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Marine and Coastal Systems of the Quoddy Region, New Brunswick

Edited by
Martin L. H. Thomas

MARINE AND COASTAL SYSTEMS OF THE QUODDY REGION, NEW BRUNSWICK

Students studying the intertidal zone on the St. Croix Estuary. The Fisheries and Oceans Canada Biological Station St. Andrews is in the background.

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Marine and Coastal Systems of the Quoddy Region, New Brunswick[1]

Edited by
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DEPARTMENT OF FISHERIES AND OCEANS
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To the Province of New Brunswick as a contribution to its Bicentennial in 1984.

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Abstract

THOMAS, M. L. H. [ed.]. 1983. Marine and coastal systems of the Quoddy Region, New Brunswick. Can. Spec. Publ. Fish. Aquat. Sci. 64: 306 p.

The book describes the main marine and coastal biological systems of Passamaquoddy Bay and adjacent waters and the oceanographic and meteorological characteristics of the area. The 17 chapters, written by scientists active in this region, are grouped to cover general subject areas beginning with meteorology and oceanography. The second group covers the intertidal systems with chapters on rocky intertidal shores, rock pools, coarse sedimentary shores, and salt marshes. The third general section, containing two chapters, covers hard and sedimentary sublittoral habitats. The following four chapters discuss pelagic systems under the headings fishes, phytoplankton, larger zooplankton, and microzooplankton, respectively. Subsequently three chapters deal with the birds, amphibians and reptiles, and marine mammals. Finally coastal vegetation is described. Each chapter presents basic scientific background material, describes appropriate methods, gives particular attention to the local situation and, if appropriate, gives specific information on particularly useful or interesting localities. This wide subject treatment makes the book useful to naturalists, students, teachers, and researchers. The unique conditions fostered by the high tidal range and vigorous water exchange in the area, dominating the oceanography and moulding the biology, will be of interest to scientists throughout the world. Although the coverage is primarily a review of the general subject areas, a great deal of original research is presented here for the first time. Numerous illustrations, and keys to groups not served by existing literature, are included.

Résumé

THOMAS, M. L. H. [ed.]. 1983. Marine and coastal systems of the Quoddy Region, New Brunswick. Can. Spec. Publ. Fish. Aquat. Sci. 64: 306 p.

Dans le présent ouvrage sont décrits les principaux systèmes marins et biologiques côtiers de la baie de Passamaquoddy et des eaux avoisinantes, avec les caractéristiques océanographiques et météorologiques de la région. Les dix-sept chapitres, rédigés par des scientifiques oeuvrant dans cette région, qui constituent ce volume ont été groupés par domaines généraux, à commencer par la météorologie et l'océanographie. Le deuxième groupe comprend les systèmes intertidaux, avec chapitres traitant des rivages rocheux, de mares dans le rocher, des rivages à sédiments grossiers et des marais salés. La troisième section est constituée par deux chapitres, l'un sur les habitats sublittoraux durs et l'autre sur les habitats sédimentaires de cette zone. Dans les quatre chapitres suivants, on examine les systèmes pélagiques sous les rubriques poissons, phytoplancton, macro et microzooplancton respectivement. Viennent ensuite trois chapitres consacrés aux oiseaux, aux amphibiens et reptiles, et aux mammifères marins. Enfin, on décrit la végétation de la côte. Chaque chapitre contient une information de base, des descriptions de méthodes appropriées, une mention spéciale de la situation locale et, dans certains cas, des renseignements particuliers à des endroits utiles ou intéressants. Parce que le sujet est couvert de façon exhaustive, ce volume sera utile aux naturalistes, aux étudiants, aux professeurs et aux chercheurs. Les conditions uniques que créent des marées de forte amplitude et un vigoureux échange d'eau dans cette région, influant à la fois sur l'océanographie et la biologie, intéresseront les scientifiques du monde entier. Bien qu'il s'agisse avant tout d'une revue de domaines généraux, on y présente pour la première fois beaucoup de recherche originale. Le volume est abondamment illustré et contient des clés d'identification qu'on ne trouve nulle part ailleurs.

CHAPTER 1

Introduction

M. L. H. Thomas

University of New Brunswick Saint John, N.B.

The need for this book has arisen from the rapid expansion in the use of the Quoddy Region for teaching and scientific research and as a site for general natural history activity, with St. Andrews as the main base. It is also an area of great intrinsic natural interest, being situated on the Bay of Fundy which boasts the highest tides in the world, reaching a range of over 20 m at the head of the bay. These tides undoubtedly contribute to the wide diversity in biological and physical features in the area, and the naturally varied geology is well exposed along the shores. The daily tidal exchange of water through the mouth of the bay from the Gulf of Maine is immense and helps to introduce new species and disperse others. The tides are also of economic interest, since the generation of electricity from tidal power is clean and renewable. Another feature linked to the tides is the large system of coastal marshes, which are of both scientific and agricultural interest. Indeed, these marshes attracted early settlers, particularly the Acadians who dyked and reclaimed large areas of the marshes for agriculture. Once dyked and drained, the marshes offered a rich soil and excellent yields. Many marshes are still used and others show evidence of former use in the shape of breached dykes and relicts of buildings, bridges, roads, etc.

While the high tidal range has many useful and interesting attributes, it has some undesirable facets. Tidal mixing prevents effective thermal stratification and consequently the water mass warms only slightly in summer, rendering saltwater bathing only a brief exhilarating experience except in sheltered coves with less tidal exchange. Cold surface waters contribute to the high incidence of fog, especially near the bay mouth in summer and fall. Tidal currents are very strong and may constitute a hazard to shipping, particularly in restricted passages, e.g. the two main entrances to Passamaquoddy Bay — Letite Passage and Head Harbour Passage. The currents in the latter, particularly, are legendary, giving rise both to the "old sow" off Deer Island Point, reputed to be the world's largest whirlpool, and to a vigorous controversy concerning the use of Head Harbour Passage as an access route for oil tankers en route to a proposed refinery at Eastport, Maine. Even where there is no restriction to flow, the tides affect shipping by restricting access to some wharfs at low tide and by creating strong currents.

The general area was settled early and has been extensively developed. There are numerous small ports housing fishing vessels and some larger ones with more varied roles. Saint John is the largest port in the area and a major east-coast shipping link. In the Quoddy Region, Blacks Harbour and St. Andrews are intermediate-sized ports with expanding roles and there are numerous smaller ports.

The Quoddy Region has been defined only relatively recently (Trites 1962), in relation to the need to delimit an area which may be strongly influenced by natural or man-made changes in Passamaquoddy Bay. It is a more useful area for consideration in this book, however, than Passamaquoddy Bay alone. The latter area, although interesting and varied, does not exhibit the tremendously wide range of features and conditions available within a short travel distance of St. Andrews. As shown in Fig. 1, the Quoddy Region lies within a line extending from Point Lepreau to the northeast tip of Grand Manan Island and proceeding to West Quoddy Head in Maine. It therefore encompasses Passamaquoddy Bay, the Deer Island Archipelago, Campobello Island, the Wolves, and all coastal waters from Point Lepreau to West Quoddy Head. The area contains several estuaries, the largest being that of the St. Croix extending between St. Stephen and St. Andrews. Others, such as those of the Digdeguash, Magaguadavic, and Letang rivers, are also of significant size. The Saint John Estuary lies northeast of the Quoddy Region but at times of high runoff its influence extends well down the coast within the Quoddy area.

The most complete and useful information source for Quoddy Region coasts and waters is *Sailing Directions, Nova Scotia (S.E. Coast) and Bay of Fundy* (Anon. 1976) provided by the Canadian Hydrographic Service, who also prepare the *Canadian Tide and Current Tables* (Anon. 1981) for publication.

This introduction would be incomplete without a brief resume of the historical development of marine science in the area. Although scientific interest was always present, several significant developments fostered progress. The first and most important of these was the establishment, under the auspices of the Canadian government, of what is fondly referred to as the Biological Station, which was a portable unit from 1898 to 1907 and a permanent station after 1907.

Before 1898 only 17 papers were published on scientific aspects of the Bay of Fundy: the first on geology in 1836, on biology in 1854, and on oceanography in 1867. At first the main thrust of work was in fisheries and biology, but gradually and with especial impetus during the second world war, oceanography gained in importance. First handled by the navy, then by the Fisheries Research Board and finally by Mines and Technical Services, its importance grew. Unfortunately, the change in responsibility for oceanography on the east coast resulted in a diminished role for St. Andrews, especially until the establishment of the Bedford Institute in Dartmouth in 1962 (Campbell 1976).

The bibliography prepared by Moyse (1978) clearly shows the accelerating pace of research in the Bay of Fundy and in the Quoddy Region in particular. From 1800 to 1900 there were about 20 papers; from 1900 to 1950, 130; from 1950 to 1970, 240; and from 1970 to 1980, 440. Of 153 papers on specific geographical areas of the bay, over 60

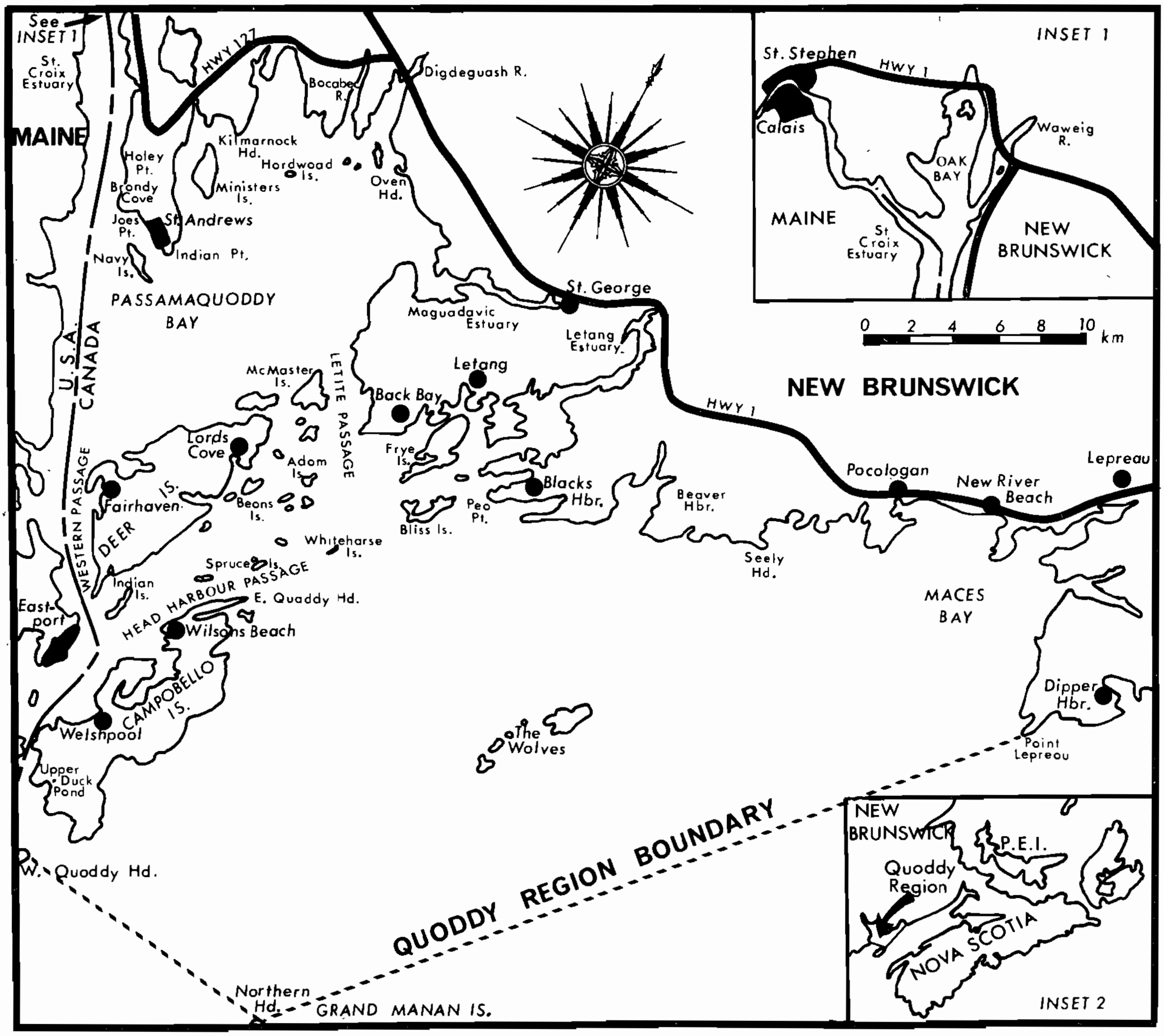

FIG. 1. The Quoddy Region, New Brunswick, Canada, showing the principal features and the main locations mentioned throughout the text. Inset 1 is a continuation, on the same scale, of the northern portion of the St. Croix Estuary. Inset 2 shows the location of the Quoddy Region in the Canadian Maritimes.

concern the Quoddy Region and many of the general papers also contain relevant data.

The acceleration in the publication rate of data on the Bay of Fundy started with the establishment of the Biological Station at St. Andrews, but it received impetus from several other important events and developments. A major group of these was a series of energy-related projects and studies. Several of these, notably the Passamaquoddy Tidal Power study of 1930–1969, the Point Lepreau and Coleson Cove nuclear and thermal power station projects (from 1973 on) and the Eastport, Maine refinery proposal (from 1974 on) concern the Quoddy Region. The general Bay of Fundy Tidal Power Studies and Annapolis River Tidal Power project, which began in 1976, have also had spin-off benefits.

Also of significance has been the steady growth of universities in the area. The University of New Brunswick has been most active in the Quoddy region, particularly since the development of its Saint John campus in 1969. However, other regional universities, notably Mount Allison, Acadia and recently the Université de Moncton, have been active in the Fundy region as a whole. Dalhousie, McGill, Guelph, McMaster, and Toronto universities have also been active in the Quoddy region, the work being fostered by ties with the Biological Station and the Huntsman Marine Laboratory.

The Huntsman Marine Laboratory (H. M. L.) is a key institution in the recent history of scientific work in the Quoddy region. This institution is a consortium of eastern Canadian Universities, provincial and federal government agencies and private organizations. It was started in 1969 when Dr. J. M. Anderson, then the director of the Biological Station, initiated a series of meetings and negotiations which culminated in the signing of a lease to the Ambridge property in December 1969 and in the official opening in August 1970. In 1971, Dr. A. W. H. Needler became the first fulltime executive director and the institution commenced to contribute scientifically. Among early developments were the hosting of university field courses from member institutions and in 1971 the inauguration of the H. M. L.'s own marine science field courses. Since 1970 over one hundred courses have been run by member universities and the H. M. L.'s own course has continued. As a result, thousands of students have had firsthand experience of the Quoddy Region, particularly in marine biology, but also in geology and oceanography. In latter years H. M. L. has hosted a wide range of courses and seminars on almost every conceivable subject. Dr. W. B. Scott became the second director in 1976 and has guided the institution into an active research role in the area. The early history of the Huntsman Marine Laboratory is detailed in Anderson (1980).

The continued expansion of H. M. L. and its role, more than any other event, dictated the need for more information on the biology, geology and oceanography of the Quoddy Region. Since its inception, H. M. L. has published or assisted in the publication of a series of titles useful to workers in the area, including *Introducing the Sea* (Thomas 1973), *Common Canadian Atlantic Fishes* (Scott and Messieh 1976) and *A Checklist of Marine Flora and Fauna of the Bay of Fundy* (Linkletter et al. 1977). These publications and the continuing series *A Guide to the Flora and Fauna of the Bay of Fundy*, published as a series of Fish and Marine Service Technical Reports by the Biological Station, St Andrews, provide a baseline for local studies, but the need for a more comprehensive guide to local systems is clearly evident and it is hoped that this volume will fill that need.

Marine and Coastal Systems of the Quoddy Region, New Brunswick attempts to present up-to-date knowledge on the structure and functioning of local marine systems — biological, oceanographic, and geological. It has been designed to provide a description useful to scientists, teachers and natural historians, whether they be in research or educational roles. Despite the wide spectrum in the intended uses, the work has been designed to be thoroughly scientific in approach. It provides descriptive information on the systems, elaborates on methods in general and in particular those fitted to local needs, and gives thorough descriptions of key localities where appropriate.

The authors chosen are at the forefront of their subject and have firsthand knowledge of the Quoddy Region. The majority are pursuing or have had active research programs in the area. To ensure top-quality content, all substantial contributions have been refereed by an international board of referees of global reputation. Their names appear earlier in this volume.

Despite the wide interest and activity in the Quoddy Region, there are some aspects for which we could not find authors. Intertidal mudflat systems are not covered, although some aspects are covered in saltmarsh descriptions (Chapter 7) and in relation to coarse sedimentary shores (Chapter 5) and sublittoral sedimentary substrates (Chapter 9). It must also be admitted that the international boundary, running down the St. Croix Estuary and close to the southwest shore of the bay, is a very real one and that the U.S.A. shore is not adequately covered. For this I apologize, but except in a few instances, available authors worked mainly in Canadian waters. Also largely ignored are phenomena intrinsically associated with the hundreds of islands in the bay. This archipelago presents many unique opportunities for study and observation which have not yet been undertaken.

It is hoped that these omissions will encourage future work. The authors regard the book not as a determinate volume, but as a stimulus to a better understanding of the Quoddy Region. In conclusion, I would be remiss if mention were not made of sources of information on the area. There are two indispensable source documents: the *Bay of Fundy Environmental and Tidal Power Bibliography* by C. M. Moyse (1978) and the *Bay of Fundy Environmental Data Inventory* by R. H. Loucks (1979). These documents present titles and summaries of previous work and contain references to smaller pertinent bibliographies. The former is a direct result of the Fundy Environmental Studies Committee, a subcommittee of the Atlantic Provinces, Inter-University Committee on the Sciences. The Fundy Environmental Studies Committee (or Group) publishes supplements to the bibliography, arranges at least annual meetings of Fundy area researchers, and sponsors workshops on topics of special interest. Membership is open to all interested workers.

The chapters are essentially self-contained, but Fig. 1 provides a general reference map showing the entire Quoddy Region and most of the specific localities mentioned in various chapters. Many chapters provide more detailed larger-scaled maps or sketch maps of specific locations. Readers requiring further detail and bathymetric information are referred to Canadian Hydrographic Service Charts No. 4011, Approaches to the Bay of Fundy, and No. 4331, Passamaquoddy Bay and Saint Croix River, New Brunswick. The United States Department of Commerce, National Ocean and Atmospheric Administration, National Ocean Survey Chart No. 3328 is also useful.

Acknowledgments

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TABLE 1. Long-term mean weather conditions for Saint John N.B., 45°19′N., 65°53′W. (Anon. 1976).

		Temperature							Precipitation		Days with					Wind Direction									
			Mean Daily		Extreme											% of Observations From									
Month	Mean Sea Level Pressure	Average	Max.	Min.	Max.	Min.	Relative Humidity	Cloud Amount Scale 0-10	Total	Max. in 24 H	Rain	Snow	Precipitation	Fog	Thunder	N	NE	E	SE	S	SW	W	NW	Calm	Mean Speed
	MB	°C	°C	°C	°C	°C	%		mm	mm															Knots
January	1014	-7.4	-2.3	-12.6	11.1	-31.1	82	6.4	145.0	69.3	6	14	17	3	0.2	22	6	7	4	5	7	18	27	4	11.3
February	1012	-7.5	-2.1	-12.9	10.6	-36.7	80	5.9	130.8	95.0	5	12	14	3	0.1	19	7	8	5	8	9	18	22	4	11.1
March	1013	-2.6	2.0	-7.3	13.9	-30.0	77	6.3	104.7	54.6	7	10	14	5	0.1	22	8	9	5	9	8	15	21	3	11.5
April	1014	3.1	7.9	-1.8	20.0	-16.7	75	6.5	111.8	125.5	11	4	13	6	0.7	20	7	8	8	16	11	11	14	5	10.4
May	1014	8.8	14.3	3.2	30.0	-7.8	72	6.8	101.9	62.0	14	1	14	10	0.8	12	6	9	9	25	16	7	11	5	10.1
June	1013	13.6	19.1	8.0	31.7	-2.2	77	7.0	94.5	54.1	13	0	13	12	2.7	10	6	8	9	33	17	5	7	5	9.7
July	1014	16.9	22.3	11.4	32.8	1.1	80	6.5	89.4	72.6	12	0	12	17	3.0	7	3	6	8	39	17	7	7	6	8.8
August	1015	16.3	21.7	10.9	31.1	-0.6	82	6.0	98.8	125.2	12	0	12	14	2.5	9	4	4	8	33	16	9	10	7	8.6
September	1018	12.7	17.8	7.4	28.9	-6.7	82	5.7	102.6	74.9	12	0	12	13	1.1	12	6	7	7	25	13	9	13	8	9.0
October	1017	7.9	12.7	3.1	25.6	-9.4	83	5.7	109.7	85.3	11	1	12	9	0.6	15	7	5	7	19	14	14	14	5	10.1
November	1015	2.6	6.6	-1.6	21.7	-14.4	85	6.8	154.4	73.4	13	4	15	5	0.2	19	7	7	8	12	8	16	19	4	10.8
December	1015	-4.6	-0.2	-9.1	15.0	-26.7	82	6.2	156.7	105.7	8	12	16	3	0.1	22	7	5	5	7	7	17	26	4	11.2
Means	1015	5.0	10.0	-0.1												15	6	7	7	20	12	12	16	5	10.3
Totals									1400.3		123	58	164	99	12.1										
Extremes					32.8	-36.7				125.5															
No. of Years of Observations	20	22	22	22	22	22	10	13	22	22	22	22	22	30	20	18	18	18	18	18	18	18	18	18	18

mainder snow equivalent. Snowfalls are frequent from December to March and may be heavy, but periodic winter thaws, especially along the coast, prevent heavy accumulations.

Very heavy rainfalls, and occasionally snowfalls, may be associated with storms, particularly those of tropical origin. Up to 126 mm in 24 h have been recorded in this region.

Inland in New Brunswick snowfalls are the heaviest in Canada and tend to accumulate to a total depth of 250–350 mm. In spring, melting snow may provide the water equivalent of 125–180 mm and thus results in very heavy freshets and seasonal floods in many rivers. That from the St. John affects a large area of the SW Bay of Fundy. Those from the St. Croix and other rivers have a marked effect on Passamaquoddy Bay.

Fog

Fog is a notable feature of the Bay of Fundy weather. It is usually most severe in spring and early summer. In July, the worst month, ship reports indicate fog 40% of the time. From May to August, 10–14 d/mo are foggy but in winter this figure declines to 2–4 days/month. Fogs are most frequent in southerly winds of low to moderate velocity (7–10 kn, 13–19 km/h) and rare in winds over 21 kn (39 km/h).

Fog density varies greatly on a local basis. It is usually less to the leeward of fairly high shores, e.g. to the NE of Grand Manan Island. Fog is often less dense in the inland portion of Passamaquoddy Bay and the St. Croix Estuary than it is close to Deer Island, Campobello Island and beyond.

Freezing Spray

From December to March, conditions in the Bay of Fundy favor the formation of freezing spray. Freezing spray can be a severe hazard to work at sea, particularly in January and February, making the vessel slippery and, if prolonged, affecting stability. The condition is most serious at air temperatures below −9°C and winds over 30 kn (56 km/h) but can be a problem at any temperature below −2°C, combined with wind over 20 kn (37 km/h).

Table 1 shows long-term mean weather conditions for Saint John. These apply well to the Quoddy Region, except that local conditions at Saint John promote prevailing S winds in summer, rather than SW which are more general.

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CHAPTER 2

Meteorology

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Introduction

The climate of the Quoddy Region is generally similar to that of the Bay of Fundy as a whole, as it results from meteorological conditions affecting much of the Maritimes and Maine. However, there are certain local effects which modify this general pattern.

There are two general air masses which govern the weather of the region: the continental air mass moving from the west and the Atlantic air mass moving in from over the ocean. These two air masses are very different in character and thus there is often a comparatively wide range in temperatures, humidities, winds, etc. from day to day and season to season. Fog occurs frequently in spring and summer and results in cooler temperatures over and near open water than inland. However, winter temperatures are milder in the bay and along the coast. The variable weather can result in large daily temperature ranges. In winter these occasionally exceed 20°C.

Spring is usually characterized by cool but changeable weather, often with a sudden transition to summer conditions. Early fall, however, is normally very settled and pleasant, with a comparatively gradual transition to winter. Snow normally starts in October or November, becomes more frequent from December to March and then declines. Frost is general from December to April, although there are brief periods with temperatures well above freezing.

As a consequence of the large tidal range and intense mixing there is negligible formation of sea ice, except in the deep bays and estuaries. Most shipboard activities are possible throughout the year. Shores ice up in intense cold but usually clear on the next tide. Shorelines and their communities such as salt marshes, headlands, etc. are usually frozen and snow-covered from January to March. In very sheltered locations, sampling from the ice is possible.

Winds and Storms

The prevailing wind pattern is a result of the regional pattern of atmospheric pressure. The mean seasonal atmospheric pressure patterns for the region are shown in Fig. 1. In winter, the general low-pressure area toward Iceland results in NW to W prevailing winds. In summer, a high pressure area over the Atlantic from Bermuda to the Azores produces mainly SW winds. Local conditions affect prevailing wind direction: for example, in summer both Eastport, Maine and Saint John experience chiefly south winds.

These wind patterns greatly affect the weather. The northwesterly winter winds are often strong but accompanied by clear weather. The summer south westerlies are usually gentle but bring fog. At any season winds may shift to NE or SE, a change generally accompanied by precipitation.

The region is the site of convergence of depressions that move both up the east coast of the continent and across the land mass from the west. The passage of these depressions produce marked variations in wind patterns and very variable weather. Depressions from the W move down the St. Lawrence valley and out to sea over the Gulf of St. Lawrence, resulting in south winds, rain in summer and rain or snow in winter. The passage of a depression is frequently accompanied by gales, beginning from the NE on E and shifting through S to SW. The other type of disturbance, moving up the eastern seaboard, may pass S of Nova Scotia or directly over the region. Winds accompanying the first type of depression start from the NE and move to the NW. In winter these conditions produce very cold conditions, which in New Brunswick may fall to −18°C inland. Over the bay conditions become squally with showers or flurries. When depressions pass through the region, winds to the east of the track become SW and to the west of the track NW. This may be accompanied by very sudden temperature changes.

Gale force winds (force 8, 34 knots, 63 km/h, or more) occur at sea 10–15% of the time during the winter months but are extremely rare in summer. Winds of 70 kn (129 km/h) have been recorded at Eastport and of over 87 kn (161 km/h) at Point Lepreau and Saint John. Such storms, such as that of February 2, 1976, can cause extensive damage to natural and man-made coastal features. The average wind speed in the bay is about 20 kn (38 km/h) in winter but closer to 10 kn (19 km/h) in summer.

In late summer storms or hurricanes of tropical origin occasionally pass through the region. Others move well off shore but still affect coastal waters. These storms are often accompanied by high winds and heavy rainfall.

Temperatures

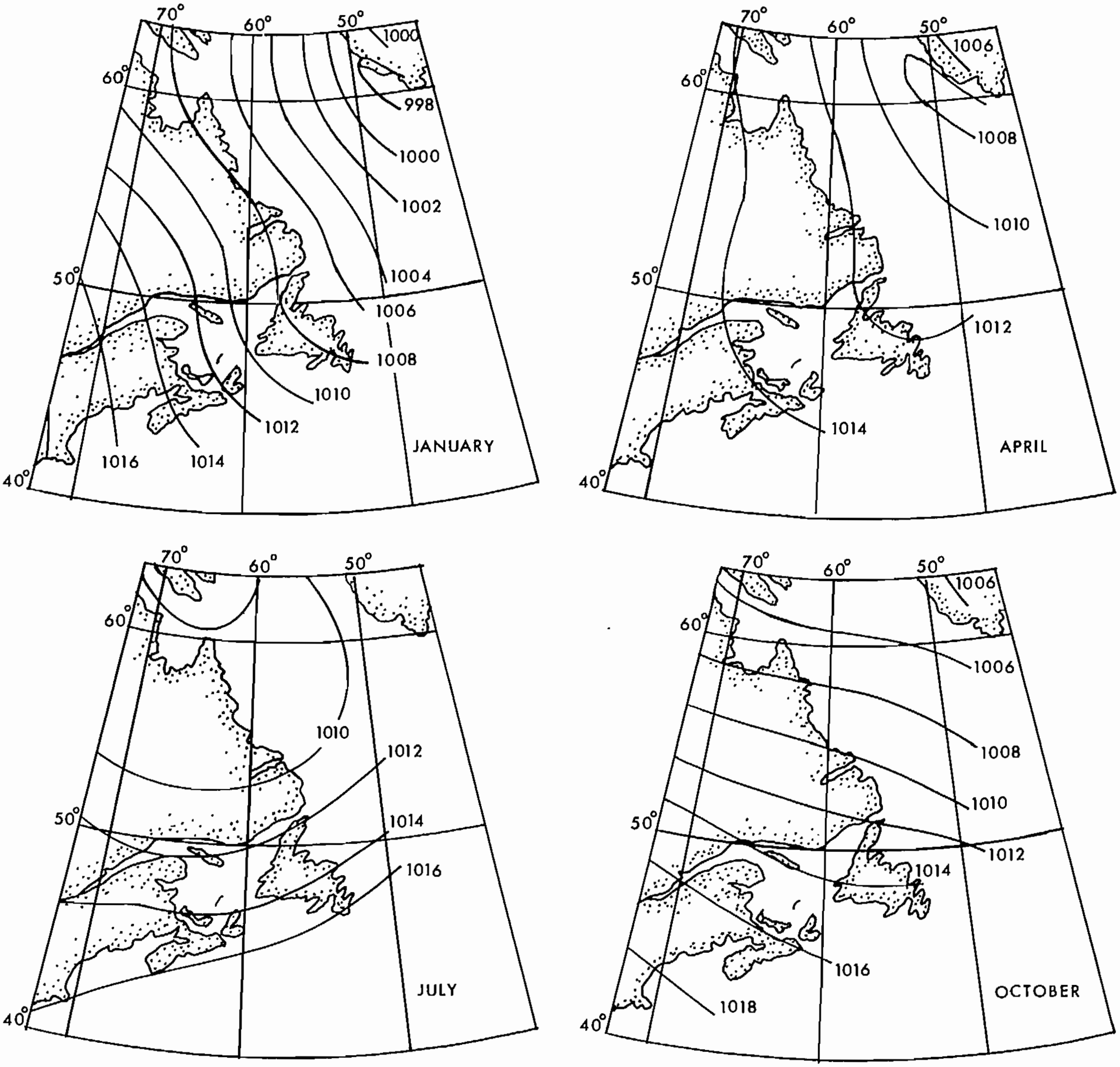
The average annual temperature is very constant throughout the region at about 5°C. The warmest period is normally July or early August, while the coolest is late January to mid-February. Temperatures in the bay are considerably more constant than on land or even along the coast. Recordings from ships show seasonal means as follows: February, −3°C; May, 8°C; August, 14°C; November, 6°C. Temperatures over the water rarely fall below −20°C whereas those inland fall well below this figure.

Humidity

Humidity is partly controlled by oceanic influences and rarely falls to low levels. Minimum values of about 72% occur in spring and maxima average 85% in fall. At sea the figures are slightly higher.

Rain and Snow

Precipitation is fairly steady throughout the year, although at times extended dry or wet spells occur. Precipitation occurs on about 160 d/yr and averages about 1400 mm/yr, about 75% of which is rain and the re-



NOTE : ATMOSPHERIC PRESSURE IN MILLIBARS
MEAN SEA LEVEL PRESSURE OF PERIOD 1940 TO 1953
FROM ATLAS OF CANADA, DPT. OF MINES AND TECH. SURVEYS, 1957

FIG. 1. Mean seasonal atmospheric pressure (from Neu 1972).

CHAPTER 3

Physical Oceanography of the Quoddy Region

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Introduction

Perhaps the single most striking oceanographic attribute of the Quoddy Region (Fig. 1) is the large tide. The visual impact from the shore is most striking, and the first impression of a town like St. Andrews may vary, depending on whether one arrives at high water or low water. In fact, if one were arriving by water aboard a ship of any great size, the arrival time would have to be timed to coincide with high water to permit docking. One can thus immediately appreciate that the tides play an important and direct role in determining man's activities in the area. The tide also plays an important but indirect role through its effect on living marine resources, and through effects on local climate and weather. Indeed, the Quoddy Region provides a small-scale demonstration of man's use of the oceans. It sustains a valuable fishery, both commercial and recreational, which creates problems of resource management. It provides port facilities and has been suggested as a site for an oil refinery and a supertanker terminal. The basins of Passamaquoddy and Cobscook bays have been proposed for tidal power development. The St. Croix Estuary receives the effluent from the pulp mill at Woodland, as well as from the human settlements on its shores. The area attracts many tourists and has served since the early 1900s as a base for research into fisheries and oceanography. All of these present and potential uses depend on, or are influenced by, the oceanographic conditions of the region. These conditions need to be understood to permit wise management, as well as for their intrinsic interest.

From a physical oceanographic point of view, the area is diverse and interesting. The St. Croix Estuary in particular shows the competing effects of fresh water discharge and the mixing associated with strong tidal currents. There are major seasonal and inter-annual variations in the water properties. For the student, the St. Croix Estuary provides a natural laboratory for the investigation of many of the physical processes that occur throughout the world's oceans.

This chapter summarizes briefly what is known about the physical oceanography, and suggests projects which could provide some interesting insights.

Tides and Tidal Currents

TIDAL ELEVATION

The Bay of Fundy is well-known for its tides, the largest in the world. The range from low water to high water sometimes exceeds 16 m in Minas Basin at the head of the bay. The main reason for this is that the whole Bay of Fundy/Gulf of Maine system, out to the edge of the continental shelf, has a natural period of oscillation of a little over 13 h, and so is nearly in resonance with the 12.4 h tidal forcing from the North Atlantic (Garrett 1972).

The tidal range in Passamaquoddy Bay is not as great as further up in the Bay of Fundy, but is still impressive, with a maximum range of 8.3 m. Predictions of times and heights of high and low water may be obtained from tide tables published by the Federal Department of Fisheries and Oceans. It should be emphasized that these predictions are only for changes in water level associated with the predictable forcing of the moon and sun, and do not include the changes in sea level associated with meteorological forcing. A sample of predicted tides is shown in Fig. 2. The zero is the chart datum, chosen such that "the daily mean water level will seldom fall below it during the season of navigation" (Anon. 1970). It is taken as the lowest normal tide, so that negative values are uncommon in Canadian tide tables, and the water depth at any location is unlikely to be less than that shown on the chart. (Given the location of the Quoddy Region it should be remarked here that the U.S. chart datum is the mean low water; thus minus tides are quite common in U.S. tide tables, and the water depth at low tide may be less by a corresponding amount than that shown on a U.S. chart).

The lunar, semidiurnal tide (M_2), with a period of 12.4 h, is the principal tidal constituent. The small difference between the two high tides each day demonstrates the unimportance of the diurnal tide in this area. A more unusual feature is that the familiar fortnightly spring/neap variation in the amplitude of the semi-diurnal tide, associated with the beating of the 12.4 h lunar tide M_2 with the 12.0 h solar tide S_2, is less important than the modulation over a month associated with the variation in the moon's distance from the earth (in oceanographic jargon the tides are anomalistic rather than synodic). This effect is shown in Fig. 2: the change in tidal height between apogee on 14 January and perigee on 28 January (and the previous 30 December) is greater than the change associated with the phase of the moon. In terms of the tidal constituents, the semidiurnal lunar elliptic tide (N_2) is greater than S_2, with an amplitude of 0.62 m compared to 0.44 m.

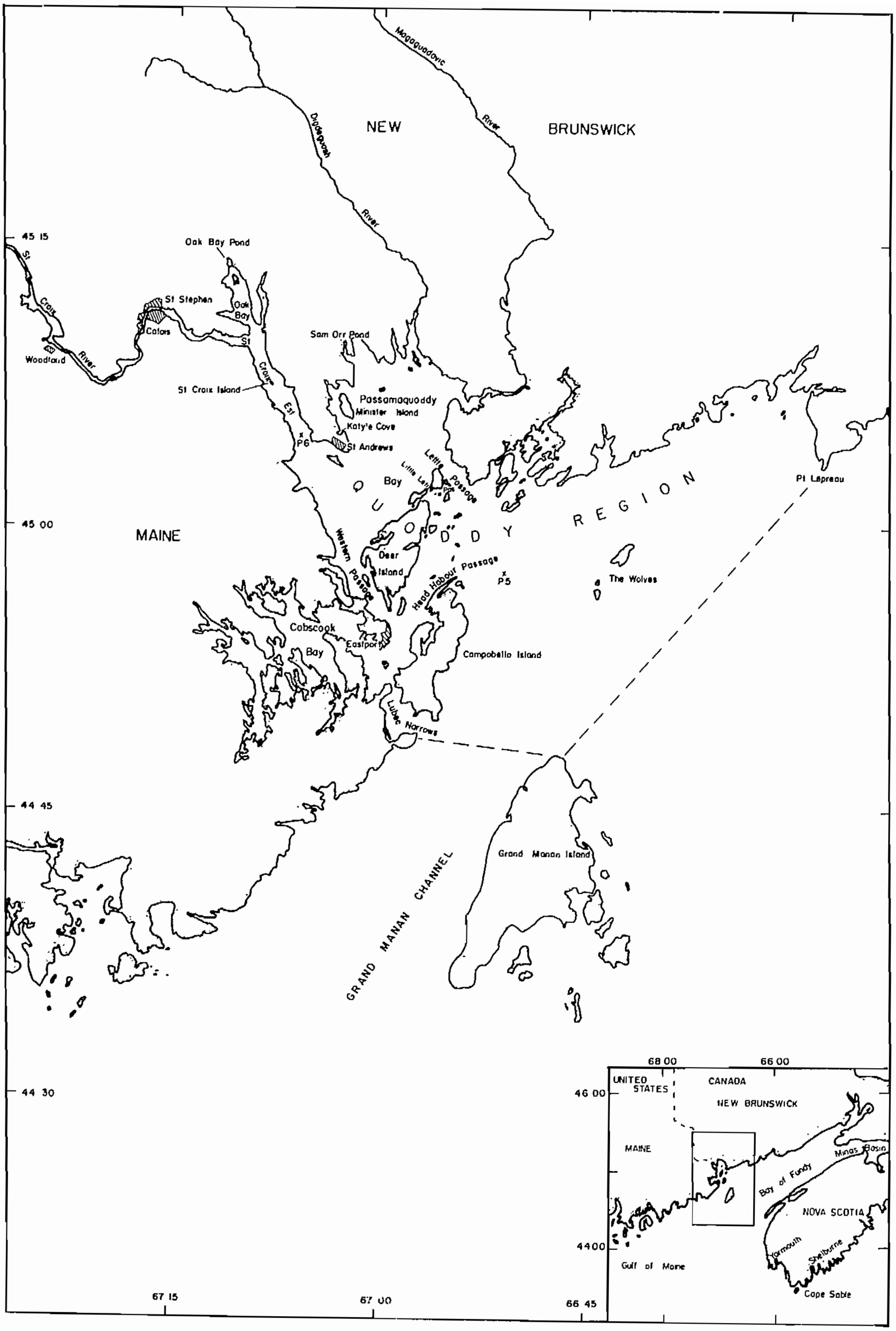

FIG. 1. The Quoddy Region.

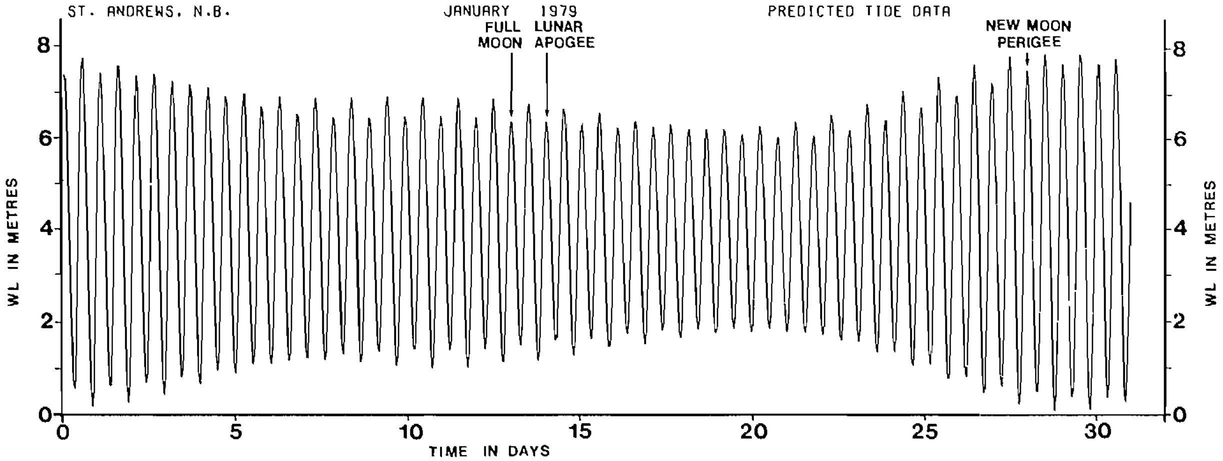

FIG. 2. Predicted water level at St. Andrews for January 1979.

NONTIDAL VARIATIONS IN SEA LEVEL

Changes in sea level caused by variations in atmospheric pressure and wind are known, at least when they are large, as storm surges. In the Bay of Fundy these tend to be buried in the large purely tidal variations, but surges of up to 1 m on top of high tide occur from time to time (D. L. DeWolfe, personal communication). More typically in the Bay of Fundy, the residual of observed minus predicted tide still looks rather tidelike, with a period of about 12.5 h. The amplitude varies over a time scale of a few days, but typically amounts to as much as 10% of M_2 (Lung-Fa Ku, personal communication). A possible reason for this is that the tidal response of the Bay of Fundy on any given day is affected by changes (particularly surface wave amplitude and hence bottom friction) induced by meteorological forcing. Further research is required, but it is probably correct to say that much of the sea level variability at St. Andrews not predicted by the tide tables (or equivalently, departures from the predicted times and heights of high and low water) is associated with modulation of the tide, rather than a superimposed and independent storm surge.

TIDAL CURRENTS

The strong ebb and flood tidal currents typically observed (Forrester 1959) in the Quoddy Region are shown in Fig. 3A and 3B. We note in particular the $2 \mathrm{m \cdot s^{-1}}$ currents in Letite Passage between Deer Island and the mainland. The effects on navigation and on the mixing of the water column can only be fully appreciated by direct observation. A good indication of the highly variable and turbulent flow is readily apparent in Plate 1. The currents do not vary much with depth, except within a metre or two of the sea floor. In time, the speeds are modulated about the averages shown in the same proportion as the tidal range shown in Fig. 2.

TIDAL ENERGETICS

The role of the tides in generating residual currents and in mixing fresh and salt water will be discussed later in this chapter, but it is appropriate to mention at this stage McLellan's (1958) estimate that the tidal power transmitted into Passamaquoddy Bay is 1260 MW. This is equivalent to the output of the Point Lepreau nuclear power station and is largely dissipated by bottom friction (and ends up as Joule heating), with a small fraction being used to mix the salt water up into the fresh water from the rivers. (McLellan's estimate is very rough, and could probably be improved using the data from Forrester (1959) and Trites and MacGregor (1962), or, better still, by developing a numerical model of the tides of the region). The actual power extracted from the tides by a tidal power scheme could, of course, be greater than the power presently being dissipated.

Freshwater Discharge

The St. Croix, Magaguadavic, and Digdeguash rivers account for nearly all of the freshwater discharge into the Quoddy Region. The largest, the St. Croix, has a drainage basin above Baileyville of 3420 km^2, and a total above St. Andrews of 4300 km^2. The Magaguadavic and Digdeguash have drainage basins of about 1860 and 440 km^2, respectively. Figure 4 shows details of the annual discharge cycle of the St. Croix, as recorded at Grand Falls, 13 km upstream from Woodland (Fig. 1). The April peak associated with meltwater from winter snow and ice stands out clearly; a secondary peak in December is the result of heavy autumn rainfall.

The interannual variability for each month is also shown on Fig. 4. The variability in the annual average discharge over a much longer term is shown in Fig. 5. There appears to be a jump, both in the annual average discharge and in the interannual variability, in the late 1940s. It would be interesting to compare this with precipitation data.

Temperature and Salinity

SEASONAL AND SPATIAL VARIATIONS

The oceanographic features in the Bay of Fundy are determined by the tide-producing forces, the earth's rotation, the fresh water discharged by the rivers, the meteorological conditions, and the bottom topography. Of

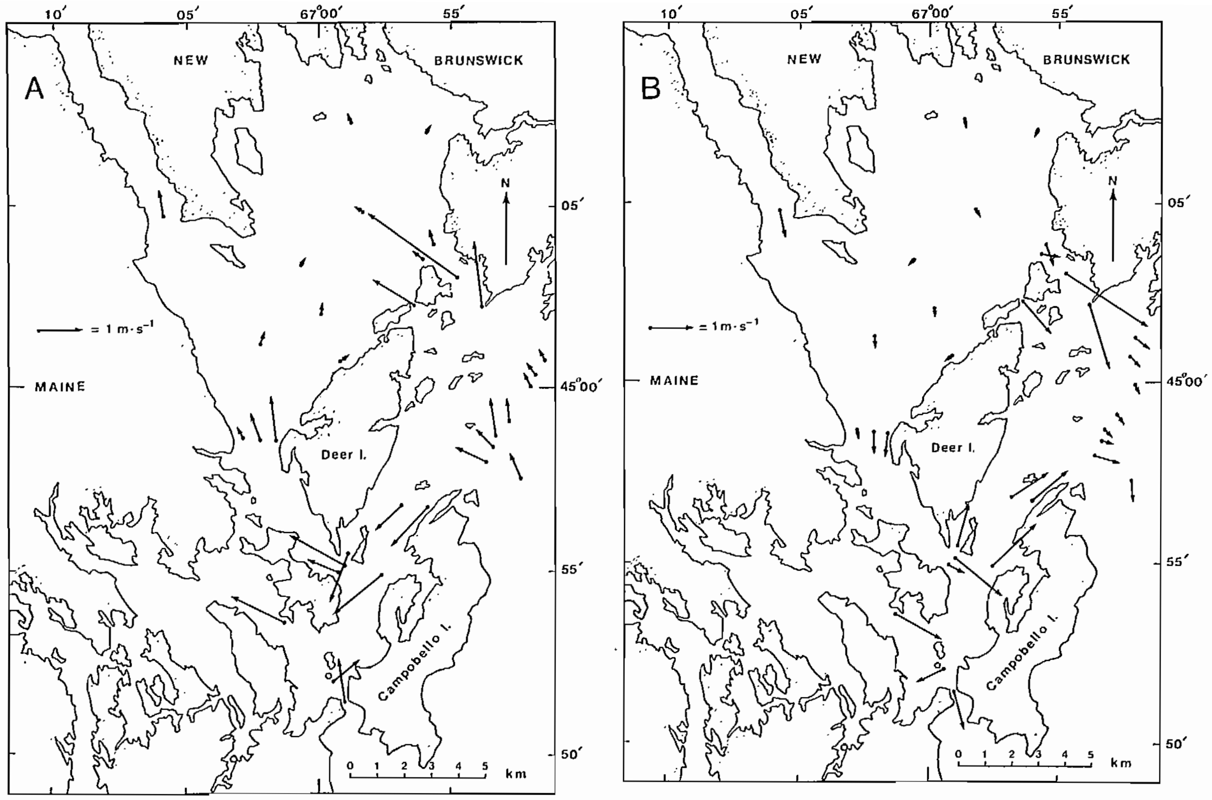

FIG. 3. *A*, Average surface tidal currents 3 h before high water; *B*, Average surface tidal currents 3 h after high water (Forrester 1959).

these factors, the strong tidal currents exert a major influence on the temperature and salinity structure.

The seasonal surface temperature and salinity variations throughout the Quoddy Region are illustrated in Fig. 6A and 6B, respectively. These figures incorporate all data available for the months of February, May, August, and November, 1958. There are several features to be noted: the temperature generally decreased seaward in May and August, while the gradient was reversed in November and February; salinity generally increased seaward at all times of the year; and maximum spatial temperature variation occurred in August, whereas maximum salinity variation occurred in May.

Although there is appreciable year-to-year variation in the temperature and salinity patterns, the features seen in 1958 are generally repetitive and can be summarized fairly succinctly using data from two stations — one near St. Andrews (Prince 6), indicative of the inner Quoddy Region, and one between Campobello Island and The Wolves (Prince 5), representative of the outer Quoddy Region (P5 and P6 in Fig. 1). Both of these stations have been occupied monthly since 1921. Mean monthly variations in temperature and salinity, surface and bottom, for Prince 5 and 6 stations are shown in Fig. 7. The temperature curves are approximately sinusoidal, with an average surface range of 13 and 10°C and a bottom range of 11 and 9°C, respectively. Temperatures in the region usually reach a maximum in late August or early September and a minimum in late February or early March. Maximum thermal stratification occurs during the late spring and summer months, when heating tends to be at or near the maximum, wind-induced mixing at a minimum, and the effects of the spring freshet on increased vertical stability are still important.

The surface and bottom salinities for Prince 6 in the inner Quoddy Region vary by 5.7 and 1.5‰, respectively, in the course of a year (Fig. 7). In the outer Quoddy Region, at Prince 5, the average range over the year at the surface is 1.4‰ and at the bottom 0.9‰. Salinities in the region generally reach a maximum in October and a minimum in April or May.

DAILY VARIATIONS

Temperatures and salinity variations below low and high water are largely due to tidal advection of spatial patterns and are generally small, except within the estuaries and the near-shore shallow areas, where there may be changes of a few degrees in temperature and several parts-per-thousand in salinity. Between April and October there is usually an inverse correlation between salinity and temperature changes from high water to low water. For the remainder of the year the temperature and salinity changes occur in the same sense. Throughout the year the lowest salinity over a tidal cycle occurs near low water.

Plate 1. Aerial photo of flood tide entering Passamaquoddy Bay through Letite Passage (National Air Photo Library, Ottawa).

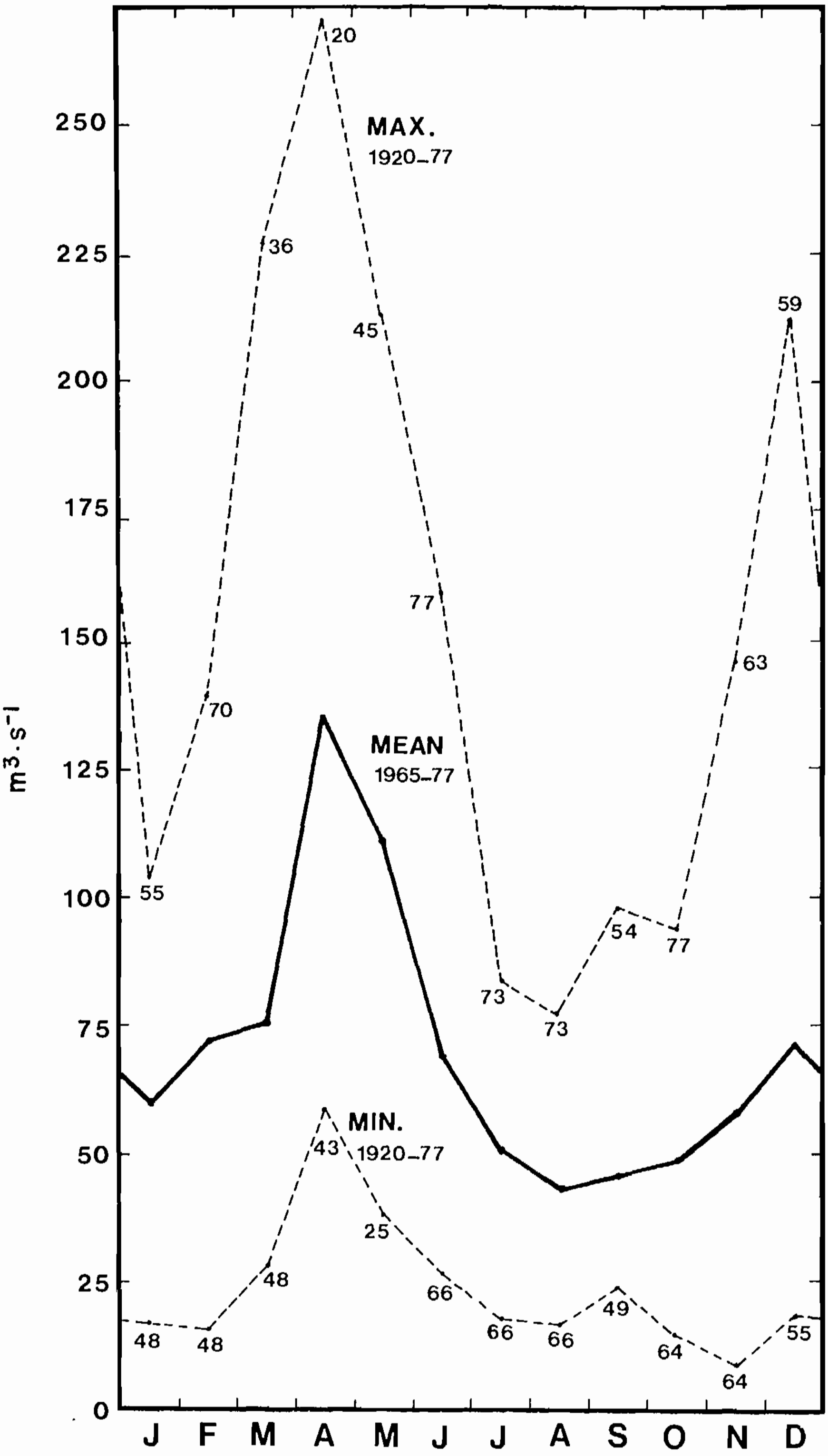

FIG. 4. Annual discharge cycle of the St. Croix River, based on data from recording gauge at Station 1AR-3 (Surface Water Data, Water Survey of Canada, Inland Waters Directorate, Canada). Solid line: mean monthly discharge (1965–77); broken line: maxima and minima for individual months (1920–77); numbers: year of occurence.

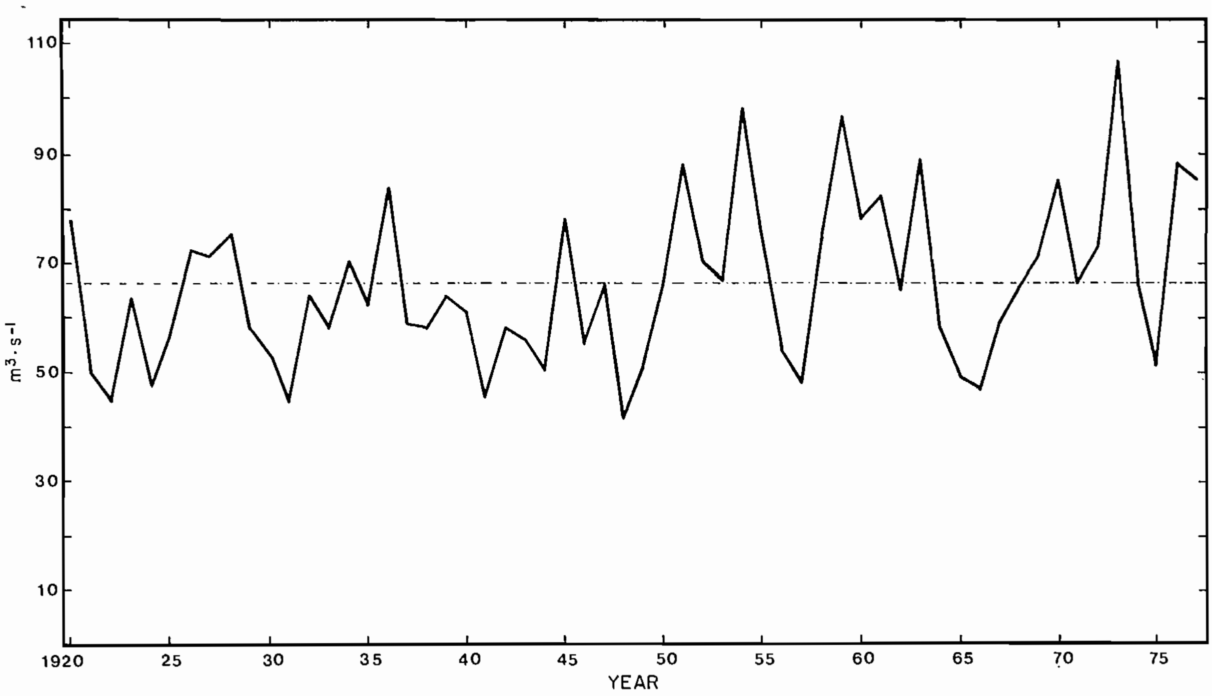

FIG. 5. Annual mean discharge of the St. Croix for 1920–77 inclusive.

LONG-TERM VARIATIONS

Twice-daily observations of surface water temperatures at St. Andrews, which began in 1921, form the longest continuous data series of water temperature along the Canadian Atlantic coast. Annual mean temperatures for the 1921–78 period, derived from the 12 monthly means, are shown in Fig. 8. Compared to the average for the total period (7.0°C), temperatures were below normal from the early 1920s to the mid-1940s; from the mid 1940s to about 1960 values were above normal. Subsequently no clear trends are readily apparent. The records reveal that rather large year-to-year variations in temperature occur (up to 1.8°C), which is a sizable fraction of the maximum change (2.7°C) between the coldest year (1923) and the warmest (1951).

A summary of monthly temperatures is shown in Fig. 9. In addition to the mean monthly values, the extremes and the year in which they occurred are shown. It is interesting to note that of the 24 extremes, 18 of them occurred in one of three years. For the period from November 1922 to September 1923, nine of the eleven months were record cold ones. Conversely, the period from December 1950 to April 1951 was a record warm spell. The period from May to September 1976 produced record high temperatures, although the months of July, August, and September, 1951 were nearly as warm.

To gain an appreciation of the geographic scale of these longer-term temperature changes, it is useful to look first at air temperatures, as the records are longer and are available for more sites than are water temperatures. Examining year-to-year variability in air temperature, one finds that it is correlated over relatively wide geographic areas. For example, the relatively close correlation between the 3-yr running means of the annual averages of air temperature for Ottawa, Fredericton, Eastport, and Sable Island is readily apparent (Fig. 10). Similarly, the correlation between air and water temperatures is generally good when running means over several years are used (Fig. 11). A number of investigators have studied these large-scale variations. Rodewald (1972) analyzed decadal changes from 1951–60 to 1961–70 for the North Atlantic and found coherent changes over the entire region. He found, however, that the changes were much greater for the winter months than for the summer ones.

While air and water temperatures correlate well for long-time scales and over wide geographic areas, the correlations at higher frequencies (e.g. monthly) are usually low. However, Sutcliffe et al. (1976) developed correlation coefficient matrices between monthly sea temperatures and St. Lawrence River discharge lagged from 0 to 12 mo, and found that the effects of the St. Lawrence River discharge could be traced through the Gulf of St. Lawrence onto the Scotian Shelf and through the Gulf of Maine. The speed of propagation was consistent with the known coastal currents (Fig. 12).

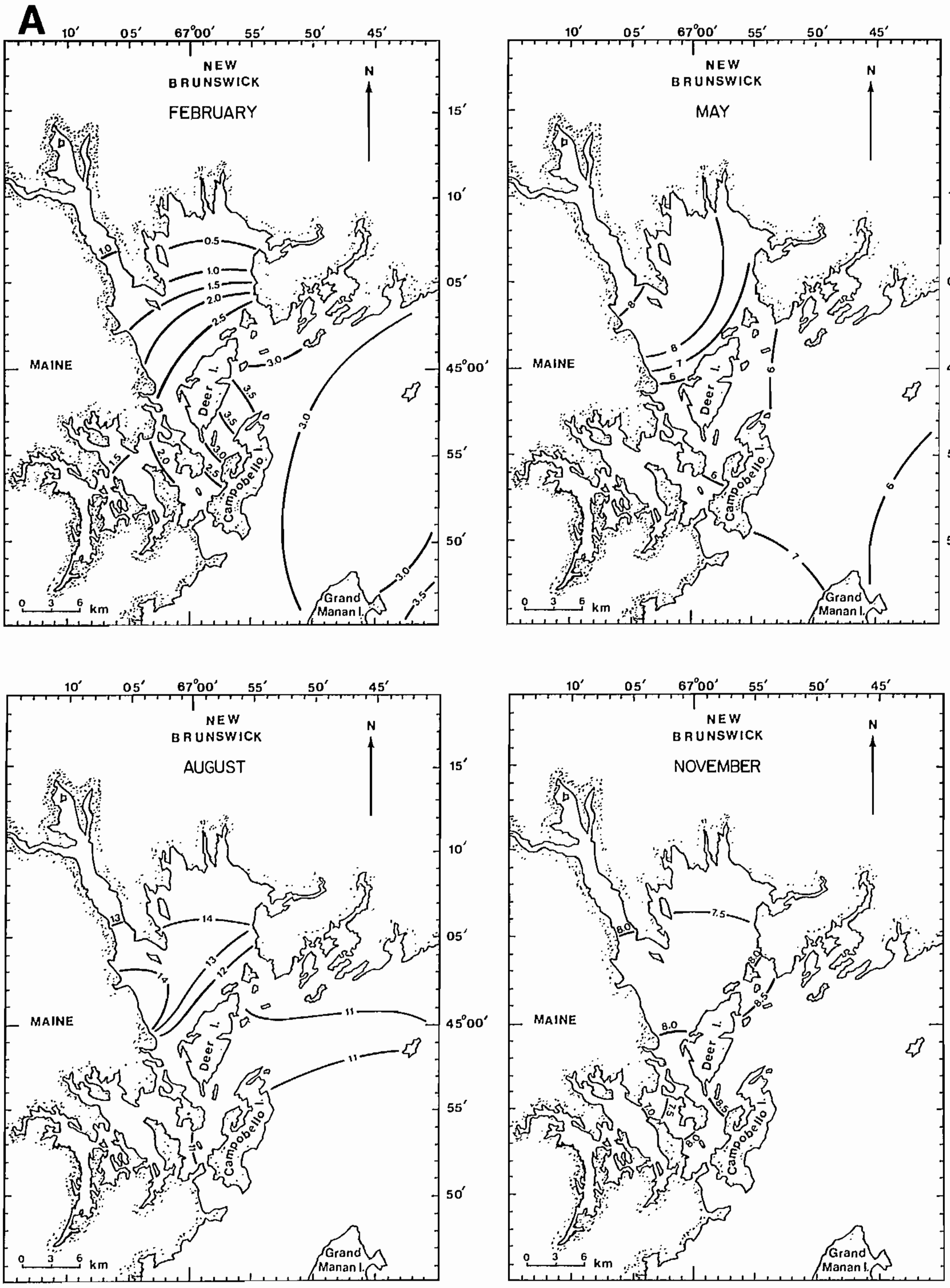

FIG. 6. *A*, Surface temperature distribution in the Quoddy Region for February, May, August, and November, 1958; *B*, Surface salinity distribution in the Quoddy Region for February, May, August and November, 1958.

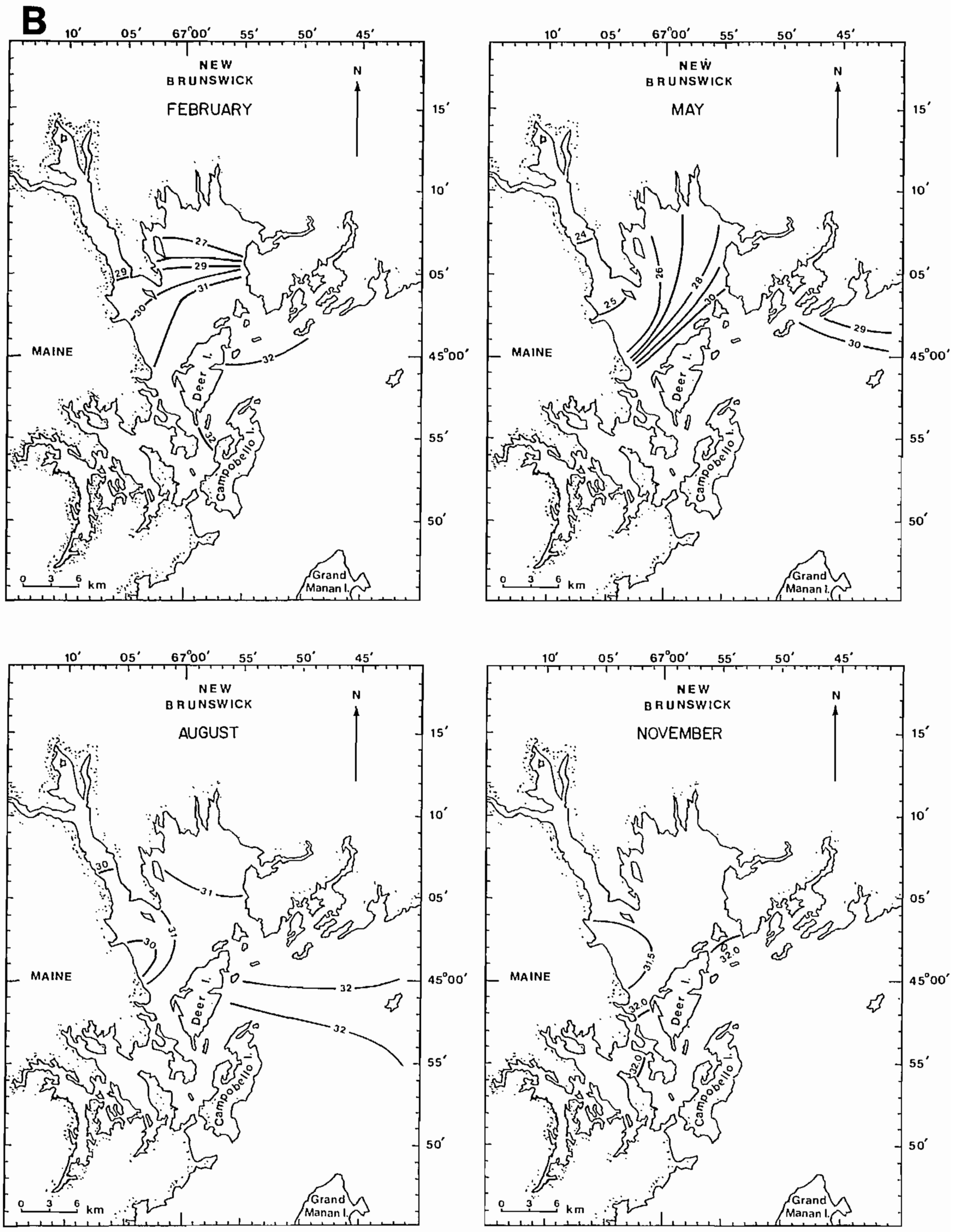

FIG. 6. (*continued*)

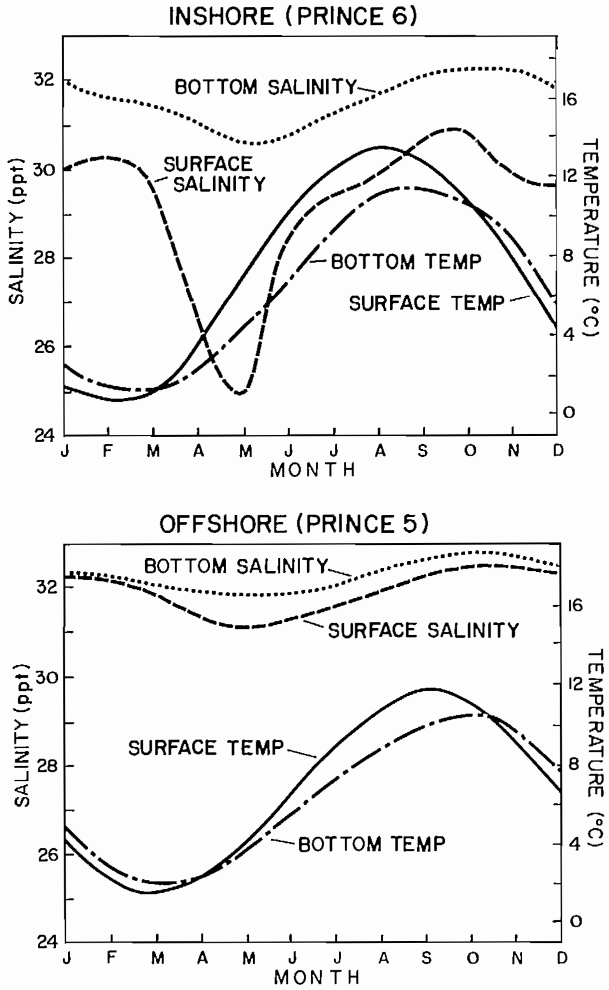

Fig. 7. Seasonal variation in temperature and salinity of surface areas of the Quoddy Region (Trites 1962). and bottom waters in the inshore (Prince 6) and offshore (Prince 5)

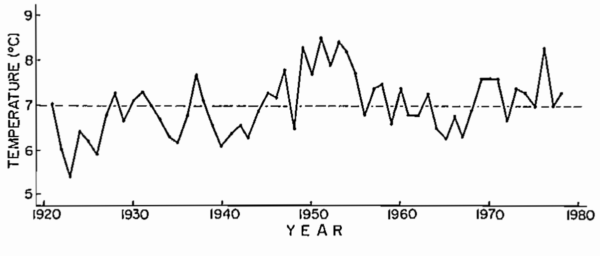

Fig. 8. Mean annual sea surface temperature, St. Andrews, N.B., 1921–78.

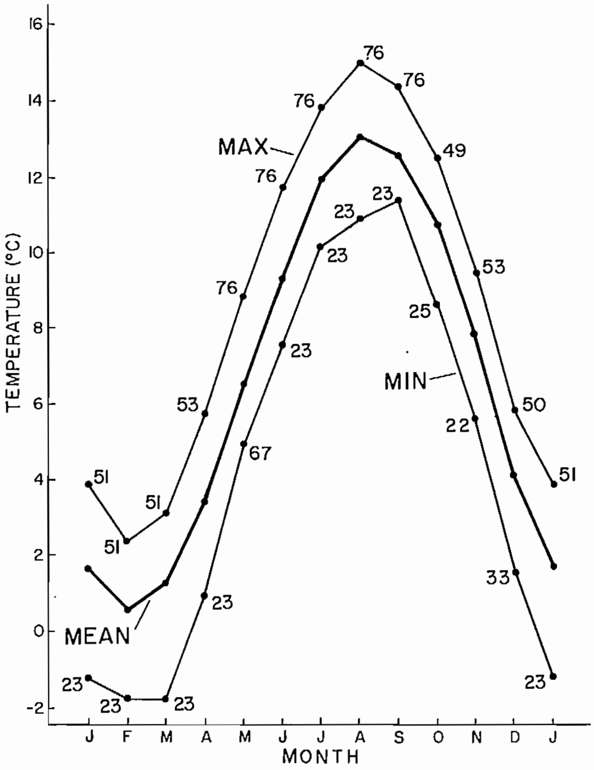

Fig. 9. Mean monthly surface temperature, St. Andrews, N.B., 1921–78, including monthly maxima and minima and the year of occurence.

Residual Currents

Bay of Fundy-Gulf of Maine

Information about the general surface current patterns on a seasonal and yearly basis has been derived mainly from drift bottles, which have been utilized sporadically in the Bay of Fundy area since the 1920s. Seabed drifters were first deployed in the area in the 1960s. Current meters have been employed as well, but only in the past two decades have self-recording units, capable of being deployed for weeks or even months at a time, been available.

Typically, residual motion displays a lot of variability, both temporally and spatially. It is therefore difficult, expensive, and time-consuming to acquire a good description of the circulation pattern and its variation seasonally and from year to year. Drift bottles and seabed drifters are relatively cheap to use, but provide limited information — a launching position and time, and for about 5–25%, a recovery position and time. From this, one attempts to construct their pathlines and speeds.

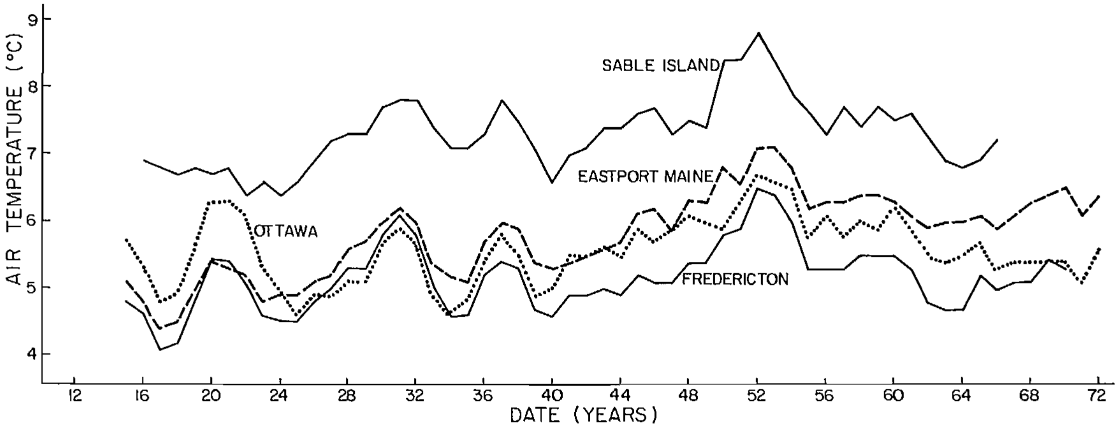

FIG. 10. Plots of 3-yr equally weighted means of the annual averages of air temperature at Eastport, ME., Fredericton, N.B., Ottawa, Ont., and Sable Island, N.S. (Sutcliffe et al. 1976).

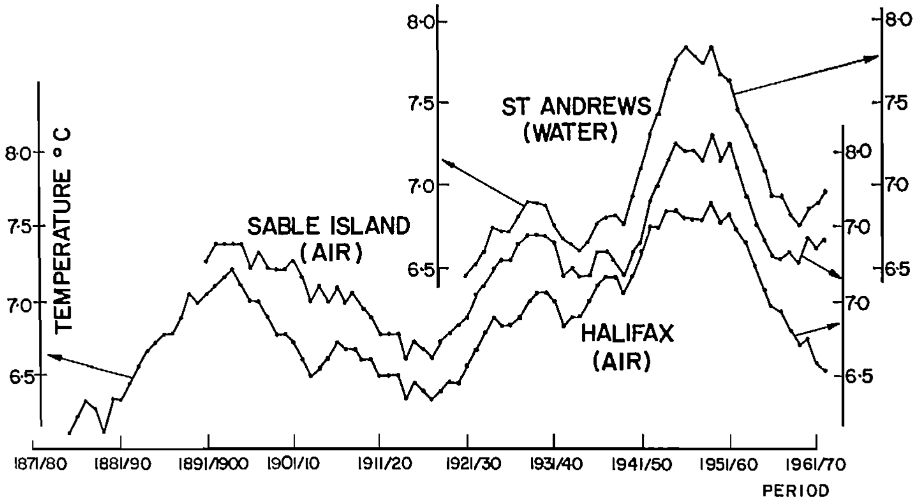

FIG. 11. Surface water temperature at St. Andrews, N.B., and air temperatures at Sable Island and Halifax, N.S. Ten-year moving averages of annual means are credited to the last year of the period (Lauzier 1972).

The seasonal pattern of surface currents, deduced from drift bottles, has been summarized for the Bay of Fundy–Gulf of Maine by Bumpus and Lauzier (1965). An extract from their publication is shown in Fig. 13. With respect to the Bay of Fundy, Bumpus and Lauzier comment as follows:

> "The circulation in the Bay of Fundy is related to that of the eastern half of the Gulf of Maine. At all times, there is an inflow along the southern entrance of the Bay. This inflow reaches a minimum during the winter months and a maximum during summer and autumn. The outflow from the Bay to the northern Gulf of Maine also exhibits a seasonal variation, being minimal during the winter and maximal during the spring and summer.
>
> "In the Bay itself, the winter surface drift is composed of one large or a few small eddies, that retain within the Bay what has been released there or what has previously drifted into it. At that time a definite movement from the northwest to the southeast side of the Bay is observed. During the spring there is an increase in the average speed of the westerly component along the northwest side of the Bay. This is accompanied by a more or less straightforward inflow along the southeast side of the Bay. This 'U turn' type of circulation is continued during the summer. The autumn circulation is an intermediate one between the 'open' circulation of the summer months and the 'closed' circulation of the winter months."

Compared to the surface, less information exists about the bottom circulation in the Bay of Fundy–Gulf of Maine system.

Lauzier (1967) summarized the available seabed drifter data (Fig. 14). In some respects the pattern is similar to that of the surface, although with speeds of an order of magnitude lower (usually between 0.1 and 1.0

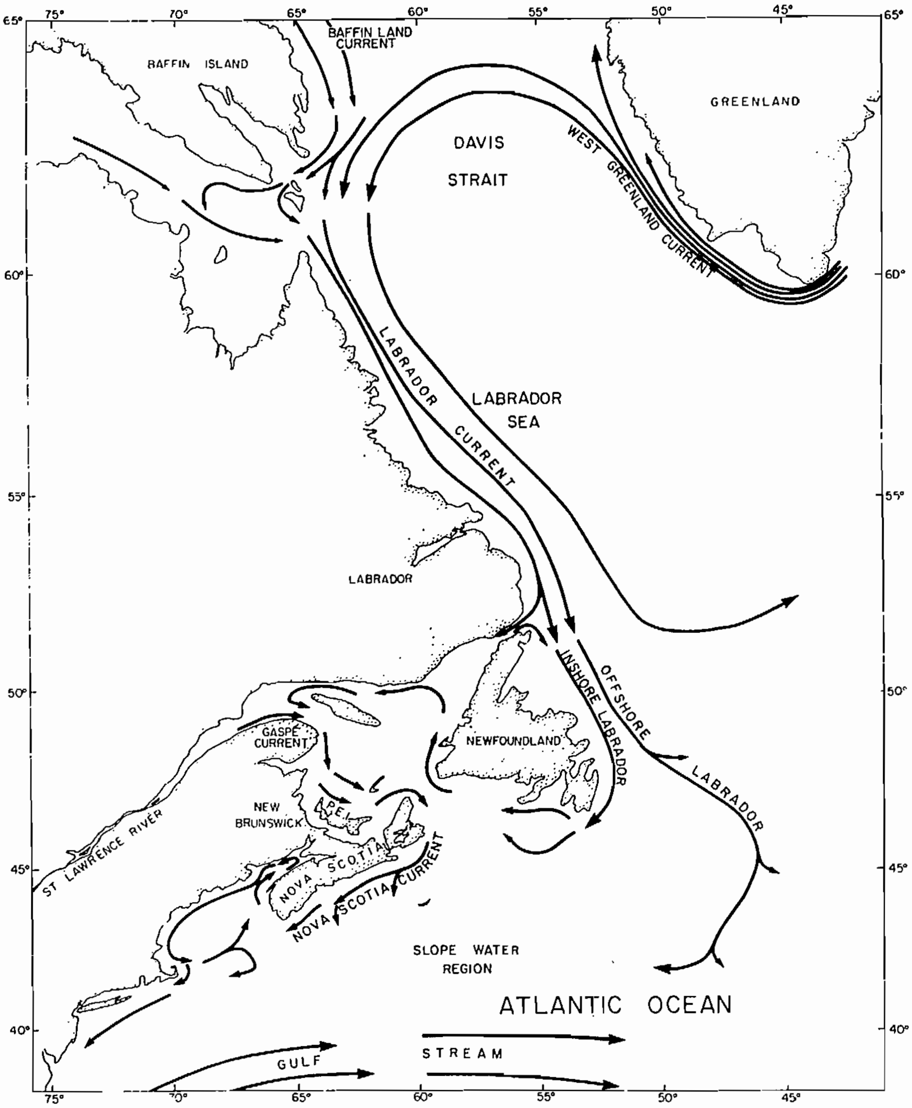

FIG. 12. The northwestern Atlantic coast showing the general surface circulation pattern (Sutcliffe et al. 1976).

nautical miles/d). One of the most striking differences in patterns of recovery of surface and bottom drifters was found for the New Brunswick side of the inner Bay of Fundy, where upwelling is pronounced (as evidenced by many seabed drifter returns and few drift bottles). On the Nova Scotia side of the Bay of Fundy, both surface and bottom drifters are recovered ashore in comparable proportions.

QUODDY REGION

Within the Quoddy Region an intensive drift-bottle release program was undertaken in 1957–58 (Chevrier and Trites 1960). Data from 48 release cruises showed some dominant circulatory features, as well as a general dispersion. These were combined to show seasonal patterns, and as certain features tended to persist throughout the 2-yr period, a general surface circulation pattern was inferred (Fig. 15). In Passamaquoddy Bay, the surface circulation is usually counterclockwise around the periphery. Frequently two cyclonic eddies are present, the larger one in the eastern side of the bay, and the smaller one in the western part. A relatively free exchange of water apparently occurs between the eddies. There is evidence that the wind modifies the situation markedly. Since the wind varies seasonally in strength and direction, from a dominant southwest in summer months to northwest in winter months, a corresponding effect on circulation in Passamaquoddy Bay can be expected. The drift-bottle results further suggest an outflow in the St. Croix Estuary, Western Passage, Cobscook Bay, and Lubec Narrows, and a variable flow in the Letite Passage. Flow in Head Harbour Passage consists of a major outward movement on the Campobello side and a minor inward flow along the

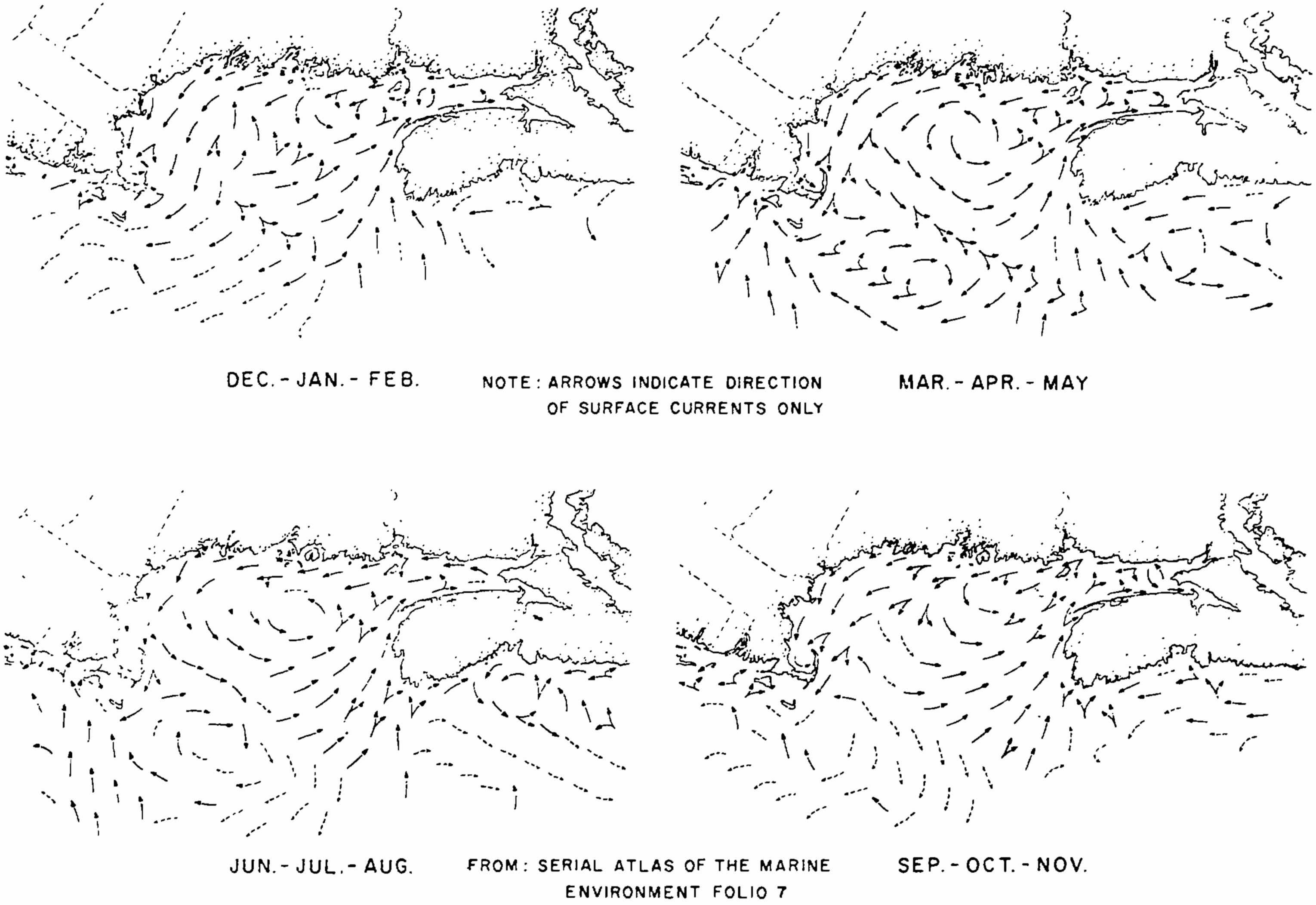

FIG. 13. Mean seasonal surface currents for the Bay of Fundy and the Gulf of Maine (Bumpus and Lauzier 1965).

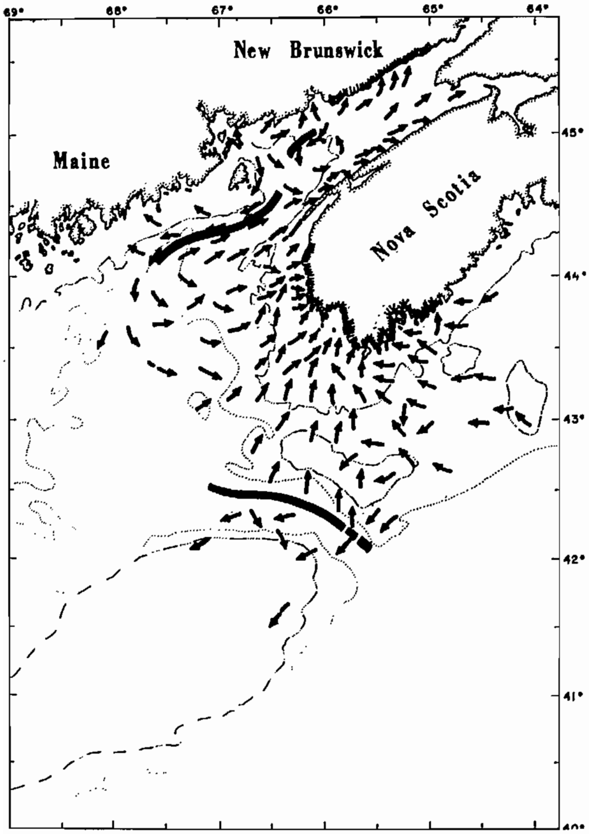

FIG. 14. Inferred residual bottom drift from southwestern Nova Scotia to the Bay of Fundy (Lauzier 1967).

Deer Island side. In the outer Quoddy Region, The Wolves appear to be at the center of a clockwise gyre. Most often surface water exiting from Passamaquoddy and Cobscook bays, through Head Harbour Passage, tends to move eastward along the New Brunswick coast before turning offshore between Pt. Lepreau and The Wolves; it then joins the general outflow from the Bay of Fundy, which moves seaward east of Grand Manan Island.

The residual flow through Grand Manan Channel is variable (McLellan 1951; Trites 1961), and it is suggested that wind plays an important role in determining the magnitude and direction of flow. Only along the coast of Maine are there indications that the net flow is usually southwestward.

Efforts were made in 1957–58 to determine total transports simultaneously in Letite and Western passages by measuring the electrical potential differences induced in the water moving across the earth's magnetic field (Trites and MacGregor 1962). Although the calibration was not entirely satisfactory, it was concluded from several months of continuous records that the residual flow in the passage, although not large, was predominantly out of Western Passage and inward through Letite Passage.

SMALL-SCALE CURRENT PATTERNS

The features described in the foregoing sections present a "smoothed" oceanographic picture, both in time and space. However, there are many areas in the Quoddy Region where interesting and important small-scale processes occur. Features such as "tide lines" or "tide rips" are often readily observed from a vessel or from shore. These are surface expressions of a convergence and may only exist for a few hours, typically at the same state of the tide.

One such feature occurs frequently at the mouth of Oak Bay on the ebb tide (Plate 2). Water leaving Oak Bay tends to be more dense than the water flowing down the St. Croix River, and so tends to sink beneath it, producing a convergence and foam line.

Some of the small-scale current patterns are induced by the shape of the coastline, as in Brandy Cove (Fig. 16). Casual observation and some work in H.M.L. summer courses suggest that, while the ebbing tide follows the shoreline, the flooding tide separates at the Fisheries Research Board wharf and causes a continuing southward flow near the shoreline in Brandy Cove. Similar asymmetry between the ebb and flood tides may be found at other headlands, near islands, and on either side of the passages into Passamaquoddy Bay. Good examples are apparent in Plate 1, where visible turbidity differences mark the separation of the flood tide past a small island in Letite Passage and the jet-like inflow through Little Letite Passage.

Remote sensing techniques are sometimes useful in providing a detailed synoptic view of variations at the sea surface. For example, even simple black-and-white aerial photographs frequently show marked patterns. An indication of the variation in lateral structure is vividly displayed in Plates 3 and 4, which show a small portion of the St. Croix Estuary near St. Andrews and the Letite Passage area. Both plates show marked surface convergences and variations in turbidity. Plate 3 also illustrates how variations in surface roughness, due to sheltering or the damping effect of surface films, show up in the variation in sun glitter. It would have been interesting to have had in situ measurements of temperature, salinity, turbidity, currents, and wave patterns at selected sites within the area photographed. Given some "ground-truthing," aerial photography and other forms of remote sensing become powerful oceanographic tools to reveal synoptically and in detail the small-scale variations.

Other Properties

WIND-GENERATED WAVES

In describing the wave climate of a region statistical properties are used. For example, "wave height" generally means "significant wave height," which is the average height of the highest one-third of all waves. Thus, nearly one-sixth of all the waves are larger than this value. For fully developed wind waves, the height of the maximum wave is roughly double the significant height.

Wave conditions in Passamaquoddy and Cobscook bays will obviously be markedly different than those in the outer Quoddy Region. The locally generated waves will be of limited height, length, and period owing to the

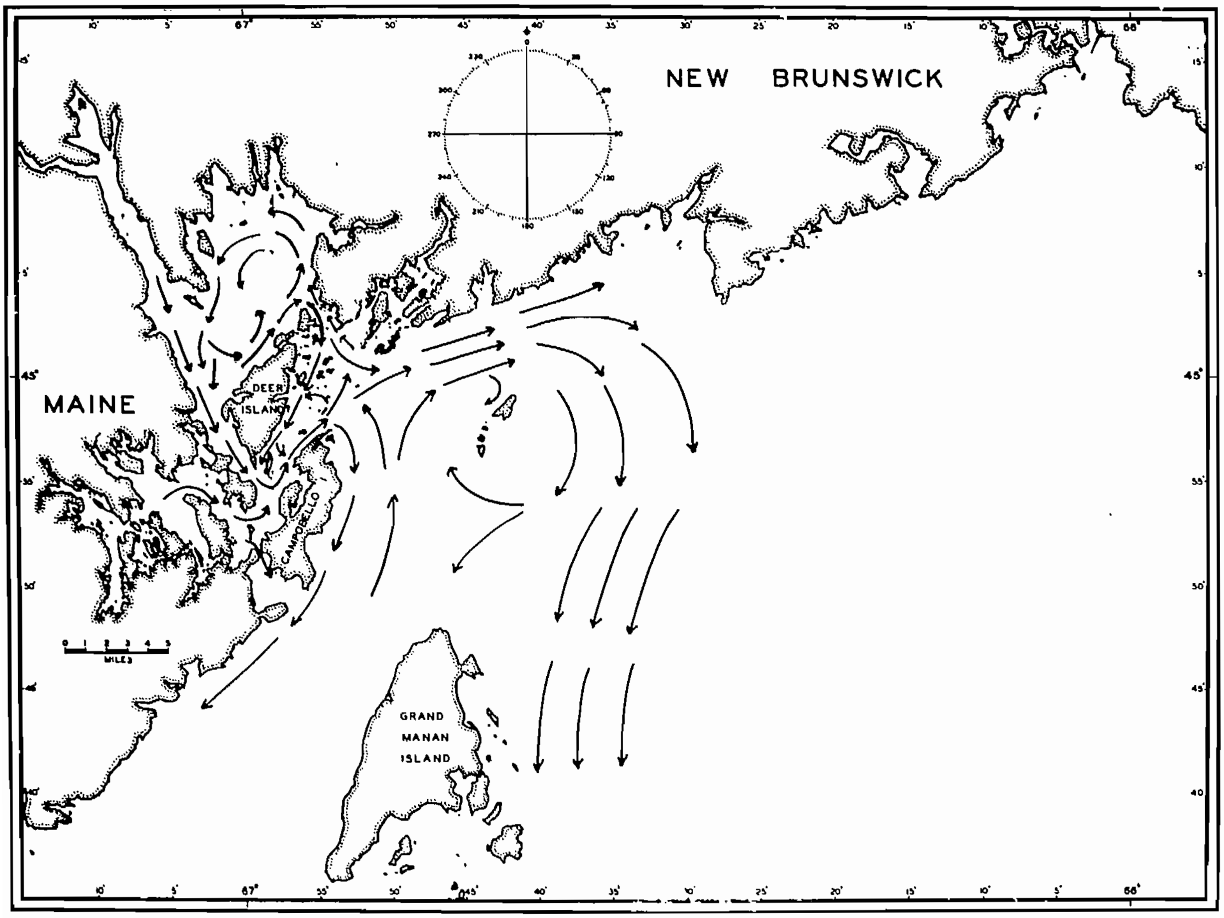

FIG. 15. General surface circulation in the Quoddy Region for 1957–58 as indicated by drift bottles (Chevrier and Trites 1960).

very short fetch. Swell from distant storms will be virtually absent, as it will be dissipated within the channels connecting the offshore region to the bays. An indication of the maximum seas developed in Passamaquoddy Bay, compared to those generated in the open Bay of Fundy, may be derived from Table 1. At low wind speeds (<10 knots) maximum heights are comparable for the two areas, whereas under high wind speeds, maximum heights outside will be nearly three times greater than those found in an area like Passamaquoddy Bay.

Wave climate studies indicate that wave heights decrease, on average, as one moves from the Gulf of Maine into the Bay of Fundy. (Fig. 17A, B). Analyses over a 1-yr period, and by 1° squares of latitude and longitude, have been undertaken by the Bedford Institute of Oceanography (H.J.A. Neu, personal communication). The results for two of these areas are shown in Fig. 17A. Significant wave height, plotted against percent exceedance, indicates not only that the larger waves occur in the Gulf of Maine, but also that waves of any given height occur more than twice as often in the Gulf of Maine as in the Bay of Fundy.

Waves in the outer Quoddy Region, when examined on a climatic basis, are found to be comprised of both sea and swell. Wave measurements, taken over a 1-yr period near Lorneville using a waverider buoy (Neu and Vandall 1976), indicate conditions in the outer Quoddy Region. A frequency diagram showing the wave period distribution is shown in Fig. 17C. Although the most frequently occurring waves have a 4–6-s period, nearly one-third of all waves come from outside the Bay of Fundy in the form of swell, with periods of up to 15 s.

INTERNAL WAVES

The vigorous tidal mixing and weak stratification of the Quoddy Region make it a generally poor environment for internal waves. However, wherever stratification exists, internal waves can be expected and are frequently visible from above, due to the effect of their associated currents on surface waves. Plates 5 and 6 show sea-surface patterns that are almost certainly caused by internal waves.

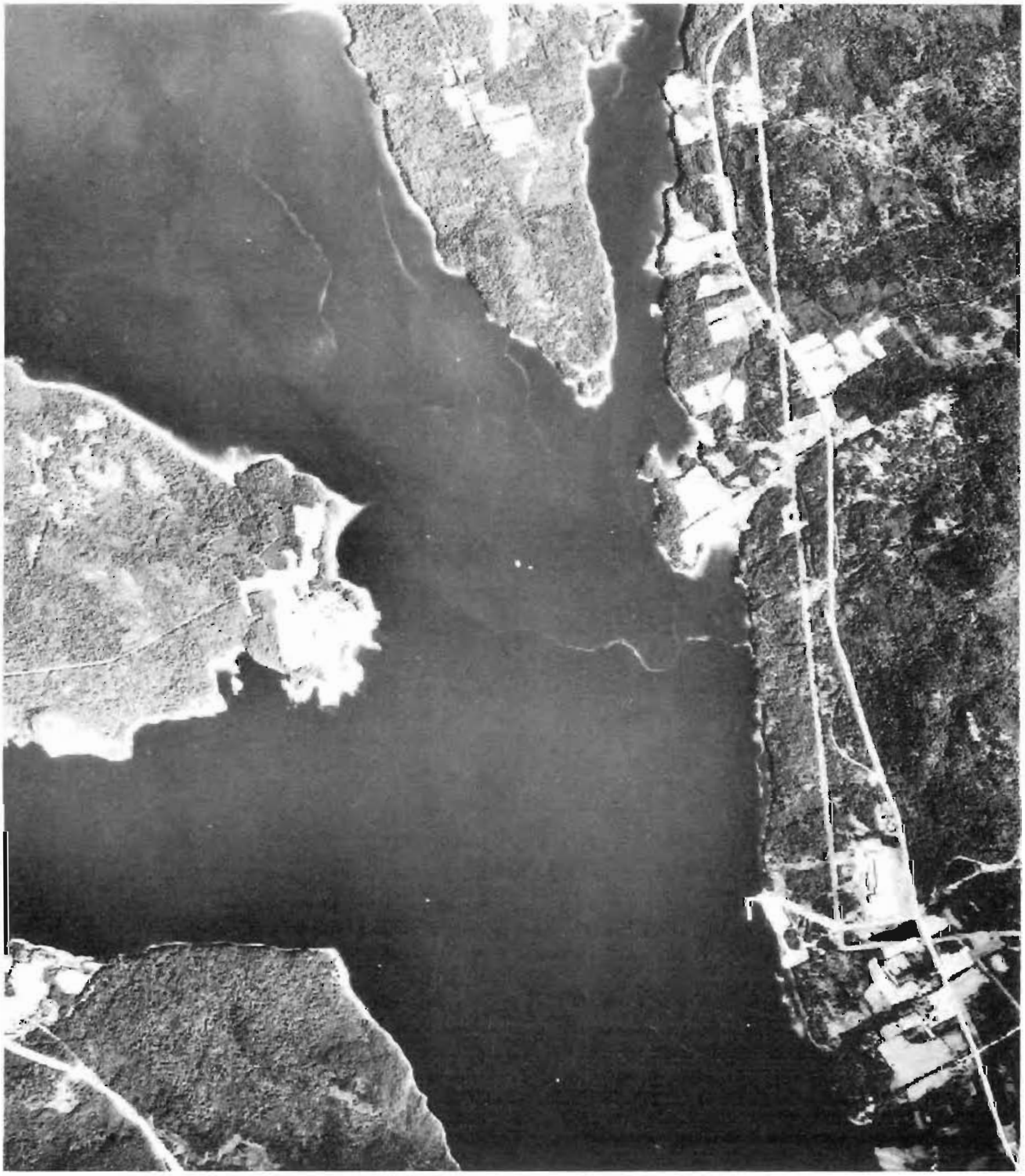

PLATE 2. Surface convergence marked by a foam line at the mouth of Oak Bay (National Air Photo Library, Ottawa).

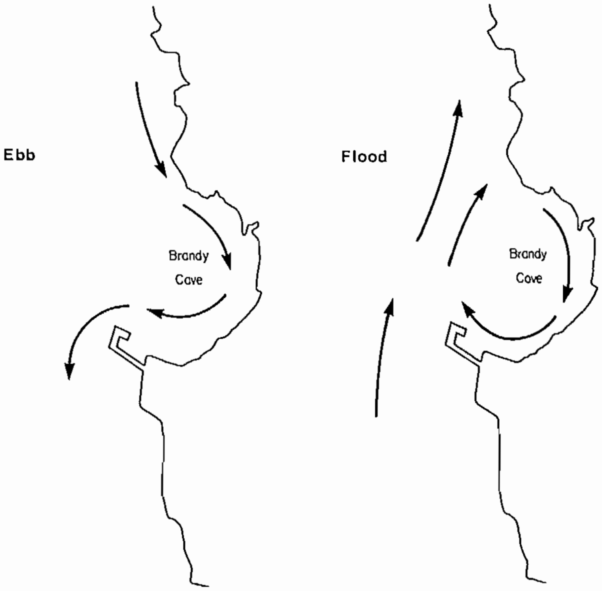

FIG. 16. Ebb and flood tidal currents in the vicinity of Brandy Cove.

ICE

Along all of our Canadian Atlantic seaboard at least some ice normally forms for short periods each winter. In the Bay of Fundy region the ice-forming areas are usually confined to near-shore areas, small embayments, and estuaries. Wind and tide may move the ice away from its formation area and into more open water some miles from shore. In areas with restricted tides and currents (e.g. Katy's Cove, Oak Bay Pond, and Sam Orr Pond) ice cover is normally complete for several months.

In the past, ice cover has occasionally been much more extensive. For example, in 1922–23 Passamaquoddy Bay was entirely ice-covered for part of the winter, and people were able to cross on the ice from Deer Island to St. Andrews. As noted above, the 1922–23 winter was a record cold one in terms of water temperatures. In the early 1930s ice formation in the St. Croix Estuary was extensive enough to remove the wharf at the Biological Station (H. B. Hachey, personal communication).

Estuarine Circulation

The whole Bay of Fundy could be regarded as an estuary in the sense that the water in it is significantly fresher than offshore ocean water. Indeed Ketchum and Keen (1953) have calculated the "flushing time" for the Bay of Fundy to be about 76 d. Passamaquoddy Bay may then be regarded as an estuary off the Bay of Fundy, and smaller systems such as the St. Croix may be regarded as estuaries discharging into the "ocean" of Passamaquoddy Bay.

THE ST. CROIX ESTUARY

Figure 18 shows a salinity section of the St. Croix Estuary obtained during a summer course in July 1976 and based on data from stations 1 to 7. The section is far from smooth as the data were collected without regard for the stage of the tide (ideally one would like the average salinity over a tidal cycle at each station), and in fact the salinity inversion at Station 6 suggests changes in water properties during the time required to complete the station. However, the section does illustrate the rapid mixing of the fresh water discharged by the St. Croix River, caused by the turbulence associated with the strong tidal currents in the estuary.

In the standard estuarine classification scheme (Pickard 1975) the St. Croix would be described as "slightly stratified," with the salinity increasing seaward at all depths and with a weak vertical salinity gradient. The competing effects of freshwater discharge (tending to stratify the estuary) and tidal currents (tending to mix it) may be quantified through the "estuary number", E_s, defined by

$$E_s = \frac{U^3 b}{g Q_f}$$

where U is the mean tidal current, b is the width of the estuary, g is gravity, and Q_f is the freshwater discharge rate (Turner 1973). A small value of E_s (weak tides or high discharge) would lead to a stratified estuary, and a large value would be associated with well-mixed conditions. The transition occurs in the range 0.03 to 0.3. The mean tidal current, U, is related to the "tidal prism" (the volume of water entering the estuary, or passing a given cross section, on the flood tide) by $1/2\ UbHT = AZ$, where T is the tidal period, Z the tidal range, H the mean depth, and A the upstream surface area. This formula or direct measurements of tidal currents leads to an estimate of $U \simeq 0.25$ m·s^{-1} as a typical average value. With $b \simeq 2$ km and $Q_f \simeq 70$ m^3·s^{-1} we obtain $E_s = 0.04$, in the transition range. A detailed explanation of the observed salinity structure in terms of the tidal currents, freshwater discharge, and topography would require an elaborate mathematical model (see Dyer 1973; Fisher 1976). It should also be borne in mind that heat or momentum transfer at the air–sea surface may produce a significant change in the vertical stratification.

FLUSHING TIME

A detailed numerical model could be useful for predicting the fate of pollutants, but a useful and usually adequate quantity is the so-called "flushing time." This is defined as the time taken for the river flow to replace the "freshwater fraction," which is the amount of freshwater required to produce the observed salinity by dilution of the external (Passamaquoddy Bay) water. Using this freshwater fraction technique, Ketchum and Keen (1953) found a flushing time of 8 d for the St. Croix Estuary (a value confirmed on many occasions since by students of

PLATE 3. Sea surface patterns in St. Croix Estuary (N.B. Department of Natural Resources).

PLATE 4. Sea surface patterns as the tide ebbs through Letite Passage (N. B. Department of Natural Resources).

Table 1. Significant wave heights (m) theoretically produced by winds of various strengths blowing over different fetches (Bigelow and Edmondson 1947).

Wind speed (kn)	Fetch (nautical miles)		
	10	100	500
10	0.5	0.6	0.6
20	0.9	2.3	3.0
30	1.5	4.0	6.1
40	2.1	5.8	9.5
50	2.6	7.3	13.4

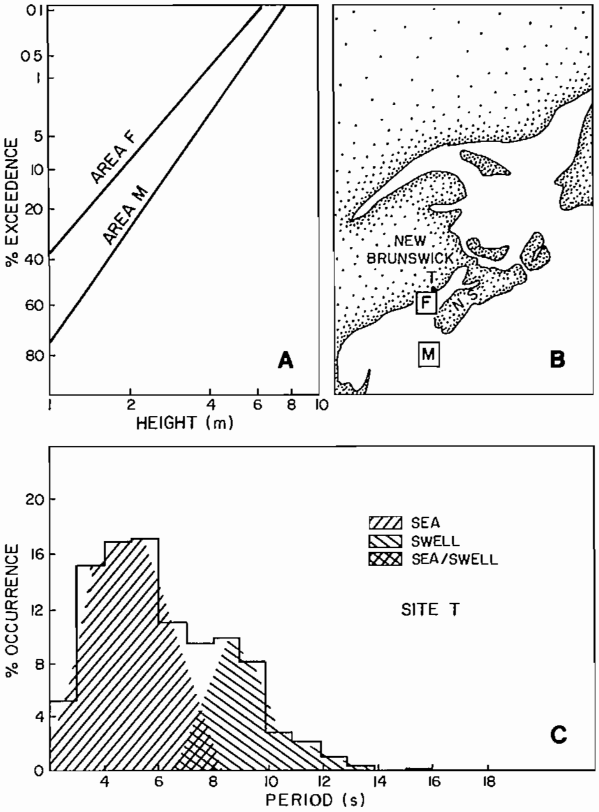

Fig. 17. *A*, Percent exceedence vs. significant wave height (m) for two areas — one in the Bay of Fundy (F) and one in the Gulf of Maine (M) — for the period June 1977–May 1978 (H. J. A. Neu, personal communication); *B*, Locations where wave climate data have been extracted; *C*, Wave period distribution for Tiner Point (T), taken over a 1-yr period using a Waverider buoy (Neu and Vandall 1976).

the H.M.L. summer course) using observed salinities in the estuary. It is interesting that this time agrees well with their a priori estimate based on their "modified tidal prism" technique, in which it is assumed that in each tidal cycle complete mixing occurs over each length of estuary, determined by the tidal excursion of a water parcel (Roman numerals in Fig. 18).

For Passamaquoddy Bay, Ketchum and Keen (1953) use observed salinities and a reference salinity from the Bay of Fundy to estimate a flushing time of about 15 d.

Temperature – Salinity (T–S) Diagram

The vigorous mixing that occurs in the St. Croix Estuary is further demonstrated by the T–S diagram shown in Fig. 19. To a first approximation the T–S diagram for the whole estuary is linear, representing mixing between warm, fresh, river water (the temperature of which may be predicted by extrapolating the line for station 1 or 2 to zero salinity) with cold, salty, Passamaquoddy Bay water. Departure from a linear T–S relationship is probably largely due to the effect of solar heating of the water as it proceeds down the estuary.

Turbidity

The turbidity of the water column affects the depth of penetration of sunlight and hence the thickness of the euphotic zone. Figure 20 shows contours of the percentage of surface illumination reaching a given depth (from photocell measurements made on an H.M.L. summer course in July 1976). The increasing attenuation with depth as one proceeds up the estuary suggests that the freshwater contribution to the estuary is more turbid than the salt water. In fact, if the turbidity itself is measured with a light attenuance meter and plotted against salinity, a linear relationship is often found, with very low values of the turbidity at salinities representative of Passamaquoddy Bay water. This suggests that in midsummer the turbidity is almost entirely associated with river water rather than with particles from erosion or biological productivity further down the estuary.

Mixing and Dispersion

The vigorous mixing associated with the strong tidal currents in the St. Croix Estuary was discussed in the previous section. Some mixing also occurs in Passamaquoddy Bay, particularly in the passages leading into it. The vertical mixing, associated with a tidal current of amplitude U in water of depth H, may be roughly parameterized by an eddy diffusivity of about $10^{-3}UH$ for homogeneous water, decreasing with increasing density stratification (Csanady 1976). The horizontal eddy diffusivity is of order $10UH$, again reduced by stratification (Csanady 1976).

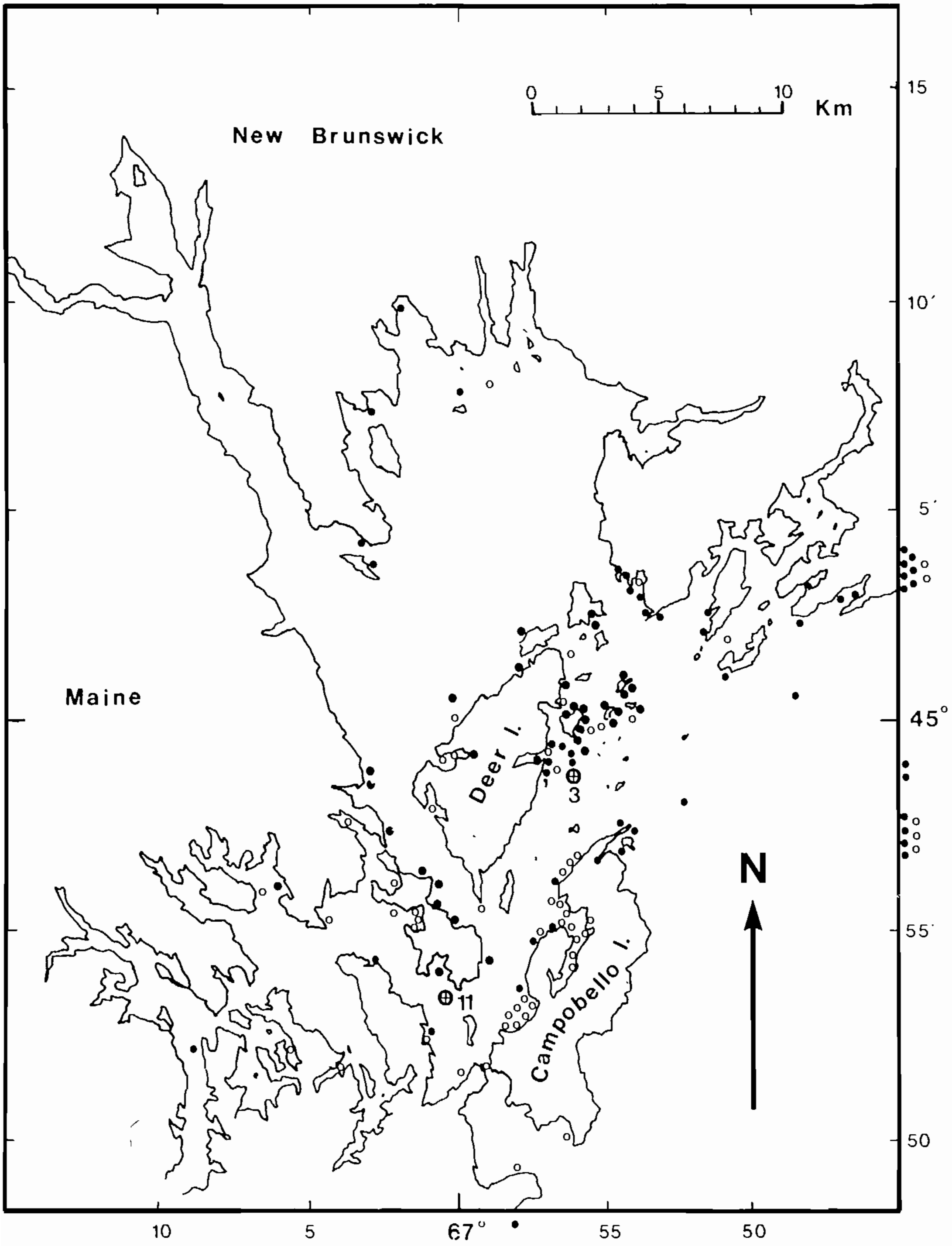

Fig. 21. Recapture points of drift bottles released at stations QP3 (solid dots) and QP11 (empty circles) (Anon. 1974).

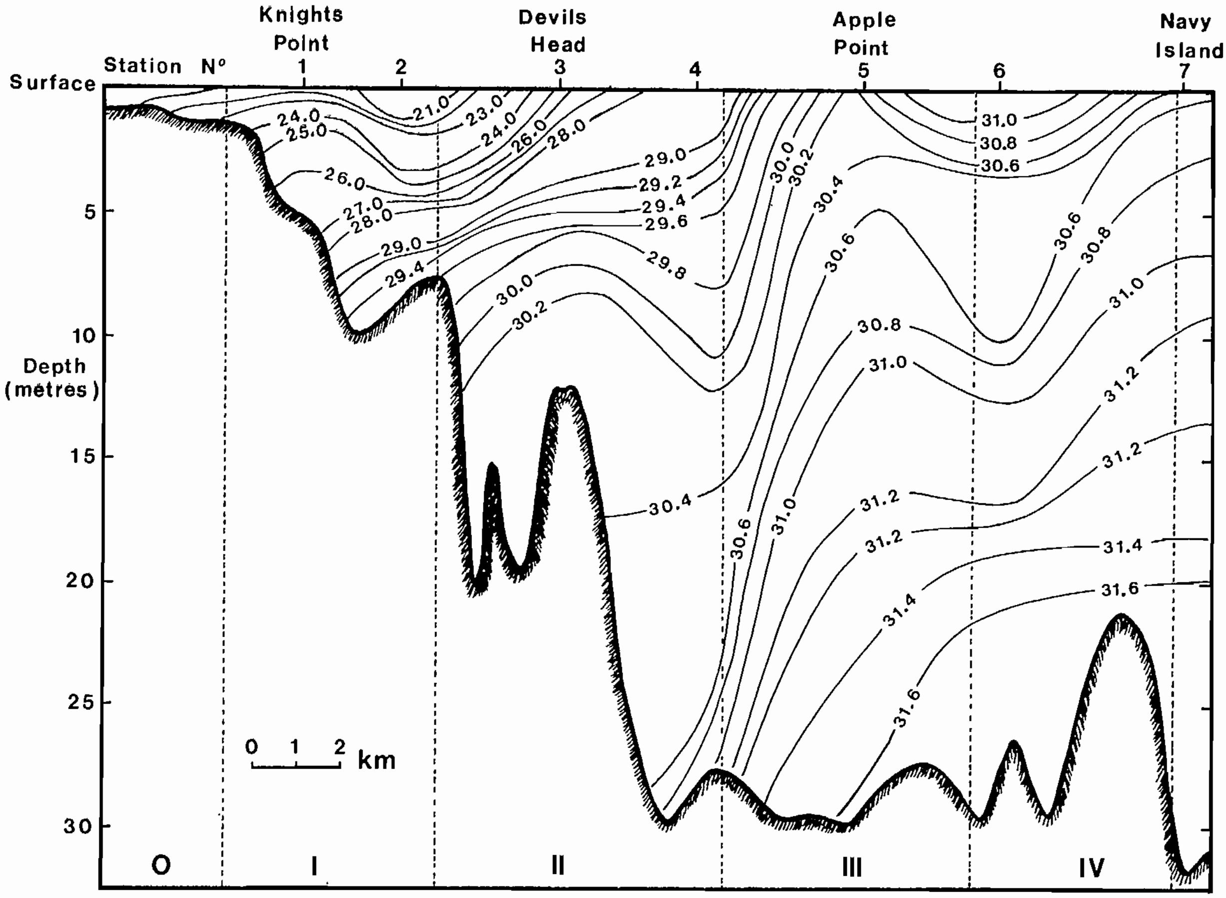

Fig. 18. Salinity section of the St. Croix Estuary based on data from Sections 1 to 7 in July 1976.

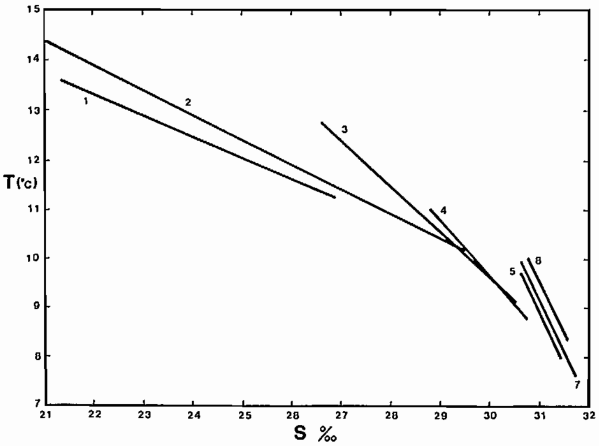

Fig. 19. T–S diagram for the St. Croix Estuary, corresponding to the data and stations of Fig. 18.

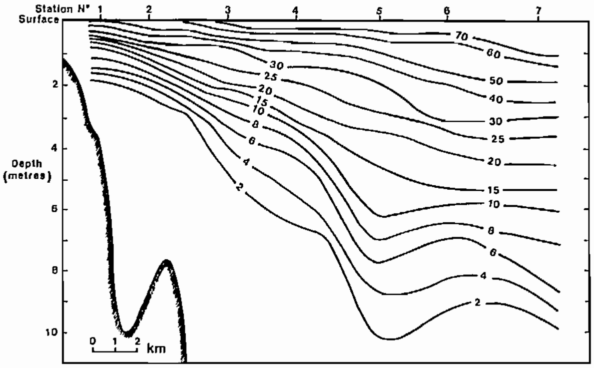

Fig. 20. Percentage of surface illumination reaching a given depth in the St. Croix Estuary in July 1976, for the stations indicated in Fig. 18.

Plate 5. Internal waves east of Minister's Island (National Air Photo Library, Ottawa).

PLATE 6. Internal waves in Passamaquoddy Bay south of St. Andrews (National Air Photo Library, Ottawa).

In the Quoddy Region much of the tendency towards stratification is associated with the freshwater input. However, solar radiation alone will produce stratification in midsummer, against the mixing effect of tidal currents, if H/U^3 is more than about $70 m^{-2} \cdot s^3$ (Garrett et al. 1978). For the center of Passamaquoddy Bay we might take H as $30 m$ and U as $0.25 m \cdot s^{-1}$, giving $H/U^3 \simeq 2{,}000\ m^{-2} \cdot s^3$. A temperature difference of about 4°C from top to bottom does develop in summer (Forgeron 1959), but this is less than would be expected without the mixing in the passages leading into the bay.

Horizontal dispersion in the Quoddy area, whether of herring larvae or, potentially, of spilt oil, is due to a combination of tidal mixing, residual circulation, and transient wind-driven circulation. An example of the dispersion of surface drift bottles is shown in Fig. 21, but this gives no indication of the rapidity of the process. Loucks et al. (1974) have estimated that much of the Quoddy Region would be contaminated within a week should oil be spilt in Head Harbour Passage.

Suggested Projects

This section is intended mainly for the guidance of students and teachers at H.M.L. summer courses. Many interesting scientific problems will suggest themselves to the enquiring reader of this chapter, or to anyone who begins to make oceanographic observations in the Quoddy area; below are listed some ideas that have occurred to us during scientific investigation or teaching in the region. Many of the projects suggested are meant to use the St. Croix Estuary as a natural laboratory for the study of fundamental physical oceanographic effects, rather than being aimed at specific local problems. In identifying these projects, we have not attempted to consider relative importance. Rather we have restricted our suggestions to those that should be amenable to study with limited time, manpower, and facilities and within easy reach of St. Andrews.

1) If you have installed a tide gauge, compare the observed time and height of high and low water with the predictions of the tide tables. Do the differences appear to be related to any local meteorological effects or to freshwater discharge?

2) Recalculate the tidal dissipation occuring in the Quoddy Region. If all this energy goes into Joule heating of the water, how fast is it warming up? (Would you consider thermal pollution from nuclear power stations situated on the Bay of Fundy to be a potential problem?)

3) Sutcliffe et al. (1976) have related St. Andrews water temperature to the St. Lawrence discharge 8 mo earlier. What effect does the St. Croix River have?

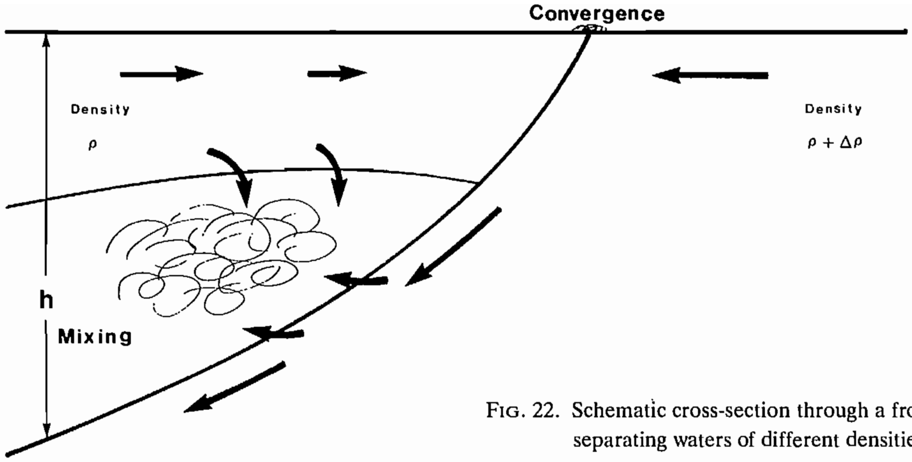

FIG. 22. Schematic cross-section through a frontal zone separating waters of different densities.

4) Study the circulation in Brandy Cove at various stages of the tide using surface drifters (oranges and grapefruit are excellent), drogues (made of, for example, a single sheet of plywood 1-m. deep by ½-m wide, with bricks for weight at the bottom and a bridle at the top attached to a small surface float; or two sheets of plywood in the form of a cross), and direct reading current meters.

5) Study the circulation past St. Croix Island with the same techniques as those outlined for project 4.

6) The flow past river bends is interesting, with faster flow on the inside bend and a bottom flow towards the inside bend (see Scorer 1958, p. 79, for a discussion). Can you confirm this in the St. Croix Estuary?

7) Small scale "fronts," or boundaries between water masses of different properties (particularly density), are often seen in the St. Croix Estuary, marked by foam lines (see Plates 2 and 3). Measure temperature and salinity profiles on either side of the front and the speed of convergence towards the front of surface drifters placed on either side of the front. Relate the convergence rates to theory (see Turner 1973 and Britter and Simpson 1978, but basically expect speeds proportional to $[g(\Delta\rho/\rho h]^{1/2}$, with symbols defined in the oversimplified sketch in Fig. 22). Set up laboratory simulations.

8) Notice the interaction between surface waves and the current field near fronts and elsewhere. What is happening? (see Phillips 1977)

9) Small plexiglass tanks can be used in the laboratory for a number of simple experiments on surface and internal waves which help one understand field observations. See Turner (1973) for ideas.

10) Obtain temperature and salinity sections for the St. Croix Estuary. Compute the flushing time. Try to evaluate a heat budget for water in the estuary. (Up-to-date values for the daily freshwater discharge may be obtained by telephoning the engineer in charge at the Grand Falls power station.)

11) Relate the St. Croix to estuarine classification schemes in more detail than by just using the estuary number discussed in the section on estuarine features (see Dyer 1973).

12) Measure the turbidity of the water and relate it to the turbidity of the fresh and salt water sources, or to local input. How much of the turbidity is due to natural causes and how much is generated by man's activity?

13) Complete your section of the estuary by measuring temperature, salinity, and turbidity profiles from the International Bridge between Calais and St. Stephen. (A salt wedge will be found near high tide for moderate or low freshwater discharge rates; if not, the freshwater temperature and turbidity are still useful end points for T–S and turbidity–S diagrams).

14) If a salt wedge is found at the International Bridge progressing upstream on the rising tide, with the river water flowing downstream over the top of it, measure the current difference ΔU and density difference $\Delta\rho$ between the two layers and, if possible, the thickness h of the interface. Compute the Richardson number $g\ (\Delta\rho/\rho)h/U^2$ (see Turner 1973).

15) Investigate the physical oceanography (heat and salt budgets, circulation, mixing) of small bodies of water such as Katy's Cove, Sam Orr Pond, and Oak Bay Pond.

16) Compare the results obtained using the freshwater fraction technique of Ketchum and Keen on the flushing time in the St. Croix Estuary with the results obtained using an independent method.

Acknowledgments

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CHAPTER 4

Rocky Intertidal Communities

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Introduction

Among the marine communities, those occurring on rocky intertidal shores probably receive the most attention. They are easily accessible from the land, well drained, and offer a great diversity and abundance of biota. From a teaching point of view the advantage of accessibility is augmented by the wealth of life available, which demonstrates a great variety of taxonomic, morphological, physiological, and ecological principles and processes. They are prime collecting grounds for laboratory work on both fauna and flora.

However, despite this concentration of attention at a fairly elementary level, the ecosystem is not well understood. It seems that specific adaptations may be rather obvious but that the factors governing the structure and function of the whole system are complex and often unknown. This may partly explain the relatively low level of scientific research on rocky shores on the east coast of Canada. For the Quoddy area, despite the presence of a federal government research laboratory, an independent research laboratory, and a university, there are less than half a dozen published studies on the rocky intertidal zone. The level of effort has expanded greatly in recent years, largely owing to the need to gather scientific information on the possible harmful effects of shoreline energy-related projects and proposals. Those of importance have been the Passamaquoddy Bay Tidal Power Proposal (Anon 1959), the Colson Cove Thermal Electric Generating Plant at Lorneville (Anon 1973a), the Eastport, Maine, Oil Refinery Proposal (Anon 1974), the Point Lepreau Nuclear Electric Generating Station (Anon 1976) and the Fundy Tidal Power Proposals (Anon 1977a, b.). Unfortunately, few of these projects have yielded published reports.

With this paucity of information, it is therefore fortunate that the intertidal zone has many universal features on a world-wide basis (Stephenson and Stephenson 1949, 1972: Lewis 1964: Southward 1966) so that studies elsewhere are applicable here.

However, Bay of Fundy shores are unique in many respects. The very large tidal range results in an unusually wide and important intertidal zone. Of the total coastline of 2745 km in the bay there are 1052 km^2 of intertidal zone (Thomas 1977) — a relatively huge area.

The lengths of various types of shoreline in the Canadian Quoddy Region have been tabulated by Thomas (1973) and are shown in Table 1. As the table shows, the dominant shoreline type is material ranging from broken rock to sand. Probably half of this distance consists of stable shores of large rock fragments and supports a rocky shore community. This, together with 35.2 % of bedrock shores, shows that about half the shoreline is rocky intertidal. Thus there is a large area available for study. It should be emphasized that this table gives lengths of shoreline: areal relationships would show different proportions.

This chapter includes a general description and discussion of this rocky intertidal community, appropriate study methods, and detailed descriptions of a variety of specific locations. The ecosystem described will be only that of the well-drained shore. The ecology of pools on rocky shores is markedly different and will be the subject of a separate chapter (Chapter 6).

TABLE 1. Extent (km) of shores of various types on the large islands and mainland of the Canadian Quoddy Region (after Thomas 1973).

Type	Grand Manan	Campobello	Deer	Mainland	Total	%
Bedrock	41.2	19.2	21.6	76.0	157.9	35.2
Coarse sediment	29.1	31.5	16.1	169.9	246.7	55.1
Mud	1.8	9.0	5.6	24.6	41.4	9.2
Salt marsh	—	1.9	—	0.2	2.1	0.5
Totals	72.1	61.6	43.6	270.7	448.0	100.0

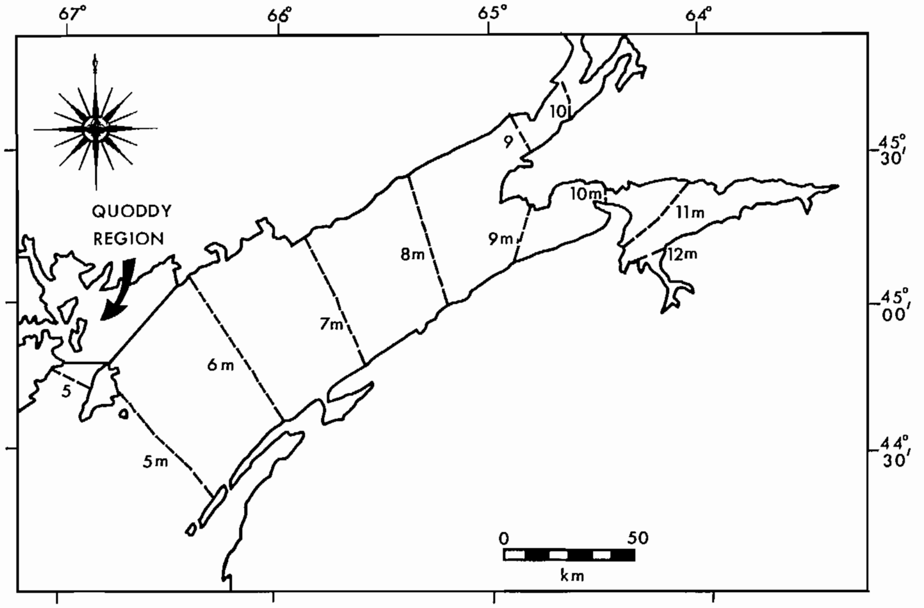


FIG. 1. Mean tidal range within the Bay of Fundy.

The Rocky Intertidal Ecosystem

The intertidal zone is, strictly speaking, the area covered and uncovered by the tides; however, a wider zone — the littoral, that is directly affected by the sea, including wave and splash action — really constitutes the rocky shore ecosystem. As discussed below, typical marine shore communities extend beyond the true intertidal into the upper littoral areas. The immense variability of the tides makes intertidal and littoral areas hard to separate. The two terms will be used as synonyms herein.

The well-drained rocky intertidal zone is characterized by one overwhelming ecological feature: vertical zonation of members of its community. This vertical zonation is a universal feature of intertidal areas and certain genera or groups of similar organisms tend to occupy similar positions all over the world. Thus, intertidal gastropods of the periwinkle group are found with lichens at the top of the shore, and are displaced lower down by barnacles or rockweeds and other algae. It is generally true too that diversity — measured simply as the number of species present — decreases moving upward to about mean high-tide level and then increases again as vascular maritime plants appear.

This intertidal or littoral zone is a meeting place of terrestrial and marine systems and its community is enriched by members from both. This is one reason for the great diversity of species and the great abundance and biomass of organisms. Other advantages contributing to the better-than-expected conditions for life in this harsh zone are the regular wetting by the sea, high light levels (although these may be harmful to some species), and good nutrient supplies from land and sea. Nutrients are supplied in coastal run-off and from the stirring of coastal sediments by wave action. High diversity is also promoted by the normally high physical heterogeneity of the shore. This results in numerous microhabitats in crevices, overhangs, shaded places, etc. Many shores also retain considerable reserves of sea water in cracks, porous substrates, and the like. These reserves, draining at low tide, help to offset drying influences at low tide.

This luxuriant system is exposed to wide variations in the physical conditions of its environment.

THE PHYSICAL ENVIRONMENT: TIDES

Tides form the dominant physical variable on the shore and there is excellent evidence and wide agreement that tides are the main influence on zonation (Lewis 1964; Stephenson and Stephenson 1972; Southward 1966; Carefoot 1977; Yonge 1949). That the tides are not the direct cause of most intertidal zonation phenomena is also widely accepted, the main evidence being that the zones vary greatly in position even in a constant tidal regime.

The tides are caused by the combined gravitational forces of heavenly bodies on the oceans, modified by the natural period of oscillation of the oceans, seas, and bays of the earth. The main effect is from the moon, the next most important one from the sun, and much smaller modifying forces from the other planets.

The relative motions of the earth, moon, and sun result in a cycle of tides each lunar month (28 d). The normal sequence is that spring tides, which have a large range, occur every 14 d and neap tides, which have a small range, are interspersed with these. Thus there are two sets of springs and two sets of neaps each lunar month. Spring or high-range tides occur when the gravitational forces of sun and moon augment each other, and neap or low-range tides occur when these forces are roughly at right angles to each other. Because the relative positions of sun and moon are rarely ideal for maximum effect, the ranges of spring tides vary from month to month and year to year. Rare

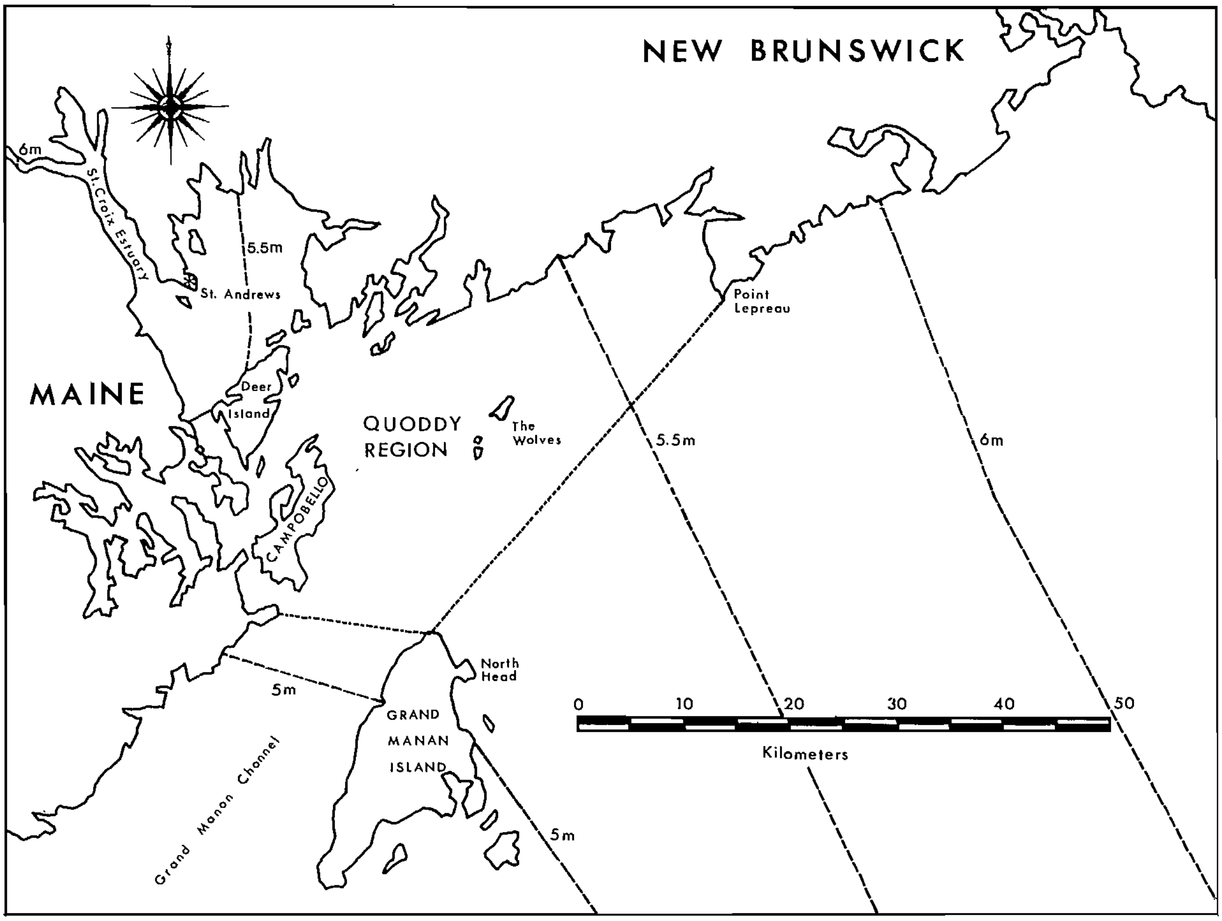


FIG. 2. Mean tidal range in the Quoddy Region of New Brunswick.

ideal conditions may result in exceptionally large-range tides.

On a daily basis, there are high tides at approximately 12.5-h intervals; thus low tide occurs about 6 h 15 min after each high tide.

Because the magnitude of tide-producing forces depends on the highly predictable motions of heavenly bodies, tide times and heights can be predicted with great accuracy. For the Bay of Fundy, tide predictions are published annually in *Canadian Tide and Current Tables, Vol. 1., Atlantic Coast and Bay of Fundy* (Anon 1979a).

Tides within the Bay of Fundy have an unusually large range because the natural period of oscillation of the bay approximates that of the tide. As a result, the tidal wave within the bay takes the form of a standing wave of increasing range toward the head of the bay resulting, in the Minas Basin, in the highest tides in the world. The general tidal range within the Bay of Fundy is shown in Fig. 1 and, in more detail for the Quoddy Region, in Fig. 2.

Practical aspects of the use of tidal tables and the interpretation of tidal levels are provided below in the section on methods.

Meteorological conditions such as strong or prolonged winds, abrupt changes in barometric pressure, or prolonged periods of high or low pressures affect water levels. These changes may affect both heights and times of tides but tend to be of small magnitude where tidal range is high, as in the Bay of Fundy.

The rise and fall of the tide does not occur at a steady rate but follows a harmonic curve. The rate of change of level is at a maximum at mean tide level and reaches zero at times of high and low water. Calculations made on this basis allow the prediction of water level at any state of the tide. Figure 3 shows the height and distance traversed by the tide for each hour of rise or fall for a typical Quoddy Region shore. Table 2 gives the percentage of the range traversed per hour by a typical tide.

The shape of the tidal curve has implications for wave action and water movement at various levels which will be discussed below.

The main result of the rise and fall of the tides is the creation of a gradient of exposure to atmospheric conditions between approximately extreme low-tide level and approximately extreme high-tide level.

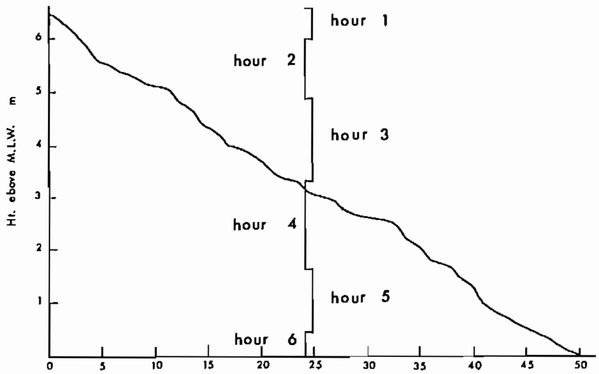


Fig. 3. Height and distance traversed by the tide for each hour of rise or fall, of a 6-h tide on a typical transect in S.W. New Brunswick.

TABLE 2. Percentage of the range of tide traversed per hour for a 6-h tide. HW, high water.

Time period	% of range
1 h around HW	4.0
Next 1 h	13.0
Next 1 h	21.0
Next 1 h	28.0
Next 1 h	21.0
Next 1 h	13.0
Next 1 h	4.0

THE PHYSICAL ENVIRONMENT: FACTORS RESULTING FROM TIDAL CHARACTERISTICS

Alternating immersion and emersion in the littoral zone inevitably imposes gradients of other environmental parameters on resident organisms.

Desiccation potential rises with height on the shore but is greatly modified by other factors, notably temperature and wind. However, marine organisms above high water of neap tides will be exposed to the air for periods of several days and those at extreme high water of spring tides may be exposed for months.

The temperature range also increases with height on the shore, increasing at the high end and decreasing at the low. Just subtidal organisms in the Bay of Fundy may be exposed to a range of 2–20°C, depending on location. Those high on the shore may encounter air temperatures ranging from +30 to −30°C or more. Low temperatures may be augmented by wind chill and high temperatures may be ameliorated by the same effect. Abrupt changes may occur in early summer when seawater at 5°C washes over organisms heated to 30°C in the sun (Carefoot 1977).

Salinity along the shore is relatively constant except in the upper reaches of estuaries; thus subtidal biota may encounter a range of 27–30‰, and intertidal organisms are exposed to water of low salinity during rain and fog or where terrestrial runoff flows over the shore. Salinity in the littoral zone may fall to zero anywhere in a heavy downpour but the potential duration of exposure to low salinity increases with height.

A fourth major variable associated with the rise and fall of the tides is the quantity and quality of light reaching the intertidal community. This variable is particularly evident in the Bay of Fundy where the tidal range is high and the rapid tidal currents can maintain a high suspended sediment load in the water. An intertidal community low on the shore may be below the photic zone at high tide.

These are the principal factors associated directly with tidal rise and fall; others may have minor effects.

THE PHYSICAL ENVIRONMENT: FACTORS MODIFYING THE TIDAL INFLUENCE

The principal environmental factor modifying the direct effect of tidal rise and fall is wave action. This factor is frequently referred to as exposure, but exposure has many facets of which wave action is only one. Wave action acts in several ways. First, it tends to broaden the zone subject to immersion in water or emersion in air. At the top of the shore waves carry water above the tide level and at the bottom waves expose subtidal organisms to transitory contact with air. A second feature affecting the upper limit of marine influence is the production by breaking waves of spray, which is carried by wind to even higher shore levels, producing a further upward broadening. Wave and spray action on open coasts may double the vertical extent of the littoral zone. A third aspect of wave action is its direct physical effect on the shore. Plunging breakers on exposed rocky shorelines may exert forces up to about 274 kg/m^2 (Thomas 1976). These forces erode rock and detach organisms not firmly attached. This aspect of exposure to waves decreases environmental stability and reduces species diversity.

Another locally important modifying factor is the effect of fog. Fog maintains high humidity in the air without precipitation, and thus does not dilute available sea water. This reduces the drying effect of exposure to air.

Wind modifies tidal effects in a variety of ways. In dry weather it increases desiccation; in any weather onshore winds carry spray inshore and vice versa.

Many studies have shown that tidal effects are greatly modified by the slope of the shore. The two extremes — gentle slope and cliff — have very different effects on both wind and wave. In general, the gentle slope allows extensive wave swash and broad spray-affected areas while the cliff causes reflection of waves and has a narrower spray zone. Gentle slopes are slower to drain than steep ones, thereby modifying the drying actions of sun and wind.

Lastly the nature of the rock itself modifies the effects of tidal action. Porous rock may hold water and reduce desiccation or, conversely, may increase it by allowing water loss by capillary action from an organism through the rock to air. Soft rock is more easily worn by waves, and organisms are more easily torn from it, although some may burrow into the soft rock and create protective hollows. Hard impervious rock dries rapidly but provides a more stable substrate unless it is very smooth, and thus makes attachment insecure.

The overwhelming influence of the tides is responsible for other environmental variables, and the tidal effect itself, as well as associated parameters, may in turn be greatly modified by other physical influences. It is not surprising, therefore, that the relationship between zonation and the tides is not a simple one. As we shall see below, the effects of this multi-variate physical environment are further modified by various biological factors.

GENERAL FEATURES OF BIOTIC ZONATION

The general characteristics of zonation have been best described by the late T. A. Stephenson and A. Stephenson (1949, 1972) who devoted 30 years to the study of zonation on a world-wide scale. They found that although zonation bore no constant relationship to the tide, it did show certain very general biological characteristics. These they termed the "universal scheme of zonation," a phrase they later changed, in response to widespread criticism, to "general scheme of zonation." Although the scheme is not absolutely universal, it does have widespread applicability, and certainly applies to the Bay of Fundy of which the Stephensons described several localities (1954a, 1954b). The nomenclature of their scheme has been slightly modified by Lewis in his monograph (1964). Both schemes are presented in Fig. 4, although the Stephensons' scheme has received wider acceptance. Both include a zone at the bottom extending below the influence of tides but having certain features in common with the intertidal zone; neither they nor later authors define its lower limit. This zone is discussed in detail in Chapter 8 below. The lower limit of this infralittoral zone (sensu Stephenson and Stephenson 1972) or sublittoral zone is approximately coincident with the bottom of the photic zone, a readily determined depth, and we propose to define it as such. Deeper waters are part of the inner continental shelf (Hedgpeth 1966).

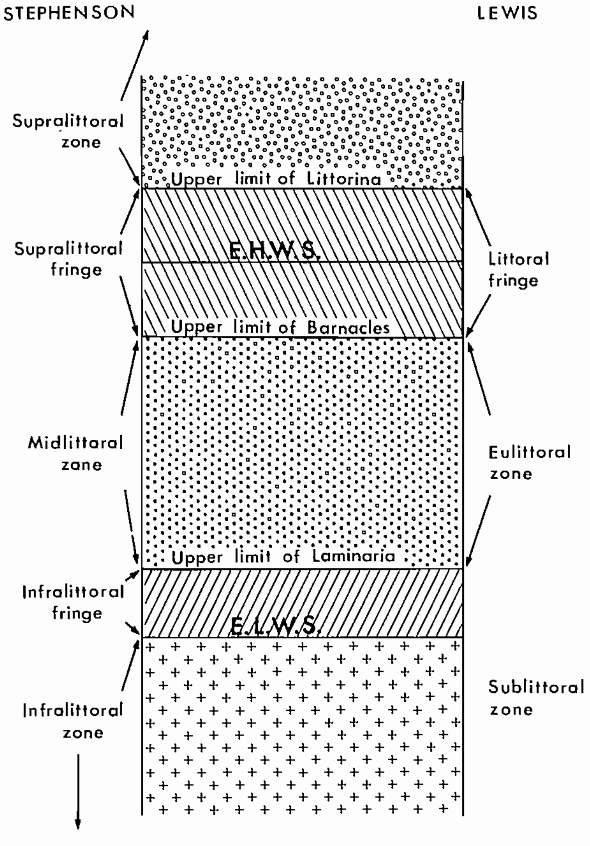


FIG. 4. General scheme of intertidal zonation (after Lewis 1964).

In the "universal" scheme are three main biologically defined levels and one tidal level dividing the shore into five major horizontal bands. The highest of these levels is the upper limit of periwinkles (e.g. *Littorina* sp.) above which lies the supralittoral zone; below the upper limit of periwinkles, the supralittoral fringe extends until the upper limit of barnacles is reached. Below this latter level, the main, generally extensive midlittoral zone extends to the upper limit of kelps (e.g. *Laminaria* sp.). The infralittoral fringe then extends to extreme low water of spring tides, below which lies the infralittoral zone (sublittoral zone).

THE GENERAL CHARACTERISTICS OF THE ZONES IN THE BAY OF FUNDY

The following descriptions follow the Stephensons' (1949) zones and are taken from data published by them (1954a,b) and by Thomas (1975, 1976), as well as additional information gathered for this book.

Supralittoral zone — In this zone the biota is typically of terrestrial origin. The commonest organisms on bare rock are a variety of grey and yellow lichens including the brilliant orange-yellow *Xanthoria parietina*. Where there are pockets or patches of sediment several vascular plants occur, the commonest of which are *Plantago maritima* (Goose Tongue Greens), *Empetrum nigrum* (Black Crowberry), and *Deschampsia flexuosa* (Hairgrass). On many islands in the Quoddy Region the lichens *Xanthoria parietina* and *Caloplaca elegens* form a well-defined orange band in the lower supralittoral zone.

Supralittoral fringe — This zone, as shown in Fig. 4, extends down from the upper limit of *Littorina* to the upper limit of barnacles. It is often referred to as the black zone and in many parts of the Quoddy Region, in Letite for example, there is a distinct black cast to the zone. The black color results from a community of lichens such as *Lichina* sp. and *Verrucaria* sp. and blue-green algae such as *Callothrix* sp., *Phormidium* sp., *Gleocapsa* sp., and *Nodularia* sp.

The characteristic animal of this zone, along the entire North Atlantic coast, is the rough periwinkle (*Littorina saxatilis*) (although this population may be an aggregate of four different spp.). This small snail is often extremely abundant, with almost no associated marine fauna. Although it is the dominant organism in this zone it frequently extends down the shore to at least mean tide level. The dominant plants of the zone are normally *Verrucaria* sp. or *Callothrix* sp. on which the *L. saxatilis* graze. In the upper part of the zone the lowest individuals of *Xanthoria parietina* are often conspicuous, and at the lower edge the smooth black encrusting lichen *Verrucaria maura* normally forms smooth, oil-like growths. On porous, moist rock surfaces the blue-greens usually dominate the lichens and may form a continuous carpet of microflora.

Just at the bottom of this zone in the Quoddy Region is an almost universally present but narrow band of the brown fucoid alga, *Fucus spiralis*. This alga is generally less than 10 cm tall, lacks bladders, and has a somewhat yellowish cast. However, it is difficult to distinguish from *Fucus vesiculosus forma linearis* except when it is fruiting.

In mature plants the irregular ridge around the vesicles is diagnostic when coupled with bisexual receptacles.

Midlittoral zone — The midlittoral zone, commencing at the upper limit of the common barnacle, *Balanus balanoides*, is a broad, usually obvious zone. It may be dominated in Atlantic Canada by barnacles (*B. balanoides*), blue mussels (*Mytilus edulis*), knotted wrack (*Ascophyllum nodosum*), or bladder wrack (*Fucus vesiculosus*). Generally, mussels dominate where wave action is highest and slope is steep, barnacles occupy an intermediate position, and the fucoid algae dominate in sheltered locations and on shallow slopes. However, in the Bay of Fundy, the fucoid algae, particularly *A. nodosum*, dominate irrespective of exposure to waves. Only occasionally, on steep slopes or cliffs, barnacles show the characteristic abrupt cessation of white colour we would expect to see. Usually, in the Bay of Fundy, the zone is a uniform olive brown from the continuous algal cover.

The top of the zone is, by definition, the upper limit of the barnacles. In eastern Canada the species is always *B. balanoides* on open coasts, but sometimes *B. improvisus* occupies a similar position in estuaries. Barnacles are usually sufficiently common that the zone can be clearly seen, but if not, the top of *F. vesiculosus* is almost always within a few centimeters of this level. Where blue mussels (*M. edulis*) do occur they are tiny and are normally found considerably lower down the zone.

In the Quoddy Region, *F. vesiculosus* may dominate the upper part of the midlittoral (Thomas 1975) but is always quickly superseded by the knotted wrack (*A. nodosum*) which normally comprises 90% of the biomass. Several animals are characteristic of, and normally abundant in, this zone: the smooth periwinkle (*Littorina obtusata*) is found throughout the zone, always on the fucoid algae; the common or edible periwinkle (*Littorina littorea*) is less constant in position, frequently abundant, and normally concentrated in the lower areas of the zone. The tortoise shell limpet (*Acmaea testudinalis*) and dog whelk (*Thais lapillus*) usually occur below mean tide level and vary greatly in abundance. *T. lapillus* is reduced in abundance in wave-washed locations. On the stalks of the fucoids, the hydroid *Sertularia pumila* and the bryozoan *Flustrellidra hispida* are almost universally present. Micro-crevices on the rock surface are normally lined with the tiny tubicolous polychaete worm, *Potamilla neglecta*. Ubiquitous throughout the zone is the highly active and abundant amphipod *Gammarus oceanicus*, which is usually the dominant herbivoire–omnivore. When drying is severe, *G. oceanicus* will only be found in damp microhabitats but in fog or high humidity will be scattered everywhere.

Seaweeds other than the dominant fucoids are common and several species of lichen also occur. The black crustose lichen *V. maura* extends well down from the supralittoral fringe, but is gradually replaced by the green *V. mucosa*, which traverses the entire zone. On the fucoid alga *A. nodosum*, the epiphytic red alga *Polysiphonia lanosa* extends almost as high as its host and higher than any other red alga except the thin red encrusting *Hildenbrandia prototypus* which appears almost black when dry. In the lower part of the zone other red algae such as *Chondrus crispus* and *Gigartina stellata* are often common, the latter often forming dense mats in the lower 5% of the zone. These two species, particularly *C. crispus*, vary greatly in color: they may be very dark or very light red. Two other reds, *Porphyra umbilicalis* and *Palmaria palmata* or dulse, have a more scattered distribution but also increase in abundance moving down. The green algae of the genus *Enteromorpha* are often common, especially if freshwater seepage occurs, and the flat green sea lettuces *Ulva* sp. and *Monostroma* sp., are frequently found.

Infralittoral fringe — In Fig. 4 the topmost extent of this zone is defined as the upper limit of *Laminaria*. In the Quoddy Region of the Bay of Fundy, this is a frequently unsatisfactory criterion to use because *Laminaria* sp. are rarely abundant. On exposed headlands and other places of active water movement another kelp, *Alaria esculenta*, may be particularly prominent if not exposed to severe drying. Other large brown algae which might be expected elsewhere are not common, a situation generally atributed to the abundance of the green sea urchin (*Strongylocentrotus droebachiensis*), a voracious grazer in this zone. Rather the zone is often characterized by a diversity of red and green algae and is most easily located as the part of the shore below the lowest *A. nodosum* plants.

The commonest red alga is often *Gigartina stellata*, beginning beneath the *A. nodosum* cover and extending lower as a more or less continuous band on exposed shores in the Quoddy Region or in patches elsewhere. Dulse, *Palmaria palmata* and its tubular relative *Halosaccion ramentaceum*, irish moss, *Chondrus crispus*, and *Cystoclonium purpureum* are most prominent among the soft-bodied red algae. They may be accompanied by extensive patches of the encrusting pink coralline alga, *Phymatolithon lenormandii* and the feathery pink, *Corallina officinalis*. Most common among the green algae are *Spongomorpha arcta*, *Enteromorpha* sp., and the sea lettuces *Ulva lactuca* and *Monostroma grevillei*, and *M. pulchrum*. The commonest browns are *Scytosiphon lomentaria, Petalonia fascia, Fucus edentatus,* and a kelp, *Alaria esculenta*. *Fucus evanescens* and *Laminaria* sp. are also common. The fauna is very diverse in this zone but the echinoderms are the most characteristic. With the green sea urchins, the common seastar, *Asterias vulgaris*, is common as are *Asterias forbesi* and *Leptasterias littoralis*. The northern rough whelk, *Buccinum undatum*, is very characteristic of this zone.

Infralittoral zone — Below extreme low water of spring tides the diversity of fauna and flora increases. The characteristics of this community are described in chapter 8 below.

MODIFICATION OF THE BASIC FEATURES OF ZONATION IN THE QUODDY REGION

The relative positions of the boundaries between the zones are modified by many factors, often quite dramatically. For instance, a change in slope or aspect may alter zone positions and change dominance patterns. The causes and effects of such differences are a complex of variables which defy simple explanation. However, the sequence of changes seen on a series of shores of similar character and aspect but with increasing exposure to wave action has been thoroughly described and is reasonably predictable for typical situations. Unfortunately the Bay of Fundy as a whole, and the Quoddy Region in particular, do not conform to described patterns. The general situation found elsewhere is illustrated in Fig. 5 and 6. The two tide levels, extreme high water of spring tides and extreme low water of spring tides, shown in Fig. 4 as being associated with certain zones, do not have such a precise relationship. As shown in Fig. 5 the positions of these tidal levels relative to biotic zonation vary with the degree of wave exposure. The midlittoral zone may have its upper limit anywhere from mid-tide level to over twice the spring tide range up the shore. In locations extremely exposed to waves, the height of the littoral zone may be at least four times the mean tidal range. However, in the Quoddy Region such extreme examples do not occur. Figure 6 depicts the change in community structure on a series of rocky shores in Scotland. The community studied there by Ballantine (1961) is similar to that in the Quoddy Region except that the barnacle *Chthamalus stellatus* and the seaweeds *Himanthalia* and *Pelvetia* do not occur here. On highly exposed Atlantic shores in Canada the area dominated by *Chthamalus* would be a blue mussel community. Note that in Fig. 6 the relative heights of the zone boundaries are held constant to make comparison easy. In practice, the midlittoral zone expands with increased exposure.

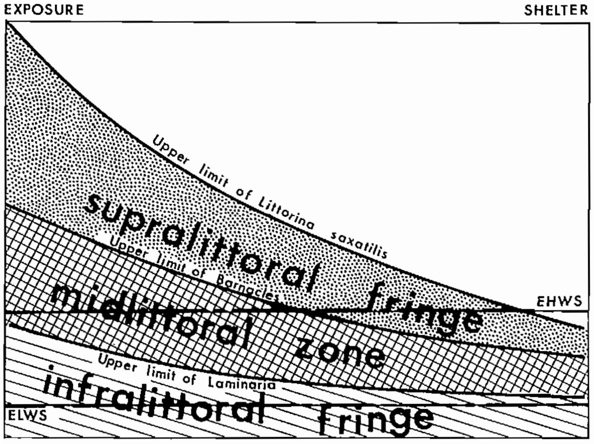


FIG. 5. Effects of exposure on intertidal zonation. EHWS, extreme high water spring tide; ELWS, extreme low water spring tide.

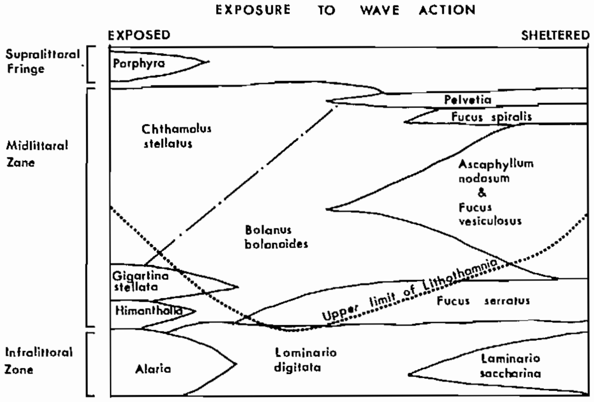


FIG. 6. Changes in the distribution of intertidal algae and barnacles with exposure in Pembrokeshire, Scotland (after Ballantine 1961).

It has also been demonstrated by many authors that the abundance of barnacles normally increases with increased exposure to waves, that overall diversity decreases as exposure increases, and that the biomass of fucoid algae decreases with increasing wave exposure.

Thomas (1975) drew attention to the fact that in the Quoddy Region the zone boundaries do not expand upwards with exposure. This phenomenon has been further investigated by Shaw and Thomas (unpublished data) and Thomas (1976). They confirmed that the organisms chosen by the Stephensons (1949) as indices of zone boundaries do not respond to increasing wave exposure by expanding up the shore but rather maintain a constant level along a gradient of increasing wave exposure. This appears to apply to most midlittoral zone species in the Quoddy Region. For example, *Balanus balanoides, Ascophyllum nodosum,* and *Fucus vesiculosus* show virtually constant upper and lower limits throughout the gradient of exposure to waves. Organisms of the supralittoral fringe and supralittoral zone do elevate their upper and lower limits as exposure to waves increases. For example, *Littorina saxatilis* extends over a metre higher at Letite (exposed) than at Holey Point (sheltered) and the black microalgal carpet of the supralittoral extends over 1.5 m higher at Letite than at Holey Point. It is thought that the large tidal range in the Bay of Fundy reduces the effect of wave action in the midlittoral zone, as the rapidly changing sea level allows only transitory wave action there. Wave action is concentrated at high and low tide levels. That wave action acts principally at these levels is further evidenced by the reduction in diversity around mean low tide level, reported by Thomas (1975). The extension of zones upward in the supralittoral is mainly an expression of spray action and is independent of tidal range. Thus, the effect of exposure to wave action is not as important in the Quoddy Region as elsewhere.

Figure 7 shows the typical features of zonation in the Quoddy Region. Zones dominated by the principal intertidal species or communities are shown, rather than the upper and lower limits of these species. This avoids overlap which confuses the situation. In effect the species and/or communities shown are dominant from their upper limit to where the upper limit of the next lower zone commences. The one exception to this is *Ascophyllum nodosum* which dominates throughout its range. Typical infralittoral fringe species, such as *Spongomorpha arcta*, show elevation of their upper limits with increasing exposure to wave action, although this is not indicated in

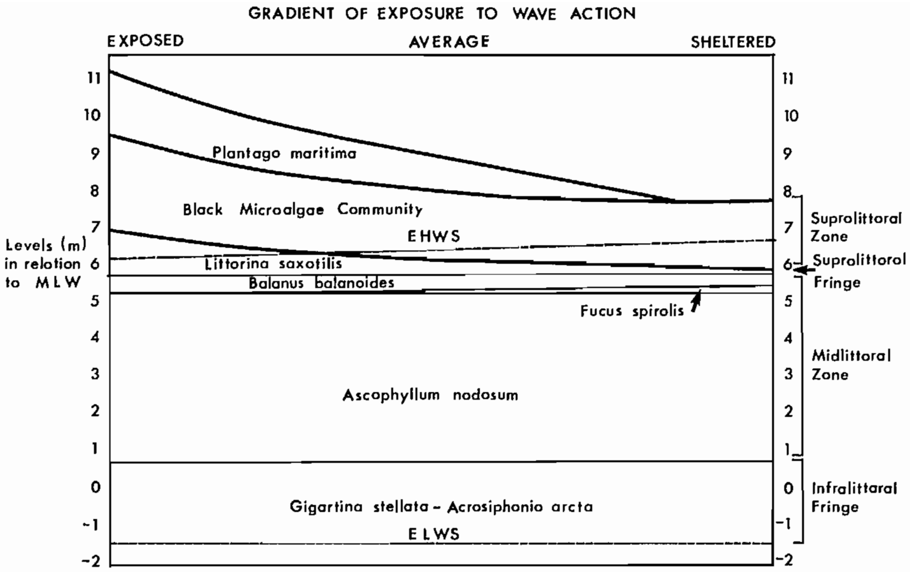


FIG. 7. Zonation of dominant organisms in the Quoddy Region in relation to tidal level and exposure to wave action. EHWS, extreme high water spring tide; ELWS, extreme low water spring tide.

Fig. 7. In practice these extensions are masked by the luxuriant growth of the dominant midlittoral fucoids *A. nodosum* and *F. vesiculosus*.

Figure 7 demonstrates another peculiar feature of zonation in the Bay of Fundy: the supralittoral fringe, normally a fairly wide band (see Fig. 5 and 6), is never very wide and in sheltered locations is very narrow. Also shown is the small extension of the *Fucus spiralis*-dominated zone above the upper limit of *Ascophyllum nodosum* in sheltered locations.

It must be emphasized that on a single or few transects, these differences may not be apparent, since local variations in rock surface texture, shading, slope, and biotic history cause rather wide differences in zonation.

ZONATION AND CRITICAL TIDAL LEVELS

In attempts to explain the very complex and variable patterns of intertidal zonation some workers have focused on what have been called critical tidal levels (Perkins 1974). Such levels were first proposed by Doty (1946) who observed that because of the pattern of tidal range change during the spring–neap cycle, there would be certain levels at which the duration of continuous emersion or immersion would suddenly increase or decrease. He termed these levels "critical tidal levels" and was able to correlate these with the distributions in level of many algae on the west coast of North America. However, attempts to test the hypothesis experimentally have not yielded conclusive results (Doty and Archer 1950). The main problem with Doty's critical levels is that, although they may exist in the short term and may be particularly noticeable on the Pacific Coast areas with diurnal tides, in the long term they move up and down the shore with constant, relatively large, variations in tidal characteristics. Certainly such levels would not stay at a constant height during the lifetime of the average intertidal organism.

Another set of critical tidal levels has been discussed by Hewatt (1937) in relation to the varying rate of rise and fall of the tide between high and low water levels. Hewatt suggested that the fast rate of rise and fall around mid-tide level, combined with the fact that the tide crossed that area most often, would result in a critical level. In the Monterey Bay area of California he found that this level marked the upper limit of two common algal species. Again, in the long term such a level would be far from constant. Elmhirst (1934), in attempting to explain the distribution of intertidal algae in Great Britain, considered that biota would be subjected to the shock of rapid changes in temperature, salinity, etc., most severely where the tide rose and fell most rapidly, at about mid-tide level. He did not consider the great modification that wave action or spray would exert in this situation.

Other authors (Druehl 1967; Carefoot 1977) have pointed out that critical levels may result from fresh or reduced-salinity surface layers in estuaries and inlets.

Although there is no doubt that for short periods the tidal régime may create on the shore quite narrow bands where the environment may change rapidly, there can also be no argument that, in the long term, other factors such as tidal variation and wave and spray action would tend to broaden and soften these "critical" levels. No long-term studies have been done to see if organisms respond to moving critical levels and we must assume in practice that these factors blend into this multi-variate environment.

As discussed above in relation to factors modifying zonation in the Bay of Fundy, we have shown that the very large tidal range may create two broad critical zones around high and low tide levels where the effects of exposure to wave action are expressed normally, whereas in the midlittoral the effect is suppressed.

THE FACTORS CONTROLLING BIOTIC ZONATION ON ROCKY SHORES

It has been emphasized that the intertidal zone is one of great environmental extremes, that organisms on the shore are likely to be responding to a complex of variables, and that these responses cause differences in zonation. We have also emphasized that on a local basis there will be great differences in zonation patterns for which there is no apparent explanation. However, it must be borne in mind that zonation is a universal feature of tidal shores and that although zones show no precise correlation with tidal characteristics, they do show the obvious influence of the tide. The zones are evidently the result of varying responses of organisms to environmental conditions that are related to the tides.

Recognizing the grave difficulties of correlating community and species distributions on the shore with the tides, the Stephensons (1949, 1972) based their "universal" zones on biotic rather than physical characteristics. Other authors, such as Lewis (1955, 1964, 1978) and Doty (1946) have concentrated on the relationship between physical factors and zonation. In recent years attention has shifted to the modifying effects of competition, predation, herbivory, and other biological interactions. Notable in this latter category are studies by Connell (1961a, b, 1970, 1972), Dayton (1971, 1975), Paine (1969, 1974), Paine and Vadas (1969), Test (1945), Menge (1972, 1976), Menge and Sutherland (1976), Jones and Kain (1967), Pace (1974) and Lewis (1978).

The general conclusions of these studies are that the upper limits of littoral species, especially above mean tide level, are controlled by physical factors, and that the lower limits of these species and perhaps also the upper limits of lower shore species are controlled by biological interactions. However, as Lewis (1978) points out, the factors controlling the lower limits of upper-shore species are still mostly unknown and may be physical. It is equally true that factors controlling the upper limits of species, thought to be physical, may in many cases be biological. It must also be remembered that where a factor such as predation or herbivore grazing is shown to control an intertidal limit, a physical factor may in turn control the presence and absence of the predator or herbivore. For instance, predatory starfish and herbivorous sea urchins are particularly important in controlling lower shore distributions, but are a group subject to severe physical constraints in their occupation of the open intertidal zone.

The principal factors known to control intertidal distributions are discussed separately below.

Desiccation — Desiccation is one of the principal factors controlling upper limits, especially in the upper part of the shore. The importance of desiccation is attested to by much evidence, both direct and indirect. The great influence of spray, splash, and wave swash in raising upper limits is an index of this importance, as is the ability to extend higher on absorbtive porous rock or where seepage of water occurs. There are many direct studies on the effects of desiccation on littoral biota. Organisms colonizing the higher levels are able to either avoid or resist drying. Those in the latter category may owe their tolerance either to an ability to withstand high water loss or to mechanisms resulting in water retention. These various adaptations to desiccation may be morphological, physiological, behavioral, or any combination of these.

Local barnacles are a good example of high intertidal organisms well adapted to resist drying. Their shells protect soft tissues and their white color helps to keep temperatures down, further reducing evaporation. Foster (1971) working in Wales found that British barnacles were situated at levels on the shore in order of their abilities to resist desiccation.

Littorina saxatilis is also remarkably adapted against water loss. It has a relatively heavy shell, the opening of which may be closed with a horny operculum. As an additional protection, when conditions are hot and dry, it closes the gap between the edge of the shell and the rock with a mucus curtain. Other species occupying high intertidal zones in other areas, such as *Littorina scutelata* on the west coast of Canada (Carefoot 1977), show similar adaptations. Both species cluster in depressions in the rock when humidity is low, a behavioral adaptation which reduces air movement past the shell.

Other animals, such as the amphipod crustacean *Gammarus oceanicus*, which are relatively poorly equipped to withstand drying, are found in the supralittoral only in foggy or very damp conditions; they retreat down the shore to congregate in damp microhabitats when humidity is low.

The upper intertidal algae, however, have extraordinary abilities to survive extreme water loss. Kanwisher (1957) showed that the intertidal species *Fucus vesiculosus, Ulva lactuca,* and *Enteromorpha linza* lost 91, 77, and 84% of their water, respectively, and that the rate of loss depended on relative humidity, temperature, and wind speed. These and other algae such as *Fucus spiralis* and *Porphyra* sp. become brittle when dry but are able to reabsorb water very rapidly on re-immersion. Southward (1957, 1966) points out that the water loss is principally from cell walls which are especially thick in high-tide forms. However, Schonbeck and Norton (1978) found in Scotland that the upper limits of both *Ascophyllum nodosum* and *Fucus spiralis* were set because of damage resulting from desiccation during neap-tide periods. They did not, however, find any evidence for such limitation in *Fucus vesiculosus*.

By electrical impedance studies, MacDonald et al. (1974) have shown that tissue of both *F. vesiculosus* and *A. nodosum* is not injured by desiccation of up to 70% water loss; this parallels their resistance to freezing damage down to −20°C, even in summer.

Once the canopy of fucoids becomes established in the midlittoral, the desiccation factor becomes much less severe. This is especially true in the Quoddy Region because of the high biomass of fucoids throughout the midlittoral. The hydroid, *Sertularia pumila* and the bryozoan, *Flustrellidra hispida* can almost always be found around the bases of *Ascophyllum nodosum* stipes, but do not extend quite as high on the shore as their host. The tiny delicate sabellid polychaete, *Potamilla neglecta* is almost ubiquitous in the midlittoral, its only protection against drying being a thin mud tube; it is found in tiny crevices and under the canopy of fucoids. Under the seaweed, the upper limits of *Lithothamnion* sp., the encrusting red algae, are also higher.

Lower down the intertidal, upper limits are also thought to be set by limited abilities to resist desiccation. For instance, among the starfish, which have little structural protection against drying, there are significant differences in water loss among littoral species, correlated with their observed intertidal ranges (Landenberger 1969). Connell (1972) found that Pacific species of *Thais* can extend higher up the shore than usual only where they are protected from desiccation by crevices or large barnacles.

The upper limits of seaweeds confined to the lowest intertidal levels are usually assumed to be related to their inabilities to withstand desiccation (Lewis 1964); Muenscher (1915) found that *Laminaria* sp. on the west coast of North America could only survive 2 h of exposure. However, observations such as those of Southward and Southward (1978) cast doubts on the assumption of a physically controlled upper limit to such species. They found that three of the common infralittoral fringe kelps — *Laminaria digitata, Laminaria hyperborea,* and *Alaria esculenta* — extended their range up to 2 m higher up the shore (well into the normal midlittoral zone) following denudation of the shore of algae and herbivores following the Torrey Canyon oil spill. They attributed the change to absence of grazing pressure by limpets. At the same time a normally low midlittoral species, *Himanthalia elongata* extended its range to mean high water.

It may be concluded that, although desiccation exerts a controlling influence over the upper limits of many species, the actual levels occupied result from both physical factors and biological interactions. These aspects need more study.

Immersion — There is no doubt that some high intertidal species cannot stand continuous immersion in seawater. This applies, for instance, to two species common in the Quoddy Region — *Littorina saxatilis* and *Fucus spiralis* (Connell 1972). However, the lower limits of these species are far above the level of continuous submergence and therefore clearly are not set by this limitation.

Temperature — Temperature has varied effects. High temperatures may be harmful in themselves or may interact with evaporation rates to increase desiccation. At the low end of the scale, comparatively few organisms are harmed by temperatures down to the freezing point, but actual freezing is a process which relatively few can survive. Another important aspect is the rate of temperature change. In the Quoddy Region in winter, a high-intertidal organism may be in seawater at 3°C one minute and in air at −20°C the next. In early summer, transitions from 6°C in water to 30°C in intense solar heating have been observed.

Some intertidal red algae are extremely sensitive to temperature change, being able to withstand sudden changes of only 2°C. Others are much more resistant (Lewis 1964). Most intertidal algae in temperate regions are resistant to freezing and, as shown by Kanwisher (1957), will function normally even after being frozen for extended periods. In very cold winter weather in the Quoddy Region, we have observed intertidal algae to freeze almost instantly on exposure and to thaw rapidly on re-immersion. MacDonald et al. (1974) found tissues of *A. nodosum* and *F. vesiculosus* to be remarkably frost-hardy throughout the year in contrast to temperate vascular land plants that are not frost-resistant in summer.

The biota of the intertidal zone are often subject to intense solar heating. Some protection to rapid change in temperature may be offered by thick shells as in *Acmaea testudinalis, Thais lapillus,* and *Littorina littorea*, or by light color as in *Balanus* sp. However, many species have both dark color and relatively thin shells: examples are *Mytilus edulis* and *Littorina saxatilis*. Experiments have shown that the internal temperatures of such animals rise rapidly when emersed (Carefoot 1977) and that some have relatively low thresholds for heat and coma death. For example, *T. lapillus* exposed to air in Britain suffered heat coma at 28°C and death at 36°C (Lewis 1964). For *L. littorea*, comparable figures were 32 and 42 and for *L. saxatilis*, 40 and 43. The extended abilities of *L. saxatilis* may partly explain its higher habitat. It should be noted that temperatures for heat coma and death normally vary with acclimation conditions and may well vary in different populations. Levels for Fundy organisms have not been established but could easily be examined in simple laboratory experiments.

Many intertidal organisms employ evaporative cooling to prevent excessive temperature rise; examples include barnacles, isopods, and limpets (Southward 1966; Edney 1953; Segal and Dehnel 1962).

Like algae, most intertidal fauna are resistant to freezing in air (Friedman 1933; Kanwisher 1955). In many species the lower lethal temperatures can be depressed by acclimation (Somme 1966). Some species, such as periwinkles and mussels, can survive extended periods frozen into ice (Kanwisher 1955; Medcof and Thomas 1974). Indeed as Medcof and Thomas (1974) have reported, dispersion of intertidal biota in ice occurs in the Quoddy Region, Antarctica, and Prince Edward Island.

One other aspect of temperature and zonation is indirect: the scouring of the intertidal zone by ice cakes and floes. This can cause considerable destruction in some areas (Stephenson and Stephenson 1954a) but is not known to occur to any extent in the Quoddy Region because the high tidal range and vigorous mixing prevents extensive ice formation.

Light — Light, of course, is essential for photosynthesis in the intertidal algae; its quality, duration, and quantity directly affect this process as well as morphogenesis and life history. Light is also important in that the ultraviolet part of the spectrum is generally harmful to living tissue. In the intertidal zone generally low light levels are probably rarely limiting, but in the Quoddy Region two important features may make limitation of algal growth due to low light levels possible. The first, which is not unique to the Quoddy Region, is the dense growth of fucoid algae in the midlittoral zone. They drape over other algae at low tide and shade them at high tide. These dominant algae all possess gas-filled bladders, which hold them up in the water to take advantage of light. The second factor limiting light availability is the very high tidal range combined with generally low light transmission in the water. Thus, low intertidal algae may at times be well below the 1% light or compensation level at high tide. The actual effect of this remains uninvestigated but it certainly contributes to a narrow subtidal zone, as described by Logan et al. in Chapter 8.

Ultraviolet light is known to bleach and kill some algae in the upper littoral areas (Carefoot 1977). Strong sunlight has also been shown to be lethal to newly settled *Balanus balanoides* which, as a result, colonize higher levels on north than south-facing shores. (Hatton 1938).

In theory, the spectral quality of light may be important in determining the distribution of seaweeds, in that red algae (Rhodophyceae) are better fitted to absorbing available light in deeper water than browns and greens. Green algae (Chlorophyceae) absorb mainly red light, which is attenuated quickly in seawater, and are therefore better adapted to higher levels. Brown algae (Phaeophyceae) occupy a somewhat intermediate position and rarely grow deeper than 15 m unless they are large and raise their fronds above this level. In practice it appears that these differences do not exert a controlling effect. It is true that throughout much of the world (Stephenson and Stephenson 1972), red algae are characteristic of the infralittoral, brown algae of the midlittoral, and green algae of the upper midlittoral; however, there are places, such as the west coast of Canada (Blinks 1955; Carefoot 1977), where the sequence is reversed. In the Quoddy Region the infralittoral fringe is frequently dominated by green algae such as *Acrosiphonia arcta* and *Monostroma* sp. Such observations suggest that light quality does not significantly influence zonation in main groups of algae.

However, the quantity of light can greatly affect the biomass of intertidal algae: in the very shaded intertidal zone of Dark Harbour, Grand Manan Island, the growth and quality of the red *Palmaria palmata* or dulse is reportedly the best in the Maritimes.

Availability of food — Some organisms, such as mussels and barnacles which extend high up the shore, are filter feeders that can only obtain food when immersed in seawater. Although they may be rapid and opportunistic feeders (barnacles for instance will filter in breaking waves — Southward 1966), limitation may stem from an inability to procure sufficient food for their maintenance requirements at high intertidal levels.

Excretion — While excretion has not generally been cited as a factor in zonation, upper midlittoral and supralittoral animals may have excretory problems. Some of these species are often not covered by the tide for days or weeks and several can stay out of seawater for months (Lewis 1964). Such species generally have adaptations to produce concentrated or dry excretory materials. For instance, in the three species of *Littorina* found in the Quoddy Region, the concentration of uric acid in nephridia has been found to increase in proportion to their height on the shore (Nicol 1969). Some high intertidal barnacles get rid of excretory and faecal material, as well as cast skins, in almost dry form (Southward 1966).

Antagonistic effects of adaptations — It should be borne in mind that some of the adaptations to intertidal existence cited above have deleterious effects in other, perhaps critical, circumstances. For example, the use of evaporative cooling results in more rapid desiccation. Additionally, the ability of many organisms to virtually seal themselves off from the environment generates immediate respiratory difficulties, as oxygen is unavailable and carbon dioxide cannot be eliminated. Organisms using gills to acquire oxygen and eliminate carbon dioxide are vulnerable to water loss.

These difficulties have led to other adaptations, such as the ability to resort to anaerobic respiration in many molluscs, combined with reaction of excess carbon dioxide with calcium carbonate from the shell (Nicol 1969). The littorinids have also developed lung-like devices of a vascularized mantle cavity which permits gas exchange with minimum water loss.

Reproductive strategies — Most marine animals and plants shed reproductive products into the seawater; fertilization is normally external and zygotes, larvae, and spores are commonly planktonic for varying periods. Although these methods may be ideal for subtidal forms they became increasingly disadvantageous as we move up the intertidal zone. It is not surprising, therefore, that other reproductive mechanisms have evolved among the intertidal community. For those retaining the typical reproductive pattern, complicated and highly adaptive larval behavior patterns, enabling colonization of suitable habitats, have been demonstrated.

The least-modified type of life cycle is typified by the common starfish (*Asterias vulgaris*) and the blue mussel (*Mytilus edulis*). In these and many other species, eggs and sperm are released into the water where fertilization takes place. The larva proceeds through a process of metamorphosis in the plankton and after a few weeks settles on the bottom to grow to adult form.

A common modification of this scheme involves internal fertilization or fertilization of eggs retained by the female. In barnacles such as *Balanus balanoides*, which are all hermaphroditic, fertilization is internal by adjacent individuals; more rarely self-fertilization may occur, followed by development of eggs inside the shell cavity. The larvae, however, are released to the sea. In many of the gastropods, fertilization is internal followed by: (1) development of eggs to young snails internally in a brood pouch, as in *Littorina saxatilis*; (2) deposition of eggs in a gelatinous mass where they develop to crawling snails, as in *Littorina obtusata* and *Lacuna vincta*; or (3) deposition of eggs in a protective egg capsule where they develop to juvenile crawling snails, as in *Thais lapillus* and *Buccinum undatum*.

Several intertidal species develop young in a brood pouch from which they are released at a stage when they can retain their position on the shore. The abundant *Gammarus oceanicus* employs this mechanism; it is made more secure by a behavioral adaptation in which the male amphipod carries the female for long periods. The interesting intertidal starfish *Leptasterias littoralis*, often abundant at Letite in spring, broods its young in a pouch formed of the disc and upper legs.

Many intertidal worms lay eggs in capsules or sticky eggs that adhere to the substratum and develop directly into bottom-living forms. Intertidal hydroids often have no free-swimming sexual medusa stage, eggs and sperm being produced by the hydroid stage.

In contrast to many intertidal invertebrates, most algae have complex life histories; these may involve production of both gametes and spores and an alternation of a spore-producing and a gamete-producing stage or, in most red algae, even a sequence of a gametic and two sporic phases. In addition, many have different responses to differing conditions of temperature and daylength. In some green (e.g. *Enteromorpha* sp.), brown (*Ectocarpus* sp.), and red algae (e.g. *Polysiphonia* sp.) sporic and gametic phases are morphologically identical; in other examples from all three groups the two phases are utterly different (as *Acrosiphonia* sp. a green alga, *Laminaria* sp. a brown alga, and *Porphyra* sp. a red alga — all common in the Quoddy area). In *Fucus* sp. the plant is diploid and has a life history like that of vertebrate animals, producing sperm and eggs. *Laminaria* plants on the shore are all spore-producing and alternate with delicate, microscopic sexual plants to bring about the complete life history.

A strange life history is that of *Porphyra* — a common, thin, flat, red, sheet-like plant which may reproduce asexually or also sexually. If it reproduces sexually, spores produce a microscopic, filamentous, boring stage that infects shells, from which spores can again reproduce the large, flat, freeliving plants; control of these developments resides in temperature and photoperiod relationships.

Many intertidal algal species are adapted to release their reproductive cells when wetted by the rising tide so that newly fertilized zygotes (as in *Fucus* and *Ascophyllum*), which become denser, sink to the bottom and become attached by mucilage secretion at the appropriate level of the shore, near where they were successfully formed. Spores, some motile, are also released and then disperse and settle.

The rapid production of adhesive mucilages and effective holdfasts by settling spores and gametes is most important in ensuring the successful propagation of littoral algae in their difficult wave-swept environment.

A great many dominant algae, such as *Fucus* sp., *Ascophyllum* sp., and *C. crispus* (irish moss) are obviously perennial and are constantly producing new upright fronds. Many other algae are less conspicuously perennial; these appear to die down but persist as prostrate filaments or crusts that actively produce new upright plants when the conditions again become favorable. Some succeed, as in *Sphacelaria* sp., in reproducing by releasing fragments or propagules.

Along-shore currents ensure the lateral distribution of many algal spores. Some algae, such as palmelloid chrysophytes, alternate littoral and truly planktonic stages. Thus, different littoral algal species have evolved a remarkably wide variety of successful reproductive adaptations (Bold and Wynne 1978; McLachlan 1974; Edelstein and MacLachlan 1975; Bird 1973).

Although many algal spores appear to drift randomly in the plankton and settle indiscriminately (Carefoot 1977), many animal larvae have an elaborate settlement behavior which concentrates them in the proper zone or the correct substrate. For instance, the larvae of *Spirorbis borealis*, a worm that has a relatively short larval life of 6–12 h, are initially photo-positive and later photo-negative. In the photo-negative phase, larvae proceed to the bottom where they are attracted to fronds of *Fucus vesiculosus* or *Fucus serratus* (Williams 1964).

In the case of *Balanus balanoides*, the cypris larvae settle to the bottom after a larval life of several weeks. The larvae test surfaces for suitability and may swim off to find other locations. They settle most readily after contact with other barnacles of their own species or with the bases of dead barnacles of their own species. Crisp and Meadows (1962) determined experimentally that the larvae could recognize the molecular configuration of a substance from the cuticle of the adult. Crisp (1961) also determined that settling *B. balanoides* larvae normally space themselves at a reasonable distance (1–3 mm) from other barnacles. This avoids juvenile competition for space but such competition may still occur as barnacles grow.

Some other larvae have been shown to possess elaborate settlement mechanisms but our knowledge of this aspect of intertidal biology is quite sparse.

Competition — There is no firm biological evidence that lower limits of any species in the intertidal zone are determined by physical factors, although this is probably true for many species whose lower limits occur in the supralittoral zone. All species having lower limits below the top of the supralittoral fringe, with the possible exception of species of terrestrial origin such as most lichens, can certainly function normally further down the shore. A good example is *Fucus spiralis*, the highest intertidal fucoid, which occupies a zone at the very top of the midlittoral; it can settle, grow, and reproduce to the base of the midlittoral (Burrows and Lodge 1951). Nevertheless, in the Quoddy Region, *F. spiralis* usually stops abruptly near the upper limits of *Ascophyllum nodosum.* It is assumed (Southward 1957; Lewis 1964) that this is a result of competition, although there is no experimental evidence to support this conclusion. More work on this aspect needs to be done.

It has generally been assumed that competition increases in severity at lower levels on the shore. The growth of both fauna and flora are normally faster there and this should increase the rates of competitive processes such as shading, smothering, and crushing (Connell 1972). It is reasonable to assume that this competition is as effective in setting the upper limits of low intertidal species as in setting lower limits of upper species. The evidence of Southward and Southward (1978), cited earlier, certainly suggests that the upper limits of infralittoral fringe and lower midlittoral algae are biologically controlled.

Most of the experiments on competitive processes in the intertidal zone have concentrated on the fauna. Connell (1961a, b; 1970; 1972) has pioneered this work and has documented the types of interactions taking place. Connell (1961b) investigated competition between the two high intertidal barnacles common in the British Isles, *Balanus balanoides* and *Chthamalus stellatus*, by measuring the survival of *C. stellatus* at a variety of tidal levels both alone and with *B. balanoides*. Observing what happened when individuals of the two species grew after touching, he found that all but the uppermost level *B. balanoides* grew faster and eliminated *C. stellatus* by undercutting the shells, thus breaking them free of the substrate by overgrowing and smothering or by crushing. Thus, *B. balanoides* outcompeted *C. stellatus* for space, except at the very top of the midlittoral where *C. stellatus* could survive owing to its greater tolerance to temperature extremes and desiccation.

On the Atlantic coast of North America *C. stellatus* does not occur and this type of competition is absent. In an examination of rocky intertidal communities in New England, Menge (1976) found that intraspecific competition for space in *B. balanoides* was important in structuring the high intertidal community. In the midlittoral zone, the lower limit of barnacles was determined in less wave-exposed places by predation by *Thais lapillus* and at more wave-exposed places by competition for space with *Mytilus edulis*. Also, in exposed locations, exclusion of mussels allowed persistence of barnacles. The dominance of mussels took only 1 or 2 mo on sloping shores but was slower on vertical faces, taking up to 2 yr there. Menge also notes the curious fact that in a sequence of colonization of wave-exposed, smooth, bare rock, *B. balanoides* must precede *M. edulis* or the juvenile mussels fail to survive. Both Menge (1974) and Paine (1974) believe that the roughness afforded by the small barnacles is essential for mussel survival. In looking at the role of the fucoid algae in this situation, Menge found that although "whiplash" from fucoids does affect barnacle settlement it does not alter the eventual outcome. *Fucus* sp. survival on all shores was found to be enhanced by barnacles but inhibited by mussels. He attributed the paucity of *Fucus* sp. on wave-beaten coasts to competition with mussels. This latter observation may have implications for Fundy shores where, as we have pointed out, fucoids are abundant at exposed locations but mussels rarely, if ever, are. It is possible therefore that some other factor influencing mussel settlement, survival, and growth is critical on our shores. This would repay investigation.

Menge (1976) found that on Atlantic barnacle-dominated shores, community structure is determined by intraspecific competition. Lewis (1978) suggests that this may proceed to the point where *B. balanoides* populations may be self-eliminated where fast growth follows heavy recruitment; he also noted a similar process in mussels and suggested that survival of these species at upper levels may depend on harsh physical conditions reducing competitive pressures.

There are many other excellent studies of competition on rocky shores, but these concentrate on American Pacific shores. Particularly noteworthy are studies by Harger (1970a, 1972), Dayton (1971, 1975), and Paine (1974); these concern interactions of Pacific coast species of mussels, barnacles, etc. Lewis (1978) rightly points out that Atlantic and Pacific shores are generally very different, especially as Pacific shores lack a zone dominated by an equivalent of *Ascophyllum nodosum*. He suggests that this creates a community more influenced by variable, biological interaction and that the Atlantic situation is much more stable. Unfortunately, the factors governing *A. nodosum* settlement, growth, and dominance have not yet been investigated.

Predation — There are of course a wide range of predators on local rocky shores. These range from the dog whelk, *Thais lapillus* through various seastars such as *Asterias vulgaris* to more active forms such as the green crab, *Carcinus maenas* and various fish such as butterfish, *Pholis gunnellus* and winter flounder, *Pseudopleuronectes americanus*. Some of these (e.g. *Thais*) are resident; others move in seasonally or with the tide. Some predation also occurs from terrestrial species, such as the herring gull (*Larus argenteus*), which feed in the zone at low tide.

Thais lapillus is a common Quoddy Region predator known to affect intertidal distributional limits of prey species such as *Balanus* sp. and *Mytilus edulis*. Connell (1961a, b) found that exclusion of *T. lapillus*, by the use of cages, increased survival of both species of barnacle present (*B. balanoides* and *Chthamalus stellatus*). On the open shore, however, the effect on *B. balanoides* was more pronounced, as that species dominated lower areas of the shore where *T. lapillus* occurred and because the whelks preferred the larger *B. balanoides* over the smaller *C. stellatus*. This preference for large barnacles also influenced the size distribution of *B. balanoides*: individuals over 2 yr old were selectively eaten. This work led to the idea of "refuges," or areas or situations where predators could not reach their prey. In the case of *B. balanoides* one refuge exists in the high intertidal where *Thais* cannot function, owing to an assumed vulnerability to desiccation. A second "refuge" exists in heavily wave-washed areas, because of the whelk's inability to crawl and adhere under extreme wave action. The refuges show up as areas of increased survival and abundance. Connell (1970, 1972) and Dayton (1971) also studied predation by several species of *Thais* on Pacific coast barnacles with similar results, except that the barnacle *Balanus cariosus* had no "size refuge" and survived predation only because large specimens were safe from predation by *Thais lamellosa*. They also observed that periods of harsh weather, which reduced *Thais* populations, were followed by periods of greater barnacle abundance. The entire system was greatly influenced by factors controlling *Thais* distribution, which were assumed to be vulnerability to desiccation at the upper limit and predation by starfish at the lower limit.

Through examinations of studies such as those cited above and work of his own, again on the Pacific coast, Paine (1974) proposed that some species at high trophic levels, usually predators, exert a disproportionately high influence in intertidal community structure. He termed these "Keystone species", and used *Pisaster ochraceus*, a Pacific starfish, as an example. In a field experiment this species was removed from a shore for a period of many years. This had a tremendous affect on zonation and community structure. *Mytilus californianus*, which had previously occupied a very narrow band, spread rapidly down the shore and had a new, much lower, limit set by

Thais sp. A second profound effect was that the species diversity of the new mussel-dominated area declined from 25 species to 1. The *Pisaster* had been responsible for maintaining the living space of a host of species by preying on *Mytilus*.

On our own shore keystone species have not been identified, but evidence suggests that *Thais lapillus* may be one. This whelk preys upon barnacles and limpets and affects the distribution of both. Both these species, in turn, influence the survival of fucoids and barnacles positively (Menge 1976) and limpets negatively. Barnacles also facilitate the settlement of mussels which, as Menge (1976) showed, in turn outcompete fucoids. These possible critical interrelationships deserve attention and may help solve the riddle of the fucoid-dominated Quoddy shores.

Herbivory — The intertidal zone is a rather unusual system in terms of the status of herbivores. The main expanse of the midlittoral on our coasts lacks large populations of herbivores, in stark contrast to the more tropical southerly shores where the midlittoral is intensely grazed. In the midlittoral of the Quoddy Region, the main herbivores are periwinkles (which consume epiphytes and macroalgae), *Gammarus oceanicus* (which is omnivorous but does graze on fucoids), and, in the lower part, the limpet, *Acmaea testudinalis* (which is principally herbivorous). In the sublittoral fringe, however, grazing is extremely heavy, mainly by the green sea urchin, *Strongylocentrotus droebachiensis*, which often forms a virtually continuous band in this zone.

Mann (1977) observed that in St. Margarets Bay, N.S., kelp beds invaded by green sea urchins were completely destroyed. Mann's observations led him to conclude that the decline in kelp beds was a permanent rather than a cyclic phenomenon, and was linked to the decline in the population of lobsters (*Homarus americanus*), a sea urchin predator.

The paucity of *Laminaria* sp. in the Quoddy Region also appears to be related to urchin activity, although this has never been experimentally checked.

Fralick et al. (1974) observed a similar phenomenon in relation to *Lacuna vincta*, the chink shell, on New Hampshire shores. This small gastropod, which can have profound effects on kelp beds, is also common on Fundy shores. These observations suggest that much more work on the effects of herbivores on seaweed populations is needed.

Although midlittoral herbivores are not abundant here, similar shores in Europe bear heavy populations of another species of limpet, *Patella vulgata*, which can profoundly affect fucoid populations. In experiments where this species was removed, great increases in algal populations followed (Jones 1948; Southward 1964). These persisted for some years but were eventually removed by limpets grazing and cutting off stipes. Southward and Southward (1978) also noted the dominant role of the limpets in reestablishing normal rocky shore communities following the Torry Canyon disaster.

Study and Collection Methods

COLLECTION

For general collections from intertidal locations, the most practical way of collecting and transporting specimens is to use polyethylene bags of various sizes. These may each be labelled with a good quality paper label marked with pencil, showing locality, habitat, and other necessary information and placed with the specimens in the bag. Normally water is not needed or recommended, but for very sensitive material, such as nudibranchs and very small and delicate algae and fish, water should be placed in a second bag or plastic jar within the main bag. If the weather is very hot, collections should be placed in a cool, shady place, preferably in a cooler. This method ensures that living material reaches the laboratory in good condition. Several cautions should be observed: (1) only a moderate biomass should be placed in each container; (2) no other material should be included with the alga *Desmarestia viridis*, which gives off sulfuric acid; and (3) before the bag is tied air should be blown in to cushion contents against crushing.

If ready access to a laboratory is unavailable, specimens should be preserved in the field as detailed below. Such practice will make it difficult to identify species with extensive powers of contraction; these should be examined alive and extended, or after careful narcotization and preservation. Narcotization is generally impractical in the field.

Laboratory identification of living specimens should be carried out promptly, unless a source of cool, running seawater is available. If refrigeration is available, small amounts of algae can be kept for awhile in moist bags or in seawater in dishes.

Collectors should exercise restraint in the collection of intertidal biota, especially rare species. Unrestrained collecting of unusual species will rapidly result in local extinction. Once lost from a particular area such species may not succeed in recolonizing it and the damage done to the organisms and to future investigations will become irreparable. Equally, irresponsible collecting of common species, which may be unrecognized key species, can quickly lead to a shift of ecological balance affecting all organisms on the shore. Also, it is important that microhabitats should not be damaged by careless exploration. In particular, loose rock must be put back in place with the original under-surface downward and seaweed masses must be returned to normal positions. Both precautions are necessary to prevent excessive desiccation of protected habitats, which are vital to the survival of the more delicate species and sometimes of the larvae of more resistant adults. Collecting is not permitted within 1000 ft of the Fisheries and Oceans Biological Station, St. Andrews.

IDENTIFICATION

The biota of this area contains arctic boreal and virginian components (Bousfield and Thomas 1975) and is remarkably diverse. No single identification manual includes all the species encountered. For fauna, the best general work is *Keys to the Marine Invertebrates of the Woods Hole Region* (Smith 1964) and Gosner's (1971) *Guide to Identification of Marine and Estuarine Invertebrates* is also useful, as is his (1978) *A Field Guide to the Atlantic Seashore*. Most of the common animals appear in *A Preliminary Guide to the Littoral and Sublittoral Marine Invertebrates of Passamaquoddy Bay* by Brinkhurst et al. (1975). Unfortunately its usefulness is limited by significant omissions. The *Field Book of Seashore Life* (Miner 1950) is also a most useful guide but identifications made from it should always be cross-checked with Smith or Gosner. For fishes, Leim and Scott (1966) discusses the entire fauna and Scott and Messiah (1976) treats the more common species.

More detailed accounts will occasionally be needed. Useful ones for various groups are: Hydroids, Fraser (1921); Polychaetes, Pettibone (1963); Isopoda, Wallace (1919) and Schultz (1969); Amphipoda, Bousfield (1973); Mollusca, Abbott (1974).

For the marine algae there is as yet no really satisfactory manual for the beginner in this area. William Randolph Taylor's classic "flora" (1957) is the most authoritative and complete key but is very much out-of-date. Current names can be checked by reference to Wilson et al. (1979) which contains a complete algal bibliography for the area. Perhaps the most useful book for beginners is *The Seaweed Handbook* by Lee (1977). Other useful illustrated guides and keys for the North Atlantic are those of Dickinson (1963), Kingsbury (1969), and Gosner (1978).

Foliose and fruticose lichens are described and a key to species is provided in Hale (1969). Terrestrial vascular plants are comprehensively treated in Gleason (1963), Gleason and Cronquist (1963), Roland (1947), and the new *The Flora of Canada* (Scoggan 1978).

A checklist of the fauna and flora of the region is given by Linkletter et al. (1977) and will be updated in the future. All new or unusual records for the region should be reported to the Identification Centre, Biological Station, St. Andrews, N.B. E0G 2X0.

NARCOTIZATION AND PRESERVATION

To maintain invertebrate animals in lifelike condition, narcotization or anaesthetization must be carried out prior to fixation and preservation. The most useful materials for this purpose are menthol, enthanol, and magnesium sulphate. Different groups and even different species within the same group react differently to various materials. Menthol is the most generally useful: a few crystals are floated on a small container of clean seawater containing the specimen. Narcotization may take several hours and can be tested by probing with a needle; unless action is complete, retraction will take place on fixation. Ethanol is added drop by drop, slowly, until reaction ceases and magnesium sulphate is used similarly as a strong solution in seawater. For a more gentle effect use 22 g/L of anhydrous magnesium sulphate or 74 g/L of hydrous magnesium chloride in distilled water mixed with an equal volume of clean seawater. During narcotization, containers must be kept cool and undisturbed, in dim light. Nudibranch molluscs are particularly difficult to fix when fully expanded, but this may be accomplished by placing the living specimen in a small dish in a freezer. The frozen block of ice containing the expanded specimen is then thawed in a container of 8% formalin in seawater. For particularly difficult examples, anaesthetics such as novocaine may work well.

Fixation is normally carried out using a solution of 8% formalin in seawater and this solution may also be used for the preservation of most species without calcareous exoskeletons. Those with calcareous shells or exposed skeletal structures should be fixed in formalin for 24 h and then transferred to 40% isopropanol in seawater. Alternatively, a formalin solution neutralized with hexamethylenetetramine (Marr, 1963) or borax is also excellent. Most fixatives and preservatives do not maintain color well; therefore, if this is important, special techniques are required for preservation.

Macroscopic algae can be preserved in 8–10% formalin in seawater (preferably neutralized) in tightly stoppered, labelled bottles. Delicate (most filamentous) forms can be preserved in formalin or in fresh F.A.A. (Formal-Acetic-Alcohol), rinsed in an appropriate solvent, and then transferred to vials of 70% isopropanol in seawater (or to 70% ethanol) for storage and further study. For general collection and record, it is usually preferable to select good representative specimens and float them on a sheet of herbarium paper of suitable size and then press them. This procedure gives good preservation of color, form, and texture of most large algae but does not readily permit subsequent observation of microscopic characters or cell measurements. For this process the specimen, carefully arranged on a labelled sheet, is permitted to drain before being placed on a blotter over a corrugated cardboard drier; it is then covered with a layer of cotton cloth (pieces of old sheets are excellent, but cheesecloth will do), and then with another blotter and drier. This process is repeated until a full press is built up; then drying is carried out under light pressure in a warm dry place. Blotters should be changed daily during drying. Dried specimens are then stored flat in folders in a dry place. Most algae produce enough mucilage in their cell walls to ensure that they stick to paper. Very coarse species, like *Fucus* and *Laminaria*, are best dried first with newspaper, instead of blotters, until their mucilage has given up most of its water. Some coarse species may have to be fixed down with mucilage and again dried under pressure after the first drying. Calcareous and other encrusting algae are best preserved by fixation in 8% formalin and preservation in alcohol as detailed above. Calcareous algae on rocks also can be kept as specimens by simply drying and labelling the rock.

Vascular plants are also preserved by drying in a press, between sheets of newspaper, but do not require floating out.

Lichens and mosses can be preserved by drying and storing in labelled paper bags or boxes.

INTERTIDAL SURVEY METHODS

The accurate description of zonation patterns and the determination of the height of intertidal study plots, in relation to tidal characteristics, involves surveying techniques.

While the use of standard survey methods using a transect or various levels (from inexpensive hand levels to more elaborate and expensive ones) may be needed for extreme precision, a simple method (Thomas 1976) is applicable to Quoddy Region shores and gives accurate results if carried out carefully. It uses the horizon as a level and the predicted height of low water to establish elevation.

Zonation studies are normally carried out on a transect, a line running at right angles to the general shoreline, from low tide level to the top of the shore. The use of the survey method to survey a transect is illustrated in Fig. 8. The transect is usually started 2 or more h before low tide and is run from the top down. A reverse procedure is possible, but will not allow ample study time. Usually the top of the transect is selected and marked. This is most easily done with bright, fast-drying spray paint, but weighted-down paper markers work equally well for a one-time survey. The transect line is normally run down a reasonably evenly sloped shore without large cliffs, boulders, caves, etc. However, slight modification of the method will accommodate most such features if desired. The survey is run in a series of steps to reference points marked on the transect. Each significant change in gradient should be a reference point, and for convenience the vertical drop between reference points should not exceed 2 m. In practice, a metre stick is held vertical at the lower of a pair of points and an observer at the higher point sights past a metre stick held vertically, resting on the rock with the 0 graduation up. The top of the lower stick and the horizon are lined up with a point on the upper stick and a reading taken. This reading is the height difference between the two points (see Fig. 8). The horizontal distance between the points may be measured directly with a tape or metre sticks. Repetition of this process for each pair of points to low water, on a continuously sloping shore, will provide a set of coordinates enabling accurate graphic reconstruction of the shore profile. Accuracy can be adjusted to suit the project but determination to ± 1 mm is possible. Figure 8 illustrates that bumps in the shore can be mapped by direct sighting over the crest of the rise. Rises or falls of over 1 m can be determined by stacking metre sticks. Other small modifications accommodate other difficulties.

In the Quoddy Region in good weather, tides are highly predictable and the water level at the time of predicted low water can be used to calculate the height of any point on the shore in relation to mean low water or chart datum. As chart datum is mean lower low water on Quoddy shores, it is advisable to work with reference to mean low water. Mean lower low water is calculated using only the lowest of the 2 low tides/day and is therefore not a true mean level.

The height of low water for the day of survey can be calculated from the *Canadian Tide and Current Tables* for the current year (Anon. 1979a, etc.). All tide calculations for the Quoddy Region are made by reference to predictions for the primary port, Saint John, with time and height corrections being made to the closest secondary port to the survey site. Interpolation between adjacent secondary ports can be made on a basis of relative distance to each port. The *Canadian Tide and Current Tables* give corrections for several secondary ports but in practice greater accuracy can be achieved by combining predictions from British and Canadian tables, as each use different secondary ports. The primary and secondary ports for the region are shown in Fig. 9 and basic metric correction data are given in Table 3. Time differences are applied to predicted times for Saint John to give high and low tide times for the survey point. Note that all predictions are standard time and 1 h must be *added* when summer time is in effect. Height corrections are applied to give the predicted height of the tide for the survey location in centimetres above chart datum. Table 4 gives the relationship between chart datum and standard tide heights for each secondary port. To correct the height above chart datum to a height with reference to mean low water, *subtract* the level of mean low water shown in Table 4. All data in Tables 3 and 4 are constants and may be used with any set of current tide tables. Note that predicted heights in tide tables are given to the nearest 0.1 m and 0.1 ft. Conversion of the foot data yields slightly more precise metric levels but in practice the level can be determined to only about ± 5 cm.

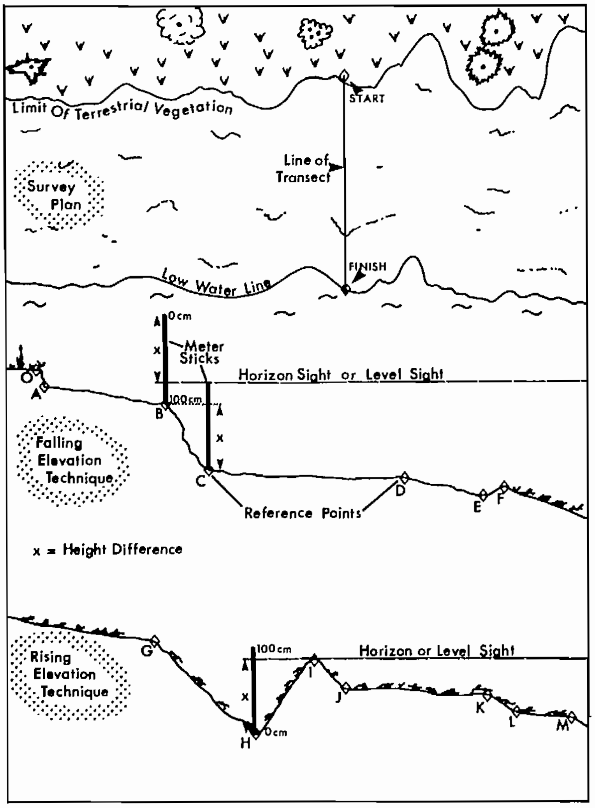


FIG. 8. Surveying a transect profile of a rocky shore.

It is also possible to calculate the tidal height of any point on the shore by recording the time at which the tide reaches it on any day when the weather is good. Such a procedure is also useful as a check on intermediate levels

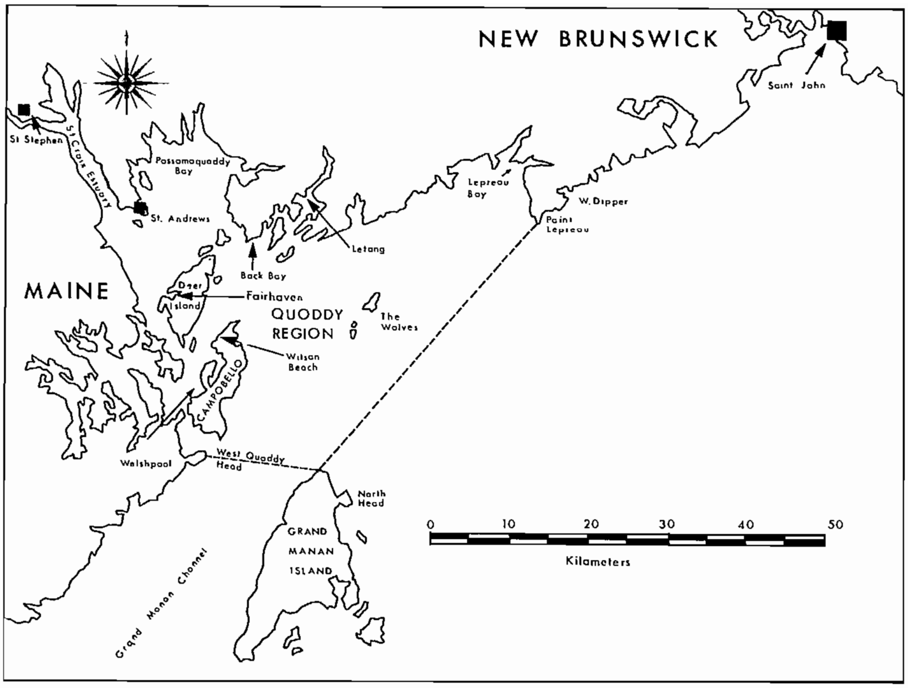


Fig. 9. Location of secondary tide prediction ports in the Quoddy Region in relation to the primary port, Saint John.

calculated as detailed above. An accurate method for this calculation is given in the British *Admiralty Tide Tables* (Anon. 1979b) and an approximate method appears in each edition of the *Canadian Tide and Current Tables* (Anon. 1979a).

Quantitative Methods

For estimation of abundance and biomass in intertidal communities, quadrats of various sizes can be employed. However, quadrats are difficult to use in very rough or fissured rock surfaces since the surface area enclosed may significantly exceed the quadrat size. Normally, the quadrat is laid parallel to the general surface and the area enclosed is sampled, irrespective of its actual area. For common species, 1/10 m^2 is an adequate sample size; for more accurate work replicate samples of 1/25 m^2 or 1/10 m^2 are advisable. Five to ten samples normally give excellent results for all but a few rare species. The adequacy of the method may be checked by a method such as that given by Weinberg (1978). Very narrow zones, such as that occupied by *Fucus spiralis*, are difficult to sample using standard techniques, and special methods must be devised.

Fresh weight biomass estimations of intertidal species are prone to bias because of the heavy shells of many species of molluscs. For these species a decalcified dry weight or a dry weight corrected by subsequent ash determination, is more satisfactory. This also applies to the calcareous algae. Data for correcting fresh weight to dry weight for various groups are given by Thorson (1957) but serve only as approximations. Fresh wt:dry wt. ratios vary greatly between species and populations.

Encrusting forms present a particular problem and are frequently quantified on a basis of their surface area as a percentage of total substrate available. However, biomass can be estimated by breaking the rock with the attached specimen. The area of specimen may be measured and the rock and specimen weighed fresh, dry, and after ashing at 435°C. The latter weight will provide a correction for all inorganic material.

In these and other cases, aerial coverage of various species may be estimated in a quadrat subdivided by a matrix of wires or by photography, with subsequent analysis of prints. Another useful method is described by Menge (1976) in which 100 random dots are marked on a plexiglass square. The square is placed over the substratum and the number of dots coinciding with the presence of a species taken as an estimate of percentage cover. Menge used 0.25 m^2 squares but 0.1 m^2 may be better in many communities.

For many algae, numerical abundance cannot be determined, because individual plants cannot be defined satisfactorily. In these cases biomass is a satisfactory substitute for abundance.

Experimental Methods

Recent intertidal ecology research has been marked by a great increase in the number of experimental studies aimed at elucidation of the effects of predators, herbivores, and competitors on intertidal species and on littoral community stucture.

TABLE 3. Height and time differences for secondary ports in the Quoddy and adjacent region to be applied to predictions for Saint John, N.B.

Port	Height correction (m)				Time correction (min)	
	MHWS[a]	MHWN[b]	MLWN[c]	MLWS[d]	MHW[e]	MLW[f]
St. Stephen	−0.6	−0.3	−0.4	−0.1	+8	+28
St. Andrews	−0.7	−0.5	0.0	+0.3	+7	+16
Welshpool	−1.4	−1.0	−0.3	+0.1	−2	+8
North Head	−1.5	−1.1	−0.4	+0.1	−5	−5
Wilsons Beach	−1.1	−0.7	−0.3	+0.1	−5	−1
Fairhaven	−0.8	−0.5	−0.2	+0.1	+3	+9
Back Bay	−1.1	−0.8	−0.2	+0.1	−7	−6
L'Etang	−1.1	−0.8	−0.1	+0.0	+1	−5
Lepreau Bay	−0.8	−0.5	−0.2	+0.2	−1	+3
W. Dipper	−0.4	−0.2	−0.3	+0.0	−7	−5
Saint John	0	0	0	0	0	0

[a] MHWS, Mean high water of spring tides.
[b] MHWN, Mean high water of neap tides.
[c] MLWN, Mean low water of neap tides.
[d] MLWS, Mean low water of spring tides.
[e] MHW, Mean high tide.
[f] MLW, Mean low tide.

Methods used in these studies are generally simple and range from manual clearing of predators, algae, or herbivores over large areas (Jones 1948; Southward 1964; Connell 1961a, b, 1970; Dayton 1971, 1975); through inclusion and exclusion experiments using cages of various sizes fastened to the substrate with stainless steel screws (Connell 1961a, b; Menge 1976); to the use of barriers which exclude certain species but not others (Dayton 1971). These experiments are often described as "elegant in their simplicity," but in fact require careful design and control. Few are suitable to short-term research or teaching use, as they require extended attention, maintenance, and observation spread over several years. Such approaches, particularly clearance experiments, may however be quite amenable to an annual inspection technique. Readers are referred to the research cited above for further details.

Measurement of primary production by plants in the rocky intertidal community presents great difficulties. Production is divided between immersed and emersed phases and varies greatly with environmental conditions. The light and dark bottle oxygen method (Strickland 1960; Vollenweider 1969) may be usefully employed to investigate the submerged phase, as may ^{14}C methods (Pomeroy 1961; Wetzel 1964). Encrusting forms must be carefully removed with a piece of underlying substratum for enclosure. The emerged phase is more difficult but may be investigated using terrestrial methods such as those described by Milner and Hughes (1968), by biomass estimates (Bellamy et al. 1973), or by controlled laboratory experiments using infrared CO_2 analysis (Anon. 1973b).

MEASUREMENT OF EXPOSURE TO WAVE ACTION

One of the main factors modifying intertidal zonation is exposure to wave action. It would therefore be useful if this parameter could be estimated in the field; however, this has proved almost impossible in practice. Various devices have been tried in attempting to measure wave action on rocky shores, such as the turbulometer of Field (1968), the dynamometer of Jones and Demetropoulos (1968), the wave impact device of Harger (1970b), the plaster of paris erosion technique of Muus (1968), and the splash monitor of Druehl and Green (1970). Menge (1976) used the novel approach of estimating wave action from the number of experimental cages lost during investigations. None of these methods is ideal: all measure different aspects of wave action and are either expensive, delicate, or insensitive. In practice we need simple, tough devices that can be left at experimental sites for extended periods. In a recent experiment using dynamometers (Jones and Demetropoulos 1968) in the Bay of Fundy no useful results were obtained.

These problems have led authors such as Ballantine (1961) to propose biologically defined exposure scales. These are potentially useful but must be modified for each new area in terms of biota present and observed local reactions to wave action. Such a modification was prepared by Dalby et al. (1978) for shores in western Norway. As midlittoral species distributions do not generally respond to wave action in the Quoddy Region, such parameters would not be useable. Dalby et al. (1978) found that the height of the black microalgal zone correlated well with exposure and this is also true in the Quoddy Region. It would also be worthwhile to check whether the Differences in shell shape of *Thais lapillus*, expressed as the ratio of shell height to external length of the aperture, found by Crothers (1973, 1974, 1975a, b, 1977) to be closely related to exposure to wave action over a wide area of Europe, hold here. If so, an exposure grade based on these two general characteristics could be devised. Figure 7 shows the general response of the black microalgal community to exposure in the Quoddy Region.

TABLE 4. Tidal data for ports in the Quoddy Region and Saint John, N.B.

Port	Mean range (m)	MLW[a](m)[b]	MTL[c](m)[b]	MHW[d]	MLWS[e]	MHWS[f]
St. Stephen	6.1	0.9	4.0	7.0	0.5	7.4
St. Andrews	5.6	1.3	4.1	6.9	0.9	7.3
Welsh Pool[g]	5.2	1.0	3.7	6.2	0.7	6.6
North Head[h]	5.1	1.1	3.6	6.2	0.7	6.5
Wilsons Beach[g]	5.1	1.2	3.8	6.3	0.9	6.7
Fairhaven[i]	5.5	1.2	3.9	6.7	0.6	7.2
Back Bay	5.2	1.3	3.8	6.5	0.6	7.0
L'Etang	5.3	1.1	3.8	6.4	0.7	6.9
Lepreau Bay	5.6	1.2	3.9	6.8	0.8	7.2
W. Dipper	5.8	1.2	4.1	7.0	0.6	7.6
Saint John	6.3	1.2	4.4	7.5	0.6	8.0

[a] MLW, mean low water.
[b] Levels are heights above chart datum for Canadian Hydrographic Charts.
[c] MTL, mean tide level.
[d] MHW, mean high water.
[e] MLWS, mean low water spring tides.
[f] MHWS, mean high water spring tides.
[g] Campobello Island.
[h] Grand Manan Island.
[i] Deer island.

Other workers have not used any direct methods and have developed exposure scales based on the arc of exposure of the shore to the open sea, modified according to fetch, distribution of prevailing winds, storms, and depth (Baardseth 1970; Grenager and Baardseth 1965). Such scales may well be useful but need correlation with actual wave action data.

Description of Specific Locations

INTRODUCTION

As detailed in the Introduction above, about half the shoreline in the Quoddy Region is rocky; thus relatively huge areas are open for study. However, access to many of these is limited by lack of roads or by their being islands. Additionally, studies on rocky-shore communities are best pursued on shores of fairly even slope, with solid rock substrata from the supralittoral zone to the sublittoral fringe (Fig. 4) and without industrial or domestic pollution. The sites described below all fit these general criteria and have yielded useful results. Their locations are shown in Fig. 10.

HOLEY POINT AREA

The Holey Point area is not accessible by road but is readily reached by walking north along the shore from the Huntsman Marine Laboratory aquarium. The general configuration of the shore and location of suitable study areas is shown in Fig. 11. Users should note that the area above high water is private; work should be restricted to the intertidal zone, unless explicit permission is obtained.

The Holey Point area is illustrated in Fig. 11. As in Fig. 10, the location is within the St. Croix Estuary and is quite sheltered. The rock structure ranges from sandstone to siltstone, being quite soft at high water and generally hard lower down. As Fig. 11 shows, a long stretch of coast is suitable for study but care should be taken to avoid pockets of sediment that occur particularly near mean low water.

As shown in Table 5, the diversity of life is generally lower than at other areas. The supralittoral fringe is particularly depauperate, owing to the crumbly rock. Nevertheless, it is a useful, typical, relatively sheltered site.

Zonation studies are also fruitful on the reef in Brandy Cove, which is slightly more sheltered than Holey Point (Fig. 11); however, work there must exclude collection of specimens.

Figures 12 and 13 show zonation patterns for common animals and plants at Holey Point. These are means of 17 transects. Figures 14 and 15 give equivalent information for the Brandy Cove reef (based on one survey). These figures also give the general shore profile for these locations with a vertical:horizontal scale ratio of 5:1. This exaggerates the slope.

JOE'S POINT

Figure 16 shows the access and general structure of the shore at Joe's Point. As shown in Fig. 10, this location is a little more exposed than Holey Point as it lies at the eastern mouth of the St. Croix Estuary. The Joe's Point location is not really good for zonation and other rocky shore intertidal studies since the habitat is limited to a series of reefs transecting the littoral, often at an angle. However, a few spots are useable. The rock is of hard sedimentary structure.

TABLE 5. Species common and useful for study at five main study locations.

Species	Holey Pt.	Joe's Pt.	Woodstock Pt.	Letite Pt.	Pea Pt.
Chlorophyta					
Spongomorpha arcta	X	X	X	X	X
Cladophora sp.	X	X	X	X	
Enteromorpha sp.	X	X		X	
Monostroma sp.	X	X	X	X	
Ulothrix sp.	X	X	X	X	
Ulva sp.	X	X	X	X	X
Phaeophyta					
Alaria esculenta				X	X
Ascophyllum nodosum	X	X	X	X	X
Ectocarpus sp.	X	X	X	X	
Fucus edentatus	X		X	X	X
F. evanescens	X	X	X	X	
F. spiralis	X	X	X	X	X
F. vesiculosus	X	X	X	X	X
Laminaria sp.			X	X	X
Pylaiella littoralis	X	X	X	X	
Scytosiphon lomentaria	X	X		X	
Rhodophyta					
Chondrus crispus	X	X	X	X	X
Dumontia incrassata	X	X	X	X	
Gigartina stellata	X	X	X	X	X
Halosaccion ramentaceum	X	X	X	X	X
Hildenbrandia prototypus	X	X	X	X	X
Lithothamnium sp.	X	X	X	X	X
Palmaria palmata	X	X	X	X	X
Polysiphonia lanosa	X	X	X	X	X
Porphyra sp.	X	X	X	X	X
Rhodochorton purpureum			X	X	X
Lichens					
Caloplaca elegans			X	X	X
Parmelia saxatilis	X	X	X	X	X
Verucaria maura	X	X	X	X	X
V. mucosa	X	X	X	X	X
Xanthoria parietina	X	X	X	X	X
Black microalgal mat	X	X	X	X	X
Vascular plants					
Deschampsia flexuosa	X	X	X	X	
Plantago maritima		X	X	X	
Porifera					
Halichondria panicea			X	X	X
Coelenterata					
Diadumene leucolena	X		X	X	X
Sertularia pumilla	X	X	X	X	X
Bryozoa					
Flustrellidra hispida	X	X	X	X	X
Annelida					
Potamilla neglecta	X	X	X	X	X
Mollusca-gastropoda					
Acmaea testudinalis	X	X	X	X	X
Buccinum undatum	X			X	X
Littorina littorea	X	X	X	X	X
L. obtusata	X	X	X	X	X
L. saxatilis	X	X	X	X	X
Thais lapillus	X	X	X	X	X

TABLE 5. (Continued)

Species	Holey Pt.	Joe's Pt.	Woodstock Pt.	Letite Pt.	Pea Pt.
Mollusca pelecypoda					
Modiolus modiolus	X	X		X	X
Mytilus edulis	X	X	X	X	X
Arthropoda crustacea					
Balanus balanoides	X	X	X	X	X
B. crenatus		X		X	
Gammarus oceanicus	X	X	X	X	X
Echinodermata					
Asterias forbesi			X	X	X
A. vulgaris	X	X		X	X
Cucumaria frondosa	X			X	X
Strongylocentrotus drobachiensus	X	X		X	X

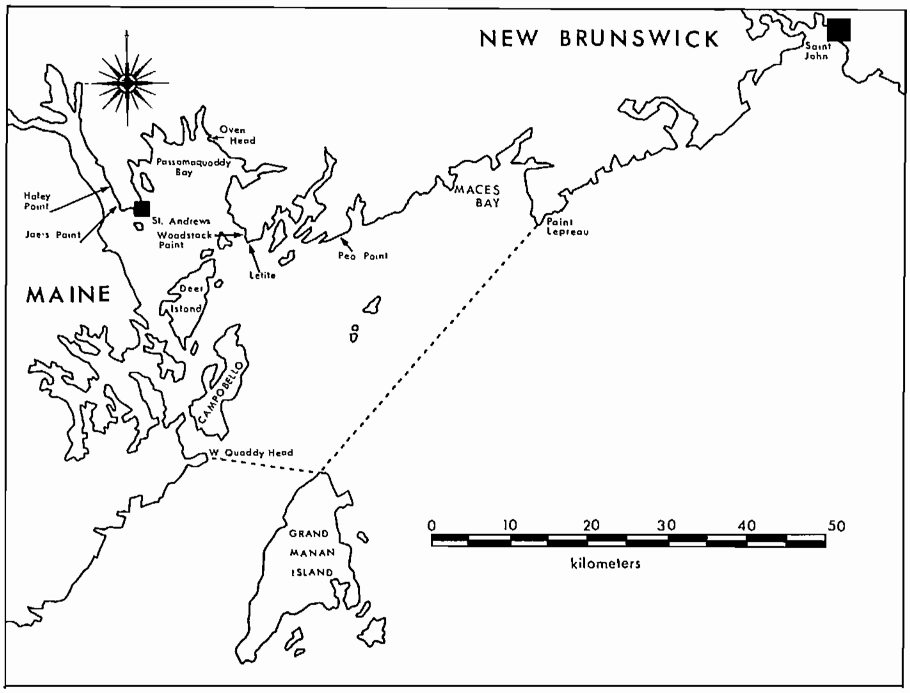
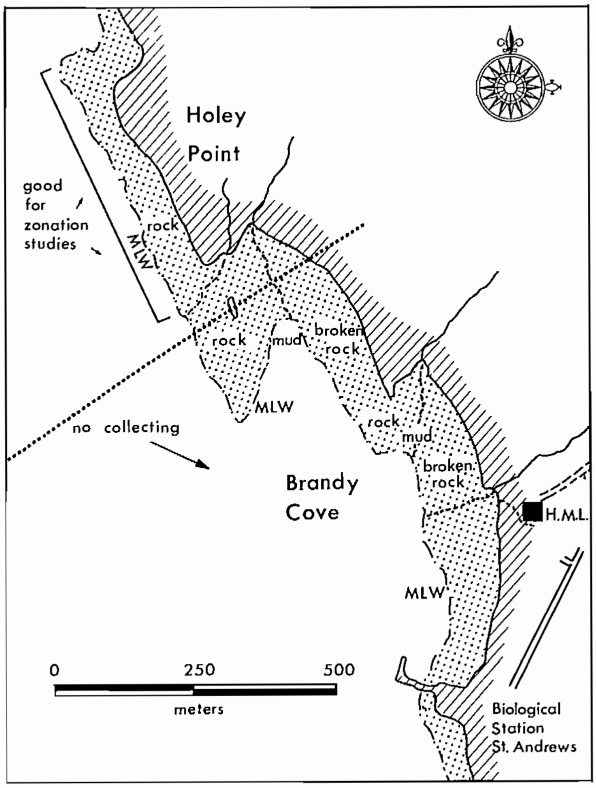


FIG. 10. Locations of specific intertidal locations described in the text.

FIG. 11. The Holey Point area showing access and study sites.



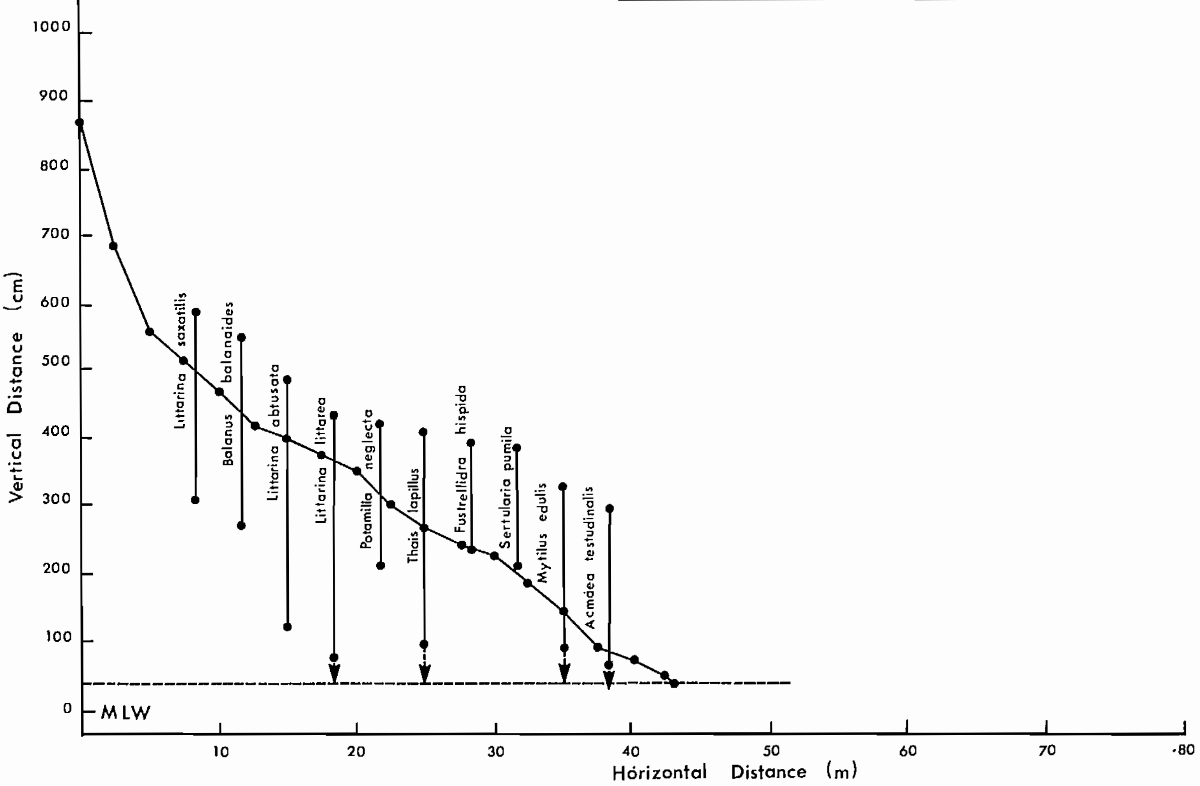


FIG. 12. General shore profile and the zonation patterns of common fauna at Holey Point. MLW, mean low water.

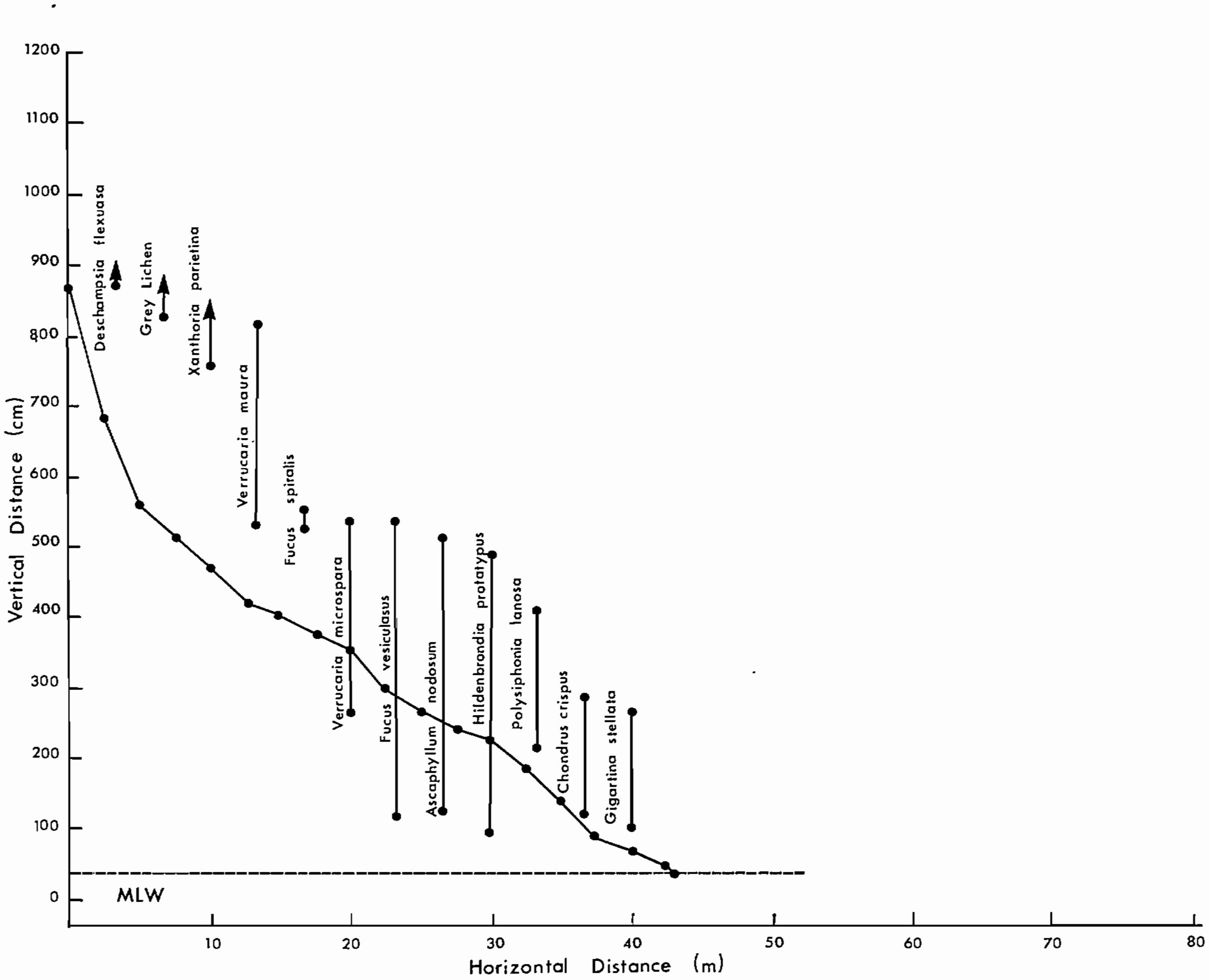


FIG. 13. General shore profile and the zonation patterns of common flora at Holey Point. MLW, mean low water.

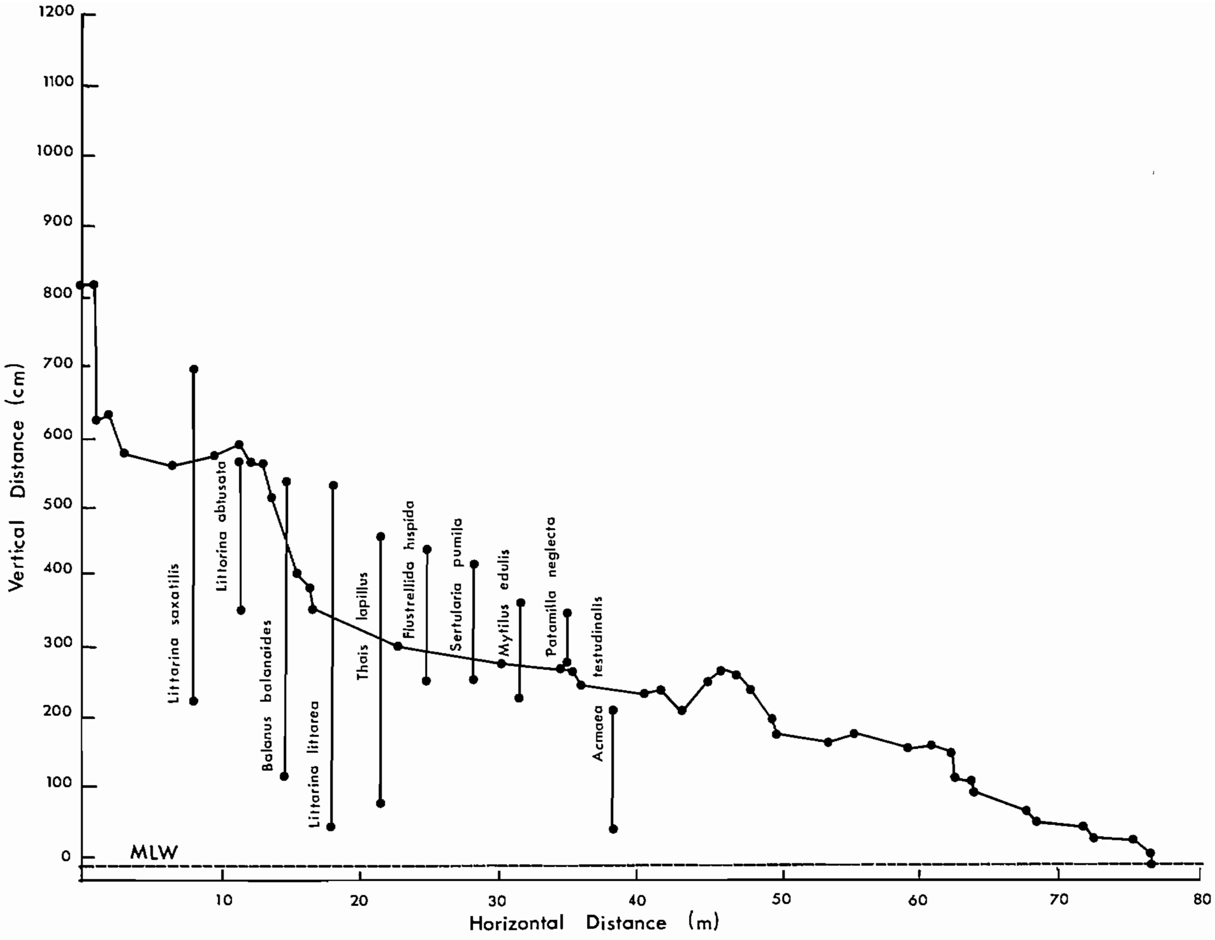


Fig. 14. General shore profile and the zonation patterns of common fauna at Brandy Cove. MLW, mean low water.

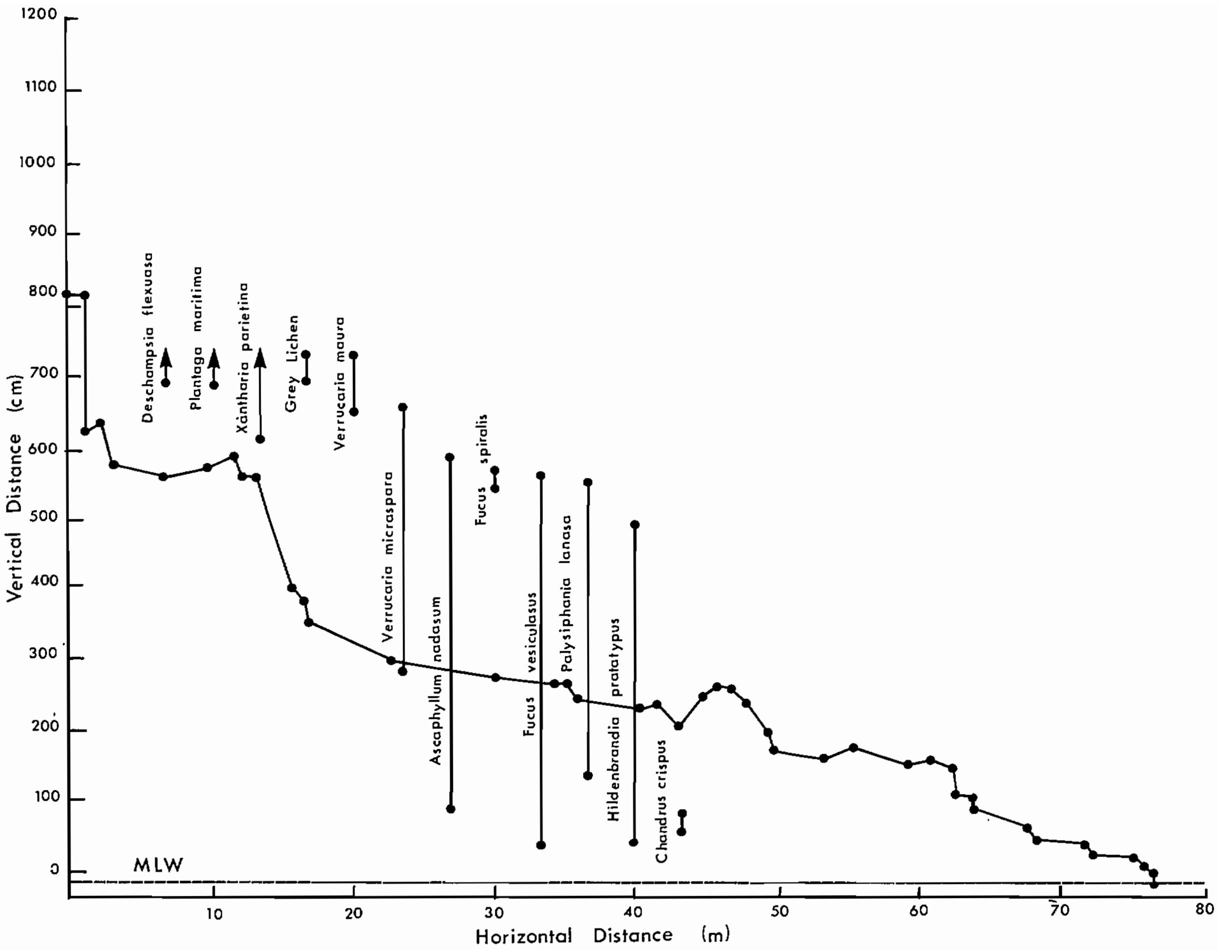
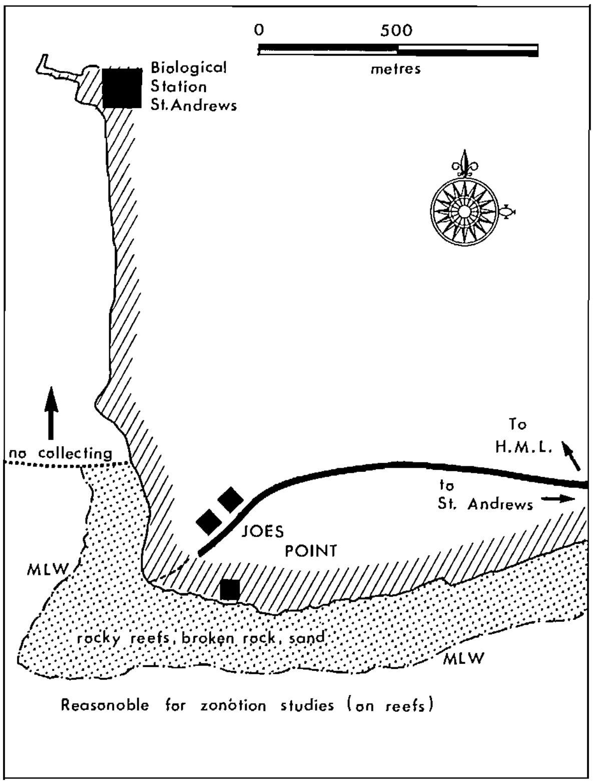


FIG. 15. General shore profile and the zonation patterns of common flora at Brandy Cove. MLW, mean low water.

FIG. 16. The Joe's Point area, showing access and study sites.



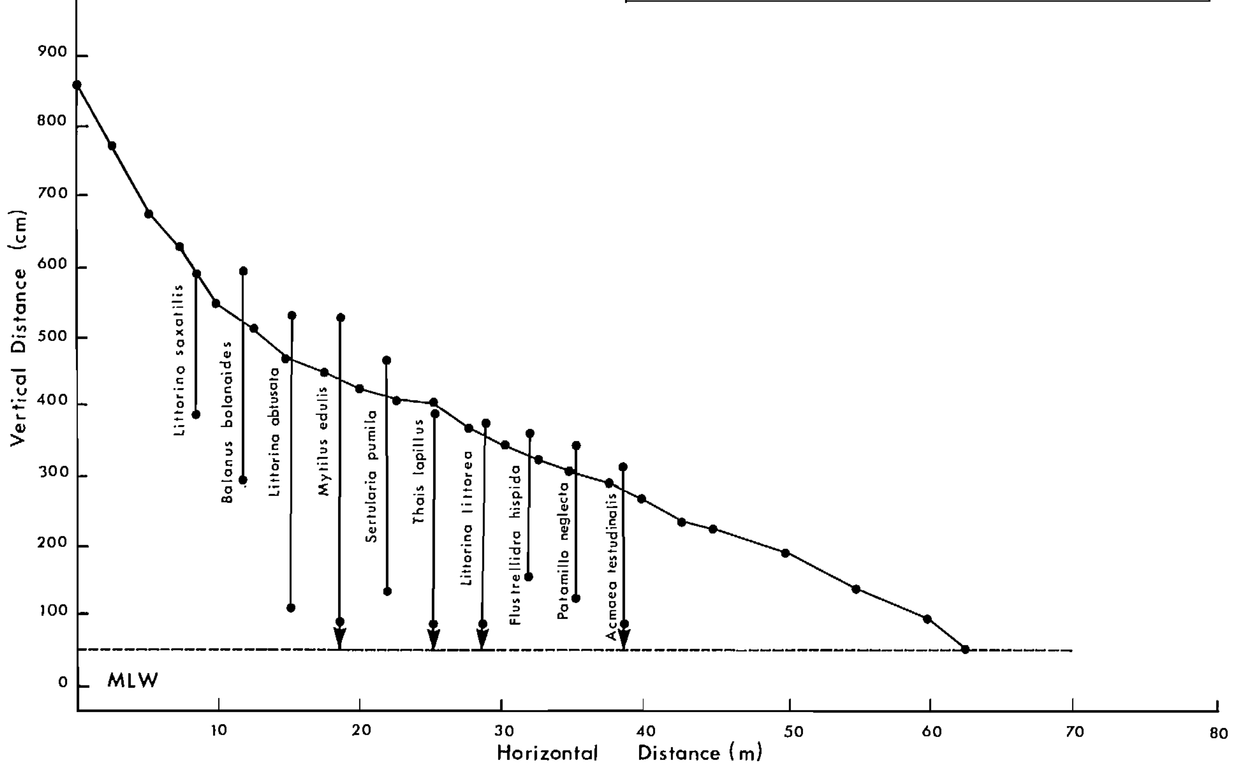
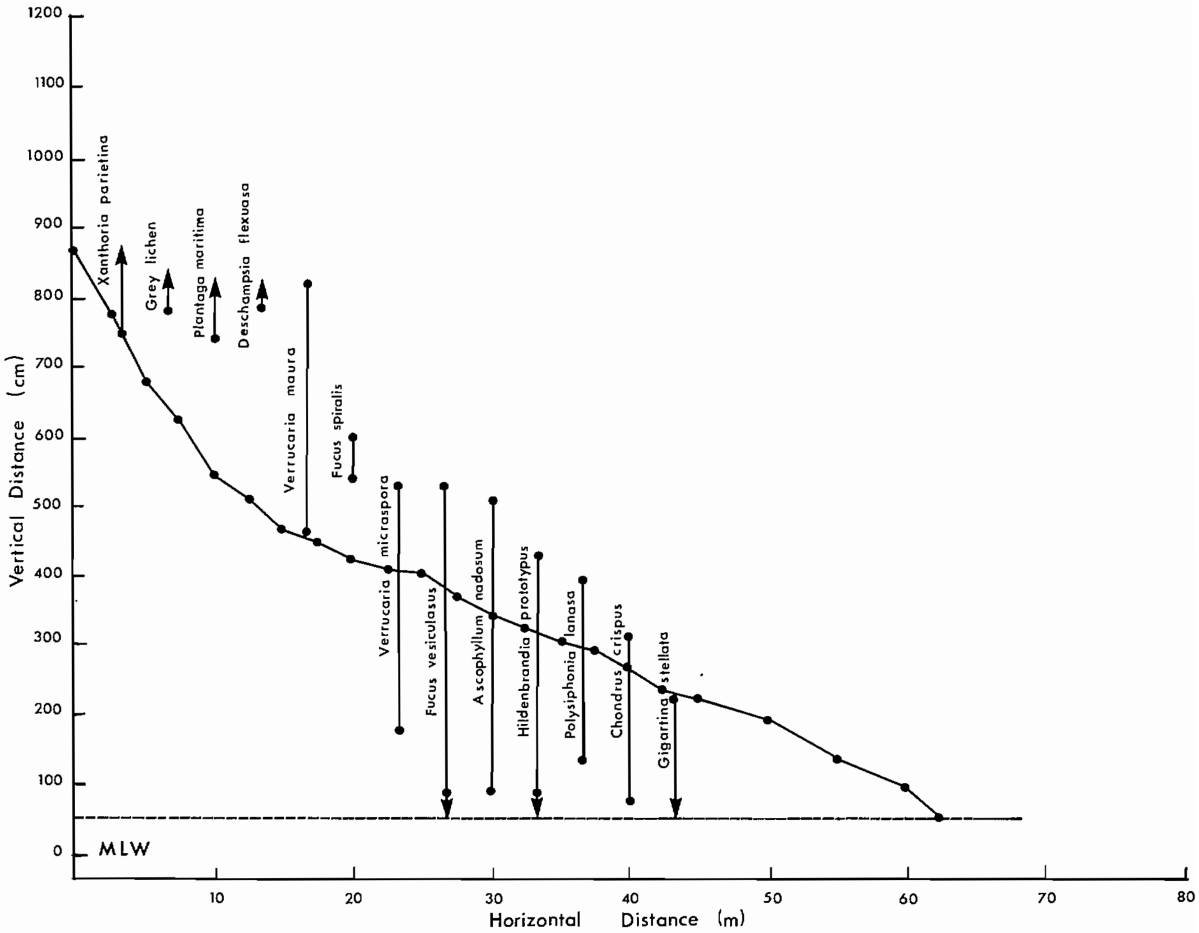
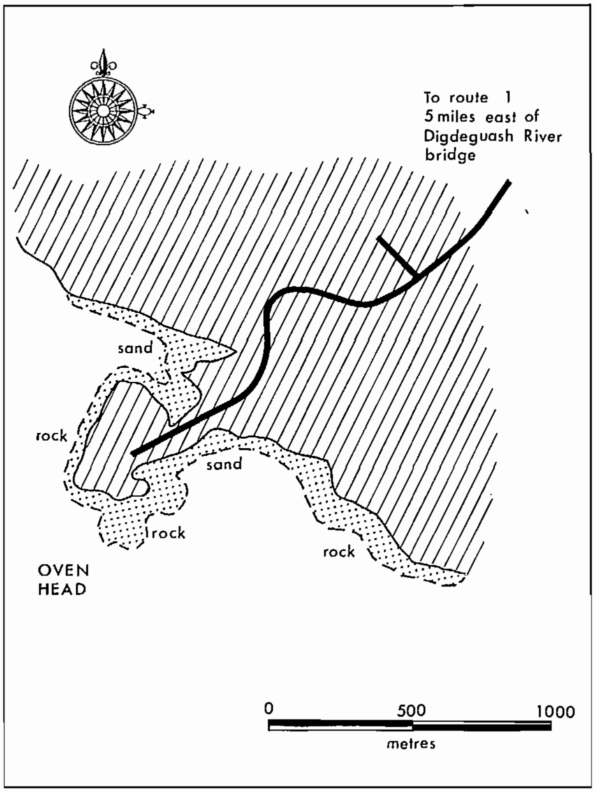


FIG. 17. General shore profile and the zonation patterns of common fauna at Joe's Point. MLW, mean low water.



.FIG. 18. General shore profile and the zonation patterns of common flora at Joe's Point. MLW, mean low water.

FIG. 19. The Oven Head area showing access and study sites.



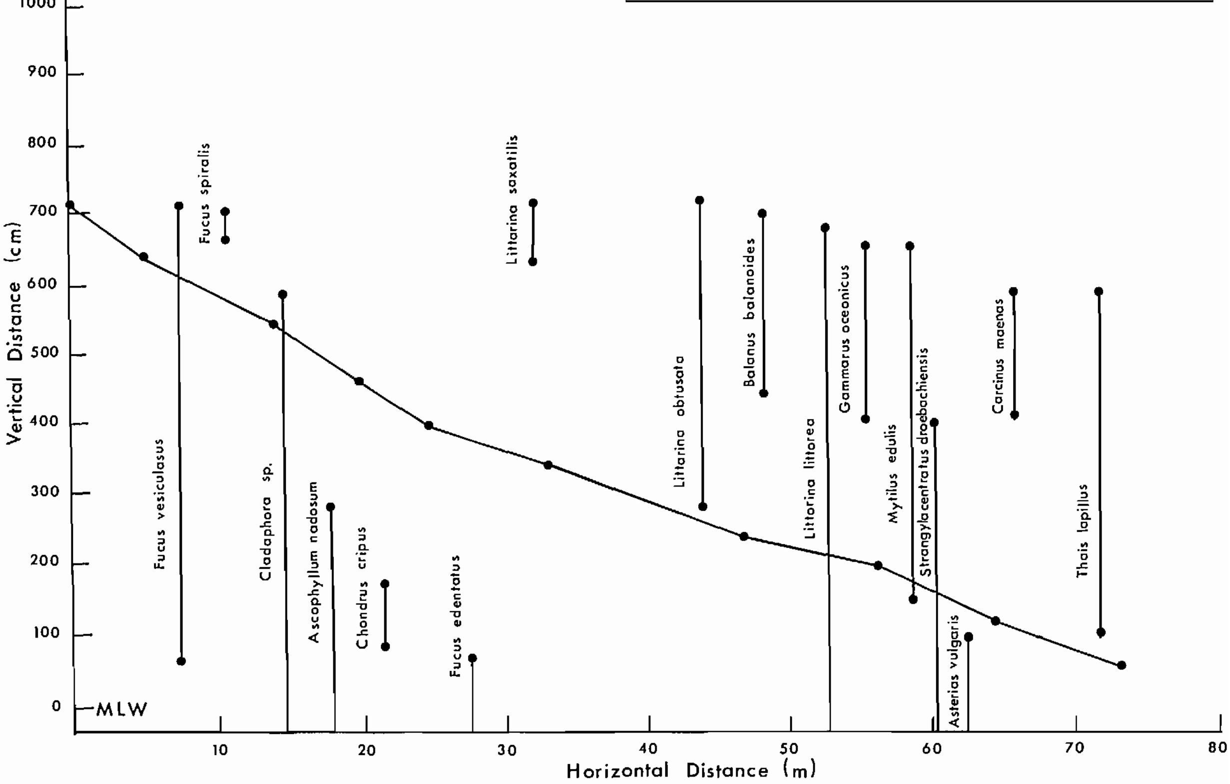


FIG. 20. General shore profile and the zonation patterns of common fauna and flora at Oven Head. MLW, mean low water.

Table 5 and Fig. 17 and 18 present species composition, diversity data, and zonation patterns for common fauna and flora, respectively. Data are based on 8 surveys.

OVENHEAD

This site is on the innermost shore of Passamaquoddy Bay, facing south into the open waters of the bay. It is thus one of the most sheltered of available shores outside of the tributary estuaries. Access to the shore can be obtained by following a dirt road off the main St. Stephen–Saint John Highway (Route 1) near Digdeguash (Fig. 19). However, this road is soft and washouts occur after rain. Vehicles may have to proceed with caution and at some seasons the approach must be completed on foot.

Ovenhead was formerly an island, separated from the mainland by a sand bar awash at mid-tide. This bar has been built up to a permanent roadway, separating two small bays with sandy, gently-sloping shores. On the outer, southern, side of Ovenhead the shore is rocky, sloping gently from high to low water. A characteristic profile for a transect at right angles to the shore with vertical ranges of the more common flora and fauna is shown in Fig. 20.

WOODSTOCK POINT

Woodstock Point (named by us) provides a fairly exposed location of ready access and with an excellent intertidal zone. The road to Woodstock Point leaves the Letite road about 0.5 km after passing the Deer Island Ferry Terminal. As shown in Fig. 10, Woodstock Point is within Letite Passage but close to the mouth of Passamaquoddy Bay. The rock structure is hard and igneous in nature and resists weathering.

Figure 21 gives details of the varied intertidal habitats at Woodstock Point. Rock slopes of varied gradient and aspect are available, enabling comparative studies of zonation and community structure. It is also useful for studies of the small lagoon and the sand beach.

Table 5 details the wide variety of species readily observed. The diversity is higher than at Joe's Point or Holey Point.

The generally even shore profile and the typical zonation patterns of common fauna and algae are illustrated in Fig. 22 and 23.

LETITE

Letite, also known as L'Etete, Mascabin Point, and Greens Point, has long been the preferred site for intertidal studies in the Quoddy Region. Access is easy at all seasons from an extension of the Deer Island Ferry Terminal road. As shown in Fig. 24, the nature of the intertidal zone is varied and presents several habitats in addition to the rocky intertidal. Fine rock pools are available at all tidal levels, as are sand and broken-rock shores. At many locations, the rocky intertidal presents superb sites for zonation studies, having relatively steady slopes. Additionally, as shown in Fig. 24, sites available for study range from almost the most exposed mainland site to relatively sheltered ones. It is possible to use this one location to run several transects to illustrate the modifying effect of wave action on the littoral biota.

Table 5 lists the wide diversity of common biota available for study and Fig. 25 and 26 show zonation patterns for common fauna and flora, respectively (based on means of 27 transects). As with other profiles the vertical scale exaggeration is 5X and the slope is, therefore, less

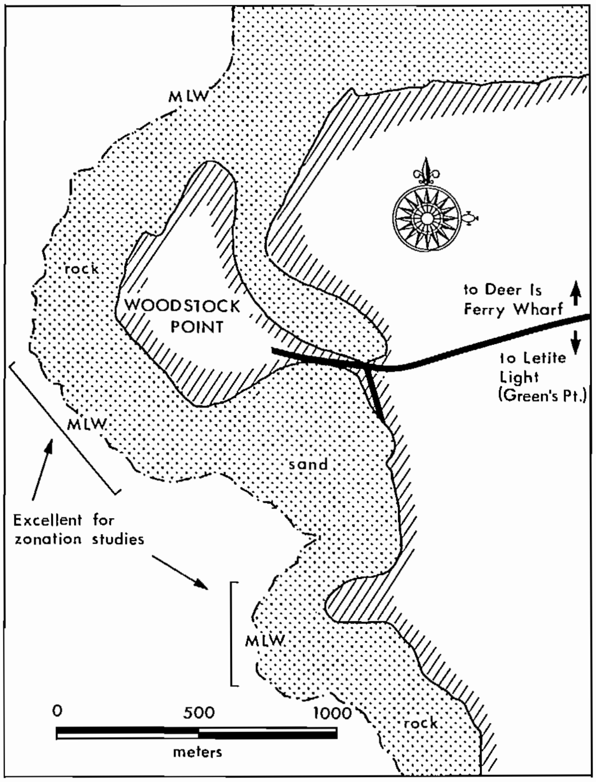


FIG. 21. The Woodstock Point area showing access and study sites. MLW, mean low water.

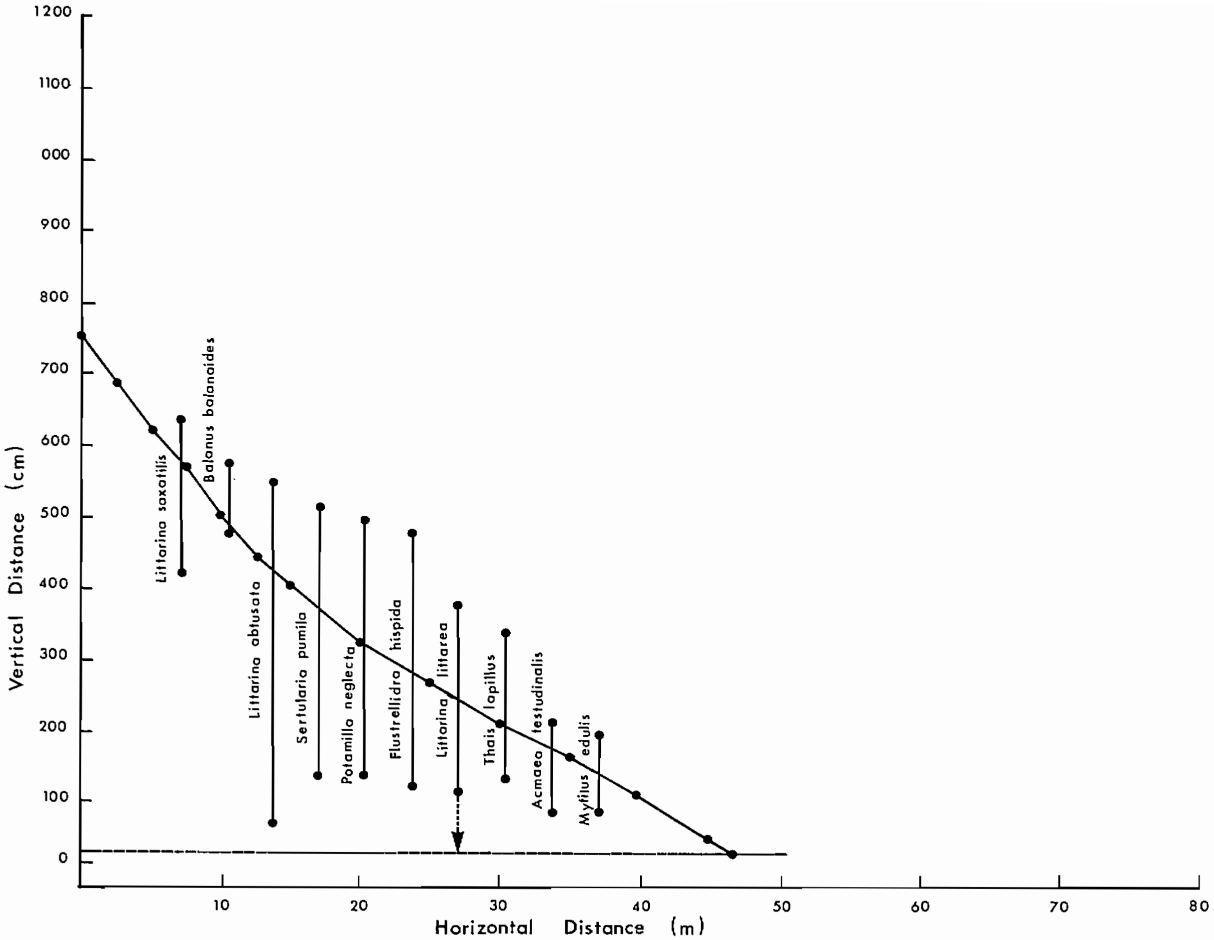


FIG. 22. General shore profile and the zonation patterns of common fauna at Woodstock Point.

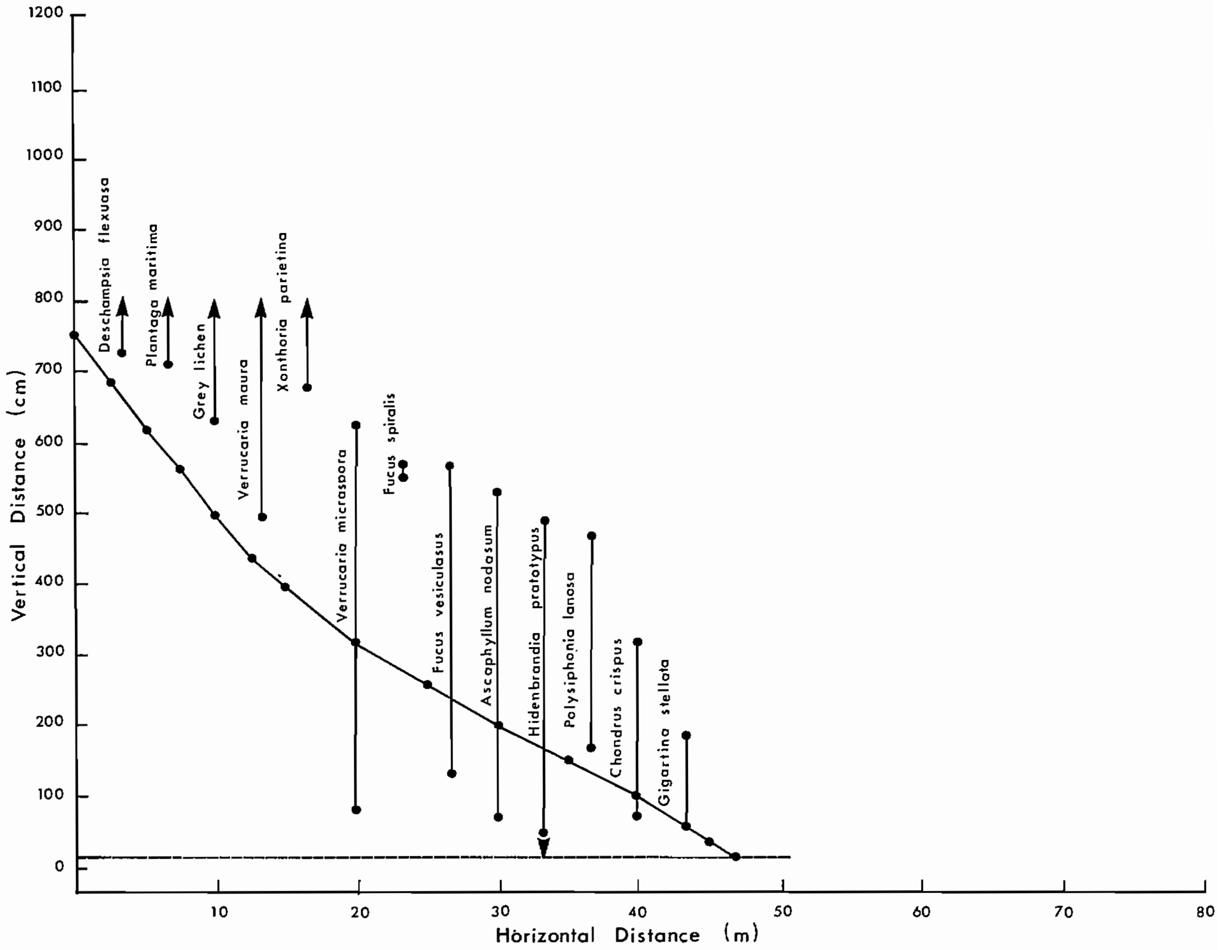
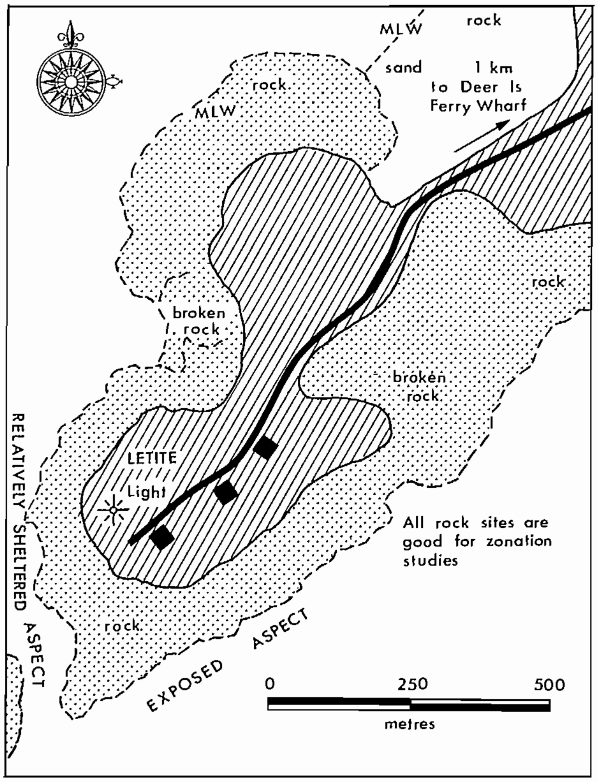


FIG. 23. General shore profile and the zonation patterns of common flora at Woodstock Point.

FIG. 24. The Letite area showing access and study sites. MLW, mean low water.



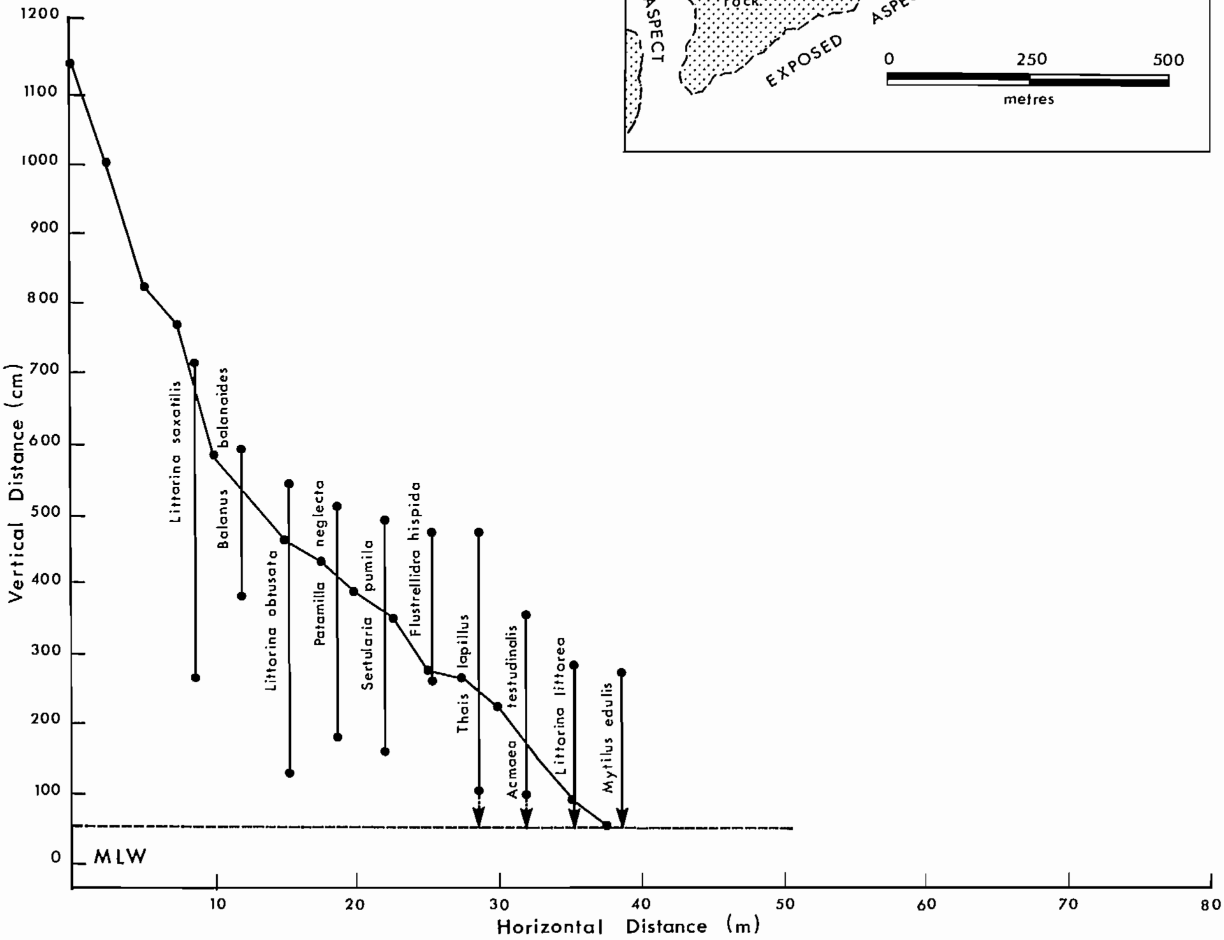


FIG. 25. General shore profile and the zonation patterns of common fauna at Letite.

formidable than depicted. However, the location is rugged and care is required. On no account should shore-based surveys of the islet joined to the point at low tide be carried out. It is quickly separated from the mainland by a channel with very powerful tidal currents.

PEA POINT

Pea Point is one of the most exposed sites in the Quoddy Region. It lies outside Passamaquoddy Bay, close to Black's Harbour, and faces south to the mouth of the Bay of Fundy (Fig. 27). Access is by a rough and narrow dirt road which turns off the paved road to Black's Harbour and serves the lighthouse on Pea Point Island. Parking and turning space is limited.

The shore is very rugged and care on the rocks is essential, particularly on the steep, seaward side of Sea Point Island where knife-edge ridges angle steeply to the sea. The channel between the island and the mainland is narrow and exposed at mid-tide level. The sheltered, northern end of the channel opens onto an area of rocks still awash at low tide and a small sand beach. The exposed, southern end of the channel formerly opened onto a small *Laminaria* bed, but this was destroyed by the urchin, *Strongylocentrotus droebachiensis*, and has not yet regenerated (Arnold 1976).

Unlike Letite, the shores do not show steady slopes but considerable variety, from small cliffs to almost horizontal ledges. They accommodate in a small area a wide variety of midlittoral patterns, including areas dominated by *Balanus balanoides*, fucoids, and *Mytilus*. The supralittoral fringe contains abundant lichens, and the infralittoral fringe is also rich in flora and fauna. Owing to the steepness of the shore, however, this fringe is extremely narrow and should be approached with caution. No one should work alone on this or any comparable shore.

Owing to the varied nature of this shore the studies, largely undertaken by undergraduates, have followed a different pattern from that employed elsewhere, and are still incomplete. Figures 28 and 29 show the vertical distribution of fauna and flora on the most exposed part of the shore. More detail of the area, including the results of a study by students with a minimum of direction, are given in Arnold (1977).

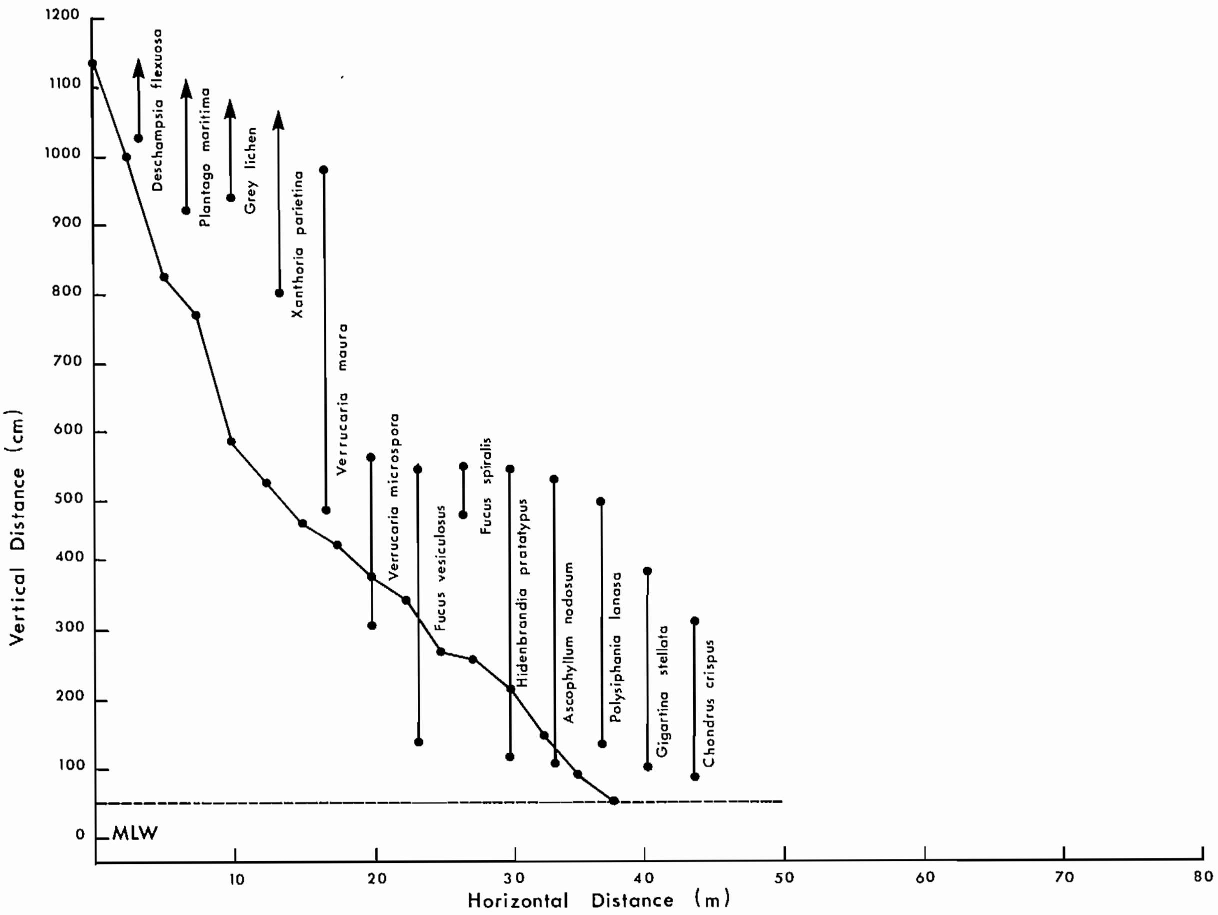
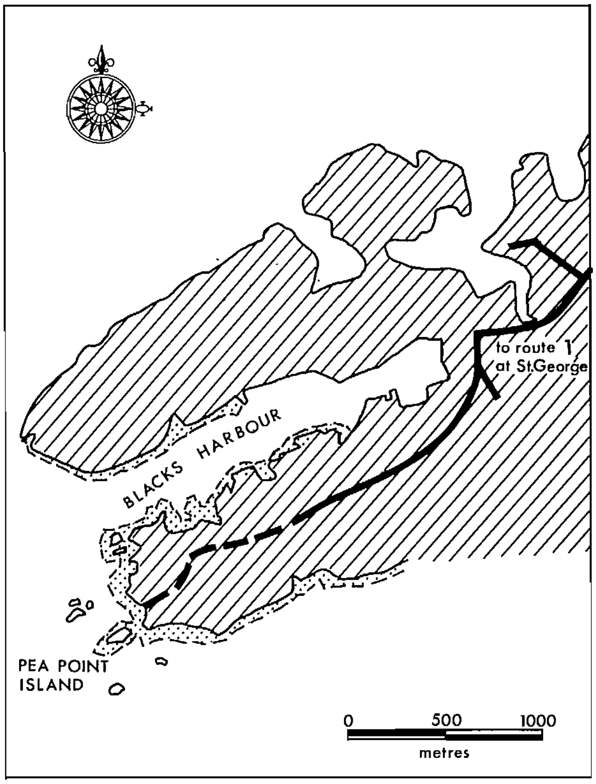


FIG. 26. General shore profile and the zonation patterns of common flora at Letite. MLW, mean low water.

FIG. 27. The Pea Point area showing access and study sites.



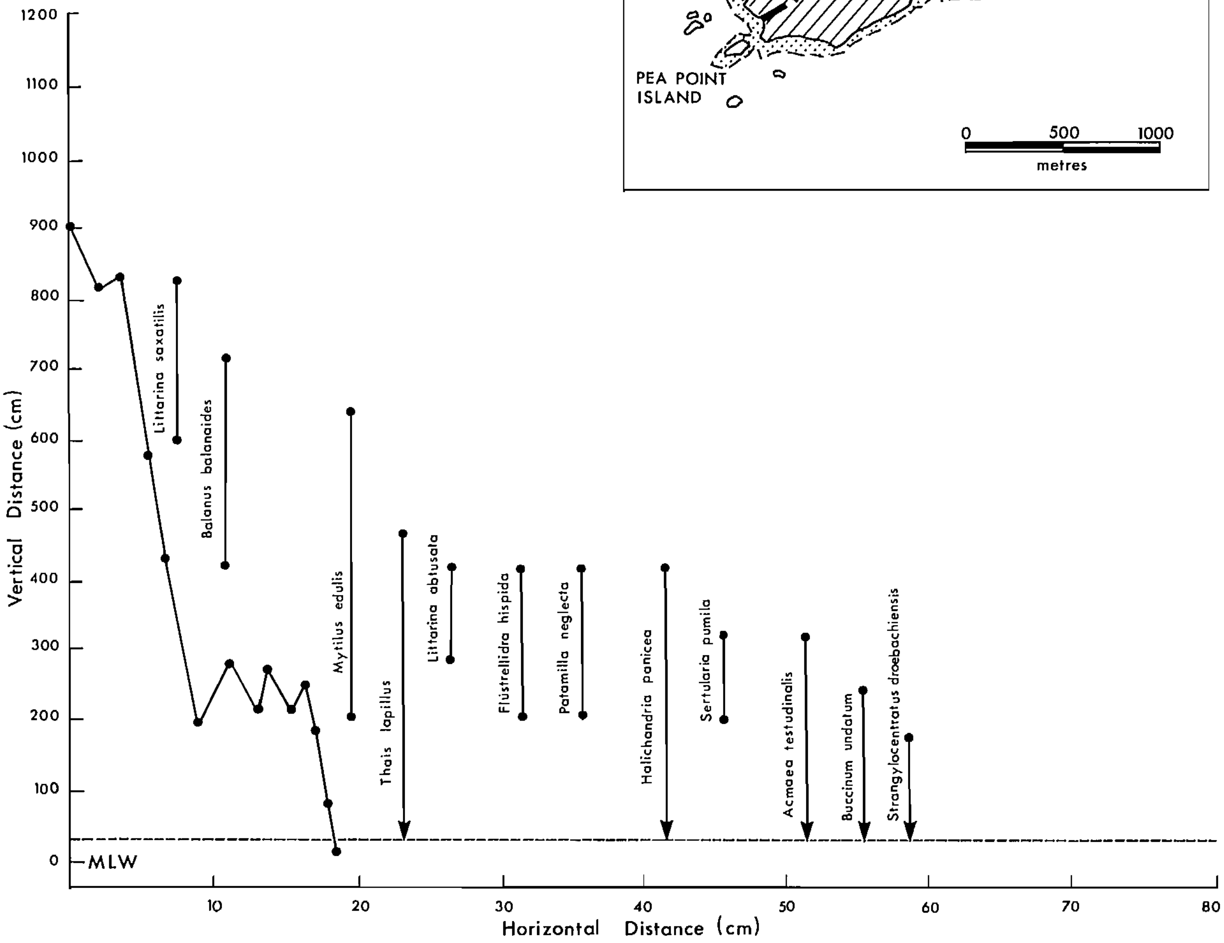


FIG. 28. General shore profile and the zonation patterns of common fauna at Pea Point. MLW, mean low water.

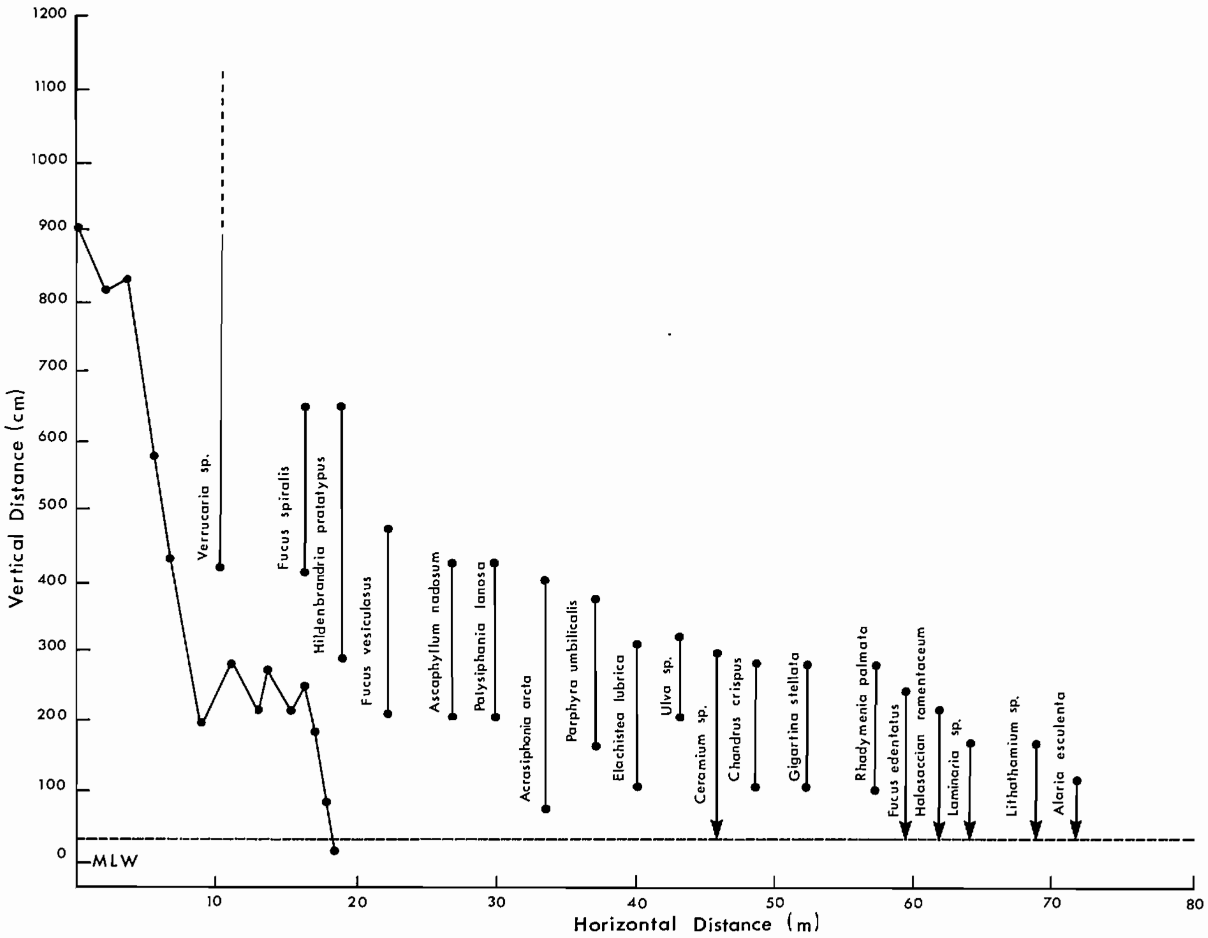


FIG. 29. General shore profile and the zonation patterns of common flora at Pea Point. MLW, mean low water.

TABLE 6. Species diversity of common biota for each 10% of the mean tidal range in the Quoddy Region.

% of range	Zone	Number of species
190–200	Supralittoral zone	8
180–190		5
170–180		3
160–170		3
150–160		6
140–150		6
130–140		7
120–130		7
110–120		7
110–110	Supralittoral fringe	13
90–100	Midlittoral zone	17
80–90		21
70–80		23
60–70		34
50–60		43
40–50		47
30–40		48
20–30		41
10–20		40
0–10		39
−10–0		42

GENERAL ASPECTS

The general, somewhat peculiar features of intertidal zonation in the Quoddy Region have been discussed above and Fig. 7 summarizes the general dominance of intertidal areas by the major species. On Fig. 7 the exposed end of the gradient is Letite and the sheltered end Holey Point. Joe's Point and Woodstock Point provided intermediate exposures. It is expected that study of certain islands in the region would provide examples of even greater exposure to wave action; it is certain that more sheltered areas may be found in the Digdeguash Harbour area (Fig. 2).

The general picture of the changing species diversity pattern with tidal height is shown in Table 6. There is a zone of very low diversity in the lower supralittoral zone. Diversity increases both above and below this zone of minimum environmental stability. Moving seaward, maximum diversity is achieved in the lower midlittoral; it drops somewhat in the infralittoral fringe before increasing again subtidally (Logan et al., Chapter 8). Areas of declining or low species diversity reflects greater environmental instability and all the combined factors modifying zonation. The decline in diversity at low water probably reflects the increased effect of wave action as the low tide turns. This difference is reflected not only in diversity but in an elevation of upper limits of fringe species such as *Acrosiphonia arcta*, *Gigartina stellata*, various echinoderms, and the Northern Rough Whelk, *Buccinum undatum*.

Acknowledgments

We thank many students who have contributed to our knowledge of Quoddy Region shores during participation in the field courses. Ms Carol Bagnall has meticulously surveyed many transects, providing invaluable data. Miss Winnifred Shaw, first as an honours student at Mount Allison University and then as a graduate student at the University of New Brunswick, Saint John, has helped in many ways. We are grateful to Ms Ronalda Higgins who has painstakingly checked, collated, and analyzed field records and prepared figures and tables. Part of this work was financed through a Natural Science and Engineering Research Council Grant (A6389) and part through a U.N.B. Research Grant (11-45) to M. L. H. Thomas.

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CHAPTER 5

Coarse Sedimentary Shores

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Introduction

When bedrock is exposed above the surface of the ocean it is immediately subject to erosion. The most important agents are the waves that wear away the rock and hurl loose fragments at the surface, grinding it away. Weak points in the rock structure are worked on and the more resistant sections that then lack support tumble down. The rate of erosion is therefore determined by the amount of wave energy at work on the rock and by the hardness of the rock itself.

The Quoddy Region is not normally subject to high wave energies, as the winds are not usually strong (mean velocity in the windiest month is only 20 km/h compared, for example, to 31 km/h in the Magdalen Islands). Also, the maximum fetch for most wind directions is limited. Campobello and Deer islands shield Passamaquoddy Bay from the Bay of Fundy, and the Grand Manan archipelago partially screens the eastern shore of Campobello Island. Only on the outer coasts of these islands and on the eastern shore of the mainland is the coast not sheltered. Here the maximum fetch varies from 120 to 400 km but the exposure is easterly, whereas the prevailing winds are from the west. Thus, high-energy shores with a potential for rapid erosion do not occur in the Quoddy Region.

In addition, the bedrock consists of old hard rocks that are not easily eroded. These are mainly Devonian and Silurian sedimentary and volcanic rocks, but granite occurs just to the north of the region and outcrops along the coast in the eastern portion of the region (Cumming 1967).

During the Pleistocene, the Quoddy Region was traversed by glaciers and is now mantled by glacial and fluvioglacial deposits. In contrast to the bedrock, these unconsolidated deposits erode readily and supply a rich source of sedimentary material for the beaches.

Sediments

Many variables determine the physical environment of a sedimentary beach. Particle size can vary from large boulders, similar in character to the bedrock, down to the finest particles of clay, and all possible combinations can occur together. The particles themselves may be in almost continuous motion and in the process of being further eroded or they may be resting quietly in a deposit. Spaces under rocks and between particles can vary enormously in extent and may be filled with water of varying temperature, salinity, and oxygen content. The different levels of the beach are alternately submerged and emerged and exposed to waves for different periods of time due to the rise and fall of the tides, which in the Quoddy Region are quite high.

Of all of these physical factors, the texture of the sediment is the most significant: it directly influences other factors such as porosity and the availability of water and is itself largely a reflection of the wave energy experienced by the beach.

Textures of sediments have been studied intensively by geomorphologists and their techniques and terminologies have generally been adopted by biologists. However, biologists are primarily interested in organisms and their environments on the beach, and thus their emphasis is different and such techniques may not be appropriate.

In general usage, sediments are named after the particles that dominate their texture (e.g. gravel, sand, etc.). Since this procedure is not very precise geomorphologists have developed more exact schemes, both for naming the particles and for describing the textural qualities. Size of particles can be measured on an arithmetic scale, but because so many of the grades of sediments of interest to geomorphologists are small, a logarithmic scale is commonly used to give a clearer representation. The logarithmic scale uses 2 as a base and again, because of the fineness of most particles, a negative logarithm is used so as to change the sign of the units. The units were designated by Krumbein (1936) as phi (ϕ) and defined as "the negative logarithm to the base 2 of the particle size in millimeters." The names applied to the various categories are those introduced by Wentworth and the whole series is known as the Wentworth Scale (Table 1).

TABLE 1. Modified Wentworth scale of particle sizes.[a]

Name				
Grade	Subdivision	ϕ	mm	µm
Boulder		−8	256	
Cobble		−6	64	
Pebble		−4	16	
Gravel		−1	2	
Sand	Very coarse	0	1	1000
	Coarse	1	0.5	500
	Medium	2	0.25	250
	Fine	3	0.125	125
	Very fine	4	0.0625	62.5
Silt	Coarse	5		31.3
	Medium	6		15.6
	Fine	7		7.8
	Very fine	8		3.9
Clay	Coarse	9		1.95
	Medium	10		0.98
	Fine	11		0.49
	Very fine	12		0.26

[a] Cummins (1962) eliminated Wentworth's term granule and introduced the widely used term gravel to replace it and part of Wentworth's pebble category.

TEXTURE

To determine texture a sediment sample is placed in a 63-μm sieve. Water is added and the sample is wet-sieved until the filtrate is clear. The fine material that passes through with the water is collected and analyzed separately. The coarse material remaining on the sieve is dried and sieved through a series of sieves corresponding to the phi series or fractions thereof. The material retained by each sieve is weighed and its percentage of the total weight determined. Coarse particles (larger than gravel) are not readily sieved but may be measured individually.

The name applied to the sediment is that of the most abundant particle grade by weight. Sediments that are not well sorted will have the combined name of the two most abundant fractions, such as sandy-gravel. For more precise determinations, the sample is plotted within a diagram whose sides represent the percentage composition of gravel, silt, and clay (Fig. 1).

With coarse particles, analysis by weight is not satisfactory as a single pebble or cobble may outweigh the rest of the sample. The large particles are better sampled and their dimensions measured individually, and the finer matrix, if any, analyzed separately. The emphasis depends on what is considered to be most significant for the organisms. On a high-energy beach, with cobbles and sand occurring together, only the character of the sand is likely to be important, since organisms will be unable to survive near or on the cobbles due to abrasion. However, on a beach of boulders and gravel both may be important, as organisms may live under the boulders and in the gravel.

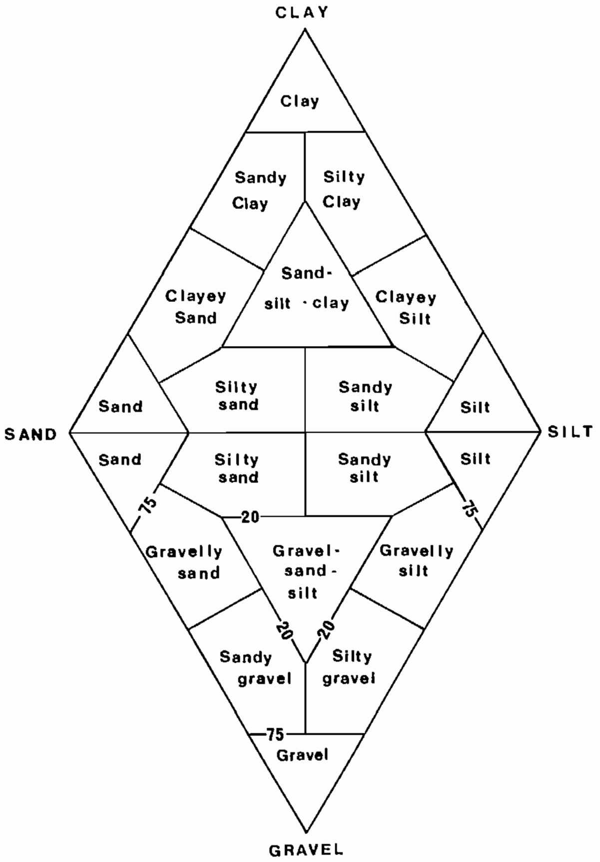

FIG. 1. Sediment names (after Holmes and McIntyre 1971 and Uchupi 1963).

Textural qualities of significance for the organisms are most readily determined by plotting the cumulative percentage composition of the sediment in phi units. On an arithmetic scale the curve is typically S-shaped, but may be transformed to a straight line, if desired, by plotting on a probability scale. From the graph it is possible to determine, by interpolation, values that can be used to calculate textural parameters (Fig. 2). Thus the 50% point ($Md\phi$) represents the median grain size, since exactly half of the particles are smaller and half are larger. The mean ($M\phi$) can be determined by averaging all the weights or can be approximated from $(\phi + \phi 50 + \phi 84)/3$. Another parameter of significance is the degree of sorting, as expressed in the particle-size distribution. This is measured as the number of ϕ units between the first (25%) and third (75%) quartiles and is known as the quartile deviation ($QD\phi$). $QD\phi = (\phi 75 - \phi 25)/2$. A sediment that has been well sorted by water movements will have a smaller quartile deviation than one that has not been well sorted. Asymmetry in the distribution of the particle sizes or skewness can be obtained as $SK\phi = (Q25\phi - Q75\phi - Md\phi)/2$. A positive value means the distribution is skewed to the right of the mean, whereas a negative value means the skewness is to the left.

MINERALOGY

The composition of the particles is of little direct ecological importance, since in most cases one type is the same as another. However, the composition has indirect effects since it influences other properties. Sand beaches are usually formed mostly of grains of quartz that have weathered out of granite or sandstone rocks. Such grains may be further rounded but when surrounded by a film of water become virtually indestructible, whereas other types of minerals continue to diminish to silt or clay-sized particles that are finally deposited in deep water offshore. Thus sand beaches are usually formed of quartz grains and tend to be most prevalent where the bedrock is granite or sandstone. The granite outcrops along the coast and the higher wave energies therefore account for the well-sorted sand beaches in the eastern part of the Quoddy Region.

SHAPE

The shape of the particles is important in assessing the wave energies affecting the sediments; it also influences some other physical features of the deposit. Erosion varies with the size of the particles and the wave energy on the beach. Large boulders and cobbles too big to roll weather slowly, whereas pebbles that roll abrade each other and erode quickly. This can be seen in pieces of broken glass that round up quickly on a beach. Particles smaller than 250 μm do not become rounded by contact

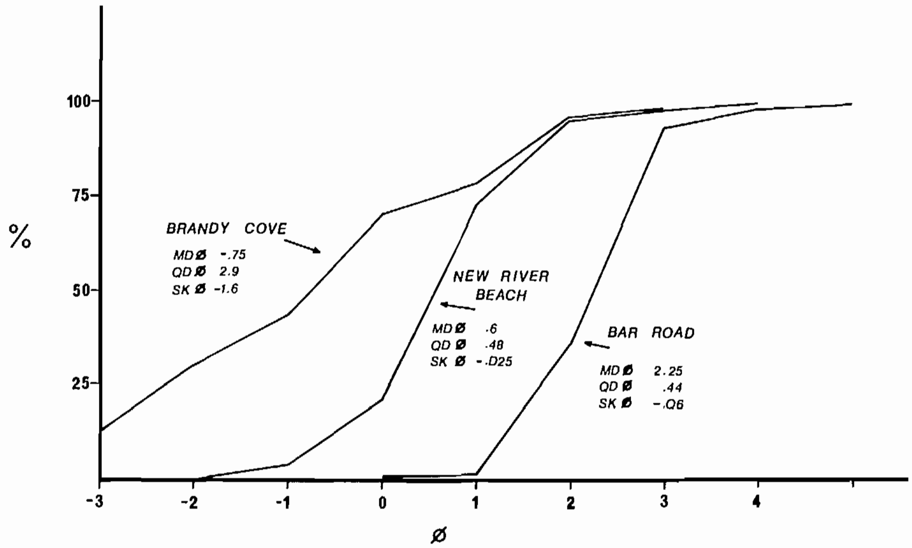

FIG. 2. Cumulative textural curves of sediments from representative sites in the Quoddy Region.

with each other but may be worn or break up on contact with larger pebbles.

The two important measurements of shape are roundness and sphericity. Roundness refers to the degree of wearing away or rounding of the corners and can be estimated by comparing the particle to a series of models of varying degrees of roundness (Shepard 1973). Sphericity refers to the degree to which a particle approaches a sphere in shape. Thus a cube is highly spherical but has a low degree of roundness. Sphericity is determined primarily by the original shape of the particle when it weathered out of the rock, and secondarily by weathering. Terms such as spherical, cuboidal, rodlike, discoidal, tabular, etc. are used to describe the particle. Three descriptive indices of shape are also used (King 1966):

1) Roundness $= 2r/l \times 1000$
2) Asymmetry $= AC/l \times 1000$
3) Flatness $= \dfrac{(w + l)}{2t} \times 100$

(l = length, w = width, t = thickness, r = least radius of curvature in the principle plane, c = where w crosses AB or l).

Differences in shape are important in determining the size and shape of the interstitial space in the sediment in which organisms can live and also the ease with which particles can roll. Sphericity of large particles is important in determining the presence and the qualities of the living space underneath them. If not small enough to be easily rolled, large spherical particles tend to become imbedded in the finer matrix, whereas tabular particles do not and have large living spaces (sublithian habitat) underneath them. Here intertidal organisms can remain cool and wet when the tide is out.

POROSITY

Another important parameter of sediments is the pore space or porosity, since it determines the space available in which organisms can live. Porosity is defined by Crisp and Williams (1971) as "the fraction of the total space left void." It is directly related to grain size and therefore coarse sediments have more porosity than fine ones. However, since the space (1) varies with particle shape, (2) may be occupied by fine particles, and (3) decreases as the sediment is compressed there is no simple relationship between texture and porosity and it has to be estimated separately. The simplest method is to saturate a dry sample with water, weigh it, and then dry it to a constant weight. The water loss gives a measure of porosity. Direct measurements of pore sizes can be obtained by sectioning samples that have been impregnated with resin and then measuring the pore spaces under a microscope (Crisp and Williams 1971).

PERMEABILITY

Although not of direct importance to the ecology of sedimentary beaches, permeability of the sediment is indirectly important since it determines the circulation of water through the deposit. It is defined by Crisp and Williams (1971) as "the rate of flow of a fluid of known viscosity through the deposit." Permeability also varies directly with porosity so it is determined by texture, particle shape, and degree of compression. Coarse sediments are generally more permeable than fine sediments but the relative amount of fine material present is also of critical importance. Thus, increasing the proportion of fine sand in the sediment decreases the permeability (Webb 1958).

Permeability is measured as the time for a head of 50 cm of water to drain through 10 cm of sediment (Hulings and Gray 1971). It can be measured by placing 10 cm of sediment in a 70–80-cm glass tube that has the end closed with gauze or netting to hold the sediment. It is filled with 65 cm of water, which is then allowed to drain to 15 cm from the bottom of the tube.

WATER CONTENT

The water content of a sediment depends on the porosity and is therefore also influenced by texture. Coarse sediments can hold more water. However, the water content also depends on the availability of water. When the tide is low the water drains out of coarse permeable sediments, especially as beaches with coarse textures have steep slopes (commonly known as flats) and capillary action keeps the water at the surface. Thus, the water content in a coarse-textured beach will fluctuate with the tidal cycle more than in a fine-textured beach, where it may remain close to saturation.

The water content of a sediment can be determined by placing 5 ml of water in a 10-ml graduated cylinder and allowing the sediment to be added until it reaches the 5-ml level. If the sediment was saturated the water will now reach 10 ml; if it was not, the level will be lower in proportion to the amount that was previously filled with air. An alternate method is to determine the weight loss of a sediment sample when it is dried to a constant weight.

HARDNESS

The hardness of a sediment determines the ease with which the macrofauna can burrow. It is determined by the size of the particles and the water content. Coarse particles (sand and coarse sand) are too heavy for small animals to move, even if abrasion by their movement is not a problem, and thus burrowing forms may be absent. Finer particles can be moved more readily, but the hardness of the sediment varies with the water content. According to Freundlich and Roder (1938) mixtures of fine particles and water form compact sediments when the water content is less than 53%. With water content between 53 and 58% they are dilatant and become harder when pressure is applied (as, for example, when wet sand whitens when it is stepped on). When the water content exceeds 58%, the mixture behaves like a viscous liquid when pressure is applied. Thus, during high tide burrowing is relatively easy but during low tide it is difficult if the water drains away, as it does on coarse, steeply sloping beaches. Gently sloping fine-textured beaches retain their water at low tide, so burrowing is still possible. Some shore birds also forage on such beaches by probing with their bills, and gulls are able to obtain clams by puddling.

Water Quality

When the tide is high, water above the sediment has the characteristics of the local sea water, but the water in the sediment may have quite different properties, depending on the permeability of the sediment and the slope of the beach.

TEMPERATURE

Large temperature variations are typical of coarse sedimentary beaches because of the influence of insolation and streams during low tide and of the ocean high tide. On a summer day insolation can raise the surface temperature of the sediments well above that of air temperature, especially when the surface dries out. Under the surface of the sediment, rocks, or patches of algae, where it remains wet, the temperatures remain much lower (Steele 1976). In winter the situation is reversed and organisms can avoid the freezing air temperatures by living under rocks or moving down into the substrate.

SALINITY

The salinity of the interstitial water depends on the position on the beach, the beach slope, and the permeability of the sediment. On fine-textured, flat beaches the sediment in the intertidal region remains saturated with seawater and has a salinity similar to that of the adjacent ocean, even at low tide. Rain and streams of fresh water flow over the surface without influencing the interstitial water very much. However, with coarse-textured sediments and their typically steep slopes, the water drains away at low tide and rain water and freshwater seeps soak into the sediment. Above the tidal region, on the upper part of the beach, the interstitial water is fresh since it is derived from rain water that drains through the sediment. The fresh water mixes with the seawater in the upper part of the intertidal region and drains out from the lower part of the beach during low tides, at about the level of low water where the slope of the beach lessens ("horizon des sources" of Delamarre Deboutteville 1960). Seeps of brackish water are conspicuous on sandy beaches at this point and some brackish-water species may predominate in this habitat.

ORGANIC CONTENT

Organic matter in the sediment is available as food for organisms living there and as a substrate for bacteria. Since it readily breaks down into small pieces it generally behaves like small mineral particles. It is kept in suspension by water movements and is found in only small amounts in the sediments of high-energy coarse-textured beaches but is abundant in the water column for suspension feeders. Low-energy beaches, with finer particles, generally have higher organic contents in the sediment where it may be consumed by deposit feeders or decomposed by microorganisms. Consumption of oxygen by the latter, combined with poor circulation of water, results in depletion of oxygen in the sediment.

The organic content of a sediment can be estimated most easily as the loss in weight when a weighed dry sample is heated in a muffle furnace to 500°C so as to burn off the organic material. However, some mineral matter, such as $CaCO_3$ in shells, may also be incinerated and cause errors in the determination. If significant quantities of shell are present they should be removed by acidification. More accurate determinations of organic matter can be made by determinations using a C, N analyser (Byers et al. 1978).

OXYGEN CONTENT

As a consequence of the stagnation of the water in fine sediments, the oxygen of the interstitial water is used up through bacterial decomposition of organic matter in the sediment. The rate of decline depends on the permeability of the beach and hence on its texture. In particular it has been found to depend on the amount of fine sand or finer particles in the sediment: when this is more than 10–20% permeability is low, as is the oxygen content (Brafield 1972). Organisms requiring high oxygen concentration have to live near the surface to be able to use the water near the surface for respiration.

Another result of the decrease in oxygen with depth is that reducing bacteria occur that reduce the sulphate (SO_4^{--}) to hydrogen sulphide (H_2S), nitrate (NO_3^-) to ammonia (NH_3^+) and carbon dioxide (CO_2) to methane (CH_4). It is the prevalence of these compounds that gives the characteristic odor to the flats when the tide is out. The H_2S in the sediment becomes fixed as iron sulphides and this produces the black layer in the sand. This may be close to the surface in fine sediments or at the surface under algae, but it is deeper or absent in coarse sediments and with higher wave energies. The position of the black layer may vary seasonally, depending on the amount of bacterial decomposition.

Beaches

The material eroded from the land varies in size from boulders to small particles. These are then sorted by waves and tidal currents. The water transports as large a particle as it is capable of moving and then deposits it when it can no longer move it. With high wave energies, the fine particles are winnowed out and the large are abraded into rounded boulders and cobbles. As the latter become progressively smaller they in turn are transported as gravel, sand, or silt to areas or depths with less motion. Areas with high wave exposure, therefore, are characterized by cliffs molded by erosion, and coarse-textured well-sorted beaches with rounded particles. Protected areas tend to have fewer cliffs and to have gently sloping flats with poorly sorted sediments in which the particles are angular.

Due to low wave energies in the Quoddy Region and especially inside Passamaquoddy Bay, cliffs are not well developed and sorting of sediments by waves is poor. The beaches have a mixture of particles of all sizes from boulders to fine particles (Fig. 3). As is evidenced from their variable mineralogy, the boulders and cobbles were mainly deposited by the glaciers or eroded out of the unconsolidated till that mantles the region. Their origin also accounts for the roundness of many of these particles. The fine particles may have had a similar origin, or may have been carried down to the ocean from the local rivers.

Beach profiles are determined by wave energy and the amount of erosion or deposition taking place. The rise and fall of the tide distributes the wave energy unequally across the profile. Also, as tidal cycles are asymmetrical, wave energy is concentrated at the tidal still stands of high water neap and low water neap.

Erosion of the land is therefore concentrated at the high water level, since waves there have the opportunity to work on the land. The eroded material is carried downwards by the backwash of the waves. During high water of spring tides the waves can work at an even higher level but this is reached much less frequently. Nevertheless, high waves combined with high tide levels, such as the storm surges associated with deep low pressure weather systems, can do a great deal of erosion in a short time. In protected areas, as in Passamaquoddy Bay, they probably do most of the erosion.

FIG. 3. Indian Point, St. Andrews. Shown are cobbles on the steep slope in the foreground, rockweeds in the middle, and the finer-textured but poorly sorted flat extending to low water beyond. Rounded boulders are scattered over the flat.

Between high and low tide the water level changes rapidly leaving little chance for erosion. The waves have to traverse the shallow eroded platform and bend to break further offshore and dissipate their energy. Consequently they tend to be constructive rather than destructive. The eroded material is sorted: the fine material is carried downwards by the backwash of the waves and gravity to lower levels, leaving behind the coarse particles. Ripple marks do not occur.

Below low water neap the fine sediment from the upper part of the beach accumulates as sand or mud. The beach slope is much more gentle and the sediment remains saturated with water during the period of exposure during spring tides. Ripple marks, formed by the oscillation of the water as waves pass over at high tide, appear on the surface.

The region near and just above low water neap is where the brackish water draining from the intertidal sediments may appear as seeps. The sediment may also be coarser and less well sorted due to the concentrated breaking of the waves at this tidal still stand.

The profile of the beach is determined primarily by wave energy and the amount of erosion that is taking place. On exposed beaches wave energy is high and may affect the profile at all levels, although it is more concentrated at high water neap. Sedimentary beaches may change from day to day and there may be marked seasonal differences related to seasonal cycles of wave energies. On protected beaches, erosion may be confined to the infrequent storms; at other times the beach remains in equilibrium, with little change evident even over a period of years.

In the Quoddy Region, wave exposure is low but the tidal range is high; thus the beaches tend to be in equilibrium and changes occur rarely. Terrestrial vegetation reaches almost to high water of spring tides (Fig. 4). The mid-tide region has a relatively steep slope and is covered with poorly-sorted, coarse-textured sediments. The pebbles and cobbles are often angular and typically imbedded in the matrix to form a kind of pavement. At the level of low water neaps the slope decreases and the texture changes to fine sand or mud with seeps obvious at low tide. Scattered over the surface are large boulders that were left behind by the glaciers. The beaches are wide and their most significant feature is the wide expanse of tidal flats exposed during periods of spring tides. Here it is possible to find animals that are never exposed elsewhere.

Fauna and Flora

It is most convenient to consider the organisms on the beach from the point of view of their roles in the beach community (i.e. producers, consumers, or decomposers) and in relation to their size.

PRODUCERS

Aside from the eelgrass (*Zostera marina*), which seems to be unimportant in the Quoddy Region, the producers consist of a diverse assortment of macroalgae and diatoms. The most conspicuous are the algae that live attached to a substrate such as bed rock, large rock particles, or each other. Their occurrence on particles depends on the amount of abrasion and hence on wave exposure.

FIG. 4. Indian Point, St. Andrews. The drift lines mark the heights of recent tides. The logs were beached in storms and extend onto the terrestrial vegetation.

Thus, cobbles on high wave energy beaches may have no macrophytes, except perhaps for ephemeral species in the summer, whereas in sheltered locations even quite small pieces of rock may bear large macrophytes. In the summer photosynthesis may produce enough trapped oxygen bubbles that plant and rock together will float and drift away. There are differences between species of algae: *Ascophyllum nodosum*, for example, does not normally occur on as small a rock as does *Fucus vesiculosus* (Fig. 5), even when both are found on the same beach. Macrophytic algae are not found on sand or gravel because of the impermanence of the surface. In sheltered locations certain species of macrophytes, such as *Ascophyllum nodosum* and *Fucus vesiculosus*, occur unattached but resting on the sand or gravel substrates.

The coarse macrophytes, such as *Fucus* spp., are not grazed to any extent when full grown, but when broken off and carried into the subtidal they are an important source of food for sublittoral animals such as sea urchins. As they become fragmented, they and their associated microorganisms form detritus that serves as food for suspension and deposit feeders. Coarse macrophytes are also important in creating cool, damp microhabitats on the beach when the tide is out. Finer algae, such as *Pylaiella littoralis* or *Dictyosiphon foeniculaceus*, are important sources of food for grazing consumers in the intertidal region.

The other important producers on sedimentary beaches are microphytes (mostly diatoms) that live on the surface of macrophytes or large rock particles. Here they serve as food for organisms such as limpets or periwinkles that graze such surfaces.

Diatoms are often the only producers on gravel or sandy beaches. Some attach to grains and the motile forms live in the interstices between the grains (Round 1971). As these microphytes are adversely affected by abrasion they tend to be most abundant where there is some shelter. Here they may be very abundant and form what is known as diatom sand. This serves as food for the sand dollar (*Echinarachnius parma*) and the green sea urchin (*Strongylocentrotus droebachiensis*).

Primary production by the phytobenthos has apparently not been measured in the Quoddy Region but might be expected to be large, due to the relative clarity of the water, the availability of nutrients, and the high tidal range. Production of the macrophytes is usually estimated by harvesting or measuring growth rates (Mann 1972). The uptake of C^{14}, either in situ or in an incubator, has been used to measure production by microphytes in sand (Steele and Baird 1968).

DECOMPOSERS

The decomposers consist of microorganisms (bacteria and fungi). These have not been studied in the Quoddy Region. As most bacteria in sediments will not grow in vitro, the usual plating methods underestimate their numbers. Direct counts of stained bacteria have been used instead but these do not differentiate between living and dead individuals. Aerobic forms are confined to a thin layer of sediment at the surface where the interstitial water is well oxygenated, and anaerobic reducing forms occur in the black sediments of the sulphide system underneath.

In Nova Scotia, Dales (1974) found with direct counts that the numbers of bacteria in sediments were inversely proportional to the mean diameter of the particles and directly proportional to the organic carbon and nitrogen contents of the sediments.

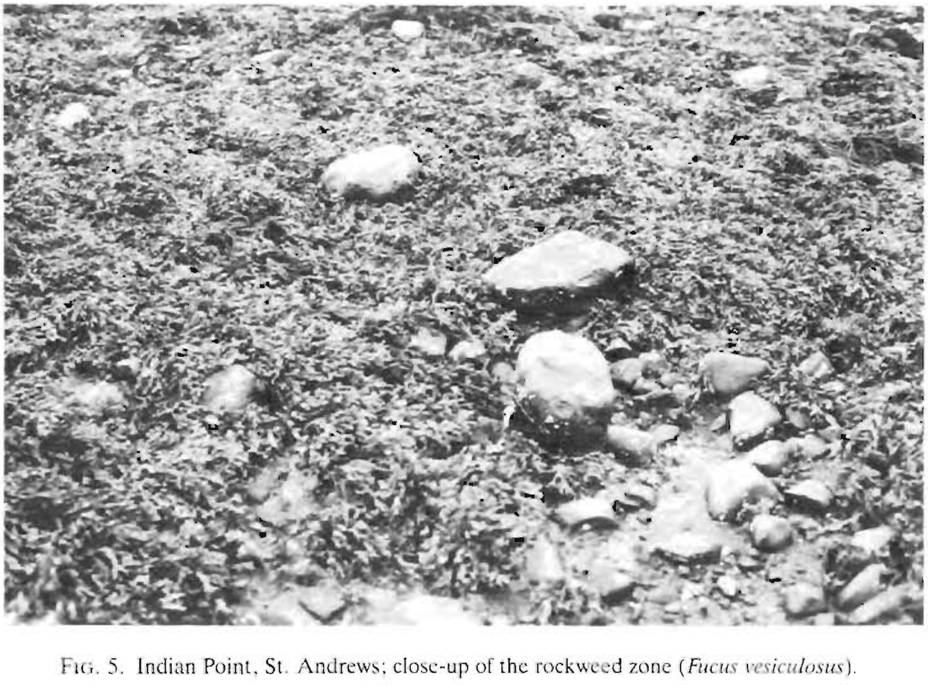

FIG. 5. Indian Point, St. Andrews; close-up of the rockweed zone (*Fucus vesiculosus*).

CONSUMERS

The animals (consumers) living on beaches occur both as epifauna (living on the surface most or all of the time) and infauna (living mostly or entirely in the sediment).

The epifauna living on coarse particles consist of macro- and microfauna; they are the same species as those found on bedrock (barnacles, mussels, etc.) and have the same intertidal zonation. Whether or not an epifauna occurs depends on the amount of abrasion. In sheltered locations even small pebbles may have barnacles attached (Fig. 6).

Underneath the large cobbles and boulders — especially those that are flat (tabular in shape) and do not become embedded in the matrix — a cool damp sublithian habitat is found, even during low tides at midday in the summer when temperatures on the exposed surface of the rock may become very high. The undersurface of the rock may be the site of attachment of hydroids, sponges, anemones, barnacles, and the egg capsules of the dogwhelk, that otherwise are found only low on the beach or in the sublittoral. Here also are small flatworms (*Procerodes* spp.), amphipods (*Gammarus* spp.), and isopods (*Jaera* spp.), crawling over the surface of the rock and the matrix beneath. Larger animals, such as the rock eel (*Pholis gunnellus*), rock crab (*Cancer irroratus*), and green crab (*Carcinus maenas*) also find shelter here in the large spaces on the lower parts of the beach. In the winter months both the common periwinkle (*Littorina littorea*) and the dogwhelk (*Thais lapillus*) shelter in these locations when they are inactive.

Quantitative sampling in this type of habitat is difficult. Samples from quadrats ($m^2 \times 10^{-1}$ being the most suitable size for intertidal studies) have high variances related to the variable nature of the substrate. As the animals are often smaller than the particles of the matrix, extraction by sieving is difficult unless the larger particles are first removed. Flotation and decantation methods of separation will work for many species. Another method that has been used is to sample the fauna associated with individual pieces of rock. The size and shape of the particle should be standardized as much as possible, as they can affect the suitability of the sublithian habitat and change the size of the area sampled (Steele 1976). Collectors and traps have also been used to make collections in this type of variable habitat. The microfauna can be obtained by filtering the water, to which some formalin has been added, that has been used to wash either particles of sediment or organisms.

Fine-textured beaches show little, if any, evidence of life during low tides. The only animals considered as epifauna are the sand shrimp (*Crangon septemspinosus*), the sand dollar (*Echinarachnius parma*), the green sea urchin (*Strongylocentrotus droebachiensis*), and the whelk (*Buccinum undatum*), and even the first two of these burrow into the sand for part of the time. The egg cases of clam drills (*Lunatia* spp.) also appear on the surface but the parents spend most of their time in the sediment.

The infauna living in the sediments are much more diverse and are separated by size into the macrofauna (retained on a 500-μm sieve), meiofauna (passing through

FIG. 6. Indian Point, St. Andrews; close-up of the cobbles at the base of the steep slope. A variety of kinds of rocks are present and some are quite angular. The cobbles are imbedded in the gravel matrix. Barnacles are attached to quite small rocks.

a 500 but retained on a 50-μm sieve) and the microfauna (passing through a 50-μm sieve). This seems to be the most practical separation that has been proposed. In sand the meiofauna is also known as the interstitial fauna, since the organisms live in the space between the particles; but in coarser sediments where the pores are larger this is also true of some of the macrofauna, so the two are not always synonymous.

The macrofauna of the Quoddy Region consists of species characteristic of sheltered-to-moderately exposed habitats and those typical of exposed and highly exposed beaches, such as the amphipod, *Amphiporeia lawrenciana*, are absent. They include a variety of molluscs (*Mya arenaria*, *Lunatia heros*, and *Lunatia triseriata*), annelids (*Nereis virens*, *Lumbrineris* spp., *Nepthys* spp., and *Pectinaria gouldi*), isopods (*Chiridotea caeca*, *Edotea montosa*), and the amphipods (*Phoxocephalus holbolli*, *Leptocheirus pinguis*, *Psammonyx nobilis*, and *Orchomenella minuta*) that burrow in the sediments during low tides. Quantitative samples are readily obtained by sieving the substrate from quadrats.

The meiofauna has not been studied in the Quoddy Region and thus is almost completely unknown. This is probably due to (1) the belief that a meiofauna is impoverished in glaciated areas, (2) the lack of well-sorted, oxygenated, sand beaches where this type of fauna has usually been looked for, and (3) the lack of tradition, as that which has developed in western Europe, for such studies. Nevertheless, an abundant fauna has been found in the Arctic in Spitzbergen (Gerlach 1965) and a cursory examination of sediments under the microscope readily reveals the presence of many small organisms, such as nematodes, showing that a meiofauna exists and its study would repay investigation.

Much of the interest in the meiofauna stemmed from the discovery that it is diverse and contains undescribed types of organisms. The adaptations that the meiofauna require for life in the interstices between particles, such as small size (0.2–3 mm) and elongate shape, have also aroused interest. More recently, studies have been extended to the anaerobic black layer in the sediments, with the realization that it also contains a previously unknown specialized fauna of its own. There are several excellent reviews of the meiofauna (Fenchel 1978; Fenchel and Riedl 1970; Swedmark 1964; McIntyre 1969; Hulings and Gray 1971) so only a brief summary is presented here.

Almost all types of marine animals — from protozoans to ascidians — have been found to have meiobenthic forms, but the dominant groups are the nematodes and the ciliated Protozoa. The novelties include the gnathostomulids (Platyhelminthes), archiannelids (Polychaeta), and mystacocarids (Crustacea).

The occurrence of various kinds of meiofauna is related to the size of pores in the sediment and hence to the texture. According to Fenchel (1978) a true interstitial fauna exists only with a median grain size greater than 100 μm in a well-sorted sediment. In finer sediments, or with the addition of significant quantities of silt and clay, the only forms likely to be present are nematodes, since they are able to burrow. A variety of other organisms may occur on the surface. With grain sizes between 100 and 200 μm the ciliated Protozoa dominate, but many nematodes also are found. In sediments with grain sizes larger than 200 μm, the ciliates and nematodes may be accompanied by a diverse array of other types of meiofauna.

Except for the plunge zone, where the waves break on exposed coarse-textured beaches, aerobic sediments rest on black anaerobic sediments. This sulphide-system

FIG. 7. Pocologan. A small pocket sand beach with rounded boulders on the upper portion in the foreground.

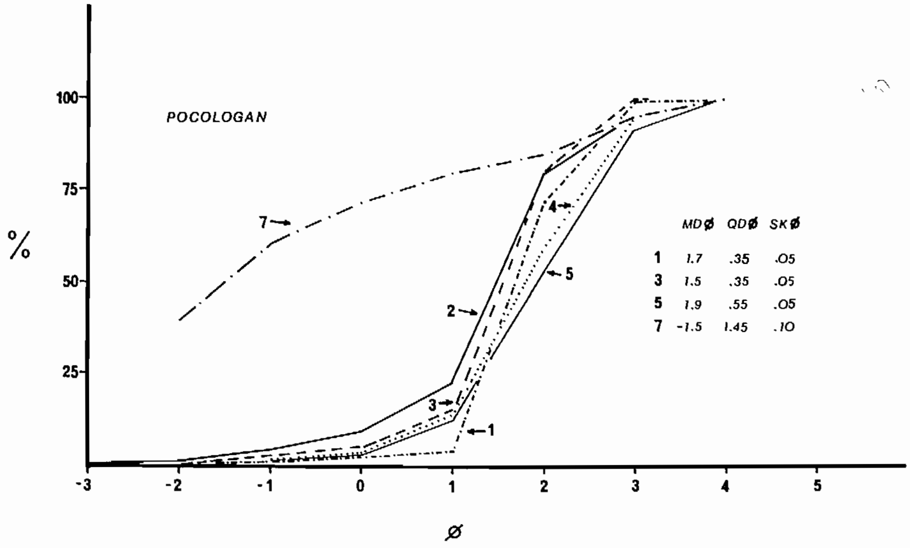

FIG. 8. Textural analysis of the sand at Pocologan.

rises towards the surface with increased protection and fine grains. The sulphide-system used to be considered lifeless except for anaerobic microoorganisms, and was largely ignored. Recent studies summarized by Fenchel and Reidl (1970) and Fenchel (1978), however, show it to have a reasonably diverse community living in a rather peculiar but very widespread habitat. All higher plants and most groups of metazoans (including all arthropods) are absent but certain groups of invertebrates — such as flatworms, nematodes, oligochaeta, and gastrotrichs — are present, especially near the oxidized layer at the redox-potential discontinuity. It is not certain if many of the species are truly anaerobic or simply "dive" into the sulphide-system. Present also are fungi, protozoans, and particularly procaryotes such as blue-green algae and bacteria. According to Fenchel and Reidl (1970), "The more the sulphide-system displaces the oxidized psammon, the more broadly the 'plant' subsystem establishes itself."

Since the meiofauna are small in size and plentiful, a small core of substrate will usually yield enough specimens. A clear plastic tube 3–4 cm in diameter is forced into the sediment to a depth of 25–30 cm and withdrawn with its enclosed core. If only the aerobic fauna is required and the sediments are fine, the depth sampled need only be shallow. Since the sediments often show marked variation in fauna, texture, and other qualities with slight differences in depth (see for example Jansson 1967) the core should be extruded and sectioned into samples shortly after it is obtained so that the fauna does not have a chance to redistribute itself.

Extraction of the animals from the sample of substrate is difficult, especially as many species are fragile and may have to be examined alive if they are to be identified. Hulings and Gray (1967) described methods for a variety of organisms in their review.

Description of Selected Beaches in the Quoddy Region

The following accounts are brief descriptions of some of the fauna and environmental properties of beaches in the Quoddy Region. Due to the high tidal range, only portions of the total intertidal were usually examined. These accounts are incomplete, as in most cases only the macrocrustacea were examined in detail. A checklist of the flora and fauna of the Bay of Fundy has been provided by Linkletter et al. (1977).

POCOLOGAN

This is a small pocket beach (Fig. 7) consisting of well-sorted, medium sand at all levels except station 7 where coarse, poorly sorted, gravelly sand was found at about the plunge point of the waves (Fig. 8). The amount of sand on the beach was small and there was no berm or supratidal fauna. The only organisms found were the isopod, *Chiridotea coeca* in the intertidal and the amphipod, *Gammarus*[1] *lawrencianus* where a small stream crossed the beach (Fig. 9). At other locations in the Quoddy Region, *Chiridotea tuftsi* has been found below LWN and in the subtidal. Only *Psammonyx nobilis* occurred below low water neap.

BRANDY COVE, ST. ANDREWS

The distribution of the fauna and flora was examined along a transect across the lower portion of the intertidal, i.e. in the rockweed zone and below (Fig. 10, 11). Much of the following description is taken from Steele (1964).

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[1] Species of this genus have been placed in a great number of genera in recent years but until there is some concensus among taxonomists it seems best to place them in *Gammarus sensu latu*.

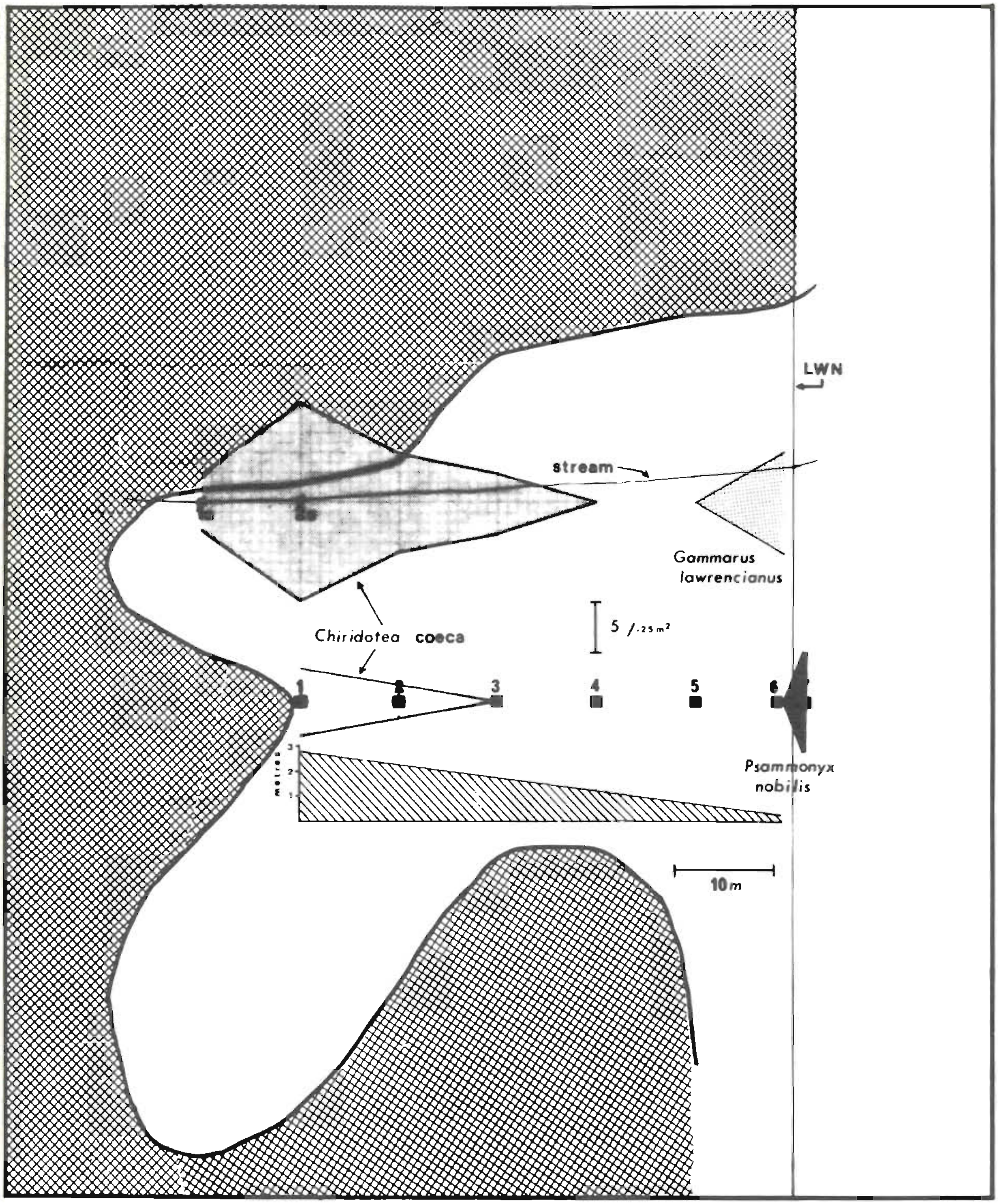

FIG. 9. The distribution of macrocrustacea at Pocologan (July 28, 1962). Samples were obtained on two transects down the beach. One transect traversed a small stream. LWN, low water neap.

FIG. 10. Brandy Cove, St. Andrews. Samples were obtained along a transect extending from the cliff on the right to the level of low water.

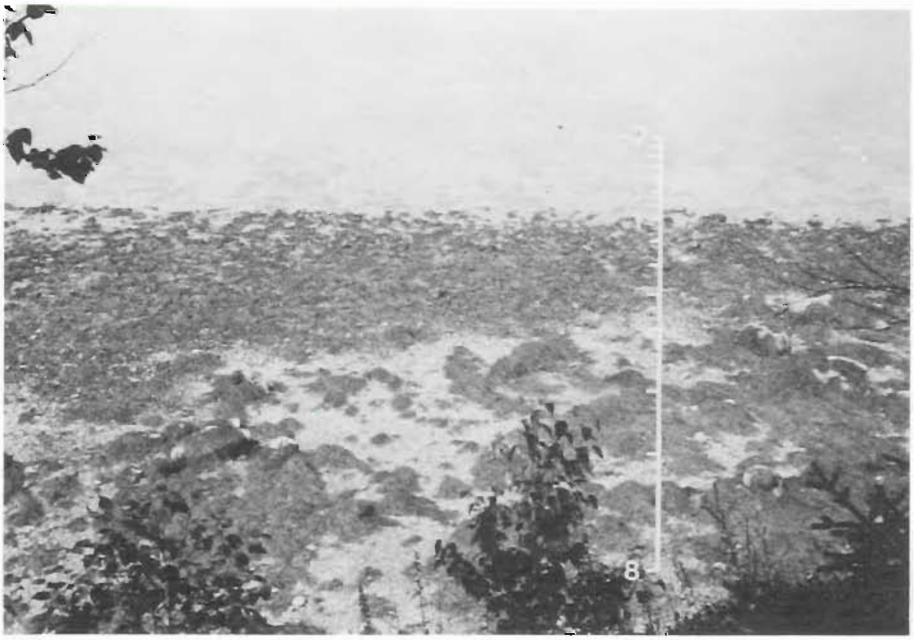

FIG. 11. Brandy Cove, St. Andrews, looking downwards along the transect from the cliff at the top of the beach. The lower stations are submerged.

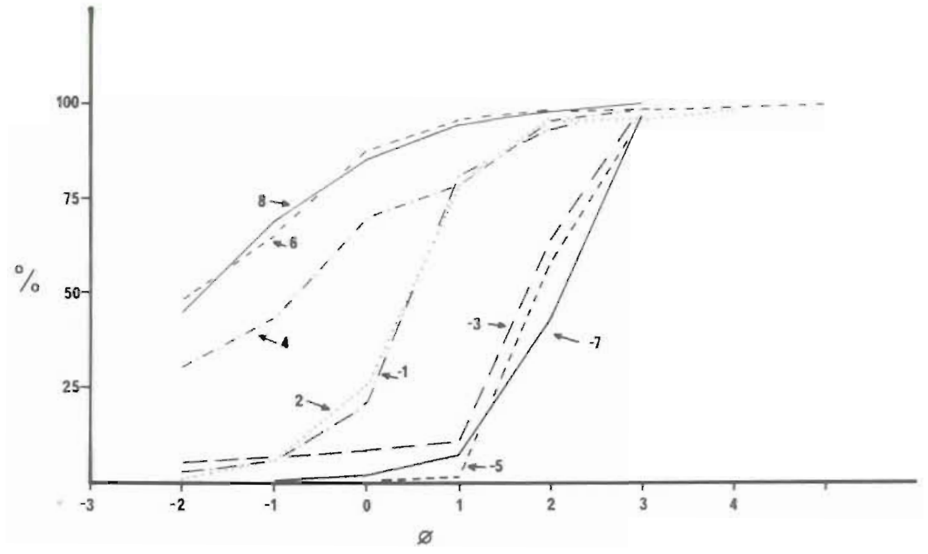

FIG. 12. Textural analysis of the matrix and sand at Brandy Cove.

FIG. 13. Cliff above station 8 with *Ascophyllum nodosum*.

FIG. 14. Station 7 imbedded cobbles with *Balanus balanoides* and *Littorina littorea*.

FIG. 15. Station 5, 6; imbedded cobbles with *Balanus balanoides* and *Mytilus edulis*.

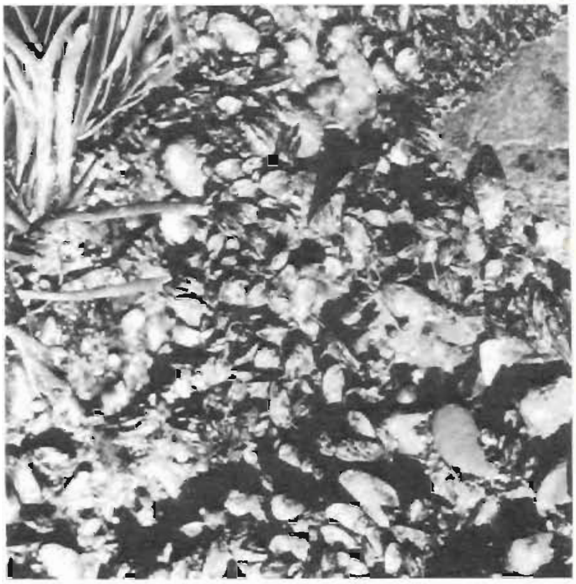

FIG. 16. Station 1, *Mytilus edulis* clumps.

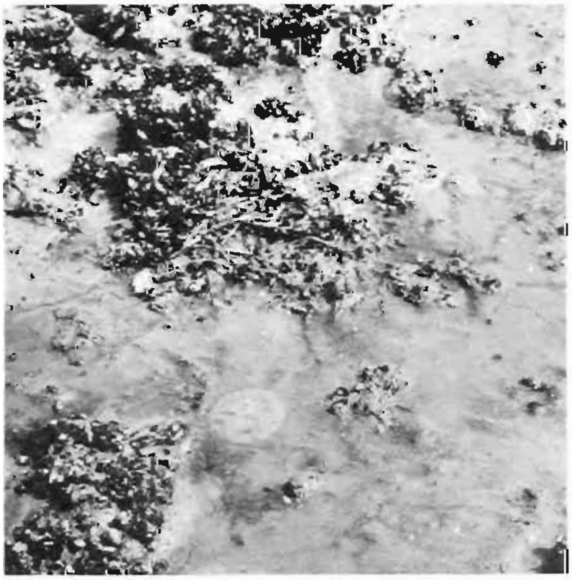

FIG. 17. Station 2, 3; sand with *Mytilis edulis* on imbedded rocks. Coverage by rockweeds is low.

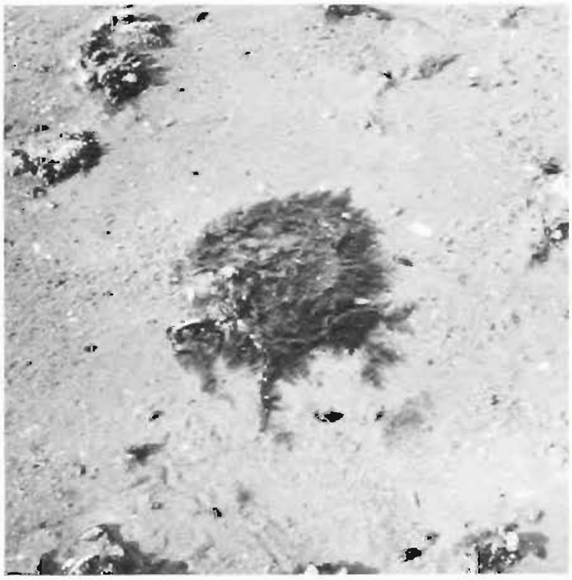

FIG. 18. Station 2; sand with *Pylaiella littoralis*. Imbedded cobbles are outlined by rings of *Mytilis edulis*.

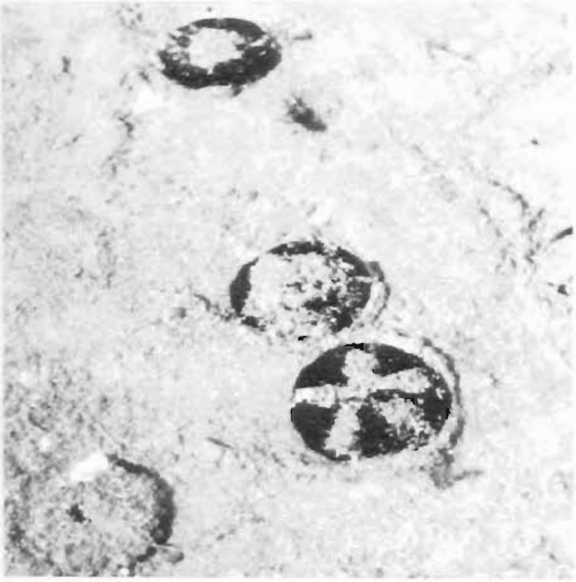

FIG. 19. Station 5; sand with *Echinarachnius parma*.

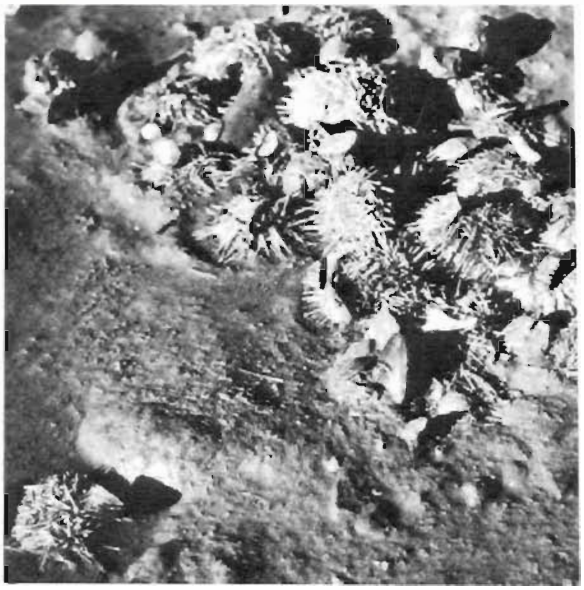

FIG. 20. Station 3; sand with *Strongylocentrotus droebachiensis*.

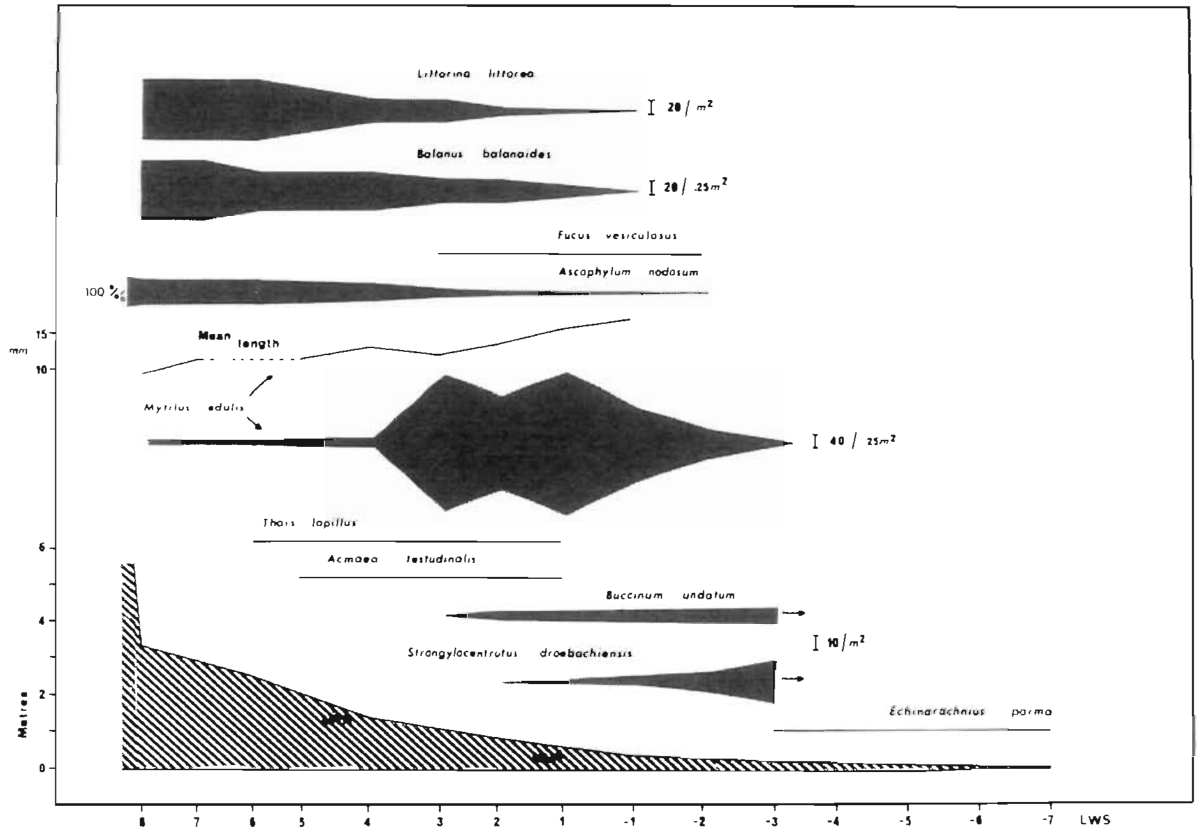

FIG. 21. Distribution of selected species of the flora and fauna at Brandy Cove (1960–1962).

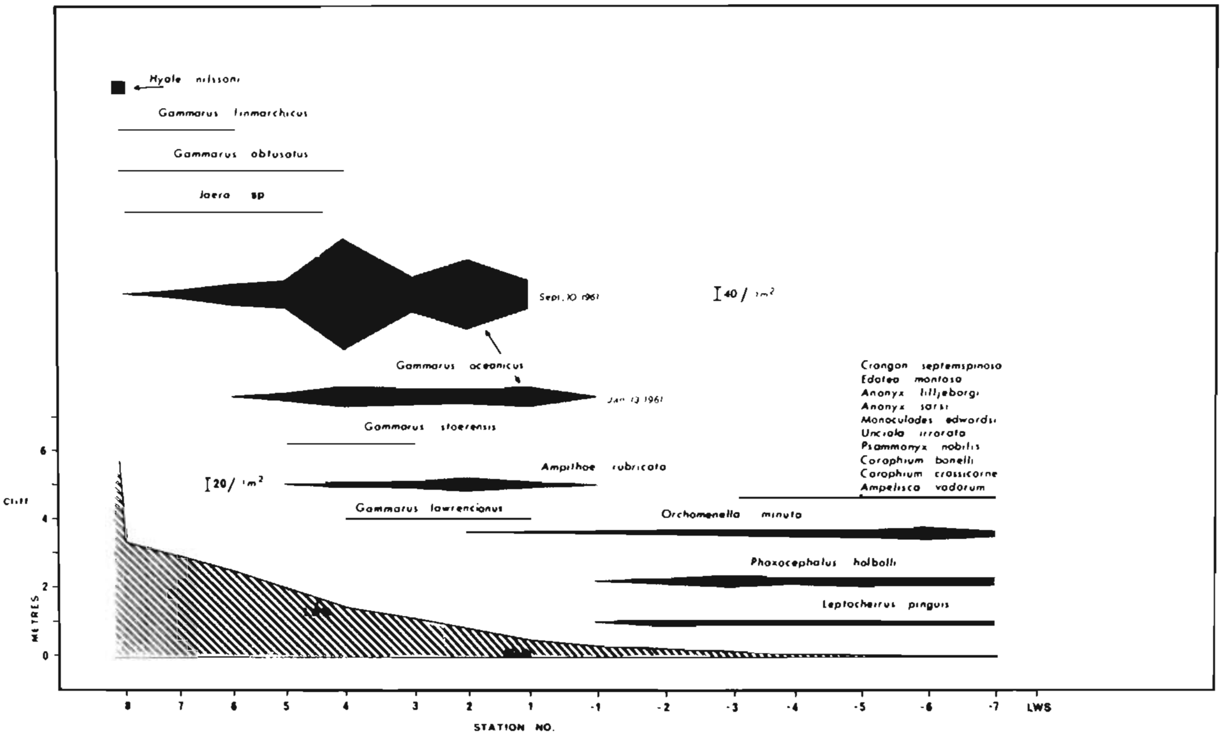

FIG. 22. Distributions of amphipods and isopods at Brandy Cove (Sept. 5, 1960), except *Gammarus oceanicus*. Only female *Jaera* were collected and could not be identified to species.

Above LWN the substrate consisted of boulders and cobbles embedded in a gravel matrix. This matrix tended to decrease in size from station 8 down to station −1. The lower stations had substrates of fine sand (Fig. 12).

The distribution of the fauna and flora is similar to what was described by Newcombe (1935) and Wells (1974) and is probably typical of much of the Quoddy Region. The upper portion is dominated by rockweeds, mainly *Ascophyllum nodosum*, with many *Balanus balanoides* and *Littorina littorea* (Fig. 13, 14, 15, 21). *Mytilus edulis* was most abundant and also most conspicuous between Sta. 3 and −1 (Fig. 10, 11, 16, 17, 18 and 21). Their mean size increased from Station 8 to Station −1 (Fig. 21). Despite the abundance of mussels and barnacles, the dog whelk (*Thais lapillus*) was present in relatively small numbers, probably because of the sheltered exposure of the site. The lower stations with a substrate of sand were sparsely populated at low tide. The edible whelk (*Buccinum undatum*) occurred on the lower portion but according to Gowanloch (1926) is poorly adapted for emersion and may not survive exposure in the spring-tide period. The green sea urchin (*Strongylocentrotus droebachiensis*) (Fig. 20) was abundant but the sand dollar (*Echinarachnius parma*) (Fig. 19) and the sand shrimp (*Crangon septemspinosus*) (not shown) were present in relatively small numbers (Fig. 21).

The fauna of isopods and amphipods along the transect was diverse (Fig. 22). The most abundant species, as is typical of this type of stable cobble-boulder substrate, is the amphipod, *Gammarus oceanicus*, which reached its maximum abundance and extended to its highest level on the beach in September (Steele 1964). In the winter it retreated downwards, as it also does in Newfoundland (Steele 1976). *Gammarus obtusatus* was found at a slightly higher level, also under the cobbles, whereas *Gammarus finmarchicus*, *Hyale nilssoni*, and an unidentified species of *Jaera* were associated with rockweeds.

Gammarus stoerensis and *Gammarus lawrencianus* were both found at about LWN and were probably associated with seepage of ground water at this level. Their occurrence in various seasons was erratic. *Ampithoe rubricata* was found amongst the clumps of *Mytilus edulis*.

The lower portion of the beach, with a substrate of fine sand, contained a diverse assemblage of burrowing species normally found in the subtidal. The most abundant species were *Orchomenella minuta*, *Phoxocephalus holbolli*, and *Leptocheirus pinguis*.

FIG. 23. Bar Road, St. Andrews; the beach flat looking towards low water. The beach remains saturated at low tide and lacks ripples. The black mounds are masses of algae (*Pylaiella littoralis*).

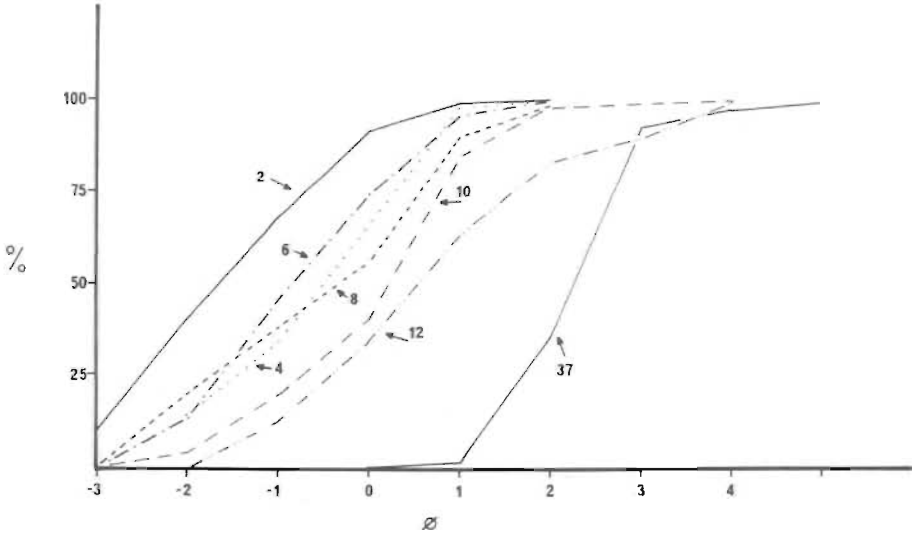

FIG. 24. Bar Road, St. Andrews; textural analysis of the matrix and the sand.

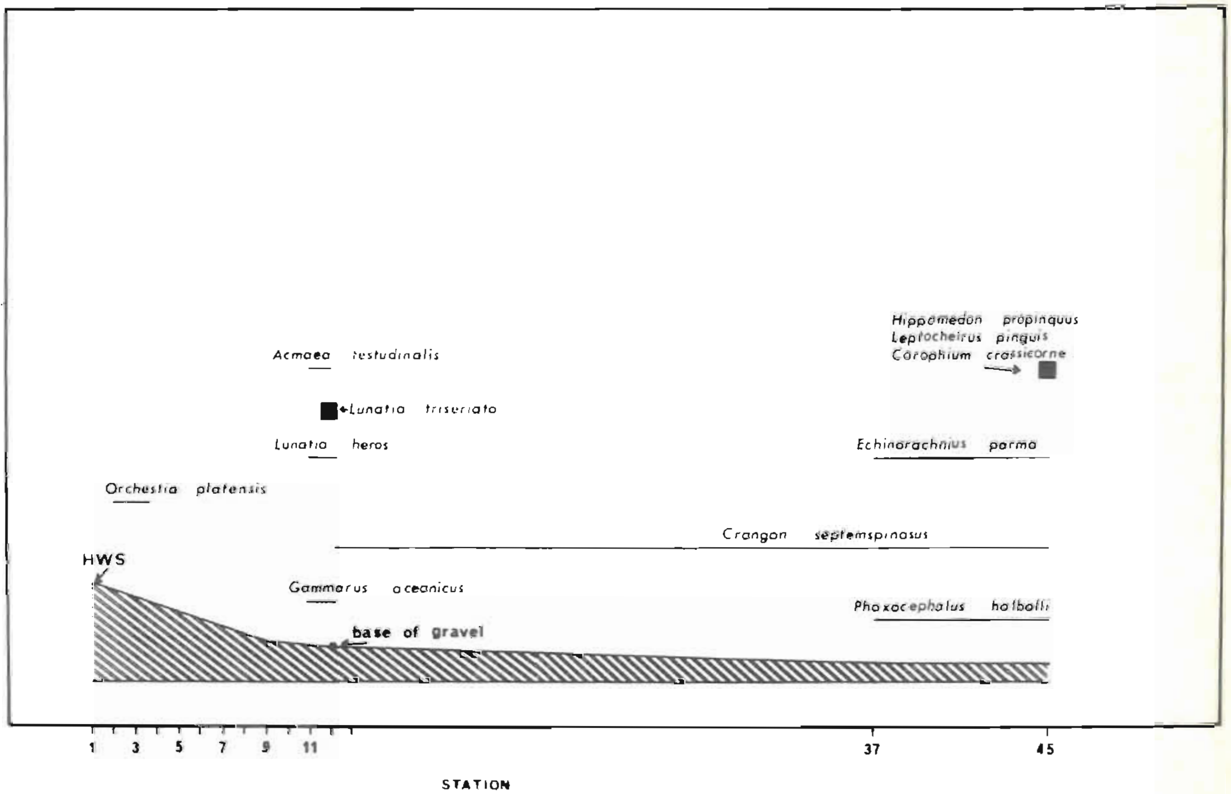

FIG. 25. Bar Road, St. Andrews; the distributions of selected organisms (Sept. 3, 1960). The profile was not measured and is schematic. As only a few samples were obtained on the flat the distributions are incomplete. HWS, high water spring.

FIG. 26. Pottery Brook, St. Andrews. The stream crosses the beach from the left. High water is indicated by the logs. A small amount of salt marsh vegetation is in the foreground. Collections were made at a series of stations along the stream.

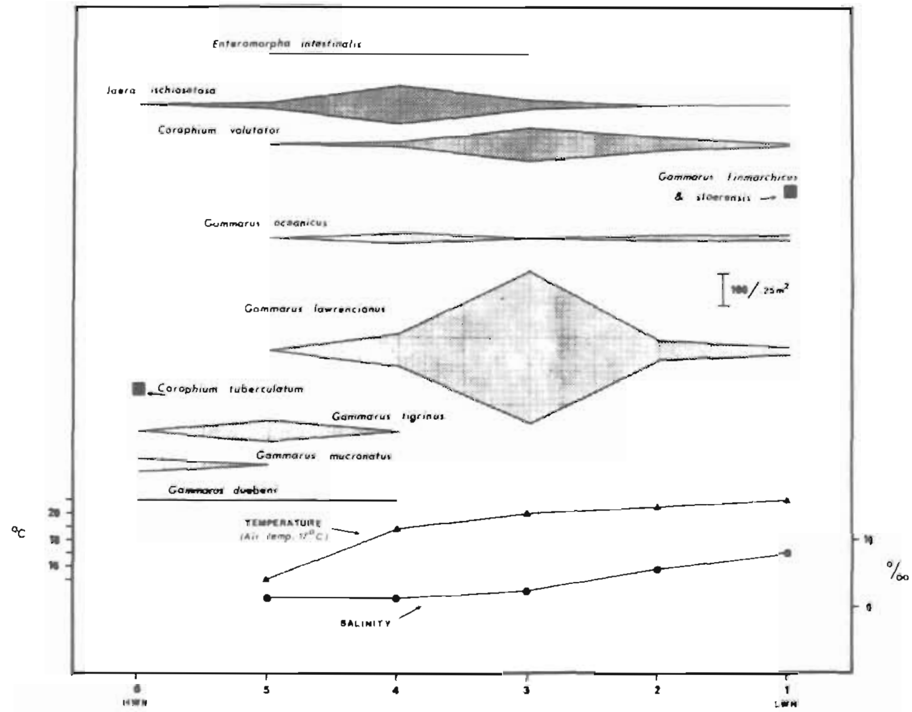

FIG. 27. Distributions of selected species in the intertidal portion of Pottery Brook (Aug. 19, 1962). *Corophium volutator* was collected in the mud beside the brook.

FIG. 28. Bocabec Cove. A small stream drains from the hill from which the picture was taken and flows over the beach.

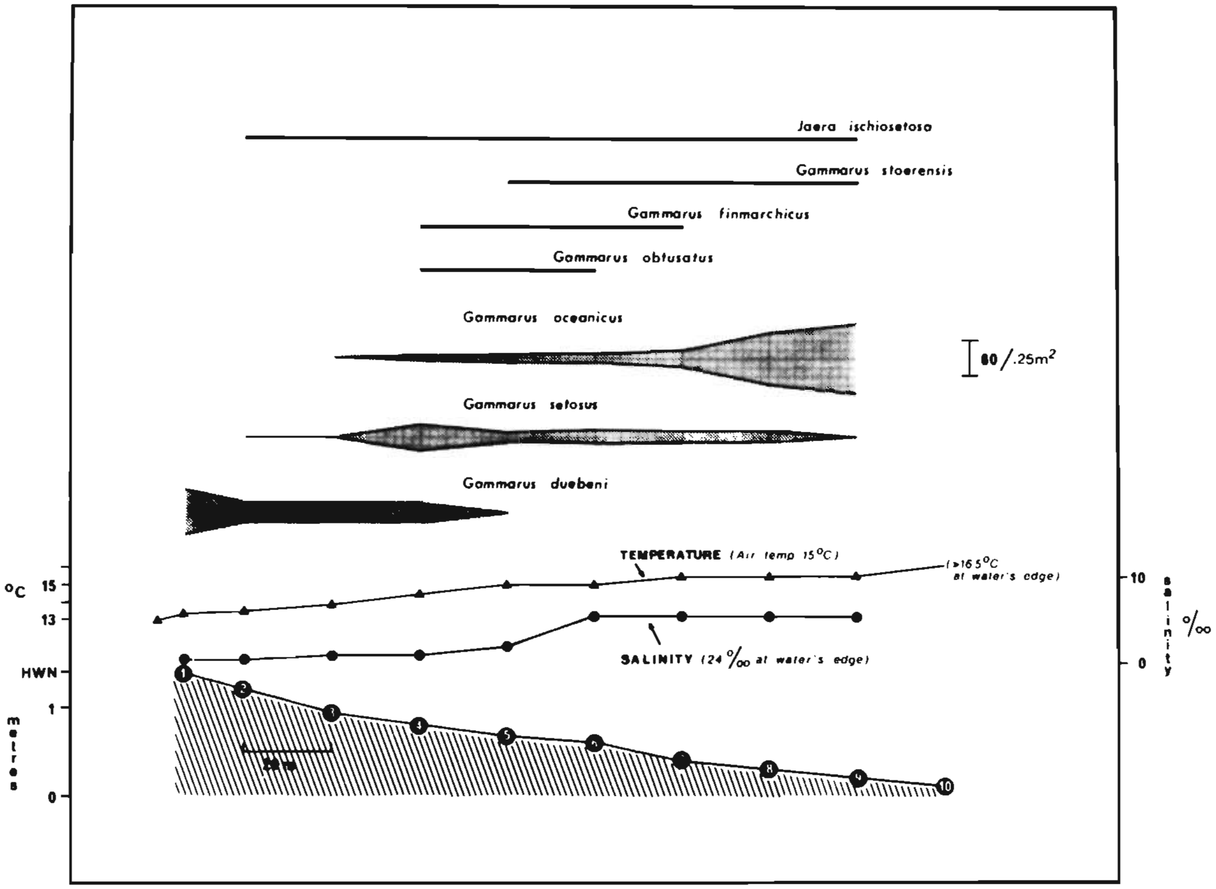

FIG. 29. Distributions of selected species at Bocabec Cove (Aug. 5, 1962). HWN, high water neap.

BAR ROAD, ST. ANDREWS

This beach is similar to that of Brandy Cove or Indian Point, with a steeply sloping coarse-textured upper portion; but this ends abruptly at the fine-textured flat (Fig. 23). The particle size of the matrix on the slope decreased with elevation (Fig. 24). Only animals associated with the drift lines at high water, such as *Orchestia platensis*, were found on the upper part of the beach (Fig. 25). A few other species, such as *Gammarus oceanicus* and *Acmaea testudinalis*, were associated with the rocks near the base of the slope near LWN.

Below low water neap the sediment is a fine sand with a very gentle slope (Fig. 23). The sand remains saturated at low tide and supports a variety of typically subtidal species. Sand dollars (*Echinarachnius parma*) were abundant and sea urchins rare in contrast to Brandy Cove.

POTTERY BROOK, ST. ANDREWS, AND BOCABEC COVE

These sites are representative of those with fresh water streams flowing over the beach. Pottery Brook (Fig. 26) is larger and open above the beach; thus the water temperatures were higher and the flow of water greater. These factors are correlated with the occurrence of the estuarine species *Gammarus tigrinus*, *Gammarus duebeni*, *Gammarus mucronatus*, *Corophium tuberculatum*, and *Jaera ischiosetosa* and the abundance of *Gammarus lawrencianus* (Fig. 27).

At Bocabec Cove the stream is smaller (Fig. 28) and is enclosed by vegetation until it starts to cross the beach. Thus the water is cooler, especially in its upper portion, and this possibly explains the presence here of *Gammarus setosus*. From the Arctic to Newfoundland *Gammarus setosus* occurs in the same habitat as *G. oceanicus*, i.e. under rocks, but south of Newfoundland to Maine it is only at sites with fresh water influence, such as Bocabec Cove. Both at Bocabec Cove and farther north to Labrador *Gammarus setosus* is slightly higher on the beach than *Gammarus oceanicus*. The only estuarine species at Bocabec Cove were *Jaera ischiostosa* and *Gammarus deubeni* (Fig. 29).

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CHAPTER 6

Tide Pool Systems

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General Introduction

Chapter four of this book covers the rocky intertidal community and it may be considered that rock pools should have been included therein. However, detailed study has shown that tide pools are a completely separate system from that of the rocky shore. Rock pools have different physical, chemical, and biotic structures and functions which make them unique. They form a sort of intermediate situation between the coastal sea and the well-drained intertidal zone, and thus give insights into factors controlling the structure and function of these two bordering systems. For instance, they show the importance of the desiccation factor on the open shore; they are also ideal for observing pH and buffering phenomena, as well as all types of diel and annual changes in environmental parameters and environmental and biological interactions in coastal waters.

N. J. Berrill, one of the fathers of marine biology in Canada, wrote: "If you look into a tide pool and comprehend what you see, you are observing the universe" (Berrill 1951). While there is much poetic license in this statement, Berrill was emphasizing the amazing diversity of life and the wealth of physical, biological, and chemical processes going on there, and amenable to study. These attributes of tide pools make them ideal objects for a wide variety of student projects. Their generally manageable proportions and simple ecosystems, at least compared to sublittoral ones, mean that thorough projects in tide pools can be undertaken in a short period.

However, there are also disadvantages in studying tidal pools. They owe their existence to the tides and most are inundated twice daily by seawater; thus observations and projects must be carefully timed. Although the pools best suited for study are in the upper intertidal, lower pools show greater biotic diversity and closer similarities with the coastal ocean. While the two simultaneous rhythms of tide and light may generate study problems, they dictate many dynamic processes in pools, demonstrating the extent of interaction between tidal pools and both marine and terrestrial systems.

Although there is a wealth of information on seashores, there is a paucity of information on tidal pools, particularly their functional aspects. There are no texts on pools and those on shores in general (Amos 1966; Carefoot 1977; Clayton 1974; Lewis 1964; Southward 1966; Stephenson and Stephenson 1972; Yonge 1949) provide little critical information about tidal pools. This undoubtedly results from the scarcity of scientific papers on tidal pools. This material has been most recently summarized by Ganning (1971) and includes only two studies of the Bay of Fundy region, those of Klugh (1924) and Bell (1927). Both studied a series of tide pools in front of the Biological Station St. Andrews, in an area now virtually obliterated by wharf and slip construction. Other regional studies are those of Williams and Williams (1976) on pools on the St. Lawrence northshore, Johnson and Skutch (1928) on pools in Maine, Sze (1980) on macrophytic algae at the Isles of Shoals, and Lubchenco (1978) on plant species diversity in tide pools in New England and on the Bay of Fundy.

The Tide Pool Ecosystem

CLASSIFICATION OF TIDAL POOLS

Despite the great variety of tidal pools, they fall into several distinct groups based on their position on the shore, their predominant water supply, and their frequency of receiving new water. Despite these natural groupings there have been few attempts to define a classification system. Most workers have been content with broad categories such as high and low (Batzli 1969) or supralittoral, littoral, and sublittoral (Gislen 1930). Other workers, such as Levander (1900), have devised systems that are more definitive but apply only to a limited geographic area. The most useful general classification is that of Forsman (1951) as modified by Ganning (1971). This classification, however, stresses pools at high intertidal and supralittoral (above high water of spring tides) levels, and the coasts where Forsman and Ganning have been working have a very small tidal amplitude. Further modification of the Forsman–Ganning system is needed to give a more generally applicable scheme. The system outlined below incorporates these modifications.

Type I: permanent saltwater pools — These pools receive seawater by tidal or frequent wave action so that their abiotic conditions resemble those in coastal waters. They lie either between mean high and low waters of spring tides or slightly above this zone where seawater gains frequent entry by wave action. They do not have a large regular influx of fresh water. Size is not critical but does affect variability.

Pools of type I show a marked gradient of characteristics depending mainly on their height in relation to mean low water but modified by their surface-to-volume ratio, a parameter which will be discussed below. These pools may be subdivided as follows:

Type IA, lying low on the shore below mean low water of neap tides;
Type IB, lying low on the shore between mean low water of neap tides and mean tide level;
Type IC, lying high on the shore between mean tide level and mean high water of neap tide; and
Type ID, lying high on the shore above mean high water of neap tides but receiving regular additions of sea water by wave and/or tide action.

All type I pools have a biota characterized by predominantly intertidal and just subtidal species. They show maximum interaction with the marine system. The majority of type I pools form in rock, as physical characteristics of sedimentary shores result in generally smooth slopes and porous substrata which do not support pools. However, varying amounts of sediment may be present, especially in pools sheltered from heavy wave action.

The species most typical of type I pools in the Quoddy Region are shown in Table 1 which includes only species attached to or living wholly within the pools. Another group of algae, notably *Ascophyllum nodosum* and *Fucus vesiculosus*, almost always dangle into pools, and species such as *Fucus edentatus*, *Fucus evanescens*, and *Fucus spiralis* do so occasionally. The highest type ID pools in exposed locations usually harbor dense growths of *Fucus distichus*.

Table 1 shows a considerable diversity but a further 103 species or varieties have been recorded from these same pools. Type I pools have a vastly greater diversity than other types. Within type I pools diversity generally decreases with increasing tidal height.

Type II: ephemeral salt water pools — These are situated high on the shore above high water of neap tides. Their source of water is infrequent wave, spray, or tidal input. They are either very small or have a high surface area:volume ratio and hence dry out periodically. Abiotic factors are variable, salinity frequently being very hypersaline. There is no regular freshwater input.

Biota are very limited, being mainly the green alga, *Enteromorpha intestinalis*, which is characteristic, the blue-green alga, *Rivularia atra*, blue-greens of the *Nostoc* sp. complex, and lichens of the genus *Verrucaria*. Animals are even more limited and most are not resident. The gastropod *Littorina saxatilis* is frequent, as is the turbellarian *Woodsholia lillei*. Insect larvae of *Eristalis* sp. occur less commonly.

Type III: Brackish-water pools — Like type II pools these are high on the shore, usually above mean high water of spring tides. The saltwater supply is from splash or spray and is infrequent. Fresh water is regularly added by runoff, seepage, or rain and hence type III pools are characteristically hyposaline. Type III pools vary widely in size and surface:volume ratio, but if small, or shallow, a regular water supply is needed.

Brackish-water pools have unstable abiotic conditions and biotic diversity is low. Additionally, some deposition of sediment is usual, reducing macroalgal colonization. The green alga, *Enteromorpha intestinalis*, is the characteristic species, often being an almost monospecific mass. Where much sediment is present, the flowering plant *Ruppia maritima* is common. The fauna is depauperate but ostracods, copepods, and turbellarians are frequent as are lymnaeid snails and the three-spined stickleback, *Gasterosteus aculeatus*.

Type IV: permanent fresh water pools — These lie very high on the shore, above extreme high water of spring tides. They are, however, under marine influence and receive some seawater in the form of spray. In exposed locations, such as the outer islands of the Deer Island Archipelago, such pools may be high above sea level. All receive a regular or continuous supply of fresh water by runoff or seepage. Size is variable but some sediment deposition is usual. Although these are marine pools, they are generally characterized by oligohaline freshwater species. Vegetation is typically dominated by vascular plants such as the burr reeds (*Sparganium americanum* and *S. angustifolium*), the cattail (*Typha latifolia*), and rushes and reeds such as *Juncus balticus* and *Scirpus americanus*. The fauna is most frequently water boatmen (*Corixa* spp. and *Notonecta* sp.) as well as various beetles and lymnaeid snails.

TABLE 1. Most common species found in type I tidal pools in the Quoddy Region, and frequency of occurrence in 62 pool studies.

Group and species	Frequency (%)
Chlorophyta	
Enteromorpha intestinalis	52
Monostroma sp.	34
Cladophora sp.	6
Phaeophyta	
Asperococcus echinatus	13
Ectocarpus sp.	26
Petalonia fascia	24
Punctaria sp.	6
Scytosiphon lomentaria	23
Rhodophyta	
Chondrus crispus	50
Gigartina stellata	8
Hildenbrandia prototypus	44
Lichens	
Verrucaria sp.	13
Platyhelminthes	
Notoplana atomata	10
Nemertea	
Lineus ruber	24
Mollusca	
Acmaea testudinalis	42
Hydrobia minuta	27
Littorina littorea	81
Littorina obtusata	52
Littorina saxatilis	71
Thais lapillus	55
Macoma balthica	19
Mya arenaria	32
Mytilus edulis	65
Polychaeta	
Potamilla neglecta	8
Crustacea	
Balanus balanoides	66
Carcinus maenas	13
Gammarus oceanicus	92
Jaera marina	13

Type V: ephemeral freshwater pools — These pools, almost invariably small and shallow, are situated high on the shore in the splash zone. They receive small amounts of seawater as spray and larger but inconsistent amounts of fresh water as rain or surface runoff. The pools often dry out and consequently range from almost fresh to a saturated salt solution. Conditions for life are extremely harsh and consequently these pools are often devoid of all macrobiota.

ENVIRONMENTAL CONDITIONS IN ROCK POOLS

The environmental characteristics of tidal pools show extreme variability. The degree of variability differs with pool type and also with its surface:volume ratio, which is an important factor: where this is high, variability is greatly enhanced. Also important is the direction of exposure and the surrounding topography of the pool, as both may modify insolation and exposure to wind. The nature of the pool bottom and the quantity and nature of biotic pool communities also have pronounced effects (Ambler and Chapman 1950; Chapman 1964; Ganning 1971; Klugh 1924; Stephenson et al. 1934).

Pools also vary on annual, diel, and tidal cycles, the latter being particularly important in lower level pools. In pools inundated by the tide, there can be dramatic and virtually instantaneous changes as tidal water enters. Higher pools show less or no tidal influence but usually more pronounced annual and diel changes.

Unfortunately there have been few long-term studies of rock pool systems except those of Ganning (1971) in Sweden, Ambler and Chapman (1950) in New Zealand, Pyefinch (1943) in Wales, and this study in the Quoddy Region. Further study will undoubtedly show tidal pools to be more variable than is now realized.

The main variables in tidal pools are as follows:

Salinity — The total range of salinity in tidal pools is from fresh water, 0‰, to saturated sea water, over 300‰. However, only type V pools would exhibit this total range.

Salinity in rock pools may be determined or altered in four main ways: addition of seawater, evaporation, addition of fresh water, and freezing. In addition Ganning (1971) has shown that pools high on the shore may have their salinities increased or decreased by rain. Increase in salinity was shown to occur in type IV pools following slightly saline rain during onshore wind.

Pools receiving an input of fresh water from runoff or rain may show pronounced stratification of salinity, particularly in very calm conditions. One type IC pool at St. Andrews has repeatedly shown almost fresh surface water overlying water of 26–28‰ at the bottom, despite its shallow depth (only 8–10 cm). Figure 1 shows a typical salinity profile of this pool with a very sharp halocline. Such pools normally exhibit distinctly different algal communities in the two layers.

However, most type I pools normally show little variation in salinity during their comparatively short exposure periods, except in torrential rain. Even then, bottom waters remain virtually at constant salinity, normally 26–30‰ in the Quoddy Region. By contrast, types II and V pools show great variations, the changes usually occurring rather quickly when compared to other marine environments. Ganning (1971) found rates of 1–5‰/wk in large high-volume pools but 1–5‰/d in small and high surface area:volume ratio pools. Ganning points out that these high level pools also show a different ionic composition to seawater; magnesium and bicarbonate levels are often high, as are phosphorus and ammonia.

Freezing increases the salinity of tidal pool water because the salt content of the ice is always reduced. During freezing, stratification frequently occurs as the ice cover effectively ensures calm conditions and allows high-salinity water forming at the ice–water interface to sink with little mixing. Similar situations exist when ice melts and the fresh water pools at the surface. Surface to bottom differences in ice-covered pools may exceed 10‰ (Ganning 1971).

The salinity extremes recorded for pools might be expected to place great stress on the biota. However, the salinity changes usually occur very slowly; and where they occur rapidly, as in a stratifying pool, they can be avoided (Newell 1979; Ganning 1971). Ganning concludes that all permanent members of tidal pool ecosystems are able to tolerate or avoid much wider flutuations in salinity than those found naturally in pools.

Temperature — In all pools except type I, the overwhelming influence on temperature is air temperature. Solar radiation is also important. Type I pools tend to approach air temperature when exposed but are at ambient sea temperature when submerged. In all pools the surface:volume ratio will be proportional to the rate of change toward atmospheric conditions. There is, of course, some temperature buffering by the rock around the pool. In pools with low surface:volume ratio, low on the shore, this effect may hold temperature close to that of the sea. Temperatures in all exposed pools may be decreased slightly by evaporative cooling. Those with shallow dark bottoms and/or abundant vegetation tend to be quickly warmed by insolation.

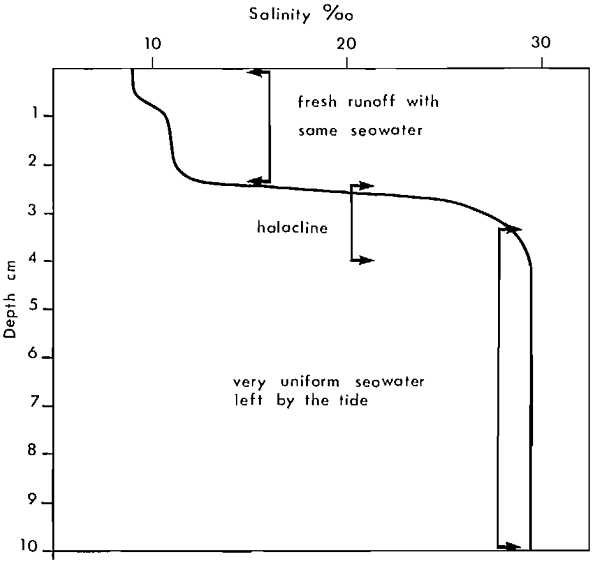

FIG. 1. Salinity–depth profile of pool 4 at Holey Point at 1655 h, April 29, 1980, 3 h after isolation by the tide.

Surface waters of pools show the greatest variation on annual or diel bases. In the Quoddy Region the greatest 24-h range in a type I pool was 3.5–20°C in April. In Sweden, Ganning (1971) found daily ranges up to 15°C and Pyefinch (1943) found differences of up to 12.5°C in Wales. In New Zealand, Ambler and Chapman (1950) recorded variations up to 15.5°C. Greater differences undoubtedly occur. On an annual basis, of course, ranges are much greater. Type I Quoddy pools have been found to range from −0.7 to 30.0°C. In Maine, Femino and Mathieson (1980) recorded an annual range of −6–31°C in a type II pool. Ganning (1971) recorded a similar range of 0–32°C in Sweden. In more temperate locations annual ranges are less, as in Japan (18–35°C, Utinomi et al. 1950) and in the Mediterranean (4–25°C, Vacelet 1969). Maximum temperatures of up to 42°C are found in tropical areas (Pearse 1932) but diel and annual ranges tend to be moderate.

In the Quoddy Region, where seawater temperatures remain cool (Chapter 2), rapid temperature reductions may occur on tidal flooding in summer. The temperature of a pool studied in July 1974 fell from 24.7 to 12.7°C in 5 min when the tide reached the pool (Fig. 2).

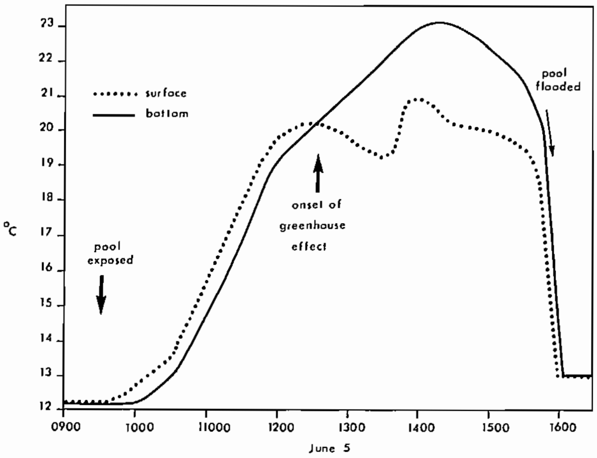

FIG. 2. Surface and bottom temperature regime of pool 4 at Holey Point from 0900 h to 1630 h, June 5, 1980.

In Quoddy pools, temperature stratification is rare except where salinity stratification has become established. Most pools are isothermal. Both surface cooling and insolative heating tend to create unstable density structures and thus mixing occurs. In other areas workers commonly found temperature stratification in isohaline pools during the day. This would be expected where direct heating by air is dominant.

An interesting phenomenon, which is often encountered in pools with reduced salinity surface layers, is inverse temperature stratification. This effect, known as the greenhouse effect, results when the saline deeper waters are heated by the sun through the fresh surface layer. The effect is most pronounced where the surface layer is flowing across the pool. In one such pool at St. Andrews, bottom water temperatures often rise to 4.5°C above surface temperatures on bright days. Much greater differences are possible. Figure 2 shows surface and bottom water temperatures in a stratified pool and the effect of tidal flooding.

Dense algal growths in pools may raise temperatures (Clark 1968) or lower them (Ganning 1971).

Temperature ranges in rock pools seldom exceed the abilities of inhabitants to withstand them. However, fauna and flora often show clear optima of activity within the range of the pools (Ganning 1971; Newell 1979).

Dissolved oxygen — Oxygen is released into pool water by autotrophic plants when the ambient light intensity rises above the compensation level. In all other natural situations oxygen shows a net utilization by all macroorganisms. Oxygen levels therefore tend to rise by day and fall at night. Wherever pool concentrations are out of equilibrium with the air, oxygen will enter or leave across the water–air interface at a rate dependent upon the difference in oxygen levels and the temperature, air, and water movement at the surface: Saturation levels are inversely proportional to temperature: thus very warm pools at night are most likely to have very low oxygen levels. In the Quoddy area concentrations below 2.4 ppm (about 27% saturated) in type I pools are rare and are usually accompanied by rotting algae. In other areas oxygen levels apparently remain well above this level. Pyefinch (1943) found no levels below 95% saturation and Utinomi et al. (1950) recorded minima of 90% in Japan. In Sweden, Ganning (1971) measured as low as 0.06 mg 0_2/L or 0.7% saturation at a depth of 40 cm, where daytime maximum was 6.2 mg 0_2/L or 75%. Ganning and Wulff (1969) recorded a minimum of 3% saturation in a Baltic pool.

Perhaps of greater interest than low oxygen levels are the extremely high ones. Tidal pools appear to exhibit routinely higher maximum oxygen levels than any other aquatic ecosystem. Ganning (1971) has recorded levels up to 361% saturation in Sweden and Utinomi et al, (1950) to 305% saturation in Japan. In Quoddy pools the maximum encountered has been 363% saturation, but on several occasions levels rose above our ability to measure them. Levels of over 200% saturation are common as levels rise over 20 ppm in warm temperatures.

Oxygen levels generally reach minimum levels at 02:00–04:00 h and maxima at 13:00–14:00 h. Figure 3 shows a typical situation in a Quoddy pool. The highest levels are typically in upper tidal level pools with abundant green algal populations in summer.

It does not appear that inhabitants of tidal pools experience any difficulty within the ranges normally encountered. However, there is little experimental evidence on this point. Available evidence, summarized by Newell (1979), suggests that some fauna encounter difficulty in hyper-oxygenated seawater (Ganning 1967). At high oxygen saturation levels, animal surfaces are often covered with a layer of small bubbles.

Carbon dioxide — Daily fluctuations in carbon dioxide show the opposite trend to those of oxygen as it is liberated in respiration and used in photosynthesis. However, its fluctuations are more complex, as CO_2 is involved in pH and carbonate equilibrium reactions (Broeker 1974). In Quoddy pools the normal cycle in exposed vegetated pools shows a fall in CO_2 levels to zero

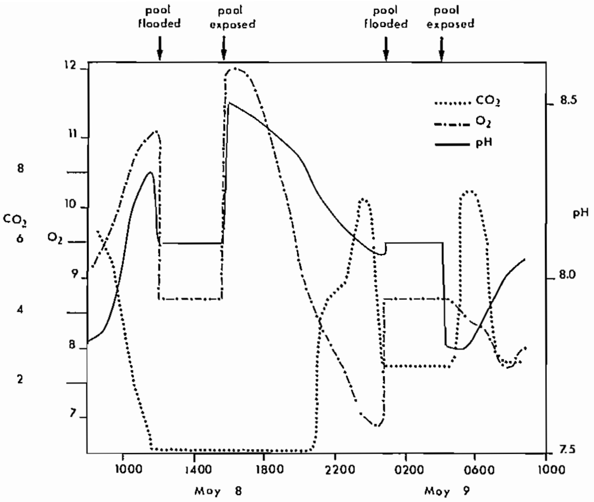

FIG. 3. Typical diel variations in pH, oxygen, and carbon dioxide in a type I Quoddy tidal pool.

(which is probably correlated to pH 7.5 above which no free CO_2 can occur) shortly after dawn; it remains at zero during daylight and rises again just before dusk. At night, levels rise steadily to as high as 50 ppm at 0200–0400 h with levels of 15–25 ppm at night being common. Figure 3 shows a typical CO_2 diel curve for a type I Quoddy pool.

Hydrogen ion concentration — In tidal pools, pH values are strongly related to oxygen and carbon dioxide levels resulting from the balance of biological activity. Both Davy de Virville (1934–1935) and Ganning (1971) found that in vegetated pools there was a daily variation of about 2 pH units. By day pH 10 was common, but it fell to pH 8 at night. However, Ganning (1971) and Ganning and Wulff (1969) have recorded summer maxima up to pH 10.3 in types II and III pools, falling to pH 7.5 in winter. Pools of type IV and V, on the other hand, exhibited lower maxima of 8.2 and 6.9, respectively. Type I pools fluctuated between 9.3 and 7.5. In the Quoddy Region, pH fluctuations in type I pools in summer are commonly between 7.5 and 9.5, but occasionally rise to 10.0 and may fall at night to low levels (3.5) in some pools, such as those with masses of rotting algae. Femino and Mathieson (1980) and Atkins (1922) suggest that pH has a profound influence on pool algae. They argue that greens with high production rates favor large pH ranges which red and brown algae are unable to tolerate.

Diurnal plots of pH against time frequently show a plateau at pH 8.1–8.3, which corresponds to the natural buffer level of seawater. Such an occurrence is shown in Fig. 3, as are typical diel changes.

Physical stability — Tidal pools always occur in depressions on the shore and are frequently surrounded by rocky ridges or prominences. All these features provide some protection against wave action. However, it is surprising that pools with almost no elevated features around them also seem to be very protected. This is a difficult attribute to measure, but in the Fundy region it has been found that fragile string grids and unsecured glass incubation bottles usually survive quite stormy weather during tidal inundation. In experiments conducted just NE of the region at Musquash Head, N.B., plaster-of-paris balls similar to those described by Muus (1967) were shown to lose weight in relation to water movement around the balls. Our balls, 2.8 cm in diameter, were moulded of Domtar plaster of paris; a screw eye was embedded, with the thread projecting from the base. These were dried and weighed and then fixed on the shore by screwing the thread into pine wedges hammered into cracks in the rock. Balls were situated at 20% increments of the mean tidal range from 0% up to 120% and also in two shallow pools at 35 and 95% of the tidal range. Both pools were unprotected laterally and seaward but had rock slopes behind. Pairs of balls were exposed for two full tidal cycles (24.5 h) and then replaced. The tests were conducted in June and July 1979. It was found that despite the fact that they were constantly immersed, the balls in pools consistently lost less weight than balls on the adjacent shore. For example, balls at the 20% tidal level averaged 70.4% weight loss during exposure and those at 40% tidal level averaged 78.3%, but those in the pool at 35% tidal level lost an average of 56.1%. For the higher pool, differences were more striking: loss at 100% tidal level in the open averaged 81.7% weight loss and at 80% tidal level, 68.0% weight loss, whereas loss in the pool at 95% tidal level showed a mean of only 33.3% weight loss. In a parallel test where vinyl surveyors' tape (2.9 cm wide and 65 cm long) was attached to the same wedges, there was no loss of tape in the lower pool, but a mean of 15.1% at adjacent shore sites. In the higher pool there was a loss of 3.2% compared to a mean of 14.5% on the nearby open shore. Although neither method can be precisely calibrated in terms of wave energy, they do give an index of the forces to which organisms are exposed. Both balls and tapes methods demonstrated the environment in even these small shallow pools to be much more sheltered than that on the surrounding shore.

Of nine pools studied at St. Andrews for 10 yr, eight have shown reasonably constant size and shape. For example, pool number 8, in a shallow rocky depression and with a sediment bottom, showed a mean area of 36.6 m^2 with a standard deviation of 3.01 m^2 over a 7–yr period. In the same time the volume averaged 1.54 m^3 with a standard deviation of 0.13 m^3. A smaller pool (No. 4) showed an average area of 3.49 m^2 ($S = 0.58$ m^2) and a volume of 0.12 m^3 ($S = 0.03$ m^3). Other pools show a similar degree of variation mainly because of differences in survey time with relation to tidal exposure time and variations of drainage patterns with algal growth. Pool No. 1, however, situated at mean high tide level, showed a steady diminution in size as follows: 1974, 0.69 m^2, 0.040 m^3; 1975, 0.64 m^2, 0.035 m^3; 1976, 0.48 m^2, 0.014 m^3. By 1977 it had disappeared. The demise of the pool was associated with increased drainage via a rock cleft in sandstone.

BIOTIC CHARACTERISTICS OF POOLS

Succession — The structure and functioning of tidal pools has not received the critical attention given the rocky shore habitat (see Chapter 4) and we know little of the processes which control development and stability in tidal-pool communities. Natural cyclical replacement and short-term successional phenomena have, however, received attention. Ganning (1966, 1971) and Clark (1968) documented annual changes in the fauna of supralittoral pools and described the typical dramatic growth of the green alga, *Enteromorpha intestinalis* in spring and early summer in these pools. Bell (1927) and Femino and Mathieson (1980) looked at annual or seasonal changes in algal populations of tidal pools at St. Andrews, N.B. and Bald Head Cliff, ME, respectively. Also Lubchenco (1978) studied plant species diversity in tide pools in New England and on the Bay of Fundy. Femino and Mathieson found that red and brown algae dominated pools low on the shore and green algae the upper pools. Most red and brown algae were perennial and most greens were annuals. Consequently upper pools showed the greatest annual variation. Some pools had double the number of taxa present in midsummer as in midwinter. Bell (1927), working in 13 pools at St. Andrews, observed conditions only from June to September 1926 and found that *Enteromorpha prolifera, Scytosiphon lomentaria, Petalonia fascia*, and *Halosaccion ramentacium* waned during the summer whereas *Ascophyllum nodosum, Fucus vesiculosus*, and *Chondrus crispus* did not. In pools studied recently at Holey Point, rapid growth of green algae, including *Enteromorpha intestinalis, E. prolifera, Monostroma* sp., and *Cladophora* sp., were observed in types IC and ID pools. Pools of types IA and IB, however, showed a remarkably constant component of taxa and a virtually constant biomass all year round.

Diversity and trophic structure — Tidal pools are generally small and relatively unstable, and consequently have relatively low diversity and simple trophic structures. The list of 131 recorded tidal pool species for the Quoddy Region is similar to that for the rocky shores. So far as is known no species are confined to rock or tidal pools; the small size of rock-pool systems would not favor the development of new species therein. Environmental variables on the open shore and in pools are similar except for factors associated with direct exposure to air, which are inapplicable to pool biota. Many algal species reach higher shore levels in pools than in the open; these include *Corallina officinalis, Halosaccion ramentaceum, Lithothamnion* sp., *Polysiphonia urceolata, Spongomorpha arcta, Laminaria* sp., *Alaria esculenta, Pylaiella littoralis*, and *Porphyra miniata*. Others, such as *Monostroma* sp., *Enteromorpha* sp., *Ectocarpus* sp., *Petalonia fascia, Ceramium rubrum, Chondrus crispus, Hildenbrandia* sp., *Palmaria palmata*, and *Petrocelis middendorfi* do not extend their ranges upward in pools (Femino and Mathieson 1980). A similar situation occurs with fauna where species such as *Taelia felina, Diadumene leucolena, Littorina obtusata, L. littorea, Acmaea testudinalis, Thais lapillus, Modiolus modiolus, Mya arenaria, Macoma balthica*, and *Carcinus maenas* extend to higher levels in pools whereas others such as *Littorina saxatilis, Gammarus oceanicus*, and *Jaera marina* do not.

A few species common on the open shore occur in pools only rarely. Among the algae these include *Ascophyllum nodosum* and *Fucus vesiculosus* (Femino and Mathieson 1980); among the animals, *Sertularia pumila, Potamilla neglecta*, and *Flustrellidra hispida* have rarely been observed in Quoddy pools.

As pointed out by Femino and Mathieson (1980) and Ganning (1971), diversity and complexity of trophic structure are greater in pools low in the intertidal area. This is also obvious in studies of Quoddy area pools, where type ID pools rarely contain over 15 species whereas in type IA pools the number often exceeds 50. Similarly food webs gain complexity moving down the shore. The trophic

TABLE 2. Mean height, area, volume, and biomass (g/m² wet wt) for tidal pools studied at St. Andrews, N.B.

	Pool number and type								
	1	2	3	4	5	6	7	8	9
	ID	IC	IB	IC	IB	IC	II	IC	IC
Height above MLW M.	5.4	3.6	1.8	4.2	1.1	4.0	5.6	4.5	4.2
Area m²	0.60	1.72	0.7	3.49	1.47	19.8	5.0	37.3	1.7
Volume m³	0.03	0.09	0.04	0.12	0.05	1.12	0.14	1.60	0.06
Mean biomass autotrophs	853.6	1086.0	559.0	1255.4	177.3	1316.0	93.5	484.0	5124.3
Mean biomass herbivores	1085.6 (20.5)[a]	295.1	34.5	101.1	24.9	417.4	52.8	121.45 (21.45)[a]	637.5
Mean biomass carnivores	5.2	4.2	1.33	0.0	0.0	0.0	0.0	0.0	0.0
Mean biomass detritivores	299.8	5.2	0.0	3.47	1.4	0.0	0.0	666.3	0.0

[a] Excluding *Mya arenaria* which may function as a detritivore.

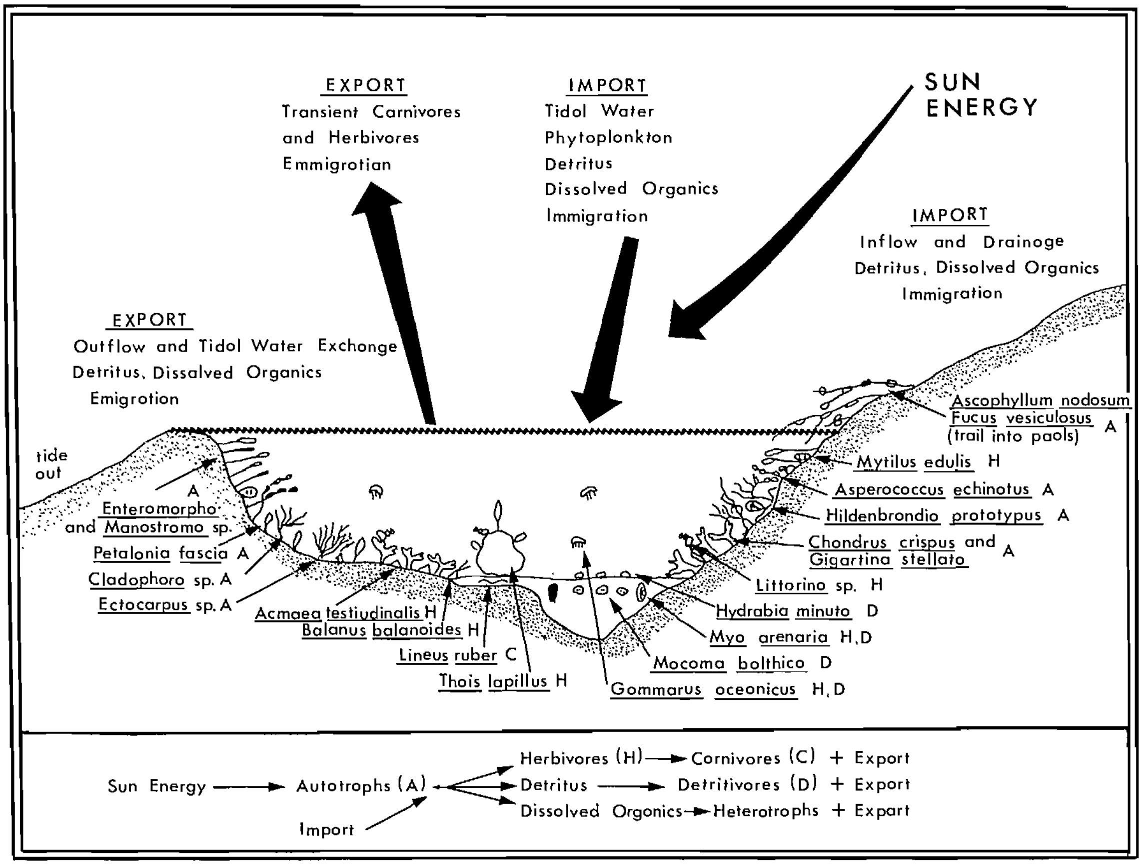

FIG. 4. Generalized biotic and trophic structure of a type I Quoddy tidal pool.

structure of the tidal pools normally shows a great preponderance of autotrophs and often few or no carnivores. It should be remembered, however, that pools have transient carnivores at both high and low tide periods in the form of fish, crustacea, birds, and mammals. The main species occurring in Quoddy pools are listed in Table 1. Biomass measurements have shown considerable variation in the biomass of autotrophs compared to that of heterotrophs in type I pool studies. Mean values are given in Table 2, as are tidal height, type, area, and volume characteristics of pools. The mean autotroph biomass varied between 5124 and 94 g/m^2 with an overall mean of 1216.49. Type IC pools had the highest biomass with an overall mean of 1853 g/m^2, whereas the only type-II pool studied had the lowest biomass. Herbivore biomass was more variable, ranging from 1085 to 25 g/m^2; however, high values in two pools were associated with populations of the soft shell clam *Mya arenaria*, which may function as a detritivore. Excluding *Mya*, the overall mean biomass for herbivores was 178.4 g/m^2. Carnivores were of consistently low biomass, ranging from 5.2 to 0 g/m^2 with an overall mean of 1.19 g/m^2. The most variable group were the detritivores, ranging from 666.3 to 0 g/m^2, and from 688 to 0 g/m^2 if *Mya arenaria* was included. The overall mean was 108.5 g/m^2 excluding *Mya arenaria* and 237.9 g/m^2 including this species. The overall ratio of autotrophs:herbivores:carnivores of 100:15:1 is very close to the "ideal" ratio of 100:10:1, and some of the difference undoubtedly results from using live weight figures. Live weight is always artificially high where shelled molluscs are involved, as they are here, among the herbivores. However, another large group of consumers, the detritivores, averaged greater biomass than the herbivores. With the inclusion of the detritivores as heterotrophs, this group becomes significantly larger than expected, being over 30% of that of autotrophs. This imbalance reflects the position of rock pools on the shore as low areas into which detritus tends to drain. Additionally, as we have shown, rock pools offer an environment with less wave energy than the surrounding shore and thus are settlement basins. It is noteworthy that detritivore-rich pools usually also have significant sediment accumulations, another indication of their collection and settlement role. A few pools show an apparent excess of autotroph production, perhaps suggesting a net export role, but most appear close to a trophic balance in an import category. However, when considered as discrete units, their general long term biomass stability suggests trophic stability, which results from interactions with surrounding systems.

The common species and their importance and known trophic relationships allow the construction of a generalized food web for Quoddy type I pools. This is shown in Fig. 4.

The fauna of tidal pools includes both mobile and sedentary forms. Many of the mobile forms move in and out with the tides. Considerable mobility of periwinkles (*Littorina* sp.) has been shown by marking experiments in the Quoddy Region. Both fauna and flora are utilized by transient herbivores and carnivores. Although there are few pool species that do not also occur on the open shore, most pool inhabitants have been observed in the stomachs of fish feeding intertidally at high tide. In the Quoddy Region these have been shown to be principally winter flounder (*Microgadus tomcod*), tomcod (*Pseudopleuronectes americanus*) and young hake (*Merluccius* sp.). *Hydrobia minuta*, a snail observed only in pools, was also present in stomachs. At low tide, herring gulls (*Larus argentatus*) have been observed feeding in pools, and raccoon (*Procyon lotor*) prints are often seen in muddy pools.

Tide pools as refuges — Dethier (1980) has drawn attention to the possibility that pools above mean high-tide level may serve as refuges from predation for some species. He found that the copepod *Tigriopos californicus* was present only in high pools but could survive and reproduce in intertidal pools. When predators of this species were transferred to high pools, rapid population declines resulted. It is probable that other species found in high pools have similar interactions.

Production patterns — The subject of primary production rates by rock pool autotrophs has not received much attention and needs further study. In the Quoddy area light and dark bottle oxygen experiments in a wide variety of pools, using pool water, normally show no results, particularly if the pool has been isolated for some time. Although the method is not very sensitive, the findings suggest little phytoplankton activity. This has been borne out by generally low phytoplankton counts in pool water. The high biomass of filter-feeding herbivores apparently crop-off phytoplankton quickly. Nevertheless, production rates of up to 35 $mgC \cdot m^{-3} \cdot h^{-1}$ have been observed in newly isolated pool water. Macrophyte production has been investigated for a number of common pool macrophytes under a variety of conditions.

Average net production rates expressed per gram of alga (live wt) and per square metre of pool are given in Table 3. Although these results show great variation, as shown by high standard deviations, they do indicate significant net production in pool environments. Generally speaking, the green algae such as *Enteromorpha intestinalis*, *Monostroma* sp., and *Cladophora* sp. show much higher rates than red and brown algae. The only red or brown species with a rate comparable to the greens was *Asperococcus echinatus* which, because of low biomass levels, contributes relatively little per unit area. When production per unit area is considered, the large brown algae, which droop into pools in large quantities, have high levels of production despite their low production rates.

Studies on Quoddy tidal pools have also shown that in the early summer, large quantities of cast *Ascophyllum nodosum* receptacles concentrate in tidal pools where they slowly decompose. This part of the detritus has been investigated using the light and dark bottle oxygen method. Detached receptacles had, on average, a low net production (0.003 $gC \cdot g^{-1} \cdot h^{-1}$) but a higher gross production (0.034 $gC \cdot g^{-1} \cdot h^{-1}$). These detached receptacles appear to contribute not only organic detritus but also some net production.

Another important source of pool production is microplants on the surface of sediment deposits. These are difficult to study in isolation but the whole sediment comminity is readily studied using oxygen levels inside a glass box (which can be light-sealed with foil) pushed into the sediment. Several such experiments have been run at St. Andrews, in pool No. 8, which has a predominantly sediment bottom. As shown in Table 2, this pool has large populations of herbivores and detritivores on and in the muddy sand (*Macoma balthica*, *Mya arenaria*, and *Hydrobia minuta*); their respiratory use of oxygen is included in experiments. In seven series of experiments using the box, the following results were obtained: ($mgC \cdot m^{-2} \cdot h^{-1}$), mean gross production 140.49 ($S = 198.08$), mean net production 10.32 ($S = 78.56$), and respiration 130.17 ($S = 256.35$). By day, therefore, net production is the general rule. These experiments excluded macroalgae around the edge of pools which tend to add to daytime net production (Ganning and Wulff 1970).

Approximate diel production respiration balances

TABLE 3. Mean net photosynthetic rates and standard deviations for common tidal pool algae in the Quoddy Region (production expressed as mg of carbon).

Species	Mean net production·/ g^{-1}/h^{-1}	Standard deviation	Mean net production/ m^2/d	Standard deviation	No. expts.
Ascophyllum nodosum[a]	0.105	0.113	711.36	1095.17	19
Asperococcus echinatus	1.017	0.833	204.44	328.46	4
Chondrus crispus	0.175	0.220	333.98	413.32	12
Cladophora sp.	0.609	0.883	2594.84	5192.52	5
Ectocarpus sp.	0.315	—	30.36	—	1
Enteromorpha intestinalis	0.994	1.985	938.21	1208.87	11
Fucus vesiculosus[a]	0.083	0.334	2063.71	10420.02	19
Monostroma sp.	1.797	1.727	5607.20	13670.96	4
Petalonia fascia	0.115	—	3262.17	—	3
Scytosiphon lomentaria	0.003	—	0.02	—	1

[a] Experiments performed on plants draped into tidal pools.

can be made by assuming production for 10 h and respiration for 24 h. On this basis, heavily vegetated pools show a net carbon surplus and pools with high heterotroph populations the reverse.

Little work has been carried out on inorganic nutrient balance in tidal pools but Ganning and Wulff (1970) have commented on high phosphate levels in some supralittoral pools. In the Quoddy Region nitrate and phosphate levels are usually low in pools, but where decomposition of algae is taking place phosphate and nitrate levels have been observed to rise. This aspect deserves further study as results suggest that some pools may be important mineralization sites.

Tidal Pool Study Methods

SURVEYING

The main objectives in making a good rock pool map are to establish its size, shape, orientation to the compass, surface area, and volume. Ideally maps should also show surrounding features such as slopes, vertical rises, etc.

A simple and accurate method for achieving these objectives is to lay a rectangular frame of wood or string around the pool, just clearing the water on all sides. The frame should be graduated at frequent intervals. The pool outline can be reproduced by measurements from frame to water on longitudinal and transverse transects. The same transects are used to determine water depths at reasonably frequent intervals. Orientation is recorded by placing a compass on one axis of the frame and recording the bearing. The pool outline and depth configuration may then be reproduced on graph paper within a scale reduction of the frame. The intervals of measurement and depth determination vary widely with the size and structure of the pool. Relatively few measurements are needed in a regularly shaped pool with an even bottom, but irregular pools require detailed coverage to produce a good map.

From the graph, surface area may be determined with a planimeter, or by the cut-and-weigh method, whereby a scale unit area of paper is weighed and compared with the weight of the pool, drawn to the same scale, and cut along the waterline.
Then:

Area of pool = Wt of paper pool/wt of unit area of paper.

This latter method is considerably faster and more adaptable than the planimeter method. It may also be simply adapted to find areas between depth contours or to determine areas occupied by species or communities.

The volume of the pool is most simply calculated as mean depth × surface area. (Note: both values must be in the same units, either cm and cm^2 or m and m^2.) More accurate volume determinations can be made by summing the volumes between depth contours, but these are seldom required.

A further important parameter is the height of the pool above mean low tide level. There are two convenient methods to determine this. The first is by using the surveying method described in detail in Chapter 4 and in Thomas (1976), which uses low tide level of the day as a reference level, with appropriate corrections for the tide height and location. The second method is somewhat faster but probably has greater error. In this method the time at which the tide is at the same level as pool water is determined, preferably on at least two occasions. The level of the pool with reference to chart datum can then be determined using the method given in the *British Admiralty Tide Tables* (Anon 1979). This method, based on the use of a series of cosine curves for interpolation of tidal height between high and low water levels, is much more accurate than the method given in the Canadian tide tables (Anon. 1980) which involves a tabular method requiring approximation. However, the latter method can give reasonable results if means of several determinations are used.

In all methods care should be taken to express height as distance in metres above mean low tide level (MLW). The height of MLW above chart datum for various locations in the Quoddy Region is given in Table 4 of chapter 4. Time and height differences for various locations are presented in Table 3 of chapter 4.

PHYSICAL AND CHEMICAL PARAMETERS

General — The main constraint on the use of standard field techniques in tidal pools is the small size of most pools and their generally shallow nature. If phenomena such as stratification are of interest, the sampling location becomes even smaller. Thus most normally used instruments and techniques are inapplicable. Those used must be carefully selected so that they will provide useful results without destroying the natural pool environment. Care should also be taken to see that pools are not physically disturbed prior to taking readings or samples, unless only general results are needed.

Temperature — Temperatures are best determined with electronic thermistor thermometers. These are normally available with very small sensors and have the added advantage that they can be left in the pool and read remotely (e.g. during tidal flooding). For most accurate results, the sensor should be held horizontally rather than vertically in the water, as the probe is normally of elongated design. With care, temperatures can be measured at 5-mm depth intervals by moving the sensor down a rule resting on the bottom. Temperature differences on a lateral basis can be conveniently mapped using the same points used in mapping the pool.

Salinity — Salinity is probably the most difficult parameter to measure accurately in pools. The most satisfactory results are obtained using either a conductivity type salinometer or a refractometer. Conductivity probes on the former are normally quite compact and, providing the two electrodes within the probe are held horizontal, salinity stratification can be documented. It should be remembered that determination of salinity from conductivity requires temperature correction. This is normally an automatic instrument function, but inaccuracy will result if the thermistor sensor and conductivity electrodes are in different conditions. Other instruments require ambient water temperature to be set on a dial; again, it is essential that this is set at the temperature of the water around the electrodes.

The refractometer offers the advantage that temperature correction is built into the instrument and only about 0.1 mL of sample is needed. Water samples can be carefully drawn by pipette from levels as close as 5 mm apart. As samples are tiny, care must be taken not to contaminate them within the pipette or on the refractometer cell. In practice it is best to draw three times the volume needed and to use the center part of the pipette sample for analysis. The profile shown in Fig. 2 was obtained using a refractometer. In extremely tiny ephemeral pools a refractometer provides the only practical method.

In large pools, samples for salinity titration can be collected but induction salinometers should never be used because of interference with cell function near the surface and bottom.

Dissolved oxygen — Both widely used methods of oxygen determination, the Winkler titration method and the oxygen electrode, are applicable to pool situations. However, unless modified, neither can be used to investigate microstratification. The Winkler titration normally requires a 30-mL sample and the electrode requires vigorous water movement across the electrode face. In practice, for either method, it is best to remove 300-mL samples from the pool for assay. Samples must be taken so as not to induce changes in oxygen. On the shore this is most readily accomplished by carefully siphoning water from the required level into a 300-mL B.O.D. bottle. The first part of the sample should be discarded. The siphon tube should then be led to the bottom of the sample bottle and the bottle allowed to fill and overflow for a few seconds; this protects the measured sample from contact with air. Other methods involve large syringes or automatic samplers and often result in considerable water mixing.

In all methods, problems will inevitably be encountered when oxygen levels rise over 20 ppm. In the Winkler method, standard quantities of reagents become exhausted before all oxygen is fixed. With meters, scales rarely extend above 20 ppm. The problem in titration can be circumvented by doubling concentrations or volumes of reagents. (There is some loss of accuracy if volumes are doubled). With meters, the most practical solution is to set the calibration at 50% of true concentrations and then double all readings. Most meters allow this, but some may have to be set at some higher fraction, say 75%, and the correction altered appropriately.

With all methods, standardization or calibration should be checked frequently. Meter drift often occurs but can be corrected for if the rate of drift is known and if the time each reading is taken is recorded.

All meter readings for dissolved oxygen require temperature and salinity correction. Some instruments correct for temperature automatically, and some by setting a dial. Salinity correction is never automatic in small portable instruments and must be made arithmetically or by setting a dial. The arithmetic method and the required nomograph are given in Thomas (1976). At any rate, salinity and temperature readings must always be taken with oxygen levels.

Carbon dioxide — Carbon dioxide is not easy to measure accurately. Approximate concentrations may be determined by titration of a water sample against NaOH with phenolphthalein as an indicator. More accurate results may be obtained by calculation from alkalinity, pH, salinity, and temperature data. Details are given in Strickland and Parsons (1972).

pH — The hydrogen ion concentration may be determined by the use of a pH meter with an electrode suitable for use in sea water, or by the use of narrow-range indicators. The latter have proved more reliable than meters, which are prone to malfunction in the field. Provided the pool water is not naturally colored, indicators will give results interpretable to 0.1 pH unit.

Illumination levels — Again small sensors are essential. Instruments are available to measure light in three different ways. The simplest meters are set at the pool surface to 100% and levels within the pool are read as a percentage of surface light. Used carefully in conjunction with a standard incident light meter at the pool surface, these instruments are satisfactory. A second group of instruments will measure light intensity underwater. As with the previous type most sensors gather light through an angle of 180° or less and may underestimate total available light. The third type of meter measures light from all angles and will either give intensity or will sum quanta of light over a given period. Choice of instrument depends on availability and accuracy considerations.

Inorganic nutrients — Analysis requires complex procedures such as those described by Strickland and Parsons (1972).

BIOTIC CHARACTERISTICS

Most species in rock pools are readily observed and collected. Where sediment is present samples should be screened through a mesh of 0.5 mm opening to isolate burrowing forms. Details of collection, preservation, and identification techniques are given in Chapter 4.

Quantitative samples are best taken with the aid of quadrats from 0.01 to 0.1 m^2. Larger sizes are inappropriate. Sampling patterns must vary with study objectives, but for critical work sampling should be on a random design with several replicates. Workers should be aware that pools are small enough that too intense sampling may destroy the pool system. Quadrat sampling, however carefully carried out, will miss very active species such as *Gammarus oceanicus*. Special techniques are required for such species. Encrusting species are also difficult to sample and are best quantified by determining the area covered. The simplest and most effective method for this involves using an overlay of 100 randomly spaced dots on a perspex sheet (as described by Menge 1976). The size of the overlay can be varied to suit the situation but sizes from 0.01 m^2 to 0.1 m^2 are usually best for pools. The number of dots overlying each species gives percentage cover directly. Dry weight biomass of encrusting species can be estimated by removal of a piece of encrusted rock, drying at 100°C to constant weight, ashing at 435°C, and re-weighing. The weight difference is dry weight of organic material. Live weight is commonly 10 × ash-free dry weight but is very variable. Biomass of samples collected from quadrats may be expressed as live, dry, or ash-free dry weight per unit area. Further refinement toward estimation of organic material weight can be obtained by chemical or mechanical decalcification before weighing. Techniques are discussed in Thomas (1976). Quadrat samples also yield estimates of abundance per unit area.

Tidal pools are particularly suitable for the investigation of the rates of primary production and respiration by macroalgae. The best method is undoubtedly the light and dark bottle oxygen method described in detail in Thomas (1976). Pairs of 300-mL B.O.D. bottles, one blacked out with foil wrap, are used with similar algal samples, in situ. Best results are obtained with samples of about 1 g wet wt of alga over a 2–4 h incubation. Small algae can be used whole; large ones should be cut carefully to damage the sample as little as possible. Cut pieces should be allowed to stabilize in the pool for half an hour before use. With large algae, different rates of production and respiration occur in different portions of the thallus. Full investigation will require several samples. It is wise to start the experiment when oxygen levels in the pool are below saturation. Heavily supersaturated samples are difficult to analyze for oxygen and give erratic results. Incubation locations should be such that the bottle is in light conditions typical for the species under investigation. Oxygen levels are determined at start and finish, and algal samples must be weighed. Results may be expressed on a wet or dry-weight basis and production per unit area of pool can be estimated from quadrat biomass data in comparison to sample weight. Encrusting species can be tested on fragments of rock of known area and compared to typical coverage of the species per unit area of the pool.

A variation of the method may be used for community production and respiration on sediments. A shallow glass or perspex open-ended box of known area is carefully embedded in the sediment around an oxygen electrode; the glass top of the box is sealed on, using petroleum jelly or silicone grease, so that no bubbles are enclosed. After initial equilibration, production and respiration rates can be calculated from a series of dissolved oxygen readings in the light and blacked out with foil. Calculation requires the determination of the effective volume and area of the box (total area or volume–electrode area or volume).

Used carefully, and with appropriate corrections for diel periods of production and respiration and the effects of temperature and light, an energy budget for primary producers in pools can be constructed.

The diel oxygen change method described by Talling (1969) may also be used, with appropriate corrections for atmospheric exchange and respiratory uptake.

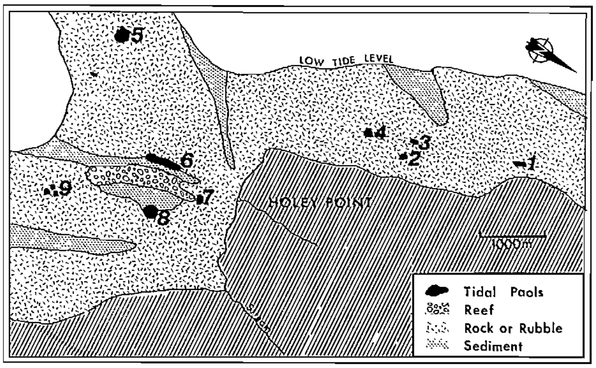

FIG. 5. Location of nine tidal pools, mentioned in the text, in the Holey Point area, St. Andrews, N.B.

Food webs can be determined by careful observation in the pool, reference to appropriate literature, and determination of losses while the pool is immersed. Stomach analyses of pool and shore inhabitants at both high and low tide are often necessary.

Specific Study Locations in the Quoddy Region

Fortunately, tidal pools are extremely common on the rocky shores of the Quoddy Region. Almost any location will yield a fine selection of type I and type II pools. Type III, IV, and V pools are difficult to find in this area. One of the best study sites is Holey Point (see map, Fig. 11, Chapter 4). General characteristics of pools studied there are presented in Table 1 and 2 of this chapter. Figure 5 is a sketch map of the Holey Point area showing the location of the nine pools studied there. Excellent pools are also available on the rocky areas of Woodstock Point (Fig. 21, Chapter 4) and at Letite (Fig. 24, Chapter 4). Letite is especially good for large type I and type II pools.

Acknowledgments

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CHAPTER 7

Salt Marsh Systems

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Introduction

Salt marshes are not well represented in the Quoddy Region, as most bays and estuaries have shores with relatively steep profiles which are not conducive to marsh formation. However, the Bay of Fundy area as a whole, as shown in Fig. 1, has extensive areas of extremely well-developed and interesting salt marshes. Some are quite close to the Quoddy Region, such as the ones at Dipper Harbour and Musquash just southwest of Saint John. Within the Quoddy Region itself there are several small but well-developed salt marshes (for instance near St. George and on Campobello Island) and, in addition, most sedimentary shores have a narrow fringe of salt marsh species at about high-water mark.

Salt marshes have been extensively studied around the world, as shown by a number of comprehensive reviews of their structure and functioning (Chapman 1964, 1977; Ranwell 1972; Teal and Teal 1969). This attention has resulted partly from their wide occurrence and great ecological importance but also because they are one of the most readily studied marine systems. Being on shore and high in the intertidal zone they are inaccessible for only a few hours a day.

Good basic information and ready access are the main requirements for field teaching sites. This fact, combined with the local importance of salt marshes, dictates their inclusion in this book.

Salt Marsh Distribution

On a worldwide basis salt marshes are found where there is at least some protection from severe wave action. They are best developed on sedimentary, low-profile coasts and in estuaries. Although they may occur at any latitude except the polar ice caps, they are typical at latitudes higher than 30°; in lower latitudes mangrove swamps develop where salt marshes develop farther to the N. or S. Large areas of the world with steep rocky coast lines (for example the west coast of South America) have no well-developed salt marshes.

In the Bay of Fundy, salt-marsh formation has been fostered by the high tidal range and extensive supplies of sediment, particularly near the head of the bay. It has been estimated that before colonization Fundy salt marshes occupied 35 700 ha. These areas were prime targets for early agricultural development. The Acadian and later settlers dyked the majority of marshes, reducing their area to a present total of 5210 ha (Fig. 1) — 3670 in Nova Scotia and 1540 in New Brunswick (Thomas 1977).

However, the Fundy salt marshes still represent a significant area of salt marsh on a continental basis. The entire U.S. coast south from Canada to the border of New York state contains only 5008 ha of marshes. South of this area the low-lying sedimentary coastline of the eastern United States has some of the largest and best-developed salt marshes in the world; there are 192 508 ha in Georgia alone. The entire east coast of the United States contains 589 429 ha of salt marsh (Reimold 1977) and represents one of the main salt-marsh concentrations in the world.

Chapman (1977) has classified the salt marshes of the world into a series of groups and subgroups. Within the western Atlantic group he recognizes three subgroups: the Bay of Fundy, the New England, and the coastal plain subgroups. The Bay of Fundy subgroup encompasses all Canadian Maritime salt marshes. In the Quoddy Region, marshes are transitional between Fundy and New England subgroups, sharing some characteristics of both.

Physiography, Structure and Soils

PHYSIOGRAPHY AND STRUCTURE

Well-developed salt marshes are generally almost level areas, sloping only gently out to sea; they develop mainly above mean high water of neap tides. The top of the marsh usually lies at about extreme high-tide level. The shape and extent of the marsh is strongly influenced by tidal range. The vertical extent is proportional to tidal range but maximum width generally is not, since with increasing tidal range marsh slopes become steeper. Thus some of the widest salt marshes in the world occur in Georgia, with a mean tidal range of 2.2 m; those of the Bay of Fundy, with mean ranges up to and over 7 m, while formerly very extensive, do not rival those of Georgia.

Tidal range also affects drainage patterns, these being complex with intermediate tidal ranges but generally simple with high and low ranges. Biotic zonation is most distinct in marshes of high tidal range.

As well as requiring shelter and a source of sediment, salt marshes are associated with low-profile coasts, since steep coasts do not provide suitable substrata for shallow-water sediment deposition even if they are extremely sheltered and have a good supply of sediment. Thus coasts of steep topography, such as fjord areas, generally show only tiny marshes at the extreme landward end of inlets. While the Quoddy Region is not an extreme case, coastal topography is frequently charaterized by steep slopes into the water (as in the St. Croix estuary), and despite adequate sediment supply, salt-marsh formation is limited to small areas of lower slope. The source of sediment to salt marshes may (1) be fluvial, from land drainage: (2) be derived from marine erosion of local coastlines, or (3) be coastal sediment deposits of glacial origin. The first and the last are the main sources. In the Fundy and Quoddy regions, the last constitutes the main sediment supply. Its

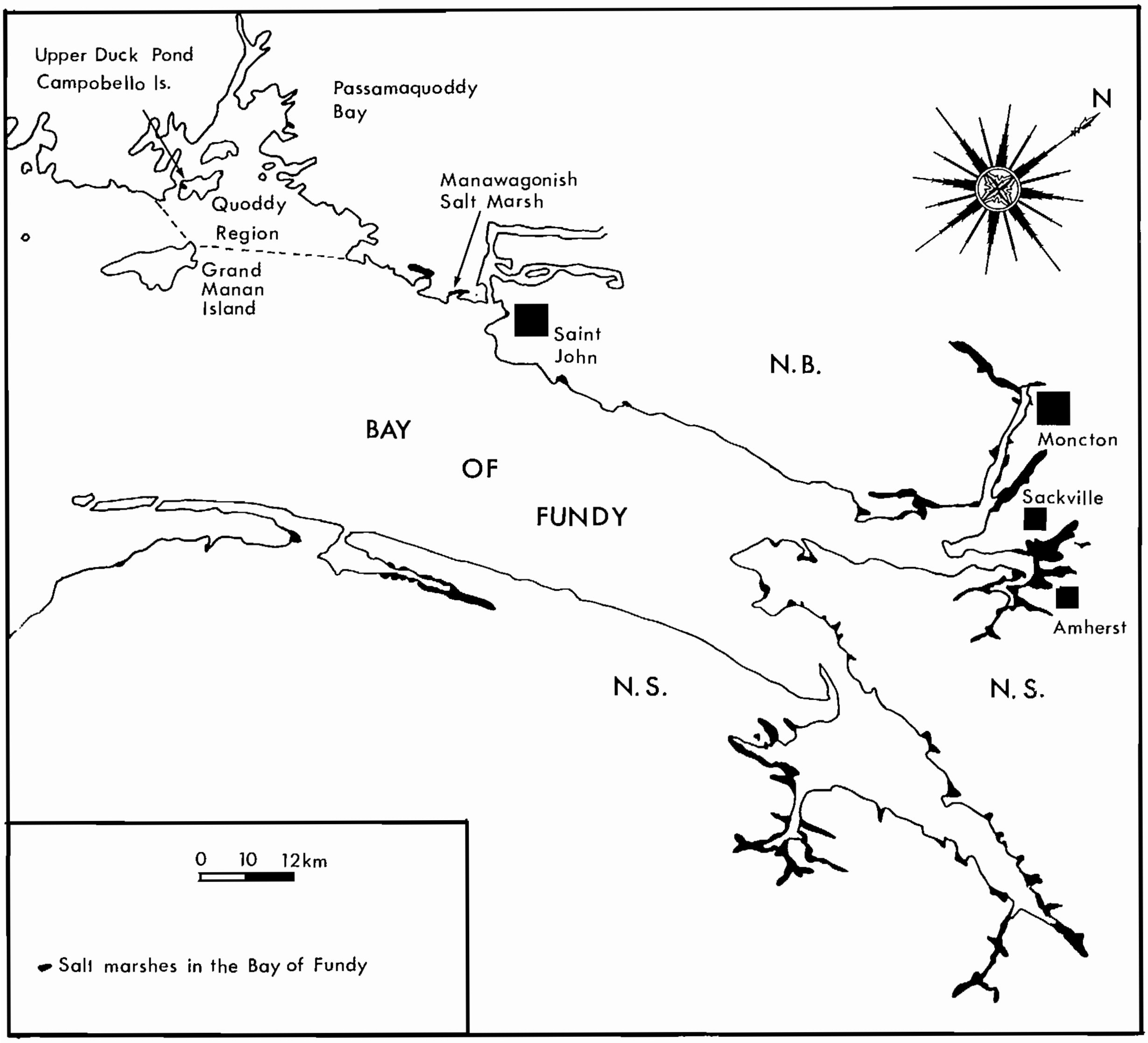

FIG. 1. The Bay of Fundy, showing location and extent of present salt marshes. The two specific locations described in the text are indicated by arrows.

availability to marsh formation is enhanced by the large tidal range, currents, and exchange which continually suspend and resuspend large volumes of subtidal and intertidal sediment.

Salt marshes are charaterized by extensive mud flats to seaward. The lower edge of the marsh proper is often marked by an increase in slope and usually by the disappearance of submerged vascular plants such as eelgrass (*Zostera* sp) or, further south, turtle grass (*Thalassia* sp.). Grasses are usually present. Within the marsh itself there are three main structural components: flat areas, drainage channels of various sizes, and pannes or pools of various sizes. Figure 2 shows a generalized profile of salt marsh and gives the commonly used names for universal features. Several of these require further explanation. The emergence and submergence marshes correspond to the terms upper and lower marsh; the dividing level is that of mean high tide level.This results in different physical environments in the two areas. The submergence marsh is under water more than 360 times/yr while the emergence marsh is submerged less than 360 times/yr. The submergence marsh has a maximum *continuous* exposure of less than 9 d and the emergence marsh greater than 10 d. The submergence marsh is under water for more than 1.2 h/d and the emergence marsh less than 1 h/d (Chapman 1960). These differences result from the normal tidal regime. There is a marked difference in the biotic composition of the two marshes but many charateristic marsh species colonize both levels.

The strandline or zone is a narrow band around mean high water of spring tides and is often sparsely vegetated and littered with floating debris. The sediment is exposed

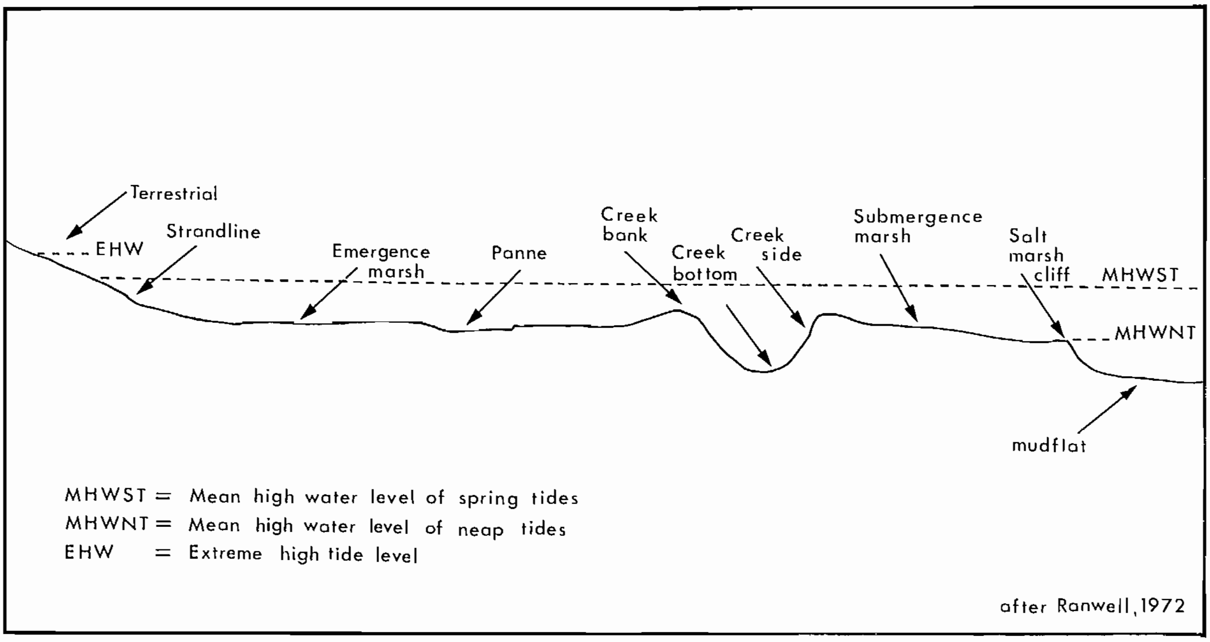

FIG. 2. Generalized profile of a well-developed salt marsh showing characteristic features and their names.

and is frequently coarser than at lower levels. The strandline results from the interaction of tide, wave action, and the level on the marsh. Only at high-water level of spring tides is the whole marsh water-covered to a depth sufficient to allow the development of significant waves. These waves may be quite severe on the strandline, limiting biotic colonization there. The salt-marsh cliff is a feature found at the lower extremity of parts of marshes exposed to a significant fetch at high water of neap tides, and results from wave erosion at that level. Above the cliff, dense vegetation protects the marsh.

The profile shown in Fig. 2 represents average conditions of a variable situation. The actual profile varies according to the slope of the coast, the tidal range, and the age of marsh. Mature, well vegetated marshes form effective sediment traps in their seaward regions. Much of the suspended sediment on the incoming tide is deposited there or close to creeks. This results in a progressive flattening of the marsh profile and the buildup of banks or levees along creek margins. These changes, in turn, affect drainage creek patterns, which grow more complex with time.

Creeks are the drainage channels of salt marshes. They carry the waters of the rising and falling tides and of any local land drainage into the system. Creeks may arise in minor surface depressions, but once formed, erosion along the channel deepens and widens them. The interaction of stabilizing vegetation and creek is such that these features, especially when of intermediate size, are often steep sided or, in more extreme cases, undercut or roofed over. The sides of wider, undercut creeks collapse, in time, to give a charateristic step-sided profile. (Chapman 1964; Steers 1977). (In Quoddy and adjacent marshes, roofed-over and very deep creeks are common, and present a somewhat dangerous situation: they should be crossed with caution). As mentioned above, the complexity of drainage creek systems is highly variable. The most highly developed forms are associated with mature marshes. Fine sediments, intermediate tidal ranges, and vigorous growth of *Spartina* grass species assist in the formation of a system which is dendritic, or tree like, in which creeks frequently subdivide to finer and finer creeks. The main creek is the primary, which gives rise to secondary, then tertiary creeks, and so forth. In our area a simpler pattern is normal, involving usually no more than tertiary creeks. Here this simplification is associated with high tidal range, but in other areas is associated with sandy substrata or paucity of vigorous salt-marsh grasses. In marshes where the tidal range is small, such as along the north shore off Prince Edward Island, there are only a few short, direct creeks. Many Fundy marshes have large primary channels or creeks with meandering paths through the marsh. These large creeks have action erosion on the outside of bends and deposition on the inside. This results in a slowly but continuously changing channel position. The banks of large channels have lower slopes than the creeks but are still steep and exceedingly difficult to climb.

The final main feature of salt marshes are the tidal pools — pannes or pans. These pannes vary greatly in size but are usually numerous and cover significant areas of mature marshes, particularly in the emergence portion (Pethick 1969). Studies have shown that pannes may form as marshes progress seaward, in association with creeks or spontaneously on the mature marsh surface (Chapman 1964; Ranwell 1972; Steers 1977). Several types of pannes occur. (1) Primary pannes are formed in low areas of a new marsh surface as a result of sediment compaction or a rise in level to seaward or toward a creek, resulting from differential sediment deposition. (2) Pannes may form from erosion and natural repair of the salt marsh cliff. (3) "Creek pannes" may form in a series along an old creek path where vegetation grows over and dams the creek. (4) "Pethick pannes" develop on the mature marsh surface where mats of debris or vegetation collect, rot, and by creating anoxic conditions, kill underlying vegetation. Root binding of sediments is destroyed and the bare patch may erode to form a panne. (5) In temperate marshes, long-lasting snow patches or ice cakes may result in panne formation in a manner similar to Pethick pannes. (6) Ice rafting pannes result from stranded ice floes freezing to the surface of the marsh in severe climates. On a subsequent large tide the ice cake, together with the underlying turf, may be lifted off to form a panne. This process is very active in local marshes and has been described for the upper Bay of Fundy by Bleakney (1972). Ice rafting for the Quoddy Region and in Prince Edward Island has been described by Medcof and Thomas (1974).

Whatever the mode of formation, pannes generally have a well-defined margin and often a steep-sided profile, which may result from miniature waves under strong winds and from the swirl of the entering tide. Steep-sided pannes in local marshes are often anoxic in deeper portions.

In terms of long-term stability, salt marshes may be stable in extent or may progress seaward, landward or both. Much depends on the stability of the coastline and the supply of sediment. The most tenuous situation exists on a rising coastline with poor sediment supply. There, only narrow marshes exist and may disappear. On stable coasts marshes have the best chance to increase areal coverage. They progress seaward as sediments are built up. On falling coastlines such as that of the Fundy area, salt marshes can form only if sedimentation rates exceed sinking rates. In such situations, marshes progress landward and remains of formerly terrestrial communities may be present in the marsh or its sediments. In the Manawagonish marsh just SW of Saint John, many dead spruce stumps project from the marsh surface, an obvious indication of a falling coastline.

SEDIMENTATION AND SOILS

Salt marshes are natural sediment traps because of their dense vegetation. Sediment settles most rapidly where water first flows over the marsh flats from the open sea or creeks. The effect of this on marsh profile was discussed above. The net effect of sediment deposition on marsh surface level is a combination of sediment deposition and compaction of deposits through time and weight of overlying material. Deposition has been measured in a variety of locations but compaction only rarely. In a 20–yr study, Stearns and MacCreary (1957) found that deposition of 0.64 cm/yr was exactly balanced by a similar rate of surface settlement. Depths of annual sediment accumulation have been measured on a wide variety of marshes and found to show wide variability both between and within marshes. Sparsely vegetated marsh areas, such as seaward pioneer bands dominated by *Salicornia* sp., show much less deposition than areas colonized by dense *Puccinellia maritima*. In comparing these two communities in a European marsh, Jakobsen et al. (1955) found sedimentation rates of 3 and 10 cm/yr, respectively. Ranwell (1972) reports rates of settlement of up to 15 cm/yr for *Spartina*-dominated areas but points out that the average for emergence zone marshes in Europe and eastern North America lies between 2 mm and 1 cm/yr. In marshes showing high rates of deposition this may be a limiting factor for plant colonization and growth. Kuenzler (1961) has shown that in many eastern North American marshes the bivalve *Modiolus demissa*, common in submergence areas, is active in sedimentary processes. Through filter feeding and the production of pseudo-feces, sediments are trapped, bound, and deposited. He showed that this process was important in supplying phosphate to the marsh. This species is absent throughout the Fundy area.

On a seasonal basis, a variety of studies have shown marked annual patterns of sediment acretion. These are summarized by Ranwell (1972) who stresses the complex interactions resulting from density of vegetation, filter feeding processes, variations in natural sediment supply, and flocculation rates dependent on salinity. The following general pattern emerges. In spring there tends to be differential settlement on the outer fringes of marshes and along creek margins resulting from filter feeding, mechanical trapping in new growth, and flocculation of particles. This continues in summer, but in fall, biological filtering activity declines and flocculation also declines in response to lower salinities, while marsh biomass has reached a maximum and mechanical silt trapping is effective over the entire marsh surface. In winter, with declining biomass and frequent rough weather, some sediment is remobilized and moves into coastal waters.

Such seasonal variations in sediment deposition rates, combined with differences in grain size of deposits at different seasons, may give rise to clearly defined seasonal laminae in sediments (Evans 1965). However, biogenic processes generally result in thoroughly reworked sediments (Phleger 1977). South of the Quoddy area, extensive reworking is accomplished by fiddler crabs *Uca* sp. (Teal and Teal 1969). Their burrowing activities (summarized by Daiber 1977) result in extensive reworking of subsurface sediments. Throughout the well-vegetated parts of marshes, root growth, decay, and infilling of root cavities results in effective reworking of all sediments. As a result most salt-marsh soils lack distinct annual or seasonal laminae. If present at all, such features are most likely to be found in sparsely vegetated seaward or creek margin communities.

Soil types in salt marshes show extreme variation from gravel to clay and some are composed almost entirely of peat. This variation reflects the origin of sediments and the local energy regime. Within the marsh differences are evident too. Normally, there are coarser sediments at the seaward fringe and along creek banks. Differences may be marked enough that sediments along creek margins are sandy and firm whereas farther into the marsh they are clayey and soft (Phleger 1977). In some marshes the deposit is calcareous, composed mainly of biogenic skeletal material; in others it is acid peat. Peat predominates only in areas with low input of inorganic sediments. Many New England salt marshes have peat soils (Chapman 1977).

Most salt marshes contain soils of small particle size or mixed size; thus pore space is small and permeability to air and water is low. Chapman (1964) emphasises that marshes normally have an aerated layer overlying a waterlogged base. The depth of the aerated layer decreases but does not disappear at high tide. Chapman (1960), Adriani (1945), and Ranwell (1972) have examined the concentration of air, O_2, and CO_2 in the aerated layer. Air makes up 2–45% of the soil volume and is reduced in O_2 and enriched in CO_2 compared to atmospheric air. Air enters salt marsh soils partly through natural spaces, but also through animal borrows and cavities created by dying roots; especially important is transport through living tissues of salt-marsh plants such as *Spartina* sp. (Baker 1970).

Below the aerated layer the soil is waterlogged and frequently anaerobic; however, there is little evidence that anaerobic soils are limiting to normal salt-marsh flora.

SALINITY STRUCTURE

The salinity of water in creeks and over marshes at high tide reflects water sources in the marsh area. Upper estuarine marshes are bathed in water of low salinity and generally have soils of low salinity. However, coastal marshes are usually flooded with water of coastal salinity and show higher soil salinities. Water enters marsh soils laterally from creeks, vertically when flooded, and also laterally from adjacent land. The effect is principally localized at high tide. The situation of marshes at high-tide levels results in a gradient of exposure to sea water across the marsh, as discussed above, in relation to submergence–emergence phenomena. Higher levels exposed to atmospheric conditions are more influenced by weather than the sea and in most locations show a gradient of decreasing salinity toward the land. At times the effects of evaporation can be marked and can result in increased soil salinity, especially in submergence marsh flats. In the Fundy area, salinities of 33–36% are common in surface soil water at neap tide periods in summer. However, salinities in soils adjacent to creeks carrying freshwater drainage may be quite hyposaline, even in the outer marsh.

Chapman (1964) gives data showing that most salt-marsh plant seeds germinate better at salinities below that of seawater, a noteable exception being *Salicornia* sp. which shows good percent germination in full seawater and up to 100‰ salinity (3 × normal seawater). It should be noted that inability to germinate in full salinity conditions does not limit plants to upper marsh, because spring rains at neap tide periods may provide good low-salinity germination conditions throughout the marsh.

Biotic Characteristics of Salt Marshes

The ecology of salt marshes has received extensive study. This is reflected in several monographs such as those of Chapman (1960, 1964, 1977), Ranwell (1972) and Teal and Teal (1969) and a vast associated literature. The biota of temperate Atlantic coastal marshes is particularly well covered by Ursin (1972) who describes and illustrates all important local species as well as those occurring somewhat farther south. Various authors, including Chapman (1937), have conducted local or specialized studies on Fundy marshes but only Ganong (1903) has published a comprehensive description. Modern analytical studies are lacking. For marshes close to the Quoddy Region the only published description is that of Thomas (1973).

Salt marshes are characterized by low-growing plants, especially grasses. The animal component is much less noticeable than the plant, but includes species that visit the marsh as well as residents. In the Quoddy Region, resident fauna are particularly depauperate but the system is visited by numerous birds and mammals.

Plant communities of the genera *Spartina*, *Puccinellia*, and *Distichlis*, as well as rushes and reeds of the genera *Juncus* and *Scirpus* dominate marshes. Species of these genera commonly occur in almost monospecific stands. Other perennials are characteristically scattered in other communities. The genera *Armeria, Plantago, Triglochin, Limonium, Cotula*, and *Selliera* are common. Some annuals are also characteristic, the main genera being *Salicornia, Sueda*, and *Atriplex*. Of these, only *Salicornia* sp. form large almost monospecific stands, particularly in new colonization of low-level areas. Algae are also important, prominent genera being *Fucus, Bostrychia, Ulva, Enteromorpha, Ulothrix, Cladophora*, and the blue-green genus *Microcoleus* (Lyngbya). Not all of these genera are found in Bay of Fundy marshes.

Faunal communities are diverse and consist mainly of species not confined to salt marshes but which occur in other littoral communities. In temperate marshes several molluscs are distinctive, such as gastropods of the genera *Hydrobia* and *Melampus* and, in eastern North America, the pelecypod *Modiolus demissus*. Worms, particularly *Nereis* sp., are frequent in the lower marsh. In pannes and creeks fishes of the genera *Fundulus* and *Gasterosteus* are often abundant. In pannes the salt marsh saccoglossan *Alderia modesta* occurs (Bleakney and Bailey 1967). Throughout much of the marsh, insects are numerous. In North Carolina Davis and Gray (1966) found 250 salt marsh species; of these, grasshoppers and sucking bugs were most important. Salt marshes are particularly important feeding and breeding grounds for many birds and mammals which may visit there for feeding purposes. Readers are referred to Ursin (1972) and Teal and Teal (1969) for accounts relevant to local conditions.

In placing the Fundy marshes in their own subgroup, Chapman (1977) stated that they are characterized by extensive growths of *Puccinellia americana* and *Juncus balticus* at upper levels and by transition to bog rather than swamp at their upper limits. Soils were generally of muddy clay. Chapman states that to the south, soils generally change to peats, *P. americana* is never dominant, and terrestrial transition is to reed swamp. These generalizations reflect Chapman's familiarity with upper Fundy Marshes. In the Quoddy Region *P. americana* is never dominant, but *J. balticus* often is.

COMMUNITIES AND ZONATION IN MARSHES FROM SAINT JOHN TO THE UNITED STATES BORDER

The salt marshes of this area are generally estuarine in origin, although the size of the river may be large or small. Consequently, there is a dominant primary channel wandering through the marsh center which exerts a dominant influence on marsh profiles. Almost all marshes were dyked in the past and subsequently used for agricultural purposes; therefore the lower border of these marshes are abandoned dykes. In other cases seaward borders are formed by barrier beaches. No major marshes have lower borders grading into mud flats without substantial interference by artifacts. Because of this, profiles from margin to central creek give a better representation of natural conditions than transects toward the sea. Such transects, however, normally do not show a newly colonized pioneer zone at their outer limit.

Starting at the primary creek, the first community is typically a monospecific stand of the tall form of *Spartina alterniflora*, salt marsh cord grass, which commences at a level corresponding to 80% of the mean tidal range. Thus the marsh proper starts below mean high low water of neap tides which lies at 85%. *Spartina alterniflora* tall form grows on the upper part of the steep creek but does not extend on to the creek bank or levee. Associated with cord grass are blue-green algae, and at its lower edge, in the mud, appear burrows of the bivalve *Macoma balthica*. Gastropods such as the rough periwinkle (*Littorina saxatilis*) may occur on the stems.

There is generally a sharp lip at the creek edge, where the community changes abruptly to one of several others.

1) In many situations (for example much of the Manawagonish and Musquash marshes S.W. of Saint John) the second community is strongly dominated by *S. alterniflora* short form with few associated species. This sequence appears to predominate where the creek bank is not significantly raised above the landward marsh.

2) Where the bank is markedly raised, as it is in many areas, *S. alterniflora* gives way to a mixed community, the most frequent members of which are *Spartina patens, Triglochin maritima, Plantago maritima, Atriplex patula, Suaeda maritima,* and *Limonium nashii, Salicornia europaea,* and *S. bigelovii* (which is found not in New Brunswick but elsewhere in the Maritimes). This assemblage represents a mixture of species found in the emergence marsh and reflects the fact that the creek bank levee often rises higher than mean high water. In places the levee has almost pure stands of *Salicornia* sp. in summer. This appears to reflect erosion or damage to the bank during the previous winter.

3) In areas where there is no conspicuous levee, but the marsh adjacent to the bank is above mean high tide level, the community is a virtually monospecific sward of salt marsh hay, *Spartina patens.*

Beyond the bank lip or levee, marshes are invariably flat and dissected with series of small creeks. The marsh surface undulates slightly and a mosaic of communities results. Typical features are a border of *S. alterniflora* tall form along creek margins, giving way to the short form as levels rise away from the creek. On the flats of the submergence marsh, *S. alterniflora* short form is normally dominant. Common here also are *Plantago maritima, A. patula, S. maritima, Glaux maritima, L. nashii,* and *T. maritima. Salicornia* sp. are often scattered but where there are slight elevations in the marsh surface it becomes dominant and is associated with *P. maritima* and *L. nashii.* Rarely does *P. maritima* dominate in similar locations.

As the marsh level rises, *S. alterniflora* short form gives way to *S. patens* on flat areas, but *S. alterniflora* tall form continues to dominate creek margins. The same assemblage of associated species is retained as in the submergence marsh, but species other than *Salicornia* sp. and *Plantago maritima* decline in abundance above mean high tide level and disappear by mean high level of spring tides. At the same time, several species make their appearance in the emergence marsh and increase in abundance to extreme high tide level. Notable among these are *Distichlis spicata* (Spike grass), *Scirpus americanus, Juncus gerardi* (Black rush), and *Potentilla anserina* (Silverweed): the latter three may occupy almost pure stands, the former two damp lows, and the last better-drained highs. *D. spicata* is comparatively rare. Between extreme high-tide level and mean high-tide level of spring tides a third *Spartina* species, *S. pectinata* (sloughgrass), may be abundant in a narrow band. In wetter places at this level is also found the characteristic but uncommon *Cotula coronopifolia* and where salanities are very low *Typha latiolia* and *T. angustifolia* (Bull Rushes) and *Phragmites communis* (Giant Reed). Around the edges of most marshes, the salt marsh goldenrod (*Solidago sempervirens*) is common, as is the salt marsh aster (*Aster borealis*).

Encroaching down to extreme high-tide level the alders (*Alnus crispa* and *A. rugosa*), spiraea (*Spiraea latifolia*), and sweet gale (*Myrica gale*) are common, often together with stunted white spruce (*Picea glauca*).

In pannes vegetation is usually limited, but some support widgeon grass (*Ruppia maritima*) in abundance. Steep sided pannes may be entirely devoid of higher plants but support intense bacterial colonies of pink or black color.

Marine resident fauna are extremely limited in Quoddy marshes. In creek sides, the bivalve *Macoma balthica* and the polychaete *Nereis diversicolor* are often abundant. A few blue mussels (*Mytilus edulis*) are often found among the lowest zone of *S. alterniflora*, but the characteristic ribbed mussel (*Modiolus demissa*) is absent. In pannes, *Hydrobia minuta*, a tiny snail, is often abundant along with the mommichog (*Fundulus heteroclitus*). The rough periwinkle (*Littorina saxatilis*) is perhaps the most generally distributed marine form and is found throughout the submergence marsh on the substrate, on grass stalks, and in pannes. *Melampus bidentatus*, the salt marsh ear shell, is absent but occurs elsewhere in the Maritimes. Many other species occur but are rarely very common. The green crab *Carcinus maenas* may occasionally be found along creek margins and the isopod *Idotea phosphorea* in vegetated lower pannes. The amphipod *Corophium volutator* is frequent in aerobic panne bottoms and creek sides. In the latter environment *Corophium lacustre* also occurs. The gammarid *Gammarus mucronatus* is occasionally abundant in vegetated pannes and two other species, *G. setosus* and *G. tigrinus*, occur occasionally in upper creek banks under vegetation. Another gammarid amphipod, *Orchestia grillus*, is characteristic of salt marshes but is not often abundant. It occurs in the emergence marsh under debris and among marsh grasses where it builds nests and runways. It is often most easily found under debris at the strandline (Bousfield 1973). The tiny saccoglossan *Alderia modesta* probably occurs in pannes as it does in the upper Fundy area (Bleakney and Bailey 1967).

The small fauna is poorly studied, but farther to the south protozoa and nematoda are often abundant. They would repay study here.

SUCCESSION

There is no doubt that in many areas, salt marshes are increasing their extent. However, in the Quoddy Region, subsiding coast lines and generally low suspended sediment supplies mitigate against expansion. Succession, therefore, is not a universal phenomenon and is most commonly seen in areas damaged by storms, ice, or man. Chapman (1960) considered the normal sequence of dominant species, as marsh elevation increased in this area, to be *S. alterniflora, S. patens, D. spicata, Juncus* sp., and *S. pectinata.* In the Quoddy Region, the most usual pioneer species is *Salicornia europaea.* This species also persists for years in monospecific stands on roadways laid in the submergence portion of Manawagonish Marsh.

Ranwell (1972) discusses the processes involved in the principal change with increasing elevation — that of change of dominance from *Spartina* sp. to others. He points out that the change is sudden, with minimal overlap. Transplant experiments demonstrate that dominant species can survive, grow, and reproduce well above or below their area of dominance. In this instance evidence suggests that the upper limit of *Spartina* sp. is set by the shading of detritus and taller vegetation and susceptibility to frost damage. In shade, *S. alterniflora* will neither tiller nor flower.

PRIMARY PRODUCTION PATTERNS

Salt-marsh energy flow and production patterns have been extensively studied, as has the role of detritus in marsh production patterns. Turner (1976) reviewed the literature on salt marsh macrophyte production and found an overall N–S gradient paralleling solar energy input with a net conversion efficiency of 0.2–0.35%. This gives salt marshes a relatively high rate of net production on a worldwide basis. Turner points out that these estimates largely ignore production by underground portions and production losses in the form of dissolved organic material. Both of these loss routes may be important and it is estimated that total net production may be three times measured production.

Among the salt-marsh species, *S. alterniflora* has been most intensively studied. It accounts for a majority of production in eastern North American marshes and its net production for 45°N, the latitude of the Quoddy Region, is in the order of 400–500 g dry$\cdot$m$^{-3}\cdot$yr^{-1}.

The pattern of production within the marsh also varies with latitude. North of 38°N, Turner (1976) found that no live *S. alterniflora* above ground biomass survived the winter. North of 38°N, therefore, *Spartina* production is essentially seasonal, peaking in summer. Teal (1962) and Teal and Teal (1969) point out that although *Spartina* growth is seasonal, algal production rises in winter when shading by grasses is reduced.

Great interest has been shown in the percentage of net production exported in the form of detritus and other material on the receding tide, as this represents a food energy source to coastal ecosystems. Teal (1962) found export in Georgia to be 45% of net production. This may be higher than average, but Turner (1976) found that the amount of dead organic material retained within marshes fell as tidal amplitude increased. It therefore seems likely that export from Fundy area marshes is a significant amount.

Detritus is acknowledged to be the main agent of energy export. Its formation from dead vegetation, particularly *Spartina* sp., has been studied in detail. May (1974) showed that fungi were of paramount importance in breakdown aided by bacteria. The process is also supplemented by the actions of herbivores and detritivores such as salt-marsh molluscs and crustaceans. Teal (1962) found that decomposition rates were highest on submergence marsh, with breakdown occurring in less than 3.5 mo. At higher levels complete breakdown took up to 5.5 mo. Teal worked in Georgia, and in the more northerly latitudes breakdown rates are slower. As breakdown proceeds, carbohydrate, fat, and caloric content fall, but the percent of protein rises as microbiotic populations build up.

SALT MARSH NUTRIENT RELATIONSHIPS

Ranwell (1962) points out that in salt marshes and other coastal systems the most frequent limiting nutrient is nitrogen. Phosphorous and the micronutrients are normally not limiting although iron may be in certain cases. Thus the dynamics of nitrogen in salt marshes is of paramount importance and has received considerable attention. Total nitrogen normally increases in salt-marsh soils moving from the seaward margin inland (Ranwell 1962); this probably reflects higher rates of nitrogen uptake in the submergence marsh. Natural nitrogen levels and reuse through mineralization are supplemented by two main sources: organic particles carried in from the sea and nitrogen fixation in the salt marsh ecosystem. The gain from the former is probably more than offset by detrital export. Nitrogen fixation in association with salt marsh vascular plants has been studied by Patriquin (1977), Patriquin and Keddy (1978), Teal et al. (1979), and others. Carpenter et al. (1978) looked at the role of blue-green algae in the process. Working in Nova Scotia, Patriquin and Keddy (1978) found nitrogen fixation in association with the roots of 15 common salt-marsh plants. Although these excluded *Spartina* species, other authors have demonstrated activity in association with them. Carpenter et al. (1978) found significant nitrogen fixation on the marsh surface by the blue-green alga, *Brachytrichia quoyi* and in algal mats by *Calothrix crustacea.* These combined methods of fixation result in a high total nitrogen fixation rate in salt marshes, which certainly contributes to their high productivity.

Salt Marsh Study Methods

Salt-marsh flora can be readily identified by reference to Hotchkiss (1970), Roland and Smith (1969), Scoggan (1978), and Ursin (1972). Fauna and algae may be identified with the aid of the group of manuals referred to in Chapter 4.

The field study of salt marshes does not require a

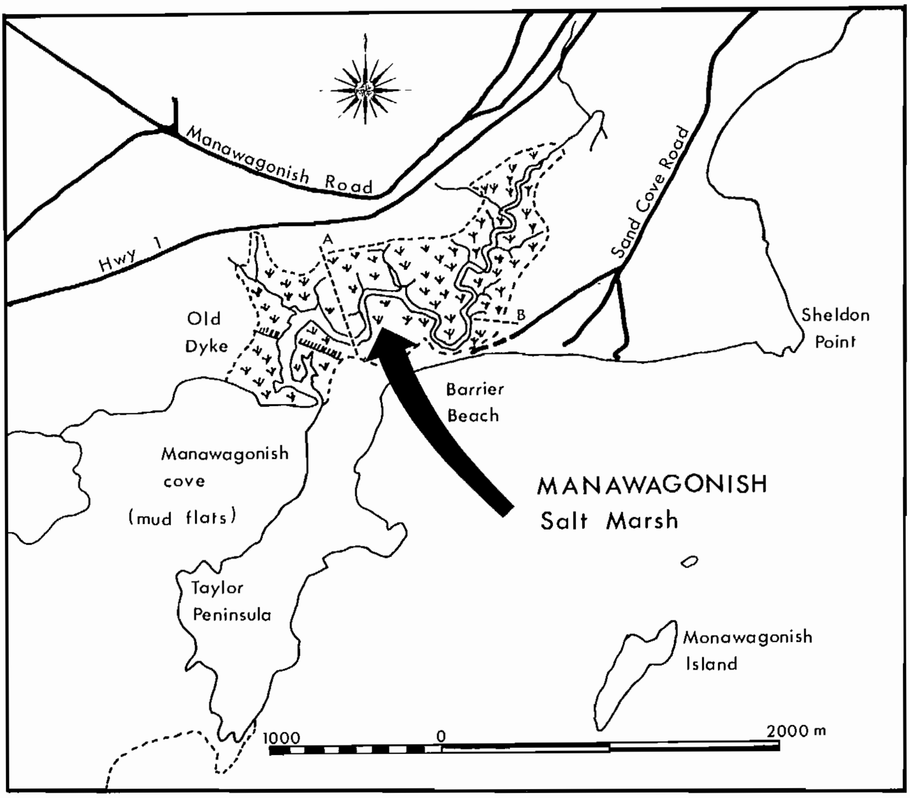

FIG. 3. The west Saint John area, showing the Manawagonish salt marsh and access roads. The two transects discussed in the text are marked A and B.

great deal of specialized equipment or the use of special techniques. For determining cross-sectional profiles, the methods described by Thomas in Chapter 4 are applicable; however, the lack of a horizon on many profiles necessitates the use of a level for sighting.

For estimates of abundance, the use of multiple 1/10 m^2 quadrats at closely spaced stations along transect lines is appropriate. Care should be exercised to ensure that samples are randomly distributed.

Biomass presents more of a problem, especially if below-ground portions are to be included. Normally ⅒ m^2 sample sizes are satisfactory.

Physical parameters such as temperature, soil particle size, etc. can be determined with standard techniques. Soil salinity, however, may present a problem. The low permeability and interstitial space of salt marsh soils makes collection of anything but tiny samples difficult. Soil may have to be pressed or centrifuged to obtain material. A refractometer is the most convenient means to determine salinity in small samples.

For techniques applicable to production estimates, nutrient studies, etc. workers are referred to summaries by Chapman (1960, 1964, 1977), Ranwell (1972), Reimold and Queen (1974), etc.

Descriptions of Specific Locations

MANAWAGONISH MARSH

Although somewhat outside the Quoddy Region, the Manawagonish Salt Marsh (see Fig. 1), lying within the S.W. part of Saint John, is an ideal study and teaching location. Figure 3 indicates its shape, location, and access. Access to its N.W. long side is from highway No. 1, and to its S.E. parts from Sand Cove Road. The flora and fauna of the marsh are typical of the area. In some areas the marsh shows disturbance by man and the effects of nutrient enrichment. A barrier beach advances inland over its surface. It is the best local marsh in which to observe the results of coastal subsidence. The lower extremity of the marsh is an old dyke, now breached, and to seaward of this are extensive mud flats. Some interior parts of the marsh were altered by the construction of a (now long-abandoned) rifle range.

The biotic composition does not differ greatly from the typical situation described in the section on communities and zonation, above, except that much of the marsh

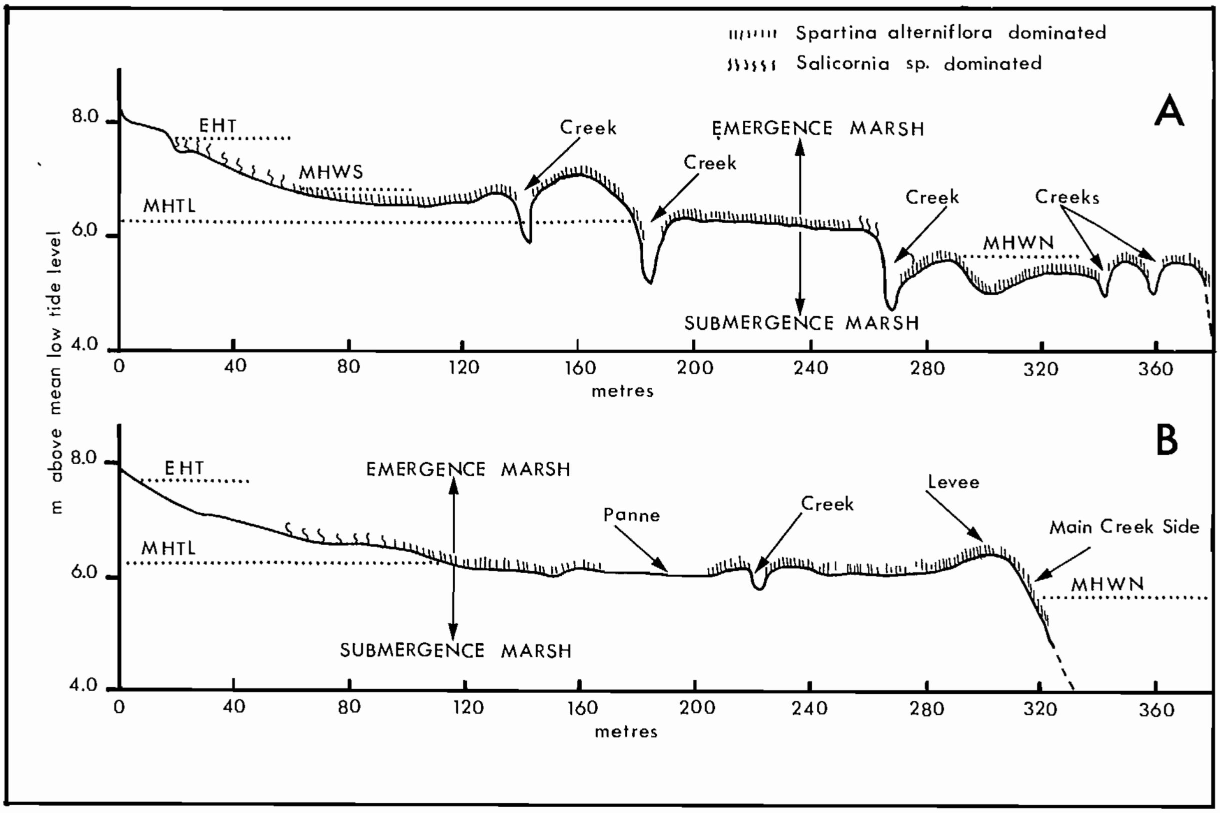

FIG. 4. Cross-sectional profiles of two transects of the Manawagonish salt marsh showing surface features and dominant vegetation. EHT, extreme high tide level; MHWS, mean high tide level of spring tides; MHWN, mean high tide level of neap tides; MHTL, mean high tide level.

border is either a road embankment or a barrier sand–gravel beach. In these locations the marsh edge communities are reduced or absent, and slough grass (*S. pectinata*) is present only occasionally.

Figure 4 shows two typical profiles from the edge of the marsh to the main channel. Their locations are shown in Fig. 3. One (3A) is situated where the main channel bank is eroding and thus the bank or levee is absent. The other shows a well-developed levee typical of a stable or acretion situation.

Figure 4 also shows a situation typical of this marsh, with dominance based on biomass chiefly vested in two species: *S. alterniflora* and *Salicornia* sp. *S. alterniflora* dominates both emergence and submergence marshes but *S. patens* does occur in patches on the emergence marsh. Common on the submergence marsh, and associated with *S. alterniflora*, are *Suaeda maritima, Atriplex patula, Plantago maritima, Triglochin maritima*, and *Limonium nashii*. On the emergence marsh *S. patens, Glaux maritima*, and *Potentilla anserina* are common. The latter species and *Salicornia*, which is more abundant here than at submergence levels, make striking shows of red and silver color following the first fall frosts.

It should be emphasized that almost all the salt-marsh species in Manawagonish Marsh show significantly over-dispersed (clumped) distribution patterns with high variance/mean ratios. The only exceptions, having random distributions, were *S. alterniflora* on lower creek banks only (elsewhere it was pronouncedly over dispersed), *Suaeda marina*, and *Atriplex patula*, as well as some terrestrial arthropods of the upper marsh. These over-dispersed distributions of major biota give the marsh flats a typically mosaic appearance.

Biomass levels reach maxima in late summer and show a pronounced falling gradient from submergence to emergence marsh. Characteristic levels at the main creek margin are 840–880 g/m^2 dry wt. In mid-marsh areas levels are typically from 350–680 g/m^2 and in the upper emergence marsh 150–388 g/m^2. These levels are only attained where *Spartina* sp. are present; elsewhere levels rarely exceed 100 g/m^2 and are frequently below 50 g/m^2.

Sediment samples taken along transects such as those shown in Fig. 3 and 4 show pronounced changes in particle size distribution. On the main creek side, median particle size is typically <3 μm, rising to about 30 μm on the creek bank or levee; a median of 23–28 μm is typical of submergence marsh flats rising steadily through emergence marsh to exceed 1000 μm by extreme high tide level. The percent sand and gravel (particles over 63 μm) rises along the same gradient from 2–3% on the creek side, to 2–9% in lower flats, 20–50% in upper flats, and over 50% on the marsh margin. The remainder of particles (silts and clays below 63 μm) show the opposite trend, with clays (<4 μm) dominating only creek side sediments.

The percentage of organic material in soils rises from about 5% (dry wt) on the creek side to 5.5–7.5% on the flats and then declines to 1–1.5% at the landward margin.

On flats, the aerated soil layer averaged about 8 cm deep and was underlain by black, anoxic deposits.

UPPER DUCK POND, CAMPOBELLO ISLAND

Figure 5 shows the location of the Upper Duck Pond salt marsh on Campobello Island (see Fig. 1 for general location). It lies within the Roosevelt–Campobello International Park and is thus protected from encroachment and alteration. It is cut off from the sea by a well developed barrier beach of sand and gravel, below which are extensive flats of muddy sand. A freshwater creek flows through the marsh and flows into the sea through a gap in the west end of the barrier beach. Nowhere does the marsh grade into the muddy sand flat. The marsh exhibits most typical communities and is excellent for demonstrating transition from salt marsh to terrestrial spruce forest. Great Duck Pond, lying just to the east, is of similar form but larger. However, it lacks an active freshwater stream and the barrier beach is complete. This marsh is therefore fresh. The two marshes are excellent for comparison and demonstrate the importance of a stream in maintaining a barrier beach gap which allows the sea to enter at high tide.

Figure 6 shows a cross-sectional profile of the marsh from the terrestrial edge to the creek side; the position of the transect is shown in Fig. 5. Upper Duck Cove is entirely an emergence marsh of very flat profile (note that the vertical scale is exaggerated) containing numerous large pannes over most of its surface. There is only one creek of significant size. Nevertheless, the marsh shows two distinct zones — a lower *S. alterniflora*-dominated one and an upper zone dominated by alternating areas of *S. patens* and *Plantago maritima*. Figure 6 also shows the distribution of common species on the marsh and these also tend to show a lower and upper group.

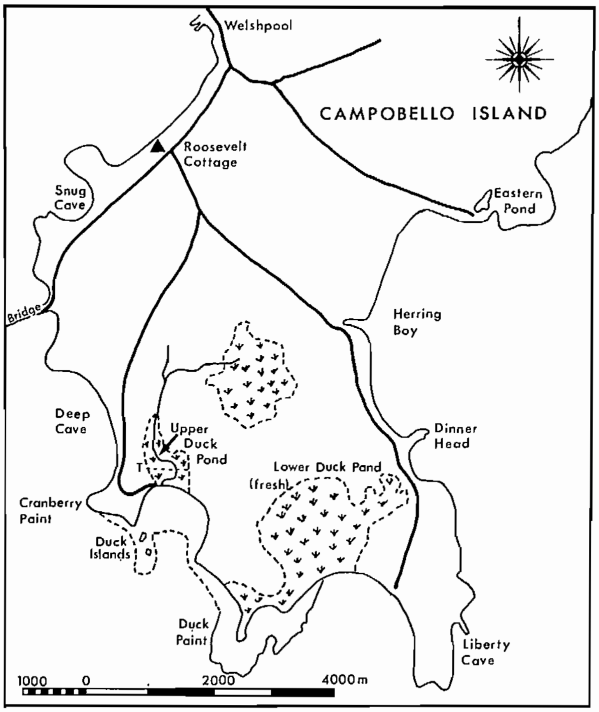

FIG. 5. The southern end of Campobello Island, showing the location of the Upper Duck Pond salt marsh and access roads. The transect discussed in the text is designated T.

The Upper Duck Pond marsh seems to have a compressed zonation. This may result from the very flat, wet conditions which retain sea and runoff waters efficiently. The soil within the marsh is very peaty in places, similar to marshes farther south.

Acknowledgments

I thank University of New Brunswick students Fred Page and Gary Thompson for their permission to incorporate data collected on field trips. I am also grateful to my assistant, Donna Baxter, who helped in the field and in laboratory analyses.

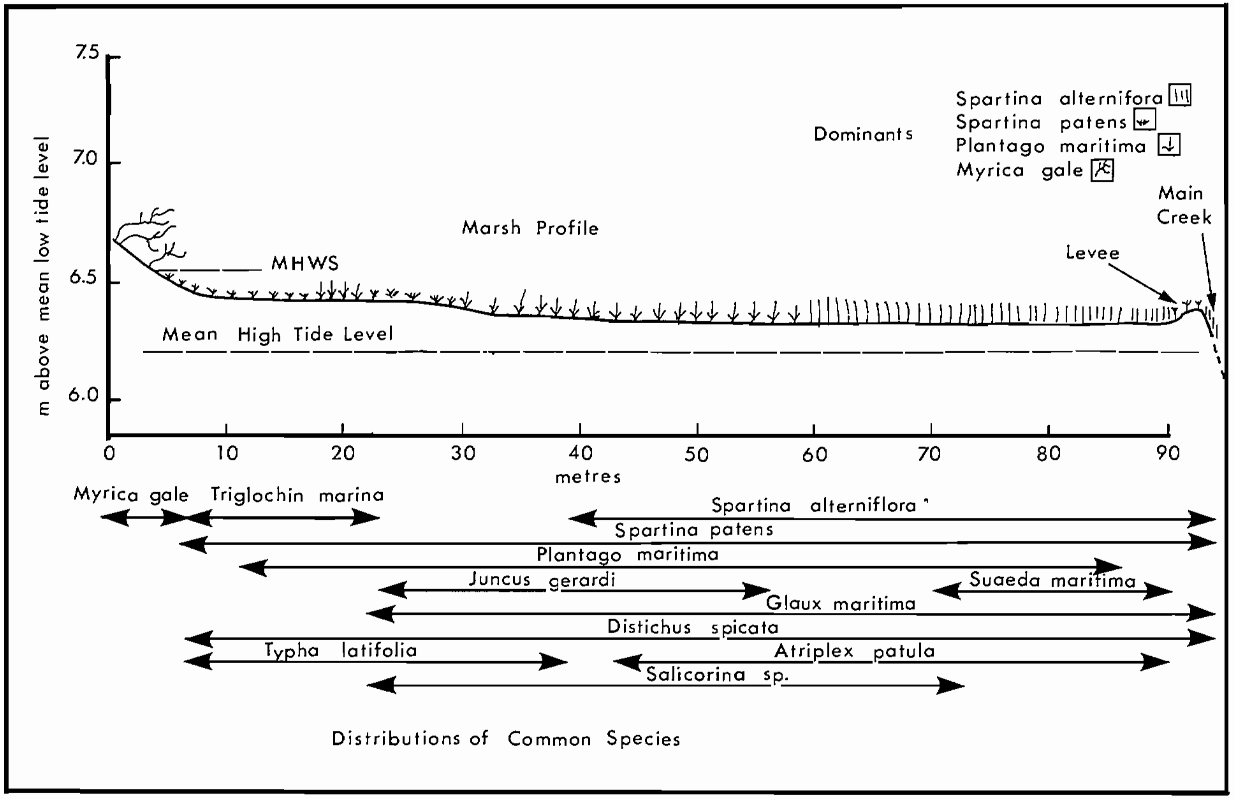

FIG. 6. Cross-sectional profile of a transect of Upper Duck Pond salt marsh, showing surface features and dominant plants. The distributions of common species are also shown (tidal level abbreviations as in Fig. 4).

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CHAPTER 8

Sublittoral Hard Substrates

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Introduction

Sublittoral hard substrates occur extensively in shallow coastal waters in the western part of the Bay of Fundy, particularly on the northwest shore; they are usually coincident with rocky or cliffed shorelines of resistant rocks, where the dominant destructive agent is subaerial weathering rather than marine erosion. Under these conditions rock rubble, ranging from boulder to pebble size, falls to the base of the cliff and forms a relatively steep zone of submerged rock debris, grading seawards into sand and mud at depths beyond about −30 m. Occasionally, submarine rock outcrops may occur as jutting "ledges", exhibiting both inclined and vertical faces, depending upon the attitude and joint directions of the rock stratum. Isolated hard substrates also occur in some deeper water areas, where coarse relict glacial tills have remained free of mud due to strong bottom currents (Fader et al. 1977).

The geographic distribution of various coastline types in the Bay of Fundy, based on aerial photographs, was first compiled by Welsted (1974) and subsequently described in greater detail by Owens (1977) and Owens and Bowen (1977). The complex shoreline of bays, headlands, and islands in the Passamaquoddy Bay area is the result of a combination of many factors, most prominently the southwest–northeast structural trend, the resistant nature of the Paleozoic rocks, the effects of glaciation, and the gradual submergence of the terrain during the geologically-recent rise in sea level. In the southwestern part of New Brunswick, the character of the coastline is strongly influenced by the bedrock geology of the region (Logan and Noble 1971). Thus pre-Acadian[1] igneous and metamorphic rocks tend to produce rocky resistant coastlines with bouldery substrates, whereas post-Acadian sedimentary rocks result in coastlines dominated by substrates of sand and mud (Fig. 1). In the immediate vicinity of St. Andrews and western Passamaquoddy Bay, the weathering and erosion of post-Acadian sedimentary rocks of Late Devonian age and sediments of Quaternary age, combined with low energy wave conditions in the lee of Deer Island (Owens 1977; Owens and Bowen 1977) and the discharge of river-borne sediments into the Bay have produced mainly sand and mud substrates. The more resistant pre-Acadian rocks farther south and east of this region have resulted in hard rocky substrates, which are particularly well developed around the off-shore islands of Deer Island, Campobello Island, and Grand Manan. It is in these areas of relatively clear waters that most existing studies on sublittoral hard substrates in the Bay of Fundy have been done (Logan and Noble 1971; Noble et al. 1976; MacKay 1978). In this review however, we confine our descriptions of hard substrates to the St. Croix Estuary, Passamaquoddy Bay, western Letite Peninsula, and Deer Island–Campobello Island.

Sublittoral hard substrates are of great interest to biologists, because they provide a firm attachment for a very diverse epifauna and epiflora. Sessile and encrusting forms include coelenterates, sponges, bryozoans, brachiopods, barnacles, annelids, bivalves, and tunicates; motile forms include echinoderms, gastropods, amphineurans, and arthropods. In shallow water, where sufficient illumination reaches the bottom, encrusting calcareous red algae are common on exposed surfaces, together with occasional stands of seaweeds. Between and beneath boulders and below overhangs are numerous microhabitats, each microenvironment exhibiting differences in illumination, temperature, water energy, food supply, sedimentation rates, and other factors which produce a wide diversity of cryptic (shaded) habitat biota. In addition, some rock or shell surfaces are bored by endolithic species, which construct a network of holes or tunnels and contribute to the sediments by bioerosion.

Modern sublittoral hard substrates are of less interest to geologists, because such bottoms represent transient stages of erosion rather than sedimentation, and are therefore rarely preserved in the geological record except as beds immediately above depositional breaks. However, recent recognition in the geological record of ancient sea floors which were lithified and hard prior to burial has prompted renewed interest in these so-called "hardgrounds"; Noble et al. (1976) demonstrated many similarities between Jurassic and Cretaceous hardground biotas and those from modern-day sublittoral hard substrates in the Bay of Fundy, suggesting that such a modern rocky community is a reasonable model for any hard substrate community. Clearly there is value in the study of modern sublittoral hard substrate communities for paleoecological reconstruction and yet, apart from those on coral–algal reef habitats, such studies have been relatively

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[1] The term "Acadian" does not refer to a geological time period but to an orogenic event, which is generally recognized by geologists as having occurred during late Middle and early Late Devonian time (Poole et al. 1970).

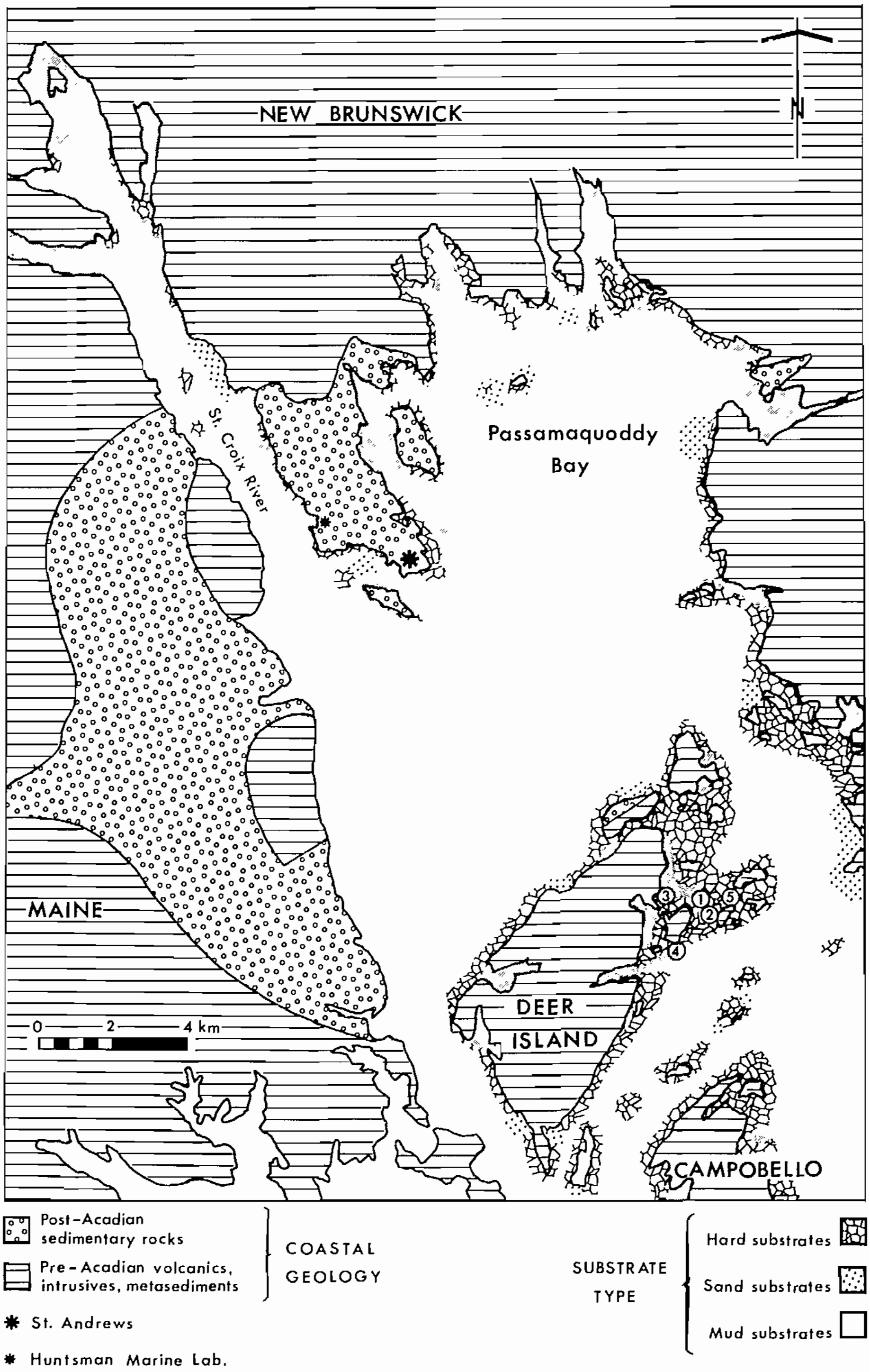

FIG. 1. Passamaquoddy Bay and adjacent areas, showing relationship of shallow sublittoral substrates to coastal rock types. Location 1, Haddock Ledge A; 2, Haddock Ledge B; 3, Hathaway Head; 4, Bean Island; 5, Nub Island (after Noble et al. 1976; MacKay 1978.).

few. Notable exceptions include studies by French and Scandinavian investigators during the last 20 yr, some of which are referred to below.

We do not propose herein to discuss in detail the validity or lack thereof of the community concept as applied to marine benthos (see Jones 1950; Mills 1969; and Stephenson 1973 for comprehensive reviews of this subject). In this study we have adopted the biocoenotic concept of a community, following the dominance–constancy school (Thorson 1957; Stephenson 1973). In the Bay of Fundy, predominantly hard substrate communities may be distinguished from predominantly soft substrate communities, but within the hard substrate communities there are both discrete and gradational variations which are probably related to parameters of the physical environment such as temperature, salinity, light, and substrate and to biotic factors such as species interactions and trophic relationships.

For the purposes of discussion we regard sublittoral hard substrates in the Bay of Fundy as comprising rock outcrop (ledges), boulders (free rocks over 256 mm in diameter), cobbles (64–256 mm in diameter), and pebbles (2–64 mm in diameter), as well as organic hard substrates such as shells, both living and dead. We also include the substrates afforded by man-made objects such as wharfs, pilings, and weir poles, which allow attachment of benthic organisms.

We use the terminology of French authors (Pérès 1967) to divide the sublittoral zone into vertical zones based on biotic composition rather than depth. Thus the infralittoral zone extends from extreme low water spring tide (ELWS) to the limit of existence of photophilous algae, this limit coinciding approximately with the 1% level of surface illumination; the infralittoral zone is therefore approximately equivalent to the photic zone, and extends to about −15 m in depth in the Deer Island region. The circalittoral zone extends from the lowest level of photophilous algae to the approximate edge of the continental shelf; although aphotic, it is theoretically possible for sciaphilous algae to live in these light-poor conditions, as in the Mediterranean.

Sampling Methods

The collection and subsequent study of the biota and associated sediments of sublittoral hard substrates has proved more difficult than that of soft sediment bottoms. First, there is the difficulty of sampling rocky bottoms effectively, even in shallow water, using conventional remote sampling methods such as dredging. Second, the numerous microhabitats produced by such substrates impose severe problems for the investigator attempting to discriminate between physical limiting factors and biological interactions. For example, Drach (1958) has recognized eight different microhabitats from sublittoral rocky substrates from Britanny, based on differences in inclination of rock surfaces and their effect on environmental factors. Because of these difficulties, biological studies of hard, non-carbonate, sublittoral substrates have been relatively few and and were rare prior to the invention of SCUBA. The gradual refinement of free-diving techniques has allowed the marine scientist direct access to shallow water rocky bottoms down to a depth of about −40 m, the approximate limit for safe diving with conventional air-breathing apparatus. Below that depth, direct observation and some sampling may be made from submersibles (Laborel et al. 1961; Vaissière and Carpine 1964); otherwise sampling must still be attempted by remote collecting methods, with their concomitant unreliability.

REMOTE SAMPLING METHODS

Holme (1971) reviewed remote (indirect) sampling methods such as dredges, trawls, and grab samplers, but pointed out the inadequacy of such methods for obtaining a representative undamaged sample from rocky bottoms. We have used rock dredges with metal rings successfully in deep-water areas for benthic sampling, but trawls and grab samplers are highly unsatisfactory on hard substrates larger than pebble size. In the deeper parts of the Bay of Fundy, Caddy (1970) obtained some success with a scallop dredge for collecting biota attached to shell substrates, while Emery et al. (1965) and Fader et al. (1977) photographed and brought up occasional boulders from deep water off the eastern coast of North America by means of remote-control cameras attached to grab samplers.

MANUAL SAMPLING METHODS

In shallow water, sublittoral hard substrates are best sampled by divers employing SCUBA. In this way, direct observation, photography, and census-taking may be performed by a trained diver (who is preferably also a marine scientist) and samples of biota, substrate, and associated sediments may be subsequently brought to the surface for laboratory examination. Surveying or monitoring methods for sublittoral areas, using diving, have recently been summarized by Hiscock (1979). If only certain members of the benthos, such as echinoids, are being studied, they may be counted and then picked up along transect lines (Forster 1959; Larsson 1968; Mackay 1976). Hiscock and Hoare (1973) and Gulliksen and Derås (1975) have described diver-operated suction samplers for rocky bottom faunas; following pre-collection photography, the weakly-attached forms are removed easily by the suction device, but the strongly-attached forms must first be loosened with a scraping knife. We have used a modified Brett sampler (Holme 1971) for sampling shell-rich sediments where it is not important to collect the fines.

On very large boulders or rock outcrops, where rock removal is not practicable, it may be necessary to remove the biota by scraping, especially where attached or encrusting species predominate. A variety of techniques have been employed for this procedure, mainly by French investigators studying Mediterranean sublittoral hard substrates (Vacelet 1967; True 1970; Harmelin 1976). Removal of biota should always be preceded by photography of the surface to be sampled. One of us (A.L.) uses the following technique for investigation of attached ledge biotas in the Bay of Fundy sublittoral zone. The in situ population is initially photographed using both single-frame and stereo-pair imagery, with an amphibious 35-mm Nikonos camera with a 28-mm lens and a close-up

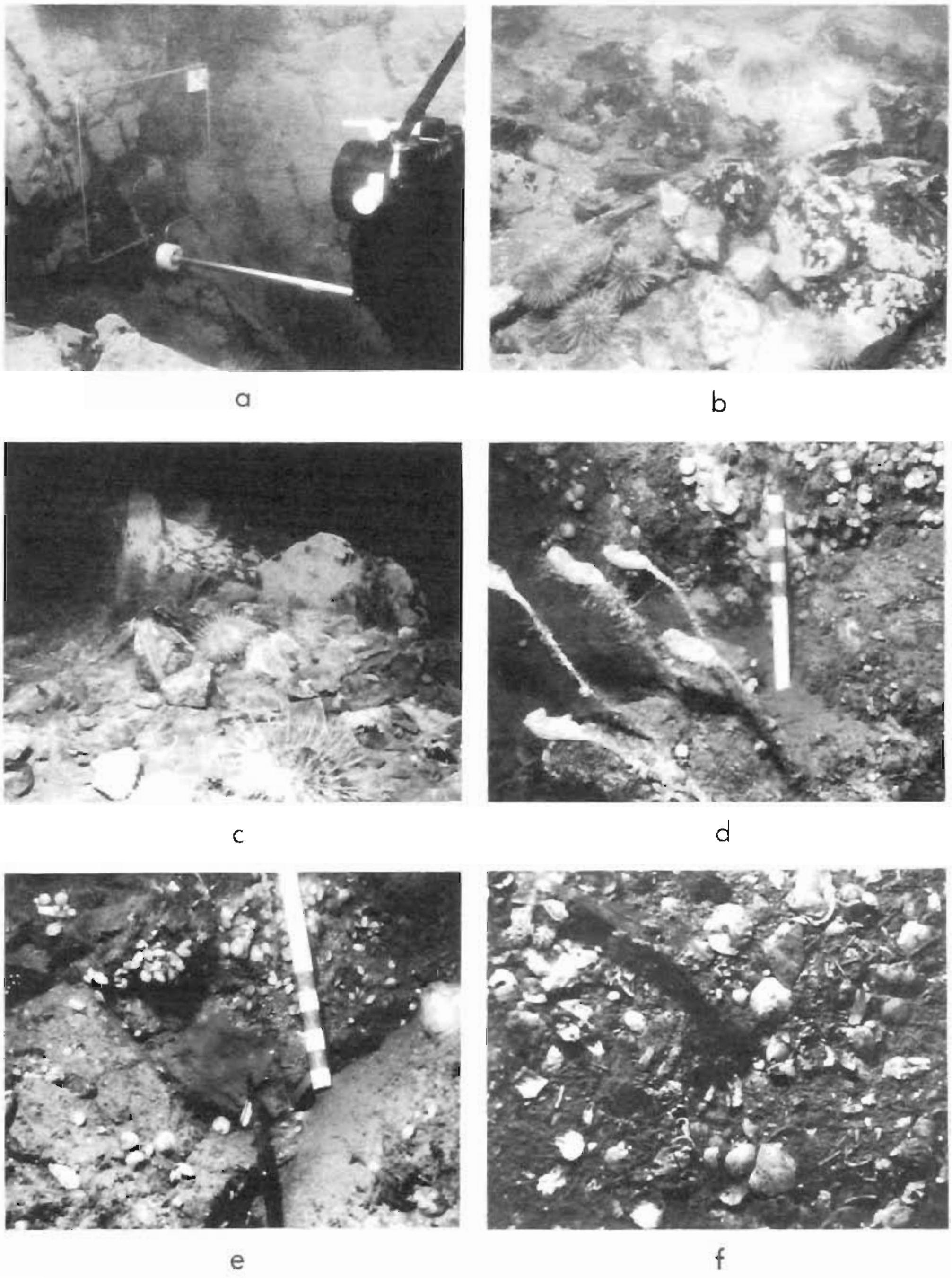

FIG. 2. (a) Close-up photography of steeply-dipping rock outcrop using Nikonos system, −3 m, Nub Island; (b) algal-covered boulders, shell-rich sediment pockets, and sea urchins, −8 m, Nub Island; (c) boulders, sediments, and biota on narrow shelf, −10 m, Nub Island; (d) biota attached to vertical ledge, −18 m, Nub Island (scale 12″ long, current right to left, as indicated by inclination of stalked tunicates); (e) brachiopods, sponges, and anemones attached to ledge, −26 m, Nub Island (scale 12″ long); (f) shell-rich sediments at base of ledge, −30 m, Nub Island (*shrimp* approximately 15 cm long).

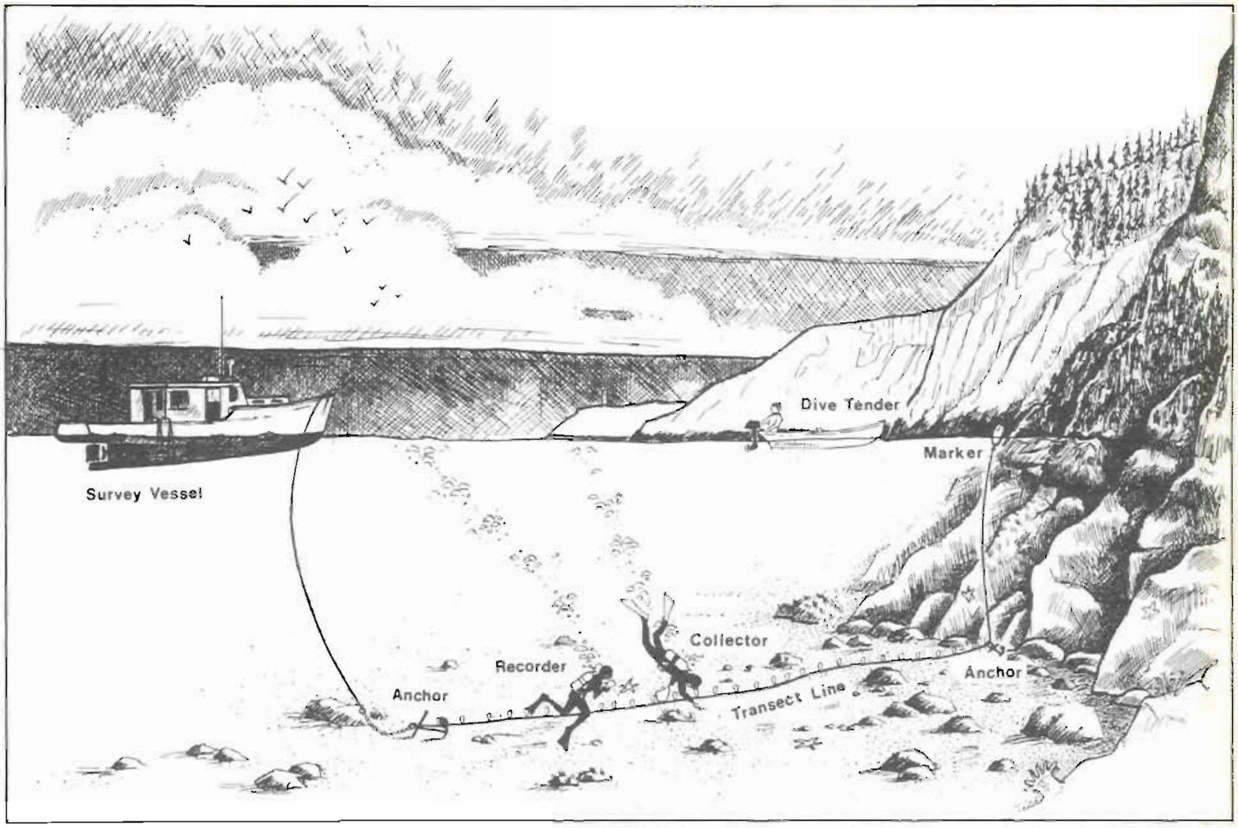

FIG. 3. Methodology for making transects along sublittoral rocky floor, Bay of Fundy (after MacKay 1975, 1978).

photographic system employing electronic flash and fine-grained color film (Fig. 2a, 11). This system incorporates a frame of 310 cm^2, the enclosed area of which can first be photographed to record spatial relationships, density, etc. (see also Gulliksen 1974, 1978); the area can then be scraped, using a knife, and a sample net can be attached to an underwater light to collect the biota. The photographs are valuable for subsequent analysis, as diving time is short in cold water, visual impressions are fleeting, and organisms are sometimes lost or damaged beyond recognition during the scraping process. Photography also enables test areas to be monitored periodically; thus single-frame and stereo-pair imagery has been used by Lundälv (1971), Torlegard and Lundälv (1974) and Rørslett et al. (1978) to quantitatively measure density, areal coverage, and size distribution over intervals of time, using photogrammetric techniques. Such periodic photographic quantitative sampling offers great potential for studying the dynamics of communities, as well as for in situ experimental manipulation of populations inhabiting test areas (Bohnsack 1979). A recent review of photography as a potentially-valuable research tool in marine biological research has been given by George (1980).

Line transect techniques involve the counting and/or collection of biota along a line laid across the sea floor. The various procedures used in setting up transects have been reviewed by Holme (1971). Quadrats of various sizes are often employed in conjunction with line transects and have long been used in sampling coral reefs (Loya 1978). The methodology used by MacKay (1975, 1978) for a transect in the Bay of Fundy is shown in Fig. 3. Transects have advantages over random spot sampling in that all substrate types are sampled and any zonation based on depth should emerge. MacKay (1975, 1978) and Noble et al. (1976) both employed line transects directed perpendicular to the shore, with sampling stations at fixed intervals along the transect lines.

Finally, the technique of sampling a developing community by submergence of artificial settling panels over varying lengths of time has been in general use for many years and is still being used in current biofouling studies (e.g. Anger 1978).

Laboratory Procedures

Laboratory procedures on collections of macrobenthos usually consist of preservation, identification, and determination of fresh weight and/or ash-free dry weight biomass (for detailed description of technique see Thorson 1957). Areal coverage of individual species can be obtained from analysis of photographs (Bohnsack 1979) or can be calculated by using a grid system on the rocks collected. Point sampling is also useful for determining areal coverage on surfaces (Sutherland 1974). Numerical counts of individuals attached to hard substrates present some difficulties, especially where colonial animals — such as encrusting bryozoans — occur. Noble et al. (1976) counted all such colonies as individuals, admitting that the accuracy of relative abundance and dominance measures is influenced by such procedures. Grain counts on sediment samples likewise pose problems: the test of a single sea urchin may be broken into hundreds of plates and spines, while molluscs and brachiopods are more durable. Differential fragmentation caused by variable skeletal durability may also account for the low bryozoan content in all but the finest sieve fractions of sediment samples (Noble et al. 1976). The loss of any record of sessile tunicates and coelenterates in the sediment is clearly related to the virtual absence of calcareous skeletons in living representatives of these groups in the Bay of Fundy; this must be taken into account in comparative studies of communities (biocoenoses) and the death assemblages (thanatocoenoses) in adjacent sediments.

The Biotic Communities

The recognition of distinctive sublittoral hard substrate communities in the Bay of Fundy is based mainly on studies in the Deer Island region (Logan and Noble 1971; Webb 1976; and Noble et al. 1976) and on 15 yr of long-term collecting and transect work by MacKay (1975, 1978) off mainland southwestern New Brunswick and offshore islands.

Noble et al. (1976) initially regarded the sublittoral hard substrate benthos in the Deer Island region as belonging to a single community, which was named the *Terebratulina septentrionalis* Community[2], after the widespread, conspicuous, and recurrent presence of the articulate brachiopod *Terebratulina septentrionalis*, a distinctive species exhibiting extremely high fidelity to hard substrates. At that time they divided the community into three subcommunities: the cavity, rock-face, and upper-surface subcommunities. The community as a whole is spatially and temporally heterogenous and is spread over two zones, the shallow infralittoral zone and the deeper circalittoral zone. The *Terebratulina septentrionalis* Community of the infralittoral zone occurs cryptically on the undersides of rocks and also within crevices and beneath overhangs down to about -20 m. In the deeper circalittoral zone below -50 m, the community begins to colonize the upper surfaces as well as the sides of boulders and ledges. Evidence for its occurrence at this depth is based on dredgings by Caddy (1970) and Bedford Institute of Oceanography personnel (unpublished data), on photographs taken by Emery et al. (1965) and Fader et al. (1977), and on unpublished photographs recently taken by Logan. In waters of intermediate depth (-20 to -50 m) within the circalittoral zone the community may occupy a transitional zone of more or less vertical shaded rock faces. Thus gradational subcommunities ("facies" of Pérès and Picard 1964), based upon variations in physical and perhaps biotic factors, may be recognized in this community.

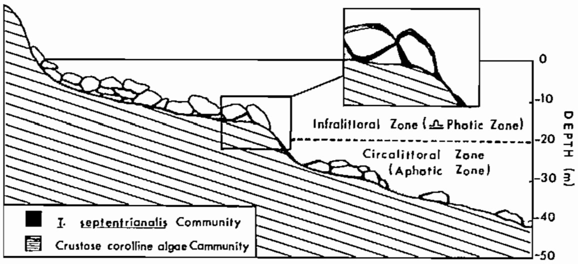

FIG. 4. Profile showing divisions of sublittoral zone, and spatial relationships between the two hard substrate communities (horizontal distance not to scale).

The other distinctive community which is now recognized is the crustose coralline algae Community (formerly the upper surface subcommunity of the *Terebratulina septentrionalis* Community of Noble et al. 1976), which is dominant on upper surfaces in the infralittoral zone down to depths of about -20 m (the exact limit depending upon turbidity and resultant light penetration). Within this zone it is closely associated with the *Terebratulina septentrionalis* Community, although it occurs on upper surfaces and sides of rocks and ledges exposed to illumination, whereas the *Terebratulina septentrionalis* Community is more or less confined to the undersides of boulders. Below about -20 m, the crustose coralline algae Community gradationally passes into the *Terebratulina septentrionalis* Community, which begins to emerge from the cryptic habitat to spread over the sides and, at still greater depths, the upper surfaces of rocks and ledges. The relationship between these two communities is shown diagrammatically in Fig. 4.

Not included in the above classification are the biotas attached to man-made objects such as wharf pilings, weir poles, and floats or those attached to shell substrates, which are not as yet sufficiently studied to be defined.

Table 1 shows the distribution of biota of these communities on hard substrates in the Deer Island–Campobello Island area and in the Passamaquoddy Bay–Letite area, together with the frequency of occurrence of each species in the Deer Island, Campobello Island, and Passamaquoddy Bay–Letite areas; many of the commonest species are illustrated in Plates I and II. Figures 5 and 6, respectively, show the distribution of organisms on a generalized subtidal rocky bottom and on wooden man-made structures, such as floats and pilings. The data in Table 1 suggests a higher diversity, abundance, and frequency of species in the Deer Island region compared to Passamaquoddy Bay–Letite and Campobello Island. MacKay (1978) believes this results from a combination of several factors, principally a varied bottom topography, narrow channels between islands, and vigorous tidal exchange. This leads to efficient vertical mixing, which distributes nutrients and food to all levels and makes surface phytoplankton available to bottom suspension feeders.

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[2] This community appears to be equivalent, at least in part, to the Offshore Hard Bottom Community of the Eastern Atlantic (Jones 1950) and the *Modiolus modiolus* Community of the same region (Roberts 1975; Hiscock and Mitchell 1980).

TABLE 1. Distribution of biota belonging to sublittoral hard substrate communities, Bay of Fundy. P, Passamaquoddy Bay; L, Letite area; D, Deer Island; Co, Campobello Island; R, rare; C, common; A, abundant. Frequencies are based on 72 localities for Passamaquoddy Bay–Letite, 96 for Deer Island, and 46 for Campobello — mostly from spot dive observations (MacKay 1978).

Group	Species	Crustose coralline algae community		*Terebrat. septent.* community		Man-made substrates		Shell substrates		% Freq. occurrence		
		P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D	Co.
Porifera	*Leucosolenia botryoides*	—	—	C	R	C	R	—	—	5.6	3.1	0.0
	Scypha ciliata	—	—	R	R	R	R	—	—	1.4	3.1	4.3
	Haliclona (Chalina) oculata	A	C	—	—	A	C	—	—	12.5	53.1	21.7
	Halichondria sp.	A	C	A	C	A	C	—	C	33.3	89.6	37.0
	Suberites sp.	R	R	—	—	—	R	—	—	2.8	1.0	2.2
	Iophon pattersoni	—	C	—	R	—	C	—	—	0.0	60.4	0.0
	Myxilla-like	R	C	—	—	R	C	—	—	1.4	68.8	4.3
	Melanochora-like	—	R	—	—	—	R	—	—	0.0	4.2	0.0
	Cliona celata	R	R	—	R	—	R	—	R	0.0	3.1	0.0
Coelenterata	*Tubularia* sp.	A	C	—	—	C	C	—	C	12.5	91.7	10.9
	Coryomorpha pendula	—	C	—	—	R	A	—	—	12.5	49.0	0.0
	Obelia sp.	C	A	C	A	C	A	—	A	26.4	52.1	8.7
	Antennularia sp.	R	C	—	—	—	—	—	C	2.8	58.3	2.2
	Hydractinia sp.	—	—	—	—	—	—	—	R	0.0	2.1	0.0
	Aurelia schyphistoma	—	—	—	C	—	C	—	C	0.0	7.3	2.2
	Alcyonium digitatum	—	C	—	—	—	—	—	C	0.0	27.1	0.0
	Gersemia rubiformis	C	C	—	—	—	—	—	A	2.8	44.8	4.3
	Tealia felina	C	C	—	C	C	C	—	—	6.9	93.8	26.1
	Metridium senile	A	A	—	A	A	A	—	—	38.9	91.7	32.6
Nem.	*Amphiporus* sp.	—	—	R	C	—	—	—	—	6.9	35.4	0.0
Bryozoa	Subtidal erect species	A	—	A	C	A	C	—	C	15.3	85.4	30.4
	Subtidal encrusting species	—	—	A	C	A	C	—	C	13.9	58.3	15.2
Brach.	*Terebratulina septentrionalis*	—	—	R	A	—	R	—	C	1.4	91.7	28.3
Mollusca	*Ischnochiton alba*	C	—	C	C	—	—	—	—	9.7	75.0	4.3
	Ischnochiton ruber	A	C	A	A	—	—	—	—	54.3	95.8	29.2
	Tonicella marmorea	R	R	R	—	—	—	—	—	2.8	1.0	0.0
	Acmaea testudinalis	C	C	C	C	—	—	—	—	47.2	85.4	60.9
	Margarites sp.	C	C	C	C	—	—	—	—	8.3	34.4	6.5
	Crucibulum striatum	R	R	—	—	—	—	—	R	1.4	2.2	2.2
	Crepidula fornicata	—	R	—	—	—	—	—	R	4.2	2.2	2.2
	Velutina sp.	R	R	—	—	—	—	—	R	2.2	1.0	2.2
	Buccinum undatum	C	C	C	C	C	C	—	—	45.8	96.9	43.5
	Neptunea decemcostata	C	C	—	—	—	—	—	—	22.2	94.8	34.8
	Colus stimpsoni	—	C	—	—	—	—	—	—	0.0	68.8	8.7
	Dendronotus sp.	C	—	C	—	C	C	—	—	2.8	46.9	6.5
	Coryphella sp.	C	C	C	C	C	C	—	—	11.1	44.8	6.5
	Aeolidia papillosa	R	R	—	—	R	R	—	—	1.4	13.5	0.0
	Puncturella noachina	R	—	R	R	—	—	—	—	1.4	1.4	0.0
	Nassarius obsoletus	R	—	—	—	—	—	—	—	1.4	0.0	0.0
	Acanthodoris pilosa	C	C	C	C	C	C	—	—	5.6	?	?

	Species	Crustose coralline algae community		*Terebrat. septent.* community		Man-made substrates		Shell substrates		% Freq. occurrence		
		P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D	Co.
Mollusca	*Onchidorus* sp.	C	C	C	C	C	—	—	—	5.6	29.2	4.3
	Musculus sp.	—	R	R	—	R	R	—	—	1.4	1.0	2.2
	Modiolus modiolus	C	A	—	—	—	—	—	—	9.7	85.4	26.1
	Anomia sp.	C	—	C	C	C	C	—	C	2.8	33.3	2.2
	Hiatella arctica	C	C	C	C	C	C	—	—	6.9	64.6	2.2
	Zirphaea crispata	R	—	—	—	—	—	—	—	1.4	0.0	0.0
	Chlamys islandicus	—	C	—	C	—	—	—	—	0.0	61.5	4.3
	Mytilus edulis	C	C	—	—	—	—	—	—	43.1	94.8	21.7
Annelida	*Lepidonotus* sp.	C	—	C	C	C	C	—	—	13.9	92.7	8.7
	Harmothoe sp.	—	—	R	C	R	C	—	—	4.2	19.8	0.0
	Nereis pelagica	—	—	—	—	—	R	—	—	0.0	1.4	0.0
	Potamilla sp.	R	C	—	—	—	—	—	—	1.4	65.6	0.0
	Myxicola infundibulum	C	A	C	C	C	A	—	—	11.1	93.8	28.3
	Filograna sp.	R	R	R	R	—	—	—	—	1.0	1.0	2.2
	Spirorbis sp.	C	C	C	C	C	C	—	C	22.2	88.5	4.3
	Amphitrite johnstoni	C	—	C	C	C	—	—	—	8.3	85.4	0.0
Arthropoda	*Balanus balanus*	C	C	C	C	C	C	—	C	19.4	92.7	15.2
	Balanus crenatus	—	C	—	—	—	C	—	C	0.0	29.2	0.0
	Caprella sp.	—	—	—	—	C	C	—	—	2.8	28.1	0.0
	Spirontocaris spinus	—	C	—	—	C	C	—	—	4.2	16.7	0.0
	Pandalus montagui	C	C	—	C	C	C	—	—	9.7	90.6	19.6
	Homarus americanus	C	C	C	C	—	—	—	—	11.1	77.1	15.2
	Pagurus sp.	C	A	—	—	—	—	—	—	29.2	95.8	67.4
	Hyas sp.	C	C	—	—	C	C	—	—	8.3	93.8	2.2
	Cancer sp.	C	A	C	A	C	A	—	—	31.9	100.0	32.6
	Carcinus maenas	C	—	—	C	C	C	—	—	30.6	28.1	0.0
	Nymphon sp.	—	R	—	R	—	—	—	—	0.0	1.0	0.0
Echinodermata	*Psolus fabricii*	C	C	—	—	—	—	—	—	26.4	39.6	28.3
	Cucumaria frondosa	C	C	C	—	C	—	—	—	33.3	71.9	21.7
	Strongylocentrotus droebachiensis	A	A	—	R	A	A	R	R	62.5	100.0	84.8
	Hippasterias phrygiana	—	R	—	—	—	—	—	—	0.0	18.8	4.3
	Solaster endeca	C	C	—	—	—	—	—	—	9.7	50.0	6.5
	Solaster papposus	R	C	—	—	—	—	—	—	2.8	77.1	4.3
	Pteraster militaris	—	C	—	—	—	—	—	—	0.0	39.6	0.0
	Henricia sanguinolenta	C	C	C	C	C	C	—	—	22.2	93.8	43.5
	Asterias forbesi	C	R	C	—	C	—	—	—	38.9	2.1	0.0
	Asterias vulgaris	C	A	—	—	C	A	—	—	52.8	96.9	69.6
	Gorgonocephalus arcticus	—	C	—	—	—	—	—	—	0.0	64.6	6.5
	Ophiopholis aculeata	—	A	C	A	—	—	—	—	19.4	95.8	23.9
	Amphiopholis squamata	—	—	R	R	—	—	—	—	1.4	1.4	0.0

	Species	Crustose coralline algae community		*Terebrat. septent.* community		Man-made substrates		Shell substrates		% Freq. occurrence		
		P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D-Co.	P-L	D	Co.
Protochordata	*Ciona intestinalis*	—	—	R	—	—	—	—	—	1.4	0.0	0.0
	Botryllus schlosseri	—	R	—	R	R	R	—	—	2.8	1.0	2.2
	Boltenia ovifera	C	A	—	—	C	A	—	—	6.9	89.6	23.9
	Boltenia echinata	R	C	R	C	R	C	—	C	2.8	82.3	6.5
	Halocynthia pyriformis	C	A	—	—	C	A	—	—	34.7	91.7	23.9
	Molgula sp.	—	C	—	C	—	C	—	C	0.0	16.7	2.2
Chordata	*Raja* sp.	—	R	—	—	—	—	—	—	0.0	2.2	2.1
	Hemitripterus americanus	—	C	—	—	—	C	—	—	0.0	65.6	15.2
	Myoxocephalus sp.	C	C	—	—	—	—	—	—	25.0	39.6	15.2
	Cyclopterus sp.	—	R	—	—	—	—	—	—	0.0	2.1	4.3
	Liparis sp.	—	R	—	—	—	R	—	—	0.0	1.0	2.1
	Pseudopleuronectes americanus	A	C	—	—	A	—	—	—	38.9	72.9	17.4
	Anguilla rostrata	—	—	C	—	—	—	—	—	4.2	0.0	0.0
	Pholis sp.	—	—	C	C	—	—	—	—	11.1	32.3	26.1
Algae	*Gigartina* sp.	R	—	—	—	—	—	—	—	1.4	0.0	0.0
	Lithothamnion polymorphum	A	A	—	—	—	—	—	—	48.6	99.0	84.8
	Phycodrys sp.	R	C	—	—	R	—	—	—	1.4	33.3	8.7
	Desmarestia sp.	R	C	—	—	—	—	—	—	1.4	50.0	23.9
	Laminaria sp.	C	—	—	—	—	C	—	C	12.5	49.0	39.1
	Agarum sp.	C	C	—	—	C	C	—	C	9.7	66.7	63.0
	Porphyra sp.	R	C	—	—	—	C	—	—	4.2	14.6	8.7
	Alaria sp.	—	C	—	—	—	C	—	—	0.0	5.2	32.6
	Ulva sp.	R	C	—	—	R	C	—	—	23.6	63.5	28.3

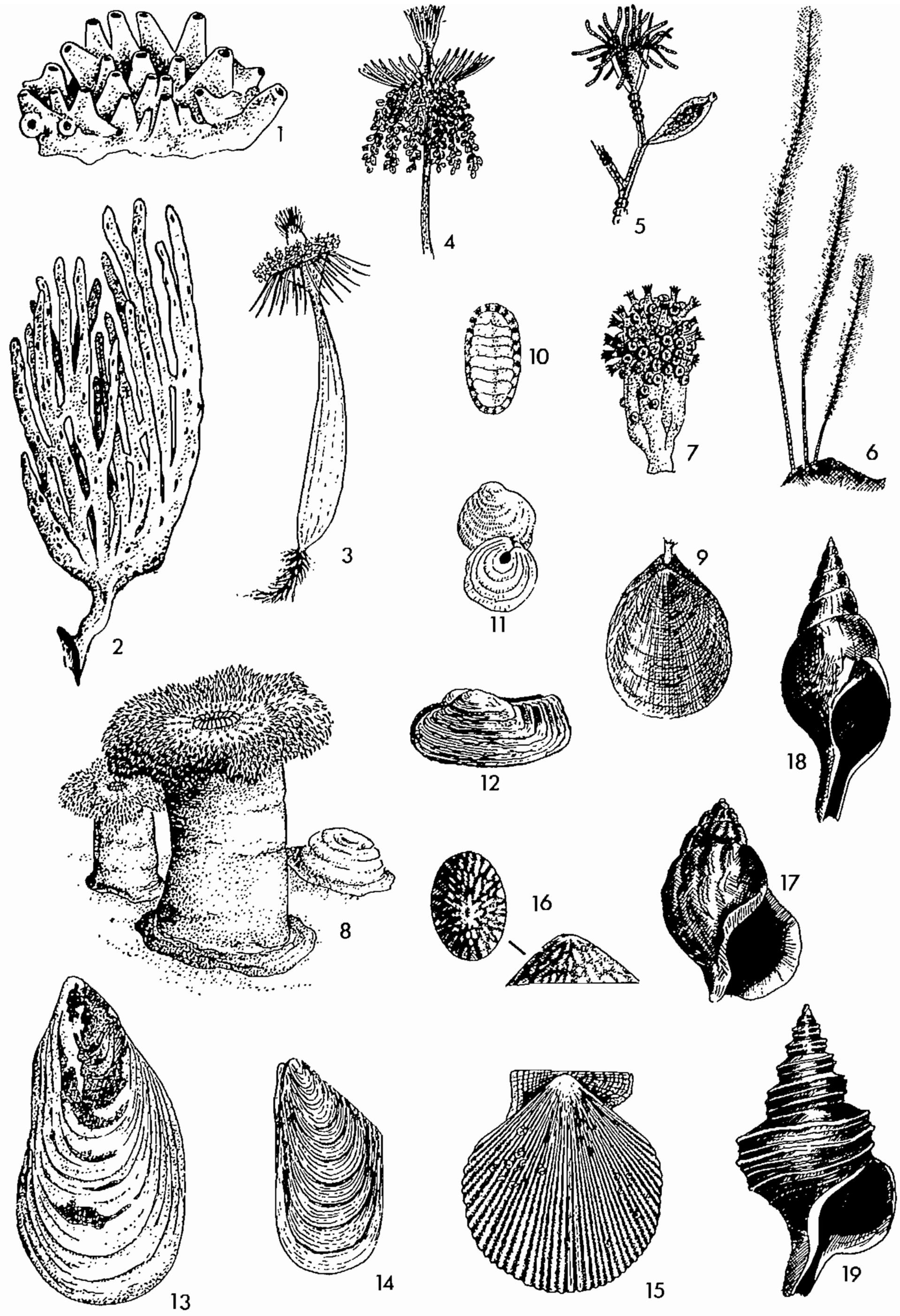

PLATE I. 1, *Halichondria* sp., × 1; 2, *Haliclona oculata*, × 0.25; 3, *Coryomorpha pendula*, × 1; 4, *Tubularia* sp., × 2; 5, *Obelia* sp., × 4; 6, *Antennularia* sp., × 0.75; 7, *Gersemia rubiformis*, × 0.5; 8, *Metridium senile*, × 3; 9, *Terebratulina septentrionalis*, × 1; 10, *Ischnochiton ruber*, × 1; 11, *Anomia* sp. × 1; 12, *Hiatella arctica*, × 1; 13, *Modiolus modiolus*, × 0.5; 14, *Mytilus edulus*, × 1; 15, *Chlamys islandicus* × 0.5; 16, *Acmaea testudinalis*, × 0.5; 17, *Buccinum undatum*, × 0.5; 18, *Colus stimpsoni*, × 0.5; 19, *Neptunea decemcostata*, × 0.5 (© A. A. MacKay 1973).

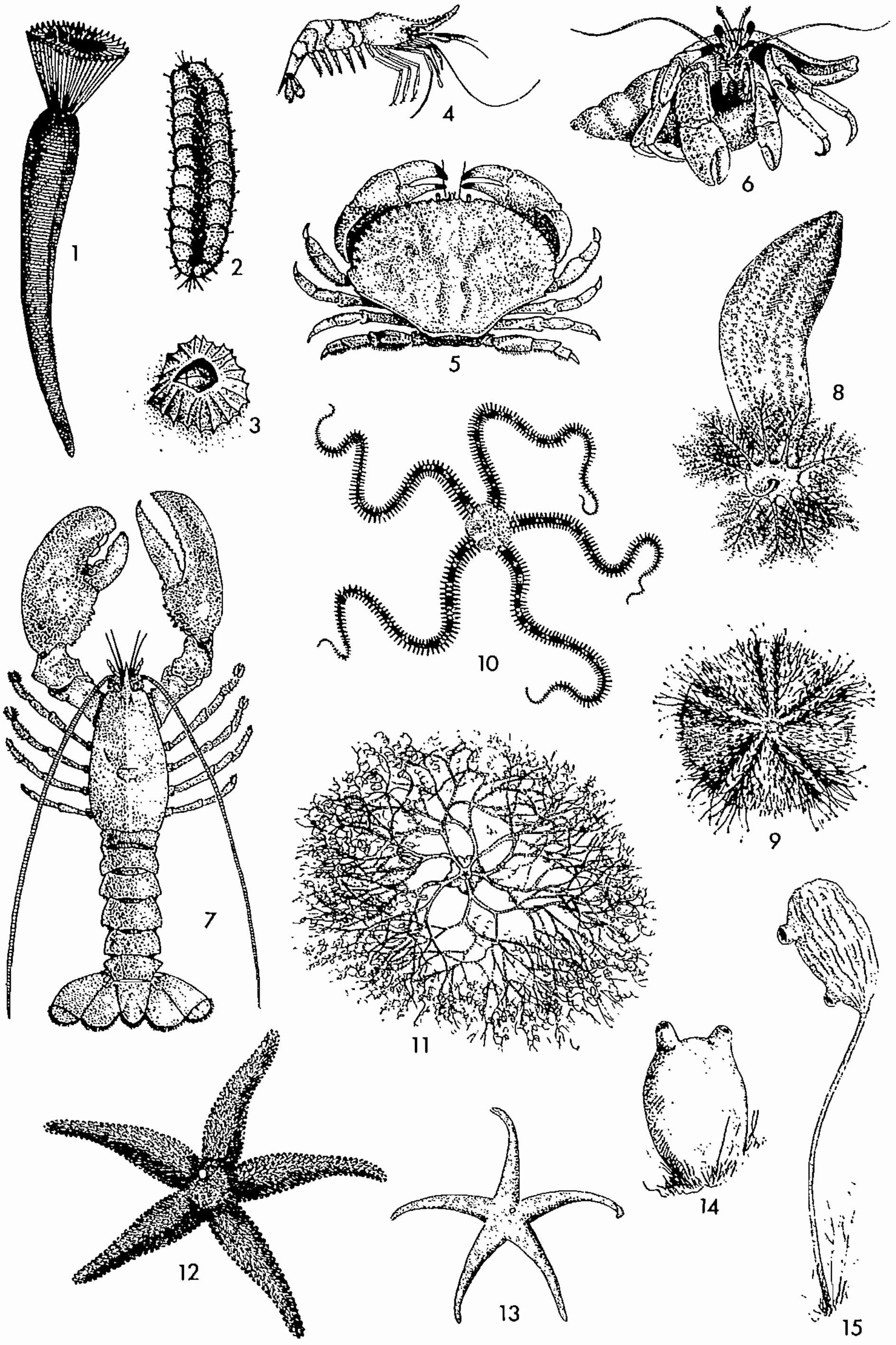

Plate II. 1, *Myxicola infundibulum* × 0.5; 2, *Lepidonotus* sp., × 0.5; 3, *Balanus balanus* × 1; 4, *Pandalus montagui*, × 0.5; 5, *Cancer* sp., × 0.25; 6, *Pagurus* sp., × 0.5; 7, *Homarus americanus*, × 0.1; 8, *Cucumaria frondosa*, × 0.25; 9, *Strongylocentrotus droebachiensis*, × 0.5; 10, *Ophiopholis aculeata*, × 0.5; 11, *Gorgonocephalus arcticus*, × 0.25; 12, *Asterias vulgaris*, × 0.25; 13, *Henricia sanguinolenta*, × 0.25; 14, *Halocynthia pyriformis*, × 0.25; 15, *Boltenia ovifera*, × 0.25 (© A. A. MacKay 1973).

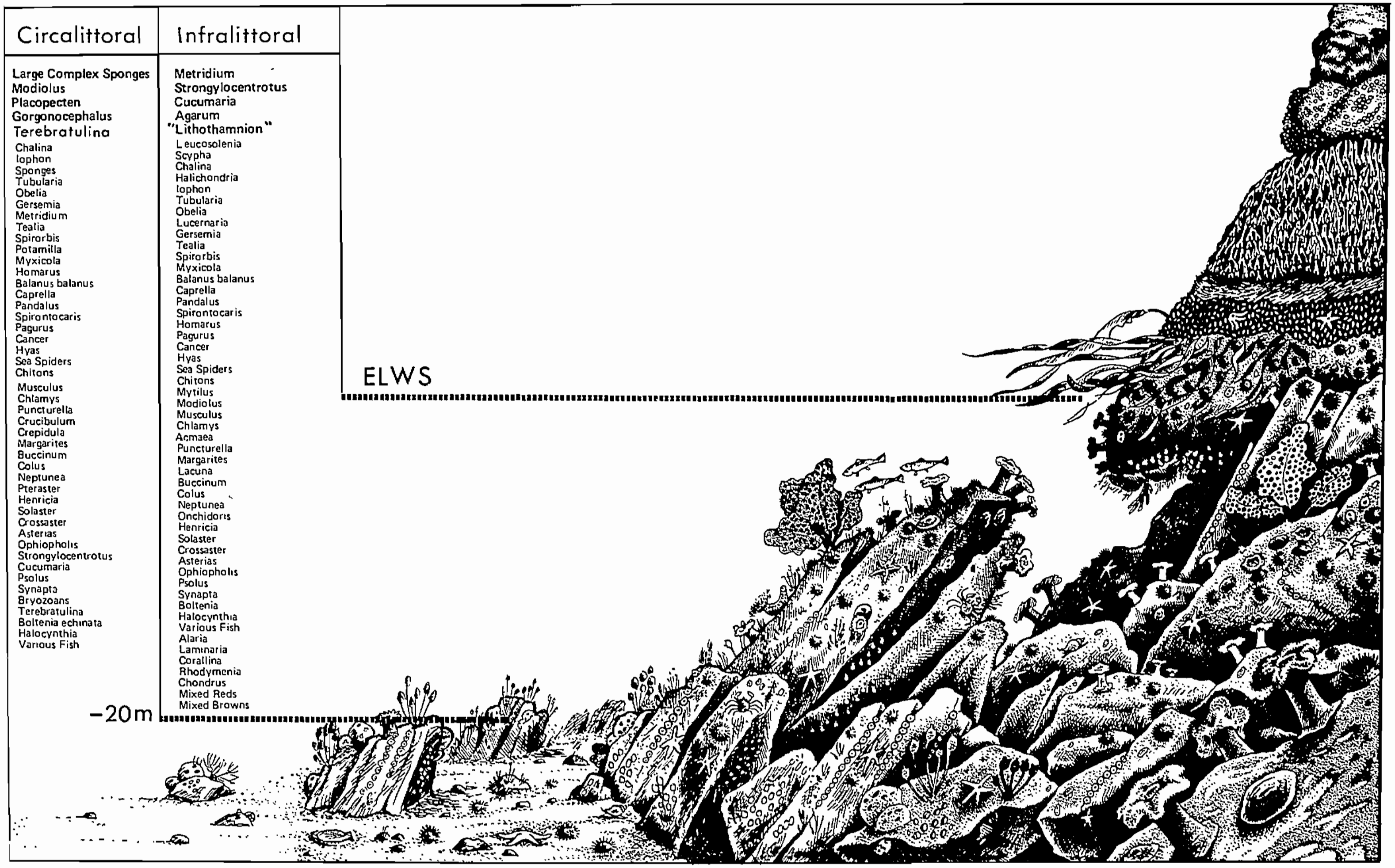

FIG. 5. Generalized profile of a sublittoral hard substrate and principal benthic biota, Bay of Fundy (after MacKay 1975, 1978).

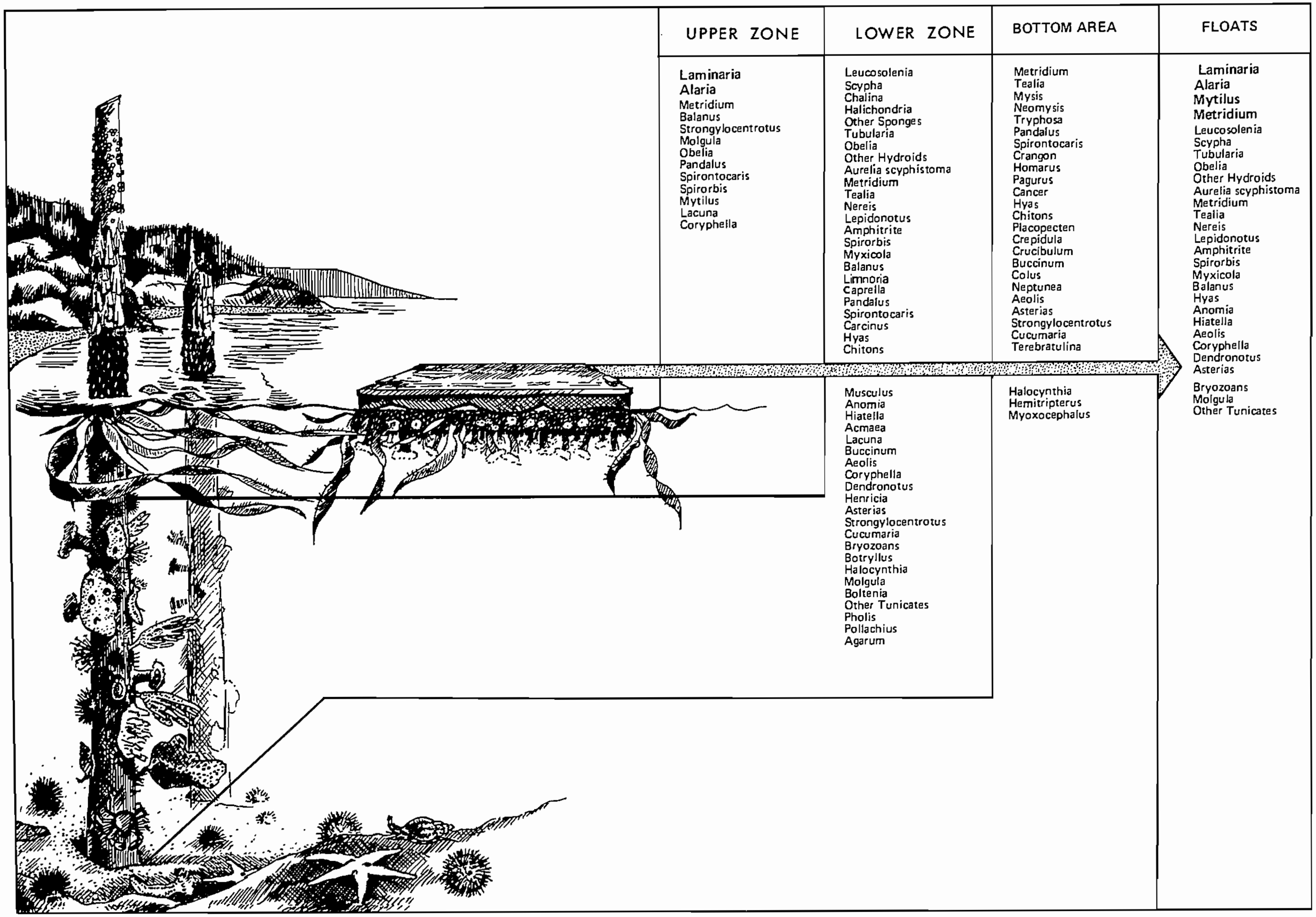

FIG. 6. Generalized profile of biota occurring on wooden man-made structures, Bay of Fundy (after MacKay 1975, 1978).

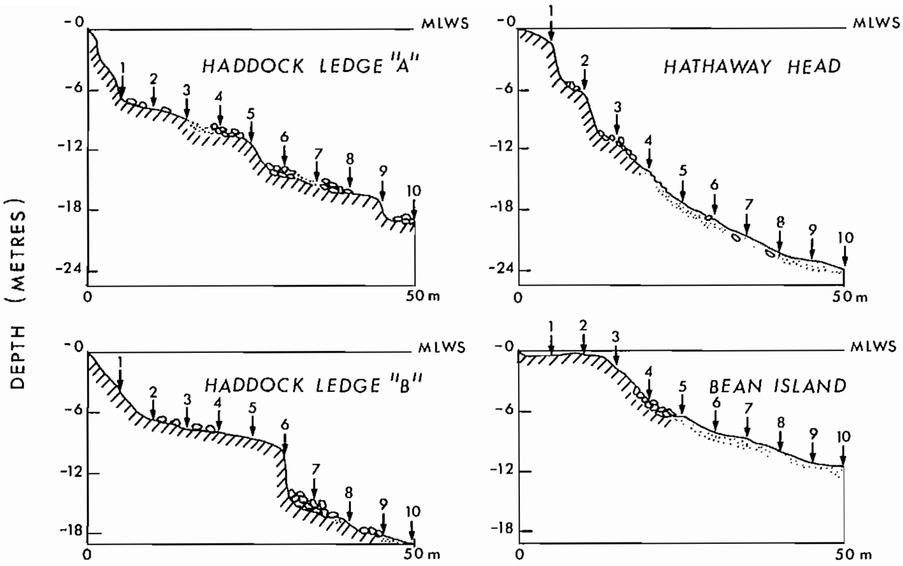

FIG. 7. Bathymetric profiles of four transects (Locs. 1–4, Fig. 1), east side of Deer Island, N.B., showing distribution of rock outcrop, boulders, and sediment, and position of quantitative sampling stations (after Noble et al. 1976). MLWS, mean low water spring tide.

THE CRUSTOSE CORALLINE ALGAE COMMUNITY

This community, recently described by Page (1981), is characterized by the widespread occurrence of several as yet unidentified species of encrusting coralline algae. MacKay (1978) has used the term *Lithothamnion* Zone for exposed surfaces down to about −20 m, where areal coverage by encrusting coralline algae often approaches 100%. Other algae include filamentous brown and red forms, as well as *Agarum* sp. and *Laminaria* sp. — holdovers from the lowest intertidal zone — which occur in very shallow water. Also common (but not always universally present) in the shallow part of the depth range are the limpet *Acmaea testudinalis*, the edible mussel *Mytilus edulis*, the sea anemone *Metridium senile*, the sea peach *Halocynthia pyriformis*, and vagile species such as the chitons *Ischnochiton alba* and *I. ruber* and the echinoderms *Asterias vulgaris, Cucumaria frondosa*, and *Strongylocentrotus droebachiensis*. At the lower end of the depth range algae gradually diminish in importance[3] and common forms include a variety of sponges, such as species of *Halichondria, Haliclona,* and *Iophon*; the sea potatoes *Boltenia ovifera* and *B. echinata*; and the basket star *Gorgonocephalus arcticus*. The large horse mussel *Modiolus modiolus* and the Iceland scallop *Chlamys islandicus* are byssally attached to rocks, and a variety of arthropods, both sessile (barnacles) and mobile (crabs, lobsters, shrimps, sea spiders), occur extensively throughout the depth range on hard surfaces.

In terms of feeding habits, the crustose coralline algae Community is dominated by suspension feeders (both active and passive), which are almost continuously filtering sea water for suspended food particles. Examples include the barnacles, bivalves, coelenterates, and tunicates. Various feeding levels relative to the bottom can be shown; for instance, the stalked tunicates *Boltenia ovifera* and *Halocynthia pyriformis* are raised above the level of the substrate and therefore feed at a higher level in the water column than species close to the substrate. The concept of resource (food) partitioning based on feeding levels relative to the substrate, as envisaged by Turpaeva (1957) for level bottom communities, is more difficult to apply in hard substrate communities where the substrate is of variable relief and organisms vary in their distance from this substrate because they are often attached to each other.

The second main feeding group comprises the herbivorous browsers, such as the rock-dwelling limpet *Acmaea testudinalis*, the chitons, and the sea urchin *Strongylocentrotus droebachiensis* which is able to feed on rock or sediment surfaces (MacKay 1976). Next in importance are carnivore-scavengers such as *Asterias vulgaris* and the whelks *Buccinum* and *Neptunea*. Some of the arthropods which rework the sediments, such as *Hyas* and *Pagurus*, may be regarded as detritus-feeders or scavengers. The difficulty in applying a rigid classification of feeding types is illustrated by such organisms as barnacles or sea anemones, which are probably capable of selecting particles mainly on size rather than type and thus may be suspension feeders and carnivores (using the classification criteria of Walker and Bambach 1974a). Other forms, such as sponges and tunicates, which are active suspension feeders, often augment their own feeding currents by orientation to water currents (Vogel 1974; Warner 1977)

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[3] Although the crustose coralline algae Community is restricted to about the upper 20 m in the Deer Island region of the Bay of Fundy, it may go down to greater depths in areas where water is clearer. For instance, off southeast Newfoundland, at a depth of −44 m, many elements of this community are clearly visible in photographs taken by L. H. King.

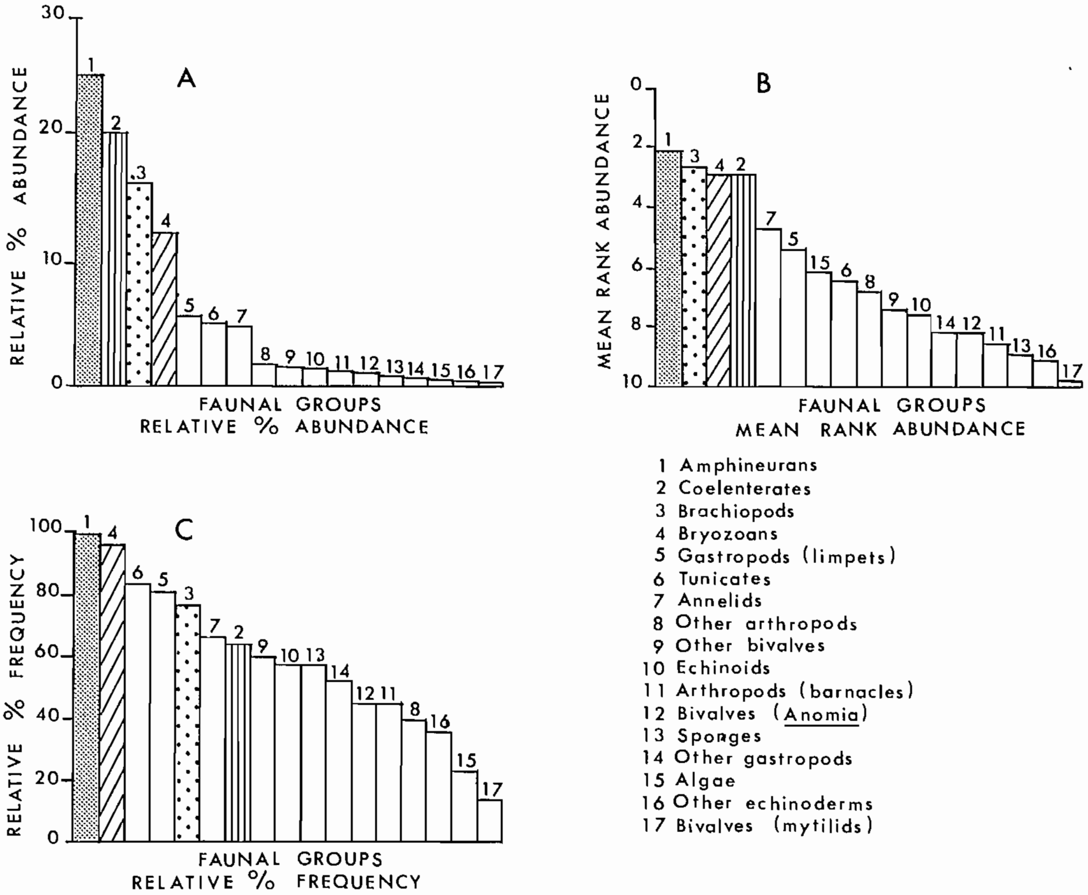

FIG. 8. Biotic composition of *Terebratulina septentrionalis* Community, in terms of 17 most abundant faunal groups, and comparison of (A) relative abundance, (B) mean rank abundance (Walker and Bambach 1974b), and (C) relative frequency, based on quantitative analysis of Deer Island samples (after Noble et al. 1976).

and may employ a variety of shapes to help maximize particle capture.

THE TEREBRATULINA SEPTENTRIONALIS COMMUNITY

This community has been sampled quantitatively by Noble et al. (1976) by running four transects at four different localities on the east side of Deer Island (Fig. 7, localities 1–4 of Fig. 1). Each transect was run perpendicular to the shoreline, from 0 to 24 m deep. Figure 7 shows the profiles of these transects, and the locations of the sampling stations at each of which 5 boulders were randomly collected every 5 m along the bottom. A total of 40 samples (200 boulders) of biota and sediments were obtained and these yielded data on the relative abundance, dominance, and frequency of the main groups (Fig. 8). It is apparent that the most abundant groups (amphineurans, coelenterates, brachiopods, and bryozoans) are also the most dominant; amphineurans and bryozoans occur most frequently, the brachiopods and coelenterates somewhat less so.

The *Terebratulina septentrionalis* Community is the most important hard substrate community in terms of total biomass, especially in the shallow cryptic habitat, and is dominated by chitons (amphineurans), hydroids and anemones (coelenterates), the brachiopod *Terebratulina septentrionalis*, and a host of encrusting and arborescent ectoproct bryozoans. It is typically developed beneath boulders in depths of 0–20 m, becoming progressively more emergent to inhabit shaded rock faces below −20 m. It is totally emergent at depths below about −50 m in the circalittoral zone, as mentioned earlier. The reasons for this gradual emergence are probably a combination of larval behavior, reduced competition from algae, and possibly reduced predation with increasing depth (see below). The rock-face subcommunity is similar to the shallower sub-boulder subcommunity, except that sponges and brachiopods are relatively more abundant, many of the sponges encrusting the brachiopod shells (Fig. 11), while because of the increased space available elements more typical of the crustose coralline algae Community, such as tunicates, anemones, and starfishes, may often spread over onto inclined or vertical faces from nearby upper surfaces. Algae are virtually absent, except

TABLE 2. Feeding type distribution of main elements of subboulder subcommunity of *Terebratulina septentrionalis* Community, Deer Island, N.B. (after Noble et al. 1976).

Taxonomic group	Feeding Type	Relative abundance (%)
Amphineurans	Browsers	24.6
Coelenterates	Predators/ Suspension feeders	20.5
Brachiopods	Suspension feeders	16.5
Bryozoans	Suspension feeders	12.4
Gastropods (limpets)	Browsers	4.8
Tunicates	Suspension feeders	4.2
Annelids	Suspension feeders and predators (minor)	4.2
All other groups	Varied	12.8

at the very edges of boulders in shallow water. The chitons are vagrant forms, crossing and recrossing from upper to lower boulder surfaces in search of food, and are thus represented in both the *Terebratulina septentrionalis* and crustose coralline algae communities.

The distribution of feeding types for the main subboulder faunal elements of the *Terebratulina septentrionalis* Community is shown in Table 2.

OTHER BIOTIC ASSEMBLAGES

The biota attached to wooden man-made structures, such as weir poles, wharf pilings, and floats, comprise an assemblage of forms not yet studied in detail. The broad distribution of these species is listed in Table 1 and shown diagrammatically in Fig. 6. Notably absent from shallow well-lit waters are the calcareous algae, which seem to have difficulty in attaching successfully to a wooden substrate. With increasing depth and diminishing light and water energy, various elements typical of the *Terebratulina septentrionalis* Community, such as sponges and bryozoans, begin to appear; however, *Terebratulina septentrionalis* itself is rare on wooden substrates, the wood apparently serving as a poor holdfast for the ramifying pedicle strands of this species. Such man-made objects offer great opportunities for the study of community development where the exact age of the structure is known. Such studies are planned in the near future.

Shell substrates are rare in this region but occasional abandoned valves of such species as *Modiolus modiolus, Mytillus edulis*, and *Placopecten magellanicus* serve as substrates for a variety of encrusting forms such as *Halichondria* sp., hydroids, limpets, byssate bivalves (*Anomia*), the coil worm *Spirorbis*, barnacles, and sessile tunicates (Table 1). *Cliona celata* occasionally bores into shell substrates, both living and dead, and individuals of the brachiopod *Terebratulina septentrionalis* are often attached to living *Modiolus modiolus*; they are also commonly attached to valves of the living sea scallop *Placopecten magellanicus* between −20 and −30 m in depth and may disperse geographically in this way (Logan et al. 1975). In shallower water, coatings of calcareous algae or isolated stands of *Laminaria* or *Agarum* may occur on upper surfaces of larger shells.

Possible Factors Controlling the Distribution, Species Diversity, and Composition of the Hard Substrate Communities

Possible physical (environmental) factors include substrate (its size, composition, micro-relief and disturbance rate), light, water energy, salinity, water temperature, and sedimentation. Biotic factors may include larval behavior, modification of substrate by organic films, predation, food supply, competition for space, and differential growth rates of species. The establishment and development of marine epifaunal communities on hard substrates in other regions have been studied over long periods using artificial settlement plates to simulate rock surface and monitoring all possible parameters (Osman 1977; Sutherland and Karlson 1977; Jackson 1977a, b). This has yet to be done in a systematic long-term way in the Bay of Fundy. Noble et al. (1976) speculated on possible factors controlling the distribution and composition of the hard substrate communities and concluded that, given a suitable substrate, the vagaries of surface relief of a boulder-and-cavity system will result in sufficient variation in exposure to light and water energy to differentiate communities and subcommunities mainly on the basis of these two factors.

There is ample evidence to support the contention that the larvae of some members of hard substrate communities exhibit substrate selection (see review of literature in Osman 1977). Noble et al. (1976) conducted short-term experiments on larval selectivity using artificial crevices, constructed of various materials which were anchored near living communities in the eastern Deer Island region. These were periodically examined for spat populations. Scallop shells, rough-textured rock surfaces, and self-curing plastic casts of irregular rock surfaces (Risk 1973) were tried, but none were extensively colonized. Colonization may depend on sufficient time for the surfaces to become covered with a bacterial or algal film.

Light is probably the most important factor reponsible for the difference between the two hard substrate communities in the Bay of Fundy. Light-dependent algae predominate on the upper surface of rocks, and are absent on the under-surfaces of rocks or the shaded faces of rock outcrop in shallow water. At least some of the elements occupying the cryptic habitat undergo negative phototaxis during their late larval stages. The larvae of selected species of brachiopods and bryozoans (Thorson 1964), along with *Spirorbis* (Knight-Jones 1951), become photonegative just before settlement, seeking out poorly-illuminated settling sites even when such sites are scarce. The gradual disappearance of algae and emergence of cryptic habitat elements to colonize more exposed surfaces with increasing depth off eastern North America has been mentioned previously and is also documented for cryptic habitat brachiopod elements of hard substrate communities in the Caribbean (Logan 1977) and Mediterranean (Logan 1979).

Relatively strong water movement and the resultant mixing associated with diurnal tidal flushing results in relative uniformity in water temperature and salinity on a seasonal basis near the bottom in shallow coastal waters around the offshore islands of southwestern New

Brunswick. Under these conditions thermoclines and haloclines rarely form; moreover, the high water energy conditions result in low sedimentation rates in the upper 30 m, except in the lee of outcrops or beneath large boulders. Biota of the upper surface crustose coralline algae Community are thus adapted to life in water which is frequently moving and are dominated by suspension feeders, many of which passively strain food particles from the flowing water without undue expenditure of energy, as described earlier. It should be noted that some elements of the *Terebratulina septentrionalis* Community dwelling on shaded rock surfaces at depths of −20 to −30 m, such as brachiopods, may also orientate to water currents to augment their regular active filter-feeding mechanism (LaBarbera 1977).

Pockets of sediments rich in fines beneath boulders testify to low water energy values in this protected cryptic habitat; here the sub-boulder subcommunity of the *Terebratulina septentrionalis* Community is dominated by suspension feeders, which must actively pump to draw in food-bearing currents. Differences in water energy must therefore be regarded as a significant factor in controlling the composition of the hard substrate communities.

Little is known about the biotic factors affecting the composition of sublittoral hard substrate communities in the Bay of Fundy, although it is clear from intertidal hard substrate studies elsewhere that biological interactions are of great importance in controlling the composition of the community (Connell 1972; Dayton 1971; Menge and Sutherland 1976; Paine 1966, 1969). We have briefly alluded to larval behavior in some cases and possible preparation of substrate by organic films. Predation may also be a significant factor, because elements of the crustose coralline algae Community may be prone to greater potential predation than those of the *Terebratulina septentrionalis* Community occupying the more protected cryptic habitat. Paine (1966), Sutherland (1974), and others have demonstrated the role of predation in increasing species diversity and affecting species composition, respectively. Long-term studies need to be done in the Bay of Fundy on predation effects on members of the hard substrate communities, including periodic observations on over-turned boulders. Much research also needs to be done in the Bay of Fundy on the effects of periodic substrate disturbance on species composition and diversity (Riedl 1964; Rützler 1965; Osman 1977); the areal extent of substrate available for settlement and its effect on community structure (Jackson 1977a, b); the possibility, through artificial substrate experiments, that succession (in the classical sense) (Odum 1971) may not occur in benthic marine communities (Sutherland and Karlson 1977; Anger 1978); and the feeding habits, growth rates, and biotic interactions of almost all members of both communities. Many questions remain unanswered and this review paper, in summarizing our present knowledge, should also serve to identify areas where information is deficient or totally lacking.

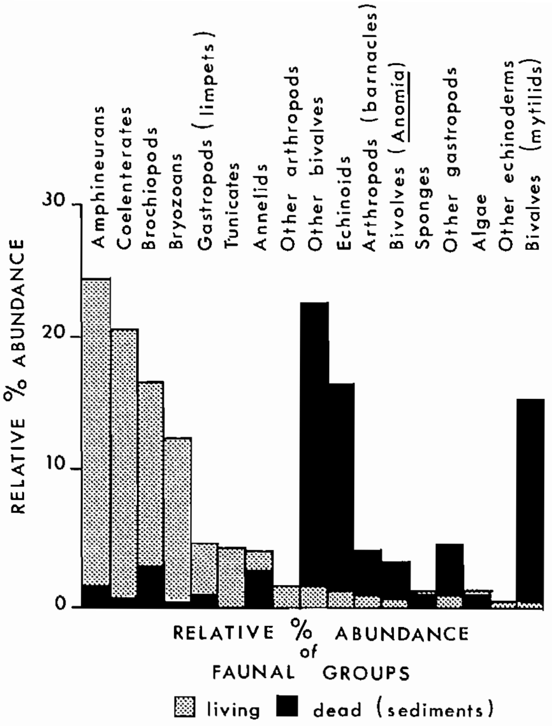

FIG. 9. Composition of sub-boulder subcommunity of *Terebratulina septentrionalis* Community compared with associated death assemblage accumulating in adjacent sediments. Based on quantitative analysis of four transects, east side of Deer Island, N.B. (after Noble et al. 1976).

Sediments Associated With the Hard Substrate Communities

The sediments associated with hard substrate communities in the eastern Deer Island region were studied by Noble et al. (1976). They compared the composition of living communities with the death assemblages in adjacent pockets of sediments, to assess the relative significance of the principal processes changing living communities to fossil communities. Biotic components of the sediments were found to reflect the individual components of *both* communities (Fig. 9) rather than the dominant (in terms of biomass) *Terebratulina septentrionalis* Community, in terms of differential preservation, differential fragmentation, variation in rates of growth and turnover of the individual community members, and transportation of shell fragments from living sites to their position between and beneath boulders. Microscopic examination of shell fragments showed that rates of abrasion, fragmentation, and disarticulation of shells are generally low (but see Noble and Logan 1981), suggesting

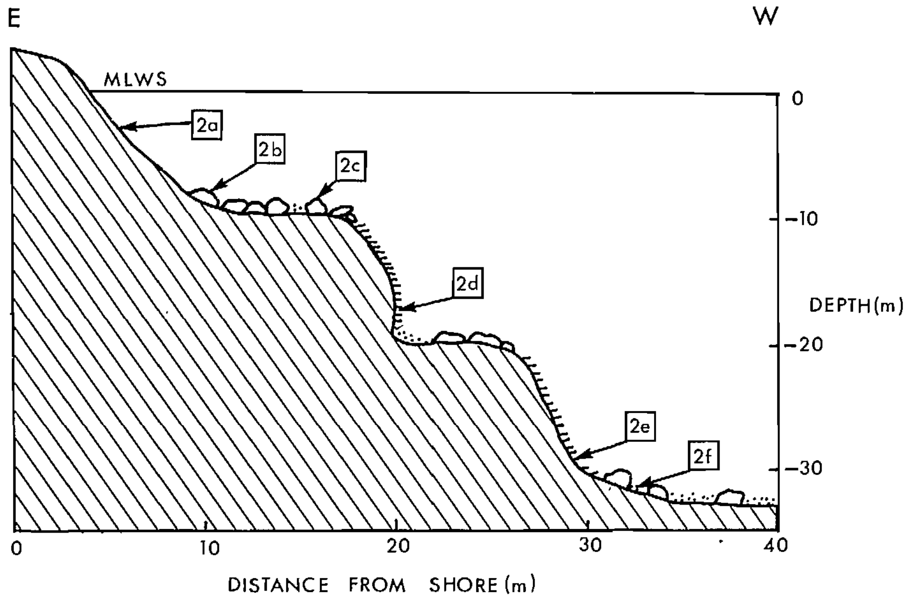

FIG. 10. Generalized profile of west side of Nub Island, N.B. (Loc. 5 of Fig. 1) showing typical substrate types. Numbers refer to photographs in Fig. 2. MLWS, mean low water spring tide.

that the death assemblage accumulates more or less in situ. The significance of these observations for fossil assemblages is that *all* communities which are closely associated spatially may contribute to the death assemblage, making reconstruction of hard substrate communities from fossilized remains more difficult than those of soft substrate communities.

Detailed Description of a Selected Locality

Typical bathymetric profiles of four localities off the east coast of Deer Island have been shown in Fig. 7. Also described in some detail is a site on the west side of Nub Island (locality 5 of Fig. 1). Figure 10 shows the generalized profile of this locality from 0–30 m depth, and typical photographs of the bottom and biota are included in Fig. 2.

The profile is one of initial steeply-dipping rock outcrop (Fig. 2a) and boulders (Fig. 2b), to about −10 m in depth, where there is a narrow shelf (Fig. 2c) followed by a vertical ledge to −18 m (Fig. 2d) and then a narrow, gently sloping shelf about 10 m wide with rubble, sediment, and occasional outcrop extending to −20 m depth. A second vertical ledge drops to −27 m, where sediment and boulders on a gently sloping bottom again predominate and continue beyond −30 m, the limit of observation of the profile.

The boulders are mainly of volcanic rock. There is usually high current activity parallel to the ledge faces. Exposure to wind is mainly from the north, with a maximum fetch of about 3 km. Light intensity values reach about 1% of surface illumination at approximately −20 m in depth. Benthic biota are abundant at this site. The surface of the rocks in the 0–12-m zone is dominated by crustose coralline algae, together with starfishes, sea urchins, and some stands of fleshy algae (Fig. 2b, c). The undersides of boulders support the sub-boulder subcommunity of the *Terebratulina septentrionalis* Community. Below −12 m *Halocynthia pyriformis* and *Boltenia ovifera* also become abundant on upper surfaces, along with serpulid worms. The horse mussel *Modiolus modiolus* is common, reaching densities of up to 25/m^2, and isolated stands of *Boltenia ovifera* attain densities of up to 100/m^2. The shallower of the two vertical ledges is heavily encrusted with bryozoans, sponges, hydroids, and brachiopods of the rock-face subcommunity (Fig. 2d, 11) and large anemones such as *Metridium senile* and *Tealia felina* are also common. The shelf at the foot of the first ledge has large stands of sessile tunicates and ball-like sponge masses, but calcareous algae are virtually absent. The lower ledge from −20 to −27 m is dominated by large encrusting sponges and brachiopods (the latter up to 500/m^2) (Fig. 2e). Below −27 m there is a general decrease in large benthic organisms, as the amount of hard substrate decreases. The basket star *Gorgonocephalus arcticus* is commonly attached to isolated rocks or stalks of individuals of the sea potato *Botenia ovifera*, and the sea scallop *Placopecten magellanicus* occurs in hollows in the sediments, which are still shell-rich (Fig. 2f) below −30 m.

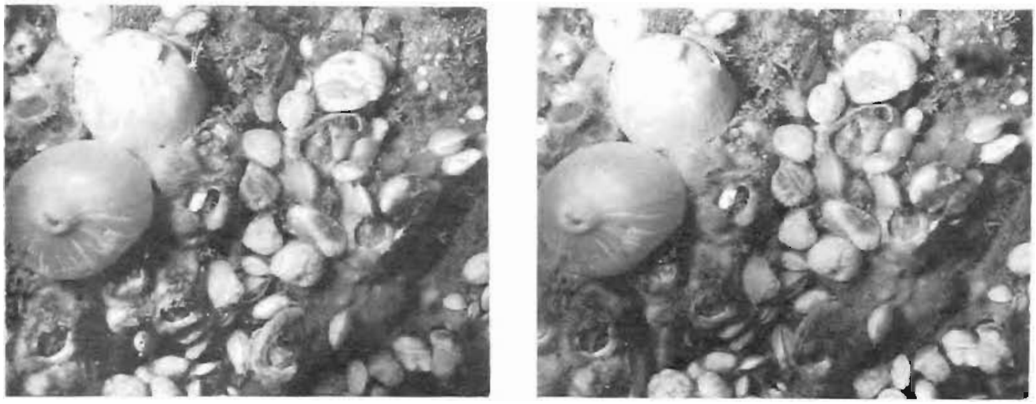

FIG. 11. Stereophotographs of attached ledge biota, mainly anemones and sponge-encrusted brachiopods, using Nikonos close-up system, −17 m, Nub Island, × 1/3.

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CHAPTER 9

Sublittoral Sedimentary Substrates

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Introduction

Study of the fauna and flora living near the interface between sedimentary substrates and seawater, below the reach of the lowest tides, dates from before the first Challenger expedition in 1872. Although the early studies were of purely scientific interest (perhaps enhanced in the minds of the pioneers by the difficulties of sampling), a renewed interest in benthic biology has blossomed in the last 25 years. This results at least partly from the realization that benthos, by their distribution patterns, provide a record of man-made impacts such as pollution because mature, benthic infauna are unable to move away from polluting sources. It was recognized early that benthic production is a major contributor to groundfish production (Petersen and Jensen 1918). Another focus of interest is from Recent sedimentary geologists who need to study comtemporary animal–sediment interactions to fully understand the stratigraphic record (see Johnson 1978).

Despite this interest in subtidal benthic biology, sampling techniques have changed little since the Challenger expedition sailed, although the introduction of the first quantitative grab (Peterson and Jensen 1911) may be said to date the origin of the subject as a scientific study. Since 1911 many novel methods have been tried, but all have limitations serious enough to discourage their general use among benthic biologists. Because of this and perhaps also because of the youth of the subject and the relatively few scientists involved at any one time, a satisfactory conceptual base has yet to emerge (Wildish 1977). This state of affairs should attract any embryonic marine biologist worth his salt to this field where so much has yet to be achieved by so few.

This chapter concerns the sublittoral animals of estuaries and the near-shore of the Bay of Fundy which live attached at the sediment–water interface, the *epibenthos*, or which live within the sediment, the *infauna*. Benthic animals may be classified arbitrarily by their body dimensions, since sieves are commonly used to separate them from the sediment matrix in which they live. The following classes are recognized throughout this work (adapted from Wolff 1977):

Class	*Size range*
microorganisms	<60 μm
meiofauna	60–1000 μm
macrofauna	>0.8 mm
megafauna	Species which cannot be adequately sampled with grab or corer

At the time of writing no data were available for the microflora and meiofauna of the Bay of Fundy. Study methods for microbenthos may be found in Rodina (1972), Rosswall (1973), and Stevenson and Colwell (1973) and for sampling both micro- and meiobenthos in McIntyre (1971).

The aim of this article is threefold. First, sampling methods for collecting macro- and megafauna are described, based on field experience, to facilitate entry of new research investigators to this field. Second, the estuaries and nearshore locations in the vicinity of St. Andrews which were investigated in the period 1970–77 are described, with emphasis on the macro-infauna. Finally, a concept of benthos in the context of the Bay of Fundy sublittoral sedimentary environment is briefly discussed.

Sampling and Analytical Methods

SAMPLING VESSELS

Vessel requirements vary — depending on the sampling area and weather conditions — from a dinghy (for work in sheltered shallow estuaries with a small hand-hauled grab) to a seagoing research vessel (for work with a heavy grab at depths greater than 10 m). Most quantitative sampling demands machine-driven winch gear to raise and lower the heavy grab; thus a small launch with facilities for power takeoff from the engine is a minimum requirement. Table 1 shows details of the vessels used in the work reported herein. The three larger vessels employed were equipped with acoustic fathometers for determining depth and substrate type. The *J. L. Hart* is also equipped with a Decca Navigator system.

POSITION FIXING

Requirements for position fixing of a vessel, to take replicated samples from a single station in successive seasonal samplings or from numerous stations over a wide spatial area, have been considered by Holme (1971).

Transits — This involves lining up clearly visible landmarks on the shore. The landmarks are recorded in the field notebook or ship log for future reference and subsequently plotted on a marine chart so that the coordinates can be ascertained. In some cases, e.g. upper Musquash Estuary, this may involve extrapolation because complete marine charts are unavailable. This method may be augmented by taking compass bearings or by taking two horizontal sextant angles between pairs of shore landmarks. Errors with this method should be within 10–100 m.

TABLE 1. Vessels from which benthic sampling has been carried out in the Bay of Fundy.

	Boston whaler	*Mallotus*	*Pandalus II*	*J. L. Hart*
Construction date	—	1951	1952	1976
Length (*m*)	5.5	16.4	16.8	19.8
Beam (*m*)	1.5	4.3	4.3	6.1
Engine (*h.p.*)	65	150	150	425
Displacement (*tons*)	?	27	27.3	86
Accessories	0	Deck mounted winch, hydrographic winch	Deck mounted winch, hydrographic winch	Hydraulic crane, auxillary engines of 70 and 30 h.p., hydrographic winch
Crew	0	2	2	4

Decca Navigation System[1] — Where shore landmarks are absent or distant, the Decca Navigator can be used to fix the position of a vessel to within 30–200 m. The actual latitude/longitude coordinates can then be found by reference to a marine chart containing both sets of coordinates. I have used latitude/longitude coordinates quoted to within 0.1 min (≈0.1 nautical mile or 185 m) which is consistent with the error range quoted above. When Decca coordinates are used in position fixing, they may also be given to facilitate repeat sampling by this method.

It is also possible to mark a spot sampled with a fixed buoy, a radar reflector, or a transponder device (see Table 2 for suppliers). The advantage of the transponder is that it can be moored safely and be free from vandalism. Care should always be taken in setting buoys which could be a hazard to shipping or to fishermen. Routine reporting of the position of any moored buoys should be made by writing the Coastguard Traffic Centre, Transport Canada, Royal Bank Building, P.O. Box 1013, Dartmouth, N.S. B2Y 3Z7, or by telephoning this center at Zenith 4900. Ship-to-shore messages and/or notices to mariners are coordinated from this location.

QUALITATIVE SAMPLING

The usual reasons for undertaking a qualitative sampling program include: to sample megafauna; to sample specific animals for autecological study; or because of unresolved difficulties in sampling on rocky or sandy substrates, which prevent quantitative sampling.

Dredges — Scallop dredges have been used (Caddy 1970) to sample epifauna, as well as specially designed epibenthic sledges (Hessler and Sanders 1967). Devices for rock dredging (see Nalwalk et al. 1962) must be robust in construction, and have a collection bag consisting of wire or iron rings with a weak link in the cable swivel attached to the dredge. The anchor dredge developed by Sanders et al. (1965) is suitable for sampling sands or firmly packed deposits. A sampler for catching organisms such as amphipods, which swim just off the bottom, has been used by Brunel (1979).

Trawls — Trawling devices such as the Agassiz (Holme and McIntyre 1971) or a beam trawl are used to catch mobile benthic animals such as shrimp or highly dispersed epifauna, such as large suspension feeders, not taken by most quantitative grabs.

Traps — Some benthic species, notably carnivorous or omnivorous scavengers, can be attracted to bait such as dead fish, and small buoyed traps of suitably sized wire netting can be used to take live specimens in good condition. For example the amphipod, *Anonyx* sp., has been collected in this way in Passamaquoddy Bay.

Underwater cameras or television — Either remotely operated from a vessel, diver operated, or on a controllable, towed sledge or diving plane, these can be used where bottom-water visibility permits. A limitation of this technique is that the few animals which show up in the pictures are not necessarily representative or dominants of the ground being studied. However, there has been little attempt to "ground-truth" the pictures by quantitative sampling at the same location. Some grabs, such as the modified Campbell or Reineck box sampler, can be supplied with a camera (Table 2) and can photograph the bottom just before it is sampled.

Further technical information on this technique is given by Barnes (1959), for towed sledges by Foulkes and Caddy (1972), and for diving planes by Foulkes and Scarratt (1972).

QUANTITATIVE SAMPLING

Diving and suction devices — As well as being a qualitative exploratory technique, SCUBA diving has been adapted for quantitative sampling on hard, rock substrates by using quadrat frames and for sedimentary substrates by using suction samplers (see Jones 1971; Kaplan et al. 1974; Tanner et al. 1977). A number of limitations serve to curtail the usefulness of this method in the Bay of Fundy. Thus the maximum working depth, without decompression facilities for humans, is 40–80 m (with a limited work time) whereas depths in the Bay exceed 200 m. The maximum working depth of the suction sampler is around 20 m and the high turbidity of many estuaries and near-shore environments reduces vision and hence the usefulness of SCUBA-based techniques.

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[1] To be replaced by the Loran C system by September 1981 in the Bay of Fundy area. Contact Mr. Bob Adams, Telecommunications and Electronics, Canadian Coast Guard, Transport Canada, Dartmouth (426–3797) for further information.

TABLE 2. Suppliers of charts, hydrographic, and benthic sampling equipment.

Description	Supplier's address
Marine charts	Hydrographic Chart Distribution, Dept. of Environment, 1675 Russel Road, P.O. Box 8080, Ottawa, Ont. K1G 3H6
Current meters	
Ott C-3100	Wild of Canada Ltd., 881 Lady Ellen Place, P.O. Box 3520, Station C, Ottawa, Ont.
Interocean Model 135	InterOcean Systems Inc., 3510 Kurty St., San Diego, CA
Calibration of current meters	Hydraulics Division, Canada Center, for Inland Waters, P.O. Box 5050, Burlington, Ont. L7R 4A6
Nansen reversing samplers	InterOcean Systems Inc., 3510 Kurty St., San Diego, CA
Miscellaneous supplies	
Plastic pails with tight sealing lids	Can-Am Containers Ltd., P.O. Box 340 Springhill, N.S.
Braided nylon rope	John Leckie Ltd., 7037 Mumford Rd., Halifax, N.S.
Field flotation jackets	Summers Co. Ltd., 635 Main St., Moncton, N.B.
Quantitative grabs	
Hunter	Valeport (Developments) Division of Valeport Services Ltd., Townstal Industrial Estate, Townstal Dartmouth, Devon, TQ6 9LX, U.K.
Smith-McIntyre	David Moir, 11/13 Broomhill Road, Aberdeen, AB1 6JA Scotl.
Van Veen	MSE Engineering Systems Ltd., 265 Canarctic Drive, Downsview, Ont. M3J 2N7
Modified Campbell	Eastern Instrument Corp., 49 Oak St., Norwood, NJ 07648
Petersen	Laboratoire Oceanographique, Skorkrogen 8, DK-2920 Charlottenlund, Denmark
Small "Petersen"	Foerst Mechanical Specialities Co., 2407N St. Louis Ave., Chicago, IL 60647
Reineck Box Sampler	Friedrick Leutert, 3141 Erbstorf-Lunenburg, W. Germany
Rock and cone dredges	InterOcean Systems Inc., 3510 Kurty St., San Diego, CA or Benthos Inc., North Falmouth, MA 02556
Coring devices	
Vibratory, modified Ewing piston and gravity types	Eastern Instrument Corp., 49 Oak St., Norwood, NJ 07648, or Benthos Inc., InterOcean Inc., or MSE Engineering Ltd.
Acoustic transponders	Geodyne Division, 151 Boar Hill Road, Waltham, MA 02154
Local workshops	
Metal	Bradfords Machine Shop Ltd., R.R. 4, St. George, Char. Co., N.B. E0G 2Y0, or Saint John Ironworks, Saint John, N.B.
Hot dip galvanizing	Atlantic Industries Galvanizing Div., Industrial Park, Amherst, N.S.
Hardwood sieving stand	H.W. Whittier and Son, Black Point, N.S.

TABLE 3. Sampling characteristics or grabs used in the present work.

Type	Maximum digging depth (*cm*)	Open dimensions (*cm*)	Surface area sampled (*m^2*)	Volume sampled (*L*)
Hunter	16	31 × 31	0.10	12.5–16.0
Smith–McIntyre	16	31 × 31	0.10	12.5–16.0
Van Veen (modified by D. Peer)	19.5	19.5 × 39	0.08	—
Small Petersen[a]	8	27 × 30	0.08	5.4–6.0

[a] This is the model supplied by Foerst Mechanical Specialities Co. (Table 2). It is a smaller version of the 0.1 m² sampler of Petersen (1913, p.44).

Grabs — A number of different designs for quantitative grabs have been described (see review by Holme and McIntyre 1971). Selection depends on relative capture efficiency, digging performance in various sediments, and grab reliability. It is not the purpose here to exhaustively review each grab. Most grabs have special features which recommend their use in particular conditions. Of the four grabs used in the work described here (Table 3), the small Petersen is unsatisfactory as a quantitative sampling device because it cannot take a deep enough "bite" of the sediment. By direct underwater SCUBA observation it was found that the biting edge of grabs such as the modified Van Veen penetrated only about one half of their maximum because the biting edge "rode-up" over deeper sediment due to an equalization of penetration forces and resistance of the substrate (Lie and Pamatmat 1965). This means that for the Smith–McIntyre and Petersen used in this study digging depths of 8 and 4 cm, respectively, were achieved when the grab contents were full. It should be remembered that living macrofauna such as the decapod, *Axius serratus* Stimpson 1852, have been found 3.0 m below the sediment–water interface (Pemberton et al. 1976) and pressure changes ahead of the grab may cause avoidance responses which take animals below the grab sampling depth. One possible solution is the use of box corers, which are now coming into wider use (see Hessler and Jumars 1974, for example). They take a relatively deep sample (50 cm) but function well only in soft, muddy sediments and are extremely time-consuming to operate.

Evidence that deeper digging grabs capture more individuals of a particular species at the same location is shown in Table 4. Rosenberg (1974) showed that about 64% of the individuals found in soft sediments of the Saltkallefjord, Norway, were limited to the top 5 cm. This may explain why grabs with effective digging depths of 8 cm are generally sufficient for soft sediments.

Another important factor affecting capture efficiency is the open dimensions of the grab. This can best be shown by considering an antagonistic distribution where significant interactions between grab size and nearest neighbor distances are evident (Table 5). An antagonistic distribution is one in which each individual is equidistant from its neighbors. Numbers in Table 5 refer to the case where the grab samples are at 45° to the orientation of the

TABLE 4. Numbers of individuals/0.1 m² and standard deviation (*SD*) based on 10 replicates through a 1-mm² mesh.

Species	Station number	Smith–McIntyre	Small Petersen
Casco bigelowi	St. Croix 11	0.9 ± 1.2	0.2 ± 0.4
Cerastoderma pinnulatum	St. Croix 11	1.0 ± 1.2	0.2 ± 0.6
Yoldia sapotilla	St. Croix 5	1.9 ± 1.3	1.1 ± 0.7
	L'Etang 5	2.1 ± 1.3	1.1 ± 0.9
Cerebratulus sp.	L'Etang 6	1.3 ± 1.5	0.3 ± 0.7
Lumbrinereis fragilis	L'Etang 6	0.7 ± 0.8	0
Nucula proxima	L'Etang 6	0.9 ± 1.1	0.1 ± 0.3
Sternaspis scutata	St. Croix 11	3.4 ± 2.7	1.8 ± 1.6
	L'Etang 5	2.2 ± 4.6	0.1 ± 0.3

TABLE 5. Antagonistic distribution of benthic macroinfauna and effect of grab size on estimated density based on 1 replicate/m² of the dimensions shown.

Grab open dimensions	Nearest neighbor distance between animals	
	5 cm	10 cm
	Estimated density/m²	
	Lowest–highest	Lowest–highest
5 × 5	0–800	0–400
10 × 10	200–500	0–400
20 × 20	300–450	100–125
30 × 30	352–451	110–143

rows. If the grab samples are in the same plane as the rows, the maximum possible numbers which can be sampled are for a 5–cm nearest neighbor distance of 539, and for a 10–cm distance of 176. Where the nearest neighbor distance between individuals is more than one half of the longest open grab dimension, single samples seriously under- or overestimate density expressed on a m^2 basis, as is shown in Table 5. This is one reason why sample replications at the same location are considered to be so important in temporal surveys. Grabs with larger open dimensions, such as the modified Campbell (Table 2), are available with a sampling area of 0.6 m^2. Antagonistic distributions of benthic macroinfauna are actually quite unusual in soft substrates although Holme (1950) has described a bivalve with such a distribution. More common are random (Levinton 1972) or contagious (i.e. clumped) distributions (Gage and Geekie 1973).

Finally, the sieve dimensions used in separating benthic organisms from sediment have a marked effect on the results, rendering them comparable only if sieved on mesh of the same size. The results are dependent on whether biomass or numbers are considered, as found by Reish (1959) who sieved replicate samples from a muddy sediment on a nest of sieves and recorded numbers and biomass retained on each sieve. Over 90% of the biomass was retained on sieves >1.4 mm square, over 90% of the numbers of individuals on a >0.85 mm square sieve, and over 90% of the species on a >0.27 mm square sieve.

Relative capture efficiencies of the small Petersen and the Smith–McIntyre grabs have been compared in samples obtained at the same time and from the same vessel in the L'Etang and St. Croix estuaries (Wildish 1978). Estimates of field and laboratory costs and further references to published comparisons of capture efficiency by various grabs and corers are also given.

Field operations — On the *J. L. Hart* the Hunter grab, originally described by Hunter and Simpson (1976), is worked from the stern using the hydraulic crane as a boom. Wire from a hydraulically operated drum is used to raise and lower the grab. The grab must be lowered slowly, and knowing when the grab has sampled properly requires skill on the part of the winchman. Tidal currents or excessive wave activity can cause the wire and grab to swing in descent and hit the sediment sideways, resulting in no sample. The deck crew land the grab on its cradle, open one of the top plates to remove a sediment subsample and/or to measure redox potential and remove animals required for special purposes, e.g. live amphipods for counting brood numbers (each is killed individually in a small vial). The rest of the sediment is washed with seawater from the grab and put into a plastic collecting bucket. The bucket contents are placed on a sieve stand. The sieve stand is made of hardwood to a design by Don Peer and is available from the source shown in Table 2. It contains two sliding drawers with brass sieve mesh of 2.5 and 0.8 mm square. After washing with seawater, the larger animals are picked off the upper 2.5 mm square mesh sieve and are placed with all of the bottom-sieve material in a plastic bucket with a watertight lid (see Table 2 for supplier). Seawater and formalin are added to make a 10% solution, and the bucket is lidded and stored until transported to the laboratory.

Sample identification. — At the laboratory a preliminary sorting is carried out to separate the macrofauna from other particles (such as worm tubes, dead shells, and detritus) and to separate the major taxa (e.g. polychaetes, molluscs, amphipods, and echinoderms). The whole sample is then placed in 30% ethanol or 5% buffered formalin, depending on the purpose of the analysis, and sent to the Canadian Oceanographic Identification Centre, National Museum of Natural Sciences, Ottawa, Ont. or to the Identification Centre, Biological Station, St. Andrews, N.B. E0G 2X0 for species (S) identification, individual enumeration (N), and wet weighing to 0.01 g (B).

For identification of local benthic macro-infauna, books by Gosner (1971) and Bousfield (1973) are useful. A local key, based mainly on littoral species, is also available (Brinkhurst et al. 1975).

Ancillary observations — Quite frequently the physical or chemical variables observed along with benthic sampling are chosen arbitrarily or because of precedent. Thus, sediment-sorting characteristics are frequently quoted in the literature as being correlated with macrobenthic distribution (see Parsons et al. 1977) — e.g. deposit feeders in silty/clay sediments; however, many cases are known where this is not the case (Wildish 1977). Quite probably the controlling factor is another variable, for example tidal energy, which controls both sediment grain size and sorting, as well as animal distribution. It has been established by Wilson (1953, 1954) that some polychaete larvae are attracted to specific sediments. The attracting factor is not related to granulometry but to the microbial–detritus complex present.

The point to be stressed here is that blanket recommendations cannot be given as to which variables should be measured. However, the variables selected should be ones which are designed to test hypotheses about benthic distribution or function.

Analytical Methods

The analytical methods used depend on the purpose of the sampling program. Different types and degrees of analysis are required for different purposes such as describing communities, determining pollution effects on a spatial or temporal scale, or searching for a particular species required for experimental purposes.

Raw data are of the kind shown in Table 6, that is, species times individuals or species times biomass matrices for different replications. A simple description may be made by ranking biomass or numerical dominant organisms and selecting the most dominant as an indicator. In Table 6 the numerical and biomass dominants are *Sternaspis scutata* and *Nepthys* sp. with a low species diversity value, $\alpha = 2.9 \pm 16\%$ (see Fisher et al. 1943 for calculation of α and its standard error). A discussion of alternative diversity measures may be found in Green (1979). Communities defined thus should be regarded as a series of species distributions along gradients (Mills 1969).

TABLE 6. Species times number matrix for station 8, Musquash Estuary, sampled by 0.1 m^2 Smith–McIntyre grab, June 1973.

	Replicate number										Total	
Species	1	2	3	4	5	6	7	8	9	10	*n*	Biomass
Nassarius trivittatus (Say, 1822)									1		1	0.09
Lunatia heros (Say, 1822)		1									1	0.02
Nucula delphinodonta Mighels and Adams, 1842									1		1	0.05
Nepthys incisca Malmgren, 1865	6	6			4				3		19	0.47
Nepthys sp.			11	6		6	6	9		3	41	1.29
Nereis diversicolor O.F. Muller, 1771				1		1					2	1.78
Goniada maculata Oersted, 1843			1		1				1	1	4	0.31
Ninoe nigripes Verrill, 1873		1			3			1			5	0.39
Sternaspis scutata (Renier, 1807)	7	14	10	11	15	14	16	15	3	7	112	28.13
Idotea phosphorea Harger, 1873									1		1	0.02
Crangon septemspinosus Say, 1818										1	1	0.11
Leptocheirus pinguis (Stimpson, 1853)							2			1	3	0.10
Accumulated total/replicate, *N*	13	35	57	75	98	119	143	168	178	191	191	32.76
Accumulated total new species/replicate, *S*	2	4	6	7	7	7	8	8	11	12		

For community description purposes over geographic areas the Czekanowski coefficient of community (CC) is useful:

$$CC = \frac{2c}{a + b} 100$$

where a is the number of species at station A, b the number at station B, and c the number of species common at A and B. Log transformation of the a, b, and c values give an improved estimate of this coefficient (Field and McFarlane 1968). Other methods of determining affinity between different stations include recurrent group analysis (Fager 1957), multivariate analysis on logarithmically transformed data (Cassie and Michael 1968), and principal component analysis (Hughes et al. 1972). It should be realized that the hierarchical groupings produced by such statistical analysis says nothing about the actual physical/biological factors which influence or control the distribution because the few parameters usually measured are chosen arbitrarily and generally with no regard to the complexities actually involved.

Because of natural variations in benthic communities only relatively gross or rapid changes can be positively identified as caused by pollution or other direct human interference. The process of this change frequently involves death of the original organisms and recolonization by pollution-tolerant fauna (Poole et al. 1978). Two general classes of analytical problem are involved: recognition of spatial differences of species composition at the same point in time; and recognition of temporal changes of species composition, biomass, or numbers at the same point in space. Statistical analytical approaches to these problems are considered by Elliot (1977), Downing (1979), and Green (1979). One difficulty with temporal observations is that the pre-operational must serve as the control for the post-operational data, implying that species composition, density, and biomass remain constant over the period of the post-operational observations. Recent data (see Buchanan et al. 1974; Lie and Evans 1974; Bagge and Ilus 1974; Eagle 1975; Livingston 1976; Whitlach 1977) as well as our own observations in L'Etang Inlet (Wildish et al. 1977) and Digdeguash Estuary (Fig. 1) show that seasonal as well as interannual changes may be large enough to invalidate the assumption of pre-operational data being a control for post-operational data.

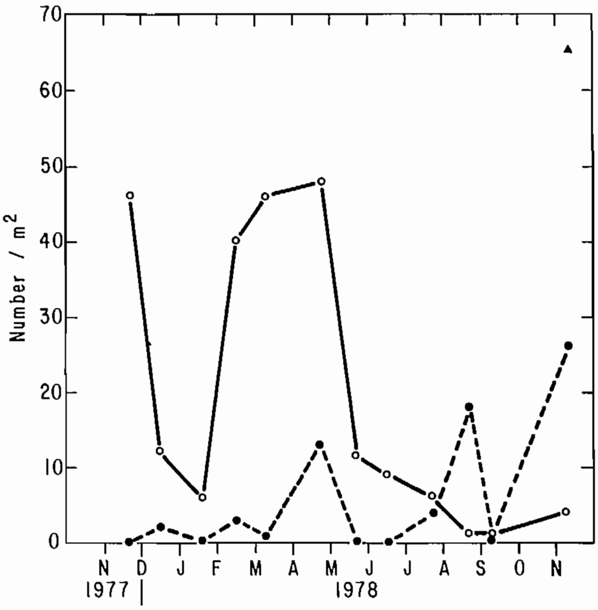

FIG. 1. Density of *Casco bigelowi* (○), *Leptocheirus pingius* (●), and *Pontoporia femorata* (▲). Taken in monthly 0.1 m^2 replicates (15–28) at station 31, Digdeguash Estuary.

Pulpmill pollution in L'Etang Inlet, observed over the period 1971–75 (Wildish et al. 1977; Wildish et al. 1979), showed a dramatic change after 1972 at the most landward station (Table 7). Such marked changes do not require detailed statistical analysis and are best appreciated by simple community descriptions (see also Rosenberg 1977) such as species/m^2, individual number/m^2, and biomass/m^2, as in Table 7. Marked hypoxia was present at station 15 from 1973 onwards.

TABLE 7. Biomass dominants at station 15, lower L'Etang, July–September, based on nine replicate 0.1 m^2 Smith–McIntyre grab samples sieved through a 3-mm^2 mesh. N = individual number/m^2, B = biomass as g wet/m^2.

Species	1971 N	1971 B	1972 N	1972 B	1975 N	1975 B
Modiolus modiolus	0	0	5	156.72	0	0
Amphitrite johnstoni	19	6.01	18	11.98	0	0
Nereis virens	9	5.20	7	2.77	0	0
Littorina littorea	1	5.99	0	0	0	0
Buccinum undatum	1	19.07	3	10.91	0	0
Gattyana cirrosa	4	0.60	0	0	0	0
Nepthys ciliata	22	2.23	8	0.42	0	0
Capitella capitata	0	0	0	0	861	?

Description of Specific Locations

In southern New Brunswick, there are six larger estuaries southward of and inclusive of the Saint John estuary (see Fig. 1, Chapter 1). All have been studied using quantitative benthic sampling methods except for the Magaguadavic Estuary which opens into Passamaquoddy Bay.

GENERAL

Satisfactory replicated sampling has been achieved during summer months with the modified Van Veen, Hunter, or Smith–McIntyre grabs, each of 0.1 m^2 sampling area, at 42 different locations and for 652 replicated samples (Wildish and Wilson 1976). Further sampling in 1976 at one station in Digdeguash Estuary and in 1977 at 15 stations in Saint John Harbour bring the total to 58 stations and 812 grab replications. Species additional to those found previously (Wildish and Wilson 1976) are recorded in Table 8.

Representative data shown in Tables 9 and 10 are from 38 stations and 376 replications, all of which have been sorted on a 0.8-mm square mesh sieve, with the exception of the L'Etang Inlet data where a 3-mm square mesh was used.

TABLE 8. Species list additional to Wildish and Wilson (1976) from Digdeguash Estuary, 1976 (one location) and Saint John Harbour, 1977 (15 locations).

Platyhelminthes	*Notoplana atomata* (Müller, 1776)
Rhynchocoela	*Lineus socialis* (Leidy, 1855) *Micrura* sp.
Mollusca	*Chaetoderma nitidulum* (Lovén, 1844) *Polinices immaculatus* (Totten, 1835) *Thyasira gouldii* Philippi, 1845 *Tellina agilis* Stimpson, 1857
Polychaeta	*Goniada norvegica* Oersted, 1845 *Scolelepis squamatus* (Müller, 1806) *Laonice cirrata* (Sars, 1851) *Scoloplos acutus* (Verrill, 1873) *Mediomastus ambiseta* (Hartman, 1947)
Crustacea	*Hippomedon propinquus* Sars 1890 *Haploops fundiensis* Wildish and Dickenson (1982) *Cancer irroratus* Say 1817 *Gammarus setosus* Dementieva 1931 *Bostrichobranchus pilularis* (Verrill, 1871)

The L'Etang Inlet is a 14-km long arm of the sea with very little freshwater flow into it, although in preglacial times it drained the present-day Magaguadavic River. Extensive studies have been made in this system (Wildish et al. 1979) in connection with the construction of a pulp mill in 1971. The St. Croix Estuary, by contrast, is longer (23.4 km) and receives large volumes of fresh water. The upper narrower part of this estuary (11.6 km long) above Raven Head is a partially stratified estuary with decreasing salinities in the landward direction. The sediment at locations 11, 12, and 14 (Table 10) is covered with wood wastes ranging from small to large strips of bark. The lower section of the St. Croix Estuary (locations 1, 5, and 10 in Table 9) is fjord-like except that it has a maximum depth of 35 m. The Digdeguash is a small estuary, 6 km long from Oven Head to the head of the tide at Salmon Falls above the main highway. It is the only estuary studied without obvious man-made interference and where a strictly deposit-feeding community has been found to date. The Musquash Estuary, 16.3 km long, drains the Musquash rivers and a small *Zostera*/*Spartina* marsh. The freshwater flow into the estuary is regulated by discharge through turbines from a small electric generating plant (Kristmanson 1976). It is eventually planned to phase out this plant and use all of the Musquash rivers flow for the domestic and industrial use of the city of Saint John. Finally, Saint John Estuary is a large, 120-km long, complex system (see Metcalfe et al. 1976). The most seaward part of the estuary — Saint John Harbour, inclusive of the area just outside the dumping buoy at Black Point to the Reversing Falls, a distance of approximately 13 km — is the only portion considered here. It has been extensively influenced by humans: industrial and municipal sewage effluents empty into the harbor, and dredging and dumping activities are carried out there (Carter and MacGregor 1978). The dredging is centered in Courtenay Bay (stations 41, 42, and 43, Table 9) and dumping near the Black Point buoy, (stations 16, 20, and 57, Table 9). Sonar traces of the sediment show that the outer harbor is flat, indicating a strong tidal-current sweeping action there. In the central channel, from below the Reversing Falls to the main harbour, deep holes (up to 20 m) are partially filled

TABLE 9. Locations with ten or more replicated samples taken at the same time. Coordinates are correct to the nearest 0.1′. LW, low water. (L'Etang inlet stations 4 and 11 are based on 9 summer replicates with a 3 mm square sieve on 3 different occasions; and St. John harbour station 7 on 7 replicates on one occasion.)

Description	Station	North		West		Depth at LW (*m*)	Sample date
L'Etang Inlet	11	45°	06.0′	66°	47.7′	5	1970–1973
	4	45	04.8	66	48.0	13	1970–1973
	6	45	04.6	66	47.3	7	July 1973
	5	45	04.6	66	47.6	13	July 1973
St. Croix Estuary	1	45	05.0	67	06.0	12	Sept. 1974
	5	45	07.0	67	07.0	28	Sept. 1974
	10	45	09.0	67	09.0	18	Aug. 1974
	11	45	09.5	67	09.2	15	July 1973
	12	45	09.9	67	10.3	13	Aug. 1974
	14	45	10.1	67	12.9	5	Aug. 1974
	17	45	10.9	67	15.3	5	Aug. 1974
	20	45	11.5	67	16.6	3	Aug. 1974
Digdeguash Estuary	31	45	09.9	66	57.6	2	Sept. 1976
Musquash Estuary	1	45	11.0	66	19.3	2	June 1973
	2	45	11.2	66	17.8	2	June 1973
	3	45	11.2	66	17.0	2	June 1973
	4	45	11.5	66	16.9	2	June 1973
	5	45	11.5	66	16.0	3	June 1973
	6	45	11.2	66	15.3	6	June 1973
	7	45	11.8	66	14.7	1	June 1973
	8	45	09.9	66	14.6	2	June 1973
	9	45	09.4	66	14.8	2	June 1973
Saint John Harbour	7	45	15.0	66	03.5	5	June 1977
	13	45	12.9	66	07.5	13	June 1977
	16	45	12.6	66		14	June 1977
	20	45	12.5	66	07.1	16	June 1977
	41	45	15.6	66	02.6	5	June 1977
	42	45	15.9	66	02.6	5	June 1977
	43	45	16.3	66	02.5	5	June 1977
	49	45	12.6	66	03.3	18	Sept. 1977
	50	45	12.1	66	03.3	18	Sept. 1977
	51	45	11.7	66	03.3	25	Sept. 1977
	52	45	11.2	66	03.1	22	Sept. 1977
	53	45	13.2	66	01.6	12	Sept. 1977
	54	45	13.2	66	01.7	9	Sept. 1977
	55	45	12.7	66	01.7	18	Sept. 1977
	56	45	12.2	66	01.8	22	Sept. 1977
	57	46	12.6	66	00.9	9	Sept. 1977

with wood particles and bark up to 2 m long, as in the St. Croix Estuary. In both places the wood piles are colonized by prodigious numbers of *Gammarus oceanicus*. Because of the nature of the substrate, it has not been possible to quantitatively sample here. In both locations there are strong tidal currents at most stages of the tide, resulting in distinct "sorting" of the wood particles — the larger pieces being present where currents are strongest. The amphipods probably use the piles as a refuge and the microbial film on the wood surface as food. Mussels, *Mytilus edulis*, also attach directly to the wood surface.

Table 10 shows mean salinity values, sediment sorting characteristics as determined by dry sieving and pipet analysis (Akagi and Wildish 1975), a relative measure of organic carbon by the Walkley Black method, as well as some biological characteristics. A classification of the sorting coefficient ($QD\phi$) and phi value is shown in Table 11 and is included to assist in interpretation of the sediment data. For the same median phi value ($Md\phi$) lower $QD\phi$ values indicate increased sorting action of sediments by greater tidal current shear stresses. A second, independent factor indicating tidal current shear stresses at a given location is the $Md\phi$ value itself. This arises because of the complex relationship between tidal current velocities — how these velocities change with time during ebb, flood, and slack tides and cause sediment mobility (Fig. 2). Thus erosion of fine sand occurs at lower current velocities (Fig. 2) but deposition is more or less linearly related to velocity and particle size. These relationships all apply to sedimentary inorganic particles with a density of ~ 2.6 g cm^{-3}; however, biologically more important organic particles, such as polysaccharides, have densities

TABLE 10. Bottom salinity, sediment, and biological characteristics of locations given in Table 14. Grab size 0.1 m², sieved on mesh of 1 mm square.

Location description	Station	Salinity S ‰	MD ϕ	QD ϕ	Skq ϕ	Organic carbon % dry w	S/m²	N/m²	α	B/m²
L'Etang Inlet	11	30.9	7.82	2.51	+1.65	2.4	17	135	5.0	154.9
	4	31.6	1.87	3.46	+2.24	0.9	35	296	10.0	99.4
	6	29.5	6.60	1.33	−0.08	1.7	68	1390	15.0	105.6
	5	29.6	6.40	1.09	+0.31	1.6	65	833	17.0	15.4
St. Croix Estuary	1	28.0	5.80	3.16	−0.46	2.8	28	207	9.5	218.2
	5	28.5	6.75	3.02	−1.12	2.6	33	137	13.0	64.8
	10	28.5	7.40	2.01	−0.26	2.0	24	200	7.5	197.8
	11	28.5	6.80	3.12	+1.38	5.1	64	861	14.0	316.4
	12	28.5	7.60	1.28	−0.25	5.0	17	56	8.0	3.1
	14	28.5	6.80	2.52	−0.77	26.5	12	1,208,479	—	220.4
	17	22.5	2.23	3.08	+1.59	3.4	4	682	2.5	274.4
	20	22.0	2.00	2.97	+1.39	1.8	3	17	1.0	0.9
Digdeguash Estuary	31	30.0	7.94	0.79	−0.13	3.1	22	449	5.0	18.5
Musquash Estuary	1	1.0	6.08	1.44	+0.26	0.8	7	76	2.2	31.64
	2	9.0	6.85	2.65	+1.85	0.9	2	4	—	0.45
	3	12.0	1.27	2.65	+1.85	0.7	11	75	3.1	23.02
	4	15.0	1.66	0.16	−0.14	0.1	12	55	4.5	42.75
	5	20.0	6.80	1.35	+0.42	0.4	11	44	4.5	2.85
	6	24.3	0.30	2.38	−2.13	0.1	3	55	0.4	2.25
	7	25.0	5.92	0.09	+0.07	0.6	17	217	4.5	26.78
	8	27.5	6.22	0.72	+0.39	1.7	12	191	2.9	32.76
	9	28.0	5.63	0.93	+0.32	0.5	5	12	—	0.21
Saint John Harbour	7	24.8	5.39	0.63	+0.01	0.5	6	73	0.8	3.60
	13	24.5	4.56	1.18	+ .11	0.6	3	4	—	0.15
	16	30.8	7.01	1.14	+ .13	2.2	2	3	—	0.03
	20	28.0	6.23	1.58	+ .04	1.9	4	7	—	0.76
	41	26.0	6.18	1.39	+ .31	1.6	9	85	2.3	29.18
	42	24.3	5.59	1.22	+ .31	1.5	9	78	2.4	10.66
	43	24.9	7.40	1.08	− .10	2.0	6	296	1.0	29.95
	49	30.0	6.29	1.34	+ .40	0.7	16	262	3.6	313.60
	50	30.7	5.84	1.76	+ .06	0.4	17	95	5.5	30.69
	51	30.0	5.18	2.01	+ .26	0.5	22	50	13.0	4.86
	52	30.7	3.05	1.57	+ .60	0.4	9	11	—	1.49
	53	30.7	5.88	1.56	− .09	0.6	14	33	8.0	1.09
	54	30.0	6.29	1.57	+ .32	0.9	13	65	5.0	2.80
	55	30.7	4.84	1.72	+ .28	0.5	8	12	—	0.54
	56	30.9	6.13	1.89	− .27	0.8	21	141	7.0	97.67
	57	28.2	6.80	1.34	+ .13	1.7	7	14	—	0.31

lower than this. Organic particles of lower density may be selectively removed or deposited in sediments; at these locations there is a linear relationship between QDϕ values (x) and a measure of organic carbon. Where the latter is expressed as percentage volatile solids (y) the relationship is (Wildish et al. 1980):

$$y = 0.5650 + 1.4531x$$

Two confounding factors serve to limit a universal application of this relationship to other Bay of Fundy estuaries: differences in supply of organic carbon to different estuaries and changes in Mdϕ values at different stations which may invalidate direct comparison of QDϕ values. Data for the estuaries shown in Fig. 3 — Musquash, Saint John Harbour, and Digdeguash (additional data from Wildish et al. 1980) — indicate that at some stations in all three estuaries tidal currents do not differentially erode organic particulate matter. Such stations, which occur above the regression line in Fig. 3, indicate that net depositional sedimentation is occurring here. Whether a given location undergoes net sediment erosion or deposition is postulated to strongly influence the type of macrofauna community to be found there (Wildish and Kristmanson 1979).

TABLE 11. Classification of the phi value (ϕ) and sediment sorting coefficients (QDϕ) according to Swift et al. (1973).

ϕ	Median diameter μ	Description	QDϕ	Description
−1–0	2000–1000	Very coarse sand	0.50 ≤	Very well sorted
0–1	1000–500	Coarse sand	0.51–0.80	Well sorted
1–2	500–250	Medium sand	0.81–1.25	Moderately sorted
2–3	250–125	Fine sand	1.30–2.29	Poorly sorted
3–4	125–62	Very fine sand	2.30 ≥	Very poorly sorted
4–8	62–4	Silt		
>8	<4	Clay		

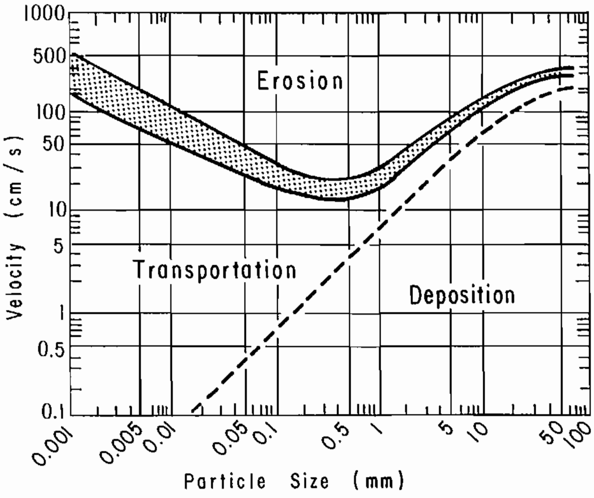

FIG. 2. Approximate relationships between current velocity (cm/s) and its ability to erode, transport, and deposit sedimentary particles of various sizes (after Perkins 1974).

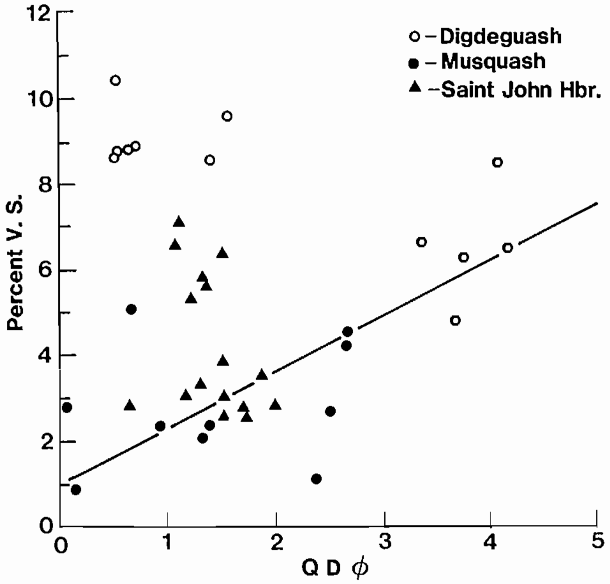

FIG. 3. Plot of percentage volatile solids based on sediment dry weight (%V.S.) versus the sediment sorting coefficient (QDϕ) in three estuaries. The fitted regression and additional data are from Wildish et al. (1980).

A notable difference between the stations shown in Table 10 is the wide variation in biomass values. One reason for this is the presence together of large suspension feeders and small deposit feeders. Thus suspension-feeding dominants, such as *Cyclocardia borealis* at station 11 St. Croix Estuary, make up 227.0 g/m^2 of the total of 316.4 g/m^2. Occasionally the biomass dominants are large deposit feeders such as the holothurian *Molpadia oolitica*, which represents 73.5 g/m^2 of the total biomass of 105.6 g/m^2 at station 6 in L'Etang Inlet. *Molpadia* was taken in only 3 of the 10 replicate grabs and hence is spatially distributed on a scale greater than the grab dimensions, i.e. is megafaunal. The low biomass values at Digdeguash station 31 and L'Etang station 5 are due to the small size of all species. Thus at the L'Etang station the biomass dominants are *Cyclocardia borealis* (3.5 g/m^2, all small specimens), *Yoldia sapotilla* (2.5 g/m^2), *Leptocheirus pinguis* (2.1 g/m^2), and *Lumbrinerus fragilis* (1.9 g/m^2) — all except the first-mentioned species being deposit feeders.

COMMUNITY CLASSIFICATION

The sublittoral benthic fauna of inshore locations near St. Andrews has previously been characterized as impoverished, mixed, or deposit ingesting (Wildish and Kristmanson 1979). Two key factors were involved in this characterization: a relative degree of impoverishment caused by physical disturbance such as low salinity, high tidal energy, and pollution; and an absolute measure of the proportions of the two major trophic groups — suspension and deposit feeding. (Further consideration of the trophic group concept is given on page 15.)

As regards the second factor, a test of the idea expressed in Wildish and Kristmanson (1979), the trophic ratio estimate is presented for selected locations (Table 12). Ideally such an estimate should be based on the

TABLE 12. Trophic ratio (TR) estimates of deposit feeders as a percentage of the total number $>5/m^2$ (N) biomass >1.0 g/m^2 (B), and number of species (S/m^2). For location coordinates see Table 9.

	TRN		TRB		TRS	
Location and station	N	%	B	%	S	%
Saint John Harbour, 7	73	100	2.24	100	6	100
Musquash Estuary, 6	55	100	1.40	100	3	100
Digdeguash Estuary, 1	449	100	18.50	100	22	100
L'Etang Inlet, 4	261	63	69.53	72	24	75
L'Etang Inlet, 11	115	43	137.92	6	17	50
St. Croix Estuary, 5	137	71	38.96	7	20	50
St. Croix Estuary, 10	200	20	195.27	6	24	50

TABLE 13. Specific limiting factors causing impoverishment of benthic populations and supporting citations.

Descriptor	Citation
Hypo-haline	Thomas and White (1969)
Strong tidal current	Wildish and Kristmanson (1979)
Strong wave action	Tyler and Banner (1977)
Hypoxia	Barr and Knull (1973)
Predation	Virnstein (1978)
Pollutants	
heavy metals	Lande (1977)
xenobiotic chemicals (e.g. D.D.T.)	Croker and Wilson (1970)

proportions of annual production produced by each trophic group but, unfortunately, this information is not available for any Bay of Fundy locations. Estimates based on proportions of species in each trophic group may also be acceptable. A difficulty with all of these methods is that the benthic fauna is sometimes facultative in its choice of trophic method. The fundamental classification of benthic communities, expressed by the trophic ratio (*TR*) is:

$$TR\% = \frac{D}{D + S} \times 100$$

where D = total deposit feeders, S = total suspension feeders. As shown in Table 12, the units used to make this calculation markedly influence the results because of the basic physiological differences between many suspension feeders (high biomass, age >1 yr) and many deposit feeders (low biomass, age <1 yr).

Impoverishment may result from specific limiting factors of which at least six can be recognized (Table 13). Naturally caused impoverishment is due to low salinity conditions at four stations: stations 1 and 2, Musquash Estuary, and stations 17 and 20, St. Croix Estuary (Table 10). The phenomenon of sharply decreased numbers of species in hypo-haline conditions in estuaries has frequently been reported (see Den Hartog 1960), sometimes with a concomitant increase in numbers or biomass of the euryhaline survivors. This appears to be the case at station 17, St. Croix Estuary, where a large population of freshly set mussels thrives. A second natural limiting factor is high tidal energy (Wildish and Kristmanson 1979). This is present in Musquash Estuary (stations 6 and 9) and Saint John Harbour (stations 7, 13, 16, 20, 41, 42, 43, 52, 55, and 57). Correlated biological/physical factors here are low diversity and a low sediment carbon level (Table 10), consistent with the observation that strong tidal currents selectively remove organic, in preference to heavier inorganic, particles. High tidal energy impoverishment is indicated by QDϕ and percent volatile solids where net erosion of organic particles occur, as previously described (Fig. 3). Many stations in the Musquash Estuary and Saint John Harbour border on being high tidal energy limited. Quite possibly stations of this kind have not been recognized previously because of the difficulty of sampling in such locations, as was experienced in the Digdeguash Estuary (Wildish et al. 1980).

Anthropogenically-caused impoverishment has been recognized in the L'Etang Estuary (Wildish et al. 1977) although those stations are not shown in Table 10: the three most landward stations experienced hypoxia from 1972 onwards due to secondary heterotrophic, aerobic metabolism of the poorly treated waste from a pulp mill.

Concepts of the Benthos

Much of the recent literature of benthic zoology consists either of descriptions of animal associations in relationship to single limiting factors, or of more theoretical accounts of these associations in terms of their community structure, diversity, successional stage, or stability/time relationships. Reasons have been presented for rejecting such approaches (Wildish 1977) in favor of a multiple limiting factor theory. Prominent among the major biotic factors involved in this theory is the food supply, and this is why the trophic group concept is stressed below.

TROPHIC GROUPS

The trophic group concept originated with investigators who described the feeding methods used by the dominant animals in their samples (Hunt, 1925, was one of the first). Such designations were often not directly observed but were inferred from stomach contents or mouthpart morphology. The importance of the few trophic "groups" to which the macrobenthic species could be referred was realized by Sanders (1960) and Rhoads and Young (1970). Most of the species seen by these authors could be classified trophically either as suspension or deposit feeding species. The fundamental importance of this distinction lies in the fact that inputs of energy reach the sea floor in

TABLE 14. Tropic group classification of some Bay of Fundy sublittoral macrofauna based on mouthpart morphology and/or gut content analysis. Trophic method key: S, suspension feeding; D, deposit feeding; C, carnivore; O, omnivorous scavenger; A, algal scrapers.

Species	Trophic method code	Species	Trophic method code
Polychaeta		*M. niger*	S
Nepthys incisa	D/C	*Mulina lateralis*	S
Sternaspis scutata	D	*Buccinum undatum*	C
Pectinaria granulata	D	*Littorina littorea*	A
Clymenella torquata	D	*Lunatia pallida*	A
Lumbrinereis fragilis	D/C	*Acmaea testudinalis*	A
Praxillella praetermissa	D	*Margarites costalis*	A
P. gracilis	D		
Ninoe nigripes	D	Amphipoda	
Spio filicornis	D/C	*Corophium volutator*	D
Tharyx acutus	D	*Unciola irrorata*	D
Paraonis gracilis	D	*Leptocheirus pinguis*	D
Ampharete acutifrons	D	*Casco bigelowi*	D
Nereis diversicolor	D/S	*Pontoporeia femorata*	D
N. virens	D/?O	*Haploops tenuis*	S
Amphitrite johnstoni	S	*Ampelisca vadorum*	S
Spirorbis	S	*A. macrocephala*	S
Nephtys ciliata	C/D	*A. abdita*	S
Eteone heteropoda	C	*Edotea montosa*	A/O
Goniada maculata	C		
		Echinodermata	
Mollusca		*Cucumaria frondosa*	S
Macoma balthica	D	*Chiridota laevis*	S
Yoldia sapotilla	D	*Molpadia oolitica*	D
Y. myalis	D	*Amphipholis squamata*	D
Nuculana tenuisulcata	D	*Strongylocentrotus droebachiensis*	A
Nucula proxima	D		
N. delphinodonta	D	Sipuncula	
Modiolus modiolus	S	*Phascolion strombi*	D
Musculus niger	S		
Mya arenaria	S	Ascheliminthа	
Cyclocordia borealis	S	*Priapulus caudatus*	D
Lyonsia hyalina	S		
Astarte undata	S	Chordata	
Crenella glandula	S	*Dendrodoa carnea*	S
Artica islandica	S	*Dendrodoa grossularia*	S
Periploma sp.	S	*Bostrichobranchus pilularis*	S
Cerastoderma pinnulatum	S	*Ascidia callosa*	S
Musculus discors	S		

only one of two ways: either in the form of current-transported particles (seston), which are thought to be the "food" of suspension feeders; or as sedimented particles, which deposit at the sediment–water interface and are then selectively or nonselectively ingested directly by the deposit feeders. Other trophic groups (Table 14) are either basically dependent on one or both of these groups (carnivores or omnivorous scavengers) or of minor importance in sublittoral environments (algal scrapers and some scavengers). Further classification of the two major trophic groups is possible: suspension feeders may (1) actively draw water and seston across a filter, or (2) be passive species, which utilize the actual water currents and trap seston on their passive filters (Jorgensen 1966). Deposit ingesters may be characterized by the degree to which they mix or recycle the sediment (Rhoads 1974). Thus species which ingest particles deep in the sediment, often below the redox discontinuity layer, are referred to as "conveyor belt" species. They deposit sedimentary material, after passage through the gut, at the sediment–water interface. Examples include *Praxillella praetermissa* and *Maldane* sp. Other species such as *Casco bigelowi*, move actively through and displace, as well as eat, the sediment. Surface deposit feeders such as *Macoma balthica*, subsurface deposit feeders such as *Nucula proxima*, and tubicolous species such as *Haploops* sp. all influence the sediment–water interface by their feeding and tube-building activity.

TROPHIC GROUP AMENSALISM AND MUTUAL EXCLUSION HYPOTHESES

The trophic group amensalism hypothesis of Rhoads and Young (1970) suggests that deposit feeders inhibit suspension feeders and sessile epifauna, either by discouraging larval settlement or by killing early benthic stages during reworking activities. Rhoads and Young (1970) specifically limit their hypothesis because "it does not adequately describe the factors that separate deposit feeding and suspension feeding groups, where food is actually limiting to suspension feeders". The mutual exclusion hypothesis is compatible with this statement because the biotic interactions implied by the trophic group amensalism may well be important, particularly at the intermediate current velocities (say mean values up to 10 cm/s) present in Buzzards Bay where these authors worked. However, they further state that: "The hypothesis of amensalism is limited to areas of high primary productivity on the continental shelves, where food is not limiting to suspension feeders" (Rhoads and Young 1970), and with this the mutual exclusion hypothesis is not compatible. Moreover, the "biotic groups" of Rhoads and Young (1970) — homogenous suspension feeder trophic groups, homogenous deposit feeder trophic groups, and mixed trophic groups—are defined differently from the categories of animal associations recognized herein and by Wildish and Kristmanson (1979). In the Bay of Fundy soft sediments examined to date, a homogenous suspension-feeding community has not been found. Quite possibly a strictly homogenous suspension-feeding community is absent in soft sediments and present only on hard substrates such as rock surfaces or coral reefs.

The trophic group mutual exclusion hypothesis (Wildish 1977) suggests that sublittoral macrofaunal community composition, biomass, and productivity are limited by a master controlling factor, the tidal current velocity, through its control on the supply of food and its direct inhibition of both major trophic groups. The mutual exclusivity arises because each of the two major trophic groups can tolerate a different range of tidal velocities. Hence, deposit feeders (Fig. 4a) are favored in low mean current velocities (less than the critical erosion velocity for the sediment in which they live) and suspension feeders (Fig. 4b) in higher mean current velocities (~5–30 cm/s). At mean current speeds, above ~30 cm/s, suspension feeders are inhibited, giving rise to the strong tidal current impoverished community (Fig. 4c).

The specific limiting factors for deposit feeders are considered to be the net sedimentation rate and the rate of aerobic microbial activity in the sediment, which is affected by animal–microbe interactions (Hargrave 1976; Poole and Wildish 1979). Levinton et al. (1977) have suggested that the rate-limiting step in deposit feeding by *Hydrobia* is not the rate of microbial activity per se but the rate of faecal pellet breakdown. Food limitation of suspension feeders depends on the concentration of ATP-seston and its rate of supply by turbulent processes to the sediment–water interface. Direct limiting factors include the physical damage to suspension feeders, caused by currents in excess of 12–25 cm/s, and possible larval settlement problems in conditions of high shear stress. For deposit ingestors any sustained currents greater than a few cm/s will tend to carry away the bioturbated sediment, which is then not available as food for them. On the other hand, re-suspended sediment or faecal pellets are exposed to clean seawater, richer in dissolved oxygen and nutrients, in which active metabolism may be enhanced. In addition, tidal currents influence the rate of exchange of dissolved gases or nutrients, as well as particulates across the sediment–water interface (Vanderborght and Wollast 1978).

According to the multiple limiting factor theory (Wildish 1977), a number of biotic factors besides food supply may influence macrobenthic community composition, biomass, and productivity. Factors would include the supply and timing of colonizing larvae, inter- or intraspecific competition, and predation not only by other benthic carnivores but by free-moving fish and invertebrates.

Recently, Virnstein (1977) experimentally investigated predation in Chesapeake Bay by using wire-mesh cages to exclude predators or to include selected predators such as the blue crab (*Callinectes sapidus*) and the spot (*Leiostomus xanthurus*). In the benthic community severe predation was found, resulting in rapid growth, short generation times, and rapid population turnover times of the macrobenthos, whose biomass was at all times well below the carrying capacity of the area. Tyler (1972), working in Passamaquoddy Bay, has shown that 13 species of demersal fish feed extensively on sublittoral macroinfauna, each species having 3–9 principal prey. All of the preyed-upon macrofaunal species were deposit feeders (*Aphrodite, Nephtys, Lumbrinereis, Praxillella, Unciola, Yoldia, Leptocheirus, Maera, Nuculana, Ophiura*) except for *Arctica, Musculus*, and *Venericardia* which are suspension feeders. The three last species form part of the diet of the ocean pout (20–65 cm long) during summer. Tyler (1972) noted that the ocean pout fed only on animals with hard coverings and is presumably specialized for this. These results are consistent with the view that deposit-feeding animals are the major prey items amongst benthic macrofauna. These experimental data serve to emphasize why the trophic ratio values (see p. 149) based on individual numbers, biomass, or production (where this is determined by biomass and a P/B conversion) may not be a good means of testing the relationship between physical factors and benthic trophic function.

Conclusions

The "quantitative" sampling methods used throughout this work contain sources of error which prevent an absolute measure of benthic standing crop biomass. The errors may be caused by insufficient sampling depth, insufficient sampling surface area, and/or variations in sieving efficiency. Specifications for an "absolute" sampling device, viz. digging depth ~3 m and surface area sampled of many m^2, are difficult to meet in a single sampler. Even if such a sampler were designed and used (e.g. a commercial dredging hopper) it would cause extensive local destruction of benthic habitats and would also be impractical for sieving. Probably the best approach in these circumstances is to use two samplers: one optimized for deep digging but of limited sampling area, such as a corer, and the other taking a reasonable surface area of 0.1 m^2 or greater. Those undertaking autecological studies should use the efficiency of various samplers to obtain some idea of the depth and surface area occupied by the species involved. In reporting benthic data, details of the digging depth and surface area sampled should always be given, as well as the mesh size of the sieve used.

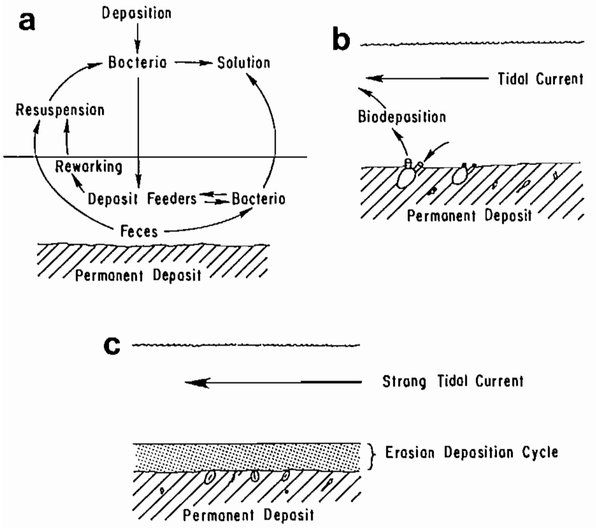

FIG. 4. Concept of major sublittoral macrofaunal communities in sediments: a, deposit-feeding (modified from Rhoads 1974); b, mixed; c, impoverished.

The comparative method used in this work was found to be useful when attempts were made to correlate physical parameters and biological characteristics. Thus, communities impoverished by low salinity, high tidal current energy, and hypoxia resulting from pulpmill pollution, were readily recognized. Used in conjunction with the trophic group concept, the comparative method promises to be useful in providing biological predictions for other Bay of Fundy estuaries where less intensive sampling of physical parameters would be needed.

The search for a central conceptual basis for sublittoral benthic biology is considered to depend on three factors: use of the trophic group classification, which is central to the idea of feeding limitation; detailed field observations of physical phenomena in relation to benthic distribution and productivity; and field and laboratory experimentation to test hypotheses in this field. Such a concept would facilitate predictions about the behavior of sublittoral macrofauna when perturbing factors are applied. It is on such a basis that a successful coastal zone resource management strategy can reliably be based.

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CHAPTER 10

Fishes

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A Review

The fishes and the fisheries of Passamaquoddy Bay and adjacent waters have been investigated extensively since the early days of this century, largely because of the existence of a highly productive commercial fishery and the early establishment (about 1899) of a biological station at St. Andrews.

The comparative richness of the Quoddy fisheries has been documented for many years. According to Huntsman (1952) the Quoddy Region had the most productive fishery for the whole of the Bay of Fundy, the Charlotte County waters yielding 147 lb/acre. (The Digby waters of Nova Scotia were next with 33 lb/acre.) The reasons advanced for such high productivity were the combination of heavy freshwater discharge, cold salt water, and strong tides for mixing.

If the fishery itself is unique, what of the fishes that make up the fishery? How does the fauna compare with other parts of Canadian Atlantic waters or even with Canadian Pacific waters?

The fauna of the North Atlantic Ocean is generally less speciose than that of the North Pacific. There was much greater continuity of faunas between these areas in Cenozoic times but during the late Miocene and Pliocene, Middle America was uplifted, closing the seaway connection between the two oceans (Durham and Allison 1960). Prior to that time, the Atlantic Ocean received its faunal contributions from the Pacific and Arctic oceans. The cooling of the seas during the Miocene allowed for replacement of the rich tropical fauna (Ekman 1953). Such a replacement was made possible during the Pliocene when the opening of the Bering Strait and favourable climatic conditions permitted movement of the Pacific fauna into the Atlantic via the Arctic Ocean (Briggs 1970).

This can be demonstrated by comparing the fish faunas of Canada's Atlantic and Pacific coasts. Of those families represented in both areas, the Pacific families are generally more speciose. The following families, shown with the number of species for each area, will serve as examples:

Family	Atlantic	Pacific
Scorpaenidae	4	37
Osmeridae	2	7
Cottidae	14	42
Pleuronectidae	7	19

However, the family Gadidae, the codfishes, is represented by 19 species on the Atlantic coast, but by only 4 on the Pacific. Because of the localities and age of the fossil remains, the Tertiary history of the seas where the fossils have been found, and the recent distribution and ecology of the cods, this group of fishes is considered to have an Atlantic or even an Atlantic–Arctic basin origin (see Svetovidov 1948, 1956).

The zoogeography and distribution of one Atlantic coast species, *Pungitius pungitius*, the ninespine stickleback, believed to have a Pacific basin origin, was studied in detail by McPhail (1963). He postulates that the present Atlantic coastal distribution resulted from a coast-wise movement from Alaska through Canadian arctic waters (including Hudson Bay), along Ungava shores of Quebec, and down the Labrador coast to the Maritimes and New England.

On a comparative basis, however, the waters of the Northwest Atlantic are considered faunistically sparse. The marine environment of the Bay of Fundy–Gulf of Maine is harsh and is usually classified as "boreal" (Bousfield 1960; Briggs 1974; Lubinsky 1980). For additional information relating to historical changes in the environment of the region see Bousfield and Thomas (1975).

The paucity of fish species, therefore, results not only from the relatively recent geologic and climatologic history, which limited the number of species available, but also from an environment nonconducive to speciation. The influential Labrador current floods cold arctic water into the region, many rivers discharge freshwater (creating salinity changes), and surging tides ensure continuous mixing — all in the presence of seasonal climatic changes. Faunal diversity is related to climatic or environmental stability, as well as to geographic area (Sanders 1968); the more stable the environment, the greater the faunal diversity.

The factors limiting the number of species that occur in the Canadian Atlantic area are the same factors responsible for the exceptionally high biological productivity of the region. Thus, although the number of species may be limited, those that have adapted may be exceedingly successful and numerous, making the Canadian Atlantic area one of the world's richest fishing grounds.

Fishes occurring in the Quoddy Region may be grouped in the following categories: 1) those of cold-water origin that have become adapted to life in the region, some of which spawn during the cool winter months (Gadidae) and some in early spring (Pleuronectidae, Cottidae); 2) those of warm-water origin that have become adapted to life in the region (Labridae) and spawn during summer; and 3) those of northern or southern origin that enter the region in winter or summer, respectively, and may or may not spawn there. The last, especially those arriving in summer, enter the region primarily to take advantage of the rich food supply.

This chapter is concerned only with marine fishes, including anadromous and catadromous species; freshwater fishes are not included. For information on the fresh waters of the area see Scott (1967), Scott and Crossman (1959), and Scott and Crossman (1973). Information on preservation and documentation of specimens is contained in the last publication.

Checklist of Fishes of Quoddy Region

The following checklist includes 104 species in 47 families. Some are based on literature reports, some are from the files of the St. Andrews Biological Station, Fisheries and Oceans Canada, and still others are from personal observations. Among the literature records, Huntsman's (1922) paper, *The Fishes of the Bay of Fundy*, is particularly important. He gives details on the ecology and distribution of 89 species. Other pertinent works include papers by Bigelow and Schroeder (1953), Kendall (1914), Leim (1960), Leim and Day (1959), Leim and Scott (1966), Linkletter, et al. (1977), Scattergood (1948, 1951), Scattergood and Coffin (1957), Scattergood and Goggins (1958) and Tyler (1971).

The study of the fish community by Tyler (1971) is of special interest. A selected site in Passamaquoddy Bay was sampled monthly by trawl. Tyler applied the terms "regulars" to those species present on every or nearly every sampling date, "summer periodic" to those present only during the warm months (July–November), and "winter periodic" to those present only during the months of minimum temperatures (December–April). "Occasionals" was the term applied to those species present irregularly in the samples and in low numbers.

These terms were used by Tyler to indicate the frequency of occurrence of fishes in a particular study area, using a specific type of fishing gear over a 16-mo period. The present study describes the occurrence of fishes that are known to have been in the region since about 1850. Consequently new terms are necessary and the following are proposed:

common — found somewhere in region throughout year but not necessarily in large numbers;

occasional — sporadic occurrence, sometimes 10 or more specimens, often seasonal;

unusual — recorded once or twice a year in most years, often seasonal;

rare — recorded less than 15 times from the region, possibly once every 3–5 yr, generally seasonal;

doubtful — incompletely documented single record, usually prior to 1925;

resident — a species that occurs in the region throughout the year in one or more stages of its life history, and that may move bathymetrically according to season; and

migrant — a species that occurs in the region for periods of one to a few months in the year, usually of seasonal occurrence. Migrants may come from the north (Arctic), the south (temperate), or from deeper offshore waters (offshore).

A total of 104 species make up the fish fauna of the region. Four of these, all salmonids (pink salmon, coho, rainbow trout, and brown trout) are introduced. Of the remaining 100 species, 57 are considered to be permanent residents and 35 of these, or more than half, are derived from just seven families: herrings, cods, sticklebacks, sculpins, lumpfishes, left-hand flounders, and right-hand flounders.

The group that moves into the region from southern waters — the temperate migrants (such as white shark and bluefin tuna), with 29 species — is the second largest component, followed by eight species (such as Müller's pearlside) that move in from offshore and another 6 species (including the Greenland shark and the capelin) that move in from northern waters.

The checklist attempts to provide maximum information in an abbreviated or cryptic form. For example, the sea lamprey, *Petromyzon marinus* is not common in the area but the larvae may be found at most times of the year living in the bottom mud of a few brooks, such as Dennis Stream. At this stage of its life, the sea lamprey is benthic. In spring, adult sea lampreys return from the sea. This shoreward pelagic movement terminates when they locate a suitable stream, spawn, and die. Adult sea lampreys are therefore anadromous like Atlantic salmon and other salmonid fishes, whereas the larvae spend the 3–5 yr of larval life as benthic infauna. The cryptic annotation for the sea lamprey is therefore:

Occasional; resident; anadromous; benthic and pelagic.

CHECKLIST

Class AGNATHA

Order MYXINIFORMES

Family Myxinidae — hagfishes

Myxine glutinosa Linnaeus — Atlantic hagfish
Common; resident; benthic

Order PETROMYZONTIFORMES

Family Petromyzontidae — lampreys

Petromyzon marinus Linnaeus — sea lamprey
Occasional, resident; anadromous; benthic and pelagic

Class CHONDRICHTHYES

Order SQUALIFORMES

Family Odontaspididae — sand tigers

Odontaspis taurus (Rafinesque) — sand tiger
Rare; migrant; temperate; pelagic

Family Alopiidae — thresher sharks

Alopias vulpinus (Bonnaterre) — thresher sharks
Rare; migrant; temperate; pelagic

Family Lamnidae — mackerel sharks

Carcharodon carcharias (Linnaeus) — white shark
Rare; migrant; temperate-tropic; pelagic

Cetorhinus maximus (Gunnerus) — basking shark
Unusual; migrant; temperate; pelagic

Lamna nasus (Bonnaterre) — porbeagle
Common; resident; pelagic

Family Carcharhinidae

Mustelus canis (Mitchill) — smooth dogfish
Rare; migrant; temperate; pelagic

Rhizoprionodon terraenovae (Richardson) — Atlantic sharpnose shark
Rare; migrant; temperate; pelagic

Family Squalidae

Somniosus microcephalus (Bloch and Schneider) — Greenland shark
Rare; migrant; arctic; pelagic

Squalus acanthias Linnaeus — spiny dogfish
Common (in summer); migrant; temperate; pelagic

Order RAJIFORMES

Family Rajidae — skates

Raja erinacea Mitchill — little skate
Common (in winter); migrant; offshore; benthic

Raja laevis Mitchill — barndoor skate
Occasional; migrant; offshore; benthic

Raja ocellata Mitchill — winter skate
Occasional; migrant; offshore; benthic

Raja radiata Donovan — thorny skate
Common; resident; benthic

Raja senta Garman — smooth skate
Occasional; resident; benthic

Family Torpedinidae — electric rays

Torpedo nobiliana Bonaparte — Atlantic torpedo
Rare; migrant; temperate-tropic; benthic

Class OSTEICHTHYES

Order ACIPENSERIFORMES

Family Acipenseridae — sturgeons

Acipenser oxyrhynchus Mitchill — Atlantic sturgeon
Unusual; resident; anadromous; benthic

Family Albulidae — bonefishes

Albula vulpes (Linnaeus) — bonefish
Doubtful; migrant; temperate-tropic; pelagic

Order ANGUILLIFORMES

Family Anguillidae — freshwater eels

Anguilla rostrata (Lesueur) — American eel
Common; resident; catadromous; benthic

Order CLUPEIFORMES

Family Clupeidae — herrings

Alosa aestivalis (Mitchill) — blueback herring
Occasional; resident; anadromous; pelagic

Alosa pseudoharengus (Wilson) — alewife
Common, resident; anadromous; pelagic

Alosa sapidissima (Wilson) — American shad
Unusual; migrant; temperate; anadromous; pelagic

Brevoortia tyrannus (Latrobe) — Atlantic menhaden
Rare; migrant; temperate; pelagic

Clupea harengus harengus Linnaeus — Atlantic herring
Common; resident; pelagic

Etrumeus teres (Dekay) — round herring
Rare; migrant; temperate; pelagic

Family Salmonidae — trouts

Oncorhynchus gorbuscha (Walbaum) — pink salmon
Rare; introduced; migrant; anadromous; pelagic

Oncorhynchus kisutch (Walbaum) — coho salmon
Rare; introduced; migrant (and resident?); anadromous; pelagic

Salmo gairdneri Richardson — rainbow trout
Rare; introduced; migrant; anadromous; pelagic

Salmo salar Linnaeus — Atlantic salmon
Common; resident; anadromous; pelagic

Salmo trutta Linnaeus — brown trout
Occasional; introduced; resident; anadromous; pelagic

Salvelinus fontinalis (Mitchill) — brook trout
Common; resident; anadromous; pelagic

Family Osmeridae — smelts

Mallotus villosus (Müller) — capelin
Unusual; migrant; arctic; pelagic

Osmerus mordax (Mitchill) — rainbow smelt
Common; resident; anadromous; pelagic

Family Gonostomatidae — lightfishes

Maurolicus muelleri (Gmelin) — Müller's pearlside
Rare; migrant; offshore; bathypelagic

Order LOPHIIFORMES

Family Lophiidae — goosefishes

Lophius americanus Valenciennes — monkfish (goosefish)
Occasional; resident; benthic

Order GADIFORMES

Family Gadidae — codfishes

Brosme brosme (Müller) — cusk
Unusual; resident; benthic

Enchelyopus cimbrius (Linnaeus) — fourbeard rockling
Occasional; resident; benthic

Gadus morhua Linnaeus — Atlantic cod
Common; resident; benthic

Melanogrammus aeglefinus (Linnaeus) — haddock
Common; resident; benthic

Merluccius bilinearis (Mitchill) — silver hake
Occasional; migrant; offshore; pelagic

Microgadus tomcod (Walbaum) — Atlantic tomcod
Common; resident; anadromous; benthic

Pollachius virens (Linnaeus) — pollock
Common; migrant; offshore; temperate; pelagic

Urophycis chuss (Walbaum) — red hake
Common; resident; benthic

Urophycis tenuis (Mitchill) — white hake
Common; resident; benthic

Family Macrouridae — grenadiers

Nezumia bairdi (Goode and Bean) — marlin-spike
Rare; migrant; offshore; benthopelagic

Family Zoarcidae — eelpouts

Lycenchelys verrilli (Goode and Bean) — Wolf eelpout

Rare; migrant; temperate (off shore); benthic
Macrozoarces americanus (Schneider) — ocean pout
Common; resident; benthic

Order ATHERINIFORMES

Family Exocoetidae — flyingfishes

Hyporhamphus unifasciatus (Ranzani) — halfbeak
Rare; migrant; temperate; pelagic

Family Cyprinodontidae — killifishes

Fundulus heteroclitus (Linnaeus) — mummichog
Common; resident; inshore pelagic

Family Atherinidae — silversides

Menidia menidia (Linnaeus) — Atlantic silverside
Common; resident; inshore pelagic

Order ZEIFORMES

Family Zeidae — dories

Zenopsis conchifera (Lowe) — buckler dory
Unusual; migrant; temperate; pelagic

Order GASTEROSTEIFORMES

Family Gasterosteidae — sticklebacks

Apeltes quadracus (Mitchill) — fourspine stickleback
Common; resident; pelagic
Gasterosteus aculeatus Linnaeus — threespine stickleback
Common; resident; euryhaline; pelagic
Gasterosteus wheatlandi Putman — blackspotted stickleback
Common; resident; pelagic
Pungitius pungitius (Linnaeus) — ninespine stickleback
Common; resident; euryhaline; pelagic

Family Syngnathidae — pipefishes

Syngnathus fuscus Storer — northern pipefish
Unusual; resident; benthic

Order PERCIFORMES

Family Percichthyidae — temperate basses

Morone americana (Gmelin) — white perch
Common; resident; inshore, estuarine
Morone saxatilis (Walbaum) — striped bass
Occasional; migrant; temperate; pelagic

Family Serranidae — sea basses

Centropristis striata (Linnaeus) — black sea bass
Rare; migrant; temperate; pelagic

Family Sparidae — porgies

Stenotomus chrysops (Linnaeus) — scup
Rare; migrant; temperate; pelagic

Family Labridae — wrasses

Tautoga onitis (Linnaeus) — tautog
Rare; migrant; temperate; pelagic
Tautogolabrus adspersus (Walbaum) — cunner
Unusual; resident; pelagic

Family Stichaeidae — pricklebacks

Lumpenus lumpretaeformis (Walbaum) — snakeblenny
Common; resident; benthic
Lumpenus maculatus (Fries) — daubed shanny
Common; resident; benthic
Ulvaria subbifurcata (Storer) — radiated shanny
Occasional; resident; benthic

Family Pholidae — gunnels

Pholis gunnellus (Linnaeus) — rock gunnel
Common; resident; benthic

Family Anarhichadidae — wolffishes

Anarhichas lupus Linnaeus — Atlantic wolffish
Common; resident; benthic
Anarhichas minor Olafsen — spotted wolffish
Rare; migrant; arctic; benthic

Family Cryptacanthodidae — wrymouths

Cryptacanthodes maculatus Storer — wrymouth
Unusual; resident; benthic

Family Ammodytidae — sand lances

Ammodytes sp. — sand lance
Rare; resident; benthic

Family Scombridae — mackerels

Sarda sarda (Bloch) — Atlantic bonito
Rare; migrant; temperate; pelagic
Scomber scombrus Linnaeus — Atlantic mackerel
Occasional; migrant; temperate; pelagic
Thunnus thynnus (Linnaeus) — bluefin tuna
Rare; migrant; temperate; pelagic

Family Stromateidae — butterfishes

Peprilus triacanthus (Peck) — butterfish
Occasional; resident; pelagic

Family Scorpaenidae — scorpionfishes

Sebastes spp. — redfishes
Common; resident; benthic

Family Triglidae — searobins

Prionotus carolinus (Linnaeus) — northern searobin
Rare; migrant; temperate; benthic
Prionotus evolans (Linnaeus) — striped searobin
Rare; migrant; temperate; benthic

Family Cottidae — sculpins

Artediellus uncinatus (Reinhardt) — Arctic hookear sculpin
Occasional; resident; benthic
Gymnocanthus tricuspis (Reinhardt) — Arctic staghorn sculpin
Rare; migrant; arctic; benthic
Hemitripterus americanus (Gmelin) — sea raven
Common; resident; benthopelagic
Icelus spatula Gilbert and Burke — spatulate sculpin
Rare; migrant; arctic; benthic
Myoxocephalus aeneus (Mitchill) — grubby
Common; resident; benthic
Myoxocephalus octodecemspinosus (Mitchill) — longhorn sculpin
Common; resident; benthic
Myoxocephalus scorpius (Linnaeus) — shorthorn sculpin
Common; resident; benthic
Triglops murrayi Gunther — mustache sculpin
Common; resident benthic

Family Agonidae — poachers

Aspidophoroides monopterygius (Bloch) — alligatorfish
Common; resident; benthic

Family Cyclopteridae — snailfishes

Cyclopterus lumpus Linnaeus — lumpfish
Common; resident; benthic
Eumicrotremus spinosus (Müller) — Atlantic spiny lumpsucker
Rare; migrant; arctic; benthic
Liparis atlanticus (Jordan and Evermann) — seasnail
Unusual; resident; benthic
Liparis inquilinus Able — inquiline snailfish
Unusual; resident; benthic

Order PLEURONECTIFORMES

Family Bothidae — lefteye flounders

Paralichthys dentatus (Linnaeus) — summer flounder
Rare; migrant; temperate; benthic
Paralichthys oblongus (Mitchill) — fourspot flounder
Rare; migrant; temperate; benthic
Scophthalmus aquosus (Mitchill) — windowpane
Common; resident; benthic

Family Pleuronectidae — righteye flounders

Glyptocephalus cynoglossus (Linnaeus) — witch flounder
Common; resident; benthic
Hippoglossoides platessoides (Fabricius) — American plaice
Common; resident; benthic
Hippoglossus hippoglossus (Linnaeus) — Atlantic halibut
Common; resident; benthopelagic
Limanda ferruginea (Storer) — yellowtail flounder
Common; resident; benthic
Liopsetta putnami (Gill) — smooth flounder
Occasional; resident; estuarine; benthic
Pseudopleuronectes americanus (Walbaum) — Winter flounder
Common; resident; benthic
Reinhardtius hippoglossoides (Walbaum) — Greenland halibut
Rare; resident; benthic

Order TETRAODONTIFORMES

Family Balistidae — leatherjackets

Monacanthus hispidus (Linnaeus) — planehead filefish
Rare; migrant; temperate; pelagic

Family Tetraodontidae

Sphoeroides maculatus (Block and Schneider) — northern puffer
Rare; migrant; temperate; pelagic

Family Molidae — molas

Mola mola (Linnaeus) — ocean sunfish
Unusual; migrant; temperate; pelagic

Keys to the Fishes of the Region

The keys are intended to assist in identifying those species more commonly encountered, and consist of a series of choices in the form of couplets, numbered on the left-hand margin. To use the key, compare the characters of the specimen in hand with the first statement. If the statement agrees, follow the indication given at the end of the statement, which will be either a name or the number of the next couplet. If the statement is not in agreement, proceed to the second part of the couplet. Continue until an identity is made.

An asterisk following the family name indicates that there is an additional key on the following pages to assist in identifying the members of the family.

KEY to CLASSES and ORDERS of Fishes

1 Jaws absent; fins without rays, paired fins absent; body elongate and snake-like; skin smooth, with one or 7 pairs of pore-like gill openings; a single median nostril; length to about 76.2 cm (30 inches) .... Hagfishes and Lampreys, class AGNATHA*

Articulated jaws present, lower jaw movable; typically with paired pectoral and pelvic fins 2

2 Gill openings slit-like, 5 pairs, either on sides or on ventral surface of body; body fusiform (sharks), or flattened (rays); skin more or less rough with small and/or large spines, never with overlapping scales........ Shark and Rays, class CHONDRICHTHYES........ 3

One gill opening on each side, with a bony flap (the operculum); body fusiform; skin typically with overlapping scales, but sometimes naked or plated; fins with rays; skeleton ossified (except in sturgeons)...................... Bony fishes, class OSTEICHTHYES*

3 Body shape fusiform (i.e. spindle-shaped or shark-like); gill openings on both sides of body; caudal fin distinct and heterocercal; teeth usually sharp and strong. . . . . Sharks, order PLEUROTREMATA*

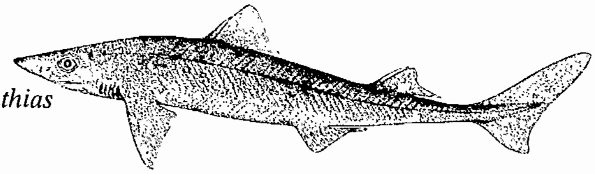
Body shape flattened dorso-ventrally with gill openings on lower surface; pectoral fins broad and winglike, attached throughout length to head and body; tail whip-like. . . . . Rays, order HYPOTREMATA*

KEY to HAGFISHES and LAMPREYS — Class AGNATHA

Three pairs of barbel-like tentacles about mouth and nostrils; one gill opening on each side, far behind head; mouth not cup-like. . . . . Atlantic hagfish, *Myxine glutinosa*

No barbels on head; 7 distinct gill openings on each side behind head; mouth cup-like and lined with horny teeth (in adults) . . . . Sea lamprey, *Petromyzon marinus*

KEY to SHARKS — Order PLEUROTREMATA (Squaliformes)

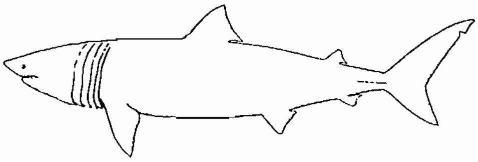


1 Anal fin absent. . . . . Spiny dogfish, *Squalus acanthias*

Anal fin present. 2

2 Dorsal lobe of caudal fin greatly enlarged, as long as head and body combined . . . . Thresher shark, *Alopias vulpinus*

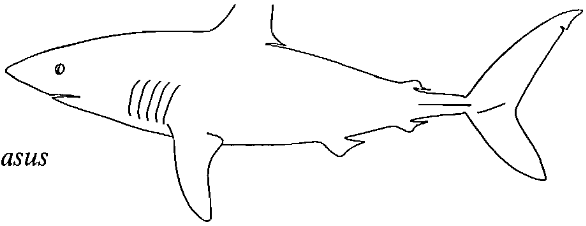
Dorsal lobe of caudal fin nearly equal in size to lower lobe, or only 2 or 3 times larger . 3



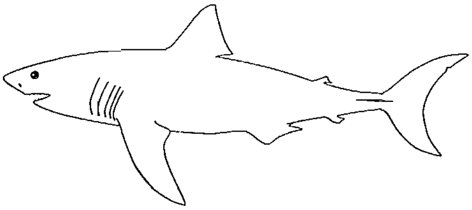
3 Gill slits or openings greatly enlarged, the first pair nearly meeting over the throat, and all 5 seeming to almost sever the head; teeth minute and numerous; well-developed lateral keels on caudal peduncle. . . . . Basking shark, *Cetorhinus maximus*

Gill slits of moderate size, not extending almost around body; teeth not minute but well developed; caudal peduncle and caudal fin with one or more distinct lateral keels 4

4 A second smaller lateral keel below primary keel, on lower lobe of caudal fin; teeth slender, pointed, smooth-edged, with sharp denticle near base on each side of individual tooth..... Porbeagle, *Lamna nasus*

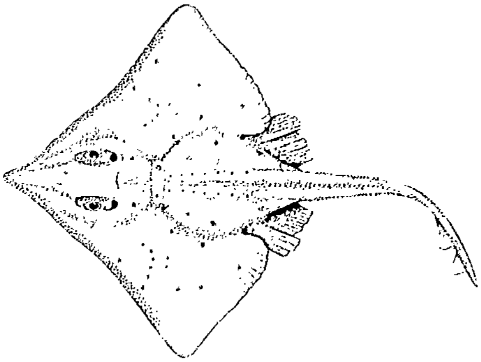


No secondary keel below primary keel; teeth broad and triangular, margins strongly serrate providing sharp cutting edges..............................
.... White shark, *Carcharodon carcharias*



KEY to RAYS — Order HYPOTREMATA (Rajiformes)

1 Anterior outline of snout usually pointed, and with an angle less than 90°; dorsal fins usually separated at base; lower surface speckled with pigmentation around mucous pores .... Barndoor skate, *Raja laevis*

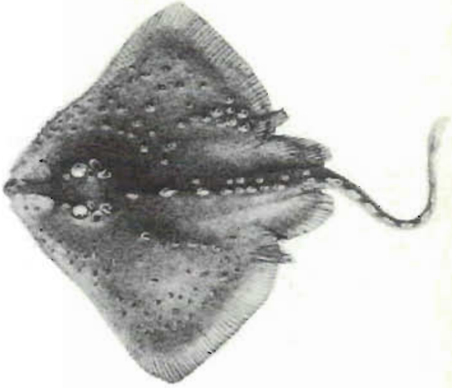


Anterior outline of snout obtuse or blunt, with an angle usually greater than 90°; dorsal fins sometimes joined at base; lower surface white, not pigmented 2

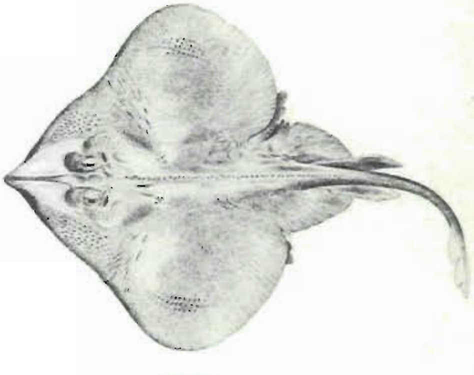
2 Skates of 30.5 cm (12 inches) or more in length, with a row of distinct spines along midline of body and tail (young skates of many species, up to a length of about 30.5 cm, (12 inches), have a midline row of spines); tooth rows in upper jaw 36–46....................... 3

Skates of 30.5 cm or more in length without a row of distinct spines along midline of body and tail; tooth rows in upper jaw 38–110 4

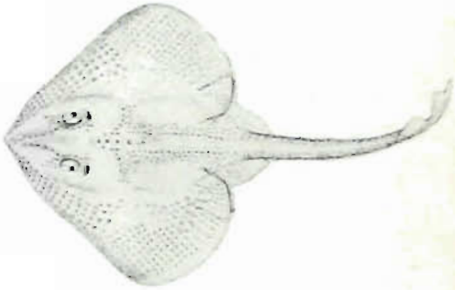
3 Large spines along midline of body and tail, no more than 10 posterior to axils of pelvic fins, extending along length of tail, not diminishing in size posteriorly; body with large conspicuous spines. . . . .
. . . . Thorny skate, *Raja radiata*



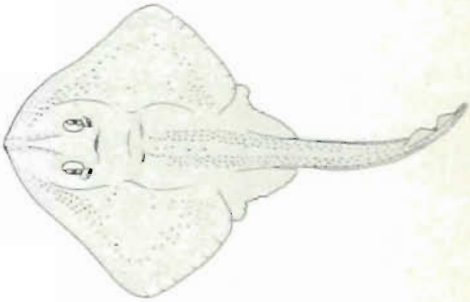
Small spines along midline of body, spines diminishing in size posteriorly, becoming indistinguishable on posterior half of body; body with mostly small, inconspicuous spines (young with 1 or 2 conspicuous pale crossbars on tail near body)
. . . . Smooth skate, *Raja senta*



4 Tooth rows in upper jaw 38–64; males with alar spines; distance between orbits greater than 12 times tail length; mouth outline strongly bowed; maximum size to 6.10 cm (24 inches) . . . .
. . . . Little skate, *Raja erinacea*



Tooth rows in upper jaw 72–100; males without alar spines; distance between orbits less than 12 times tail length; mouth outline gently bowed; maximum size to 109.2 cm (43 inches) . . . .
. . . . Winter skate, *Raja ocellata*



KEY to Families of BONY FISHES — Class OSTEICHTHYES

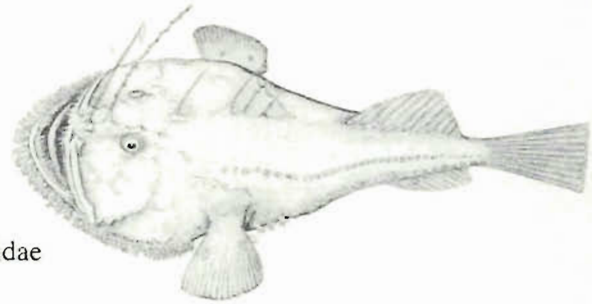
1 Caudal fin heterocercal (shark-like); 5 longitudinal rows of bony plates along body; skeleton cartilaginous; mouth inferior, preceded by 4 barbels. . . . .
. . . . Sturgeons, family Acipenseridae

Caudal fin when present is homocercal 2

2 Body strongly compressed laterally and asymmetrical, with both eyes on one side..... ....Flatfishes, families Bothidae and Pleuronectidae*

Body shape variable but symmetrical, usually of conventional shape; one eye on each side of head 3

3 First dorsal fin spine elongated and located far forward on top of the head and modified to form an illicium or movable fishing lure (anglerfishes), or this spine modified; pectoral fin usually stalked and limb-like; body rather flattened dorso-ventrally.......................... ....Goosefishes, family Lophiidae



First dorsal fin spine, if present, not far forward and not modified to form an illicium; body not flattened dorso-ventrally 4

4 Pelvic fins present (sometimes reduced to a few rudimentary spines) 5

Pelvic fins absent.. 21

5 Adipose fin present; pelvic fins usually abdominal 6

Adipose fin absent; pelvic fins abdominal, thoracic, or jugular...................... 7

6 Pelvic axillary process well developed... ....Salmons and Trouts, family Salmonidae*

Pelvic axillary process absent...................... ....Smelts, family Osmeridae*

7 Pelvic fins abdominal; fins soft rayed, without stiff or pointed spines 8

Pelvic fins thoracic or juglar; fins with or without spines 9

8 Caudal fin forked, pelvic axillary process present, medium-sized (76.2 cm (30 inches)) silvery fishes..Herrings, family Clupeidae*

Caudal fin rounded or square; pelvic axillary process absent; small (up to 12.7–15.2 cm (5–6 inches)) fishes. .....Killifishes, family Cyprinodontidae

9 Fins soft rayed, without spines or stiff rays; no spines on head 10

Stiff spines or spine-like branched rays in dorsal, anal or pelvic fins; sometimes with strong spines on head and gill covers 11

10 Dorsal and anal fins distinct from caudal fin; dorsal fins usually 2 or 3 (only *Brosme* has one); anal fins one or 2; chin barbel usually present. . . . . Codfishes, family Gadidae*

Dorsal and anal fins long and continuous with caudal fin, no separate caudal fin; elongate fishes. . . . . Eelpouts. family Zoarcidae

11 No distinct caudal fin, body tapering to a pointed tail; mouth inferior and snout distinctly projecting. . . . . Grenadiers, family Macrouridae

A distinct well-formed caudal fin present 12

12 A series of dorsal and anal finlets, behind the dorsal and anal fins. . . . . Mackerels and Tunas, family Scombridae

No dorsal or anal finlets. 13

13 Soft dorsal fin preceded by individual sharp spines; pelvic fin reduced to one spine and 0–2 inconspicuous rays; small fishes . . . . Sticklebacks, family Gasterosteidae*

Soft dorsal fin not preceded by individual sharp spines; pelvic fin not reduced to a single spine 14

14 Body completely covered with rows of hard overlapping plates; small, slender fishes. . . . . Poachers, family Agonidae

Body scaled, naked, or with dermal denticles; spiny-rayed fishes of variable shape and size 15

15 Anal fin rays soft and flexible, not preceded by short stiff spines; pelvic fin rays usually 3; body usually tadpole shaped . . . . Sculpins, family Cottidae*

Anal fin preceded by 1–4 stiff spines, pelvic fin usually having one spine and 1–5 soft rays; body shape variable, not tadpole shaped. 16

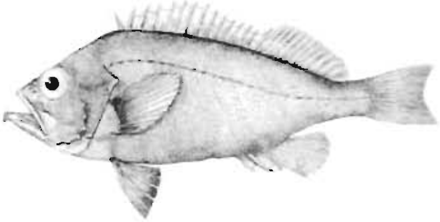
16 Pelvic fin of one spine and 5 soft rays; body somewhat laterally compressed 17

Pelvic fin reduced to one spine and 1–3 soft rays. 20

17 First dorsal fin small, of 4 spines, separated from second soft dorsal by a space equal to its own base length; anal fin preceded by a single slender spine; small slender fishes. . . . . Silversides, family Atherinidae

First dorsal fin joined to second soft dorsal or separated from it only by a narrow space 18

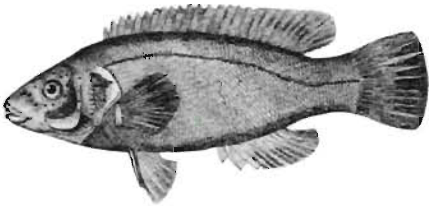
18 Head spiny, with 4 or 5 spines on the posterior margin of preopercle; spiny and soft-rayed portions of dorsal fin broadly joined; pelvic fins inserted directly below insertion of pectoral fins. . . . .
. . . . Scorpionfishes, family Scorpaenidae



Head not spiny; spiny- and soft-rayed dorsal fins separate or joined; pelvic fin inserted behind pectoral fin insertion 19

19 Spiny- and soft-rayed portions of dorsal fin separated by a narrow gap, forming 2 distinct fins; lower incisor teeth not prominent. . . . .
. . . . Temperate basses, family Percichthyidae*

Spiny- and soft-rayed portions of dorsal fin broadly joined; lower incisor teeth somewhat prominent and protruding. . .
. . . . Wrasses, family Labridae



20 Pelvic fin usually moderately well developed but composed of few rays, and fin located in advance of pectoral fin. . . . . Pricklebacks, family Stichaeidae*

Pelvic fin greatly reduced in size, of one spine and one soft ray only, located under or behind pectoral fin base. . . . .
. . . . Gunnels, family Pholidae

21 A well-developed sucking disc on breast, formed from modified pelvic fins. . . . .
. . . . Lumpfishes and Snailfishes, family Cyclopteridae*

No sucking disc on breast 22

22 Body covered with bony plates, forming a series of bony ridges; mouth small, located at end of a prolonged snout . . . . Pipefishes, family Syngnathidae

Body not covered with bony plates; body scaleless or with small inconspicuous scales . . 23

23 Dorsal fin originating on posterior part of head, in advance of pectoral fins. . . . . . .
. . . . Wolffishes, family Anarhichadidae

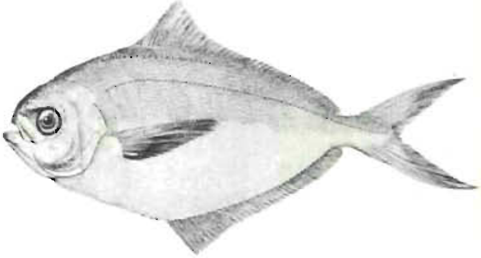
Dorsal fin originating on back behind pectoral fin origin 24

24 Dorsal fin not continuous with caudal fin, caudal fin forked; small fishes, usually less than 25 cm long 25

Dorsal fin continuous around caudal fin, caudal rounded or pointed, elongate fishes, to 60 cm or more long 26

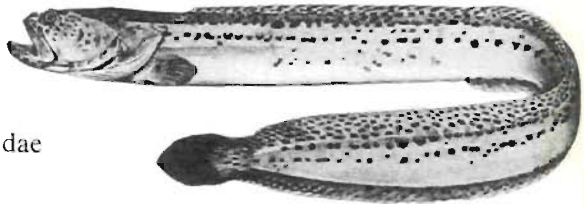
25 Slender, lancet-like fishes, with pointed snout and projecting lower jaw, low fleshy ridge above ventral outline .... Sandlances, family Ammodytidae

Deep bodied, laterally compressed fishes, ovate in lateral view, rounded snout with lower jaw included.................. .... Butterfishes, family Stromateidae



26 Body and head unspotted; gill opening restricted, not extending above pectoral fin base; mouth horizontal .... Freshwater eels, family Anguillidae

Body and head distinctly spotted with small brown spots; gill openings not restricted; opening extending well above pectoral fin base; mouth at oblique angle ...... Wrymouths, family Cryptacanthodidae



KEY to HERRINGS — Family Clupeidae

1 Belly outline not sharply saw-toothed but with a knife-edge ridge............... .. Atlantic herring, *Clupea harengus harengus*

Belly outline sharply and strongly saw-toothed 2

2 Lower jaw fitting into notch in upper jaw when mouth closed; gill rakers more than 55 .... American shad, *Alosa sapidissima*

Lower jaw projecting; gill rakers less than 55.................................. 3

3 Peritoneum silvery; eye diameter usually greater than snout length. . . . . Alewife, *Alosa pseudoharengus*

Peritoneum sooty or black; eye diameter usually as long as snout length. . . . . Blueback herring, *Alosa aestivalis*

KEY to SALMONS and TROUTS — Family SALMONIDAE

1 Light spots on body, spots may be red, pink or rusty in color but not black; overall colouration silvery in the sea; scales present but not conspicuous; lower fins with snow white leading edges; caudal fin square or nearly so. . . . . Brook trout, *Salvelinus fontinalis*

Black spots present on head and/or body; overall coloration silver in the sea; scales conspicuous; lower fins without white leading edges 2

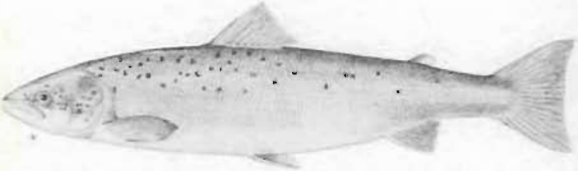
2 Primary anal rays 7–12. 3

Primary anal rays 13–19 (usually 14–16). . . . . Pacific salmons, *Oncorhynchus* spp.

3 Caudal fin usually distinctly marked with radiating rows of black spots; never red spots, but spawning males may have red blush on sides; adipose fin often with a black margin; gill cover usually unspotted . . . . Rainbow trout, *Salmo gairdneri*

Caudal fin without radiating rows of black spots; red or rust colored spots may be present on sides especially of young fish; gill cover usually with spots; spotting often masked by silver when caught in sea 4

4 Maxillary to below center of eye in 6 inch fish, seldom far behind eye, except on large males; branchiostegal rays usually 12; dorsal fin rays usually 11; vomerine teeth weakly developed; gill cover with a few large spots; small fish have red spots between parr marks. . . . . Atlantic salmon, *Salmo salar*



Maxillary to below last half of eye in 5 inch fish, extending well beyond eye in larger fish; branchiostegal rays usually 10; dorsal fin rays usually 9; vomerine teeth well developed; gill cover with many spots; rust-red spots sometimes on adults and often on margin of the large adipose fin. . . . . Brown trout, *Salmo trutta*

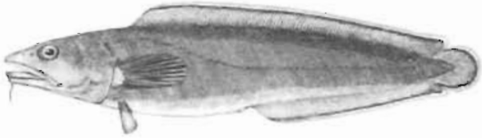
KEY to SMELTS — Family Osmeridae

Well-developed fang-like teeth on jaws and especially on tongue; adipose fin base smaller than eye diameter. . . . . Rainbow smelt, *Osmerus mordax*

Teeth on jaws and tongue weak; adipose fin base greater than eye diameter. . . . . Capelin, *Mallotus villosus*

KEY to CODFISHES — Family Gadidae

1 One dorsal and one anal fin only, each joined to caudal and separated from it by a notch; median fins dark toward margin, with white edging. . . . . Cusk, *Brosme brosme*

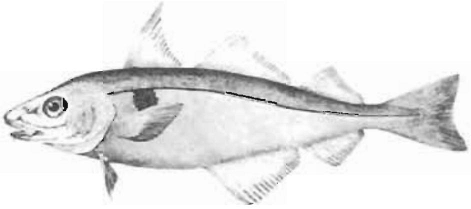


Two or 3 dorsal fins; one or 2 anal fins 2

2 Three separate dorsal fins; 2 anal fins 3

Two separate dorsal fins (first dorsal may be reduced to a short base); one anal fin 6

3 Lateral line black; black blotch on side ('shoulder') above pectoral fin. . . . . Haddock, *Melanogrammus aeglefinus*

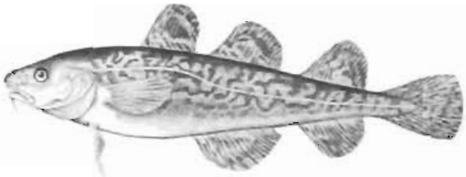


Lateral line pale; no black blotch on shoulder 4

4 Lower jaw projecting beyond upper jaw; chin barbel minute . . . . . . Pollock, *Pollachius virens*

Upper jaw projects beyond lower; chin barbel apparent, not minute 5

5 Pelvic fins with second ray prolonged as filamentous 'feeler' as long as the rest of fin; caudal fin rounded posteriorly. . . . . Atlantic tomcod, *Microgadus tomcod*



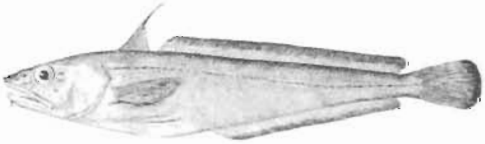
Pelvic fins with second ray prolonged to less than 1/3 the length of the rest of the fin; caudal fin slightly concave posteriorly . . . . Atlantic cod, *Gadus morhua*

6 Pelvic fins of only 2 prolonged feeler-like rays, the longer one reaching to or beyond vent 7

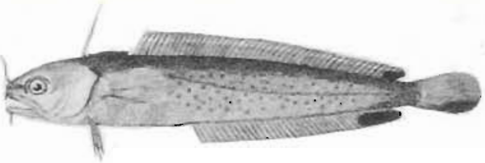
Pelvic fins small but without prolonged rays. 8

7 Scales larger, 98–117 in lateral series; 3 gill rakers on upper limb of gill arch; maximum size to about 55 cm; reddish brown coloration . . . . Red hake, *Urophycis chuss*

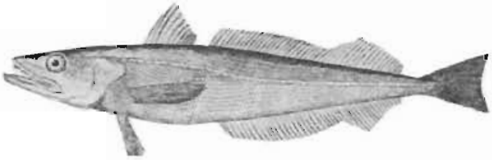
Scales smaller, 119–148 in lateral series; 2 gill rakers on upper limb of gill arch; maximum size to about 125 cm; grayish brown coloration . . . . . . White hake, *Urophycis tenuis*



8 Three barbels on snout, one in front of each nostril and one in midline; chin barbel present; black blotches at posterior extremities of dorsal and anal fins; mouth and teeth moderate in size. . . . .
. . . Fourbeard rockling, *Enchelyopus cimbrius*

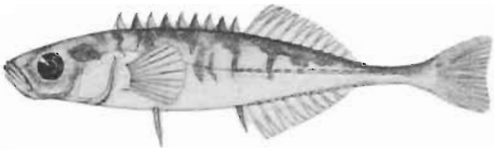


No barbels on snout or chin, nor black blotches on fins; mouth and teeth large
. . . . Silver hake, *Merluccius bilinearis*



KEY to STICKLEBACKS — Family Gasterosteidae

1 Dorsal spines usually 9 (7–12), short and inclined alternately to left and right; gill membranes entirely free from isthmus; a median ventral plate present; no bony plates on sides. . . . .
. . . Ninespine stickleback, *Pungitius pungitius*

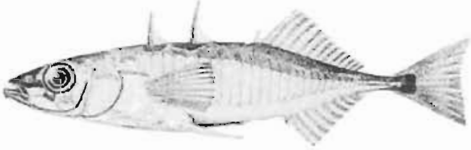


Dorsal spines 3–6; gill membrane united to isthmus; usually bony plates along side and between pelvic fins (except in *A. quadracus*) 2

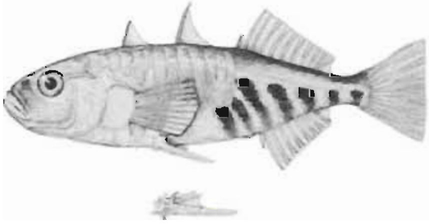
2 Dorsal spines 4 or 5 (rarely 6), last spine attached to soft dorsal, spines inclined alternately to left and right side; a bony stay directed posteriorly from base of each pelvic fin; no median ventral plate. . . . . . .
. . . . Fourspine stickleback, *Apeltes quadracus*

Dorsal spines 3 (rarely 4), last spine not attached to soft dorsal, all spines in line; a strong median ventral plate extending posteriorly from pelvic base 3

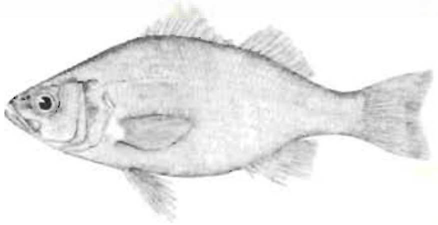
3 Dorsal spines 3 (rarely 4), last spine short; pelvic fin of one spine and one soft ray, spine with one pointed cusp at base; caudal peduncle with a keel; body without round black spots; color in life green, blue, or silvery. . . . .
Threespine stickleback, *Gasterosteus aculeatus*



Dorsal spines 3 (rarely 2); pelvic fin of one spine and 2 soft rays, spine with 2 well-developed pointed cusps at base; caudal peduncle keelless; many round black spots along sides; color in life lemon-yellow. . . . . Blackspotted stickleback, *Gasterosteus wheatlandi*



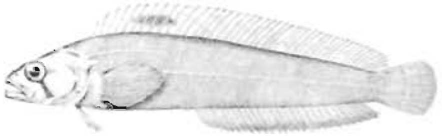
KEY to TEMPERATE BASSES — Family Percichthyidae



Anal fin rays usually 9; anal fin spines not graduated in size, stout, the longest spine 3/4 or more the height of anal fin; body without longitudinal stripes. . . . .
. . . . White perch, *Morone americana*

Anal fin rays usually 11; anal fin spines graduated in size, slender, the longest spine less than 1/2 the height of anal fin; body with about 7 longitudinal lateral stripes. . . . .
. . . . Striped bass, *Morone saxatilis*

KEY to PRICKLEBACKS — Family Stichaeidae



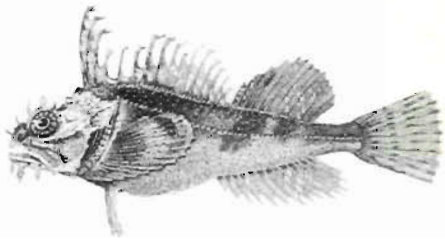
1 Oblong black blotch anteriorly on dorsal fin (about 5th–10th spines); a black band extending downward and backward from eye; one complete lateral line at mid flank, a second incomplete lateral line ending above tip of pectoral fin or beyond
. . . . Radiated shanny, *Ulvaria subbifurcata*

No pronounced blotch on 5th–10th spines of dorsal fin, nor black band from eye; one inconspicuous lateral line. 2

2 Lower rays of pectoral fins elongated, free from membrane and almost finger-like; caudal fin square posteriorly. . . . .
. . . . Daubed shanny, *Lumpenus maculatus*

Lower rays of pectoral fins not elongated; caudal fin pointed posteriorly. . . . .
. . . . Snakeblenny, *Lumpenus lumpretaeformis*

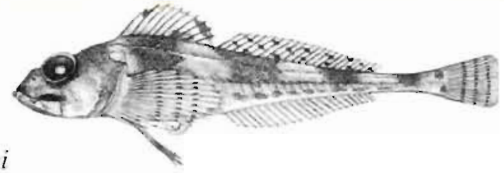
KEY to SCULPINS — Family Cottidae



1 Head and chin with fleshy tabs; skin on body and head rugose or pebbly. . . . . . .
. . . . Sea raven, *Hemitripterus americanus*

Head and chin without fleshy tabs; skin mainly smooth or spiny 2

2 Lateral line armed with rows of plates, each with backwardly directed spines; area below lateral line with folds arranged in oblique rows; head and opercular spines not well developed. . . . . Moustache sculpin, *Triglops murrayi*

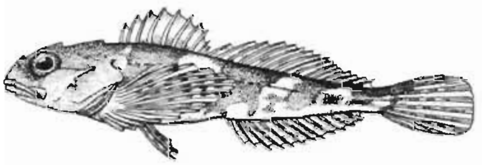


Lateral line not armed with rows of plates, area below lateral line not in folds; head and opercular spines usually well developed 3

3 Upper preopercular spine long, about 4 times as long as spine below it; all head spines sharp. . . . . Longhorn sculpin, *Myoxocephalus octodecempinosus*

Upper preopercular spine not conspicuously long, at most twice as long as spine below it 4

4 Second dorsal fin rays 13–14; anal fin rays 10–11; dorsal spines stiff; length seldom over 15.2 cm (6 inches) . . . . Grubby, *Myoxocephalus aenaeus*

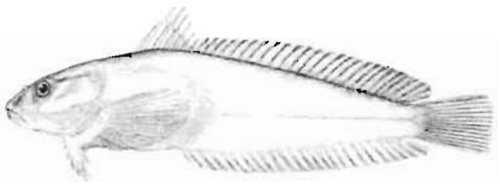


Second dorsal fin rays 15–19; anal fin rays 12–16; dorsal spines flexible; length to 50.8 cm (20 inches) or more . . . . Shorthorn sculpin, *Myoxocephalus scorpius*

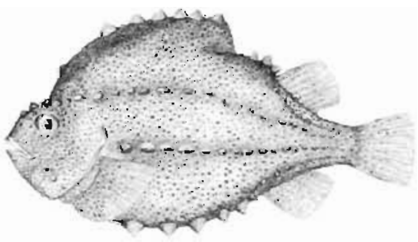
KEY to LUMPFISHES and SNAILFISHES — Family Cyclopteridae

1 Skin with conical tubercles; dorsal and anal fins short and posterior in position and clearly separated from caudal fins; lower rays of pectoral fin not prolonged 2

Skin smooth, without tubercles; dorsal and anal fins long and closely associated with caudal fin; lower rays of pectoral fin prolonged providing a secondary lobe to the fin. . . . . Snailfishes, *Liparis* spp.



2 Gill openings large, extending to below top of pectoral fin base. . . . . Lumpfish, *Cyclopterus lumpus*



Gill openings small, not extending downward to base of pectoral fin. . . . . Atlantic spiny lumpsucker, *Eumicrotremus spinosus*

KEY to FLATFISHES — Families Pleuronectidae and Bothidae

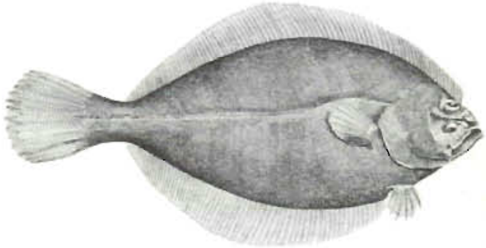
1 Eyes and pigment on right side.......... 2

Eyes and pigment on left side.......... 8

2 Mouth large, maxillary extending to below middle of eye or beyond; teeth well developed 3

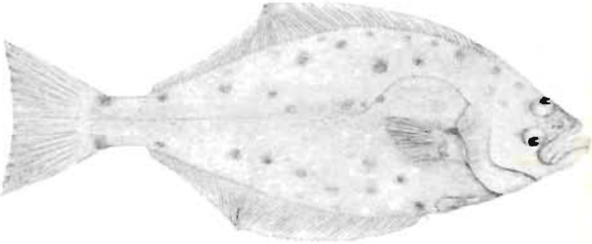
Mouth small, maxillary extending at most to front of eye.......... 5

3 Caudal fin distinctly rounded; lateral line almost straight but curving slightly over pectoral fins; dorsal fin rays 75–96; body reddish-brown..........
American plaice, *Hippoglossoides platessoides*



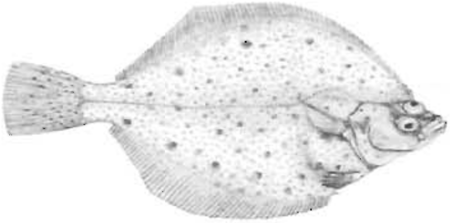
Caudal fin slightly forked, not rounded, corners of caudal fin angular; dorsal fin rays 98–105; body color gray-brown or dark brown to olive.......... 4

4 Lateral line arched above pectoral fin; dorsal fin rays 98–105; body color dark and blotchy above, distinctly white below
..Atlantic halibut, *Hippoglossus hippoglossus*



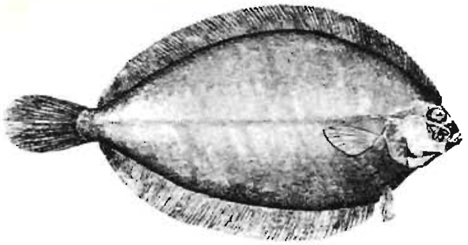
Lateral line straight, even slightly decurved above pectoral fin; dorsal fin rays about 100; body color grayish-brown; creamy below but not white..........
.... Greenland halibut, *Reinhardtius hippoglossoides*

5 Lateral line distinctly arched over pectoral fin; anal fin preceded by a short spine directed forward; body usually spotted..........
..... Yellowtail flounder, *Limanda ferruginea*



Lateral line more or less straight.......... 6

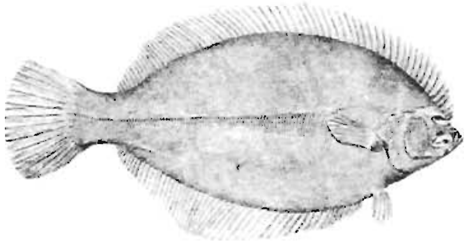
6 Lower blind side of head with circular depressions (sometimes called "pits"); right pectoral fin with conspicuous black pigment toward tip visible on fish 5 inches long and over; dorsal fin rays more than 100. . . . . Witch flounder, *Glyptocephalus cynoglossus*



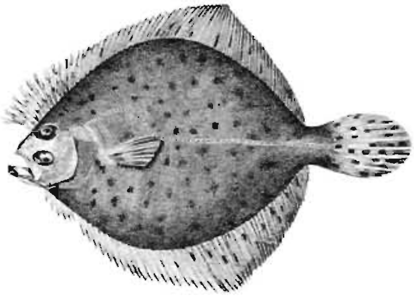
No depressions on lower or blind side of head; pectoral fin without black pigment; dorsal fin rays less than 75. 7

7 Region between eyes without scales (smooth to the touch); dorsal fin rays 53–59; anal fin rays 35–41; body color uniformly brown to almost black. . . . . Smooth flounder, *Liopsetta putnami*

Region between eyes with scales (rough to the touch); dorsal fin rays 60–76; anal fin rays 45–58; body color usually dark brown to black with spots or blotches. . . . . Winter flounder, *Pseudopleuronectes americanus*



8 Body very deep (and thin), being almost round in outline; anterior 10 rays of dorsal fin free of membrane, long branched and fringe-like; left pelvic fin very broad at base, appearing almost as part of anal fin . . . . Windowpane, *Scophthalmus aquosus*



Body longer than deep; anterior dorsal fin rays not fringe-like; pelvic fins distinct and with narrow bases (*Paralichthys*) 9

9 Eyes small, interorbital distance about equal to diameter of pupil; number of gill rakers on outer arch 16–24; pigmented side with a number of black spots of different sizes. . . . . Summer flounder, *Paralichthys dentatus*

Eyes large, interorbital distance much less than the diameter of pupil; number of gill rakers on outer arch 9–13; pigmented side with four prominent black spots only. . . . . Fourspot flounder, *Paralichthys oblongus*

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CHAPTER 11

Phytoplankton of the Quoddy Region

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Introduction

Phytoplankton forms an important component in the production of waters. This chapter describes the phytoplankton of Passamaquoddy Bay and neighboring waters, and the methods most commonly used for phytoplankton collection, examination, counting, and biomass and primary productivity determinations in coastal and marine waters. The methods, taken from the literature (some with slight modifications), will allow students and other interested persons to undertake phytoplankton research in the field.

The Phytoplankton System

THE QUODDY REGION

The Quoddy Region includes the area from West Quoddy Head to the northern extremity of Grand Manan Island and on to Point Lepreau (Chapter 1, Fig. 1). This is a very important sardine fishery area (Graham 1936). Passamaquoddy Bay (Fig. 1) lies inside Deer Island and does not include any of the passages connecting it to the outside waters of Grand Manan and Point Lepreau (Gran and Braarud 1934). The St. Croix, Magaguadavic, and Digdeguash rivers flow into the bay, the St. Croix River discharging over half of the freshwater flow. The bay is essentially glacial with an average depth of 28 m, the maximum depth being 60–75 m. Mackay et al. (1978) discussed in detail the bathymetry, substrates, and oceanography of this enclosed basin. The bay, with an assymetrical bottom in a North–South section, is shallow in the north and slopes steeply to maximum depths in the south. The tides, with a mean tidal range of 6.1 m at the head of St. Croix Estuary, reach Passamaquoddy Bay through Letite and Western passages. In summer, the southwest winds keep the northeast part of the bay warmer but the cold northwest winds of winter quickly change this (Forgeron 1959). High loads of suspended matter restrict light penetration. For example, in November 1979 and February 1980 80% of the light disappeared by 5 m in all four sampling stations (Fig. 2). (Figure 1 shows station locations.) This turbidity, due to high tidal current mixing (Huntsman 1918), possibly attracts herring (Graham 1936).

Details of oceanographic conditions in the area are given by Trites and Garrett (Chapter 3). The wide range of salinity in the bay waters is reflected in the presence of many estuarine species, some of which are unique to the bay (MacKay et al. 1978). The association of species in outer Passamaquoddy Bay resembles that of the coastal region of the Gulf of Maine (Bigelow 1926; Fish and Johnson 1937), although events take place later in the north. The association of species in the St. Croix Estuary resembles that of other estuaries in the Gulf of Maine and Bay of Fundy area (Legare 1961). Copepods and other dominant zooplankters depend on the ample supply of diatoms which are represented by a large number of species (Legare 1961).

PREVIOUS ACCOUNTS OF PHYTOPLANKTON

General sources for eastern Canada are included in the references. Davidson (1934) studied phytoplankton of the Quoddy Region for 7.5 yr consecutively, and Fritz (1921) made a detailed study of the phytoplankton of Passamaquoddy Bay from seven stations. Studies by Bigelow (1926), Gran (1933) and Gran and Braarud (1935), are the main sources of information for the Gulf of Maine, Quoddy Region, and Bay of Fundy. Hulbert (1964), Hulbert and Rodman (1963), and Marshall (1971, 1976, 1978) focussed on the phytoplankton of the northwest Atlantic, including the Gulf of Maine. Linkletter et al. (1977) reported on some of the phytoplankton of Passamaquoddy Bay.

DISTRIBUTION OF PHYTOPLANKTON SPECIES IN PASSAMAQUODDY BAY

Some data on the winter phytoplankton of Passamaquoddy Bay were reported by McMurrich (1917). *Coscinodiscus radiatus, C. concinnus, C. centralis,* and *C. normani* occurred most often. *Biddulphia aurita* and *B. mobiliensis* were less frequent. At rare intervals *Chaetoceros laciniosum, C. curvisetum,* and *C. decipiens* appeared in the collections. *Thalassiosira nordenskioldii, Rhizosolenia setigera*, and *R. styliformis* were most frequent at the end of March and the beginning of April. Among the dinoflagellates, *Ceratium tripos, C. fusus, C. furca, Peridinium depressum*, and *Dinophysis norvegica* occurred infrequently.

The studies of Fritz (1921) on Passamaquoddy Bay and adjoining waters revealed that *Pleurosigma strigosum* and *Chaetoceros danicum* persisted throughout the year. *Chaetoceros* lead both in diversity and numbers although in winter only *C. debile, C. diadema, C. laciniosum,* and *C. decipiens* were observed. Species which attained dominance at one season and then either appeared at rare intervals or disappeared were *Ditylum brightwelii* (September to December), *Rhizosolenia hebetata* and *Chaetoceros debile* (August), *Rhizosolenia setigera* (spring), *Pleurosigma strigosum* (February to April), and *Actinoptychus senarius* and species of *Coscinodiscus* (winter). During April and May, *Thalassiosira gravida* and *T. nordenskioldii* dominated the phytoplankton. In every

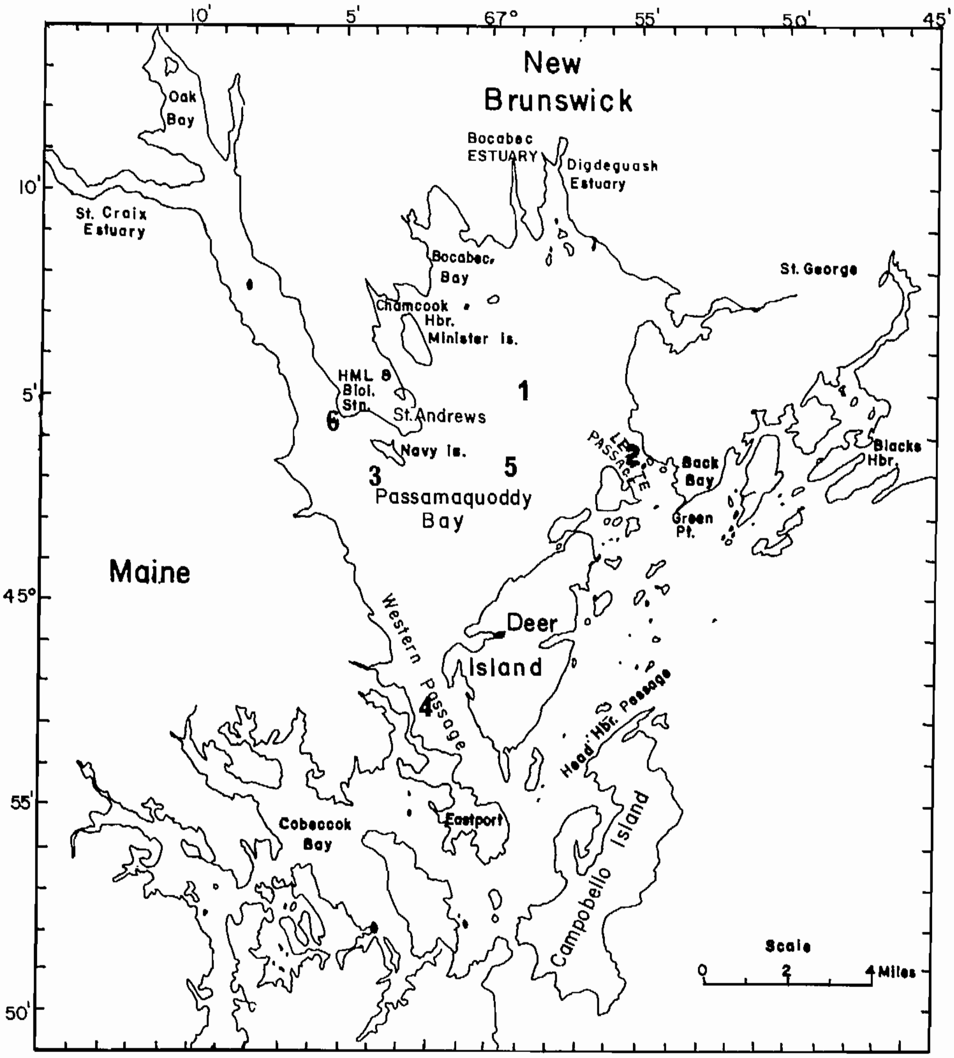

FIG. 1. Passamaquoddy Bay, showing sampling locations 1 to 6, mentioned in the text.

winter collection *Skeletonema costatum* and species of *Melosira* were noted. Throughout the bay in autumn, *Thalassiothrix longissima, Rhizosolenia shrubsolei,* and *Ditylum brightwelii* prevailed. Species of *Biddulphia* were often observed in spring along with species of *Thalassiosira*. There were strong similarities between the flora of Passamaquoddy Bay and the exposed waters of the Bay of Fundy although the latter waters were poorer in regard to total population and number of species.

Davidson's (1934) studies revealed that dinoflagellates, when compared to diatoms, were not important contributors in net hauls in the Quoddy Region. Diatoms were represented by a large number of species and had a characteristic composition. Davidson reported over 100 species of phytoplankton, the majority being arctic-neritic and boreal in character. Usually diatoms increased with the onset of spring and reached their maximum in late June or July in Passamaquoddy Bay. *Thalassiosira nordenskioldii, T. gravida,* and *Chaetoceros debile* dominated in the collections. *C. diadema, C. compressus, C. constrictus,* and *C. sociale* contributed to the summer populations. The diatoms most common during late summer and autumn were *Nitzschia seriata, Skeletonema costatum, Leptocylindrus danicus, Rhizosolenia setigera,* and *R. shrubsolei* (Davidson 1934). The previous works of Bailey and MacKay (1921), McMurrich (1917), and Fritz support Davidson's (1934) observations that the spring diatoms were essentially of the same arctic-neritic and boreal character, and stationary in the region. In St. Margaret's Bay, N.S., Platt and Subba Rao (1973) recorded similar spring blooms dominated by *Chaetoceros debile, Thalassiosira gravida,* and *T. nordenskioldii.* Saifullah and Steven (1974) also reported multispecific spring blooms in St. Margaret's Bay and several of these species were the same as those of Pasamaquoddy Bay waters. *Skeletonema costatum* solely dominated the late summer

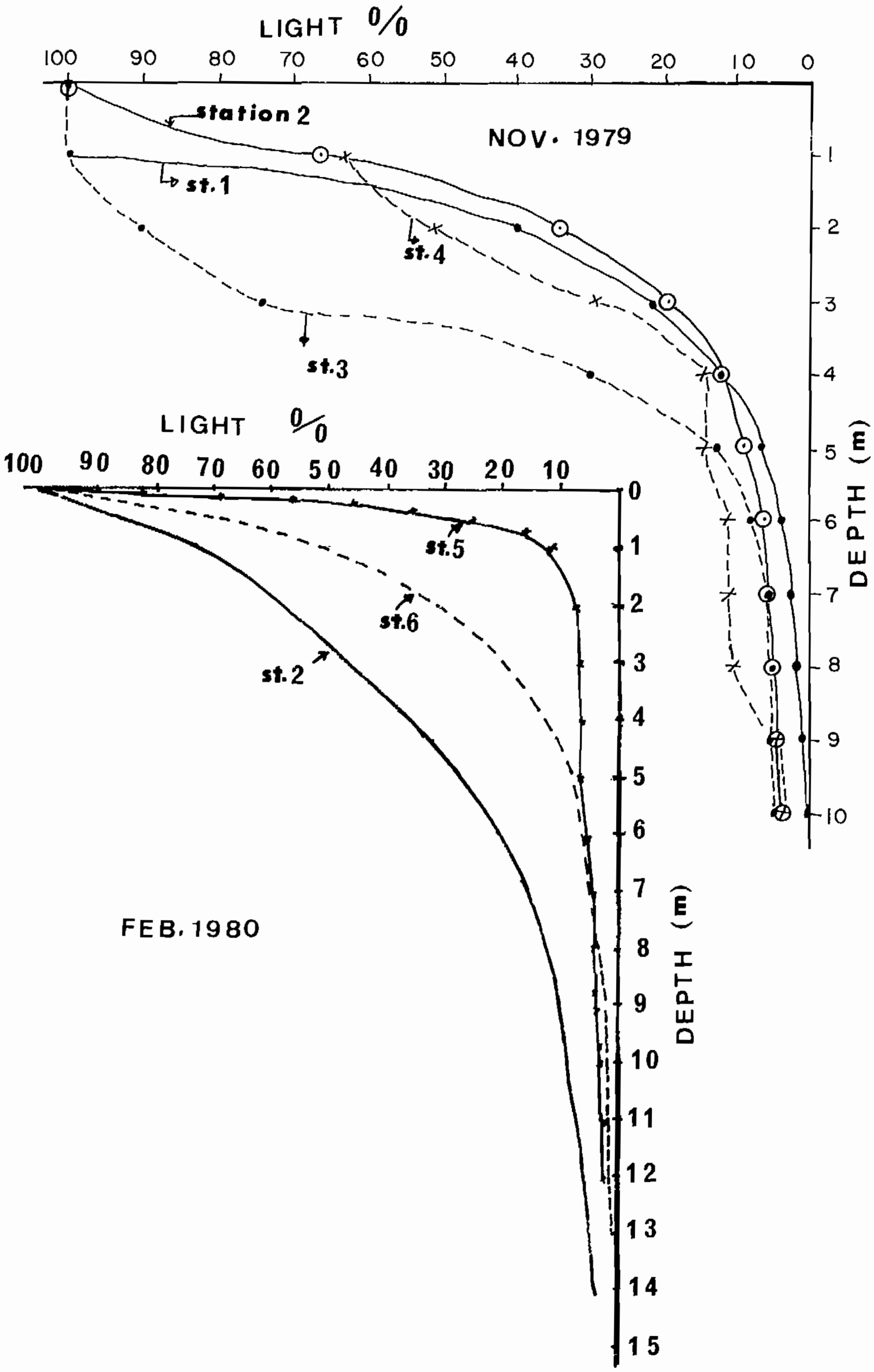

FIG. 2. Light curves at stations 2 and 3.

waters of St. Margaret's Bay (Saifullah and Steven 1974) and was present in the same period in Passamaquoddy Bay waters (Davidson 1934). The outer part of the Quoddy Region, which is colder than the inner, Passamaquoddy waters, showed *Chaetoceros debilis* dominance over *Thalassiosira nordenskioldii* (Davidson 1934).

Pleurosigma, Thalassiothrix, Rhizosolenia, Ditylum, Chaetoceros, Skeletonema, Melosira, Thalassiosira, Biddulphia, Actinoptychus, and *Coscinodiscus* were in greater numbers in 5-m collections and all showed the same irregularity of distribution (Fritz 1921). In March the 6-m collections showed *Disphanus speculum*, the only silicoflagellate noted (McMurrich 1917).

Skeletonema costatum, Thalassionema nitzschioides, Thalassiosira nordenskioldii, Guinardia flaccida, Chaetoceros compressus, and *Rhizosolenia setigera* are the common east coast ubiquitous species (Marshall 1976). Characteristic neritic cold-water assemblages include *Amphiprora hyperborea, Biddulphia aurita, Chaetoceros atlanticus, C. compressus, Rhizosolenia stolterfothii, Skeletonema costatum, Thalassionema nitzschioides, T. nordenskioldii, Ceratium lineatum, C. longipes, C. macroceros, Dinophysis acuta, D. norvegica, Peridinium brevipes, P. depressum, Cyclococcolithus leptoporus*, and *Coccolithus huxleyi* (Marshall 1978). Representation within some of the association of the above phytoplankton species and the succession of flowering in Passamaquoddy Bay and its outer regions resembles that of the coastal margin of the Gulf of Maine.

RED TIDES IN THE BAY OF FUNDY REGION

Red tides are sudden outbursts of excessive growths of phytoplankton which impart peculiar discoloration, giving a red-brown color to the coastal waters, seas or oceans. These occur in many oceanic and coastal waters around the world (Braarud and Heimdal 1970; Quayle 1969; Prakash et al. 1971; Schantz 1975). Some of these organisms produce deadly poisons which, when accumulated by fish or shell fish and subsequently eaten by man, cause sickness and, in the case of shellfish, sometimes death. The toxicity of these organisms may be a defense mechanism against herbivores.

Gonyaulax catenella on the northwest Pacific coast of North America, *G. acatenella* in several coastal areas of British Columbia, and *G. excavata (tamarensis)* on the northeast Atlantic coast of North America (including the Quoddy Region and the coasts of the North Sea) are the known common poisonous dinoflagellates. *Gonyaulax excavata* is known to bloom during summer and fall in the southern Bay of Fundy and in the estuary of the St. Lawrence River. Prakash et al. (1971) described the effects of toxins of *G. excavata* on warm-blooded animals. White (1977) reported a herring (*Clupea harengus harengus*) kill in the Bay of Fundy probably caused by *G. excavata* toxins. These may have been accumulated by pteropods which were found to be in abundance in the stomachs of the herring. The survey revealed that the kill occurred from about White Head to North Head, off the coast of Grand Manan Island. The dominant alga in this region at the time of the herring kill was *G. excavata*, which also occurs in Passamaquoddy Bay.

SPECIES DIVERSITY

This chapter includes a checklist of 127 species of phytoplankton of Passamaquoddy Bay, based on the research cited above. This far from exhaustive list includes 120 diatoms, 6 dinoflagellates, and 1 chrysophycean. Future work will certainly add more. For details of identification, consult Brunel (1962), Cleve (1894 and 1895), Cleve–Euler (1915, 1951–55), Cupp (1943), Griffith (1961), Hustedt (1927–30, 1930), Hendey (1964), Huber—Pestalozzi and Hustedt (1942), Lebour (1925, 1930), Patrick and Reimer (1966), Schiller (1937), and Vanlandingham (1967-69, 1971, 1975).

Methods

SAMPLING PHYTOPLANKTON: GENERAL CONSIDERATIONS

Phytoplankton vary greatly in size and abundance. A sample of a few litres may suffice for an abundant species but a much larger sample must be taken for rare forms. In deep waters, sampling at 3–6-m intervals throughout the euphotic zone to an arbitrary depth below the thermocline is generally satisfactory, but other intervals may be required under special circumstances. Tow or net sampling should be carried out at 90° to the wind direction. Estuarine phytoplankton should be sampled at regular intervals from the surface to the bottom three or four times during one or more tidal cycles (Weber 1973).

For ecological and distributional studies, the sampling program should include the determination of chlorophyll, nutrients, and primary productivity.

FIELD NOTES AND SAMPLE LABELLING

Notes should include weather information, water surface condition, turbidity, total depth at station, depth of the sample taken, a list of all types of samples taken at the station, and general descriptive information (e.g. direction, distance). Sampling stations should be plotted on a map, or position (latitude and longitude) or Decca coordinates noted.

Both labels and marker should be waterproof. Insert the labels into sample containers immediately after the samples are collected. Record the following information on all labels: location or station number; date, time and ship; depth, wire angle; type of sample (e.g. grab, vertical plankton net haul, etc.); sample volume, tow length; preservatives used and concentration; and name of collector or observer.

SAMPLING EQUIPMENT

Cylinder-type samplers like the Kemmerer, Juday, Niskin, and Van Dorn bottles are recommended for water sampling. These leave the ends open to allow free passage of water during lowering. A messenger released at the desired depth closes the bottle. Non-metallic samplers are best for metal analysis, algal assays, or primary productivity measurements. For surface samples in shallow waters, the sampler can be held in a horizontal position and operated manually. For deep-water sampling, the Nansen reversing water bottle may be used if only small samples are needed. Series of bottles set to desired depth intervals speed work but require a hydrographic winch and meter block.

For collecting net phytoplankton, Clark-Bumpus or Wisconsin nets or Juday traps are often used. A No. 25 mesh plankton net (nylon or bolting silk, 64-μm aperture, 200 meshes/in) is best. Nets are used primarily for qualitative work. Very rough quantitative estimates can be made by calculating water volume in the path of the net, but filtration efficiency decreases as resistance increases with the accumulation of material in the net. A flow meter, properly placed in the net mouth, increases accuracy. Net collection of phytoplankton is not recommended for quantitative work except for large species. Nanoplankton and many diatoms could pass through the mesh and thus must be counted from water samples. The use of a suction-pump and on-deck filtration is possible but presents problems when the water is stratified, as the tubing must be flushed between samplings and delicate algae are damaged. Nets help in assessments of species composition, diversity, and geographic distribution. Surface films of phytoplankton may be sampled by using a skimming net or by suspending glass plates or microscopic slides. Contamination from the ship or boat must be avoided in such sampling (UNESCO 1974).

Differential filtration or fractional filtration using nylon bolting cloth of different apertures (10 μm to 365 μm) can give samples of phytoplankton of graded sizes (Subba Rao 1980). Culturing phytoplankton will yield large numbers of flagellates not found in preserved samples. Germanium oxide will inhibit diatom growths in cultures. A general sample of the water column may be taken with a plastic hose (inside diameter 8 mm) with an appropriate weight lowered to a depth (e.g. 15 m). The upper end is sealed and the hose pulled aboard and emptied (Carlsberg 1972).

The volume required from sample bottles depends on the numbers and kinds of analyses to be carried out, e.g. cell counts, chlorophyll, dry weight. When phytoplankton densities are less than 500/mL approximately 6 L of sample are required for Sedgwick-Rafter and diatom species proportional counts. A 1–2-L sample will suffice for more productive waters (Weber 1973).

SAMPLE PRESERVATION

There are a variety of preservatives, each having advantages. Samples to be stored for more than 1 yr should be preserved in formalin neutralized with sodium tetraborate (ph 7.0–7.3). Sodium bicarbonate and calcium carbonate may also be used as buffering agents. Five mL of neutralized formalin are added to each 100 mL of sample. This preservative may cause many flagellated forms to lose their flagella. The addition of 1 mL/L of saturated cupric sulfate solution to the preserved samples maintains the green color of phytoplankton and aids in distinguishing phytoplankton from detritus. Adding detergent solution prevents clumping of settled organisms. Use 5 mL of 20% surgical detergent solution per litre of sample. Do not use detergent when diatom slides are to be made (Weber 1973).

Merthiolate is a preservative offering the advantage of staining cell parts and simplifying identification. It also causes algae like blue-greens to lose gas from their vacuoles, thus aiding settling. Samples preserved with merthiolate may be stored for 1 yr. Merthiolate solution is prepared by dissolving, in 1 L of distilled water (Weber 1973): 1.0 g merthiolate (sodium ethyl-mercury thiosalicylate), 1.0 mL aqueous saturated iodine-potassium iodide solution prepared by dissolving 40 grams of iodine and 60 grams of potassium iodide in 1 L of distilled water, and 1.5 g Borax (sodium borate).

Aqueous saturated iodine solution (Lugol's solution) alone may be used for immediate fixation of phytoplankton. As well as coloring the starch, it fixes cilia and flagellae, if present.

To make Lugol's solution dissolve 10 g potassium iodide in 20 mL distilled water. Add 5 g double sublimated iodine and 5 g sodium acetate (CH_3 COO Na). After all the crystals have dissolved make the volume up to 100 mL.

Kiefers solution may be used as a long-active preservative. In 900 mL of ethanol (50%), dissolve 50 mL formaldehyde (40%), 25 mL glycerol, 25 mL acetic acid, 50 g cupric chloride, and 15 g Uranyl nitrate ($UO_2(NO_3)_2$ $6H_2O$). Usually 5 mL of this solution is added to 100 mL of sample. The appearance of the organisms is altered somewhat by this preservative but with experience no problems are encountered.

PREPARATION FOR IDENTIFICATION

The identification of phytoplankters to species is often difficult and is limited by methods used for preservation, concentration, and microscopial examination. If the organisms are very small (<10 μm) and unrecognizable due to bad preservation, they may be classified as monads (without cilia) or flagellates (with cilia). For information on identification problems, consult Hasle (1978). The use of phase contrast, or oil or water immersion objectives, may help in distinguishing species. Serial dilution-culture methods are necessary to identify fragile plankters which cannot be preserved or concentrated by any other means.

Heating of the phytoplankton sample on microscopic slides to 45°C usually clears the slides of excess suspended organic matter for preliminary examination. Fresh mounts may be prevented from drying by applying sealing compound (made by heating two parts of vaseline and one part of beeswax) around the coverglass (Hendey 1964).

Diatoms should first be examined alive under the low and high powers of the microscope. Valve view is diagnostic for diatoms.

Water samples containing diatoms can be coagulated with a 5% ferric alum solution stirred for 10 min and allowed to settle in pyrex glass separating funnels for 24–36 h. The concentrated particle fraction is separated to 5 or 10 mL fractions depending upon the quantity of the concentrate. Portions of these are washed with distilled water until all possible preservatives and salt have been removed. This permits the examination of more delicate forms and preceeds further treatment.

Diatoms may be cleaned as follows: If there is much calcium present (as in samples from warm waters) add as much concentrated HCl as there is sample, agitate, and rinse twice with distilled water (centrifuge). Then follow Procedure A or B.

Procedure A

1) Add twice as much concentrated H_2SO_4 as there is sample. Agitate.

2) Add a very small quantity of saturated $KMnO_4$ (there should be crystals in the bottle) slowly (to prevent boiling over) until the liquid is dark brown-purple. Agitate.

3) Add a small quantity of oxalic acid until sample is colourless. Agitate.

4) Rinse twice with distilled water (centrifuge), then examine the material under the microscope. If not clean, repeat the above procedure. If clean, continue to rinse until blue litmus paper does not turn red in the solution.

Procedure B

1) Rinse the sample with distilled water.

2) Add as much saturated $KMnO_4$ as there is sample. Agitate. Leave for 24 h.

3) Add as much HCl as there is sample. Heat gently over an alcohol lamp until sample is transparent and colorless or light yellow-green in color.

Diatoms are mounted in CUMAR R-9, a chemically inert and neutral coumarone-indene resin resistant to oxidation, salt, and moisture. Pleurax, Euperol, Canada Balsam, Hyrax, and Glycerine jelly may also be used for differential clarity. For the preparation of permanent slides and material to examine under Scanning Electron Microscopy (SEM) and Transmission Electron Microscopy (TEM), see Hasle (1978).

Sources for the identification of phytoplankton are given by Sournia (1978) and in the references and bibliography of this chapter.

CULTURING PHYTOPLANKTON

Culturing phytoplankton may be necessary for proper identification as some of the species in the collections may not be present in all stages of development. Culture media provide the basis for the observation of different stages of development of certain species, frequent or rare, in phytoplankton collections. Algae can be cultured either on gelatin, agar, or silicagel media, or in nutrient solutions. To obtain good results, it is necessary to provide correct salt concentration, pH, light intensity, and temperature. To grow unialgal or pure cultures free from bacteria, work has to be done in sterile conditions. To clean glassware or culture vessels, soak until clean in ethyl alcohol saturated with potassium hydroxide or in a solution made up with 35 mL of saturated sodium dichromate solution (technical grade) and 1 L of concentrated sulfuric acid. Rinse glassware well in tap and distilled water and sterilize in dry heat at 160–190°C or autoclave at 15-lb pressure for at least 20 min. Nutrient media and solutions could be sterilized in an autoclave at 15 lb. pressure for 20 min. If organic compounds are present in the nutrient substrates, sterilization should be carried out by filtration or in a steam chamber.

Only aged natural water or glass-distilled water should be used. Age the waters for a few months in the dark at 5 to 10°C. Natural waters may be freed from organics and toxic materials by adding activated charcoal (USP Grade) and then filtrating. Depending upon need, use any combination of the following treatments: deionization, activated charcoal filtration, aging, pasteurization, or filter sterilization.

Most algae grow well at natural environmental temperatures. Phytoplankton of Atlantic waters grow well at 10 to 20°C. Cool-white fluorescent daylight tubes (200 to 400 candles) are generally good for growth of cultures. For purification of algal cultures, dilution, centrifugation, antibiotics, or UV light, filter, or ultrasonic treatment techniques could be used. Potassium telleurite (K_2teO_3) at concentrations of 1 mg/L could be employed to obtain pure algal cells for cultures. For a detailed treatment of algal cultivation, see Bold (1942), Pringsheim (1949), Provasoli et al. (1957), Starr (1964, 1971), Wiedeman et al. (1964), Stein (1973), and Bold and Wynne (1978), among others.

Formulas and instructions for preparing a few commonly used media for nanoplankton and phytoplankton are given in Van Valkenburg et al. (1977), Guillard and Ryther (1962), and Bold and Wynne (1978).

COUNTING METHODS

Phytoplankton consists of large forms (>60 μm diameter), nanoplankton (<60 μm) and ultraplankton (only a few micrometres in diameter). Depending upon the sample variability, alternate methods and analyses such as random, stratified, cluster, systematic, ratio, and regression sampling should be considered (Sournia 1978).

Preserved samples may be concentrated by sedimentation or centrifugation (using plankton centrifuges or continuous flow centrifuges) or by filtration through a membrane filter (APHA 1976). Addition of 0.05 mL of 1% solution of potassium aluminium sulphate crystals to 10 mL of the sample to be centrifuged could help in flocculation and sedimentation of the sample (Ballantine 1953). The calibration of light microscopes is given in APHA (1976). The apparatus and techniques used for counting phytoplankton are varied.

Sedgwick–Rafter method — The Sedgwick-Raftér (S.R.) Counting Chamber is the most commonly employed device for plankton. The S.R. cell is 50 mm long, 20 mm wide, 1 mm deep, and has a total bottom area of 1000 mm^2 and a total volume of 1 mL (1×10^{12} cubic μm^3 or 1000 mm^3). The whipple micrometer outside limits cover 1 sq. mm on the stage and the smallest square covers an area of 400 μm^2 (20 × 20 μm) known as the "aerial standard unit". A strip is the length of the S.R. cell 1 mm deep and the width of the whipple field. Four strips are usually counted, depending upon the density of phytoplankters. A 20× objective is generally used for counting. To calculate the concentration of organisms for the strip count:

$$\text{No./mL} = \text{Actual count} \times \frac{1000}{\text{Vol of strip (mm}^3\text{)}}$$

If random field counts are to be made, make sure to examine at least 10 whipple fields in two identically prepared S.R. cells. The concentration of the organisms with the field count:

$$\text{No./mL} = \text{Avg count/field} \times \frac{1000}{\text{Vol of field} \times \text{No. of fields}}$$

Always multiply or divide the number of cells per mL by a correction factor (including the preservative factor) for dilution or for concentration.

Palmer–Maloney cell method (Weber 1973) — The Palmer-Maloney (P-M) Nanoplankton Cell is designed for enumerating nanoplankton with a high-dry objective (45×). It has a circular chamber 17.9 mm deep with a volume of 0.1 mL. More counts may be required to obtain a valid estimate of the larger, but less numerous, organisms present. Count at least 20 whipple fields.

To calculate the concentration of organisms:

$$\text{No./mL} = \frac{C \times 1000 \text{ mm}^3}{A \times D \times 1}$$

where:

C = number of organisms counted (tally)
A = area of a field (whipple grid image), mm^2
D = depth of field (P–M cell depth), mm
F = number of fields counted.

Hemacytometer method (Weber 1973) — Hemacytometers are counting cells or machined glass slides with a finely ruled grid on a counting plate and a specially-fitted ground cover slip. The counting plate proper is separated from the cover slip mounts by parallel trenches on opposite sides. The grid is ruled such that squares as small as 1/20 mm (50 μm) to a side are formed within a larger 1-mm square. With the cover slip in place, the depth in a Petroff–Hausser cell is 1/50 mm (20 μm) and the hemacytometer 1/10 mm (100 μm).

Count all the forms that fall within the gridded area of the cell. To calculate the number or organisms per millilitre, multiply all the organisms found in the gridded area of the cell by the appropriate factor. For example, the multiplication factor for the Petroff–Hausser bacterial counting cell is based on the volume over the entire grid. The dimensions are 1 mm × 1 mm × 1/50 mm which gives a volume of 1/50 mm^3 and a factor of 50,000. Follow the manufacturer's instructions. The disadvantage of this type of counting cell is the extremely limited capacity, which results in a large multiplication factor. A sample must be either concentrated or a large number of mounts per sample should be examined.

Membrane filter method (McNabb 1960) — This method of phytoplankton counting requires a vacuum filtering apparatus. To determine the proper amount of sample to be filtered, use 0.45 or 0.5 μm pore size cellulose acetate membrane filters. This method permits the use of conventional microscopes for enumeration of small phytoplankton and increases the probability of counting the less abundant forms. The method is very suitable for use on water samples with low phytoplankton and silt contents. However, substantial quantities of suspended matter could obscure the phytoplankters. The membrane filter technique is used as a preparative step in scanning and electron microscopy (Fournier 1978).

The sample is filtered at a vacuum of 1/15 atmosphere (50 mm Hg), and the wet filter is removed and placed on top of 2 drops of immersion oil on a microscopic slide. Two drops of immersion oil are placed on top of the filter. The filter is air-dried at room temperature until clear. A cover slip is added prior to examination.

If the sample contains a mixture of fragile and robust forms, basic distilled water (pH 7.1–7.5) should be used for dilution of seawater. The organisms may be stained with Fast Green (alcoholic or aqueous) to make it easier to locate organisms on the filter (Fournier 1978).

When the filter is examined, the magnification and sampling field or quadrat must be such a size that the most abundant species will appear in at least 70 but not more than 90% of the microscopic quadrats. The occurrence of each species in 30 random microscopic fields is recorded. Table 1 gives a conversion table and calculations to give frequency and abundance of species.

To make a permanent slide, do not let the sample dry on the filter. Leave at least 5 mL of water in the filter apparatus and add 10–15 mL of glutaraldehyde–ethanol mixture (made by combining 5 drops of glutaraldehyde and 50 mL distilled water, cooling, and mixing in 50 mL ethyl alcohol). Filter, and leave until a thin film of water remains on the filter. After removing the filter from the apparatus, saturate it with beechwood creosote–ethanol mixture (7 mL of 95% ethanol + 3 mL beechwood creosote), add cover slip, and set aside until it is clear. (Clean filtration apparatus with 95% ethanol).

Filters may also be passed through an alcohol series and mounted in Canada Balsam.

Inverted microscope count method — The inverted microscope permits the use of short-focus and high-magnification objectives. By altering the height of the chamber, different concentrations can be obtained. Details for the use of this instrument for counting phytoplankton are available from Hasle (1978). As in the S.R. technique, strip or field counts can be used. Count a minimum of two strips perpendicular to each other over the bottom of the chamber and average the values. For counting, the Whipple eyepiece micrometer is also used. As a general rule, a minimum count of 100 of the most abundant species is necessary. After counting, total the tallies and calculate the percentages of the individual species. To calculate the number of plankters per millilitre (APHA 1976):

$$\text{Strip count (No./mL)} = \frac{C \times FA}{L \times W \times S \times V}$$

$$\text{Field count (No./mL)} = \frac{C \times FA}{F \times A \times V}$$

Where:

C = Number of organisms counted
FA = Total area of the bottom of the settling chamber (mm^2)
L = Length of a strip, mm
W = Width of a strip, mm (whipple grid image width)
S = Number of strips counted
V = Volume of the sample settled
A = Area of field, mm^2 (whipple grid image area)

TABLE 1. Conversion table for membrane filter technique (based on 30 scored fields) (APHA 1976).

Total occurrence	*F*%	*DN*
1	3.3	0.03
2	6.7	0.07
3	10.0	0.10
4	13.3	0.14
5	20.0	0.22
6	16.7	0.18
7	23.3	0.26
8	26.7	0.31
9	30.0	0.35
10	33.3	0.40
11	36.7	0.45
12	40.0	0.51
13	43.3	0.57
14	46.7	0.63
15	50.0	0.69
16	53.3	0.76
17	56.7	0.83
18	60.0	0.91
19	63.3	1.00
20	66.7	1.10
21	70.0	1.20
22	73.3	1.32
23	76.7	1.47
24	80.0	1.61
25	83.3	1.79
26	86.7	2.02
27	90.0	2.30
28	93.3	2.71
29	96.7	3.42
30	100.0	?

$$\text{Where } F = \frac{\text{total number of species occurrence} \times 1000}{\text{total number of quadrats examined}}$$

Calculation: Number of of organisms per millilitre = density (*DN*) from above table × number of quadrats or fields or membrane filter ÷ number of millilitres filtered × formalin dilution factor (0.96 for 4% formalin).

Particle counters — Particle counters facilitate automated counting and sizing of phytoplankton. Other types of particles suspended in a fluid can also be counted by sense zone counters. There is no single instrument which can perform all phytoplankton counting measurements equally well, but any one instrument will be good for a specific task (Sheldon 1978). These instruments can be used effectively for counting pure cultures of algae. Leslie (1978) compared electronic (Model B Coulter Counter and Millipore Particle Measurement System) and Utermohl techniques in quantitative analysis of freshwater particulates, and found that the counting and characterization of particles varied with size and shape in each technique. The counting of unknown detrital particles is a problem and to some extent contributed to the variation of results obtained.

Lackey drop microtransect method (APHA 1976) — In this simple method the sample is settled, and 0.1 mL is transferred to a glass slide and covered with a 22 × 22-mm glass cover slip. The organisms are counted in 3 or 4 strips under the cover slip. The number of a particular type of organism in 1 L of water can be determined as follows:

$$\text{No./L} = \frac{\dfrac{(\text{Avg No./field})\ (\text{No. fields/coverslip})}{(\text{No. drops/mL}) \times 1000}}{\text{Concentration factor}}$$

$$\text{The concentration factor} = \frac{\text{mL of original sample}}{(\text{mL of concentrate})\ (0.94)}$$

where 0.94 accounts for the dilution of the sample by the addition of formalin and the detergent.

Average volume in cubic microns of each species is obtained by measuring 20 individuals. The volume contributed by each species can be expressed in parts per million by use of the following formula:

$$\text{Volume (ppm)} = (\text{No. org/L})\ (\text{avg species vol in } \mu\text{m}^3 \times 10^{-9})$$

Fluorescent microscopy — Fluorescence occurs when energy, absorbed by atoms, molecules, or ions of various substances which are capable of fluorescing, is transformed into light. Light rays, electron bombardment, X-rays, and radioactive emission are capable of providing energy necessary for fluorescence. Fluorescent microscopy can use both ultraviolet and visible light. Plant and algal cells fluoresce because of chlorophyll. External fluorescence may be induced by specimens which are treated with fluorescent dyes or fluorochromes (e.g. acridine orange, auramine 00, acridine yellow, coriphosphine, aurosphosphine, berberine sulphate, neutral red, acriflavine hydrochloride, rhodamine B, primuline, fluorescein, sodium fluorescein, eosin, and erythrosine). Living algae fluoresce with a bright blood-red light. Total cells, with or without chlorophyll, can be counted after staining with a DNA-binding fluorochrome, acridine orange. The use of the fluorescence microscope is detailed in Sournia (1978). However, there are problems of cell rupturing and poor phytoplankton distributions on filters. Identification of organisms rather than the mere counting of cells is difficult, as the outlines of the cells are hard to see, and 4–5 L of water sample are required when dealing with sparse populations (UNESCO 1974).

Scanning electron microscopy — The scanning electon microscope is invaluable in showing fine surface detail not visible with the light microscope. The freeze-etching technique yields a three-dimensional view of the phytoplankton. Special procedures are given for diatoms in Hasle (1978) and Sournia (1978), for dinoflagellates in Taylor (1978), and for other flagellates in Leadbeater (1978).

MEASUREMENT OF PHYTOPLANKTON PIGMENTS

Chlorophyll *a* is present in all algal groups. The concentration of chlorophyll *a* provides an important estimate of biomass or standing crop of the phytoplankton.

The chlorophyll *a* concentration varies with species and certain algae also contain chlorophyll *b* and *c*. Chlorophyll can be estimated by fluorometry or spectrophotometry (SCOR–UNESCO 1964; Holm-Hansen and Reimann 1978).

Procedure: (Weber 1973; Holm-Hansen and Riemann 1978) —

1) Concentrate the algae with a membrance filter (0.45 μm pore size) or a glass fiber filter (0.45 μm effective pore size).

2) Store the samples at – 20°C. These may be kept in storage for a maximum period of 2–3 wk.

3) Transfer the sample to a screw-capped centrifuge tube, add sufficient reagent grade methanol to bring the volume to 5 ml, and keep it in the dark at 4°C for 24 h. Use the solvent sparingly to avoid unnecessary pigment dilution. Agitate midway during the extraction period and again before clarifying.

4) Centrifuge 20 min at 500 *g*. Decant the supernatant into a clean, calibrated vessel (1–5 mL, screw-capped, calibrated centrifuge tube) and determine the volume. Minimize evaporation by keeping the tube capped.

Pigments may be determined by trichometric or fluorometric methods.

Trichometric determination — Determine the optical density (*OD*) of the extract at 750, 663, 645, and 630 nanometers (nm) using a 90% aqueous acetone blank. Dilute the extract or shorten the light path if necessary, to bring the OD_{663} to between 0.20 and 0.50. The 750-nm reading is used to correct for turbidity. A suitable blank is used for turbidity correction. Spectrophotometers having a resolution of 1 nm or less are preferred. Minimize evaporation during the time readings are being made.

Calculations — The concentration of pigment in the phytoplankton is expressed as mg/m³ or μg/L and is calculated as follows:

$$\text{mg chlorophyll } a/\text{m}^3 = \frac{C_a \times \text{volume of extract (L)}}{\text{volume of sample (m}^3)}$$

The chlorophyll concentrations in the extract are determined by inserting the corrected 1-cm *OD*'s in the following equations.

$$C_a = 11.64D_{663} - 2.16D_{645} + 0.10D_{630}$$

$$C_b = 3.94D_{663} + 20.97D_{645} - 3.66D_{630}$$

$$C_c = -5.53D_{663} - 14.81D_{645} + 54.22D_{630}$$

where C_a, C_b, C_c are the concentrations, in milligrams per liter, of chlorophyll *a*, *b*, and *c*, respectively, in the extract, and D_{663}, D_{645}, and D_{630} are the 1-cm *OD*'s at the respective wavelengths, after subtracting the 750-nm blank.

Fluorometric determination (Yentsch and Menzel 1963; Holm-Hansen et al. 1965; and Weber 1973) — The fluorometric method is much more sensitive and permits accurate determination of much lower concentrations of pigment and the use of smaller sample volumes. To obtain optimum sensitivity use excitation and emission wavelengths of 430 and 663 nm, respectively, using a R-136 photomultiplier tube. Corning CS-5-60 excitation and CS-2-64 emission filters or their equivalents should be employed. Calibrate the fluorometer with a chlorophyll solution of known concentrations of approximately 0.002, 0.006, 0.02, and 0.06 mg chlorophyll *a*/L of extract, so that a minimum of two readings are obtained in each sensitivity range of the fluorometer (1/3 and 2/3 of full scale). Using these values, derive factors to convert the fluorometer readings in each sensitivity range to milligrams of chlorophyll *a* per litre of extract.

$$F_s = \frac{\text{Conc chlorophyll } a \text{ (mg/L)}}{\text{fluorometer reading}}$$

where F_s is the fluorometric conversion factor and *s* is the sensitivity range (door).

The filter is dried in the dark and extracted by grinding with 85% acetone (Yentsch and Menzel 1963). The final volume of the extract is 10.0 mL exactly. The fluorescence of the extract (Rb) is measured on the fluorometer. If the reading (scale deflection) is over 90 units, use a lower sensitivity setting, e.g. 30 × 10 × 1 ×. Conversely, if the reading is less than 15 units, increase the sensitivity setting. If the samples fail to fall in range, dilute accordingly. The extract is then acidified by shaking with 0.1 mL (2 drops) 1.0 NHCl and the fluorescence is read again (Ra). Acidification converts all the chlorophyll initially present in the extract to phaeophytin. Chlorophyll and phaeophytin exhibit different fluorescence per unit weight. The initial extract contains some phaeophytin in addition to chlorophyll and the effect of its fluorescence must be subtracted from R_b before the true fluorescence due to chlorophyll alone can be determined.

Acidification of a solution of pure chlorophyll *a* results in a 40% reduction in the OD_{663}, yielding a "before:after" *OD* ratio ($663_b/663_a$) of 1.70. Samples with $663_b/663_a$ ratios of 1.70 are considered free of phaeophytin *a*, and contain algal populations consisting mostly of intact, nondecaying organisms. Samples containing phaeophytin *a* but not chlorophyll *a* show no reduction on OD_{663} upon acidification, and have a $663_b/663_a$ ratio of 1.0. Samples containing both pigments will have ratios between 1.0 and 1.7.

PRIMARY PRODUCTIVITY

Primary productivity is the rate at which inorganic carbon is converted to an organic form by the chlorophyll-bearing plants. Primary productivity can be determined by measuring the changes in oxygen or carbon dioxide concentrations in aquatic environments. The pH rises along with the removal of carbon dioxide from the waters and carbon dioxide uptake may be determined from pH. However, high concentrations of carbonate content of the waters renders the method impracticable. The two commonly used in situ methods for measuring the carbon dioxide uptake are the carbon^{14} method and the oxygen method (APHA 1976).

^{14}C method (Vollenweider 1971; Carlsberg 1972; Gargas 1975; APHA 1976) — Determination of photosynthetic production by the ^{14}C method is based on the

TABLE 2. Secchi disc disappearance depths, approximate extinction coefficients, % transmission, and levels of illumination. Secchi (m) is the mean of depths at which Secchi disc disappears and at which it reappears upon raising after it has been lowered beyond visibility, when viewed from the shaded side of the boat.

			Depths for percentage of surface irradiance (m)				
Secchi (m)	*K*[a]	% Transmission	100%	60%	30%	16%	1%
5	.340	71	0	1.5	3	6	16
6	.284	75	0	2	4	7	18
7	.243	78	0	2	4	7	19
8	.212	80.5	0	2.75	6	8	21
9	.188	82.5	0	3	6.5	10	23
10	.170	84.5	0	3.5	7	12	26
11	.154	86	0	3.5	8	13	29
12	.142	86.8	0	4	8.5	14	30.5
13	.131	88	0	4.5	9	14	32.5
14	.121	88.5	0	4.5	9.5	15	34
15	.113	89.5	0	4.75	11.5	17	39
16	.106	90	0	4.75	11.5	17	42
17	.100	90.5	0	5	13	17.5	43
18	.095	91	0	6	15	18	45
19	.089	91.5	0	5	13	19	48
20	.085	91.8	0	6	14	20	50
21	.081	92	0	6	15	22.5	54
22	.077	92.5	0	6	16	24	60
23	.074	92.8	0	7	18	25	65
24	.070	93	0	7	20	28	70
25	.068	93.5	0	8	22	30	75

[a] *K*, extinction coefficient.

assumption that labelled carbon has been assimilated by the algae in proportion to normal CO_2. The total amount of carbon fixed during a period of time can be calculated by determining the amount of ^{14}C present in the phytoplankton when the experiment ends. This technique is very sensitive and quite accurate particularly in oligotrophic waters. Long-term experiments are not necessary as with the oxygen method.

Photosynthetically active radiation occurs between 390 and 710 nm (Wetzel and Likens 1979). The intensity or irradiance is usually measured as g cal/cm²/min (= langley/min). Surface irradiance upon the waterbody may be measured by pyrheliometer or solarimeter. Underwater light intensity is usually measured with photometers containing selinium photocells or silicon photovaltaic cells. Some photometers with quantum sensors can measure photosynthetically active radiation in the 400–700 nm portion of the spectrum directly in $\mu E \cdot m^{-2} \cdot s^{-1}$.

Particles in water, living or dead, and dissolved organic compounds such as fulvic and humic acids absorb and/or scatter the light. There is greater light penetration in less productive waters than in more productive waters. The compensation depth is also affected by latitude, season, and time of day. Light is absorbed logarithmically in seawater; in the upper 10-m depth, about 80% of the total solar radiation is absorbed and of the visible wavelengths, only 50% remains even in the clearest water. One percent incident visible light reaches about 120 m in clear tropical oceans. The same reduction to 1% is reached at 50 m in boreal waters, and in turbid inshore areas the 1% level could be reached between 10 and 20 m (Raymont 1966). Secchi disc (white disc, 20–25 cm in diameter) visibility is a function of reflection of light from the surface of the disc. Secchi disc visibilities correlate well with percentage transmission but may differ by 1–15% from measurements with underwater photometers (Wetzel 1975). Table 2, showing Secchi disc readings and % light transmission, may be used to calculate depths for primary productivity experiments with ^{14}C. The appropriate secchi disc reading allows the determination of the depths at which specific percentages of surface irradiance occurs. Collect water for ^{14}C experiments at depths corresponding to 100, 60, 30, 16, and 1% illumination.

Water samples are immediately transferred to two 300 mL glass B.O.D. bottles, one transparent and one black. The latter is for determination of dark fixation. Normally dark fixation should be determined at each depth but for repetitive work it may be sufficient to have dark bottles at every second depth. Bottles are kept in a dark box to avoid radiation from the sun. To each sample add 1 mL of $NaH^{14}CO_3$ solution (4 μC). The working strength ranges between 1 and 110 μC/ml. (To calculate the actual radioactive carbon added to incubation bottle, consult Strickland and Parsons 1972). Introduce the solution with a small pipette with a rubber bulb at the bottom of the bottle, being careful to avoid spills. Rinse the ampoule with a small volume of the sample, and add the pipette to the sample bottle. Put the bottles back into the dark box until all samples are ready. Then attach them to a rope and suspend them from a float at their original depths.

Incubation time is generally 4 h anytime between 9 AM and 3 PM. Longer exposure times may decrease accuracy. At the end of the incubation period take the bottles aboard and if possible immediately filter 5 mL of each sample with a 25-mm Millipore filter apparatus at a vacuum of 0.5 Kp/cm^2 (or approximately 0.3 atm vacuum). (At stronger vacuum there is a risk that the cells are deformed or damaged.) Place the bottles in the dark and transfer them rapidly to a shore laboratory. Using uncontaminated forceps, remove the membrane, place in 20-mL glass scintillation vials, and add 0.1–1.0 mL of 5N HCL (Lean and Burnison 1979). After 2 or 3 h add 1.0 mL of solvene 350 (Packard) to each vial. After complete dissolution add 1–2 drops of hydrogen peroxide and leave for 2 h or more for bleaching. To the colorless contents of the vials add 10 mL of 90% PCS (from Nuclear Chicago) or 5 mL of any other liquid scintillator such as Dioxan based Bray, Instagel, or Bio-Solv BB3, and cap the vials tightly. The absolute activity of the ^{14}C activity of the solution in the vial is determined by counting its scintillation activity before and after adding a known amount of ^{14}C hexadecane standard.

For identification, the filters should be marked with sample numbers. Determine temperature, salinity, alkalinity, and pH from separate samples from each sampling depth. From these data it is possible to compute the total amount of CO_2 in the water from a nomogram (APHA 1976, p. 297).

The values of dark fixation (the dark bottles) are subtracted from the values for the transparent bottles to obtain the net primary production of the phytoplankton organisms. When the photosynthesis for the whole day is to be determined, the irradiance from the sun from sunrise to sunset is measured with an integrating instrument (Pyrheliometer). The exposure time is multiplied by the quotient:

$$\frac{\text{Total irradiance from sunrise to sunset}}{\text{Irradiance during the exposure time.}}$$

Integrate the productivity for the entire depth of the euphotic zone and express as grams of carbon fixed per square metre per day (cf. APHA 1976).

The probable sources of error are:

1) This procedure is for vertically placed bottles. In horizontal exposures the assimilation is 10–30% greater.

2) Rate-of-change ought to be determined in every area of investigation and at every major change in the phytoplankton stock or water milieu.

Calculations:

The rate of radiocarbon-measured photosynthesis

$$(\text{mgC/m}^3/\text{h}) = \frac{(R_s - R_b) \times W \times 1.05 \text{ or } 1.1}{R \times N}$$

Where:

R_s = counts/min on filters from the light bottle
R_b = counts/min on filters from the dark bottle
W = the total amount of inorganic carbon in the samples in mg C/m^3
1.05 or 1.1 = a factor to allow for the fact that ^{14}C isotope behaves somewhat differently than the ^{12}C isotope found in nature
R = the normal count/min ampoule
N = the time of incubation (h)

The principal disadvantages of ^{14}C method for phytoplankton photosynthesis are higher costs, the need to obtain the proper licence to use ^{14}C, and some uncertainty about the exact nature of the rates being measured.

Oxygen method — Phytoplankton production may be measured indirectly by estimating either the uptake of carbon dioxide or the release of oxygen in the photosynthetic process. One mole of oxygen is released for every mole of carbon dioxide incorporated into organic carbon. Oxygen may be added to water by photosynthetic algal activity or removed through animal and plant respiration. Oxygen can be measured most accurately by the Winkler method (Strickland and Parsons 1972). During photosynthesis, oxygen production generally exceeds the respiration of photosynthetic organisms. Hence the amount of oxygen added is a measure of net productivity or the carbon dioxide fixed as carbon.

Primary production can be measured in a 1-m^2 column of water, extending from bottom to surface, by monitoring changes in oxygen at various levels in the water column. This is accomplished by suspending two glass-stoppered B.O.D. bottles (one light and the other dark) containing water and planktonic organisms at each level in the water column and recording oxygen changes within the bottles during 3–10-h increments over a period of 24 h. Oxygen changes in the light bottle are a result of addition through photosynthesis and subtraction caused by community respiration. The dark bottle measures respiration.

Prepare 3 B.O.D. bottles (2 clear and one dark). Fill them with natural samples of water and phytoplankton from the depths where they will be suspended. Pairs of light and dark bottles should be suspended at selected depths (0.5, 1.5, 2.5, 3.5 m and so on) within the water column on a weighted line and incubated for 3–10 h. The third bottle is fixed at the start with Winkler reagents. After the incubation period, the light and dark bottles are also fixed, and the three bottles titrated for oxygen.

Community respiration, gross primary production, and net production may be calculated from observed oxygen changes according to Strickland and Parsons (1976). Vollenweider (1969) gives more information on this technique. The net primary production throughout the water column can be calculated by multiplying each net production value by the length of the water column it represents and then totaling each value throughout the water column.

Calculations (Vollenweider 1969):

$$\begin{array}{ll} \text{Net phytosynthesis} & \\ (\text{mg c m}^{-3}\text{h}^{-1}) & = \dfrac{\text{Light bottle} - \text{initial bottle}) \times K_1 \times K_2}{\text{N. PQ.}} \end{array}$$

$$\begin{array}{ll} \text{Respiration} & \\ (\text{mg c m}^{-3}\text{h}^{-1}) & = \dfrac{(\text{Light bottle} - \text{dark bottle}) \times K_1\ .}{N.} \end{array}$$

$$\begin{array}{ll} \text{Gross photosynthesis} & \\ (\text{mg c m}^{-3}\text{h}^{-1}) & = \dfrac{(\text{Light bottle} - \text{dark bottle}) \times K_1 \times K_2)}{N.\ PQ.} \end{array}$$

Where:

K_1 = Factor to convert bottle volume to m^3
K_2 = Constant to convert mg O_2 to mg c (= 12/32)
N = Number of hours of incubation
$PQ.$ = Photosynthetic quotient

Oxygen measurements in water flowing past two fixed points have been used by Odum (1956) to calculate production of plankton and attached organisms as follows:

$$Q = P - R + Din + A$$

Where:

Q = rate of change of dissolved oxygen between two sampling stations a fixed distance apart
P = Rate of gross primary production per area
R = rate of respiration per area
Din = rate of oxygen uptake into the water mass by diffusion
A = rate of drainage accrual (usually negligible)

For further details concerning this method refer to APHA (1976).

Diurnal curves of oxygen are constructed from which production values are calculated. It is generally assumed that all the area under investigation undergoes a simultaneous change in oxygen concentration.

Sources of error of the oxygen bottle method—Disadvantages of the oxygen method are:

1) The temperatures in the dark bottle series may be somewhat different, respiration proceeding at different rates in the light and dark bottles.

2) Compounds other than carbohydrates may be synthesized particularly by diatom cultures, which affects the amount of oxygen produced.

3) Growths, especially of marine bacteria, tend to increase in the enclosed bottles.

4) The oxygen bottle experiment is insensitive to low concentrations of phytoplankton as in oligotrophic areas of the sea.

5) The technique is unsuitable for productivity experiments in very rich, highly polluted, inshore waters, especially those with high bacterial populations. This has proved to be generally true in the St. Croix Estuary, where the ^{14}C method is recommended.

STANDING CROP (BIOMASS) DETERMINATION

The biomass of phytoplankton can be estimated from numbers of organisms per unit volume or biovolume (cell volume), cell surface area, dry and ash-free weight, total carbon, total nitrogen, Adenosine triphosphate in plankton, and chlorophyll content. The variations in size distribution of the phytoplankton does not permit reasonable standing crop estimates based on cell numbers (APHA 1976). The cell volume index for phytoplankton is achieved using the simplest configuration that fits the shape of the cell being measured (Vollenweider 1971) and the data is recorded on a volume-per-volume basis (APHA 1976). The cell surface areas may be used in a similar way.

The dry and ash-free weight of the phytoplankton is a most useful means of expressing plankton biomass (Lovegrove 1966). The dry weights are obtained by drying at 105°C for 24 h; the ash-free weights are obtained after igniting the dry sample at 500°C for 1 h and cooling in a desicator before weighing (APHA 1976). Ten mg of dry weight is generally considered equivalent to 100 mg of wet weight (Weber 1973). Cummins and Wuycheck (1971) recommend methods with corrections for determining caloric values (per gram wet, dry, and ash-free weight) for primary producers. Ecologists often convert caloric data to biomass data to permit correlation with other trophic levels or taxa. Thus caloric values of phytoplankton may serve as an index of biomass.

Crippen and Perrier (1974) described the use of neutral red staining to determine the live–dead ratio for diatoms. To estimate the total viable plankton biomass, a measure of the adenosine triphosphate (ATP) is useful (APHA 1976). A primary coulometric titration has been proposed as a standardization technique for the succinate dehydrogenase assay used in the estimation of respiration rates in marine plankton (Packard and Healy 1968). A review of ATP biomass estimation technique was presented by Qureshi and Patel (1976), who conclude that ATP is a reliable index of biomass, although ATP varies from species to species (APHA 1976). However, more critical studies on methodology are needed before the ATP method can be used as a routine technique (Qureshi and Patel 1976).

Indirect estimates of biomass on the basis of nutrient uptake (nitrogen, phosphorus) are possible. However, elements like phosphorus are rapidly recycled and the estimates could only yield lower limits of primary production. Cellular contents of organic carbon to cell volume or cell surface area could give a general ratio which is relatively constant to many algae (Wetzel and Likens 1979). A detailed treatment of the chemical composition of phytoplankton in relation to productivity measurements was given by Strickland (1960).

List of Phytoplankton of Passamaquoddy Bay

BACILLARIOPHYCEAE

Achnanthes longipes Agardh
A. subsessilis Kützing
A. taeniata Grunow
Actinoptychus senarius (Ehrenberg) Ehrenberg
Amphiprora alata (Ehrb.) Kützing
Amphora ovalis Kützing
Asterionella japonica cleve and Moller ex Gran
Auliscus sculptus (Wm. Smith) Ralfs in Pritchard

Bacillaria paxillifer (O.F. Muller) Hendey
Bacteriosira fragilis Gran
Biddulphia alternans (Bailey) Van —eurck
B. aurita (Lyngb.) de Brébisson
B. Bailey Wm. Smith
B. mobiliensis (Bailey) Grunow ex Van Heurck
B. pulchella Gray
Brebissonia boeckii (Ehrenberg) Grenow

Campylodiscus Grunow
Ceratulina pelagica (cleve) Hendey

Chaetoceros atlanticum cleve
Ch. boreale Bailey
Ch. compressus Lauder
Ch. concavicorne Magnin
Ch. constrictus Gran
Ch. convolutum castracane
Ch. curvisetum cleve
Ch. danicum cleve
Ch. debile cleve
Ch. decipiens cleve
Ch. diadema Ehrenberg
Ch. didymum Ehrenberg
Ch. furcellatum Bailey
Ch. laciniosum Schütt
Ch. lorenzianum Grunow
Ch. radians Schutt
Ch. sociale Lauder
Ch. teres cleve
Ch. Willei Gran
Cocconeis scutellum Ehrenberg
Corethron criophilum castracane
Coscinodiscus asteromphalus Ehrenberg
C. centralis Ehrenberg
C. concinnus Wm. Smith
C. eccentricus Ehrenberg
C. normani Gregory in Greville
C. oculus – iridis Ehrenberg
C. radiatus Ehrenberg
Cyclotella compta (Ehrenberg) Kützing

Detonula confervacea (cleve) Gran
Diatoma elongatum (Lyngbye) Agardh
Diploneis didyma (Ehr.) Ehr.
D. elliptica (Kütz.) cleve
D. smithii (de Brebisson) cleve
Ditylum brightwellii (T. West) Grun ex Van Heurck

Endictya oceanica Ehrenberg
Epithemia musculus Kützing
Eucampia zoodiacus Ehrenberg
Eupodiscus radiatus Bailey

Fragilaria capucina Desmazieres

Gomphonema acuminatum Ehrenberg
G. marinum (Kützing) Wm. Smith
Grammatophora marina (Lyngbye) Kütz.
G. serpentina Ehrenberg
Guinardia flaccida (Castr.) H. Perg.

Hyalodiscus scoticus (Kütz.) Grunow

Isthamia enervis Ehrenberg
I. nervosa Kutzing

Leptocylindrus danicus cleve
Licmophora lyngbyci (Kützing) Grunow ex Van Heurck

Mastogloia Smithii Thwaites ex Wm. Smith
Melosira crenulata (Ehrenberg) Kutz.
M. hyperborea Grunow ex cleve et Moller
M. juergensii C. A. Agardh
M. moniliformis (O. F. Müller) Agardh
M. nummoloides (Dillwyn) C. A. Agardh
M. subflexilis Kützing
M. varians C. A. Agardh

Navicula bahusiensis (Grunow) cleve
N. crucigera (Wm. Smith) cleve
N. distans (Wm. Smith) Ralfs
N. marina Ralf in Pritchard
N. peregrina Kützing
Nitzschia bilobata Wm. Smith
N. closterium Wm. Smith
N. seriata cleve

Paralia sulcata (Ehrenberg) cleve
Pinnularia major (Kütz.) Rabh.
P. viridis (Nitz.) Ehr.
Pleurosigma aesturii (de Brébisson ex Kützing) Wm. Smith
Pl. angulatum Wm. Smith
Pl. attenuatum Wm. Smith
Pl. balticum Wm. Smith
Pl. decorum Wm. Smith
Pl. elongatum Wm. Smith
Pl. fasciola Wm. Smith
Pl. formosum Wm. Smith
Pl. intermedium Wm. Smith
Pl. spenceri Grunow
Pl. strigosum Wm. Smith

Rhabdonema arcuatum (Lyngbye) Kütz.
Rhaphoneis amphiceros (Ehr.) Ehrenberg
Rhizosolenia alata Brightwell
R. alata forma *gracillima* (cleve) Gran
R. hebetata Bailey
R. obtusa Hensen
R. setigera Brightwell
R. shrubsolei cleve
R. styliformis Brightwell
Rhopalodia gibba (Ehrenberg) O. Müller

Skeletonema costatum (Greville) cleve
Stauroneis Ehr.
Striatella unipunctata (Lyngbye) Agardh
Surirella gemma (Ehrenberg) Kutzing
S. ovalis de Brebisson
S. Smithii Ralfs
Synedra pulchella Kutzing
S. radians (Kutzing) Grun

Thalassionema nitzschoides Grunow
Thalassiosira nordenskioldii cleve
T. gravida cleve
Thalassiothrix longissima cleve and Grunow

CHRYSOPHYCEAE

Distephanus speculum (Ehrenberg) Haeckel

DINOPHYCEAE

Ceratium furca (Ehrenberg) claparede and Lachman
C. fusus (Ehrenberg) Dujardin
C. tripos (O. F. Müller) Nitzseh

Dinophysis norvegica claparède and Lachmann

Gonyaulax excavata (Braarud) Balech

Peridinium depressum Bailey

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CHAPTER 12

Larger Zooplankton of the Quoddy Region

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Introduction

Zooplankton consists of the drifting animals of the sea. Weak locomotor capabilities cause these animals to be at the mercy of currents, as they are unable to swim against them. Zooplankton can be categorized or subdivided according to duration of time spent as a zooplankter and size. Those remaining zooplankton for the entire life cycle are holoplankton, e.g. euphausiids and chaetognaths; meroplankton are plankton for only part of their life cycle, e.g. larvae of benthic invertebrates such as crabs and barnacles. Microzooplankton are those less than 1 mm and macrozooplankton those more than 1 mm in size. The latter classification is arbitrary and should be used cautiously. For example, some copepods would be considered microzooplankton as larvae but macrozooplankton as adults.

Chapter 13 deals with microzooplankton and copepods. This chapter is about holoplankton of which adults are usually greater than 5 mm. Included are chaetognaths, pteropods, ctenophores, cnidarians, euphausiids, and amphipods, and also benthic species which undergo a diurnal vertical migration and hence become members of the zooplankton community at night (mysids and cumaceans).

The Quoddy Region is defined by Legaré and Maclellan (1960) as "encompassing Passamaquoddy Bay, Cobscook Bay, the passages, and outside Passamaquoddy inside a line from West Quoddy Head, Maine, to the northern tip of Grand Manan, New Brunswick and thence to Point Lepreau, New Brunswick" (Chap. 1, Fig. 1).

Both qualitatively and quantitatively, the zooplankton of Passamaquoddy Bay is far less rich than that of the adjacent Bay of Fundy. The variety and quantity, especially of the larger zooplankton, decreases drastically from the Bay of Fundy into the Passages and is generally very poor in the inner portions of Passamaquoddy Bay. None of the holozooplankton listed above form endemic populations within the Quoddy Region. Specimens occurring in this area are part of much larger populations in the Bay of Fundy. The pelagic amphipods, pteropods, and ctenophores are not endemic to the Bay of Fundy and probably originate in the Scotian shelf and/or the Gulf of Maine. As a result, the relative abundance of these taxa varies greatly in time and space, especially in the Quoddy Region. The zooplankton in Passamaquoddy Bay and the Passages is most diverse and abundant in summer, less so in fall and winter, and least diverse and abundant in the spring (Legaré and Maclellan 1960).

Other taxa frequently occurring in the zooplankton such as mysids, cumaceans, and decapods inhabit the Quoddy Region throughout the year. The jellyfish, *Aurelia aurita*, occurs seasonally. The pelagic polychaete, *Tomopteris helgolandica* occurs spasmodically and is most common during winter. Table 1 provides a brief, generalized summary of the larger zooplankton of the Quoddy Region, their respective habitats, relative depths, and seasonal abundance.

Collecting and Preserving Techniques

Methods of collecting, observing and maintaining zooplankton vary depending on individual requirements. A conical net attached to a metal hoop and tapering to the cod end, to which a jar or container is attached, is the basic net used for qualitative studies. One can modify this standard or ring trawl by placing a cylinder of canvas between the metal ring or hoop and the net. If specific depth ranges are to be investigated then a similar net equipped with a closing device is required. The diameter of the mouth may vary from 1/4 m to 1 m, and nylon mesh is available in a wide variety of sizes. The mesh size selected depends on the size of animals to be collected. The best size for obtaining the animals discussed herein is 300–500 µm. Nets of smaller mesh build up a pressure front when towed which allows the larger animals to escape.

If quantitative analysis is required, the tow net must be equipped with a flowmeter. For efficiencies of various nets and further details of design, see UNESCO (1968).

To sample the entire water column, the net is lowered from a stationary boat so that it almost touches the bottom and is then raised. This technique, the vertical haul, is good for microzooplankton but yields few larger animals. If larger numbers are needed, an oblique haul is recommended. The net is lowered to the sea bed and as it is pulled up the vessel proceeds at a speed of not more than 2 kn. This is also a valuable technique if one is sampling around the clock, as it negates any error of specific depth sampling caused by diurnal vertically migrating animals. Sampling specific depths or depth ranges requires the use of an opening and closing net. To collect surface plankton or neuston, special neuston nets of various dimensions and mesh sizes are available.

Most large zooplankton are difficult to maintain alive in the laboratory. However, short-term observations and experiments can be undertaken if special precautions are taken. First, minimize tow duration (about 5–10 min) to prevent damaging animals in the net. The animals should be returned as quickly as possible to the laboratory. Circular containers are best and overcrowding should be avoided. The water must be well oxygenated and preferably maintained at ≤ 5°C. Thermos bottles may prove useful in transporting animals.

TABLE 1. The habitats and relative seasonal abundance of the larger zooplankton found in the Quoddy Region (based on Legaré and Maclellan (1960) and personal observations).

		Depth		Season of greatest abundance			
Species	Habitat[a]	<20 m	>20 m	Spring	Summer	Fall	Winter
ANNELIDA							
Tomopteris helgolandica	P		√				—
CRUSTACEA							
AMPHIPODA							
Parathemisto gaudichaudi	P		√	—	—	—	—
Hyperia galba	P	√	√		—		
Calliopius laeviusculus[b]	P + EP	√			—	—	
Monoculodes edwardsi[b]	EP		√	—	—	—	—
MYSIDACEA[b]							
Erythrops erythropthalma	EP	√	√	—	—	—	—
Neomysis americana	EP	√	√	—	—	—	—
Mysis stenolepis	EP	√	√	—	—	—	—
CUMACEA[b]							
Diastylis sculpta	B	√		—	—	—	—
D. quadrispinosa	B		√	—	—	—	—
Eudorella sp.	B	√		—	—	—	—
Campylaspis rubricunda	B		√	—	—	—	—
Leptostylis ampullacea	B		√	—	—	—	—
Petalosarsia declivis	B		√	—	—	—	—
EUPHAUSIACEA							
Meganyctiphanes norvegica	P		√	—	—		
Thysanoessa inermis	P		√	—	—		
DECAPODA[b]							
Crangon septemspinosa	B	√	√	—	—	—	—
Pandalus montagui	B		√	—	—	—	—
Spirontocaris sp.	B		√	—	—	—	—
CHAETOGNATHA							
Sagitta elegans	P		√	—			—
CTENOPHORA							
Pleurobrachia pileus	P		√		—		—
CNIDARIA							
Aurelia aurita	P	√	√		—		
Nanomia cara	P			—	—		—
MOLLUSCA							
Clione limacina	P		√	—	—		
Limacina retroversa	P		√	—			

[a] P, pelagic; EP, epibenthic; B, benthic.
[b] Species which are benthic or epibenthic during the day and undergo diurnal vertical migration.

If the animals are to be preserved, a solution of 3–5% neutralized formaldehyde (borax or chips of chalk) is suggested. However, animals which tend to be damaged through decalcification (e.g. pteropods) if the formaldehyde is not truly neutralized should be killed in 3–5% formaldehyde and then transferred immediately to a non-acidic fixative such as 70% alcohol. Generally, 3–5% neutralized formaldehyde is the best fixative for most zooplankton. For more details on specific fixation and preservation techniques see UNESCO (1976).

The best places for general collecting in the Quoddy Region are the Passages and the Grand Manan area, especially if large numbers are required.

Biology and Distribution

The following descriptions and discussion include only those species of larger zooplankton usually found in the Quoddy Region. Other animals, originating from more northern or more southern waters, infrequently appear in this area; examples of these can be found in Huntsman (1952). General keys for identification are found in Newell and Newell (1963), Miner (1950), Smith (1964), and Smith (1977). Keys for specific groups are listed under the respective headings.

There follows separate discussions of each taxa and species and a general summary and discussion of the general biology of the larger zooplankton in the Quoddy Region.

CRUSTACEA

The most common crustaceans in this area are the copepods, which are discussed in Chapter 13. Of the larger crustaceans, the euphausiids and the amphipods are the commonest members of the holozooplankton. Mysids and cumaceans, through diurnal vertical migrations, form an important component of the zooplankton during the night.

Euphausiacea — Euphausiids are holozooplankters which form a significant proportion of the animal biomass of most oceans and are an important aspect of marine food webs. These crustaceans are an important food source for baleen whales (Nemoto 1957) and many fish such as herring, mackerel, hake, and cod (Battle et al. 1936; Tyler 1972). The euphausiids in turn are filter feeders and feed on a wide variety of food items such as organic debris, detritus, diatoms, dinoflagellates, tintinnids, and zooplankton. Particulate matter forms the greatest proportion of their diets. Detritus is consumed when the animals are close to the bottom, e.g. during the day in some areas. A seasonal change in diet generally occurs. During winter, when plankton is less abundant, they feed mainly on detritus. As spring approaches and plankton becomes more available, the amount of detritus consumed decreases and the amount of plankton consumed increases (Mauchline and Fisher 1969).

Adult euphausiids inhabit relatively deep waters during the day and perform vertical migration at night, moving into the upper regions of the water column with some animals found at all depths (Kulka et al. 1981). In the Western Passage area, because the depths are 55–100 m, the mature euphausiids are located immediately above the substratum. As a result, they provide food during the day for demersal fish such as cod, and during the night for pelagic fish such as herring and mackerel. Also, in certain areas, surface swarms of adult euphausiids are common, especially during late summer in areas around the Quoddy Passages which experience heavy tidal currents and upwelling (Battle et al. 1936; Fish and Johnson 1937; Kulka et al. 1981). Thus, these animals provide food for many marine birds at this time (Gaskin, personal communication).

Male euphausiids produce spermatophores which are transferred to the females. The eggs are fertilized during extrusion and are released into the surrounding water. The eggs and early larval stages are pelagic, being found in the upper part of the water column. As the larvae develop and metamorphose into juveniles they tend to occupy deeper parts of the sea. The overall daytime vertical distribution is as follows: eggs and early larval stages (nauplius, metanauplius, calytopis, and furcilia) are near the surface, juveniles are deeper, and adults occupy the deepest part of the species depth range.

Euphausiid eggs occur at the entrances of Passamaquoddy Bay in early summer. Small numbers of early furcilia larvae occur in mid-to-late summer. Late furcilia stages are very rare in Passamaquoddy Bay. The center of spawning of euphausiids is outside the Quoddy Region, probably in the vicinity of Grand Manan Basin (Kulka and Corey 1978).

Meganyctiphanes norvegica and *Thysanoessa inermis* are the two species of euphausiids commonly found in the Quoddy Region at certain times of the year (Table 1). The occurrence and abundance of both these species vary with time and place. The Quoddy specimens of both species belong to populations which are endemic to the Bay of Fundy and are centered in the vicinity of the Grand Manan Basin (Kulka et al. 1981). Both species undergo an annual expansion and contraction of varying degrees. They are generally found in greatest concentrations in the outer Quoddy Region and in the Passages during late spring, summer, and early fall. They are virtually absent during the winter of most years. Even during the summer they are rare in the inner parts of Passamaquoddy Bay.

As the distribution and life histories of *M. norvegica* and *Th. inermis* are different, they will be discussed separately.

Meganyctiphanes norvegica — *Meganyctiphanes norvegica* is found throughout the North Atlantic. In the northwest Atlantic, it ranges from Cape Hatteras (35°N) northwards over the continental shelf and along the continental slope to Labrador, Baffin Island, and western Greenland to about 70°N (Mauchline and Fisher 1969).

The life history of *M. norvegica* in the Quoddy Region and Bay of Fundy has been described by Hollingshead and Corey (1974). Sexual maturity is attained in 1 yr, with gonadal development taking about 3 mo. The breeding season (defined as the time when 50% of females carry spermatophores) lasts from mid-April to the end of July and spawning (release of eggs) occurs during July and August. Eggs (average diameter 0.68 mm) and nauplii and metanauplii (average lengths 0.52 and 0.55 mm, respectively) are present during early

July. During late July and August, calyptopis and furcilia stages occur. These animals reach sexual maturity in 1 yr, i.e. they breed and spawn for the first time the following summer. After breeding and spawning again the next year the animals die, having a life span of approximately 2 yr. During the early 1970's this species was present in the Quoddy Region in varying numbers from February to November, the greatest concentrations occurring from May to November; they virtually disappeared during December and January.

Thysanoessa inermis — *Thysanoessa inermis* is predominantly subarctic and arctic, with its southern boundaries in the temperate regions. It is an inshore species, found north of 40°N in the Pacific and western Atlantic (including the Gulf of Maine, the Gulf of St. Lawrence, and the Bay of Fundy) and north of 50°N in the eastern part of the Atlantic in shelf waters. Shen (1966) compiled detailed records of distributions in the Atlantic north of 50°N, including much of the inshore areas and the northern seas to 80°N.

Thysanoessa inermis inhabits the Fundy region throughout the year, the population center being in the Grand Manan Basin area. As mentioned earlier, specimens occurring in the Quoddy Region are part of the Fundy population. This species exemplifies the tremendous variability in seasonal and annual abundance in the Quoddy area (Table 1). For example, during 1971, *Th. inermis* was abundant in all months except January and February. In 1972, it was abundant only in spring and summer months. In 1973, 1974, and 1975 it was either absent or occurred only in small numbers during most months. Thus the appearance and disappearance of euphausiids in Passamaquoddy Bay were generally rapid and sporadic (Kulka and Corey 1978).

Thysanoessa inermis in the Fundy-Quoddy region has a life span of 2 yr. Spawning occurs at the end of the first and second years from March to July. This species occurs in two forms which are related to stages of the life cycle. Morphological variations occur in the shape of the eye, the length of the second thoracic leg, body shape, and mandibular structure. The *neglecta* form (first year juvenile animals) has elongated second thoracic appendages and constricted eyes, whereas the *inermis* form (second year adult animals) has round eyes and uniform thoracic legs. These changes are thought to be related to a change in niche requirements. The juveniles or *neglecta* form occur in the upper water column and the adult or *inermis* form much deeper in the water column (Kulka and Corey 1978).

Einarsson (1945) provides excellent keys to the eggs, larval stages, and adults of the North Atlantic euphausiids.

Amphipoda — Four species of amphipods, *Parathemisto gaudichaudi, Hyperia galba, Calliopius laeviusculus*, and *Monoculides edwardsi*, occur from time to time in zooplankton in the Quoddy Region (Table 1), and particularly in the Fundy waters adjacent to Passamaquoddy Bay. Of these, *P. gaudichaudi* is a truly pelagic species and *Hyperia galba* is found in the jellyfish, *Aurelia aurita*. The other two species are epibenthic and pelagic.

Parathemisto gaudichaudi belongs to the family Hyperiidae and is a polymorphic species. It tends to exist in two extreme forms, *bispinosa* and *compressa*, with all possible intermediate variations occuring. Also, until 1974 it was thought that *P. gaudichaudi* and *P. gracilipes* were two different species, the former a neritic species and the latter an oceanic species. However, Sheader and Evans (1974) showed that they were in fact one species, with *P. gaudichaudi* taking precedence. The full range of morphological characteristics in the *bispinosa-compressa* condition is not seen until the animals are greater than 10 mm. The *P. gracilipes* form matures at 3–14 mm, whereas the *P. gaudichaudi* form matures at 7–35 mm. In the Gulf of Maine, *P. gaudichaudi* breeds from February to October, with a summer peak (Bigelow 1926).

Parathemisto gaudichaudi in the western North Atlantic ranges from the Strait of Belle Isle to the Gulf of Maine. It is relatively common throughout the Gulf of Maine and Scotian Shelf waters outside the 100-m depth contour line (Bigelow 1926; Fish and Johnson 1937). Its distribution within the Fundy–Quoddy region varies seasonally and annually, and these animals are probably part of a population with the center of concentration in the Gulf of Maine and over the Scotian shelf. As a result *P. gaudichaudi* may or may not occur in zooplankton in the Quoddy region.

Parathemisto gaudichaudi is an opportunistic feeder, preying on a wide range of zooplankton including copepods, decapod larvae, euphausiids, chaetognaths, and also larval fish such as herring and sand lance (Sheader and Evans 1975).

Hyperia galba is found in association with the jellyfish, *Aurelia aurita* and therefore occurs only during late summer (Table 1).

Monoculodes edwardsi belongs to the family Oedicerotidae and is about 9 mm long at maturity. It is an epibenthic species, inhabiting fine sand to muddy sand and ranging from the Gulf of St. Lawrence to northern Florida and the Gulf of Mexico at depths less than 75 m. *Monoculodes edwardsi* ranges from truly marine to oligohaline brackish environments. It has an annual life cycle with ovigerous females occuring from May to September. Each female produces several broods (Bousfield 1973).

Monoculodes edwardsi is common in certain areas of the Bay of Fundy (e.g. Grand Manan Channel, off the mouth of the St. John River Estuary, and the upper regions of the Bay of Fundy; personal observation). It is not common in Passamaquoddy Bay but frequently occurs immediately outside, in the Grand Manan Channel.

Calliopius laeviusculus belongs to the family Calliopiidae and ranges from Labrador to New Jersey. It is both epibenthic and pelagic (Bousfield 1973). It is common on floating seaweed (M. J. Dadswell, personal communication) and has been found sporadically during summer and fall in the passages of the Quoddy area (Table 1).

Excellent references for keys and descriptions of these amphipods can be found in Sheader and Evans (1974), Bousfield (1973), and Sars (1895).

Cumacea — Cumacea are infaunal, detrital-feeding, benthic species which undertake diurnal vertical migrations, even in shallow waters. Many species have actually been taken in surface hauls during periods of darkness (Russell 1925; Corey 1970). As a result, these peracaridans are frequently caught in plankton nets. They are seldom obtained in large numbers. The species most frequently occurring in the plankton are *Diastylis sculpta*, from shallow waters, and *D. quadrispinosa*, from deep waters. Four other species — *Petalosaraia declivis*, *Campylaspis rubricunda*, *Leptostylis ampullacea*, and *Eudorella* sp. — are much smaller in size and are caught only infrequently. All six species inhabit the Quoddy Region the year round.

Diastylis sculpta and *Eudorella* sp. are both relatively common shallow-water species. *Diastylis sculpta* inhabits sand and sandy mud substrates of 7–65 m depths, from the Gulf of St. Lawrence to New Jersey (Watling 1979). In Passamaquoddy Bay they are most abundant between 10 and 30 m. *Diastylis sculpta* produces two generations per year in the Quoddy Region. The females of the overwintering generation release their young from mid-July to late August and then die. These young grow rapidly over the summer, and mature and release young in November. The overwintering and summer generations have life spans of 12 and 5 mo, respectively (Corey 1976).

Diastylis quadrispinosa is by far the most common of the deeper water Cumacea in the Quoddy area. Gravid females have been taken during the winter months (personal observation).

An excellent key for the Cumacea inhabiting this area is given in Watling (1979).

Mysidacea — The mysids *Erthrops erythropthalma*, *Neomysis americana*, and *Mysis stenolepis* are generally considered to be epibenthic and inhabit Passamaquoddy Bay the year round. As in the case of the cumaceans, these animals are detrital-feeders and also undergo a vertical migration, especially *N. americana* which is frequently taken at the surface just after sunset and just before sunrise (Herman 1963).

Erythrops erythropthalma (so named because of its brilliant red eyes) is a relatively small mysid (8 mm) and occurs only rarely in plankton samples.

Neomysis americana is slightly larger than *E. erythropthalma*, has black eyes, and inhabits coastal and estuarine waters from 1 to 250 m deep along the eastern coast of North America from Newfoundland to northern Florida (Williams et al. 1974). In Passamaquoddy Bay, *N. americana* inhabits mainly shallow water areas (0–15 m). It produces two generations per year. Breeding occurs from spring to early fall, and each female is capable of producing two or three broods (Pezzack and Corey 1979).

Mysis stenolepis is much larger (adults 25 mm), and inhabits coastal waters from the Gulf of St. Lawrence to New Jersey (Tattersall 1939). In Passamaquoddy Bay the young are released in very shallow water during the spring and grow rapidly during summer. In the fall, the young adults move out to deeper waters where they mature and breed. The males die soon after breeding but the females survive and move into shallow waters in the spring to release young. The life span is about 1 yr (Amaratunga and Corey 1975). As a result of this seasonal horizontal migration this species occurs only in very deep plankton hauls (i.e. near bottom) during the winter and conversely only in very shallow waters during the summer.

Decapoda — The three species *Crangon septemspinosa, Pandalus montagui*, and *Spirontocaris* sp. are all shrimps which live in or near the substratum. They are included in this chapter because if nets are initially set close to the bottom during darkness these shrimps are frequently obtained. *C. septemspinosa* may be taken in both shallow and deep waters, whereas *P. montagui* and *Spirontocaris* are generally found only in deeper waters. All three species occur in the Quoddy Region throughout the year. Quantitative seasonal changes have not yet been recorded.

CHAETOGNATHA

Chaetognatha (arrow worms) are true zooplankton and are frequently taken in large numbers in plankton samples. In fact, in many areas they are numerically second only to the copepods. Chaetognaths can be used as water mass indicators (Russell 1935). Although a total of 8 species have been recorded from the Bay of Fundy, only *Sagitta elegans* occurs within the Quoddy Region (Hurley et al. in preparation).

Sagitta elegans is a neritic species typical of the upper 100–150 m in arctic and subarctic regions of both the Atlantic and Pacific oceans. It is typical of cold water and ranges from the entire continental shelf of the Arctic Archipelago south in the western Atlantic to approximately 39°N (Alvarino 1965).

Sagitta elegans is an important carnivore, feeding on zooplankton such as copepods and larval herring. *S. elegans* in turn becomes food for juvenile and adult herring (Hardy 1924).

The specimens of *S. elegans* found within the Quoddy Region are probably part of a large population inhabiting the Bay of Fundy. One is therefore more apt to find *S. elegans* in the Passages than within Passamaquoddy Bay proper. Legaré and Maclellan (1960) found adults to be present throughout the year but juveniles only in summer.

The eggs (round, transparent, 0.2mm diameter) are released singly and float near the surface. The life history of *S. elegans* varies greatly throughout its range, from the Arctic where it has a life span of 2 yr and an alternating breeding cycle consisting of two distinct breeding populations (Dunbar 1962), to the English Channel off Plymouth, where it produces 4 or 5 broods annually from February to September at intervals of 2 or 3 mo (Russell 1933). In the Quoddy Region, *S. elegans* has only one major breeding season, in the spring (Hurley and Corey in preparation).

CTENOPHORA

Ctenophores are among the most characteristic of the zooplankton. They are pelagic and very weak swimmers and are frequently found in large concentrations caused by current activity. Ctenophores are also carnivores feeding on zooplankton, utilizing their long tentacles to trap prey such as crab and oyster larvae, copepods, fish eggs, and chaetognaths. The ctenophore, *Pleurobrachia pileus* is not endemic to the Quoddy Region and is generally found in late summer, fall, and winter (Table 1).

CNIDARIA

Aurelia aurita occurs seasonally within Passamaquoddy Bay. This jellyfish occurs in large numbers in surface waters during late summer, and declines rapidly in numbers during the fall. These animals occur in such heavy concentrations that they clog up or fill a plankton net.

A siphonophore, *Nanomia cara* (syn. *Stephanomia cara*) occurs commonly in the winter and spring. Greatest abundance occurs in the Passages outside Passamaquoddy Bay (Legaré and Maclellan 1960).

ANNELIDA

The pelagic polychaete, *Tomopteris helgolandica* (Syn. *T. catherina*) occurs sporadically in small numbers in the Bay of Fundy and tends to be more common during the winter months. Like chaetognaths and the ctenophores, tomopterids are transparent and carnivorous, feeding on small zooplankton, including young fish.

MOLLUSCA

Certain pelagic gastropods, called pteropods or sea-butterflies, are epipelagic, oceanic animals. Two species, *Clione limacina* and *Limacina retroversa*, may be found in the Quoddy and adjacent Fundy waters. The relative abundance of both species varies greatly with time and space and in fact may be completely absent from these waters for a year or more. Centers of populations lie outside the Bay of Fundy area.

Clione limacina, a gymnosome, is a naked carnivore which feeds mainly on other pteropods (thecosomes), protozoans, and crustacean larvae (Nicol 1969). *Clione limacina* is found sporadically in the Quoddy Region, with the numbers fluctuating greatly seasonally and from year to year. They are usually found only in small numbers and tend to occur more frequently in spring and summer.

Limacina retroversa, a thecosome, is much smaller than *Clione limacina* and has a calcareous shell. *Limacina retroversa* is herbivorous, feeding on phytoplankton, and forms very dense swarms seasonally. This pteropod is a boreal-to-temperate species, widely distributed in the Atlantic. As mentioned earlier, *L. retroversa* is a very sporadic immigrant into the Bay of Fundy and hence into the Quoddy Region. There appears to be some disagreement as to the status of this pteropod in the Gulf of Maine. Bigelow (1926) states that it is "one of the most characteristic of the permanent pelagic inhabitants of the Gulf of Maine." However Redfield (1939) found that it was not endemic, but rather originated offshore.

Summary and General Discussion

The only species of larger zooplankton endemic to the Quoddy Region are the benthic or epibenthic animals, which through diurnal vertical migration become part of the nocturnal zooplankton. These include all the cumaceans, mysids, and decapods described herein. Two species of amphipods, *Monoculodes edwardsi* and *Calliopius laevisculus*, are generally considered to be both pelagic and epibenthic (Bousfield 1973). The euphausiids, pteropods, chaetognath, and cnidarians are members of the holozooplankton and are not endemic to the Quoddy Region. The two species of euphausiids, *Meganyctiphanes norvegica* and *Thysanoessa inermis*, and the only species of chaetognath, *Sagitta elegans*, are all endemic to the Bay of Fundy and spasmodically invade the Quoddy area, being more abundant in the outer parts and the passages. Although these three species are endemic to the Bay of Fundy, their distribution is widespread over the shelf and they are considered to be boreo-arctic (Kielhorn 1952). *Parathemisto gaudichaudi, Hyperia galba, Clione limacina*, and *Limacina retroversa* are also boreo-arctic species whereas *Pleurobrachia pileus* and *Tomopteris helgolandica* are boreal species of a more southern range. None of these six species have a permanent population in the Fundy area: they are periodically brought into the area through the Gulf of Maine or over the Scotian Shelf.

It is interesting to note that only a very small percentage of holozooplankton species occurring in the Bay of Fundy actually penetrate into the Quoddy Region. For example, only 2 of the 7 species of euphausiids and only 1 of the 8 species of chaetognaths occur within the Quoddy area (Kulka et al. in preparation; Hurley et al. 1982). Also, members of the holozooplankton are virtually absent within Passamaquoddy Bay. These observations, along with the 20% decrease in abundance of zooplankton from the outer Quoddy area into Passamaquoddy Bay itself (Legaré and Maclellan 1960), suggest a barrier of some sort. This barrier is caused by a combination of factors: the very slow mixing of waters between the Bay of Fundy and Passamaquoddy Bay, as described by Watson (1936); the shifting of species in and out of the Passages concurrently with the ebb and flow of the tides; and lower salinity conditions within the bay (annual range 21.91–32.78%, Trites 1962). Analyses of the stomach contents of herring, which are opportunistic feeders, confirm the above findings: herring within Passamaquoddy Bay feed only on neritic species, whereas herring from the passages feed on offshore species (Battle et al. 1936).

Two different types of surface swarming by the larger zooplankton have been recorded in the Quoddy Region. The amphipod, *Calliopius laeviusculus*, and the mysid, *Neomysis americana* are regularly found at the surface during their respective breeding seasons (Fish and Johnson 1937). A second type of surface swarming is probably caused by tidal currents in the passages. Swarms of copepods (*Calanus*) and euphausiids (chiefly *Meganyctiphanes norvegica*) have been recorded frequently during the summer in the outer parts of the three passages (Battle et al. 1936; Fish and Johnson 1937; Huntsman 1952; Kulka and Corey 1978). The importance of such surface swarms lies in the fact that zooplankton which would normally be in deeper waters, especially during the day, are brought to the surface and become available as food for herring (Battle et al. 1936) and sea birds (Braune and Gaskin in press). In fact, during the summer months it is not uncommon to see thousands of sea birds actively feeding on the surface in Head Harbour Passage (D. E. Gaskin, personal communication).

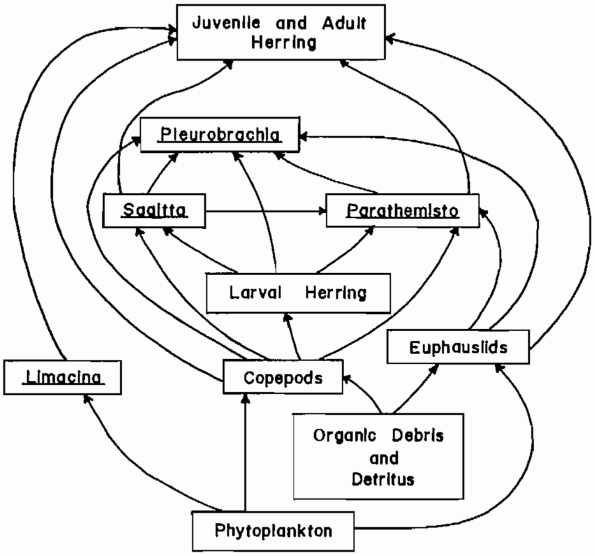

FIG. 1. A diagrammatic representation of a possible, generalized food web in the Quoddy Region centered around herring (based on Hardy 1924; Battle et al. 1936; Mauchline and Fisher 1969; and Sheader and Evans 1975).

The vertical distribution of larger holozooplankton within the water column has not been studied extensively. Legaré and Maclellan (1960) found that *Sagitta elegans* was abundant at all depths but "much more so at 100 m." They also found that euphausiids, amphipods, and herring larvae were fairly uniformly distributed throughout the water column. Regarding the euphausiids, Legaré and Maclellan (1960) did not delineate the stage of life history. It is probable that what occurred is that described by Kulka et al. (in preparation) — that there is an otogenic depth distribution in euphausiids, with the youngest being nearer the surface and the older animals being nearer the bottom. Both the euphausiids and the chaetognaths undergo an active, diurnal vertical migration (Kulka et al., 1982; Hurley et al., in preparation). This migration, plus that of many epibenthic and benthic species causes great variability in the daily component structure of the zooplankton community, which is more diversified at night.

Research on trophic and feeding interrelationships within the zooplankton community in the Quoddy Region is very much at the qualitative stage. The only thorough studies on feeding are for herring (Battle et al. 1936) and sea birds (Braune and Gaskin in press).

As most of our knowledge is centered around the food and feeding of herring, a diagrammatic generalized representation of a food web for the herring in the Quoddy Region is shown in Fig. 1. The chief predators on larval herring are *Sagitta elegans, Parathemisto gaudichaudi*, and *Pleurobrachia pileus*. The first two animals in turn become food for juvenile and adult herring. The chief competitor for adult herring food would seem to be *Pleurobrachia pileus*. Further research is needed to elucidate the trophic importance of the nocturnal zooplankton.

There is a seasonal variation in the zooplankton portion of the diet of some demersal fish inhabiting the passages of the Quoddy Region. This is coincidental with the expansion and contraction of the Bay of Fundy euphausiid populations and the seasonal horizontal movement from shallow to deep waters of the large mysid, *Mysis stenolepis*. Euphausiids are commonly found in the stomachs of demersal fish during summer, whereas *M. stenolepis* is eaten during winter (Tyler 1972).

In conclusion, the community structure of the larger zooplankton varies daily, seasonally, annually, and from location to location within the Quoddy area. It is very dependent on hydrographic conditions and on species present in the adjacent Bay of Fundy, Gulf of Maine, and Scotian Shelf waters.

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CHAPTER 13

Microzooplankton of the Quoddy Region

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Introduction

The term microzooplankton has no precise definition; Bougis (1976) presents some useful schemes for size ranking of planktonic organisms. Without specifying size too precisely, the organisms that form the subject of this chapter fall predominantly in the range of 100 μm to 10 mm, thus spanning two orders of magnitude in size. Excluded are the phytoplankton (Chapter 11) and the macrozooplankton > 1 cm (Chapter 12). For a general introduction to marine plankton, the practical guide by Newell and Newell (1963) is excellent and Smith (1977) is also useful. The general treatments of plankton ecology by Bougis (1976) and Raymont (1963) are highly recommended, and for more description, Hardy (1956). Detailed taxonomic references may be found in these texts.

The microzooplankton of the Quoddy Region has received little attention in recent years (see Legaré and MacLellan 1960 for list of older studies). The most comprehensive studies of the area are still those by Fish and Johnson (1937) and Legaré and MacLellan (1960) which deal with both micro- and macrozooplankton. The extensive report of Bigelow (1926) on the nearby Gulf of Maine is also indispensable.

The Bay of Fundy microzooplankton is a rich if somewhat unpredictable mixture of neritic, oceanic, and intermediate species including arctic, boreal, and southern forms. Several of these reach their limit of distribution in the Quoddy area. Like the macrozooplankton (Chapter 12), the microzooplankton of Passamaquoddy Bay is less diverse than that of the Bay of Fundy. However, unlike the macrozooplankton, several species of microzooplankton have substantial reproducing populations in Passamaquoddy Bay, and the populations of some estuarine species are virtually limited to the bay itself.

The largest fraction of the holozooplankton (the permanent members of the animal plankton) of the oceans consists of copepods. This is generally true also in the Quoddy Region, and the Copepoda will receive the greatest attention in this chapter. However, in order to at least give honorable mention to those planktonic organisms not covered elsewhere in this volume, the other groups of the microzooplankton, both holoplanktonic and meroplanktonic (temporary members of the plankton, as larvae), will be discussed.

Collecting Methods and Preservation Techniques

Although a variety of towed body samplers and multiple opening and closing nets is available (e.g. Longhurst et al. 1966; Sameoto et al. 1977), and although new sampling techniques are constantly being developed, the conical plankton net is still the classical method for collecting zooplankton. The UNESCO publications on zooplankton sampling (UNESCO 1968) and on fixation and preservation (UNESCO 1976) should be carefully consulted by any serious planktologist before planning collections. They provide a wealth of information on sampling design, field techniques, loss of organisms through various mesh sizes, filtration performance, and net avoidance.

For most purposes a .5–m SCOR pattern net is the most versatile gear; it has an initial filtration efficiency, when new, of about 85%, and for short tows probably filters at over 50% efficiency. Vertical, horizontal, or oblique hauls may be used for collecting, and abundances can be expressed in terms of organisms per m^3 or per m^2 for a specified depth of tow.

A towing speed of about .5 m/sec is desirable for vertical hauls, but for horizontal hauls towing speeds of up to 2 m/sec may be necessary for coarser mesh nets, to maintain the open cone configuration of the net and to achieve the highest filtration efficiency (Roff and Lam unpublished data). Towing speeds above 2 m/sec are not desirable since a plateau of filtration efficiency has been reached and higher speeds merely increase filtration pressure and hence strain on the gear.

The mesh of plankton nets varies from 50 μm to about 250 μm. For many purposes a 65-μm net is a useful lower size; this captures most of the larger copepods quite well compared to a coarser mesh, retains the younger developmental stages (including early nauplii), and also captures cladocera and tintinnids. If smaller species or early developmental stages are not required, a 200-μm mesh is adequate; this will capture most organisms larger than about copepodite stage III of *Pseudocalanus minutus*. Dimensions, patterns, and suggested suppliers for a standard SCOR .5-m net are available from the author on request.

Duration and depth of tow will depend on requirements. If live specimens are required, then tow duration must be kept short. A 5-min tow in Passamaquoddy Bay may be packed with *Acartia* and *Coscinodiscus* during August. For quantitative work a calibrated flow meter is necessary to calculate net filtration efficiency under field conditions.

Preservation techniques for marine zooplankton are fully covered in UNESCO (1976). Despite various alternatives a solution of 4% formaldehyde in sea water is still widely regarded as "the best reagent as a fixative and as a preservative for taxonomic and morphological characters of mixed marine zooplankton" (Steedman 1976). The most severe problems with formaldehyde arise because of its acidity, which dissolves skeletal calcium carbonate; if buffering is desired, $CaCO_3$ powder is most effective. However, neutralization is not necessary for most specimens, provided only external morphological characters are required. If loss of color, wax esters, etc. is not important, collections can be left in 4% formaldehyde indefinitely. If biomass estimates are to be made these should be done immediately on fresh specimens, after freeze-drying, or after about 2 wk stabilization if fixed in 1–2% formaldehyde (UNESCO 1976).

For taxonomic purposes, examination under a binocular microscope up to 80 × is generally sufficient once the species are known. For initial correct identification, dissection of legs or other body parts may be necessary, or the whole specimen may be mounted. A water miscible medium, such as Turtox low viscosity medium containing acid fuchsin, rapidly stains the appendages and makes detailed examination of setation easier. Examination of whole specimens under an inverted compound microscope may overcome the necessity for dissection of appendages.

Fine taxonomic work on the microcrustacea requires patience and practice and is best learned directly from someone familiar with the techniques. References for identification of the various planktonic groups include: Brodsky (1967), Newell and Newell (1963), Owre and Foyo (1967), Roff (1978), Sars (1903, 1918), and Wilson (1932). References to the extensive keys of the *Fiches d'identification de Zooplancton* published by ICES will be found in Newell and Newell (1963) and Roff (1978).

Groups of the Microzooplankton

MEROPLANKTONIC FORMS

With the exception of the Polychaeta, little effort has been made to identify the larval forms of the zoobenthos of the Quoddy Region, which is surprising because several species of larval fish may rely heavily on meroplanktonic forms as a food source. The Polychaete larvae (Fig. 1) of the area are relatively well known, having been described by Lacalli (1980), who includes 30 species from 17 families.

Polychaete larvae are usually encountered in the plankton from March to September, with most species liberating eggs in May and June. The basic larval form is the trochophore (Fig. 1), but this may be suppressed in favor of a more advanced worm-like larva, especially where yolky eggs are laid (Lacalli 1980) and the larva is lecithotrophic. For further details on this group see Lacalli (1980); the macroscopic planktonic polychaetes have been dealt with in Chapter 12.

Many species of Mollusca temporarily inhabit the planktonic world as veliger larvae (Fig. 2). Several species of intertidal and subtidal molluscs have been recorded in the Quoddy area (Fish and Johnson 1937; Legaré and MacLellan 1960), including *Mytilus, Placopecten,* and *Littorina*. These were chiefly observed during summer and fall. To identify the major local species use Sullivan (1948). The macroscopic species of the plankton are dealt with in Chapter 12.

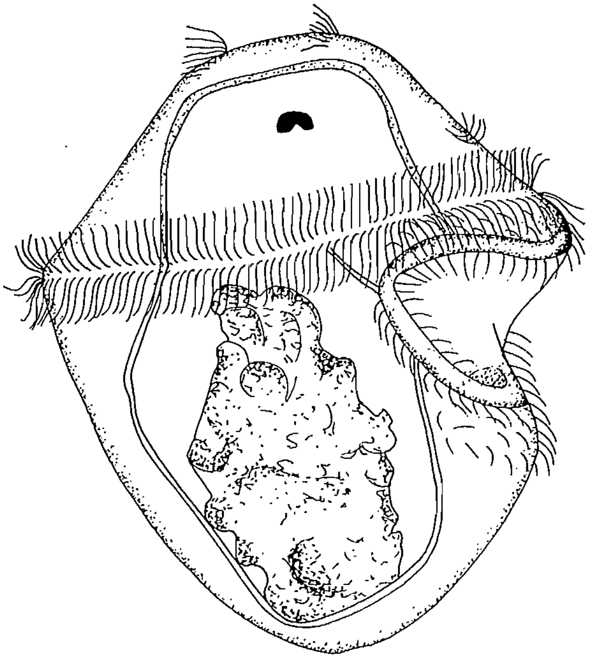

FIG. 1. Polychaete larva — trochophore of *Harmothoe imbricata*.

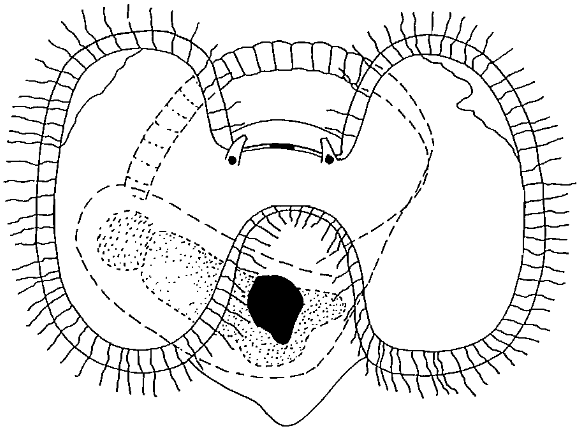

FIG. 2. Molluscan larva — veliger of *Littorina littorea*.

Almost all the Echinodermata have planktonic larvae, but after the dipleurula stage a confusing diversity of larval types is produced, with each class of echinoderms having a characteristic type (see Newell and Newell 1963). In the Quoddy region several common species are represented in the plankton with *Asterias vulgaris* (Fig. 3)

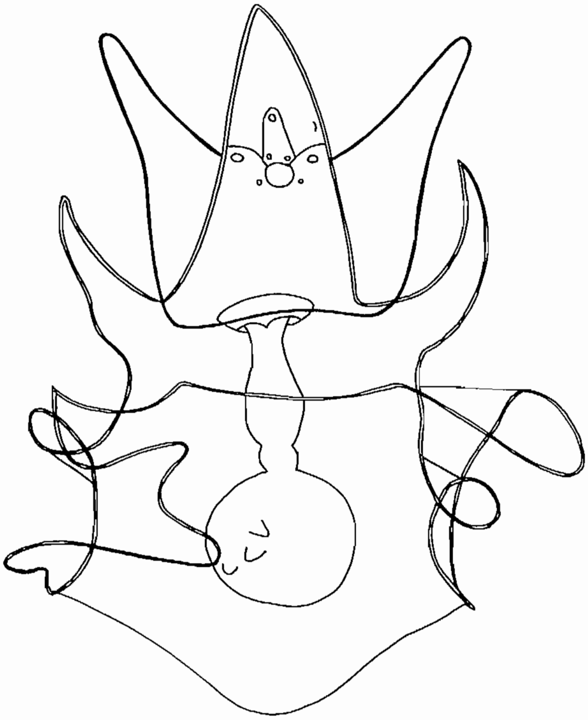

FIG. 3. Echinoderm larva — bipinnaria of *Asterias vulgaris*.

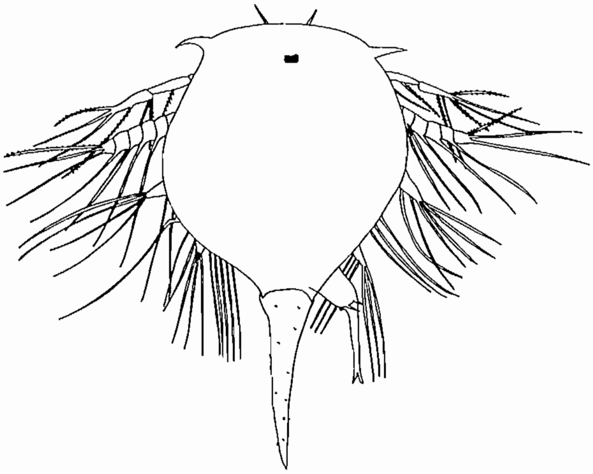

FIG. 4. Crustacean larva — nauplius of *Balanus balanoides*.

larvae appearing in the spring and larvae of *Cucumaria frondosa* from May to September.

Several members of the class Crustacea which are benthic as adults produce planktonic larvae. Barnacle larvae (order Thoracica) are common in the area, with *Balanus balanoides* (Fig. 4) appearing in the spring and *Balanus crenatus* in late summer and early fall (Fish and Johnson 1937; Bousefield, 1954; Legaré and MacLellan 1960). *Balanus improvisus* larvae have also been recorded from the Bay of Fundy (Bousefield 1954).

In the Macrura, lobster larvae (*Homarus americanus*) have been observed in Passamaquoddy Bay (Wilder 1950) but they are rare since the centers of abundance of the adult populations lie well outside the Quoddy Region. Anomuran larvae of the hermit crab *Pagurus* have been recorded in the area (Fish and Johnson 1937). In fact during the late summer, eggs of berried females may readily hatch in the laboratory. The older records of larval Brachyura (the true crabs, Fig. 5) must be viewed with some reservation. Good descriptions from laboratory-reared specimens have only recently become available, e.g. for *Cancer borealis* and *C. irroratus* (rock crab and Jonah crab) (Sastry 1977a,b) and for the two *Hyas* species *H. araneus* and *H. coarctatus* (Christiansen 1973).

Thirty-five taxa of larval Brachyura (as zoeas and megalopas) have recently been described from the Nova Scotian shelf and outer Bay of Fundy (Roff et al. 1983). These species can be divided into local indigenous species and southern imports. Recurrent group analysis of several thousand samples (Roff, unpublished data) shows that there is little overlap of these two groups. The Quoddy Region represents the northern inshore limit of distribution for the southern imports, although they are carried further north at the edge of the Scotian Shelf. The southern import group includes larvae of swimming crabs (family Portunidae) and members of the families Calappidae, Ocypodidae, etc. which are not known to occur in Canadian Atlantic waters. The zoeas or megalopas most likely to be encountered locally are *Cancer borealis* and *C. irroratus*, the two *Hyas* spp. and, especially closer to shore, *Carcinus maenas* (Fig. 5).

Among the minor phyla, larva of the Phylum Phoronidae (Fig. 6) (Wiley 1915) and Ectoprocta (≡Bryozoa, Fig. 7) are known to occur in the Quoddy area, but they have not received recent attention. In the Hemichordata a tornaria larva is usually produced but the local *Saccoglossus*, like its British counterpart, may simply produce a lecithotrophic larvae which rarely, if ever, appears in the plankton (Newell and Newell 1963).

NON-CRUSTACEAN HOLOZOOPLANKTON

Although the Pyrrhophyta and other unicellular flagellate groups are often coveted by zoologists they are more appropriately considered with the phytoplankton (see Chapter 11). The remaining important groups of single-celled organisms of the plankton (the Protozoa) include the Foraminifera, Radiolaria, Oligotricha, and Tintinnida. With the exception of Johansen (1976) these groups on the east coast have received little recent attention.

This is disappointing, especially in the face of mounting evidence that, for example, the Tintinnida may be locally significant grazers of the smaller phytoflagellates, and may contribute significantly to local nutrient regeneration (e.g. Antia et al. 1980). In the Quoddy area several species of Tintinnids, including species of the genera *Parafavella* (Jermolajev 1958) and *Tintinopsis*, occur commonly, and with practice they can be readily identified from Marshall (1969).

In the phylum Rotifera a few species have been recorded from the Quoddy area (Fish and Johnson 1937),

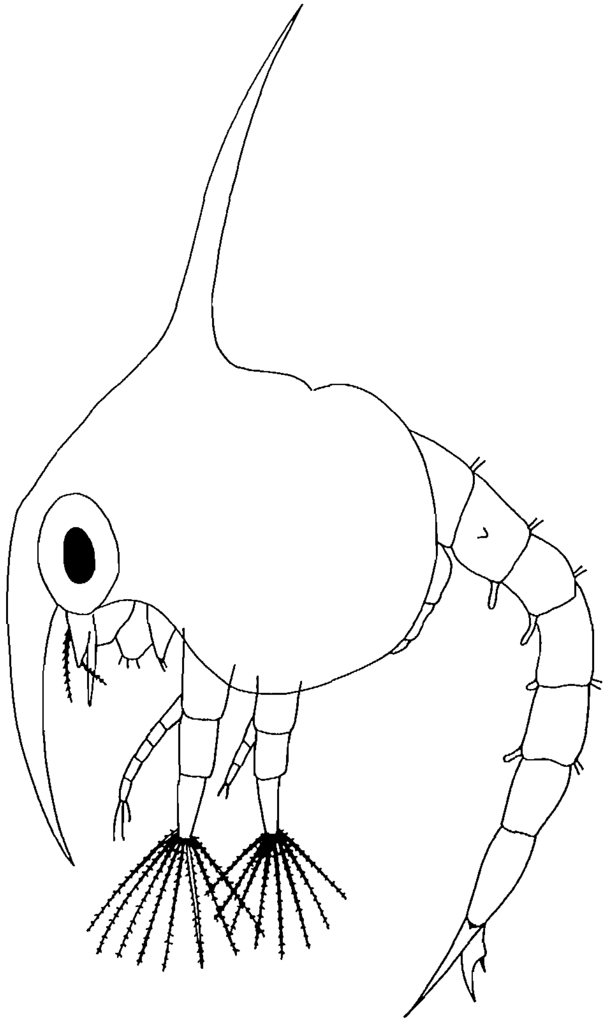

FIG. 5. Crustacean larva — zoea of *Carcinus maenas*.

although this is not a dominant group ecologically in marine waters.

The appendicularians (class Copelata (≡Larvacea) of the Phylum Urochordata) are a group of small planktonic tunicates which retain the dorsal notochord and tail of larval tunicates. These animals build a transparent house enclosing a fine filter through which water is drawn by tail movements. In plankton hauls the animal usually becomes separated from its house.

In the Quoddy Region, two species may be encountered — *Fritillaria borealis* and *Oikopleura dioica* (Fig. 8) (Fish and Johnson 1937) — although several other species are commonly observed off the eastern Nova Scotia coast.

The remaining non-crustacean holozooplankton are macroscopic and are covered in Chapter 14.

THE MICROCRUSTACEA

Small crustaceans are the dominant metazoan organisms of the plankton. A minor component is provided by the water-fleas (sub-order Cladocera) comprising locally two genera and up to five species. As a group the cladocerans are much more abundant and diverse in the fresh waters of North America. The two commonest species in the Quoddy Region, *Evadne nordmanni* (Fig. 9) and *Podon leucarti* (Fig. 10), are both easily recognizable from their single compound eye, large antennae, and phyllopodous swimming limbs (see Newell and Newell 1963). They are very common in Passamaquoddy Bay during the summer and early fall; they are generally captured by any plankton haul at or near the surface, often carrying eggs in the dorsal brood pouch. Both species are members of the main Bay of Fundy recurrent group (Fig. 13 and 14).

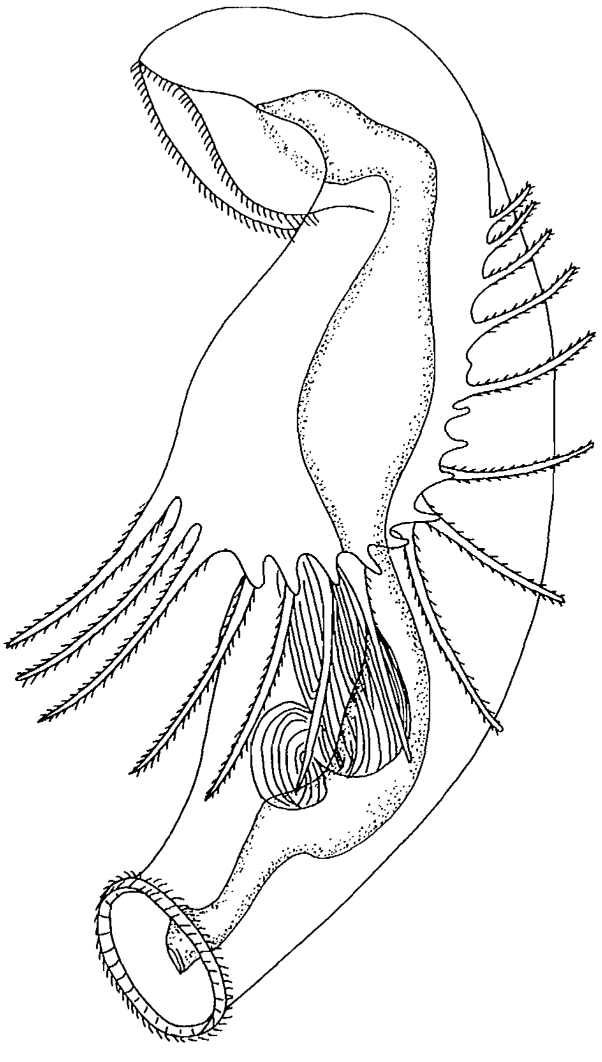

FIG. 6. Phoronid larva — actinotroch of *Phoronis* spp.

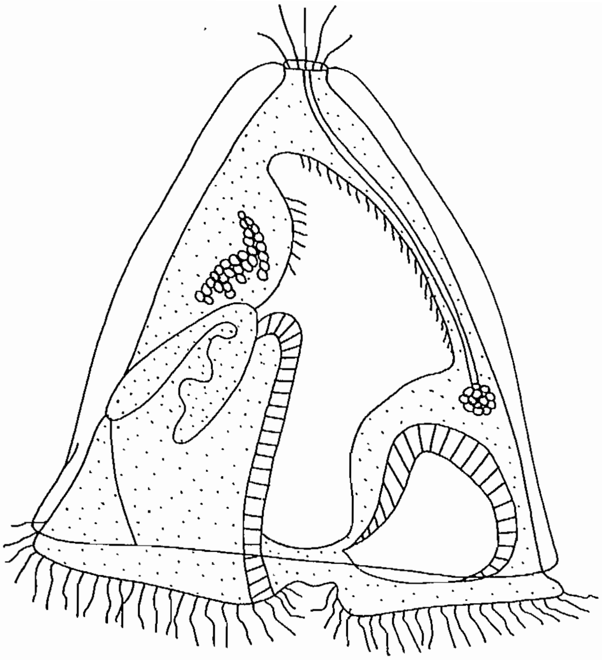

Fig. 7. Ectoproct larva — cyphonautes of *Membranipora* spp.

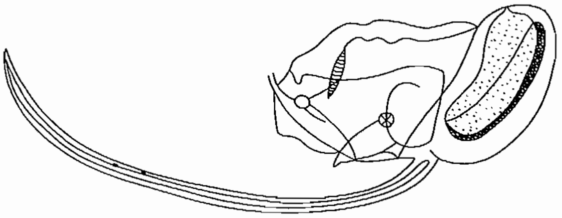

Fig 8. Appendicularian — *Oikopleura dioica*.

A second species of *Evadne, E. spinifera*, occurs commonly outside Passamaquoddy Bay where two further species of *Podon, P. intermedius* and *P. polyphemoides*, have also been recorded (Fish and Johnson 1937). The cladocera form an important food resource for larval neustonic fish (Coates and Roff, unpublished data).

Although the Ostracoda may at times comprise a significant fraction of the oceanic zooplankton (Angel and Fasham 1975) they are rarely abundant in coastal waters. The remaining group of the microcrustacea, the copepods, usually comprise the bulk of the metazoan zooplankton.

Biology and Distribution of the Copepoda

Copepods dominate the zooplankton; one species, *Calanus finmarchicus* (*sensu latu*) (Fig. 11), is a prime candidate for being the most numerically abundant metazoan in the world (Russell-Hunter 1970). Copepods of Atlantic Canada range in size from under 1 mm to about 1 cm in length. The body consists of the metasome (fused head and "thorax") which bears a single median nauplius eye and the feeding and swimming appendages, and the smaller posterior urosome ("abdomen").

There are six naupliar and six copepodite stages in a copepod life cycle, the terminal moult producing the adult copepod. Many boreal species overwinter as late copepodites or adults. At each moult, new appendages or buds are added or the existing appendages are modified progressively towards the adult condition. The process is gradual, and a major metamorphosis only occurs between the sixth naupliar stage and the first copepodite. Copepods are dioecious; the sex ratio varies considerably between species, with male numbers ranging from the same as to much fewer than females. After fertilization the female either liberates eggs singly or retains them in egg sacs attached to the urosome.

For details on life cycles of representative species, and as a general introduction to copepod anatomy and biology, see the extensive accounts by Marshall and Orr (1972) and Corkett and McLaren (1978). The taxonomy and identification of the group is not easy for the beginner, but the introductory treatment by Newell and Newell (1963) is recommended. Within the class Copepoda seven orders are recognized; four of these (e.g. the Monstrilloida, occasionally reported from the area) are parasitic as larvae or adults and will not be considered here.

Of the three free-living orders, the Harpacticoida are mainly benthic although one species, *Microsetella norvegica*, is often encountered, especially in areas of bottom turbulence or when a net strikes bottom. The order Cyclopoida is represented locally by five species. With the exception of *Oithona similis* (Fig. 12) these are southern forms; *O. similis* may be locally very abundant. Of the 48 species of Copepods listed in Table 1, the rest are Calanoids.

Although the Cyclopoida have long been recognized as predators, the Calanoida were often assumed to be entirely herbivorous. Several feeding studies have shown that many calanoid copepods are also predators and many

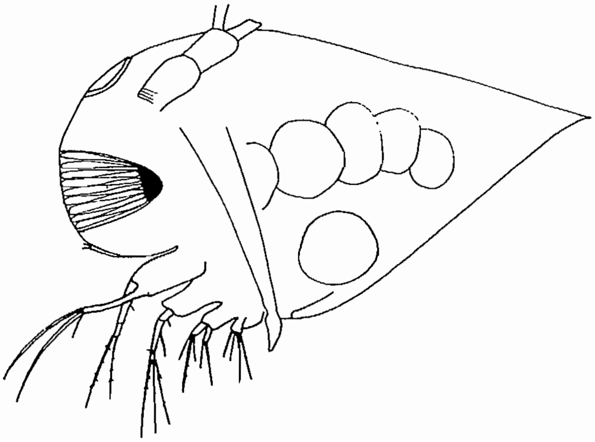

Fig. 9. The cladoceran *Evadne nordmanni*.

FIG. 10. The cladoceran *Podon leucarti*.

more are facultative predators. The range and composition of food available to these organisms is thus extensive since it includes not only phytoplankton but detritus, protozoa, and other zooplankton as well.

There has been no local study of feeding, population dynamics, or production of the copepods, and these aspects will not be covered here. The recent reviews by Edmondson and Winberg (1971), Greze (1978) and Conover (1978) should be consulted for this purpose.

Although the total species list of Calanoid and Cyclopoid copepods for the Bay of Fundy is impressive (Table 1), the greatest diversity is contributed by the southern expatriates, and any one haul will contain only a few species. A range of 6–17 species per haul, from Passamaquoddy Bay to the outer Bay of Fundy, would not be unusual during the summer.

Marine plankton distributions are by nature continuous, and any attempt to categorize species distributions by sharp boundaries must fail at some point. A continuous description of ranges as proposed by Colebrook (1964) is preferable. However, it is possible to recognize broad zoogeographical affinities for species as presented in Table 1. For the sake of continuity, the classification system of Legaré and MacLellan (1960) has been adopted here, which divides the local fauna into the following groups: the meroplankton (see above ≡ Benthonic), Neritic (i.e. Boreal neritic), Boreal (Temperate and Northern Seas), Northern (Arctic) and Southern (i.e. Tropical and Subtropical).

Several species of the boreal group are in fact intermediate to various degrees between truly oceanic and neritic as noted by Colebrook (1964). Thus the major Nova Scotia shelf species — *Calanus finmarchicus, Paracalanus parvus, Pseudocalanus minutus, Centropages typicus,* and *Metridia lucens* — are neither truly neritic nor completely oceanic.

Some species are widespread (cosmopolitan), being found in deep water in the tropics and sub-tropics, but occurring closer to the surface in subarctic waters. Thus it may not be reasonable to assert latitude of origin or exclusive membership categories. Rather, it may be useful to

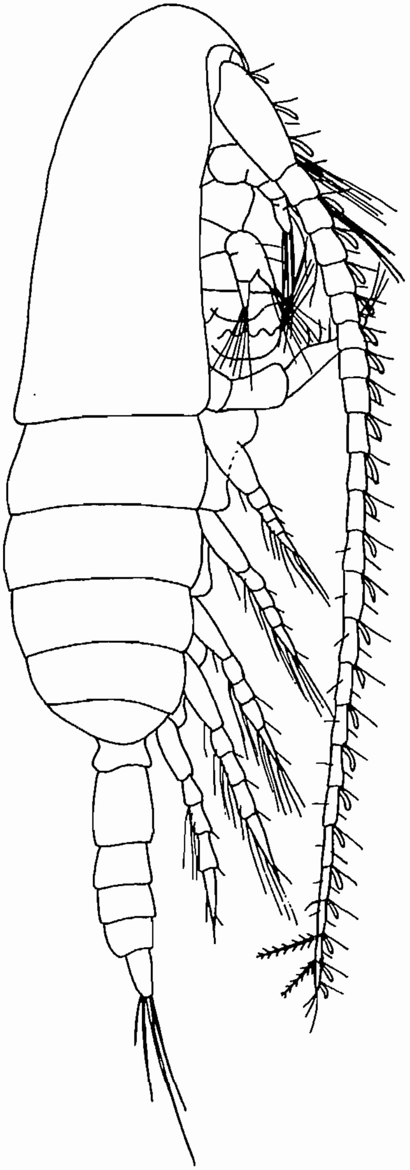

FIG. 11. The copepod *Calanus finmarchicus*.

TABLE 1. List of Copepoda (Calanoida and Cyclopodia) observed in the Quoddy Region, geographical range (No., northern; B, boreal; S, southern), and onshore–offshore range (E, estuarine, N, neritic, I, intermediate, O, oceanic; see Colebrook 1964). (From Roff 1978, unpublished data; Legaré and MacLellan 1960; and Shih et al. 1971).

Species	Authority	Geographical range	Onshore-offshore range
Acartia bifilosa	(Giesbrecht)	B	E, N
Acartia clausi	Giesbrecht	B	N
Acartia danae	Giesbrecht	S	
Acartia discaudata	Giesbrecht	B	N
Acartia longiremis	(Lilljeborg)	B	N
Acartia tonsa	Dana	B	E, N
Aetideus armatus	(Boeck)	S (Widespread)	
Anomalocera patersoni	Templeton	B	I
Calanus finmarchicus	(Gunnerus)	B (Widespread)	I
Calanus glacialis	Yashnov	No.	O
Calanus hyperboreus	Krøyer	No.	O
Calocalanus pavoninus	Farran	S	
Candacia armata	(Boeck)	S (Extends extensively into Boreal waters)	I
Centropages bradyi	Wheeler	S	O
Centropages hamatus	(Lilljeborg)	B	N
Centropages typicus	Krøyer	B	I
Clausocalanus arcuicornis	Dana	S	
Eucalanus elongatus	(Dana)	S	
Euchaeta norvegica	Boeck	No.	O
Euchirella rostrata	(Claus)	S	
Eurytemora americana	Williams	B	E, N
Eurytemora herdmani	Thompson & Scott	B	E, N
Eurytemora hirundoides	(Nordquist)	B	E, N
Gaidius tenuispinus	(G.O. Sars)	S (Widespread)	
Haloptilus longicornis	(Claus)	S (Widespread)	
Labidocera aestiva	Wheeler	B	
Lucicutia flavicornis	(Claus)	S	
Mecynocera clausil	I.C. Thompson	S	
Metridia longa	Lubbock	No.	O
Metridia lucens	Boeck	B	I
Microcalanus pusillus	G.O. Sars	No.	
Nanocalanus minor	(Claus)	S	
Oithona plumifera (C)	Baird	S	
Oithona similis (C)	Claus	B	
Oithona spinirostris[b] (C)	Claus	B	
Oncaea conifera (C)	Giesbrecht	S	
Oncaea venusta (C)	Philippi	S (Widespread)	
Paracalanus parvus	(Claus)	S, B	I
Pleuromamma borealis	(Dahl)	S	O
Pleuromamma robusta	(Dahl)	S, B (Widespread)	O
Pseudocalanus minutus	(Krøyer)	B	I
Pseudodiaptomus coronatus	Williams	B	E, N
Rhincalanus nasutus	Giesbrecht	S	O
Sapphirina gemma (C)	Dana	S	
Scolecithricella minor	(Brady)	No.	
Scolecithrix danae	(Lubbock)	S	
Temora longicornis	(O.F. Muller)	B	N, I
Temora stylifera	(Dana)	S	
Tortanus discaudatus	(Thompson & Scott)	B	E, N

[a] C, Cyclopoid.
[b] Not a valid species according to Shih et al. (1971).

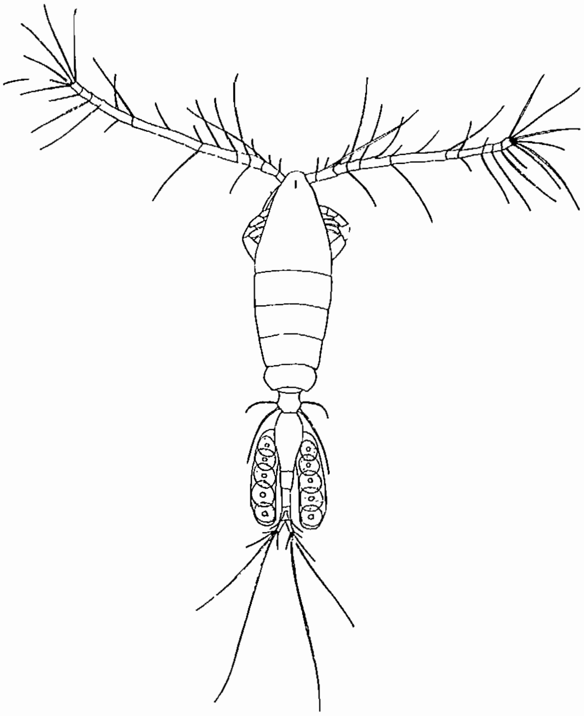

FIG. 12. The copepod *Oithona similis.*

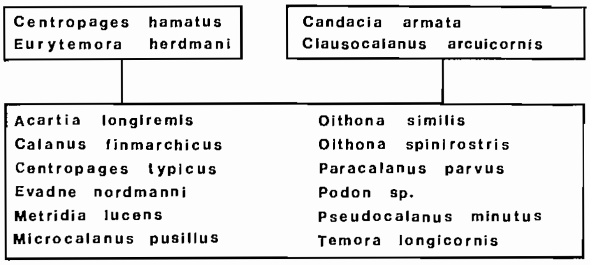

FIG. 13. Bay of Fundy recurrent groups, July–Aug. 1979 (49 stations).

recognize transitional groups, as suggested by Bary (1963). In addition some widespread species may consist of several forms or sub-species (e.g. *Rhincalanus nasutus*, Brodsky 1969), which may not be generally recognized. One species in which this problem has been adequately resolved is *Calanus finmarchicus* (*sensu latu*): it is now recognized as consisting of at least four species (Brodsky 1948, 1959; Jaschnov 1955).

Recurrent group analysis (Fager and McGowan 1963) of the Bay of Fundy microzooplankton (Fig. 13, 14) clearly shows the community to be a mixture of boreal species (intermediate of Colebrook 1964), which also belong to the main Nova Scotia shelf recurrent group (Tremblay and Roff, unpublished data), and several neritic species including *A. clausi, A. longiremis, Podon* sp., and *Evadne nordmani.* The additional influence of the truly neritic species *E. herdmani* and *C. hamatus* is also seen (Fig. 13) in a smaller associated group. Thus the coastal influence of the Bay of Fundy microzooplankton community is clear.

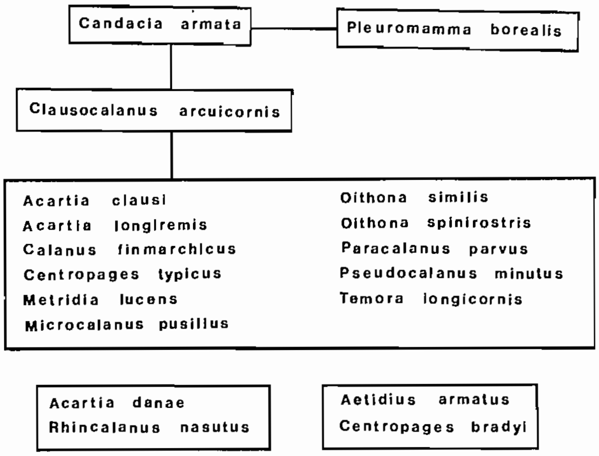

FIG. 14. Bay of Fundy recurrent groups, Nov. 1979 (57 stations).

The general trend is for numbers in the neritic species to increase into the bay or in coastal areas (e.g. *Eurytemora*, Fig. 15) while numbers in the intermediate species decline into the Bay of Fundy (e.g. *Calanus* and *Pseudocalanus*, Fig. 16, 17). Community diversity (as number of species per haul) also decreases by about 50% into the bay (Fig. 18) with the more oceanic species being replaced by fewer neritic ones. Each of the major zoogeographical groups will now be considered.

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NERITIC SPECIES

Several species can be regarded as truly neritic, that is, their distributions are effectively limited to shallow

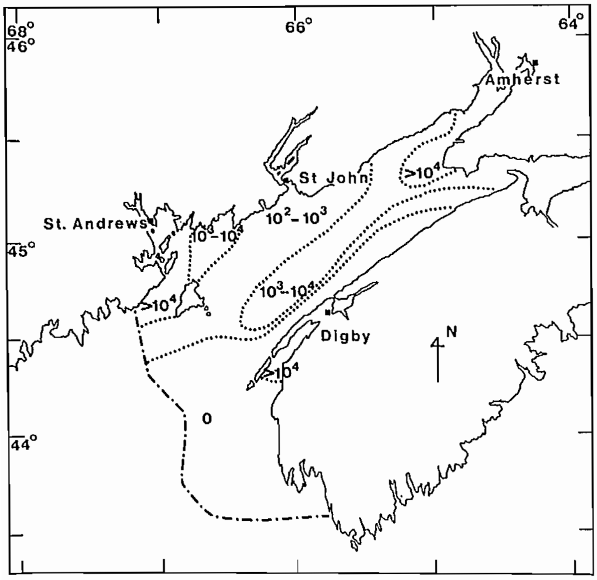

FIG. 15. Distribution of *Eurytemora herdmani* in Bay of Fundy, July–Aug. 1979. Abundances in log-scale/m^2 (49 stations). The dotted line indicates sampling limit.

coastal waters. Neritic species include the *Acartia* spp. (except *A. danae*), *Centropages hamatus*, the *Eurytemora* spp. (Fig. 15), *Pseudodiaptomus coronatus*, and *Tortanus discaudatus*. According to Legaré and MacLellan (1960), about 10% of Quoddy Region zooplankton consists of *A. clausi, E. herdmani,* and *T. discaudatus*. Although the developmental biology and life histories of the neritic species have not been investigated in the Quoddy area, several of these species have been studied elsewhere (see below).

In the Quoddy Region several species of *Acartia* have been recorded (Table 1), but *A. clausi* (≡*A. hudsonica*?, Bradford 1976) is typically the most abundant and it can be found throughout the year. It is most abundant in the summer when its highest population densities are found inside Passamaquoddy Bay and around the passages. Although *A. clausi* is also found throughout the Bay of Fundy and along with *A. longiremis* contributes to the main microzooplankton recurrent group (Fig. 13, 14), it is however certainly endemic to Passamaquoddy Bay.

The number of generations *Acartia clausi* has each year in the Quoddy area has not been determined. Evans (1977) estimates that *A. clausi* has 7 generations/yr and *A. longiremis* has 4 generations/yr in Northumberland coastal waters off Great Britain at temperatures similar to those of Passamaquoddy Bay. The number of generations any species has is variable, and certainly depends on temperature and food supply. Heinle (1966) estimates generation times for *A. tonsa* of only 7 d at 25.5°C and 13 d at 15.5°C; he further suggests that generation times derived from field collections may be underestimated. He calculated that *A. tonsa* alone probably accounted for over 50% of the secondary production of the Patuxent Estuary during the summer months. Clearly the neritic species in bays and estuaries are important secondary producers and deserve fuller attention.

Eurytemora herdmani (Fig. 15) is also abundant in Passamaquoddy Bay where it is undoubtedly endemic. It thrives in brackish water with females and nauplii found well up the St. Croix Estuary, where it is often the dominant species. It is present in the Quoddy area from March or April until October or November (Legaré and MacLellan 1960) with a population peak occurring in July or August. Its population extends throughout the Gulf of Maine and in the Bay of Fundy it forms a recurrent group with *Centropages hamatus*, which shows affinities to species in the main Bay of Fundy group (Fig. 13).

Nothing appears to be known of number of generations per year, but the closely related *E. hirundoides* (= *E. affinis*, Katona 1971) is second in abundance only to *A. tonsa* in the Delaware River Estuary (Cronin et al. 1962). In the Quoddy area *E. herdmani* is certainly multi-generational and within Passamaquoddy Bay may contribute significantly to secondary production.

Centropages hamatus is much less abundant in the Quoddy area than the more oceanic *C. typicus*. *Centropages hamatus* lays resting overwintering eggs (Pertsova 1974; McLaren 1978) and is typically a summer species, being present from late March to September. During July–August it forms a neritic recurrent group with *Eurytemora herdmani* showing affinities with the main species group of the Bay of Fundy (Fig. 13). Again, nothing is known of its local life cycle or number of generations produced in a year. In Loch Striven, Scotland, at summer temperatures somewhat above those of Passamaquoddy Bay, McLaren (1978) estimates 8 generations/yr for *C. hamatus*.

Tortanus discaudatus is also found abundantly in the Quoddy Region, with its highest population densities located within Passamaquoddy Bay and the St. Croix Estuary. It is not abundant outside Passamaquoddy Bay and does not associate with any other species in the recurrent groups of the Bay of Fundy. This species may be present throughout the year (Legaré and MacLellan 1960) but its population peaks in summer or fall. Its life history in the Friday Harbour area has been described by Johnson (1934), and more recently in New Hampshire by Phillips (1976). This species is notable as being one of the most highly colored local copepods. It can be easily recognized in the adult or late copepodite stage because of its prominent nauplius eye, reddish-purple chromatophores, and asymmetrical urosome. It is certainly indigenous in Passamaquoddy Bay.

Pseudodiaptomus coronatus, although commonly found in the inner Bay of Fundy during summer and fall (Jermolajev 1958; Roff, unpublished data), does not extend further into the Bay of Fundy (Fish and Johnson 1937). It is basically an estuarine epibenthic form, included here for the sake of completeness. Other species noted as estuarine or neritic in Table 1 are recorded from the Bay of Fundy or Gulf of Maine, but do not contribute substantially to the Quoddy Region microzooplankton. Thus species such as *A. tonsa, A. discaudata*, and *E. hirundoides* usually form locally restricted populations around specific bays or estuaries (Cronin et al 1962; Jermolajev 1958), but the factors limiting their distributions are not well understood.

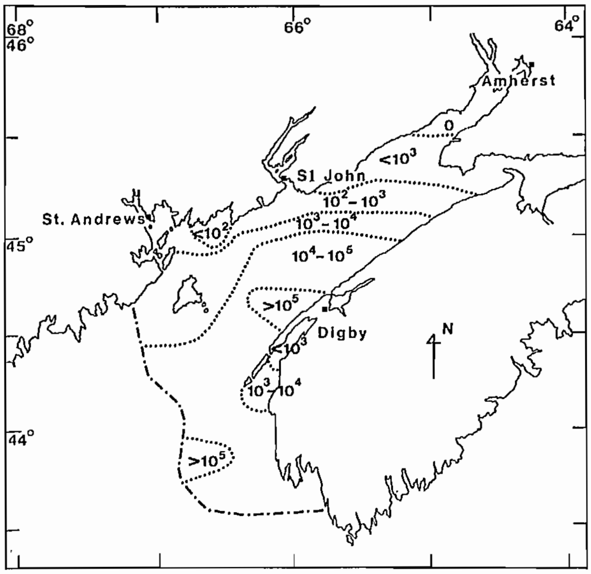

FIG. 16. Distribution of *Calanus finmarchicus* in Bay of Fundy, July–Aug. 1979. Abundances in log-scale/m^2 (49 stations). The dotted line indicates sampling limit.

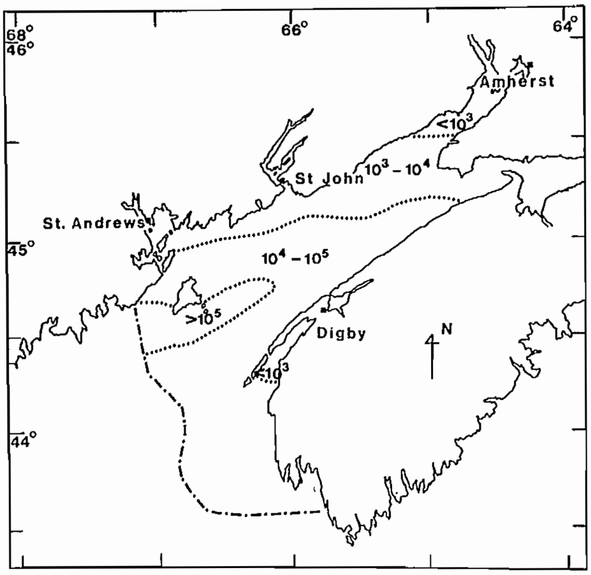

FIG. 17. Distribution of *Pseudocalanus minutus* in Bay of Fundy, July–Aug. 1979. Abundances in log-scale/m^2 (49 stations). The dotted line indicates sampling limit).

BOREAL SPECIES

In the study of the Quoddy area by Legaré and MacLellan (1960) only three species — *Calanus finmarchicus, Pseudocalanus minutus,* and *Centropages typicus* — accounted for 84% of the annual copepod catch. These species, along with *Temora longicornis* and *Metridia lucens*, comprise the dominant indigenous copepod elements of the Gulf of Maine and the outer Bay of Fundy (Bigelow 1926; Fish and Johnson 1937). In addition, *Paracalanus parvus* and *Oithona similis* must be considered as important recurrent members of the Bay of Fundy fauna (Fig. 13, 14). As noted above, the Bay of Fundy itself is heavily influenced by neritic species and the northern species *Microcalanus pusillus*, which also contribute to the main Bay of Fundy recurrent group.

Calanus, Pseudocalanus, and *Centropages* are recorded in some developmental phase year-round from the Quoddy Region; they all have multiple generations each year and all have centers of abundance outside the Quoddy Region. Typically their abundances decline as one progresses into the Bay of Fundy, with lowest concentrations along the New Brunswick shore (Fig. 16, 17). All three species serve as food for both larval and adult fish of the area.

Calanus finmarchicus predominates numerically in autumn and winter when it alone may constitute over 80% of the zooplankton both inside and outside Passamaquoddy Bay (Legaré and MacLellan 1960). *Centropages typicus* becomes most abundant in fall outside Passamaquoddy Bay and may comprise up to 80% of the zooplankton. *Pseudocalanus* is also locally abundant and may contribute up to 50% of the summer zooplankton in the passages and up to 20% of the spring population in Passamaquoddy Bay (Legaré and MacLellan 1960). Although copepodites of *Calanus finmarchicus* can be found in Passamaquoddy Bay, it is doubtful whether this is a suitable environment for the species and it probably does not complete its life cycle here. *Pseudocalanus*, despite producing eggs here, also may not complete its life cycle within Passamaquoddy Bay (Fish 1936b). In this respect there may be a clear distinction between the neritic species and these boreal intermediates.

In their study of the zooplankton, Fish and Johnson (1937) distinguished between abundance (number of organisms present) and production (in their terms involving origin and time). On the basis of currents (deduced from drift bottle studies) and seasonal fluctuations in zooplankton abundances, they concluded that the center of production of the dominant boreal species was probably the western Gulf of Maine. From this origin they considered that the spring generation of copepods physically colonized the Bay of Fundy which lagged behind in patterns of seasonal abundance. The Quoddy area was notably lower in total zooplankton volume than the Nova Scotian section of the outer Bay of Fundy (Fish and Johnson 1937).

Overall, seasonal development of the zooplankton appeared to be retarded in the Bay of Fundy compared to the Gulf of Maine, with only the central waters of the outer Bay supporting a rich zooplankton fauna in August and September (Fish and Johnson 1937). This contention is supported by Jermolajev (1958) who showed that the inner Bay of Fundy and Minas Channel were practically devoid of locally produced zooplankton. Those present were considered to originate from the Gulf of Maine or were resident estuarine species. According to Gran and

Braarud (1935) production of phytoplankton in the Bay of Fundy is low. They maintained that high turbidity and tidal mixing prevented phytoplankton growth which reduced the zooplankton food supply. Jermolajev (1958) also noted that *Calanus* were gradually losing their fat reserves going into the inner Bay; this supports the food limitation hypothesis. Certainly the dramatic decline in *Calanus* numbers approaching the inner Bay of Fundy (Fig. 16) argues that this is not a favorable environment for this species.

In a more detailed examination of seasonal distributions and abundances of *Calanus finmarchicus*, Fish (1936a) showed that the Gulf of Maine west of Mt. Desert probably produces three generations of *Calanus*; in March–April, June–July, and September. To the east of Mt. Desert only two less well-defined broods occurred, in April–May and July–August. Fish (1936a) thus considered that the spring generation of *Calanus* in the Bay of Fundy is enhanced by immigrants from the Gulf of Maine. Although reproduction of *Calanus* in the outer Bay of Fundy appears to occur in the summer, these generations also may be augmented by circulation from the Gulf, gradually and continuously throughout the summer.

The number of generations produced in a year by a copepod species is quite variable, and must depend on food supply as well as temperature. *Calanus finmarchicus* generally produces at least 2 generations/yr throughout its range. In the Baie des Chaleurs, however, it produces three generations, with the second (in summer) usually dominant (Filteau and Tremblay 1953). For a full account of the biology of this important species the work by Marshall and Orr (1972) is indispensable.

Pseudocalanus minutus produces eggs throughout the Gulf of Maine and Bay of Fundy, even within Passamaquoddy Bay. Its main center of breeding activity apparently lies in the outer gulf (Fish 1936b). Fish (1936b) suggests that despite its widespread occurrence and egg production, the Bay of Fundy population is dependent solely on recruitment from Gulf stocks, as in *Calanus*. However, due to the complexity of its population distributions, high natural mortality rates, and the uncertainties of water movements, this position should be viewed with some reservation. The population density of *Pseudocalanus* certainly does decline toward the upper reaches of the Bay of Fundy (Fig. 17) but not as dramatically as in *Calanus*. This is in keeping with the assessment of Colebrook (1964) who indicated that *Pseudocalanus* is a more neritic form than *Calanus*.

Fish (1936b) proposed that three or four generations of *Pseudocalanus* are produced each year in the Gulf of Maine. Evans (1977) indicated five generations in the North Sea, and McLaren (1978) demonstrates six and possibly more in Loch Striven. *Pseudocalanus* is an extremely "plastic" species showing great phenotypic variation and environmental adaptation. Corkett and McLaren (1978) have recently produced an exhaustive review of the biology of this important species.

The reproductive biology of *Oithona similis* has also been investigated by Fish (1936c) in the Bay of Fundy and Gulf of Maine. Four generations appear to be produced in the west of this region and three in the east. Again, Fish (1936c) concluded that there is no evidence of successful propagation by this species in the Bay of Fundy. Clearly it is time for a re-evaluation of the trophic status of the Bay of Fundy, especially with respect to its secondary production.

Paracalanus parvus, Temora longicornis, Centropages typicus, and *Metridia lucens*—all belonging to the main Bay of Fundy recurrent group (Fig. 13, 14)—also belong to the main recurrent group of the Scotian Shelf (Tremblay and Roff, unpublished) and are widespread in North Atlantic waters. They probably all have several generations per year. Thus *Temora longicornis* has a generation time of only 28 d even at 12.5°C (Harris and Paffenhöfer 1976) and produces 4–6 generations/yr (Evans 1977) in the North Sea. All these species are important as food for larval fish (Coates and Roff, unpublished data).

NORTHERN SPECIES

Of the northern species (Table 1) both *Calanus hyperboreus* and *C. glacialis* are at the southern limit of their recorded range in the Quoddy area (see Grainger 1963). Their presence clearly indicates the influence of arctic waters in the area. Both species appear to have a single generation a year (Grainger 1963; Conover 1967).

Calanus hyperboreus was common in the outer Bay of Fundy in July–August and persisted until November. *Microcalanus pusillus* and *Metridia longa* were also common in the outer Bay of Fundy during July–August, and *Scolecithricella minor* was taken here once in November (Roff 1978, unpublished data).

Among the six northern species, only *C. glacialis* is reported here for the first time. It was found at a single station south of Grand Manan. This species is common along the Nova Scotia shelf (Tremblay and Roff, unpublished data; Shih et al. 1971) and is also previously recorded from the Gulf of Maine by Matthews (1969). The five remaining species have been reported in the Quoddy area by Fish and Johnson (1937) and Legaré and MacLellan (1960). Apparently none of these species penetrates in numbers into Passamaquoddy Bay.

SOUTHERN SPECIES

A large number of southern species, whose population centers lie well to the south of the Bay of Fundy, have been recorded in the outer Bay of Fundy and Gulf of Maine (Table 1). Many of these species have been previously recognized as southern expatriates (see Fish and Johnson 1937; Legaré and MacLellan 1960; Shih et al. 1971). However, nine additional species are recorded here for the first time (Roff unpublished data, see Table 1). With the exception of *Clausocalanus arcuicornis*, which was common in both July–August and November 1979 at several stations as far into the bay as a line from St. John to Digby, the remaining species noted here were rare.

Haloptilus longicornis was taken at several stations in the Bay of Fundy as far north as the St. John–Digby line. *Acartia danae* was observed at two stations south of St. Mary's Bay, N.S., and *Oncaea venusta* was taken at one station south of Grand Manan. All three of these species were observed in the July–August and November cruises.

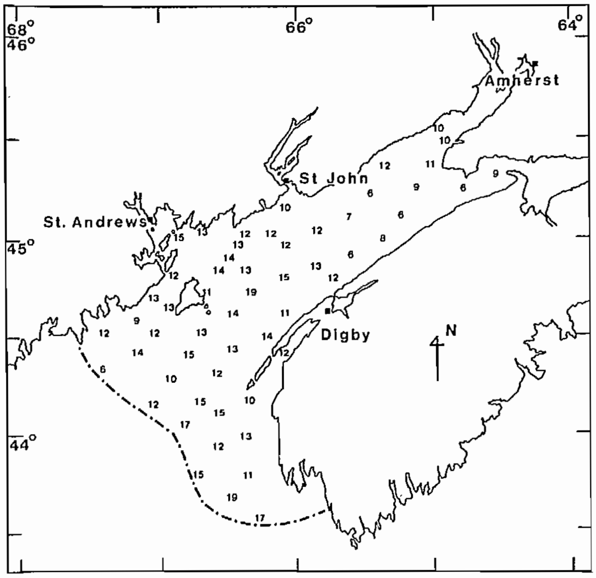

FIG. 18. Number of copepod species observed in Bay of Fundy, Nov. 1979 (57 stations).

Three additional species were only observed in November; *Mecynocera clausii* and *Centropages bradyi* were both taken at several stations in the outer Bay of Fundy southwest of Grand Manan, and *Pleuromamma borealis* was taken at several stations as far into the bay as the St. John–Digby area. Three further species were also only observed in November, each at one station only: *Eucalanus elongatus* (= *E. hyalinus*?, Fleminger 1973) off St. Mary's Bay, *Calocalanus pavoninus* east of Grand Manan, and *Lucicutia flavicornis* south of Grand Manan.

Southern zooplankton communities appear to enter the Gulf of Maine and Bay of Fundy sporadically during the summer and fall, with successive waves being composed of very different species (Fish and Johnson 1937). This is clearly shown by the recurrent group analysis (Fig. 13, 14) where *Candacia armata* and *Clausocalanus arcuicornis* form a recurrent group linked to the main Bay of Fundy recurrent group in July–August, and the same two species with *Pleuromamma borealis* show a similar association in November. In November, however, the community structure is more complex, and two additional unrelated groups of southern species occurred. Whereas the boreal species can be expected at some time of the year in all developmental stages, both the northern and southern expatriates will generally occur in the Quoddy Region only as late copepodite or adult stages.

Conclusions

The foregoing has been a broad, mainly qualitative treatment of the Bay of Fundy microzooplankton community, with emphasis on the Quoddy Region. This community is seasonally very variable and is dominated by the calanoid copepods.

In some respects the Bay of Fundy acts as a temporary, rather unretentive trap for various water masses. It is subject to internal and external influences from local neritic areas and estuaries, the Labrador Current, slope waters of the Nova Scotia area and ultimately the Gulf Stream, and the broad area of the Gulf of Maine and Nova Scotia shelf.

The main recurrent group of the bay comprises species of the neritic community and the major species of the Nova Scotia Shelf recurrent group (Tremblay and Roff unpublished data, species also common to the Gulf of Maine). The Bay of Fundy microzooplankton community can thus be characterized as a coastally influenced extension of the Nova Scotia Shelf or the Gulf of Maine.

On top of these indigenous zooplankton components are added expatriates of southern origin. However, during a semi-synoptic sampling program, we encounter not a single southern recurrent group of copepods but rather several groups which may or may not be associated, each containing one or more species. This is also the case with the Brachyura larvae of the region (Roff, unpublished data) where several small unassociated recurrent groups of southern expatriates occur rather than a single group containing all the species.

There are at least two possible explanations for this independent behavior of the species recurrent groups. One is that successive water masses, each containing its own characteristic zooplankton community, sequentially influence the outer Bay of Fundy. The second is that these unassociated southern groups differ in their ability to penetrate the shelf zone, possibly because they are oceanic to various degrees, or because they occupy different depth strata. Whatever the explanation, we are presumably seeing the end result of injections of slope water ultimately influenced by the warm core Gulf Stream rings described by Cox and Wiebe (1979), among others. The presence of significant numbers of copepod species in the Bay of Fundy which are characteristic of the Florida Current (Owre and Foyo 1967) certainly indicates Gulf Stream influence. The final fate of the "injected" southern expatriate species is presently the subject of some speculation (e.g. see Markle et al. 1980), but presumably most are lost in this "lottery" strategy.

Although additions of species from both the north and especially the south contribute to the overall diversity of the microzooplankton, it is the species of the main recurrent group common to the Gulf of Maine and the Nova Scotia shelf which dominate the biomass and production of the Bay of Fundy. However, the production of neritic and estuarine species must also be significant, at least locally, but it has not been studied. We have no estimates of the relative contribution of neritic and estuarine species to the overall secondary production of the bay.

According to Fish and Johnson (1937) and Fish (1936a,b,c), secondary production *to* the bay (i.e. additions mainly from the Gulf of Maine) is more significant than secondary production *in* the bay. There are grounds for believing that the low autochthonous secondary production, of at least the upper Bay of Fundy, may be related to its extreme tidal variations and high turbidity (Jermolajev 1958). However, these hypotheses have not been adequately reviewed.

Present local information on life histories of even the dominant species is sparse and there is no published quantitative information on biomass or production of the microzooplankton. Also, virtually nothing has been done on zooplankton feeding ecology or trophodynamics in the Quoddy area. In view of the acknowledged significance of these organisms to fish feeding this is surprising. It is clearly time for a reappraisal of the production of the Bay of Fundy, especially the contribution of the microzooplankton.

Acknowledgments

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CHAPTER 14

Birds

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Introduction

The coastal situation and varied habitats attract a large variety and quantity of birds to the Quoddy Region. Of most interest are the aquatic species of inshore marine habitats, the large numbers of phalaropes and gulls which congregate around Head Harbour Passage, and certain pelagic birds of the Grand Manan Channel. Also offering ample opportunities for study are shorebirds, of which the wintering Purple Sandpipers are most significant, and many terrestrial species that frequent coastal habitats.

The birds most poorly represented in the Quoddy Region are the dabbling ducks, rails, and other species of freshwater marshes which can be studied just outside the region at Moosehorn National Wildlife Refuge in Maine.

Despite many interesting features there has been relatively little systematic study of the avifauna of this region. With a few exceptions, the description that follows results from preliminary, restricted studies and from the casual observations of birdwatchers.

Birds in the Quoddy Region

Birds are conspicuous, highly mobile components of the ecosystems they inhabit. In the food chain, they are consumers of plants[1] and/or animals. The particular trophic level occupied varies with species and season. Because of their mobility, birds play important roles in the transport of energy and nutrients from one ecoystem to another. In a small way, seabird excrement helps to replenish the phosphate nutrients depleted in surface waters during periods of phytoplankton bloom.

The New Brunswick Museum files (hereafter NBM files) contain reports of 300 species[2] that have occurred in the Canadian portion of the Quoddy Region. I believe 220 occur regularly or numerously; the remainder are rare or accidental in the region. Appendix A indicates the approximate status, season of occurrence, and main habitats of those 220 species, 91 of which are present mainly in summer, 33 mainly in winter, 42 throughout the year, and 54 of which primarily pass through during migration.

The seaward boundary of the Quoddy Region is shown in Chapter 2, Fig. 1. The inland boundary is less well defined but for convenience it is considered to be roughly the position of Highway 2, also shown in this figure.

MIGRATION

Many birds are highly migratory. Their movements link the Quoddy Region with areas as far removed as the high arctic and the subantarctic. Thus, events in tropical rain forests and other remote habitats can influence Quoddy systems through the birds that travel to and from them. Almost all local migration involves Northern Hemisphere breeders that move southward to winter in areas with a milder climate and larger food supply. Some species (e.g. Horned Grebe, Bohemian Waxwing) have a strong west-to-east component to their migration. Exceptions to the general pattern are three pelagic species — Greater and Sooty Shearwaters and Wilson's Storm-petrel (South Atlantic breeders that spend the Southern Hemisphere winter in the North Atlantic).

Most birds seen in the Quoddy Region migrate on a broad front at night, but many of the larger waterbirds (diurnal raptors, swallows, and some other songbirds) may migrate during the day, following topographic features such as the coast or lines of hills. Flights of loons, cormorants, Canada Geese, scoters, other sea ducks, and gulls pass up and down the Bay of Fundy mainly along the outer coast, although some flocks may stop in Passamaquoddy Bay or Maces Bay to stage an overland flight to some northern region. Movements of hawks, swallows, American Robins, and blackbirds are also conspicuous along the coast.

Spring migration takes place mainly between early March and mid-June, and fall migration from mid-July to early December. There may be some movement at almost any time of year, even in midwinter when food- or weather-related influxes of finches, birds of prey, and waterbirds are sometimes observed, but those are not the predictable movements that we normally consider as migration.

Different sexes and age classes of the same species may migrate at different times or on different routes. For instance, male Red-winged Blackbirds arrive before the females in spring and adult Semipalmated Plovers move southward about a month earlier in fall than the young birds do. Herring Gulls migrate as far as the Gulf of Mexico in their first winter, but much shorter distances in subsequent years (Gross 1940). Male Common Eiders leave the nesting areas in June and move eastward to moult in the upper Bay of Fundy and southern Gulf of St. Lawrence, while the females and young remain near the nesting islands during the summer (Palmer 1976).

More detailed accounts of bird migration in the Maritimes appear in Erskine (1970) and Finch (1977).

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[1] Mainly in terrestrial habitats and in fresh and salt marshes. In Quoddy marine habitats only the Brant and perhaps the Black Duck are important primary consumers.

[2] Avian nomenclature in this chapter follows the American Ornithologists' Union (1957, 1973, and 1976) except those names in parentheses in Table 16.1 which are American Birding Association names likely to be adopted in the next revision of the checklist of the American Ornithologists' Union (1957) (Peterson 1980).

TABLE 1. Principal seabird colonies of the Quoddy Region (data from recent, preliminary, and sometimes cursory surveys.) Common Eider and Black Guillemot probably nest more widely than indicated. Breeding colonies of less than 200 pairs, mostly gulls, have been reported on eight additional islands.

Island	Species, No. pairs, and source	Island	Species, No. pairs, and source
Hog Island (45°08′N, 66°58′W)	Great Black-backed Gull (125[a]) Herring Gull (100[a])	Flat Wolf Island (44°58′N, 66°44′W)	Double-crested Cormorant (186[a]) Great Blue Heron (3[a]) Common Eider (95[a]) Great Black-backed Gull (70[a]) Herring Gull (860[a]) Black Guillemot (several[d])
Dick Island (45°08′N, 67°00′W)	Double-crested Cormorant (present[a]) Herring Gull (130[a])		
Hardwood Island (45°07′N, 67°00′W)	Common Eider (some[b]) Great Blue Heron (75–80[a]) Herring Gull (60[a])	Green Rock (44°58′N, 66°44′W)	Great Black-backed Gull (40[a]) Herring Gull (400[a]) Black Guillemot (a few[d])
Hospital Island (45°07′N, 67°01′W)	Great Black-backed Gull (10[a]) Herring Gull (230[c])	Fatpot Island (44°57′N, 66°44′W)	Common Eider (200[a]) Great Black-backed Gull (50[a]) Herring Gull (1270[a]) Black Guillemot (several[d])
Mohawk Island (45°02′N, 66°54′W)	Great Blue Heron (21[a])		
Hospital Island (44°59′N, 66°55′W)	Great Black-backed Gull (10[a]) Herring Gull (271[a]; 400[c]) Common Eider (8[a])	South Wolf Island (44°57′N, 66°44′W)	Common Eider (250[a]) Great Black-backed Gull (60[a]) Herring Gull (800[a]) Black Guillemot (several[a])
South Spectacle Island (44°59′N, 66°55′W)	Herring Gull (250[c])	West Salkeld Island (45°07′N, 66°31′W)	Common Eider (90[a]; 28[e]) Great Black-backed Gull (50[a]; 108[e]) Herring Gull (570[c]; 718[e]) Black Guillemot (9 adults[c])
Sandy Island (44°58′N, 66°54′W)	Great Black-backed Gull (3[a]) Herring Gull (38[a]; 250[c])		
White Horse Island (44°59′N, 66°52′W)	Gannet (1 — no evidence they were successful[c]) Double-crested Cormorant (112[a]; 400[c]) Common Eider (22[a]) Great Black-backed Gull (10[a]) Herring Gull (390[a]; 500[c]) Black Guillemot (35 individuals[a])	East Salkeld Island (45°07′N, 66°31′W)	Double-crested Cormorant (238[a]; 197[c]) Common Eider (28[a]; 44[c]) Great Black-backed Gull (80[a]; 115[e]) Herring Gull (330[a]; 596[c]) Black Guillemot (10 adults[c])

[a] A. R. Locke and B. Dodge, aerial and/or ground survey, 29 May–June, 1979 (Locke 1981; some quoted in Canadian Wildlife Service 1979).

[b] E. M. Majka and C. G. Majka, summer 1968, personal communication.

[c] Observations by University of Guelph research team, 1977–1979 (Gaskin and Smith 1979)

[d] D. S. Christie, from boat, 7 June 1980.

[e] P. Barkhouse, W. Barrow, and R. Milton, Maritimes Nest Records Scheme cards, 9 June 1976.

THE BREEDING SEASON

The breeding season occupies half the year, from mid-March, when Great Horned Owls begin to lay, through early September, when the young fly from late nests of certain songbirds. However, for the majority of species egg laying, incubation, and care of dependent young is concentrated in May, June, and July. Some of the small passerines raise two broods during the season but even in those species many pairs are probably single-brooded and a lot of the late summer activity may be renesting by pairs that were unsuccessful earlier in the season.

Seabird Colonies

Recent surveys suggest that a total of about 10 000 pairs of 6 species of waterbirds breed colonially or semi-colonially on 23 islands in the Quoddy Region, about 4600 pairs at The Wolves, 2500 in Head Harbour and Letite Passages, 2000 in Maces Bay, and 900 in Passamaquoddy Bay. Populations of the main colonies are outlined in Table 1. Black Guillemot numbers are least well known because of their habit of nesting in cliff niches. The numbers of Common Eiders, in the Head Harbour Passage area where they commonly breed, have not been estimated (Canadian Wildlife Service 1979).

At Grand Manan and in Maine, studies relevant to seabird breeding biology in the Quoddy Region have been carried out on Double-crested Cormorant (Mendall 1936), Common Eider (Gross 1938; Paynter 1951; Choate 1964; Clark 1968; Mirot 1980), Herring Gull (Paynter 1949), and Black Guillemot (Winn 1950; Preston 1968). Herring and Great Blackbacked Gulls, which have increased greatly in recent decades (Kadlec and Drury 1968), are the main cause of loss of Common Eider eggs and young (Bourget 1973); they exert pressure on other nesting seabirds as well.

The presence of numerous seabirds alters the vegetation structure of the islands they inhabit. The nutrient-rich excrement of herons and cormorants burns tree foliage and ultimately kills the trees in which they nest. When the trees are gone cormorants may begin to nest on the ground but herons will move to another site. The presence of a gull colony prevents invasion of open areas by woody vegetation through overfertilization and the trampling action of gull feet. Where the numbers of gulls are increasing, a lush growth of resistant vegetation, especially grasses, expands at the expense of other plants.

OFFSHORE

In the waters beyond about 5 km from the coast there exists a community of seabirds many of which are seldom seen near land except at their nesting colonies. Most characteristic are the shearwaters during late summer and fall and various alcids in fall and winter. Storm-petrels, common members of this community south of Grand Manan Island, seem to be less tolerant of conditions near the mainland and are usually rare in the Quoddy Region.

The occurrence of seabirds in our offshore waters has been discussed or mapped by Christie (1971), Baird et al. (1973), and Brown et al. (1975). Based on my observations from the Grand Manan ferry, large numbers are most apt to be encountered in the southern portion of the Grand Manan Channel during the latter stages of a rising tide when the Long Eddy, a strong tidal current, sweeps NE into the channel from the tip of Grand Manan Island. The birds move readily from place to place in response to the tides and the availability of food, so that at a given location there may be hundreds of feeding birds at one time and few or none an hour or two later.

Small fish, crustaceans, and squid are probably the principal foods of the offshore bird community and must be near the surface to be available to most birds. Many planktonic invertebrates rise close to the surface at night but the extent of nocturnal feeding by most seabirds is not known. In the Bay of Fundy, upwelling and turbulence caused by strong tidal currents, such as the Long Eddy (*cf.* Brown et al. 1979), are perhaps the most important factors making food available. The underwater feeding activity of large fish and marine mammals also forces smaller organisms to the surface (e.g. Bent 1921; 245 and 1927: 22) and some birds follow whales to glean waste from their feeding (Palmer 1962: 233). The turbulent wake of passing ships and various activities of the commercial fishery also provide feeding opportunities.

The feeding ecology of shearwaters has been studied on the Nova Scotia side of the Bay of Fundy (Barker 1976). Greater and Sooty Shearwaters are the principal species but the scarcer Manx has been increasing and is quite regular. A fourth large tube-nose, the Northern Fulmar, *Fulmarus glacialis*, thus far seldom seen in the Quoddy Region, has also been increasing in the Maritimes and may be found more frequently in the future.

The Black-legged Kittiwake, most oceanic of eastern Canadian gulls, is typical and common offshore during fall and winter. Terns are common for a month or two following their breeding season. To some extent, Great Black-backed and Herring Gulls, mainly adult birds, forage offshore throughout the year and are joined in winter by small numbers of Iceland and Glaucous Gulls. These large gulls scavenge for carrion and refuse from boats, which they often follow, and gather at surface concentrations of fish or invertebrates to feed directly on those organisms[3] or to rob other birds of food. Other food robbers are the swift-flying jaegers which pursue terns and small gulls, forcing them to drop or disgorge their food. The Parasitic Jaeger harries terns mainly, whereas the more powerful Pomarine commonly pursues birds as large as kittiwakes. Both jaegers are also predators of small birds such as phalaropes and migrant songbirds.

Storm-petrels and phalaropes select smaller prey than all the preceding species. They feed on organisms at or within pecking distance beneath the surface. Usually very few of either Wilson's or Leach's Storm-petrel are seen in the Quoddy Region but small flocks of both Northern and Red Phalaropes occur regularly offshore during migration. The phalaropes are often seen feeding at floating patches of algae in which many small animals are probably hiding.

The remaining principal offshore species are diving birds capable of obtaining food at somewhat greater depths than can shallow-plunging shearwaters, gulls, and terns. The alcids (Razorbill, murres, Dovekie and Common Puffin) feed on small fishes and crustaceans whereas the Gannet, a spectacular diver from flight, feeds mainly on fishes, these frequently up to 30 cm long (Cramp 1977).

THE PASSAGES

The passages among the islands at the mouth of Passamaquoddy Bay are exceptional for birds. The concentration of phalaropes, gulls, and terns found there from mid-summer through early winter is markedly different from bird communities of other inshore areas of the Quoddy Region. In fact, certain aspects of the food chain and bird populations resemble offshore habitat. Turbulence and upwelling associated with strong tidal currents through Western, Letite, and Head Harbour passages and the attendant swarms of planktonic crustaceans and schools of herring (discussed in other chapters) attract the birds. As offshore, the distribution of the flocks changes markedly through the tidal cycle. From early or mid-winter through early summer bird populations of the passages are not exceptional.

The importance of these passages as feeding areas for birds is indicated in Table 2. Numbers vary from year to year partly because of variations in euphausiid populations (Gasken and Smith 1979). Concentrations of most of these species are found primarily in Head Harbour Passage, Friar Roads, the southern portion of Western Passage, and less frequently in Letite Passage. Gaskin and Smith (1979) found no feeding Northern Phalaropes in Letite Passage and I have only observed it once.

Gaskin and Smith (1979) note that the area west of White Island is an important feeding ground for phalaropes on flood tide only, and that southern Head Harbour to Deer Island Point and Eastport is important only

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[3] I found that euphausiids, probably *Meganyctiphanes*, were the principal food being fed to nestling Herring Gulls at the Manawagonish Island colony near Saint John, N.B., 11 July 1974.

TABLE 2. Selected reports of large numbers of phalaropes, gulls, and terns in the Head Harbour Passage area during summer and fall.

Species	Date	Number, area, and source
N. Phalarope	21 Aug 1971	100 000 from Campobello to Deer Is. ferry[a]
	28 Aug 1973	0.5–1.0 million off Eastport[b] (incorrectly noted as 28 Sept. 1973 in Am. Birds 28:115)
	21–22 Aug 1974	500 000 off Deer Island Point[c]
	26–29 Aug 1976	2 million off Deer Island Point[d]
Great Black-backed	7 Oct 1972	7700 between Eastport and Campobello[b]
	Aug 1977	3175, count of roosts, Head Harbour Passage region[e]
Herring Gull	28 Jul 1968	5000+ off Wilson's Beach[a]
	7 Oct 1972	44 000 between Eastport and Campobello[b]
	Aug 1977	9185, from count of roosts, Head Harbour Passage region[e]
Bonaparte's Gull	13 Oct 1972	12 000 off Deer Island Point[a]
	9 Aug 1973	12 000 off Deer Island Point[c]
	26, 29 Aug 1976	25 000 to 30 000 off Deer Island Point[d]
	Aug 1977–78	peak of 5000 to 10 000 in Head Harbour Passage region[e]
Black-legged Kittiwake	11 Nov 1970	2000+ off Deer Island Point[a]
	30 Oct 1971	3200 off Deer Island Point[f]
	7 Oct 1972	2000 between Eastport and Campobello[b]
Common and/or Arctic Terns	9 Sep 1973	1000 off Deer Island Point; all those identifiable were Commons[a]
	Aug 1977	1260, maximum in Head Harbour Passage region[e]
	Aug 1978	750, maximum in Head Harbour Passage region[e]

[a] D. S. Christie et al (NBM files).
[b] W. Townsend (NBM files).
[c] D. W. Finch (NBM files).
[d] Finch 1977.
[e] Gaskin and Smith 1979.
[f] J. G. Wilson (NBM files).

on the ebb tide, whereas parts of Head Harbour Passage, north and west of East Quoddy Head, are important on all running phases of the tide. Their map shows Herring Gulls between Deer and Campobello islands to be feeding more to the northwest on the flood tide and to the southeast on the ebb, although small areas between Deer Island Point and Eastport northeast of Indian Island and north of East Quoddy Head are important at both stages.

Black-legged Kittiwakes, often common offshore by early September, are not usually numerous in Head Harbour Passage before mid- or late October. In autumns of low euphausiid surface populations, significant numbers may not enter the passages. Those factors may partially account for the failure of the University of Guelph team to observe large numbers of kittiwakes during 1977–79. Their 1977 field season concluded on 10 October and 1979 was a poor year for euphausiids (Gaskin and Smith 1979).

Often terns are not seen well enough to be specifically identified. Gaskin and Smith (1979) report that Common Terns were first to arrive but that Arctic Terns predominated during August. Arctics were more common in euphausiid-rich areas, the Commons elsewhere.

In addition to the species listed in Table 3, a few other gulls occur regularly in the passages, including the rare Black-headed and Little Gulls. Razorbill and Dovekie are sometimes numerous in winter and other offshore species occasionally enter the area. Parasitic Jaegar is reported fairly frequently. Many other birds are found in the passages, especially close to shore and in shallow water areas (see the discussion of inshore species below).

The passages are an "area of outstanding importance" on the migration route of the Northern Phalarope (Morrison 1976). The concentrations of that species are the largest known in eastern North America, and those of the Bonaparte's Gull are the largest in eastern Canada (Canadian Wildlife Service 1979).

University of Guelph personnel have studied the feeding habits of some species in the area (Gaskin and

TABLE 3. Principal waterbirds reported on the Eastport-Campobello (N 14), St. Andrews (N 20), and Lepreau (N 18) Christmas Bird Counts, giving maximum number recorded, mean number, and percent frequency.[a] Observer effort on the one-day counts varies somewhat from year to year; the Deer Island portion of the Eastport-Campobello circle is not covered.

	Eastport-Campobello			St. Andrews			Lepreau		
Species	Max.	Mean	f%	Max.	Mean	f%	Max	Mean	f%
Common Loon	42	11	79	7	2.4	70	13	5.3	100
Red-throated Loon	4	0.5	21	1	0.1	10	5	1.2	56
Red-necked Grebe	45	8.9	79	8	1.1	45	39	15	78
Horned Grebe	58	22	93	17	4.4	80	87	23	100
Great Cormorant	296	61	100	11	2.2	80	17	5.9	94
Black Duck	835	264	100	327	144	100	131	41	100
Greater Scaup	8	3.1	64	177	57	100	5	0.7	33
Common Goldeneye	235	119	100	38	20	100	109	73	100
Bufflehead	490	214	100	133	66	100	169	51	100
Oldsquaw	1077	309	93	33	5.7	60	117	20	94
Common Eider	263	39	93	1851	295	70	360	115	100
White-winged Scoter	183	44	93	343	49	100	12	2.5	67
Surf Scoter	37	11	57	376	132	100	8	1.6	44
Black Scoter	20	4.7	50	150	20	65	64	10	61
Common Merganser	13	3.6	57	12	2.4	40	59	11	56
Red-breasted Merganser	178	44	100	36	1.7	65	33	13	94
Purple Sandpiper	82	15	50	84	29	50	947	175	89
Iceland Gull	30	7.9	86	0	0	0	3	1.2	61
Great Black-backed Gull	1057	414	100	293	104	100	473	97	100
Herring Gull	5756	3190	100	1064	466	100	1236	622	100
Ring-necked Gull	52	13	71	2	0.1	5	3	0.3	17
Bonaparte's Gull	197	50	86	0	0	0	0	0	0
Black-legged Kittiwake	10052	2187	100	0	0	0	400	48	89
Razorbill	83	15	36	0	0	0	150	41	78
Thick-billed Murre	64	7.8	71	1	0.1	5	10	0.9	33
Dovekie	2725	201	57	0	0	0	2	0.4	28
Black Guillemot	28	9.6	86	0	0	0	3	0.8	50

[a] Compiled from the 1960–1980 Christmas Bird Counts reported in *Audubon Field Notes*, *Am. Birds*, *Nature News*, and *N. B. Nat.* by the count compilers for Eastport-Campobello (Wm. Townsend 1967–80), St. Andrews (N. Bourne 1960–61, 1963–64; H. W. MacCoubrey 1965–67, 1975–77; H. V. MacCoubrey and J. E. Rigby 1969; J. E. Rigby 1970; H. W. MacCoubrey and W. Stobo 1972–74; D. Linton 1978–80) and Lepreau (D. S. Christie 1960–75; 1977; K. H. Deichmann 1980).

Smith 1979; Braune 1979). Herring Gulls were found to take herring up to 25 cm long, to follow fishing boats, to join Bonaparte's Gulls in frenzied feeding on euphausiid surface swarms, and to scavenge inland at nearby garbage dumps. Bonaparte's Gulls changed their feeding method from diving to surface seizing as euphausiid concentrations increased. Common Terns fed almost exclusively on small fish, especially herring 8–12 cm long, whereas Arctic Terns took a mixture of small fish and euphausiid shrimps. Frenzied feeding activity by gulls drove the diving terns to the edge of the prey concentration. Northern Phalaropes appeared to be taking copepods and the smaller sizes of euphausiids.

Other sources of food may also be important. William Townsend observed a feeding assemblage of 1000 Herring, 500 Great Black-backed Gulls, 130 Red-breasted Mergansers, 50 Great Cormorants, 10 Bald Eagles, and a few birds of three species of alcids attracted by an early winter school of squid in a small area of Head Harbour Passage (NBM files).

INSHORE

The inshore waters of the Quoddy Region support large but not exceptional numbers of birds. Variety is significantly greater in winter than in summer because most of the few breeding species are resident year-round and because several species that nest in northern Canada winter in the region.

Christmas Bird Count results (Table 3) indicate the variation in wintering water birds among three parts of the region. Comparisons must be made with caution but the generally greater number and variety of birds and especially the prominence of gulls and Oldsquaw at the mouth of Passamaquoddy Bay (Eastport-Campobello) are obvious, as are the larger numbers of eiders and scoters and the lack of alcids and certain gulls in the St. Andrews area.

Canadian Wildlife Service aerial surveys along the coast are also useful in interpreting the distribution of waterbirds in the Quoddy Region during migration as well as in winter (Canadian Wildlife Service 1979; C.W.S. files).

Certain species are locally more common than revealed by the Christmas Bird Counts. Black Guillemots, for instance, are more numerous about The Wolves and the islands of the Letite Passage area than in the three counts reported here. The Harlequin Duck is also a regular winter resident of the region, principally at The Wolves (Squires 1976). There have been a number of reports of Harlequins at Point Lepreau and East Quoddy Head and they may occur at other exposed locations along the outer coast, most of which are seldom visited by bird students during winter.

Barrow's Goldeneye has never been reported on the St. Andrews Christmas Bird Count but observations by R. Mazzeo, H. W. MacCoubrey, and A. J. Erskine of as many as 46 birds at St. Andrews and Chamcook in various years (NBM files), as well as totals of from 4–30 birds on five of the Eastport–Campobello Christmas Counts, suggest that the estuarine situations of northern and western Passamaquoddy Bay may be a regular wintering area (perhaps the only one in the Bay of Fundy) for small numbers of this goldeneye.

Summer populations of the Quoddy Region consist primarily of Herring and Great Black-backed Gulls, Common Eider, Double-crested Cormorant, Black Guillemot, and Osprey, as well as a small number of Common Loons (see discussion of breeding colonies).

The inshore birds can be divided into four main groups according to feeding habits and principal prey. Searching for food from the air are the Osprey, Bald Eagle, and large gulls, all of which may feed around inland waters as well as coastal ones. Of these, the Osprey is distinct because its diet is exclusively of fish obtained by plunging into protected, shallow waters, whereas the others are wide-ranging and opportunistic, taking any kind of food they can catch or find as carrion. The nesting population of Ospreys in the Quoddy Region was about 30 pairs in 1974 (Stocěk 1974) and at least four Bald Eagle nests were active in the region in 1978 (Gaskin and Smith 1979). During winter the small breeding population of eagles may be increased by movement to the coast of birds that nest inland. The Bald Eagle population is significant within New Brunswick but minor compared to that of Nova Scotia (Canadian Wildlife Service 1979).

There are two groups of birds that dive from the surface, one that feeds largely on fishes (many species, of small to medium size) and the other on molluscs (especially the blue mussle *Mytilus edulis*). Various crustaceans (amphipods, small crabs, etc.) are often important components of the diet of both groups. The fish-eating species are the loons, grebes, cormorants, mergansers and Black Guillemot, and the mollusc-eating ones are the Greater Scaup, goldeneyes, Bufflehead, Oldsquaw, Harlequin Duck, eiders, and scoters.

Further details of the diet of these inshore species are given by Palmer (1962, 1976) and Bent (1919, 1937). Locally, MacKay and Bosien (1979) have investigated the foods of cormorants, eiders, gulls, and Purple Sandpiper (a littoral species).

Diets change through the season as illustrated by work in the St. Lawrence Estuary of Quebec where herring eggs were the most important food of Common Eiders in May, herring eggs and *Nereis* worms in June, periwinkles (*Littorina*) in July and August, with *Gammarus* amphipods of increasing importance through August and September (Cantin et al. 1974). That study also looked at the effect of eider predation on the food animals, finding that the females and ducklings harvested 10–30% of the standing crop biomass of periwinkles during July.

Although the diets of many of diving birds are similar, the species tend to be separated by preference for or tolerance to varying depth, water clarity, salinity, currents, wave action, and bottom type. For instance, Oldsquaws feed in deeper water than the other sea ducks, and Buffleheads prefer the most sheltered coves and harbors. Most of these species occur in both marine and estuarine situations, but Common Merganser is seldom found in marine habitats and Oldsquaw, Harlequin Duck, eiders, and Black Guillemot avoid estuaries.

LITTORAL HABITATS

Littoral habitats include the intertidal zone of rock, sand, mud, and salt marsh, as well as spray-influenced cliffs and beach dunes. The rise and fall of the tides create changes in bird populations in the intertidal zone. When the shore is covered by the sea, inshore species such as eiders and loons dive to feed on intertidal invertebrates or the fishes which have also advanced with the tide to feed. Some of those birds play an important role in the intertidal ecosystem but this section deals only with birds that visit the exposed shore or feed at the edge of the sea. These include gulls, sandpipers, plovers, and certain waterfowl, passerines, and other birds.

Most prominent year-round are the ubiquitous Herring and Great Black-backed Gulls, joined occasionally by other gulls. Those birds feed on various intertidal invertebrates as well as carrion. Food animals include all but the smallest species. Access to hard-shelled molluscs and sometimes to sea urchins may be gained by dropping them onto rocks to break the shell. Common Crows also prey regularly on invertebrates, particularly during winter when they are much more common and feeding potential is much reduced in terrestrial habitats. The Common Raven and Bald Eagle are principally scavengers but may also prey on a variety of shore animal life.

The most varied group of littoral birds consists of shorebirds, sandpipers and plovers, most species of which pass through the region during migration. Only the Spotted Sandpiper is widely distributed on coastal shores during nesting season. Breeding Killdeer and Common Snipe may feed on salt marshes or on estuary shores but they are more apt to be found in terrestrial or freshwater habitats. Most of the migrant shorebirds are most numerous on muddy shores or in salt marshes but the Sanderling prefers sand beaches and the Purple Sandpiper feeds mainly in algae-covered rocky areas.

The Semipalmated Sandpiper, commonest migrant shorebird in most parts of the Quoddy Region, is found in larger numbers on the extensive mudflats at the head of the Bay of Fundy. However, surveys of the Maces Bay shore by Evan Smith show it to be among the more important locations in the Maritimes for Semipalmated Plover, Least Sandpiper, and Ruddy Turnstone (Morrison 1978). It is also a very important wintering area for Purple Sandpipers (Morrison 1976). The Indian Point shore at St. Andrews is probably important for those species too.

Most shorebirds either pick small invertebrates from the surface or probe into the sediments for burrowing animals (Palmer 1967). Turnstones turn over small stones, seaweed, and debris to capture the organisms hiding beneath. Yellowlegs frequently capture small fish, especially the killifish and sticklebacks commonly found in marsh pools. Hicklin and Smith (1979) found the mud-dwelling amphipod, *Corophium volutator* and various polychaete and nemertean worms to be the important foods of five common shorebirds during fall migration in the upper Bay of Fundy.

In addition to a productive feeding ground, migrant shorebirds require a roosting site where they can gather to rest at high tide. The roost location is usually a sand or gravel beach. The Bay of Fundy is an important staging area where certain shorebirds gain sufficient fat reserves to fuel a migratory flight over the Atlantic to northern South America (Morrison 1977).

Aside from eiders and other diving ducks, the Black Duck is the main species of waterfowl of the intertidal zone; it feeds mainly on small crustaceans, molluscs, and various small aquatic plants such as widgeon grass, *Ruppia*, from fall through spring. Other dabbling ducks also use littoral areas, particularly the salt marshes. Brant are spring migrants, important in certain areas and particularly at Maces Bay where as many as 2000 have been reported (NBM files). They feed principally on plants — mainly sea lettuce, *Ulva*, and perhaps also *Porphyra*. Marine eelgrass *Zostera* is an important food of Brant elsewhere but it is scarce and occurs only very locally in the Quoddy Region.

Great Blue Heron and Belted Kingfisher feed on small fish along the edge of the sea and in salt marsh pools and creeks. Red-breasted Mergansers also visit saltmarsh waters to fish, principally during spring.

A wide variety of passerines feed to some degree along the shore but only a few are strongly associated with it. Most salt marshes in the Quoddy Region are rather small (Chapter 7) and usually do not support the breeding Sharp-tailed Sparrows characteristic of larger marshes farther up the Bay of Fundy. However, they may have Savannah Sparrows, which are also typical of beach grassland. On small beaches Song Sparrows may replace the Savannahs. During migration and in winter, certain open country birds such as Snow Bunting and Horned Lark feed in those natural grasslands. Insects are the main food source in summer and seeds during the remainder of the year.

One interesting feature of the intertidal zone during winter is the Starling's habit of shorebird-like feeding among the rocks and algae. I have frequently seen small flocks on the shore at Maces Bay and have also noticed them in intertidal areas at St. Andrews.

Red-winged Blackbirds and Common Grackles that nest near the shore often feed in the salt marsh or on the beach. Swallows forage above the intertidal areas and even over the sea in search of flying insects. Many other songbirds are occasional intertidal feeders, but for most the shore may be just an emergency source of food, particularly in spring when the flies and amphipods of the strand line may carry some forest insectivores through a cold weather shortage of food.

A few raptors are found in littoral habitats. Marsh and Rough-legged Hawks and Short-eared Owl hunt the salt marsh, mainly for mice. During migration Sharp-shinned Hawk, Merlin, and Peregrin Falcon frequently take birds, especially shorebirds, in intertidal areas.

The sea cliffs are little frequented by birds but where suitable ledges or overhangs occur they may provide nesting sites for Common Raven and Barn and Cliff Swallows; however, all those species nest more commonly in other locations. Coastal sand and earth banks are important nesting sites for Bank Swallows.

TERRESTRIAL HABITATS

The principal terrestrial habitat along the coast is conifer forest. The common forest birds represent several families of passerines, particularly warblers and fringillids (finches and sparrows), as well as woodpeckers. Several species occur in a variety of forest types but others are confined to either coniferous or deciduous growth. Typical of spruce and fir are Yellow-bellied Flycatcher, Boreal Chickadee, Winter Wren, Magnolia, and Bay-breasted Warblers. Typical in deciduous woodland are Least Flycatcher, Red-eyed Vireo, and Ovenbird. Boreal influences in the region become stronger south and east, where cooler summer temperatures and more frequent fog favor a more dominant spruce–fir element and its associated birds.

Other terrestrial habitats in the region include thickets of young trees or shrubs, bogs, grassland (maintained by periodic cultivation), and towns and villages. Passerine species adapted to open conditions, low vegetation, or the forest edge are found in those locations. In the forest and in more open habitats, insects are the main source of food for the summer bird community, being important to almost every songbird. Other invertebrates such as earthworms are also consumed. As the season progresses, fleshy fruits, grains, and other seeds become increasingly important foods for certain groups of birds. Several raptorial species prey on small vertebrates.

Winter populations of terrestrial habitats are smaller and less varied than those of summer. In the forest, a few resident woodpeckers and insectivorous songbirds are joined by various finches, the numbers of which fluctuate erratically depending on amounts of tree seeds available locally and elsewhere. In fact, the populations of almost all overwintering species vary considerably from year to year and most of the finches are erratic at any time of year. Many species range widely in winter and may be common wherever suitable food is available. Seeds are important to most, hibernating insects and insect eggs to a few, buds and foliage to a very few. Bird feeders and the fruits of ornamental trees and shrubs are important winter food sources in the towns and villages. A few raptors prey on birds and small mammals.

In a coastal region like Quoddy, the relationship of terrestrial birds to marine influence is of interest. Presumably certain species reach higher densities on the small islands than on the mainland or two main islands, while others are more scarce or absent. No local fieldwork has been done but in Muscongus Bay, ME, Northern Parula, Yellow-rumped Warbler and Song Sparrow were found to occupy smaller territories on small islands (0.1–4.0 ha) than on the neighboring mainland, apparently because of the absence of competing species. Other forest birds were found only on the islands that were as large as their minimum territory size on the mainland (Morse 1977).

TABLE 4. Sources of unpublished information and assistance on the study of birds in the Quoddy Region.

Canadian Wildlife Service Atlantic Region P.O. Box 1590 Sackville, N.B. E0A 3C0 (and other offices)	Maritimes Nest Records Scheme; various surveys of waterfowl, shorebirds, seabirds; library; permits for capture, marking and scientific collection.
Maine Shorebird Survey University of Maine Orono, ME.	Shorebird and phalarope surveys in and near Maine.
N.B. Dept. of Natural Resources Fish and Wildlife Branch P.O. Box 6000 Fredericton, N.B. E3B 5H1	Data on upland game birds; gun permits for scientific collection.
New Brunswick Museum 277 Douglas Avenue Saint John, N.B. E2K 1E5	Breeding Bird Survey; files of bird observation data; collection of birds, eggs, etc.; library; exhibits.
Sunbury Shores Art & Nature Centre P.O. Box 100 St. Andrews, N.B. E0G 2X0	Natural history programs; nature trail; bird checklist.
U.S. Fish & Wildlife Service Refuge Manager Moosehorn National Wildlife Refuge Calais, ME 04619	Information on the birds and management of the refuge units at Baring and on Cobscook Bay; exhibits; nature trail.
University of Guelph Dept. of Zoology Guelph, Ont. N1G 2W1	Surveys and ecological studies of seabirds.

In Fundy National Park, N.B., above rather high cliffs, Canada Warbler, American Redstart, and Dark-eyed Junco are apparently more numerous at the forest edge than within the forest (Christie 1980). Those and other species, such as American Robin, Common Yellowthroat, and White-throated and Song Sparrows, are ones that may flourish, particularly at the coastal edge of the forest in the Quoddy Region.

Study and Collection Methods

SOURCES OF INFORMATION

There is much scope for systematic study of birds in the Quoddy Region. Much information presently available consists of casual observations reported by resident and visiting birdwatchers (NBM files and Maritimes Nest Records Scheme). Details of bird observations in the region are often included in seasonal summaries in *American Birds, N.B. Naturalist*, and *The Guillemot*.

A number of Christmas Bird Counts have been conducted in the region (Table 4). There have been surveys (most rather limited) of shorebirds at Eastport, Lubec, and Maces Bay; of the phalarope and gull concentrations in Head Harbour Passage; of Osprey and Bald Eagle nests, seabird breeding colonies (Table 2), pelagic birds, wintering Purple Sandpipers, and waterfowl. There have also been studies of the feeding ecology of Bonaparte's Gull and terns and investigations of the diet of the large gulls, cormorants, Common Eider, and Purple Sandpiper. Sources of those data appear in the bibliography or in Table 4.

Books on the birds of New Brunswick (Squires 1976) and of Maine (Palmer 1949) contain details about the occurrence of birds in the Quoddy Region and provide general information on the larger surrounding region. The latter reference in particular provides many ecological insights. The status of the birds of the St. Andrews peninsula is indicated in a checklist (MacCoubrey and Moffatt 1974) and locations in the vicinity of Maces Bay are described in a birdfinding guide for the Saint John area (Christie 1978).

OBSERVATION

Birds, many species of which are highly visible and/or audible, offer more possibility for study by direct observation than most other classes of animals. A pair of binoculars (usually 6 to 10 ×) is necessary to aid in identification and observation of behavior. In open areas, a telescope of 20 or 30 power may be necessary to study birds at a distance, such as waterfowl at sea. Identification by ear is important for some species, particularly in wooded areas. Photography, often from a blind where one can be close to birds without disturbing them, helps in analyzing behavior and counting large numbers. Tape recorders and parabolic microphones can be used for vocalization studies and for detecting the presence of scarce or inconspicuous species, as many birds respond quickly when a taped song of their species is played.

In the Quoddy Region the most useful field identification guides are those of Peterson (1980) and Robbins et al. (1966). An excellent larger text is that of Godfrey (1966). A number of good recordings of the voices of eastern North American birds are available, including those by Kellogg and Allen (1971) and Borror and Gunn (undated). A wealth of general and specialized literature exists on birds and bird study. Standard ornithology texts (such as Pettingill 1970) include a review of methods and bibliography. Several references quoted in this chapter outline useful study methods.

Simple observation of birds is very useful in studies of the annual cycle, behavior, breeding biology, reproductive success, population density and trends, community structure, habitat use, and certain aspects of diet and migration. This is particularly true in open habitats, where birds are readily visible to an observer on foot or in a vehicle, or even in an aircraft (for surveys of large areas). Under such conditions virtually complete counts can sometimes be made of feeding or resting concentrations or of a breeding colony.

The passage of diurnal migrants is readily monitored by a stationary observer counting the numbers of birds passing a point on the migration route. Although nocturnal migrants can often be detected visually against the face of the moon or audibly by their calls overhead, radar is the best means for studying their movements.

It is more difficult to detect birds in woodland and other tall vegetation than in open areas, yet with patient, purposeful watching and listening, many details of a species' life history can be discovered. Determining population densities of birds in heavy vegetation presents problems because they cannot be counted like ducks on a pond. During breeding season the males of many passerines sing frequently from an established territory. The traditional method of determining their numbers is to map the location of singing males on a census plot (International Bird Census Committee 1970).

Other methods use fixed or variable width transects or point samples for determining populations in breeding season and at other times (Kolb 1965; Emlen 1971; Dickson 1978; Proceedings, Symp. Estimating the Numbers of Terrestrial Birds, October 1980; U.S. Fish and Wildlife Service and U.S. Forest Service, in press).

A population index, a number that reflects the population size, is often sufficient for environmental monitoring and wildlife management programs. Typical population index surveys, for instance the continental Breeding Bird Survey (Erskine 1978), are systematic samples of readily audible or visible indicators which, when repeated under similar conditions, should reveal population trends. Such surveys are used to study changes between years and in before-and-after studies of the effects of pesticides or other environmental treatments.

CAPTURE, MARKING AND COLLECTION

Simple observation of birds in the field falls short of fulfilling certain objectives. The study of anatomy, physiology, population dynamics, diet, pathology, dispersal pattern, and certain behavioral and ecological aspects require "a bird in the hand" for detailed examination (impossible with two or indeed any number "in a bush") or for the marking and identification of individual birds.

All wild birds in New Brunswick are protected by the provincial Fish and Wildlife Act and many also by the Federal Migratory Birds Convention Act. Permits for bird banding and for capture or scientific collection of birds are issued by the Canadian Wildlife Service. Permits to carry a gun in the field are available from the Chief Game Warden, New Brunswick Department of Natural Resources (Table 5).

With local birds ranging in size from 3-g hummingbirds to 5-kg geese and eagles, a great variety of methods can be used to capture them. The regulatory agencies can advise on appropriate techniques for the type of birds being studied. The Bird Banding Manual distributed to holders of banding permits and two journals — *North American Bird Bander* and *Journal of Field Ornithology* (formerly *Bird-Banding*) — are good sources of information on methods.

The standard method of identifying individual birds consists of placing a numbered aluminum band or ring around one leg. In studies in which it is important to be able to identify individuals in the field without recapturing them, the standard bird band is supplemented by color marking with colored plastic leg bands, wing tags, or neck collars, or dye on portions of the plumage. Anyone recovering a banded bird or observing a color-marked bird should report full details to the Canadian Wildlife Service, Atlantic Region, P.O. Box 1590, Sackville, N.B.

The traditional method of collecting birds is with a shotgun of suitable gauge and proper shot size for the bird being sought. Many times a gun is the only feasible means of collection but shooting may not be appropriate and certain species may be more easily taken with a trap or net. Anderson (1960) outlines methods of collecting and preserving bird specimens.

Specific Locations

GENERAL

There are good possibilities for bird study almost everywhere in the Quoddy Region but certain locations are good for particular studies. The comments that follow are rather general and could be improved upon when the region is more thoroughly studied.

First described are areas in the northern part of Passamaquoddy Bay, commencing with the St. Croix Estuary, then those to the south, and finally eastern areas.

St. Croix Estuary — The St. Croix, the largest river of the Quoddy Region, has a 25-km estuary extending from St. Stephen to St. Andrews. It is more easily approachable from locations along U.S. Route 1 south of Calais, ME, than from Route 127 NW of St. Andrews and The Ledge Road, SE of St. Stephen. Birds which frequent shallow waters and muddy shores are common and Barrow's Goldeneye may be regular in winter along the estuary. Oak Bay, a major bay off the estuary, is regularly frequented by Common Loons. It is crossed by N.B. Route 1 about 20 km NW of St. Andrews and 2 km W of the small Waweig River estuary.

St. Andrews — On a summer morning the lovely town of St. Andrews is filled with bird song. Its shade trees, shrubbery, and well-kept gardens provide habitat for many songbirds commonly associated with residential areas. Numerous migrants, some of them rare vagrants, stop in town during migration. In winter, many people operate bird feeders.

Most of the woodland immediately surrounding St. Andrews is second growth, of mixed composition. Sunbury Shores' nature trail at Pottery Cove, off Joe's Point Road and 1.4 km W of the center of town, runs through thickets of young trees, and 1 km farther NW the Fisheries Biological Station and Huntsman Marine Laboratory at Brandy Cove are surrounded by older woodland. Farther from town there is more extensive forest but finding mature stands of much size may be difficult. Field habitats are best represented along Route 127, west towards St. Stephen.

Ospreys, a common sight about town, often nest on Navy Island, visible from Water Street. Various gulls, shorebirds, and ducks also frequent the waterfront area but most can be found in greater numbers at Indian Point and Bar Road.

At Indian Point, the southeastern extremity of St. Andrews peninsula and about 1.5 km SE of the town center, is an extensive intertidal zone of both bedrock and soft sediments. Shorebirds feed commonly during migration (Purple Sandpiper in winter) and may roost at high tide on the gravel beach on the eastern side of the point or on the ball field across the road. However, the great amount of human activity along the shore from July through early September may cause the birds to move elsewhere. Brant are common on the shore from late March through May. Wintering ducks feed regularly in the shallows and gulls, cormorants, and loons are also conspicuous.

Along the eastern shore, about 1 km north of Indian Point is a small salt marsh, the only one close to St. Andrews and a location to be watched for dabbling ducks, shorebirds, and marsh-loving passerines. Some poorly drained woods lie along the railway between the marsh and Indian Point.

The Bar Road, off Route 127 towards Saint John (just over 2 km from the center of town), runs NE to an intertidal gravel bar which, except at high tide, joins Minister's Island to the mainland. The gravelly tidal flats seem less attractive to shorebirds than those at Indian Point but the sheltered waters may have many ducks, cormorants, loons, and grebes.

Hardwood Island — Hardwood Island, a small wooded island in the northern part of Passamaquoddy Bay, about 10 km by boat from St. Andrews, is a breeding site of herons, gulls, and Common Eider. At least three other islands in Passamaquoddy Bay are also seabird colonies (Table 2). Hardwood Island is privately owned so permission should be obtained before making an extended visit. Care must be taken so as not to unduly disturb the birds.

Cobscook Bay — A rather exceptional estuarine situation is found in Maine where the very enclosed Cobscook Bay has many arms and coves that provide a large amount of shoreline and protected water habitat. It is reached from Routes 190, 1, and 189 between Eastport and Lubec. Parts of the shoreline of two of its arms, Dennys Bay and Whiting Bay, are included in Moosehorn National Wildlife Refuge. The outer portions of Cobscook Bay are more marine than estuarine so the entire bay offers a great range of conditions for waterbirds.

The Letite Passages — Letite Passage and Little Letite Passage are narrow channels north of Deer Island through which strong tidal currents flow in and out of Passamaquoddy Bay. The Deer Island ferry (free passage) from Letite on Route 772 south of St. George travels among several islands as it crosses these passages. Black Guillemots, present year round, are conspicuous from the ferry. Common Eider, Red-breasted Merganser, and scoters are common from fall through spring when smaller numbers of other waterbirds also occur. Bald Eagles are frequently seen in this area.

The Passage Islands — East of Deer Island there are over 40 small islands (McMaster Island, with 180 ha, being the largest) and islets in and near Head Harbour and Letite passages. Double-crested Cormorants, Great Blue Herons, Common Eider, Great Black-backed, Herring Gulls, and Black Guillemots find nesting sites on several of the islands, including those in Table 2, which are accessible by power boat from nearby fishing villages.

Deer Island — Mostly wooded, Deer Island is reached year round by a free ferry from Letite on the New Brunswick mainland and in summer by toll ferries from Campobello Island, N.B. and Eastport, ME. The sheltered harbours at Lord's Cove, Leonardville, and Fairhaven are good areas for ducks. The park at Deer Island Point, the southern tip of the island near the Eastport and Campobello ferry landing, is an excellent vantage point for observing waterbirds, particularly when the gulls and phalaropes congregate in Head Harbour Passage. Gulls commonly gather to bathe and drink at Big Pond between Richardson and Leonardville.

Diurnal migration of passerines has been reported in spring when flocks were noted flying N along the eastern shore and in fall when birds were flying out across the water from Deer Island Point towards Eastport (NBM files).

Head Harbour Passage and Western Passage — Head Harbour and Western passages, situated SE and SW of Deer Island, are longer and broader than Letite Passage but have similarly strong tidal currents. These waters support numerous seabirds all year but especially in late summer and fall (p. 217–219 and Table 3). From a small boat the gulls, terns, and phalaropes can be followed from place to place, a freedom unavailable to observers on land. However, there are good observation locations at Deer Island Point, Eastport and from Wilson's Beach to East Quoddy Head. The ferries from Deer Island to Eastport and Campobello are sometimes useful for getting close to the birds if they are feeding near the ferry path.

Campobello Island — Campobello Island is reached via the international bridge from Lubec, ME, and during summer on the toll ferry from Deer Island. Spring migrants moving along the coast of Maine follow naturally onto Campobello. Presumably hawks, which have been seen flying N at Herring Cove on the eastern side of the island (NBM files), and passerines move along to East Quoddy Head where they must either fly over the water and small islands to the mainland or turn around. Sea ducks, loons, and other waterbirds migrating over the sea are probably best observed from Owens Head and Liberty Point, reached on foot 1.5 and 3 km S of Herring Cove, or on the nearby mainland at West Quoddy Head, ME. Elsewhere those migrants are likely to be rather far from shore.

The birds of Head Harbour Passage can be observed from shore between Wilson's Beach and East Quoddy Head, an exposed location where Harlequin Ducks and offshore species are sometimes seen. Mudflats south of the Lubec bridge are good for shorebirds.

Grand Manan Ferry — The car ferry to Grand Manan Island is a relatively inexpensive means of getting out on the sea to observe the offshore bird community (p. 217–219). The greatest variety of species is expected from August through December but the trip can be interesting at any time of year. The ferries make from one to a few return trips daily, depending on season, from Black's Harbour on the New Brunswick mainland.

The Wolves — The Wolves, four rocky islands and an islet in the Bay of Fundy about 10 km S of Beaver Harbour, are the major seabird nesting area of the region (Table 2). They are also a regular wintering ground for Harlequin Ducks. South Wolf Island is partly owned by Transport Canada, the others by the Hawkins family of Beaver Harbour. A good fishing boat is necessary for a visit.

New River Beach Provincial Park — The provincial park at New River, just off Route 1, 25 km E of St. George, features a fine sandy beach where Sanderlings feed during fall migration. The Barnaby Head Nature Trail in the park runs through coniferous woods and a small bog along the shore of a rocky headland. Palm Warbler and Lincoln's Sparrow nest around larger bogs on the N side of Route 1 just E of the park.

Maces Bay — Maces Bay, easily observed from Route 790 which turns S from highway 1 about 35 km E of St. George, is a good area for inshore marine birds, and the shallowly sloping, rocky tidal flats with many shallow pools attract migrant shorebirds in late summer, Purple Sandpipers in winter, and many Brant in spring. Gulls and other seabirds breed on the Salkeld Islands (The Brothers) 2 km offshore (Table 2).

Crossed by Route 790 at the northern end of the community of Maces Bay is the Little Lepreau Basin, a sheltered, muddy estuary which is a good feeding area for migrant shorebirds at low tide and for wintering Buffleheads at high tide.

Point Lepreau — The road to Point Lepreau is a 4.5-km side trip from Route 790 about 0.3 km E of Maces Bay. At this headland, which juts out into the Bay of Fundy, Razorbill and Black-legged Kittiwake can be seen regularly and murres and Harlequin Duck rarely in winter when, during strong W winds, the birds take shelter in the lee of the point.

Various other marine species occur in winter and large flights of sea ducks pass during migration when landbirds are sometimes plentiful too. N.B. Power has a nuclear generating station at the base of the point and may restrict access. It is advisable to contact the security office to obtain permission prior to a visit to the lighthouse area.

Musquash Marsh — All the salt marshes within the Quoddy Region are very small, but about 13 km E of the region a 650-ha marsh is situated S of Route 1 at Musquash. The upper portion has been partially diked and drained for pasture and hay production but the rest is flooded by spring tides. All the birds associated with Bay of Fundy tidal and diked marshland are found at Musquash except for the Willet, which breed regularly only on the Nova Scotia side of the bay. The Musquash marsh is accessible from Route 1 and from the South Musquash Road, which turns E from Route 790 about 2 km from Route 1.

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Appendix A

The status, seasons of occurrence, and habitats of 220 species in the Quoddy Region are listed below. At least 80 other species have been reported but are of very rare or accidental occurrence in the region. Abundance and status are indicated by letter abbreviations, and the season of occurrence by numerals signifying the months of the year. Months within parentheses represent periods when a species is considerably less numerous than at other times. A few individuals may be seen earlier or later than indicated.

a — abundant (200 or more may be seen in a day)
c — common (between 15 and 199 may be seen in a day)
u — uncommon (up to 14 may be seen in a day, usually seen at least once a week)
r — rare (seen less often than once a week or, if seen more frequently, the regional population small and local)
e — erratic (fluctuations in abundance from year to year; may be as numerous as indicated, scarcer, or even absent)
R — year yound resident (as a species; individuals may be migrate)
S — summer resident or visitor
B — known or presumed to breed
W — winter resident or visitor
M — migrant (both spring and fall)
Sp — spring migrant
F — fall migrant
1 — January, 2 — February, etc.

Note: The abundance designations are a function of the conspicuousness as well as the number of each species in the region. Although, for instance, Bald Eagle and Brown Creeper are both classed as uncommon, the inconspicuous creeper is undoubtedly much more numerous than the very obvious eagle.

Common Loon *Gavia immer*: cW,uSB 1–12 inshore, lakes.
Red-throated Loon *G. stellata*: uW 10–5 inshore
Red-necked Grebe *Podiceps grisegena*: uW 10–4 inshore
Horned Grebe *P. auritus*: cW 10–4 inshore.
Pied-billed Grebe *Podilymbus podiceps*: rS 4–11 ponds.
Greater Shearwater *Puffinus gravis*: aSF 7–11 offshore.
Sooty Shearwater *P. griseus*: cS,uF 7–9 offshore.
Manx Shearwater *P. puffinus*: uSF 7–10 offshore.
Leach's Storm-petrel *Oceanodroma leucorhoa*: rF 8?–10? offshore.
Wilson's Storm-petrel *Oceanites oceanicus*: rF 8?–9 offshore.
(Northern) Gannet *Morus bassanus*: uS,cF 5–11 offshore. 1977–79 breeding attempt at White Horse Island (Gaskin and Smith 1979).
Great Cormorant *Phalacrocorax carbo*: cW 9–4 inshore. Former breeding at White Horse Island (Tufts and Townsend 1924) and Maces Bay (Squires 1976).
Double-crested Cormorant *P. auritus*: aSB 4–11 inshore.
Great Blue Heron *Ardea herodias*: cSB 4–11 shallow water.
Green Heron *Butorides striatus*: rS 5–9 sheltered shores of shallow waters.
Black-crowned Night Heron *Nycticorax nycticorax*: rM 4–5, 8–10 tidal pools and creeks.
American Bittern *Botaurus lentiginosus*: uSB 4–10 marshes, swamps.
Canada Goose *Branta canadensis*: cM 3–4, 10–12 lakes, marshes, intertidal.
Brant *B. bernicla*: aSp 3–5 intertidal areas with gentle slope.
Mallard *Anas platyrhynchos*: uW 10–4 ponds, estuaries, and intertidal zone.
(American) Black Duck *A. rubripes*: cW,uSB 1–12 ponds, estuaries, intertidal.
(Common) Pintail *A. acuta*: rM 3–4, 9–10 marshes.
Green-winged Teal *A. crecca*: uM,rS 3–4 (5–8) 9–11 ponds, marshes.
Blue-winged Teal *A. discors*: uM 4, 8–10 ponds.
American Wigeon *A. americana*: rM 4, 10 ponds
Wood Duck *Aix sponsa*: rS 4–10 woodland ponds and sluggish streams.
Ring-necked Duck *Aythya collaris*: rSB 4–11 woodland ponds and small lakes.
Greater Scaup *A. marila*: cW 10–4 sheltered coves and estuaries.
Common Goldeneye *Bucephala clangula*: cW 10–4 inshore, estuaries.
Barrow's Goldeneye *B. islandica*: rW 11–3 estuaries, protected coves.
Bufflehead *B. albeola*: cW 10–4 sheltered coves and estuaries.
Oldsquaw *Clangula hyemalis*: aW 10–4 inshore marine.
Harlequin Duck *Histrionicus histrionicus*: rW 10–4 exposed rocky shores.
Common Eider *Somateria mollissima*: aRB 1–12 inshore marine.
White-winged Scoter *Melanitta deglandi*: cW 10–5 inshore marine.
Surf Scoter *M. perspicillata*: cW,aSp 10–5 inshore marine.
Black Scoter *M. nigra*: uW,aSp 10–5 inshore marine.
Hooded Merganser *Lophodytes cucullatus*: uM,rSB,RW 4–5, 10–11(6–9,12–3) ponds, sheltered coves, and estuaries.
Common Merganser *Mergus merganser*: uW, rSB 10–4 (5–9) estuaries, streams.
Red-breasted Merganser *M. serrator*: rSB 10–5 inshore, estuaries.
(Northern) Goshawk *Accipiter gentilis*: rRB 1–12 woodland.
Sharp-shinned Hawk *A. striatus*: cM,uSR,rW 4–11 (12–3) woodland, edges.
Red-tailed Hawk *Buteo jamaicensis*: uRB 1–12 woodland, open areas.
Broad-winged Hawk *B. platypterus*: cM, uSB 4–9 woodland.
Rough-legged Hawk *B. lagopus*: rW 11–4 fields, marshes.
Bald Eagle *Haliaeetus leucocephalus*: uRB 1–12 coastal.
Marsh Hawk (N. Harrier) *Circus cyaneus*: uM,rS 3–5(6–7) 8–10 marshes, fields.
Osprey *Pandion haliaetus*: cSB 4–10 shallow waters
Peregrine Falcon *Falco peregrinus*: rM 4,9–10 coastal.
Merlin *F. columbarius*: uM 4–5, 9–11 coastal.
American Kestrel *F. sparverius*: cM, uSB 3–10 fields and open areas.
Spruce Grouse *Canachites canadensis*: rRB 1–12 coniferous woodland.
Ruffed Grouse *Bonasa umbellus*: uRB 1–12 woodland.
Semipalmated Plover *Charadrius semipalmatus*: uSp,aF 5, 7–10 intertidal mud.
Killdeer *C. vociferus*: cSp,uSB 3–10 fields, drier shores.
Am. (Lesser) Golden Plover *Pluvialis dominica*: rF 8–10 intertidal flats.
Black-bellied Plover *P. squatarola*: uSp,cF 5,8–11 intertidal mud and sand.
Hudsonian Godwit *Limosa haemastica*: rF 8–10 intertidal mud.
Whimbrel *Numenius phaeopus*: rF 8–9 intertidal areas, fields.
Greater Yellowlegs *Tringa melanoleuca*: cM 4–5,7–11 intertidal pools, creeks.
Lesser Yellowlegs *T. flavipes*: uF 7–10 intertidal pools and creeks.
Solitary Sandpiper *T. solitaria*: rSp,uF 5, 7–10 pond shores, swamps, ditches.
Willet *Catoptrophorus semipalmatus*: rM 5, 8 intertidal areas.
Spotted Sandpiper *Actitis macularia*: uSB 5–10 fresh and salt shores, usually avoiding soft mud.
Ruddy Turnstone *Arenaria interpres*: uF 8–10 rocky and sandy intertidal areas.
Northern Phalarope *Lobipes lobatus*: cSp,aF 5,7–10 offshore, Head Harbour Passage area.
Red Phalarope *Phalaropus fulicarius*: uM 5, 8–11 offshore

American Woodcock *Philohela minor*: uSB 3–11 woodland, thickets.

Common Snipe *Capella gallinago*: uSB 4–10 marshes, swampy areas.

Short-billed Dowitcher *Limnodromus griseus*: rSp,uF 5, 7–9 intertidal mud.

Red Knot *Calidris canutus*: uF 8–10 intertidal mud and sand.

Sanderling *C. alba*: cF 7–11 intertidal, especially sandy areas.

Semipalmated Sandpiper *C. pusilla*: uSp,aF 5–6, 7–10 intertidal mud.

Least Sandpiper *C. minutilla*: cSp,aF 5,7–10 intertidal mud, marshes.

White-rumped Sandpiper *C. fuscicollis*: rSp,cF 5,8–11 intertidal mud.

Pectoral Sandpiper *C. melanotos*: uF 8–10 marshes.

Purple Sandpiper *C. maritima*: cW 9–5 intertidal rocks.

Dunlin *C. alpina*: cF 9–11 intertidal, especially pools and creeks.

Pomarine Jaeger *Stercorarius pomarinus*: rF 8–10 offshore

Parasitic Jaeger *S. parasiticus*: uF 7–10 offshore.

Glaucous Gull *Larus hyperboreus*: rW 11–4 marine and coastal.

Iceland Gull *L. glaucoides*: uW 11–4 marine and coastal

Great(er) Black-backed Gull *L. marinus*: aRB 1–12 marine and coastal.

Herring Gull *L. argentatus*: aRB 1–12 marine and coastal.

Ring-billed Gull *L. delawarensis*: uM,rW 8–11(12–2)3–5 estuaries, Head Harbour Passage area, intertidal flats.

Black-headed gull *L. ridibundus*: rW 9–1(4?) Head Harbour Passage area.

Bonaparte's Gull *L. philadelphia*: uSp,aF 4–5, 7–12 Head Harbour Passage area.

Little Gull *L. minutus*: rF 8–11 Head Harbour Passage area.

Black-legged Kittiwake *Rissa tridactyla*: aFW,rS (7)8–2 (3) offshore, Head Harbour Passage area.

Common Tern *Sterna hirundo*: uSp,aF 5,7–10 offshore, inshore.

Arctic Tern *S. paradisaea*: aF 8?–9? offshore, Head Harbour Passage area.

Razorbill *Alca torda*: cW 9–3 offshore, Head Harbour Passage area.

Common (Thin-billed) Murre *Uria aalgae*: rW 9–2? offshore.

Thick-billed Murre *U. lomvia*: uW 10–3 offshore, Head Harbour Passage area.

Dovekie *Alle alle*: eaW 10–2? offshore, Head Harbour Passage area.

Black Guillemot *Cepphus grylle*: cRB 1–12 inshore marine.

Common Puffin *Fratercula arctica*: uF 8–12 offshore.

Rock Dove *Columba livia*: cRB 1–12 towns, farms.

Mourning Dove *Zenaida macroura*: uSB,rW 3–11(12–2) farmland, towns.

Yellow-billed Cuckoo *Coccyzus americanus*: rF 9–11 woodland, thickets.

Black-billed Cuckoo *C. erythrophthalmus*: uSB 6–9 woodland, thickets.

Great Horned Owl *Bubo virginianus*: uRB 1–12 woodland.

Snowy Owl *Nyctea scandiaca*: erW 11–3 fields, other open areas.

Barred Owl *Strix varia*: uRB 1–12 woodland.

Long-eared Owl *Asio otus*: rM 4,10 woodland, edges

Short-eared Owl *A. flammeus*: rM 4,10 marshes, lowlying fields.

Saw-whet Owl *Aegolius acadicus*: uRB 1–12 woodland.

Whip-poor-will *Caprimulgus vociferus*: uSB 5–9 deciduous woodland.

Common Nighthawk *Chordeiles minor*: uM,rSB 5–9 feeds high in the air, nests on the ground in rather open areas.

Chimney Swift *Chaetura pelagica*: cSB 5–9 aerial feeder about towns, woods.

Ruby-throated Hummingbird *Archilochus colubris*: uSB 5–9 woodland edge, gardens.

Belted Kingfisher *Megaceryle alcyon*: cSB,rW 4–11(12–3) shallow waters.

Common Flicker *Colaptes auratus*: cSB 4–10 open woods, edge, fields.

Yellow-bellied Sapsucker *Sphyrapicus varius*: uSB 4–10 mixed and deciduous woodland.

Hairy Woodpecker *Picoides villosus*: uRB 1–12 woodland.

Downy Woodpecker *P. pubescens*: uRB 1–12 woodland, mainly deciduous.

Black-backed Three-toed Woodpecker *P. arcticus*: rRB 1–12 coniferous woods.

Eastern Kingbird *Tyrannus tyrannus*: uSB 5–8 farmland, woodland edge.

Eastern Phoebe *Sayornis phoebe*: uSB 4–10 edge habitats, usually near water.

Yellow-bellied Flycatcher *Empidonax flaviventris*: cSB 6–8 coniferous woods.

Alder Flycatcher *E. alnorum*: cSB 6–8 alder thickets.

Least Flycatcher *E. minimus*: cSB 5–9 deciduous woodland.

Eastern Wood Pewee (E. Pewee) *Contopus virens*: cSB 5–9 deciduous woodland.

Olive-sided Flycatcher *Nuttallornis borealis*: uSB 5–8 open coniferous woods.

Horned Lark *Eremophila alpestris*: uM 3–4, 10–12 fields, shores, marshes.

Tree Swallow *Iridoprocne bicolor*: cSB 5–8 aerial feeder near woods, towns, water.

Bank Swallow *Riparia riparia*: cSB 5–8 aerial feeder near sand and gravel, water, banks.

Barn Swallow *Hirundo rustica*: cSB 5–9 aerial feeder near buildings, fields.

Cliff Swallow *Petrochelidon pyrrhonata*: uSB 5–9 aerial feeder near buildings, fields.

Gray Jay *Perisoreus canadensis*: uRB 1–12 coniferous woodland.

Blue Jay *Cyanocitta cristata*: cRB 1–12 woodland, towns.

Common (Northern) Raven *Corvus corax*: cRB 1–12 most coastal habitats.

Common (American) Crow *C. brachyrhynchos*: cRB 1–12 most coastal habitats.

Black-capped Chickadee *Parus atricapillus*: cRB 1–12 woodland, shade trees, thickets.

Boreal Chickadee *P. hudsonicus*: cRB 1–12 coniferous woodland.

White-breasted Nuthatch *Sitta carolinensis*: rRB 1–12 deciduous woodland.

Red-breasted Nuthatch *S. canadensis*: ecRB 1–12 coniferous woodland.

Brown Creeper *Certhia familiaris*: uRB 1–12 woodland.

Winter Wren *Troglodytes troglodytes*: cSB 4–10 coniferous woodland.

(Northern) Mockingbird *Mimus polyglottos*: rR 81–12 thickets.

Gray Catbird *Dumetella carolinensis*: cSB 5–9 thickets.

Brown Thrasher *Toxostoma rufum*: rSB 5–10 thickets.

American Robin *Turdus migratorius*: aSB,rW 3–11 (12–2) woods, farms, towns.

Wood Thrush *Hylocichla mustelina*: rSB 5–9 deciduous woodland.

Hermit Thrush *Catharus guttatus*: cSB 4–10 woodland.

Swainson's Thrush *C. ustualatus*: cSB 5–10 coniferous woodland.

Gray-cheeked Thrush *C. minimus*: rM 5–6, 9–10 woodland.

Veery *C. fuscescens*: cSB 5–9 damp deciduous and mixed woodland.

Eastern Bluebird *Sialia sialis*: rSB 4–10 farmland, blueberry barrens.

Golden-crowned Kinglet *Regulus satrapa*: uRB,cM 1–12 coniferous and mixed woodland.

Ruby-crowned Kinglet *R. calendula*: cSB 4–10 coniferous and mixed woodland.

Water Pipit *Anthus spinoletta*: uM 5,9–10 open fields and shores.

Bohemian Waxwing *Bombycilla garrulus*: rW 11–3 around fruit-bearing trees.

Cedar Waxwing *B. cedrorum*: cSB 6–9 woodland edges and openings.

Northern Shrike *Lanius excubitor*: euW 11–4 rather open areas with scattered trees or tall bushes.

(European) Starling *Sturnus vulgaris*: cRB,eM 1–12 farms, towns, wood edges.

Solitary Vireo *Vireo solitarius*: uSB 5–9 mixed woodland.

Red-eyed Vireo *V. olivaceus*: cSB 5–9 mainly deciduous woodland.

Philadelphia Vireo *V. philadelphicus*: rM 5,8–9 woodland, thickets.

Black-and-White-Warbler *Mniotilta varia*: cSB 5–9 deciduous and mixed woods.

Tennessee Warbler *Vermivora peregrina*: cSB 5–9 woods, thickets.

Nashville Warbler *V. ruficapilla*: cSB 5–9 mixed woodland.

Northern Parula (Warbler) *Parula americana*: cSB 5–9 mixed and coniferous woodland.

Yellow Warbler *Dendroica petechia*: cSB 5–9 deciduous thickets, gardens.

Magnolia Warbler *D. magnolia*: cSB 5–9 young conifers and coniferous edge.

Cape May Warbler *D. tigrina*: uSB 5–9 coniferous woods.

Black-throated Blue Warbler *D. caerulescens*: uSB 5–9 deciduous saplings in deciduous or mixed woodland.

Yellow-rumped Warbler *D. coronata*: cSB 4–11 coniferous and mixed woods.

Black-throated Green Warbler *D. virens*: cSB 5–9 woodland.

Blackburnian Warbler *D. fusca*: cSB 5–9 mixed and coniferous woodland.

Chestnut-sided Warbler *D. pensylvanica*: cSB 5–9 young deciduous and mixed woodland.

Bay-breasted Warbler *D. castanea*: cSB 5–9 coniferous woodland.

Blackpoll Warbler *D. striata*: uM,rS 5–6(7–8)9–10 woodland (coniferous during breeding season).

Palm Warbler *D. palmarum*: uSB 4–11 coniferous scrub at bog edges, in migration widespread in thickets and woodland edge.

Ovenbird *Seiurus aurocapillus*: cSB 5–9 predominantly deciduous woods.

Northern Waterthrush *S. noveboracensis*: cM,uSB 5–9 swamps, shoreline thickets.

Mourning Warbler *Oporornis philadelphia*: uSB 6–8 low shrubbery in forest openings.

Common Yellowthroat *Geothlypis trichas*: cSB 5–10 low shrubbery, often wet.

Yellow-breasted Chat *Icteria virens*: rF 9–11 thickets.

Wilson's Warbler *Wilsonia pusilla*: uSB 5–9 wet thickets.

Canada Warbler *W. canadensis*: cSB 5–9 damp thickets in or near woodland.

American Redstart *Setophaga ruticilla*: cSB 5–9 deciduous and mixed woodland, tall thickets.

House Sparrow *Passer domesticus*: cRB 1–12 towns, farms.

Bobolink *Dolichonyx oryzivorus*: cSB 5–9 moist fields.

Eastern Meadowlark *Sturnella magna*: rSB 4–10 dry fields.

Red-winged Blackbird *Agelaius phoeniceus*: aSp,uSB 3–11 marshes, shoreline thickets.

Northern Oriole *Icterus galbula*: uM 5,8–9(–11) deciduous shade trees.

Rusty Blackbird *Euphagus carolinus*: uSB 4–10 swampy woods.

Common Grackle *Quiscalus quiscula*: aSp,cSB,rW 3–11(12–2) woods near water, towns, farms.

Brown-headed Cowbird *Molothrus ater*: aSp,cSB,rW 3–10(11–2) farms, open areas.

Scarlet Tanager *Piranga olivacea*: uM 5, 8–9 woodland, thickets.

(Northern) Cardinal *Cardinalis cardinalis*: rRB 1–12 towns, thickets.

Rose-breasted Grosbeak *Pheucticus ludovicianus*: uSB 5–9 deciduous woods.

Indigo Bunting *Passerina cyanea*: rS 5–10 thickets, woodland edge.

Dickcissel *Spiza americana*: rF 8–11 fields, towns

Evening Grosbeak *Herperiphona vespertina*: eaRB 1–12 woodland, towns.

Purple Finch *Carpodacus purpureus*: cSB,euW 4–10(11–3) woodland, towns.

Pine Grosbeak *Pinicola enucleator*: ecW 10–4 woodland.

Common Redpoll *Carduelis flammea*: eaW 10–4 thickets, fields, woods.

Pine Siskin *C. pinus*: ecRB 1–12 woods, thickets.

American Goldfinch *C. tristis*: ecRB 1–12 towns, fields, thickets.

Red Crossbill *Loxia curvirostra*: ecR 1–12 coniferous woodland.

White-winged Crossbill *L. leucoptera*: ecRB 1–12 coniferous woodland.

Rufous-sided Towhee *Pipilo erythrophthalmus*: rM 4–5,9–11 thickets.

Savannah Sparrow *Passerculus sandwichensis*: cSB 4–10 fields, grassy headlands, islands and beaches, salt marsh.

Sharp-tailed Sparrow *Ammospiza caudacuta*: rM 5–6,9–11 salt marsh.

Vesper Sparrow *Pooecetes gramineus*: rM 4, 9–10 dry fields, barrens.

Dark-eyed (Northern) Junco *Junco hyemalis*: cSB,uW 1–12 coniferous and mixed woodland, thickets.

(American) Tree Sparrow *Spizella arborea*: cW 10–4 thickets, old fields.

Chipping Sparrow *S. passerina*: cSB 5–10 woodland edge, towns.

Field Sparrow *S. pusilla*: rM 5,10–11 thickets.

White-crowned Sparrow *Zonotrichia leucophrys*: uM 5,9–10 thickets, edge.

White-throated Sparrow *Z. albicollis*: cSB,rW 4–10(11–3) coniferous and mixed woodland, edge, thickets.

Fox Sparrow *Passerella iliaca*: ecSp,uF 3–4,10–11 thickets.

Lincoln's Sparrow *Melospiza lincolnii*: uSB 5–10 bog edges, wet old fields.

Swamp Sparrow *M. georgiana*: cSB 4–10 wet thickets, marsh edges.

Song Sparrow *M. melodia*: cSB,rW 3–11(12–2) thickets, edge, gardens.

Lapland Longspur *Calcarius lapponicus*: rW 10–3 fields, salt marsh.

Snow Bunting *Plectrophenax nivalis*: ecW 10–4 fields, salt marsh, beaches.

CHAPTER 15

Amphibians and Reptiles

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Introduction

Although this is basically a marine treatise the inclusion of the amphibians and reptiles of our marine coastal shoreline is justified if only to stress the gaps in our knowledge. There has never been, in the Bay of Fundy area, quantitative research on salinities in local coastal habitats nor examination of coastal amphibians and reptiles for marine prey species in their gut contents. Few persons are aware that barachois pools on both the open coast and in protected bays can have breeding choruses of anurans in early spring. The authors have observed Wood Frogs *Rana sylvatica sylvatica*, Leopard Frogs *Rana pipiens pipiens*, American Toads *Bufo americanus*, and the Northern Spring Peeper *Hyla crucifer crucifer* in such barachois habitats where cat-tails and cranberry were present, but where extreme spring tides flooded into that vegetational zone. These coastal habitats are essentially freshwater marshes in the spray zone or saline pools with a freshwater surface layer, although some supralittoral marine species occur there and may serve as food. Even on the exposed rocky shore we have seen toad tadpoles in the highest spray zone rock pools, where salinities (although not yet measured) were probably low due to rain or runoff.

Turtles have not been reported from barachois pools. The ubiquitous Eastern Garter Snake *Thamnophis sirtalis* certainly preys on coastal frogs and probably marine fish in tide pools. This snake is highly aquatic, so there is no reason not to suspect that it fishes in tide or marsh pools, as the closely related species *T. elegans* has been observed to do in British Columbia (F. Cook personal communication). Salamanders may be more sensitive to chemical changes in water bodies near the coast; nevertheless, the stream-loving habitat-specific Northern Dusky Salamander *Desmognathus fuscus fuscus* has been reported within 10 ft of the seashore. Recent research in the Appalachian Mountains has shown that salamanders are much more sensitive to acid-rain than frogs and may be completely eliminated from ponds and lakes where frogs are still maintaining populations. A monitoring of the effect of acid-rains and saline-rains along the coast of the Quoddy Region would be a worthy project. Another aspect worthy of study is related to hibernation and involves a significant difference at the ordinal level. Frog larvae hibernate and thus escape temperature extremes, oxygen depletion, and other winter stresses; salamander larvae are active in winter, even under ice, and are subject to winter kill in ponds due to oxygen depletion and perhaps, along the coast, from winter storms, tides, and spray.

In summary, we emphasize that coastal amphibians and reptiles in New Brunswick do occupy aquatic habitats at the shore, but ones that are basically freshwater, with non-marine flora. However, these habitats can be submerged during spring tides and storms and are undoubtedly subjected to saltspray.

Information Gaps

We really know very little about size range and seasonal activity of amphibians and reptiles in New Brunswick. To obtain such information requires a great deal of patient observation and careful record-keeping. Persons who live near frog or turtle ponds can make a major contribution to our understanding of the lives of the amphibians and reptiles in eastern Canada by recording the times at which they emerge from hibernation, the times at which they breed, the length of the larval periods or egg incubations, growth rates, migrations to and from ponds, and then by relating this to temperature and weather conditions. Such information and any specimens should be sent to the New Brunswick Museum in Saint John or the National Museum of Natural Sciences, Ottawa. The collection of specimens for deposition with certified museums is certainly justified. Such incidental collection is unlikely to endanger a species of amphibians or reptiles, but habitat destruction may. Commercial exploitation is not significant in New Brunswick and it should not be permitted except under strict control. Information on the distribution and fluctuations of amphibians and reptiles in southwestern New Brunswick will allow documentation of habitat determination and will suggest possible nature reserve sites.

whole snake since skins can be easily identified to species.

6) The mixed woodland habitat and old coniferous woods have many species of amphibians and reptiles. Searches can be made in the abundant cover of moss layers, leaf litter, large stones, and rotten logs. Snakes are often found in sunny glades in woods, and a walk through a woodland on a rainy night will often reveal a number of frogs and salamanders moving about on the forest floor. Adult Wood Frogs *Rana sylvatica* in this habitat have the interesting habit of turning in mid-air when they jump and landing facing their pursuer. When lunged at they may immediately leap past legs or over shoulders, and disappear in the leaf litter before you have a chance to turn around.

Two interesting salamanders may be encountered in areas of moist forest litter and logs. The first is the red eft which is the juvenile stage of the aquatic adult Red-spotted Newt *Notophthalmus viridescens viridescens*. Efts are brick red with a rough skin and may spend 2–3 yr on land before becoming mature. The lungless Red-backed Salamander *Plethodon cinereus cinereus* is totally terrestrial and its eggs are typically laid in moist rotten logs, under rocks, or underground.

7) True bogs are a common habitat in New Brunswick and those covered with sphagnum moss and with a floating margin bordering on a stillwater or pond should be ideal for an unusual salamander that has yet to be discovered in New Brunswick, although often reported in Nova Scotia. This is the Four-toed Salamander which lays eggs in grape-like clusters in sphagnum moss that overhangs water. The larvae hatch and fall into the water below where they continue their development until they metamorphose in the autumn. These salamanders may be found by turning up the overhanging moss along the edge of water, particularly if there is a log projecting out into the water that has a blanket of sphagnum moss over it. The adults may be found curled around the egg clusters, guarding them. The adult dorsum is the same color as the brown base of sphagnum moss, but their underside is milk-white with small black spots and readily seen once the moss is flipped over.

8) In the cold, well-oxygenated streams and rivers of New Brunswick there are two salamander species which have not been recorded in the other Atlantic Provinces. These are lungless salamanders, which may be found in streams or near their margins. One is the slender Northern Two-lined Salamander *Eurycea bislineata bislineata* and the other the stouter Northern Dusky Salamander *Desmognathus fuscus fuscus*.

Twin Lakes, near Waweig, Charlotte County, is a favorite collecting area, and is easy to reach by road. If the area is visited on a number of occasions from spring until fall probably about 80% of the species known from the area can be observed.

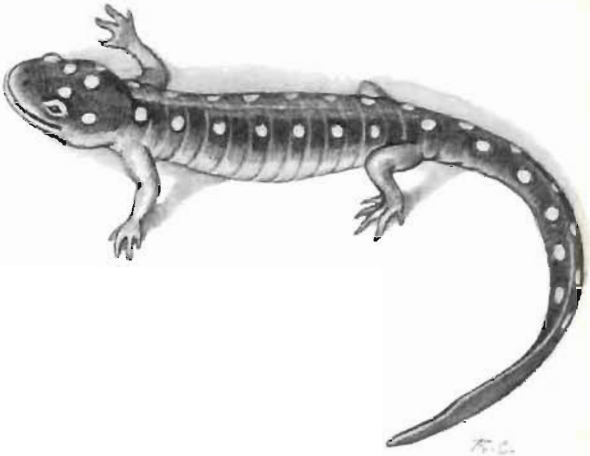

FIG. 1 Spotted Salamander, *Ambystoma maculatum*, × 0.6.

Annotated List of Species

Amphibia: Caudata — Salamanders

SPOTTED SALAMANDERS — *Ambystoma maculatum* (Ambystomatidae), Fig. 1, are the largest salamanders found in New Brunswick with females reaching 205 mm (approx. 8 inches); the males are somewhat smaller. The dorsal color is slate black with a row of large yellow spots along each side of the back.

Both sexes assemble at shallow ditches and ponds at night in early spring, sometime during the first week in April in the southern part of the province. The large firm egg masses are attached to twigs or grass in shallow water and hatch after about 4 wk. Usually each egg capsule becomes green with symbiotic algae while the rest of the egg mass remains clear or translucent, so that the entire egg mass looks like green peas in clear aspic. After mating, the adults return to a fossorial existence and are rarely seen during the rest of the year. The salamander larvae may transform anytime from the end of July to autumn. At this stage they are about 75 mm (approx. 3 inches) long and feed on small worms and insects. In some areas of Nova Scotia they commonly overwinter as larvae and are active beneath the ice cover, transforming only the following spring and summer. This phenomenon has been reported for New Brunswick populations at Oak Point, Kings County.

The Spotted Salamander is well known and widely distributed in New Brunswick.

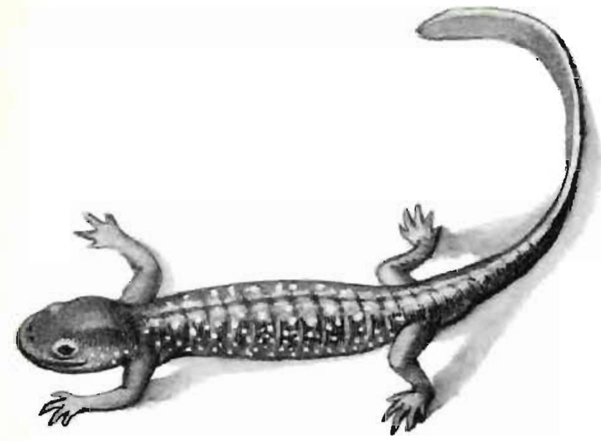

FIG. 2. Blue-spotted Salamander, *Ambystoma laterale*, × 0.7

BLUE-SPOTTED SALAMANDERS — *Ambystoma laterale* (Ambystomatidae), Fig. 2, are smaller and slimmer than the Spotted Salamanders, the females up to 153 mm (approx. 6 inches) long and the males somewhat smaller. They are slate black and have bluish white flecks on the sides.

The Blue-spotted Salamander may be found spawning in ditches and ponds during April, but is fossorial the rest of the year. The egg masses resemble those of the Spotted Salamander, but are smaller, having an average of 16 eggs/mass compared to 100 eggs/mass for Spotted Salamanders.

In certain populations of the Blue-spotted Salamander, such as that of the lower St. John River Valley, a triploid form exists; it is composed almost entirely of females, and was formerly considered a distinct species. However, Cook and Gorham (1979), following Lazzell (1968) and Shultz (1969), felt that the triploid population should not be considered as "species" but rather, quoting Schultz (1969, p. 608): "The fact remains that the all-female forms are hybrids and should be treated as such."

The Blue-spotted Salamander has been collected in most of the southern and eastern counties of New Brunswick.

RED-SPOTTED NEWTS — *Notophthalmus viridescens viridescens* (Salamandridae) Fig. 3. Aquatic salamanders range in size from 75 to 102 mm (approx. 4 inches), females being the largest. Adults are olive green to greenish above with two rows of tiny black-bordered red spots. In breeding season, May and June, the males have a pronounced crest on the tail. This species sometimes remains active during winter under the ice in ponds and lakes.

The Red-spotted Newt has an interesting life history. The eggs are usually deposited singly on aquatic vegetation, and hatch in about 30 d. Approximately 2 mo later they transform and leave the water, becoming terrestrial juveniles known as red efts, as they are brick red and have a dry rough toad-like skin. The eft may remain on land for 1–2 yr before returning to the water and changing to the adult coloration.

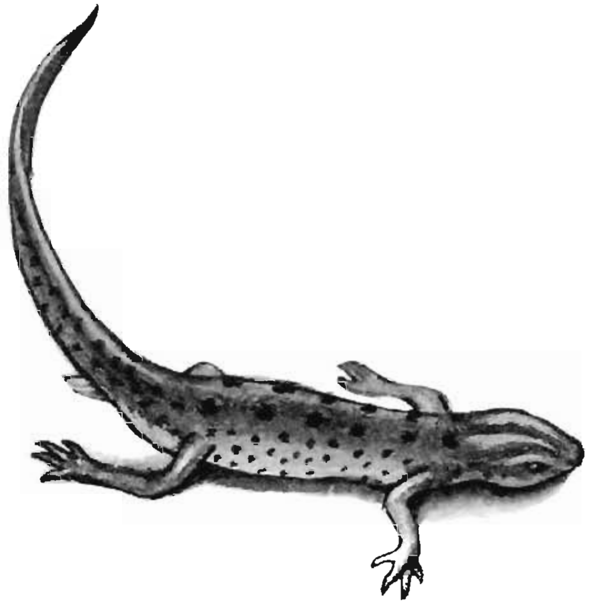

FIG. 3. Red-spotted Newt, *Notopthalmus viridescens*, × 0.6.

The Red-spotted Newt is widely distributed in New Brunswick, but except in the eft stage is limited to permanent bodies of water such as tiny oxbow ponds, acid bog ponds, alkaline gypsum ponds, rock or gravel quarry ponds, and large lakes.

NORTHERN DUSKY SALAMANDERS — *Desmognathus fuscus fuscus* (Plethodontidae), Fig. 4, vary in length from 102 mm to 133 mm (approx. 4 to 5.5 inches). The dorsal color ranges from gray-brown to almost black while the venter is sometimes mottled with gray and brown. Young specimens may be dark yellow to light brown above with small light spots and a line running down each side of the back; at this stage they could be mistaken for Northern Two-lined Salamanders but can be distinguished by the light line from eye to angle of the jaw that is very pronounced in the Northern Dusky Salamander, and by their large hind legs.

This salamander has an unusual adaptation: the upper jaw is hinged, and with this mechanism it can thrust its snout under small stones, lever them up with the upper jaw, and get at the invertebrates hiding beneath. It is believed that the poorly oxygenated waters of the Tantramar marshes have prevented these stream-dependent salamanders from crossing into Nova Scotia.

Northern Dusky Salamanders are found near springs or cold brooks, under stones or in the muddy bottom. In July or August, eggs are laid in a cluster in moist cavities near the water's edge and are guarded by the female. This species remains active from early spring to late fall; during the winter it stays in the unfrozen mud at the bottom of springs and on occasion may be seen during mid-winter.

The Northern Dusky Salamander is found in southern New Brunswick north as far as southern Carleton County and northern Westmorland County. It has not been recorded from the central and northern parts of the

Several phenomena of special interest and of which we have very little information include (1) communal nesting of Northern Ringneck Snakes *Diadophis punctatus edwardsi*, (2) nesting congregations of Wood Turtles *Clemmys insculpta* on sandbars along streams, (3) spring emergence of snakes in huge congregations, (4) triploid salamander populations of the Blue-spotted Salamander *Ambystoma laterale*, (5) the relative abundance of the three color varieties of the Redback Salamander *Plethodon cinereus cinereus*, (6) the several species from the State of Maine which have yet to be found in New Brunswick, and (7) the survival rate of overwintering turtle nestlings in frozen ground.

Preservation Methods

Adult amphibians and reptiles can be readily killed by enclosing them, with cotton soaked with ether, in an airtight container. They can also be killed by freezing, and preserved as they are thawing. After they are dead or frozen they can be transferred directly to a 10% formaldehyde solution. Tadpoles and eggs of frogs or reptiles can be placed directly in 5% formaldehyde. Larger snakes and turtle specimens should either have the abdominal region slit open or be injected with formaldehyde with a large veterinarian-type syringe. All specimens must be accompanied by a label which includes the day, month, and year in which the specimens were collected and the locality and habitat, in great detail if possible, (e.g. miles and direction from nearest town, lat., long., military and topographical maps, etc.). Unfortunately, as these specimens are in liquid, the paper labels must be waterproof or water-resistant and written on either in lead pencil or waterproof ink. Interested persons can obtain proper labels on which to record their data from museums. Specimens need not be shipped to the museum in glass jars but can be removed, wrapped in wet paper, and placed in an airtight plastic bag for shipment.

Distribution

The number of species of amphibians and reptiles in the Quoddy area does not differ appreciably from other areas in southern New Brunswick. The one exception is the Gray Treefrog *Hyla versicolor* known with certainty from Barker's Point in Lower St. Marys near Fredericton. However, this species is reported from Moosehorn Wildlife Refuge in Maine, less than 0.5 km from the New Brunswick border, and can be considered a possibility in the Quoddy area, as may the Northern Water Snake *Natrix sipedon*, which also occurs in Moosehorn Wildlife Refuge.

Maine has 32 species of amphibians and reptiles of which 9 have not been found in New Brunswick. New Brunswick and Nova Scotia each have 22 species. Three species not recorded in New Brunswick but which occur in Nova Scotia are the Eastern Ribbon Snake *Thamnophis sauturus sauturus*, Blanding's Turtle *Emydoidea blandingii*, and the Four-toed Salamander *Hemidactylum scutatum*. In turn there are three species in New Brunswick which have not spread into Nova Scotia: the Gray Treefrog *Hyla versicolor*, the Northern Two-lined Salamander *Eurycea bislineata bislineata*, and the Northern Dusky Salamander *Desmognathus fuscus fuscus*.

The islands of the Bay of Fundy have a number of species which are common on the mainland. The American Toad *Bufo americanus*, Wood Frog *Rana sylvatica*, Eastern Smooth Green Snake *Opheodrys vernalis vernalis*, and Northern Redbelly Snake *Storeria occipitomaculata occipitomaculata* are known from Grand Manan Island but all have been introduced (Lorimer 1876). Deer Island, which is much closer to the mainland, supports more species: Pickerel Frog *Rana palustris*, Green Frog *Rana clamitans melanota*, Red-spotted Newt *Notophthalmus viridescens viridescens*, Spotted Salamander *Ambystoma maculatum*, Redback Salamander *Plethodon cinereus cinereus* (Christie 1973), and other species may possibly be found there. Campobello Island probably has more species from the mainland, but there are no specimens from that island in the New Brunswick Museum and only a few in the National Museum of Natural Sciences, Ottawa, so here again more surveys are needed.

How to Find Amphibians and Reptiles

In early spring, as soon as ice has melted from ponds and pools and while snow is still in the woods, it is possible to locate the best pools for amphibian breeding by driving along quiet back roads in the evening or after dark and periodically stopping and listening for frogs. The earliest calls will be those of the Wood Frog *Rana sylvatica* and the Northern Spring Peeper *Hyla crucifer crucifer*; their presence sometimes indicates a body of water which will be used sequentially by other frogs and even turtles and snakes during the rest of the summer. After these ponds are located, their margins should be searched carefully for frogs and salamanders laying their eggs. This may occur in a very restricted area that might be readily overlooked if searching the pond during the daytime. Once a pond is located at night, a daytime search may reveal evidence of other species such as the Spotted Salamander *Ambystoma maculatum*, the males of which deposit little white blobs of spermatophores. Having located these spermatophores one can return at night with lamps and re-examine the same area. Such a pond may also have large frog tadpoles and salamander larvae which over-wintered there and are now almost a year old.

An interesting phenomenon often associated with rainy nights in early spring is the mass migration of frogs and salamanders to breeding sites. These are most readily seen crossing roadways and can be searched for by driving along roadways at night. Occasionally even Maritime Garter Snakes *Thamnophis sirtalis sirtalis* will be seen accompanying these edible migrations.

Whereas frog and salamander detection is basically a night-time activity, searching for snakes and turtles is a late spring or summer daytime activity. Snakes are usually quite difficult to locate unless basking on a road or under some artificial cover such as boards and tarpaper which can be readily overturned. If boards or sheets of plywood or tin are put out along the edges of fields or at the sides of ponds, snakes will often frequent these shelters to bask or to feed on the invertebrates which congregate under such cover, and may be observed there. Drift fences and pitfall traps may be used as well, but these are rather time-consuming and difficult to maintain. An essential piece of apparatus for locating turtles is a pair of binoculars. Turtles are often present in vegetated bays and ponds, with their heads exposed amongst the aquatic plants, but without the magnification of binoculars or more ideally, a telescope, it is difficult to distinguish the heads from the vegetation. The pigment pattern on the heads of turtles in eastern Canada is very distinct and readily identifiable to species. One can improve turtle-watching locally by adding logs or large planks to the shoreline of a pond because the turtles will soon utilize these for basking. If such basking sites are not available the turtles will simply crawl out on grassy banks or in amongst cattails, where they are nearly impossible to find. Other evidence of turtles are the remains of eggs dug out of nests by raccoons. Gravel and sand banks and even old sawdust piles should be examined for evidence of these pillaged nests, and the eggshells should be collected for identification. It is often worthwhile to dig down deeper at the nest site, as the raccoons may have overlooked some of the deeper eggs and intact eggs are easier to identify.

In late autumn and through the winter, amphibian and reptile studies and collections can be pursued at ponds and lakes. Spring-fed water sources where many of these species hibernate are often especially interesting. If one digs into the soft mud near springs or cuts holes in the ice over spring-fed ponds, larvae and adults may be found. If salamander larvae are placed in aquaria at room temperature and fed small worms, they will transform in a few weeks and then can be readily separated to species. Spotted Salamanders *Ambystoma maculatum* or Blue-spotted Salamander *Ambystoma laterale* are the only two likely to overwinter.

Typical Habitats and Their Characteristics

Included here are the species that one would be most likely to find in some of the distinct habitats of southern and western New Brunswick. Other species may be present, but due to the thickness of the vegetation or to fossorial habits they are unlikely to be discovered.

1) Deep roadside ditches, small pools, and ponds with permanent water that is typically spring-fed constitute one habitat. In early spring, at night, such species as the Spotted Salamander *Ambystoma maculatum*, Blue-spotted Salamander *Ambystoma laterale*, Spring Peeper *Hyla crucifer crucifer*, and Wood Frog *Rana sylvatica* should be present. For a brief period of several weeks, hundreds of individuals of these species may be seen or heard but during the rest of the year it is a real accomplishment to locate one. Later in spring and in early summer there will be a series of other species of frogs such as Northern Leopard Frogs *Rana pipiens*, Green Frogs *Rana clamitans melanota*, and American Toads *Bufo americanus* utilizing some of these same ponds. Various tadpole and salamander larvae may be present and quite often the Maritime Garter Snake *Thamnophis sirtalis pallidula* may be found hunting along the margins of such ponds.

2) Larger bodies of water, bays of lakes, and large bog ponds all with permanent aquatic vegetation are excellent areas for another association of amphibians and reptiles. In early spring the Northern Leopard Frog *Rana pipiens* and the Mink Frog *Rana septentrionalis* may be heard calling, followed a few weeks later by choruses of Pickerel Frogs *Rana palustris*, Green Frogs *Rana clamitans melanota*, and Bullfrogs *Rana catesbeiana*. There should also be a permanent population of adult Red-spotted Newts *Notophthalmus viridescens viridescens* which may be seen both day and night. These areas are also the favorite haunt of Common Snapping Turtles *Chelydra serpentina serpentina* and Eastern Painted Turtles *Chrysemys picta picta*. Again, the ubiquitous Maritime Garter Snake *Thamnophis sirtalis pallidula* should be found here as well. One would expect to find Northern Water Snakes *Natrix sipedon sipedon* in such a habitat, but the species has not yet been reported from New Brunswick. There is some confusion because Maritime Garter Snakes *Thamnophis sirtalis sirtalis* frequent shorelines and just prior to shedding their skins they are often very dark, resembling the dark brown Northern Water Snake *Natrix sipedon sipedon*, and thus are often locally termed "water snakes".

3) Along the rocky and gravelly shores of lakes or even on the stony beaches of recreational lakes one quite often finds small Pickerel Frogs *Rana palustris*. Adults can occasionally be heard calling in the summer: their call resembles a person snoring. Where canoes or rowboats are hauled up on a lake shore and remain there for several days, a frog which is usually discovered under them is the Pickerel Frog *Rana palustris*. Where there are areas of vegetation along gravel or rocky shores, a walk along the water's edge will flush a number of frogs into the water. Most of these are Green Frogs *Rana clamitans melanota* but if they scream as they leap through the air, they are juvenile Bullfrogs *Rana catesbeiana*. The Mink Frog *Rana septentrionalis*, so named because of a mink-musk odor which it emits when handled, seems to be confined to areas of water lilies where it most often perches on the lilypads. However, Mink Frogs are very difficult to approach and were considered extremely rare, until the techniques of using binoculars and shooting specimens with 22 skeet-shot proved them to be generally common and in some areas actually abundant. In many areas Green Frogs *Rana clamitans melanota*, Bullfrogs *Rana catesbeiana*, and Mink Frogs *Rana septentrionalis* occur side-by-side. The use of a telescope facilitates their identification in daylight; at night one can "jack" these species from a canoe.

4) Wet grassy areas and meadows are a favorite habitat for large Northern Leopard Frogs *Rana pipiens* and Pickerel Frogs *Rana palustris*. A related habitat found in woodland areas of the Maritimes are logroads, near lakes, which often have tall grassy centers: in these we have flushed the largest adults of both Northern Leopard Frog *Rana pipiens* and Pickerel Frog *Rana palustris*.

5) In grassy and shrub areas along the edges of roads or the edges of fields such reptiles as the Maritime Garter Snake *Thamnophis sirtalis pallidula*, Northern Redbelly Snake *Storeria occipitomaculata occipitomaculata*, Eastern Smooth Green Snake *Opheodrys vernalis vernalis*, and Northern Ring-necked Snake *Diadophis punctatus edwardsi* can be found by searching diligently. Cast snake skins, from rock or brush piles, are just as valuable as the

province. The Northern Dusky Salamander is common in the Quoddy area. Specimens have been collected within 10 ft of the highwater mark near Bayside.

FIG. 4. Northern Dusky Salamander. *Desmognathus fuscus*. × 0.6.

RED-BACKED SALAMANDERS — *Plethodon cinereus cinereus* (Plethodontidae), Fig. 5, may reach a length of nearly 128 mm (approx. 5 inches) but the average length is 77–102 mm (approx. 3–4 inches). Although it is called the Red-backed Salamander, this pattern occurs in only one phase as this species may also be uniformly dark gray (leadback phase) or reddish (erythistic phase, above). In New Brunswick the redback phase is the most common. The leadback phase can be confusing as it somewhat resembles a young Blue-spotted Salamander; the latter, however, is much stouter, with longer hind toes.

The Red-backed Salamander is terrestrial and inhabits moist woodlands. It is most often found under bark, logs, stones, and inside rotted logs and is active from May until early October. The eggs are laid in clusters and hung in moist cavities in rotted wood or under stones in July and August, attended by the female. Hatching occurs in approximately 3 wk. There is no free-living larval stage as the gills are completed in the egg, which is provided with an ample yolk. After hatching the young look like miniature adults, in both shape and color. Shortly after the heavy October frosts these salamanders burrow into the earth for the winter.

The Red-backed Salamander is widely distributed in New Brunswick. On the Atlantic coast of Nova Scotia it has been found under boards at the high tide strand line, where spruce forests border the sea coast.

FIG. 5. Red-backed Salamander. *Plethodon cinereus*. × 0.9.

FOUR-TOED SALAMANDERS - *Hemidactylum scutatum* (Plethodontidae), Fig. 6, are small, about 50 mm–90 mm (approx. 2–3.5 inches) long, with four toes on the hind foot. The color above is brown to reddish brown and the belly is white, spotted with black. This salamander is usually found in sphagnum bogs, but has also been found on moist hardwood ridges.

It has not been recorded from New Brunswick, but as it does occur in southwestern Quebec and in Nova Scotia, more specific collecting efforts in boggy areas might reveal some.

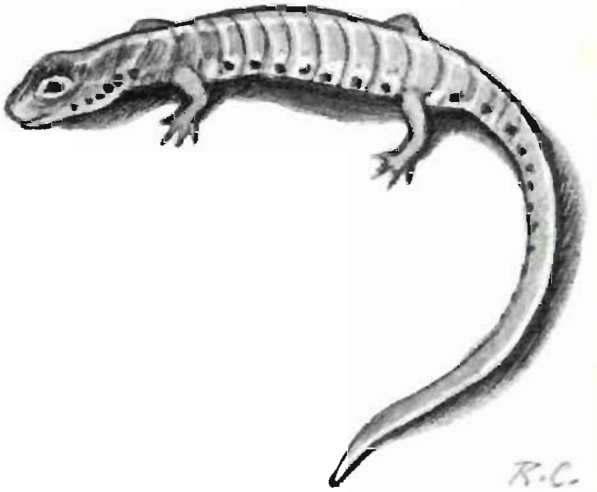

FIG. 6. Four-toed Salamander. *Hemidactylum scutatum*. × 0.1.

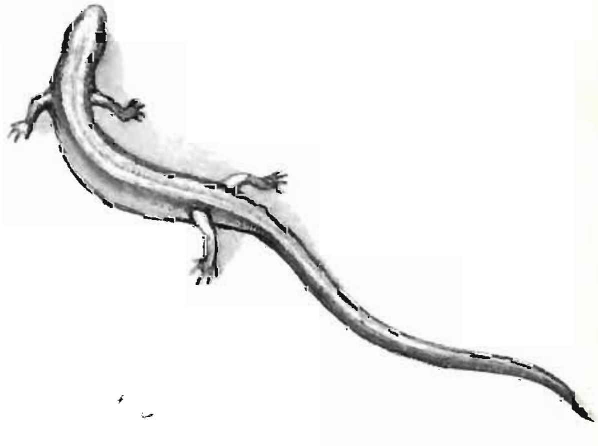

FIG. 7 Northern Two-lined Salamander. *Eurycea bislineata*. × 0.1.

NORTHERN TWO-LINED SALAMANDERS — *Eurycea bislineata bislineata* (Plethodontidae), Fig. 7, reaches a length of 100 mm (approx. 4 inches). The back is pale yellowish-brown with a distinct dark line along each side. The underside is yellowish.

The Northern Two-lined Salamander may be found in or near brooks and streams, under stones or wood. Breeding occurs from May to July and the eggs are attached to the underside of stones, usually in well oxygenated water. After hatching, the young remain in the larval stage for a year or more. They have external gills and are strictly aquatic, and spend the winter in the deeper pools which do not freeze to the bottom. The adult salamanders leave the streams in fall and hibernate during winter under rocks or in holes in the ground near the water.

The Northern Two-lined Salamander is widely distributed in New Brunswick and is reported from most areas with suitable habitat.

Amphibia: Salientia — Frogs and Toads

AMERICAN TOAD — *Bufo americanus* (Bufonidae), Fig. 8, reaches a head and body length of about 65 mm–102 mm (approx. 2.5–4 inches). Nearly everyone is familiar with the American Toad, with its roughened skin, short legs, stout body, and a large poisonous parotoid gland behind each eye. Females grow larger than males. The color varies from light to dark brown, with both lighter and darker markings on the sides and back and often a white line down the middle of the back. The underside is pale with dark spots or reticulations.

The American Toad makes its spring appearance in May and the loud trilling of the males is heard from ponds. The eggs are laid as two long strings in shallow water, and under favorable conditions hatch in 6–12 days. The young remain in the tadpole stage for approximately 60 d and then transform into tiny toads 6–12 mm long (approx. 0.25–0.5 inch). The American Toad is beneficial as it consumes many insect pests harmful to agriculture, but it also eats earthworms and beneficial insects, beetles, and ants. It hibernates in dry situations such as hillsides, where frost does not penetrate deeply.

The American Toad is widespread in New Brunswick and is well known in the Quoddy area.

FIG. 8. American Toad, *Bufo americanus*, × 0.6.

NORTHERN SPRING PEEPERS — *Hyla crucifer crucifer* (Hylidae), Fig. 9, are the smallest species of frog found in New Brunswick, ranging in size from 25 to 32 mm (approx. 1 to 1.25 inches); the females are generally larger than the males. They are brown or brownish gray with a darker X-shaped mark on the back. This frog has expanded discs on the tips of the digits which allow it to climb freely in shrubs and trees. The small adhesive discs and the small body size distinguish it from all other species, except juvenile Gray Treefrogs. The latter, however, are usually green when young.

FIG. 9. Northern Spring Peeper, *Hyla crucifer*, × 0.1

The Northern Spring Peeper makes its appearance early in April. It is amazing that this tiny frog has such a loud voice; sometimes a chorus of 100 or more may be heard calling in the evenings. The eggs are laid singly at the bottom of ponds or ditches, usually on vegetation, and they hatch quickly. The tadpoles transform in about 3 mo after which they are about 12 mm (0.5 inches) long. After the breeding season ends in June the adults leave the water and resume their arboreal life in shrubs or trees, where they feed mainly on flies and other small flying insects. Occasionally, just before summer rain storms or on warm autumn days, their distinctive shrill "peep-peep" may be heard from high in the trees. During winter they hibernate under logs, in holes in the ground, or at the bottom of ponds.

The Northern Spring Peeper is common in New Brunswick and is well known in the mainland Quoddy area.

GRAY TREEFROGS — *Hyla versicolor* (Hylidae), Fig. 10, are 40 mm–58 mm (approx. 1.5–2.25 inches) long, the females being larger than males. As the Latin name suggests, this frog can change color apparently to blend with its surroundings. The dorsum varies from gray to grayish brown or green with dark markings. The venter is pale and there is yellow or orange under the hind legs and sides of body, areas concealed when the animal is sitting but revealed when it hops. The skin is rough textured. The large adhesive discs on the tips of all digits distinguish this species from all other New Brunswick frogs except the Northern Spring Peeper which is much smaller. Although given the common name of "treefrog" the Gray Treefrog and also the Northern Spring Peeper are more closely related to toads than frogs.

FIG. 10. Gray Treefrog, *Hyla versicolor*. × 0.1.

The Gray Treefrog does not breed until the latter part of May and calling may extend into July. The call is a loud flutelike pulsed trill and once heard will not be mistaken for any other species of New Brunswick amphibian. The eggs are laid in ponds and hatch in about 1 wk. The tadpole, which transforms in about 2 mo, is about 14 mm–25 mm (approx. 0.5 to 1 inch) long. The Gray Treefrog is a great fly catcher, living mostly on flying insects and spending a good part of its time in trees.

The Gray Treefrog is restricted in New Brunswick to the mouth of the Nashwaak River and the area near Lower St. Mary's, both near Fredericton. However, it is recorded from Moosehorn Wildlife Refuge, near Calais, ME, and Vanceboro, ME. It could possibly occur in isolated pockets in mainland Quoddy.

FIG. 11. Bullfrog, *Rana catesbeiana*. × 0.4.

BULLFROGS — *Rana catesbeiana* (Ranidae), Fig. 11, is the largest species of frog found in New Brunswick; adults are 100–150 mm (approx. 4–6 inches) long, the females slightly larger than males. This species lacks the ridges along each side of the back common to other New Brunswick ranids, and the toes are webbed to the tips.

Although one may observe Bullfrogs in late April they do not begin calling and breeding until late June or early July. The voice of the Bullfrog is loud and deep — "Jug-o-Rum" — and males can be heard during warm evenings. The eggs are laid in a thin sheet and float on the surface. Tadpoles at our latitude may stay in this stage for 3 yr before transforming, at which time they may reach 100–150 mm (approx. 4–6 inches) total length. Although the Bullfrog is limited to permanent ponds and lakes, some individuals may be found in moist places quite a distance from water. The Bullfrog feeds on anything that moves including its own kind, other frogs, toads, salamanders, small snakes, turtles, mice, birds, as well as insects and earthworms.

The Bullfrog is found in southern, western, and northern New Brunswick, and is known from mainland Quoddy.

FIG. 12. Green Frog, *Rana clamitans melanota*. × 0.5.

GREEN FROGS — *Rana clamitans melanota* (Ranidae), Fig. 12, are the common frogs of ditches, ponds, lake shores, rivers, and streams; adults are 50–100 mm (approx. 2–4 inches) long. The color is usually drab green with bright green on the upper jaw. The male has a yellow throat and the female a white throat. There are narrow dorsolateral ridges along the upper sides and these distinguish it from the Bullfrog. Green Frogs can be distinguished from Mink Frogs by the hind legs: the Green Frog has a series of dark cross-bars across the long axis of the leg while the legs of the Mink Frog have blotched or spotted elongated markings parallel to the long axis of the leg.

The Green Frog breeding season lasts from late May until August. The call of the male somewhat resembles the sound of a banjo string being plucked, hence the name "banjo frog." The egg masses are attached to vegetation in still water and hatch in about 2–4 wk. The tadpole overwinters and, depending on when it hatched, transforms the following summer any time between April and September. After transformation the young frog measures about 25 mm (approx. 1 inch).

The Green Frog is one of the most widely distributed of the amphibians found in New Brunswick.

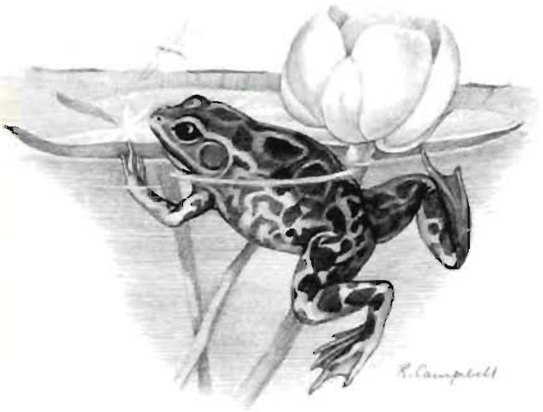

FIG. 13. Mink Frog, *Rana septentrionalis*. × 0.6.

MINK FROGS — *Rana septentrionalis* (Ranidae), Fig. 13, are medium-sized frogs measuring 50–75 mm (approx. 2–3 inches). The general color is greenish to brownish olive with dark mottling on the back and beneath. The dorsolateral ridges are poorly developed and may even be incomplete and inconspicuous. The hind legs are blotched or spotted and these markings distinguish it from the similar-sized Green Frog, which has definite crossbars on the hind legs. A Mink Frog in the hand usually emits a musky odor reminiscent of mink, hence the name.

Little is known of the breeding habits of the Mink Frog in New Brunswick, but it appears that it does not breed until late May and June. The tadpole overwinters and at transformation in July or August of the following year is about 38 mm (approx. 1.5 inches). There is little information on the food habits of this species in New Brunswick but it is insectivorous like other frogs.

The Mink Frog has been collected in most of the southern and central counties and northwestern New Brunswick. It is a common frog in Twin Lakes, near Waweig, Charlotte County, but is apparently not found in many other ponds and lakes where the habitat would appear to be suitable.

FIG. 14. Wood Frog, *Rana sylvatica*. × 0.8.

WOOD FROGS — *Rana sylvatica* (Ranidae), Fig. 14, are a medium sized species ranging from 35 mm to 83 mm (approx. 1 to 3.33 inches) in length, the females larger than the males. The color is light reddish brown to dark brown on the back and white beneath; females are usually a lighter brown or very reddish. It has a dark brown streak or mask on either side of the head and a prominent dorsolateral ridge.

The Wood Frog is one of the earliest spring callers and the loud duck-like "clack-clack" can be heard from mid-April to early May in ponds, ditches, bogs, and lakes. The breeding season lasts only a few weeks, and then the adults return to the woodlands. The eggs are laid in a round dark mass usually attached to submerged grass or vegetation in shallow water, and the incubation time is approximately 2 wk. The tadpole stage lasts about 60 d after which transformation into frogs, ranging in size from 18 mm to 25 mm (0.75 to 1 inch) takes place. They hibernate on land.

The Wood Frog is widely distributed in New Brunswick, being found in all counties. They are common in the mainland Quoddy area but it would only be by accident that one would find an adult after the breeding season.

FIG. 15. Northern Leopard Frog, *Rana pipiens*. × 0.7

NORTHERN LEOPARD FROGS — *Rana pipiens* (Ranidae), Fig. 15, are the common spotted grass frogs and are 77 mm–100 mm (approx. 3–4 inches) long. The general color is green or brown above and white beneath. There are rounded dark brown spots on the back which have light borders. The dorsolateral ridges are conspicuous.

The Northern Leopard Frog emerges from hibernation in late April or early May, and in some localities large migrations to the breeding ponds may be observed. During this migration, which usually takes place on a rainy night, sometimes hundreds are killed by automobiles on busy roads. The mating call of the male is a guttural snoring sound usually repeated about five times. Eggs are laid in shallow water in oblong masses. After hatching and a tadpole stage of about 60 d, the transformed frog is about 25 mm (approx. 1 inch) long. After breeding season, in late May or June, the adults leave the ponds and return to their terrestrial life in moist, open, grassy areas. They hibernate in and near ponds and also in moist places on land.

The Northern Leopard Frog is found in grassy and cultivated land throughout New Brunswick. It is well known in the Quoddy area.

FIG. 16. Pickerel Frog. *Rana palustris*, × 0.7.

PICKEREL FROGS — *Rana palustris* (Ranidae), Fig. 16, are the common frog of swamps, boggy ponds, and lakes, and are 50–75 mm (approx. 2–3 inches) long. The rows of dark brown spots are square or rectangular and the general color is golden bronze; the bright orange of the underside of the hind legs distinguishes this species from similar frogs, except for newly transformed individuals on which it is absent or faint.

The Pickerel Frog mates in late April and May. The call is similar to that of the Northern Leopard Frog, but is a lower, pronounced snoring sound. The eggs are laid in shallow water and after hatching the tadpoles transform in about 2.5 mo. The newly transformed young are 20–25 mm (approx. 0.75–1 inch) long. Adults leave the water after mating and can be found in moist rocky ravines, rocky lake shores, and grassy areas.

The Pickerel Frog is widely distributed in suitable habitats in New Brunswick.

Reptilia: Testudines — Turtles

COMMON SNAPPING TURTLES — *Chelydra serpentina serpentina* (Chelydridae), Fig. 17, are the largest freshwater turtles found in New Brunswick. The shell may reach a length of 260 mm (approx. 18 inches) and a long neck and equally long tail may add an additional 18 inches to the total length; some specimens weigh as much as 18 kg (approx. 30 pounds). The Common Snapping Turtle is dark gray-brown above and may have algae growing on the shell: hence the term "Old-moss Back" is often used for it. There is less ventral shell than on most other turtles and its general size and the large muscular legs, neck, and tail makes it worthwhile hunting for the meat. In some areas of North America, including parts of Ontario, it is harvested as an item for the restaurant trade but most Ontario captures are exported to U.S. markets. It also has the temperament and capability of delivering a severe bite. The Common Snapping Turtle can be distinguished from the Eastern Painted Turtle and the Wood Turtle by the conspicuous saw-toothed ridge on its long tail. The only "safe" way to pick up a snapper is by the tail or the rear of the shell. Common Snapping Turtles are found in permanent freshwater ponds, lakes, and rivers where they feed on fish, frogs, birds, vegetation, and particularly on carrion.

The Common Snapping Turtle is known in the Quoddy area in the Digdeguash and Magaguadavic river systems. A specimen from Pocologon is in the N.B. Museum Collection. It is reported from the southern and northwestern counties of New Brunswick, but is not a common species.

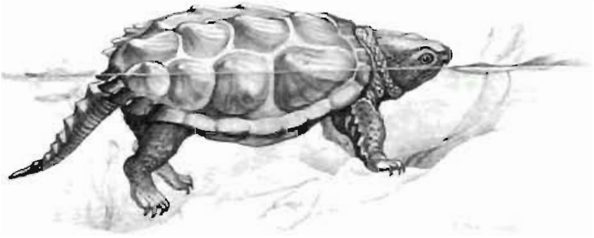

FIG. 17. Common Snapping Turtle. *Chelydra serpentina*, × 0.1.

WOOD TURTLES — *Clemmys insculpta* (Emydidae), Fig. 18, are probably the most common of the turtles found in New Brunswick. It has a shell length of up to 230 mm (approx. 9 inches). The characteristic rough appearance is due to annual growth rings prominent over each scale. The underside is yellowish with dark markings, and the neck and legs of adults orange or brick red.

The Wood Turtle is often terrestrial and may be found in the woods some distance from water. Eggs are

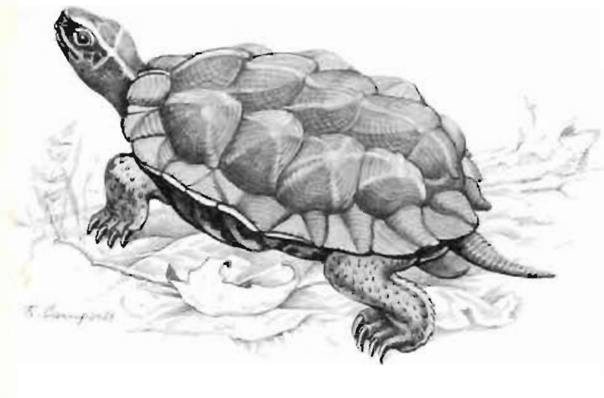

Fig. 18. Wood Turtle, *Clemmys insculpta*, × 0.2.

laid during the summer, usually in sandy places near water. Whereas the Common Snapping and Eastern Painted Turtles must be submerged in water in order to swallow food, the Wood Turtle is perfectly capable of feeding on land and lives on a variety of animal and plant life, including earthworms and wild fruits. The Wood Turtle hibernates in winter, occasionally in muskrat burrows, and individuals have been caught in New Brunswick in mink traps along brooks in January, indicating that some may move about during winter thaws.

The Wood Turtle *Clemmys insculpta* is a semi-terrestrial turtle that appears to be peculiarly habitat specific and limited to streams and rivers running through glacial till deposits. They maintain territories along these rivers and some have been reported at the same basking sites year after year. Along the River Philip near Oxford, N.S., these turtles migrate up and down the river to congregate on the largest sandbars at bends in the river. There they nest communally in such numbers that they dig out each others eggs while looking for additional nest sites. The Wood Turtle has a wide distribution in New Brunswick but very little information on its life history in that province is available. It does create runs in meadows and woodlands adjacent to rivers, similar to muskrat or rabbit runs, and it is in these that we have obtained small juvenile specimens in Nova Scotia. In contrast to the sun-loving habits of our other turtles, this species seems to be most active in the early morning and particularly on wet days or during summer thunder showers, which may explain why we have so few observations: one does not usually associate turtle-watching with rainy weather. In fact, it may be that these animals are crepuscular and most active in the evenings or early mornings, and perhaps even at night. Some are known to hibernate in muskrat burrows and occasionally muskrat trappers find these turtles in their traps.

The Wood Turtle is found in suitable habitat in most of New Brunswick and is known from mainland Quoddy near the Digdeguash and Magaguadavic rivers.

EASTERN PAINTED TURTLES — *Chrysemys picta picta* (Emydidae), Fig. 19, are small attractive turtles having a dark smooth carapace of 100–180 mm (approx. 4–7 inches) with red and black markings on the edges. The ventral shell is yellow and the head and neck are conspicuously marked with wavy yellow, red, and black stripes.

The Eastern Painted Turtle, like the Common Snapping Turtle, is limited to permanent ponds, lakes, and rivers where it feeds on aquatic insects and vegetation. During late June, July, and early August the eggs are laid, usually on sandbars, beaches, road beds, and earth dams.

The Eastern Painted Turtle is most common in the Grand Lake area of New Brunswick. It has been reported from the Digdeguash and Magaguadavic watersheds, but it is not a common species in the Quoddy area. A specimen from Magaguadavic Lake is in the N.B. Museum collection.

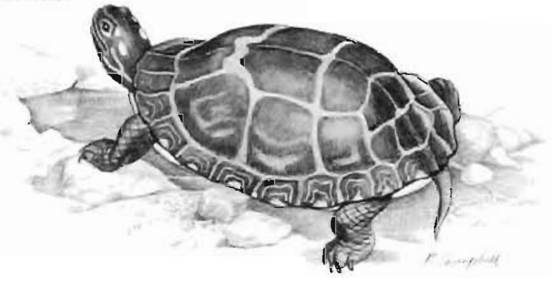

Fig. 19. Eastern Painted Turtle, *Chrysemys picta*, × 0.2.

SEA TURTLES — On rare occasions during the summer months the Atlantic Leatherback Turtle *Dermochelys coriacea coriacea* (Dermochelidae), Fig. 20, is reported in waters off the coast of New Brunswick. One specimen was taken in Northumberland Strait near Shemogue in September 1964, another near Cape Bald, Westmorland County, in October 1964, and a large specimen was taken near Escuminac in July 1969.

In July 1969 a partly decomposed specimen of Atlantic Loggerhead Turtle *Caretta caretta caretta* (Chelonidae) washed ashore at Chance Harbour, Saint John County.

It is possible that the Atlantic Ridley Turtle *Lepidochelys kempi* (Chelonidae) reported from Nova Scotia occurs in New Brunswick waters, but there are as yet no specimens.

Fig. 20. Atlantic Leatherback Turtle, *Dermochelys coriacea*, × 0.1.

NORTHERN WATER SNAKES — *Natrix sipedon sipedon* (Colubridae), Fig. 21, range from 610 mm to 1200 mm (approx. 2 to 4 ft) in length and are thick-bodied, particularly the females. The color of the back varies from gray to dark brown, with markings or bandings varying from reddish brown to black. The belly is light with blotched black and reddish markings. Some specimens appear to be uniform dark brown or black. The Northern Water Snake has keeled dorsal scales and a divided anal plate. They are found in and near ponds and lakes, are good swimmers, and feed on amphibians, fish, and invertebrates.

At present there are no specimens of Northern Water Snakes recorded from New Brunswick; however, specimens have been taken in Moosehorn Wildlife Refuge, near Calais, ME, less than 0.5 km from the New Brunswick border. This species, therefore, should be looked for in the southern Quoddy area.

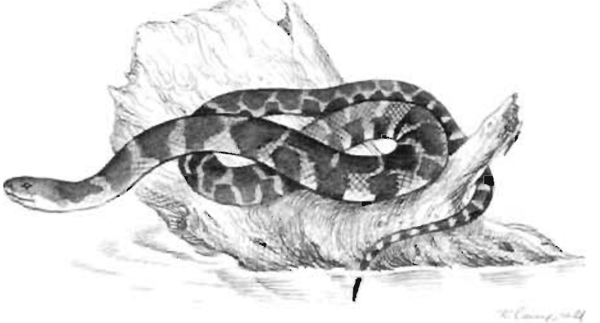

FIG. 21. Northern Water Snake, *Natrix sipedon*, × 0.2.

FIG. 22. Northern Red-bellied Snake, *Storeria occipitomaculata*. × 0.4.

NORTHERN RED-BELLIED SNAKES — *Storeria occipitomaculata occipitomaculata* (Colubridae), Fig. 22, are small, usually not over 305 mm (approx. 12 inches). It is the only species found in New Brunswick which has a reddish belly, varying in color from dark to light red. The dorsum may vary from dark brown to light brown. Usually there are three light spots on the back of the neck.

The Northern Red-bellied Snake can be found under stones and logs in the spring, shortly after the snow is off the ground. The young, up to 20 or more, are born alive in late July, August, or early September and range from 65 mm to 100 mm (approx. 2.5 to 4 inches) at birth. This species feeds on earthworms and insects. The Northern Red-bellied Snake hibernates in various dry situations — in holes in the ground, in rock piles, and also on broken ledges. Some have been seen quite late in the autumn.

The Northern Red-bellied Snake is common in New Brunswick and is well known in the Quoddy area.

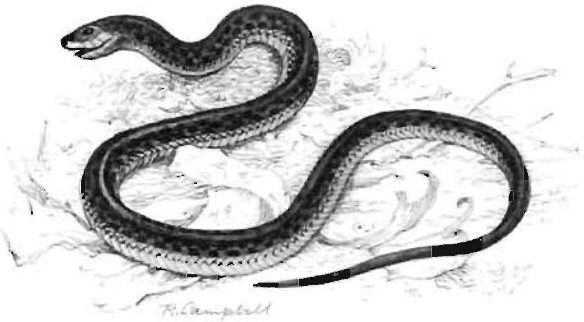

FIG. 23. Maritime Garter Snake, *Thamnophis sirtalis*, × 0.3.

MARITIME GARTER SNAKES — *Thamnophis sirtalis pallidula* (Colubridae), Fig. 23, are the common grass snake of New Brunswick, ranging in length up to nearly 1200 mm (approx. 4 ft) but usually not over 910 mm (3 ft). The dorsum varies greatly in color, being grayish olive, greenish brown, reddish brown, or dark brown with darker brownish blotches; some individuals have conspicuous light stripes running along the back and each side. The belly is a dull green or yellow.

The Maritime Garter Snake comes out of hibernation early in spring and can be found in a variety of habitats, sometimes in moist areas around ponds and sometimes on dry hillsides. They feed on frogs, toads, insects, and occasionally young mice. The young are born alive in late July, August, or September. Usually about 30 young are born at one time, but as many as 78 have been recorded. The young snakes vary from 128 mm to 205 mm (approx. 5 to 8 inches) at birth. The Maritime Garter Snake hibernates in late fall under rocks, ledges, and in other dry situations where the frost does not penetrate.

The Maritime Garter Snake is common and widely distributed in New Brunswick, including the Quoddy area.

NORTHERN RING-NECKED SNAKES — *Diadophis punctatus edwardsi* (Colubridae), Fig. 24, vary in length from 255 mm to 510 mm (approx. 10 to 20 inches). It is the only species of snake in New Brunswick having a yellow band around the neck and a bright yellow belly; the back is bluish-black or slatey.

The Northern Ring-necked Snake comes out of hibernation in early spring and frequents dry-to-moist wooded areas. This species of snake lays eggs which hatch quickly, sometimes in 10 d, because they are already well developed before they are laid. The young have been collected in late July, August, and September and are about 100–125 mm (approx. 4 to 5 inches) long. The food consists of insects, earthworms, and small salamanders.

The Northern Ring-necked Snake is secretive in its habits but is probably widely distributed in New Brunswick. Specimens have been collected from the southern counties of Albert, Kings, and Saint John and no doubt it can be found in the Quoddy area.

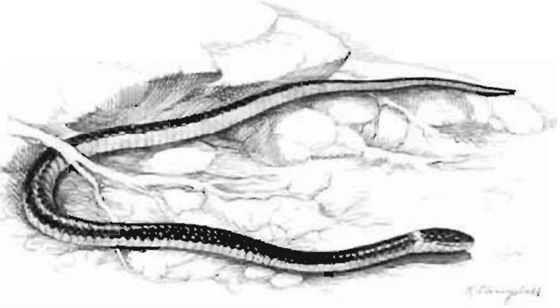

FIG. 24. Northern Ring-necked Snake. *Diadophis punctatus*. × 0.2.

EASTERN SMOOTH GREEN SNAKES — *Opheodrys vernalis vernalis* (Colubridae), Fig. 25, range in length from 305 mm to 510 mm (approx. 12 to 20 inches). No other species of snake found in New Brunswick is bright green on the back and whitish- or yellowish-green on the belly.

The Eastern Smooth Green Snake usually comes out of hibernation later than other snakes. It is found in grasslands, around rock piles, and under logs. As it feeds mainly on insects, it is very beneficial to the farmer. The young are not born alive but hatch from eggs which are laid in the latter part of July and August and are deposited in moist places under stones or wood. The eggs (already partly developed when laid), hatch in approximately 3–4 wk, the young being grayish or olive gray and from 105 mm to 115 mm (approx. 4 to 4.5 inches) long. The Eastern Smooth Green Snake hibernates early in the fall. They may hibernate singly or in groups, and as many as 70 individuals have been observed in early November in a hole in the ground under a stump.

The Eastern Smooth Green Snake is probably widely distributed in New Brunswick although specimens are known only from southern and central counties. It has been recorded from the Quoddy area near St. Andrews.

FIG. 25. Eastern Smooth Green Snake. *Opheodrys vernalis*. × 0.4.

Checklist of the Amphibians and Reptiles of Maine, New Brunswick and Nova Scotia

	Maine	N.B.	N.S.
Spotted Salamander *Ambystoma maculatum*	X	X	X
Blue-spotted Salamander *Ambystoma laterale*	X	X	X
Red-spotted Newt *Notophthalmus viridescens viridescens*	X	X	X
Northern Dusky Salamander *Desmognathus fuscus fuscus*	X	X	
Red-backed Salamander *Plethodon cinereus cinereus*	X	X	X
Four-toed Salamander *Hemidactylum scutatum*	X		X
Spring Salamander *Gyrinophillus prophyriticus*	X		
Northern Two-lined Salamander *Eurycea bislineata bislineata*	X	X	
American Toad *Bufo americanus*	X	X	X
Northern Spring Peeper *Hyla crucifer crucifer*	X	X	X
Gray Treefrog *Hyla versicolor*	X	X	
Bullfrog *Rana catesbeiana*	X	X	X
Green Frog *Rana clamitans melanota*	X	X	X
Mink Frog *Rana septentrionalis*	X	X	X
Wood Frog *Rana sylvatica*	X	X	X

Northern Leopard Frog *Rana pipiens*	X	X	X
Pickerel Frog *Rana palustris*	X	X	X
Common Snapping Turtle *Chelydra serpentina serpentina*	X	X	X
Spotted Turtle *Clemmys guttata*	X		
Wood Turtle *Clemmys insculpta*	X	X	X
Eastern Painted Turtle *Chrysemys picta picta*	X	X	X
Blanding's Turtle *Emydoidea blandingi*	X		X
Atlantic Loggerhead Turtle *Caretta caretta caretta*	?	X	X
Atlantic Ridley Turtle *Lepidochelys kempi*	?		X
Atlantic Leatherback Turtle *Dermochelys coriacea coriacea*	X	X	X
Northern Water Snake *Natrix sipedon sipedon*	X		
Northern Brown Snake *Storeria dekayi dekayi*	X		
Northern Red-bellied Snake *Storeria occipitomaculata*	X	X	X
Maritime Garter Snake *Thamnophis sirtalis pallidula*	X	X	X
Northern Ribbon Snake *Thamnophis sauritus sauritus*	X		X
Northern Ring-necked Snake *Diadophis punctatus edwardsi*	X	X	X
Northern Black Racer *Coluber constrictor*	X		
Eastern Smooth Green Snake *Opheodrys vernalis vernalis*	X	X	X
Eastern Milk Snake *Lampropeltis triangulum*	X		

Acknowledgments

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CHAPTER 16

The Marine Mammal Community

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Introduction[1]

The Bay of Fundy approaches are ecologically unique. The tidal range averages more than 7 m, and this causes extensive vertical mixing and hence cooler surface water temperatures during the summer months than in adjacent regions. Production is relatively high, and strong tidal currents and upwellings produce nutrient enrichment at certain locations which are, within broad limits, geographically constant in summer. Large local eddies also bring about concentrations of zooplankton between June and October (see Chapters 12 and 13), in amounts which attract numerous large baleen whales and keep them in the region for most of the summer and early fall. Considerable quantities of herring and mackerel enter the bay from late spring onwards, and these are prey for three or four species of small toothed cetaceans, the most abundant being the harbour porpoise, *Phocoena phocoena*. In former times, the harbour seal, *Phoca vitulina* was abundant in the region, but the population was reduced to a low level by bounty hunting. This bounty was imposed by the Federal Department of Fisheries because of the apparent involvement of the harbour seal in spreading the cod worm parasite. Despite reduction in harbour seal numbers to an insignificant level, the parasite continued to extend its range; the bounty was suspended for a time in the 1970's, and harbour seals increased in numbers. By 1979 the bounty had been reimposed, largely in response to complaints by weir fishermen that seals were interfering with the netting of herring. The grey seal, *Halichoerus grypus* occurs in small numbers in the Grand Manan area, but is not a common species in the bay. While the grey seal is also a carrier of the adult form of cod worm, a bounty imposed in the Miramichi Estuary was designed to prevent numbers increasing to the point where the seal population might significantly interfere with the salmon fishery.

A less fortunate feature of the Gulf of Maine in general, and the Bay of Fundy in particular, is vulnerability to the influences of industrial, agricultural, and forestry technologies. The prevailing major current flow up the eastern seaboard of America passes important agricultural and industrial regions and large urban conglomerates, and thus collects out-wash from river systems as it goes. Mixing occurs between this water mass and the waters of the Gulf of Maine on a significant scale for about half of the year. The Gulf of Maine Eddy carries this mixed water inshore in a counter-clockwise direction. This phenomenon is probably responsible for the relatively high levels of dieldrin and polychlorinated biphenyls found in the fauna of the region, as these compounds are not commonly produced or used locally. During the remainder of the year, exchange between the water bodies is more restricted, and outflow from Passamaquoddy Bay and river systems within the Bay of Fundy tends to remain within the region. Extensive spraying of spruce budworm in New Brunswick forests in the 1960's and pulp mill activities in that province and in northern Maine have contributed heavily to the high levels of DDT and mercury found in the fauna of the bay.

All three sub-regions of the Fundy approaches — Inner Quoddy, Grand Manan, and Brier Island — stand to be affected by three major industrial schemes recently approved for the Bay of Fundy: the deep-water port facility with supertanker capacity at Lorneville, adjacent to Saint John, N.B.; the nuclear power station at Point Lepreau, N.B., which is assumed to have the potential to attract much secondary manufacturing; and the Pittston Corporation oil refinery and tanker terminal for Eastport, ME. Construction of the first two has begun. The third is still opposed by the Canadian Federal Government, as approach to Eastport is through the Canadian territorial waters of Head Harbour Passage. Two moderate oil-spills have already occurred near Saint John, and the advent of these major projects has greatly increased concern for the environmental well-being of the region.

All the cetacean populations seem to reach a peak of abundance in the Bay of Fundy at approximately the same time: July to September. It is possible that the whole summer assemblage represents a quite fragile interrelationship dependent on fairly critical timing in zooplankton swarming, which is dependent on the success of phytoplankton bloom. If the timing is sub-optimal in some seasons, the gross result might be recognized by the nonappearance of finback and minke whales, for example, as happened in 1972 and 1973 in the inner Quoddy Region; by scattered Harbour porpoise distribution instead of the usual concentration; and by the similarly scattered distribution of herring and mackerel shoals. Far more research is required to determine the reasons for the sporadic occurrence of marine mammals in this region. At this stage we cannot attribute changes in abundance and distribution of marine mammals either to natural oceanographic fluctuations or the effects of man's activities (e.g. pollution or overfishing) with any certainty.

The species of marine mammals recorded from the Bay of Fundy approaches are listed below, and their probable status indicated.

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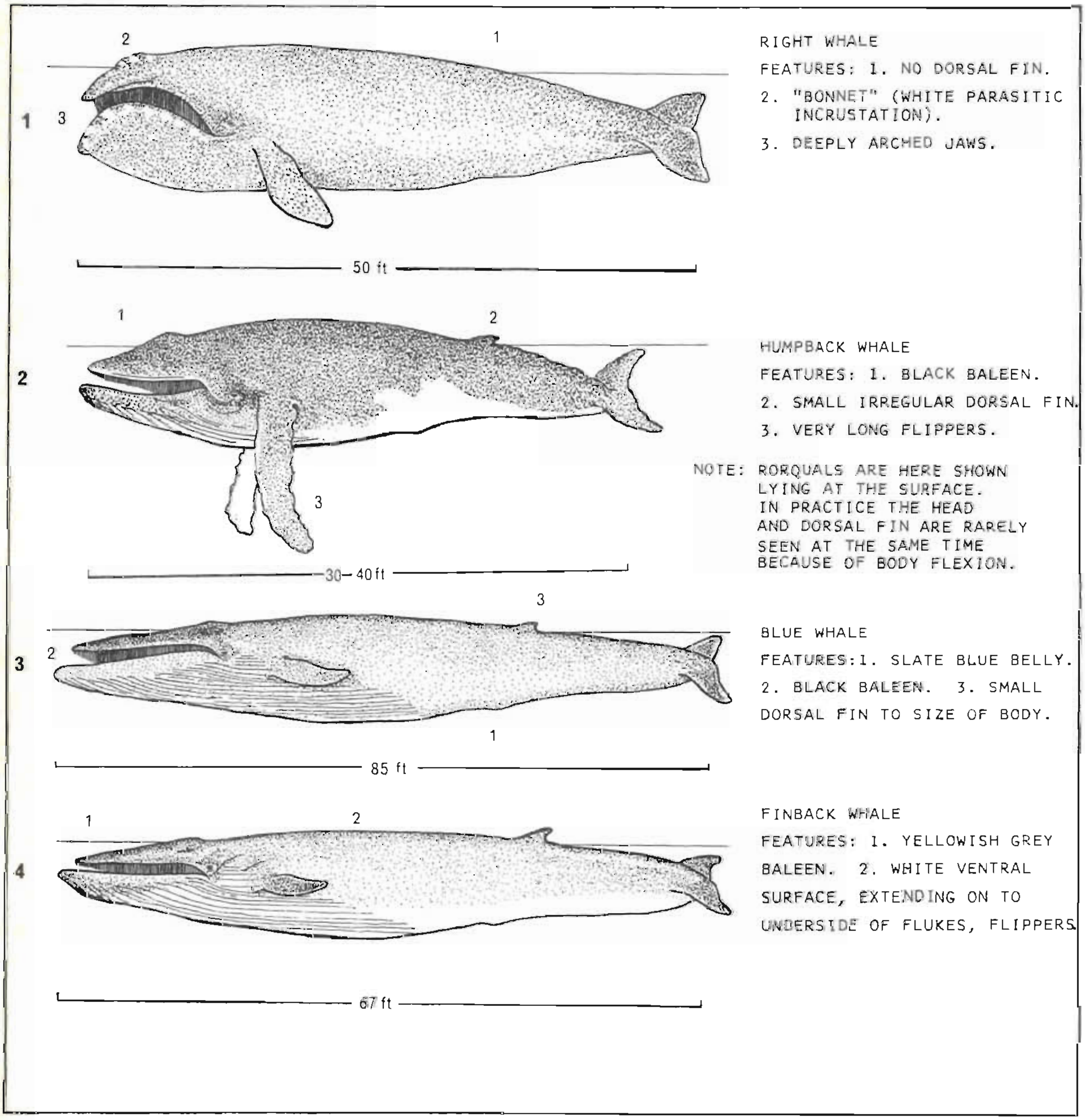
[1] Terms used: Cetacea — the order containing all whales of all sizes; Cetaceans — common language equivalent to "Cetacea"; Whale — strictly, can be applied to all Cetacea, but is usually restricted to the large species; Porpoise — a member of the family, Phocoenidae, with spatulate teeth; Dolphin — members of the superfamily Delphinoidea, which includes the killer whale as well as the "whales" rather than the dolphins. In practice, the names "porpoise" and "dolphin" have long been used interchangeably in popular literature.

Marine Mammals of the Bay of Fundy

CHECKLIST AND STATUS

i) Baleen Whales (Fig. 1–6)

Eubalaena glacialis Right whale	Sporadic visitor to Inner Quoddy region. Present around Wolves Is. and Grand Manan in most seasons. *Endangered species.*
Megaptera novaeangliae Humpback whale	Regular visitor to Brier Is. sub-region. Present in inner Quoddy Region during 1979. *Endangered species.*
Balaenoptera physalus Finback whale	Regular visitor to all three sub-regions.



RIGHT WHALE

FEATURES: 1. NO DORSAL FIN.

2. "BONNET" (WHITE PARASITIC INCRUSTATION).

3. DEEPLY ARCHED JAWS.

HUMPBACK WHALE

FEATURES: 1. BLACK BALEEN.

2. SMALL IRREGULAR DORSAL FIN.

3. VERY LONG FLIPPERS.

NOTE: RORQUALS ARE HERE SHOWN LYING AT THE SURFACE. IN PRACTICE THE HEAD AND DORSAL FIN ARE RARELY SEEN AT THE SAME TIME BECAUSE OF BODY FLEXION.

BLUE WHALE

FEATURES: 1. SLATE BLUE BELLY.

2. BLACK BALEEN. 3. SMALL DORSAL FIN TO SIZE OF BODY.

FINBACK WHALE

FEATURES: 1. YELLOWISH GREY BALEEN. 2. WHITE VENTRAL SURFACE, EXTENDING ON TO UNDERSIDE OF FLUKES, FLIPPERS.

FIG. 1–4. Baleen whales: right, humpback, blue, and finback, with diagnostic features.

Balaenoptera borealis Sei whale	Possible visitor to southern part of Brier Is. sub-region.
Balaenoptera acutorostrata Minke whale	Regular visitor to all sub-regions.
Balaenoptera musculus Blue whale	Reported sporadically but not in last 15 yr. *Endangered species*.

ii) Toothed whales (Fig. 7–17)

Phocoena phocoena Harbour porpoise	Regular resident for up to 12 mo of year, but most of population migrates offshore in fall.
Lagenorphynchus acutus White-sided dolphin	Regular visitor; may be residential in outer region.

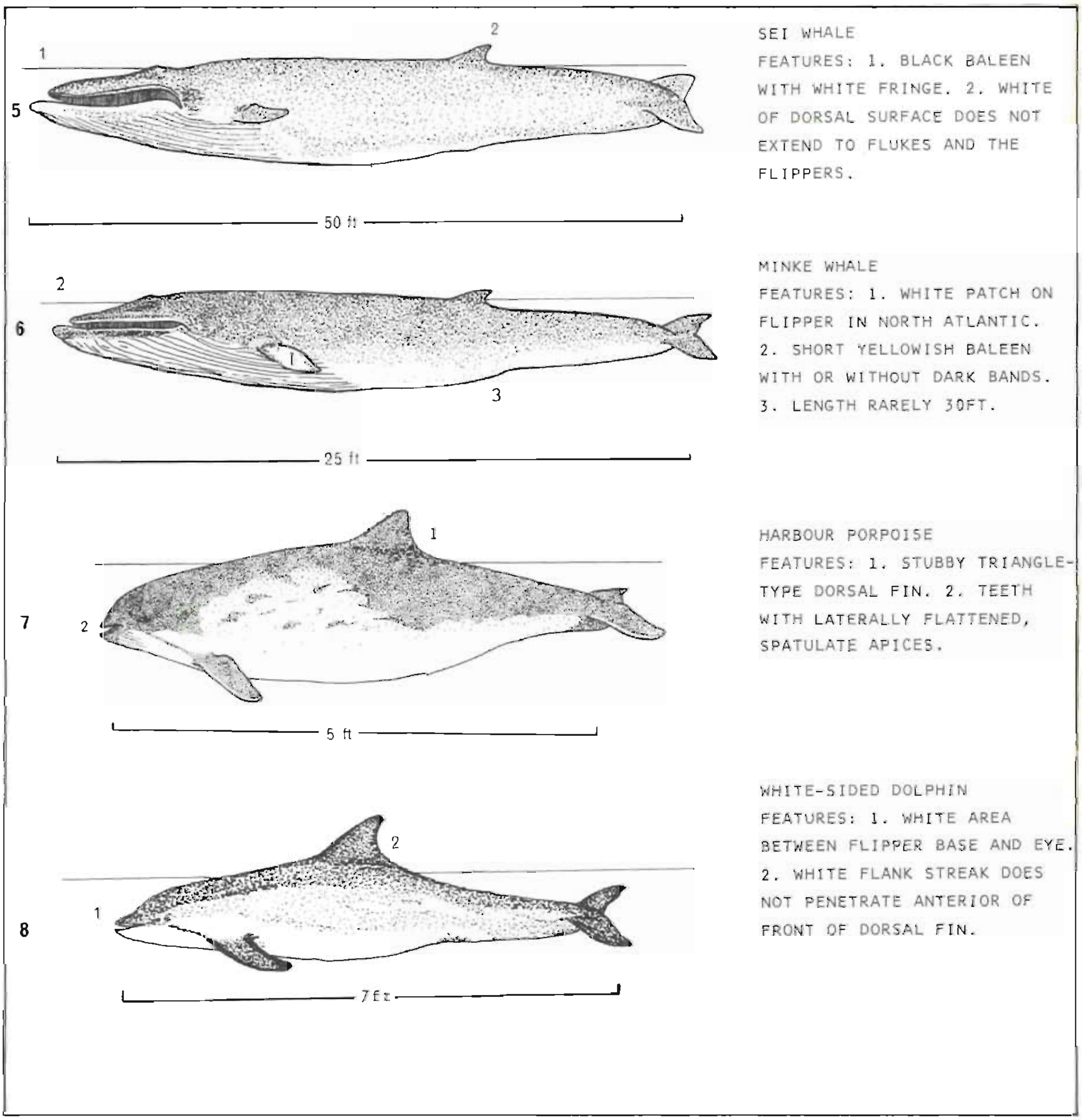
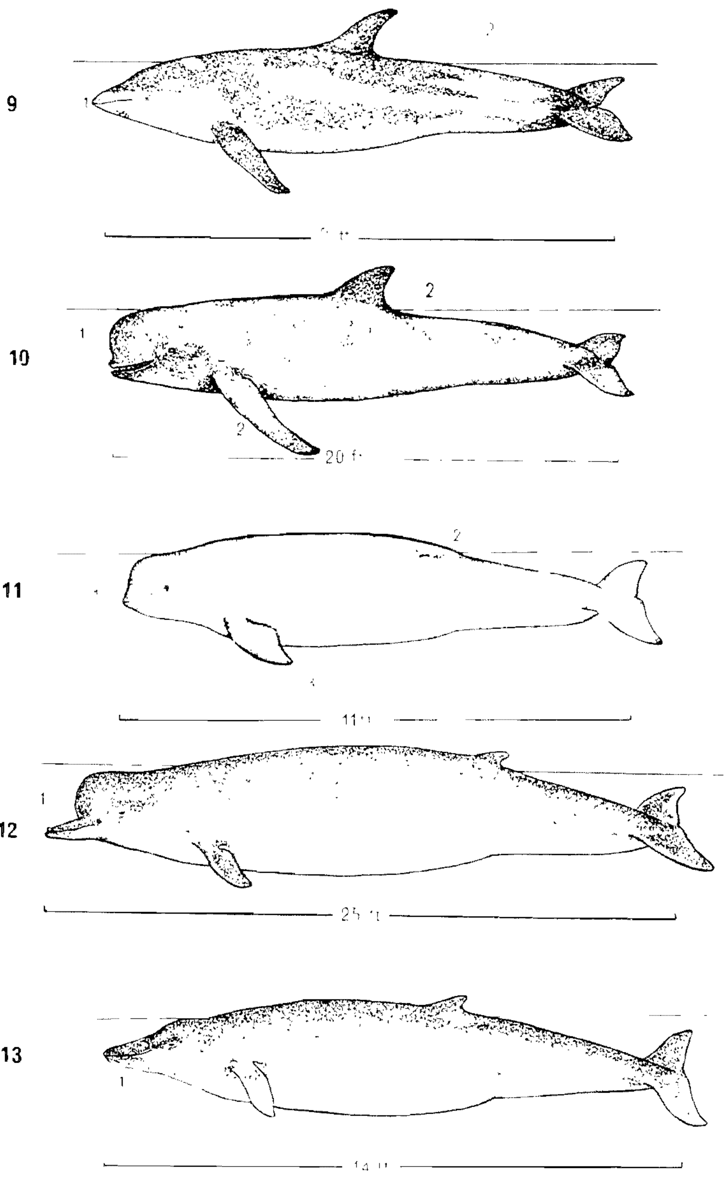


FIG. 5–8. Baleen and toothed whales: sei, minke, harbour porpoise, and white-sided dolphin, with diagnostic features.

Lagenorhynchus albirostris White-beaked dolphin	Possible sporadic visitor	*Hyperoodon ampullatus* Bottlenose whale	Known from a stranded specimen.
Globicephala melaena Pilot whale or Pothead whale	Sporadic visitor, but forms large schools.	*Mesoplodon bidens* Sowerby's beaked whale	Known from a stranded specimen
Delphinapterus leucas White whale	Occasionally strays from Gulf of St Lawrence (one in 1976).		



WHITE-BEAKED DOLPHIN
FEATURES: 1. GREY AREA BETWEEN EYE AND FLIPPER BASE. 2. WHITE FLANK STREAK PENETRATES FAR ANTERIOR OF DORSAL FIN.

PILOT WHALE
FEATURES: 1. BULBOUS HEAD. 2. LONG FLIPPERS. 3. LARGE, BROADLY TRIANGULAR DORSAL FIN.

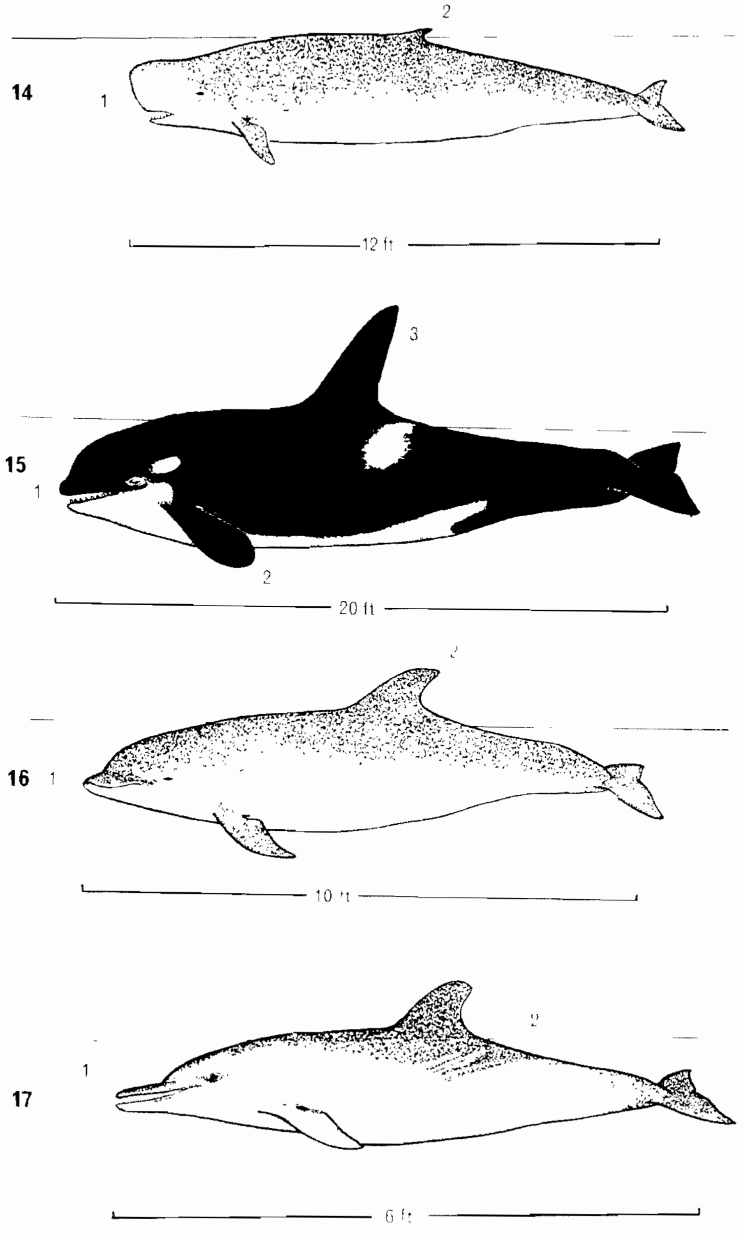
BELUGA OR WHITE WHALE
FEATURES: 1. BULBOUS HEAD. 2. NO DORSAL FIN, ONLY HUMP. 3. WHITE BODY COLOUR IN ADULT.

BOTTLENOSE WHALE
FEATURES: 1. BULBOUS HEAD WITH DISTINCT BEAK.

SOWERBY BEAKED WHALE
FEATURES: 1. LESS PRONOUNCED BULBOUS MELON OR FOREHEAD THAN BOTTLENOSE WHALE, BEAK NOT AS DISTINCTIVE. COULD BE OTHER ZIPHIID SPECIES. CALL SPECIALIST.

FIG. 9-13 Toothed whales: white-beaked dolphin, pilot whale, white whale, bottlenose whale, and Sowerby's beaked whale, with diagnostic features.

Orcinus orca Killer whale	Possible sporadic visitor.	*Tursiops truncatus* Bottlenosed dolphin	Possible rare visitor.
Kogia breviceps Pigmy sperm whale	Possible sporadic visitor.	*Delphinus delphis* Common dolphin	Possible rare visitor.



PIGMY SPERM WHALE
FEATURES: 1. SHARK-LIKE APPEARANCE OF HEAD. 2. SMALL DORSAL FIN.

KILLER WHALE
FEATURES: 1. WEDGE-SHAPED HEAD, WITH DISTINCT BLAZE BEHIND EYE.
2. PADDLE-SHAPED FLIPPERS.
3. LARGE, ERECT DORSAL FIN IN ADULT MALE KILLERS.

BOTTLENOSE DOLPHIN
FEATURES: 1. RATHER ROUNDED FOREHEAD, JAWS IN A CURVED LINE GIVING A PERMANENT "GRIN".
2. BODY RATHER UNIFORM GREY.

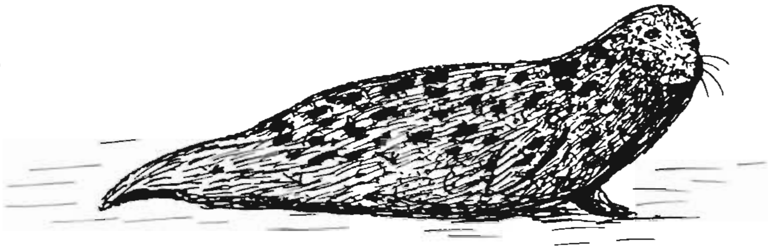
COMMON DOLPHIN
FEATURES: 1. RELATIVELY LONG, SLENDER SNOUT. 2. DORSAL SURFACE BROWNISH IN LIFE, DARK GREY IN DEATH. VENTRAL SURFACE WHITISH CREAM, YELLOWISH AND GREY SHADES AND STRIPING ON FLANKS.

FIG. 14-17 Toothed whales: pigmy sperm whale, killer whale, bottlenosed dolphin, common or saddlebacked dolphin, with diagnostic features.

iii) Phocid seals (Figs. 18, 19)

Halichoerus grypus Grey seal	Local visitor — Grand Manan region only.
Phoca vitulina Harbour seal	Previously common, much reduced by bounty hunting, now recovering.

18



HARBOUR SEAL

FEATURES: PELT MORE OR LESS BLUISH GREY, WITH DARK BLOTCHES OR SPOTS VARYING IN SIZE, AND FREQUENTLY WITH WHITISH RINGS AND WHIRLS. HEAD RATHER SMOOTHLY ROUNDED.

19

GREY SEAL

FEATURES: PELT VARIABLE, DARK GREY OR NEARLY BLACK IN SOME ADULT MALES, BUT IN MANY FEMALES NOT MUCH DARKER THAN IN HARBOUR SEAL. FEMALES MAY BE VERY PALE ON VENTRAL SURFACE. BACK AND FLANKS HAVE DARK BLOTCHES IN BOTH SEXES. THE "ROMAN" NOSE OF THE ADULT MALE GREY IS VERY CHARACTERISTIC.

FIG. 18-19. Harbour and grey seals, with diagnostic features.

ACCOUNTS OF MAJOR SPECIES

Right whale — Formerly abundant in the North Atlantic, northern right whales were reduced to a remnant stock by the beginning of this century. Despite having been completely protected for several decades, the population in the western North Atlantic has recovered only very slowly, and even now only numbers in the hundreds at the most. There is every indication that the eastern North Atlantic stock was almost completely exterminated.

During the last 15 yr right whales have apparently been steadily extending their range in the western North Atlantic, and perhaps increasing in numbers as well, although there is little real evidence for this. American researchers have kept records of their seasonal occurrence off Cape Cod since 1956 (Watkins and Schevill 1976), and animals have been reported reliably all along the east and south coasts of the United States (Reeves et. al. 1978; Moore and Clark 1963). In August 1971 about six right whales came into the inner Quoddy Region and were observed by the University of Guelph research team for several weeks before they gradually moved out towards Grand Manan. We have direct records of single animals and females with calves around the Wolves Islands in most years. Schools of 2-7 are seen each summer in the pelagic regions of the Bay of Fundy, engaged in both feeding and mating activity. In August 1979 six animals were seen in the Grand Manan Channel by workers of Marine Research Associates of Lord's Cove, N.B. Formerly, whalers of the Blandford station in Nova Scotia frequently encountered right whales over the banks of the continental shelf some 50 miles southwest of the La Have mouth, where they were feeding during their annual north-south migrations, but the numbers did not seem to be large.

Humpback whale — The Digby Neck region of southwestern Nova Scotia is well known as one of the summer feeding grounds of this species in the North Atlantic. During August–September each year humpbacks can be found within 5 miles of shore between Letite Passage and Grand Passage, and southwestwards towards the Lurcher Shoal. Sporadic sightings of humpbacks have been made off Grand Manan in most years since 1970, but prior to 1978 we know of only one reliable report of humpback whales coming into the inner Quoddy Region, about 1967.

Since 1975 the number of inshore sightings of humpback whales in waters of the Atlantic provinces has greatly increased (Lien and Merdsoy 1979), as has the incidence of collisions and entanglements in fishing gear, especially the leaders of cod traps. This has resulted in damage to gear and sometimes injury to the whales. Fisheries and Oceans Canada and other agencies have begun to study ways of forcing the whales to avoid set nets and lines, e.g. by attaching ultrasonic or sonic pingers to ropes. Some commercial fishing interests have claimed that a great increase in numbers of humpbacks has occurred since the North Atlantic population was given nearly complete protection, and it has been suggested by some that whaling operations be resumed in Atlantic Canada. A possible explanation for the increase of inshore sightings is that the capelin stocks of southern and eastern Newfoundland have been severely depleted by pelagic fleet operations in recent years; as a result, humpbacks may have moved inshore to exploit other shoaling species such as herring. Inshore cod fishing has also increased.

Whatever the reason, the inshore movement of humpbacks has also occurred recently in the western Bay of Fundy. Whale watchers from Lubec, ME, (Mr. David Pike and his friends) reported a single humpback whale off Campobello Island in August 1978. During August 1979, two females with calves were present around Campobello Island fairly consistently. They were most frequently seen between Cutler and West Quoddy Head, both localities in Maine, but on several occasions they spent extended periods in the mouth of Head Harbour Passage, between the lighthouse and Spruce Island. Frequent diving indicated that the animals were actively feeding, especially off East Quoddy Head, and apparent suckling behavior was noted by some observers, especially by Mr and Mrs T. Barto of Fairhaven, Deer Island, one afternoon in mid-August. Apparently one of the calves became trapped in a seine net near Lubec, ME, in early September 1979. It was successfully released but with considerable damage to the net.

Finback whale — This is the most common species of large whale in the Bay of Fundy at present (Fig. 4). It appears during June or July in all three sub-regions when euphausiid shrimp concentrations start to form in surface waters (Fig. 20). Up to 10 different individuals have been counted in the inner Quoddy Region at one time (in the vicinity of Deer Island and Campobello Island) although 3–6 is more usual. The maximum count off Brier Island–Long Island at any one time was 15, in August 1974. Once the animals have moved into the inshore belt of water in both sub-regions, their appearance is relatively predictable until autumnal changes break up the euphausiid shrimp shoals in surface waters and drive the schools of young herring deeper. We have fewer observations from the eastern Grand Manan area, but their occurrence there is also usually regular. Finback whales are often reported off Swallowtail Head, and further south, off the Brazil and Old Proprietor shoals (see Fig. 29). These areas are less accessible than the inner Quoddy Region and Brier Island, and one cannot rely on finding animals nearly so readily as in the other areas. Off western Grand Manan, finbacks have reportedly concentrated off Dark Harbour during the fall. We have reason to believe that these are the same animals which were present off Deer Island and Campobello a month earlier.

Finback whales are reported regularly by boats out on the very edge of the Bay of Fundy, working along the shelf region crossing the northern Gulf of Maine. From the scientific and/or recreational point of view, however, these animals are virtually out of reach except to an ocean-going vessel. One of the great natural advantages of both the inner Quoddy and the Brier Island regions is that finback whales can be studied at close quarters for extended periods of time, using inexpensive, relatively small fishing boats. This is one of the few parts of the world where such studies are possible. The feeding areas of the inner Quoddy and Brier Island animals seem to be quite

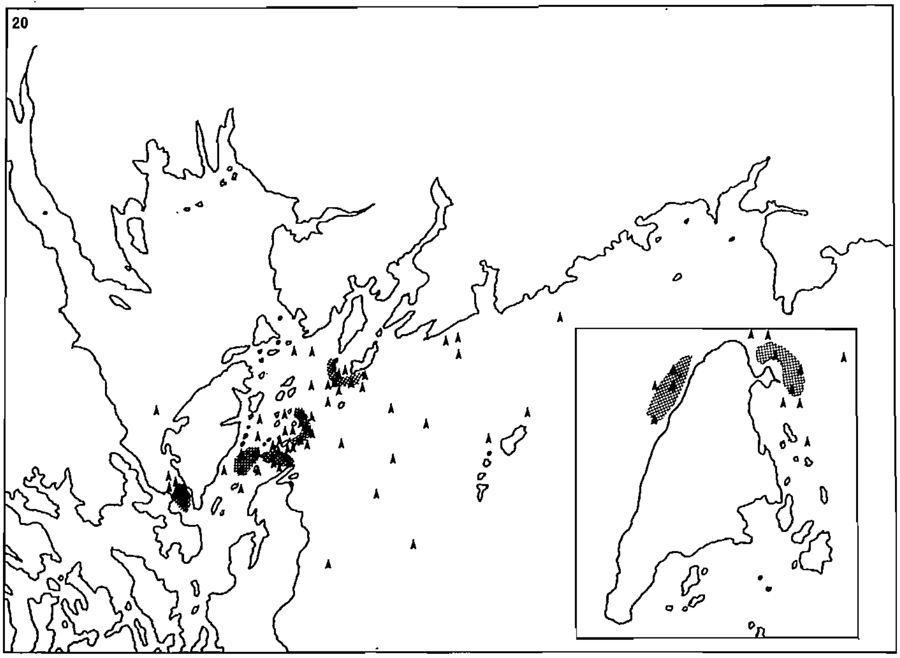


FIG. 20. Areas where finback whales regularly congregate and feed during the summer months: observation of one or more animals in the period 1970–77 indicated by points. Hatched areas indicate where fairly consistent surface swarming of euphausiid shrimps occurs in summer months. (Inset is Grand Manan Island)

limited (Fig. 20) and related to tidal conditions, according to the preliminary observations by Arnold and Gaskin (1972) and Gaskin (1976). The ledge system running parallel to the northwestern coast of Digby Neck, about 5–10 miles offshore, and on the New Brunswick coast, the shelf off White Island and the "sill" close to the tip of Campobello Island, seem to be critical features in the feeding systems for the finback whales in the two sub-regions (Fig. 20).

Finback whales were reduced to relatively low numbers by Canadian shore-whaling operations during the 1950s and 1960s, and the closing of these stations in 1972 by the Hon. Jack Davis MP, then Minister of the Environment, was protested by few outside the whaling industry itself. The decline of the western North Atlantic population was documented by Allen (1971). The species is not presently hunted, despite the Canadian Government's setting a quota for the population, and the size of the stock is thought to be slowly increasing.

The northwest Atlantic finback population appears to contain several discernible sub-populations (Mitchell 1974; Sergeant 1977), including one off Nova Scotia and another off Newfoundland. Some fractions of these sub-populations certainly migrate, and winter regularly on the eastern North American coastal shelf about as far as latitude 35°N. In summer they concentrate further north, and some penetrate into the Gulf of St. Lawrence and the Bay of Fundy. Brodie (1975) reported finback whales off eastern Nova Scotia during winter, which indicate that not all of that sub-population migrates. Adequate food supply, in the form of herring and euphausiid shrimps, is available to these animals year-round in that very productive region. Since individual food requirements for such large mammals are high, relative dispersion of individuals or small schools is a prerequisite for success and food must occur in concentrated patches to facilitate optimum exploitation.

Minke whale — Although not as commonly observed as the finback because it is smaller and frequently unobtrusive in its behavior, the minke whale is a regular summer migrant to all three sub-regions (Fig. 21). It feeds on alewives, capelin, and herring. Several individuals are usually present in the Quoddy Region each summer; one often "patrols" day after day during July–September in the vicinity of White Island and Spruce Island (Fig. 28), and others may penetrate Blacks Harbour, Letite Passage, the Western Passage, and Passamaquoddy Bay. There are several recent records of young minke whales stranded in Passamaquoddy Bay; they sometimes enter herring weirs in pursuit of fish and become trapped.

Harbour Porpoise — The harbour porpoise is by far the most abundant cetacean in the Bay of Fundy, and is almost certainly one of the most important species of the upper tropic levels in the coastal marine food web. It feeds on herring, mackerel, small gadoid fish, and squid.

Some individuals have been seen in almost every month of the year, but most arrive in the coastal areas when the surface water temperature reaches 8–10° C, and leave at the time of fall cooling. The migration pattern is essentially onshore–offshore, rather than north–south. Our studies showed that the "main herds" arrived at the

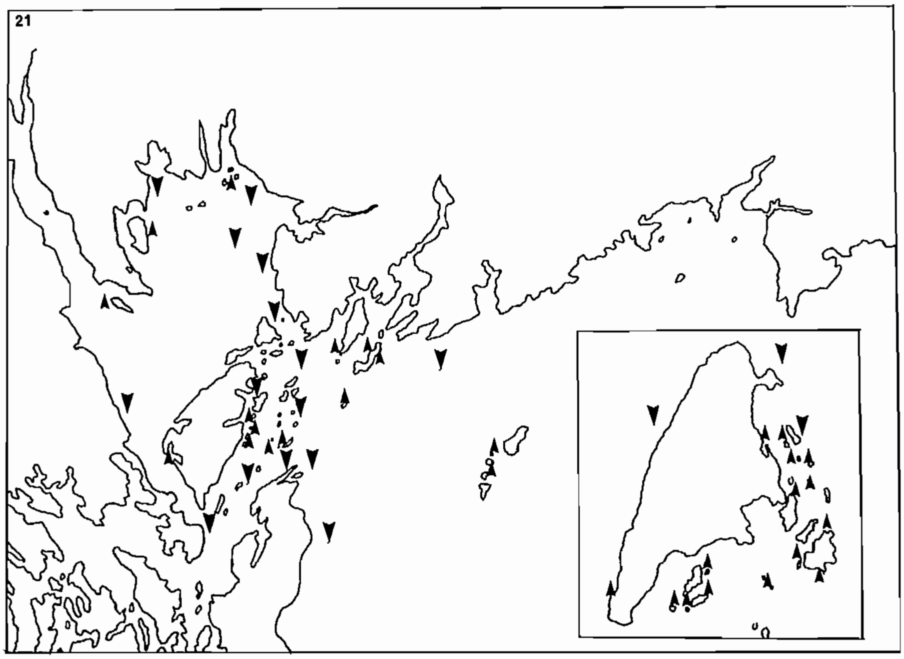


FIG. 21. Observations on minke whales during 1970–77 (large points), and harbour seal haulout ledges for the same period (small points). (Inset is Grand Manan Island)

same time of year, from southern Maine to southern New Brunswick. The wintering areas are not known, but are probably the southern edges of the Brown's Bank and George's Bank, where water temperatures are 7–9° C in most winters. This species may have a relatively high metabolic rate, and is the smallest of the cold water cetaceans. It has colonized a niche which on the whole permits it to avoid competition with the white whale to the north and the wide-ranging, more pelagic species such as white-sided, white-beaked, common, and bottlenosed dolphins to the east and south. The white whale is generally found in colder and less saline waters than the harbour porpoise; however, the latter has been recorded in the Western and Letite passages, adjacent to Deer Island, in December and February (A. MacKay and R. Bosein, personal communication). In early April 1970, with water temperatures ranging from 1.9°C to 3.8°C, as many as 14 sightings were made in Letite in one day. Thus a small fraction of the population — probably submature males—undoubtedly overwinters in the Bay of Fundy. However, density measurements in April were estimated as 0.9 animals/search h in good sighting conditions, compared with up to 12/h in late August and early September.

Mature females arrive with their calves in the immediate coastal zone; calving evidently takes place further offshore. Most years these animals leave the coastal zone again in early October, by which time a significant percentage of the females are already pregnant again. Mating also usually seems to occur in offshore waters, although it has occasionally been observed among the inner island chains and in the coves of Deer Island. In all three subregions, the harbour porpoise population peaks at the same time — between mid-July and mid-September. The population of the Brier Island region seems to be the smallest, with several dozen animals seen regularly at the Fundy mouth of Grand Passage, but only small numbers are seen in the rest of the area except for the approaches to Digby Gut, where quite large numbers occur.

The densest concentrations of harbour porpoises recorded in our studies from 1969 to 1979 were between Northern Head and Swallowtail Head, off upper Grand Manan, and in Head Harbour Passage in 1978. Concentrations in the inner Quoddy Region in August, particularly in Letite and its approaches, outside Head Harbour Passage, and over the shelf of White and Spruce Islands, are nearly as high and occur over a larger area (Fig. 22). The size of schools increases as the season progresses, with up to 15 animals/group being seen in the Letite area in September. Shortly after, these groups are encountered only on the edge of Grand Manan Channel current, about halfway between Deer Island and the Wolves Islands. They seem to stay in this outer area for a week or so and then disappear. The formation of large schools, final concentration in the Letite and Head Harbour approaches, and movement to the offshore current boundary are apparently stages presaging the start of the offshore winter migration. In fact, the overall migration pattern closely resembles that of the principal food species — herring and mackerel. Predation on squid may be heaviest in the late summer and early fall, when short-finned squid, *Illex* most commonly occur in the inner Quoddy Region. Workers at the College of the Atlantic report that later in

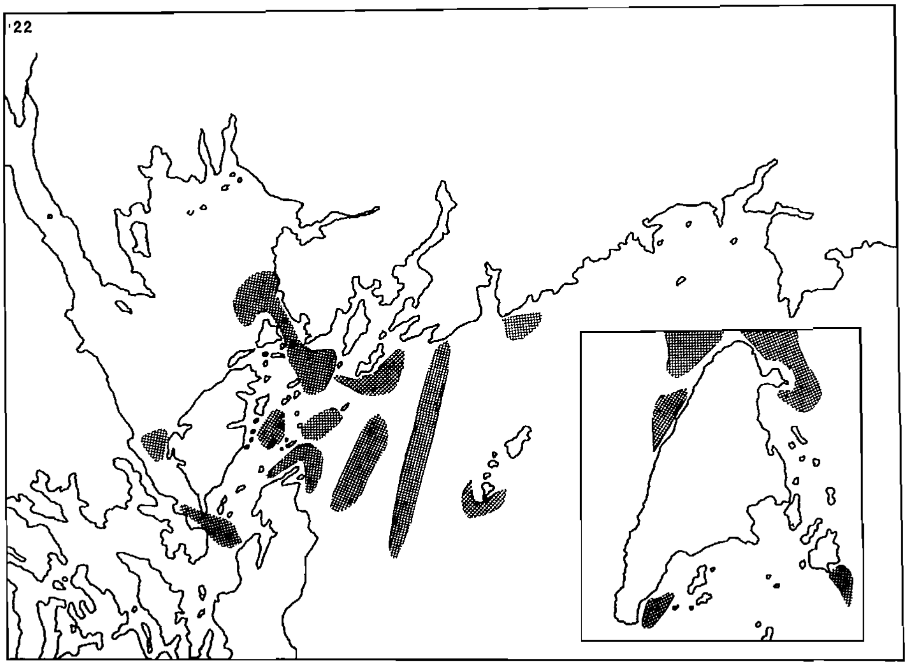


FIG. 22. Areas in the Quoddy and Grand Manan areas where harbour porpoises consistently congregate in most years between July and October. (Inset is Grand Manan Island)

the fall, large numbers of harbour porpoises occur in the Grand Manan Channel, between northern Maine and western Grand Manan.

After several years of study, the University of Guelph research group concluded that the Bay of Fundy approaches, especially the islands of southern New Brunswick, represent the real stronghold of this species in the western North Atlantic south of Newfoundland. After surveying all the Atlantic provinces during 1969–74, we concluded that while significant populations occur in the Gulf of St. Lawrence and in Newfoundland waters, nowhere else can the species be found in such numbers in a relatively small area, so regularly, and so accessibly for scientific research. Therefore, any further environmental deterioration in the western shore regions of the Bay of Fundy is viewed by us with great concern, as it would destroy a unique "field laboratory" for the study of this important species. At the 1976 Whaling Commission meetings in London, concern for the status of this species in European waters was expressed by nearly half the delegates present. The population of harbour porpoises in the Baltic Sea is believed to have collapsed, and the species now seems to be disappearing from the continental side of the English Channel and the southern North Sea, including the coast of Holland (Dr P. J. H. Van Bree, personal communication).

The species seems to be relatively short-lived; our studies indicate a maximum life span of only about 13 yr, with an average of 8–9 yr. Only one calf is produced at a time under normal circumstances; although twinning undoubtedly occurs it is unlikely that both calves could be weaned. Although we have evidence that some females may calve in as many as three successive years, others have resting years between pregnancies. Sexual maturity is attained in the fourth year of life. The short life span does not seem to be countered, therefore, by a high reproductive rate. The species is not likely to be able to respond favorably or show much reproductive flexibility if subjected to intensive exploitation or increased mortality from other sources.

White-sided and White-beaked dolphins — Sporadic, infrequent sightings of "large black and white sea dolphins" are reported to us by fisherman from all three subregions during winter and summer in the inner Quoddy Region. White-sided dolphins were seen off Whitehorse Island in summer in 1973 and 1979, and twice off the Digby Gut, N.S. in 1970 and 1972 by University of Guelph workers. A stranded specimen was found on Barnes Island by us during 1974, and a large school was stranded in Lingley Cove, ME (Geraci 1975). The species is regularly sighted in the vicinity of Long Island and Brier Island. Major items of diet are probably squid, herring, and mackerel. The white-beaked dolphin may also occur in the Bay of Fundy approaches, but its presence has yet to be confirmed by a specimen.

Pilot whale — A school of about 30 animals a few yards from the shore on Bliss Island was recorded and filmed by University of Guelph workers in August 1969, following reports of an unusually heavy run of squid into the Quoddy Region. Some pilots penetrate the Bay of

Fundy almost every year; one school stranded near Yarmouth in 1982; most were towed off alive. This species does not seem to be a resident or regular visitor to the Bay of Fundy.

PHOCID SEALS

Grey seal — While occasional strays are reported some distance into the Bay of Fundy, the only locality where the species can occasionally be seen (albeit in very small numbers) is on one or two ledges off the eastern side of Grand Manan. It is probable that shooting by fishermen once kept numbers down, but in the absence of recent reports of grey seals being shot, we must assume that some other factor restricts expansion of their range within the Bay of Fundy. The status of the species was reviewed by Mansfield and Beck (1977).

Harbour seal — The coastal terrain in the Brier Island sub-region is not well suited to this species. All the major offshore ledge systems are subsurface even at low tide, and inshore ledges are not numerous. The stronghold of the species in the area is undoubtedly Grand Manan, especially along the eastern coast which is rich in ledges suitable for hauling out. Harbour seals in the inner Quoddy sub-region were sighted much more frequently during 1973–82 than during 1969–72. This can be attributed to the removal, for several years, of the long-standing Department of Fisheries bounty during the mid-1970s, and particularly to the retirement from active hunting of the last local full-time bounty hunter. The present population in the inner Quoddy and Grand Manan sub-regions combined is estimated by us, based on observations from 1972 to 1979, to be in the low hundreds. The inner Quoddy and Grand Manan sub-regions where harbour seals are most frequently observed, based on 1970–75 records, are shown in Fig. 21. We do not have such complete records for Grand Manan, as this area has only been cursorily surveyed since 1973. Our conclusion is that the species is now slowly increasing in numbers but will probably be checked by increased shooting under the renewed bounty now operating again.

Studies and Study Methods

PUBLISHED WORK

Published studies on marine mammals of the Bay of Fundy can be summarized as follows. There are some useful allusions in eastern U.S. and Canadian regional reviews (Sergeant and Fisher 1957; Mansfield 1967; Sergeant et al. 1970; Katona 1975; Katona et al. 1975; Leatherwood et al. 1976). In a much earlier paper Gilpin (1875) reviewed the small cetaceans known to occur off Nova Scotia and in the Bay of Fundy. Fisher and Harrison (1970) published some data and useful speculation on the reproductive cycle of the harbour porpoise, largely based on specimens collected in the 1950's. Schevill et al. (1969) described phonation of harbour porpoises temporarily held in captivity in the vicinity of Pendleton's Passage, Passamaquoddy Bay. Preliminary results of long-term studies by the University of Guelph group on DDT, diedrin, PCB's, mercury, mirex, and other pollutants have been published (Gaskin et al. 1971, 1972, 1973, 1976, 1979). Some data concerning predation on harbour porpoise by white shark were published by Arnold (1972). The structure of the stomach of this species, and the nature of its diet and feeding habits in this region were published by Smith (1972) and Smith and Gaskin (1974). Aspects of diet and energetics of cetaceans have been discussed by Brodie (1975) and Gaskin (1978). Details of functional anatomy of the locomotor system of harbour porpoises have been published by Smith et al. (1976), of the structure of the heart and coronary system by Rowlatt and Gaskin (1975) and Halina and Gaskin (1978), of the vascular system of the liver by Hilton and Gaskin (1978), and of renal morphology by Hedges et al. (1979). The prolific lungworm parasites of harbour porpoise were studied by Arnold and Gaskin (1975) and the problem of age determination by Gaskin and Blair (1977). Thesis work yet to be published in primary literature by the University of Guelph group includes a study of the morphology of the adrenal of the harbour porpoise (Louisy 1973), the histology of the parathyroid and consideration of its role in calcium metabolism (Mertens 1975), and the efficiency of locomotion and energetics by Yasui (1978).

Considerable attention has also been focussed on the ecology of the species. Preliminary results of movements revealed by radio telemetric studies were published by Gaskin et al. (1975). Watson (1976) studied the behavior and distributional ecology of harbour porpoises in the Fish Harbour area of Deer Island. A detailed review and bibliography of the species was published by Gaskin et al. (1974), and the morphometrics of Pacific, Atlantic, and Baltic harbour porpoise populations were analyzed by Yurick (1977). The dynamics of harbour porpoise ecology in the Quoddy Region are currently being studied by D. B. Yurick. A preliminary analysis of population size and seasonal changes in density was published by Gaskin (1977). Some data on the baleen whales of the Inner Quoddy sub-region were published by Arnold and Gaskin (1972), and further discussion of feeding in the Brier Island region by finback and minke whales can be found in the paper by Gaskin (1976). Marine mammal research in the Bay of Fundy is currently concentrated on the ecology and acoustics of the harbour seal (Universities of Maine and New Brunswick), identification and population size in right whales (New England Aquarium, Boston), the interrelationships of upper trophic level animals (including seabirds) with prey species (University of Guelph), and specific aspects of population dynamics, behavioral ecology, and energetics of cetaceans (Guelph and Ocean Search Ltd.).

STUDY METHODS

Two methods by which cetaceans can be studied are open to the non-specialist: examination of freshly dead, stranded, or accidentally net-trapped specimens; or observation of animals at sea from boats, light aircraft, or from suitable vantage points on the land.

The stranded animal — Examining stranded animals necessitates, of course, being in the right place at the right time. Nevertheless, during the course of a calendar year at least one small or medium-sized cetacean can be expected to strand at some reasonably accessible point on the Fundy coasts. For example, in 1976–77 no less than three

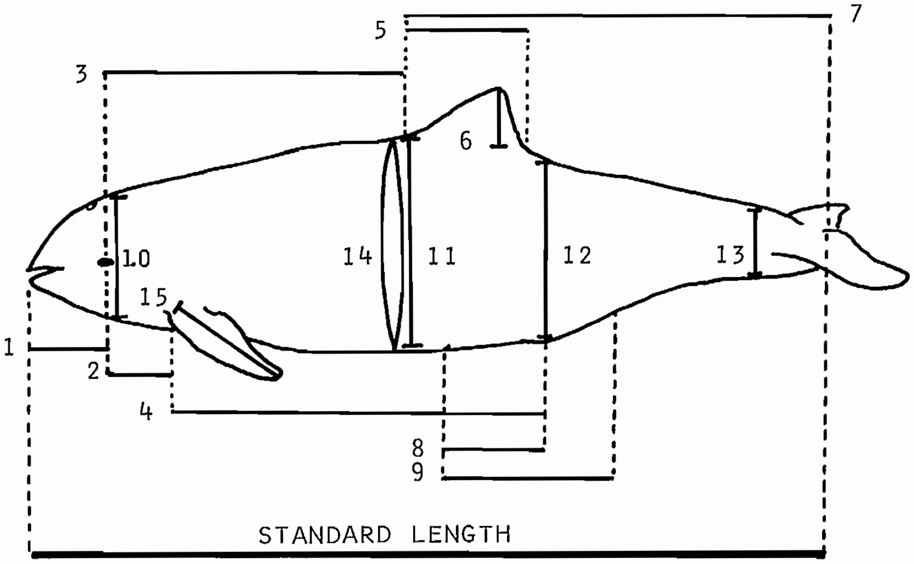


FIG. 23. Measurements from a small stranded cetacean. Reference to the numbers will be found in the text (p. 257).

minke whales and one finback whale were stranded in New Brunswick and Nova Scotia.

Certain rare or pelagic species only become available to science when they strand; some of these are hardly ever seen or recognized at sea. The potential importance of a stranded cetacean should therefore not be underestimated, and the observer should attempt to obtain maximum information about the specimen or specimens. Species such as the pilot whale and white-sided dolphin sometimes strand in whole schools, for reasons which are still not fully known. Among those suggested are (1) suicide (this seems most unlikely); (2) an ancestral desire to return to the land (even less likely!); (3) unfamiliarity with inshore environments, especially those with large tidal ranges such as the Bay of Fundy area; (4) parasitic infection; (5) confusion of their sonar navigational system in shallow waters; (6) the call of one accidentally trapped animal which lures the rest of the school to destruction; and (7) predators, such as sharks or killer whales, or even offshore thunder storms driving them ashore. It seems unlikely that there is a single cause for the phenomenon of mass strandings, and that each incident should be treated on its merits. Whatever the reason for stranding, if there is no specialist on the scene within a relatively short time, any member of the general public can collect valuable information.

The first and most important task is to establish the identity of the specimen(s). Newspaper reports abound with rough approximations and inaccurate local names such as "blackfish", "killer" whale, and so on. A number of publications, many either not readily available to the general public or out of print, provide guides to the identification of species of whales or seals. The Western North Atlantic guide (Leatherwood et al. 1976) and the Gulf of Maine guide (Katona et al. 1975) are very useful. The former can be obtained from U.S. Federal Government Information Offices (cite the NMFS number given in the chapter bibliography), and the latter from the senior author at the College of the Atlantic, Bar Harbor, ME.

A key to the identification of the whales, dolphins, and seals likely to be found in the Bay of Fundy is given below, with a worked example. With a little practice it should be possible for the reader to identify most stranded specimens to species.

When the finder has identified the animal as exactly as possible, any obvious external parasites or growths should be noted and drawn, or better still, cut out and preserved. Any scars should be carefully noted. Sketches of the color pattern of fresh specimens are very useful. Photographs of the whole animal, especially relative close-ups of the head (washed free of mud and sand) and the flukes, are the most valuable of all. Some kind of scale, (e.g. a ruler or a person) is useful in the photograph. If the specimen is in an advanced state of decay, it may be possible to salvage the skull and lower jaws for a museum. If the whole skull cannot be saved, a few teeth (if present) are useful. These must be dug from the gum, not sawn off short at the gum level. If the animal(s) have stranded alive, and there is no hope of them being returned to the sea, they should be put out of their misery with a rifle bullet through the brain or the heart. Fisheries Department wardens or the local police detachment will usually do this job; the former should be informed of the stranding in any case. Any obvious cruelty, e.g. poking the eyes of living whales with sticks, should be reported at once to the Humane Society and the police, and appropriate charges laid. In inhabited areas the disposal of large carcasses can be expensive and troublesome; if there is an onshore breeze complaints will soon be telephoned to any government department which is prepared to listen! Records of the stranding should be forwarded to the Fisheries and Marine Service (in Canada, the Arctic

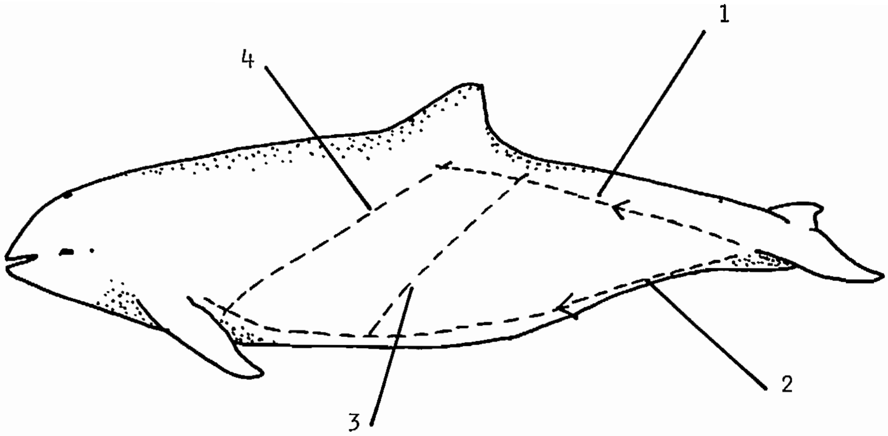


Fig. 25. Basic cuts to make at start of dissection of small cetacean.

The abdominal viscera (Fig. 26) — Keeping the point of the knife *up*, to avoid damaging organs beneath, cut through the skin connective tissue layer covering the abdominal cavity, and through the relatively thin muscle sheet. The INTESTINE, which varies from pinkish anteriorly to greenish posteriorly (there is no clear distinction between small and large intestine in cetaceans), is very long in proportion to the body size. The loops will spill from the body cavity through the incision; avoid cutting them. The KIDNEYS lie quite far forward against the ventral surface of the hypaxial muscle mass, below the vertebral column. Their lobulate structure is characteristic of cetaceans and not quite like the superficially similar lobulate condition found in some other groups of mammals. In cetaceans, the lobulation is probably associated with the increase in functional area needed to process excretory products and retain metabolic water in what is essentially a physiologically "dry" environment. At the anterior pole of each kidney, you will find the rather triangular and flattened ADRENAL GLANDS, each set within the same outer capsule membrane as the kidney with which it is associated. The DORSAL AORTA, partly set in a depression of the larger, thinner POSTERIOR VENA CAVA, can be located between the kidneys. The RENAL ARTERIES are prominent, the RENAL VEINS less so. In the wall of the abdominal cavity (and in many other parts of the body wall) you will find the tortuous networks of the elastic blood vessels, collectively called the RETE MIRABILE.

Move the intestines to one side and feel in the very base of the abdominal cavity for the relatively small BLADDER, which is usually partly filled. If the specimen is a male, a good part of the ventroposterior abdominal cavity will be taken up by the muscular and connective-tissue coated sheath of the PENIS — elongate, tapering, retractile, and usually dark grey — and the white, elongately oval TESTIS, edged with dark pinkish EPIDIDYMIS. The relative size of the testes depends greatly on the age of the specimen and whether the animal is in reproductive condition, since there is a seasonal sexual cycle in most species, including the harbour porpoise.

If the specimen is a female, it is relatively easy to locate the median CERVIX and the left and right horns of the UTERUS leading from it. The extremities of these horns run dorso-anteriorly around the wall of the abdominal cavity, attached by a mesentry. The uterine tissue is characteristically rather purplish. Trace each horn in turn to its distal extremity where the whitish OVARIES will be found. In immature animals these are smoothly elongate ovals; in mature specimens the presence of follicles and corpora make the shape irregular. Presence of a large CORPUS LUTEUM on the ovary is a good (but not invariable) indication of a FOETUS and PLACENTA being present. *Very carefully* slit open the horns of the uterus and search the interior with a blunt seeker or tip of forceps or closed scissors. The foetus may be only a few millimetres in length.

The upper right quadrant of the abdominal cavity is almost completely taken up by the large, bilobed LIVER, with the tubular DUODENUM (not clearly defined in cetaceans in the external morphological sense) closely appressed to its ventral surface. There is *no* GALL BLADDER in cetaceans. Near the anterior center of the abdominal cavity is the creamy pink, triangular PANCREAS. Palpate the liver and pancreas for hard spots (sometimes visible as white circular surface patches on the liver). Cut into these and you might encounter the pancreatic trematode *Campula oblonga*, usually in a dark greenish exudate produced by the liver tissue in reaction to the presence of the parasite. Few harbour porpoises are free of this infestation, which is often extensive, with much tissue damage. We believe it may be a significant contribution to mortality in the harbour porpoise.

In the upper left quadrant of the abdominal cavity is the complex, ruminant-like STOMACH. This has three distinct compartments. Since cetaceans have evolved as opportunistic feeders, they do not chew their food. Small prey items are swallowed whole; larger ones may be bitten into pieces by toothed whales. Digestion begins in the first compartment; under normal circumstances only liquid passes through to the second and third compartments.

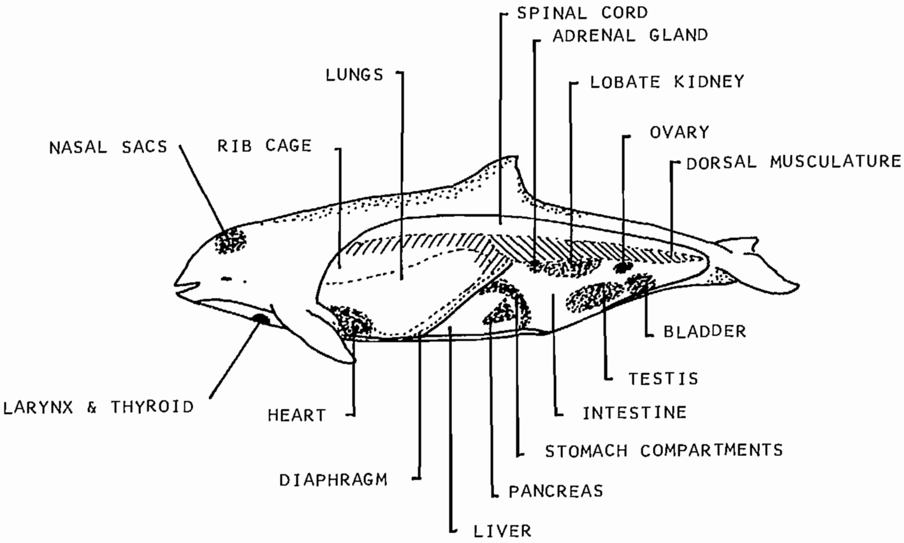


FIG. 26. Location of major organ systems in small cetacean.

Open the first compartment; note the thin, folded lining. Search for fish remains (vertebrae, gills, and especially otoliths from which identifications can be fairly reliably made), and squid remains (pens, eye lenses, and mandibles — the latter can be identified to genus and sometimes to species). Roundworms of the genus *Anisakis* may be present.

Thoracic Cavity — For the next part of the dissection, cut off the dorsal fin so that the animal can be easily rolled on its back. Note the hydrodynamic section of the fin in the process. Place a large piece of stone or wood on each side to hold the carcass in place. Remove all the blubber between the flipper bases as far forward as the middle of the "chin". Then, paring apart the muscles with knife or scalpel, snap through the ribs close to the line of the flippers on each side; carefully cut inward from the diaphram to the sternum and snip the anterior ribs near the top of the sternum; reflect the rib cage forward. Use scalpel and forceps to carefully separate the attachments to the sternum. The whole ventral section can now be severed at the top and removed. Be very careful not to cut yourself on the jagged rib stubs remaining in the lateral lines. The DIAPHRAM is thick and muscular — note how it is placed obliquely without a restraining ligament. Because of this, the tidal exchange of air is much more complete in the porpoise than in man or most terrestrial mammals.

Open the sac of the PERICARDIUM, exposing the coneshaped muscular HEART, which is quite large for the size of the animal. Study the main arterial and venous junctions with the spongy LUNGS. The latter may be congested, depending on the cause of death. They are quite likely to be significantly nodulated. Cut transversely with the scalpel in several places, and examine the cut surfaces; brush away the bronchial foam if necessary. If the specimen has been recently killed, living parasitic nematodes will be observed wriggling from the bronchioles and air spaces. *Pseudalius inflexus* occurs in the pulmonary arteries and bronchioles, *Torynurus convolutus* in the bronchioles, *Halocercus invaginatus* in nodules in lung parenchyma, and *Stenurus minor* in bronchial tubes and cranial sinuses. It is rare to find an adult porpoise without extensive infestation of respiratory system nematodes.

In the walls of the thoracic cavity note further extensive RETE. The function of these vessels is still being debated: they have been cited as glycogen stores, expansive cushions to protect the thoracic viscera during diving, and blood oxygen stores. Observe that the AZYGOUS vein is absent in cetaceans and that the carotid system is modified.

Locate the OESOPHAGUS (trace it up through the diaphram from the stomach). Use the back edge of the knife to separate it from the surrounding tissues in the neck region, but be careful not to sever anything else. Next find the hard, cartilaginous TRACHEA leading to the somewhat softer main BRONCHI. Use the tip of the index finger to locate the significant bulge of the LARYNX; use the back edge of the knife or scalpel to clean away the thin layers of muscle. The larynx is gleaming, blue-white cartilage. Associated with it are the right and left reddish purple lobes of the THYROID GLAND. Below the thyroid and back to the aortic junction of the heart, you will find traces of pinkish glandular tissue, there will be a lot of it if the animal is young. This is the THYMUS GLAND, and the cetaceans are unusual among mammals in that the thymus persists in the adult.

This completes virtually all the macroscopic examination which can conveniently be done, except for tracing out the major detail of the arterial and venous systems of the body, and studying the features of the head. The EXTERNAL OPENING OF THE EAR is a tiny, almost pinhole-opening a short distance posterior to the midline of the eye. Note the characteristic spatulate TEETH of the harbour porpoise, and the short tongue, which does

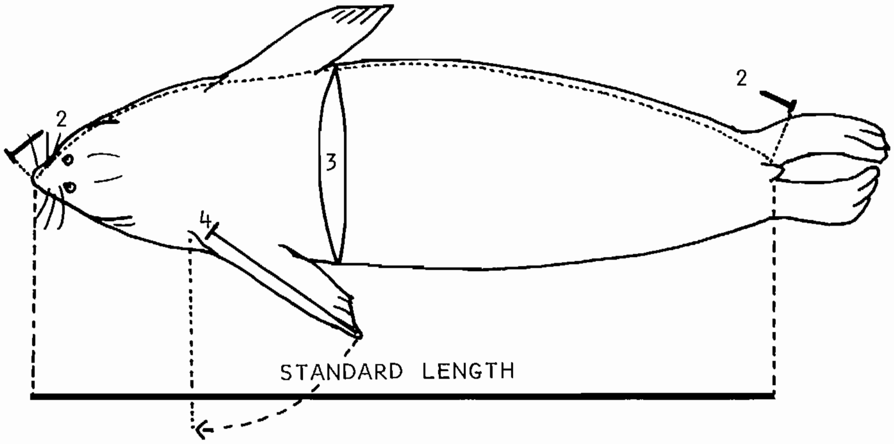


FIG. 24. Measurements from a stranded seal. Reference to the numbers will be found in the text on this page.

Biological Station, St. Anne de Bellevue, Que., c/o Dr. E. Mitchell) and a duplicate copy of the data retained in case the originals should go astray in the mails.

The next step is to take standard measurements. A guide to the standard measurements of whales and dolphins was prepared by the North American Committee of Marine Mammalogists (Norris 1961). Their format of measurements is very comprehensive, perhaps more extensive than most nonspecialists would be prepared to take. The most useful of these are given below. The single absolutely essential one is the *standard length*. This is taken *in a straight line* from the tip of the lower jaw to the crotch of the tail flukes. Other useful measurements are (Fig. 23):

1. Tip of snout to eye center
2. Eye to anterior flipper base
3. Eye to anterior edge of dorsal fin
4. Anterior of flipper base to anterior edge of vent (genital aperture)
5. Length of dorsal fin
6. Height of dorsal fin
7. Anterior edge of dorsal fin to crotch of flukes
8. Anterior edge of vent to navel
9. Navel to anus
10. Depth of body at eye
11. Depth of body at anterior edge of dorsal fin
12. Depth of body at vent
13. Depth of body over tail stem just before flukes
14. Maximum girth
15. Length of flipper
16. Width of flipper
17. Width of flukes
18. Length of flukes

The presence, shape, and number of teeth should be recorded. The shape of the head in profile, the presence and number of throat grooves, and the color pattern of this area should also be noted. If the animal is a baleen whale, a sample of whalebone plate should be taken if possible (this sounds easy — in practice it is not!). The sex of the animal should be noted; if it is possible to see the vent, or roll the animal over so that it is visible, this is easy. The male cetacean has a single deep slit; the penis may or may not be extruded. The slit starts quite high up on the abdomen. The female cetacean has a shorter vent, placed more posteriorly, and it is flanked by the pair of nipples.

If dissection is feasible, note the thickness of the blubber in several places. Slice the first stomach compartment to check stomach contents. In stranded specimens the stomach is usually empty. In a mass stranding of an unusual species, it is particularly valuable (if the carcasses are quite fresh) to take the ovaries, small foetuses which might be present, a small cube (1 cm × 1 cm) of mammary gland from the females, a similar small cube of testis from each male, and (in the case of dolphins, porpoises, or pilot whales), a tooth from each specimen. Fix all the samples in neutral 10% formalin or in 70% alcohol. Much interesting information can be obtained from such material in conjunction with accurate measurements.

The North American Committee of Marine Mammalogists has also prepared a guide to measurements to be taken from seals (Scheffer 1967) which recommends the following as a minimum (Fig. 24):

1. The standard length, taken as a straight line distance from snout to tail tip along the ventral surface.
2. The curvilinear length along the side from snout to tail tip if the animal is too heavy to roll over.
3. The girth just posterior to the fore-flippers.
4. The length of the front flipper held out at right angles to the body.
5. The weight, if practical.

As with cetacean measurements, these should be in metric units, if possible.

The number of seals likely to occur in this region is small in comparison to whales and dolphins. Attempting to key them (especially immature specimens which have not yet developed adult pelage) is difficult unless they are dead or unusually cooperative. If you are in any doubt about the identification, take notes, drawings, and preferably a photograph, and consult a specialist zoologist.

Key to Stranded Marine Mammals

(A guide to the use of the key will be found at the end.)

1 (1)	Animal with a tail but no hind limbs; a whale or dolphin	2
—	Animal with distinct hind limbs; a seal	17
2 (1)	Whale with long, fringed baleen plates in the roof of its mouth	3
—	Whale or dolphin with bare gums, or distinct teeth	8
3 (2)	Whale from about 3 — 4 m in length (much larger if an adult), with a strongly arched mouth, and lacking a dorsal fin on the back	*Eubalaena glacialis* (Right whale)
—	Whale with the mouth line slightly curved, but not strongly arched, and the back bearing a distinct dorsal fin	4
4 (3)	Flippers very long and curved, as long as total length of the head or more; body rather stout	*Megaptera novaeangliae* (Humpback whale)
—	Whale with short flippers, less than length of the gape of the mouth, and closely appressed to the body, which is elongate and rather streamlined	5
5 (4)	Baleen plates greyish-blue, except on anterior third of the right side of the jaw, where they are white. Grooves of throat white, numerous. Body basically grey above and white beneath	*Balaenoptera physalus* (Finback whale)
—	Baleen plates yellowish, or blackish	6
6 (5)	Baleen plates yellowish (N. Atlantic specimens usually have a distinct white patch on the outside of each flipper)	*Balaenoptera acutorostrata* (Minke whale)
—	Baleen plates blackish	7
7 (6)	Baleen plates black, but *with whitish hair fringe.* Body dappled grey above, white below, often with pinkish reflections when fresh	*Balaenoptera borealis* (Sei whale)
—	Baleen plates black, body surface slate blue-grey when fresh, often dappled. No white beneath	*Balaenoptera musculus* (Blue whale)
8 (2)	Whale without a dorsal fin; just a crest or ridge present. Body white with some dark pigmentation on edges of flukes, flippers and dorsal ridge if an adult, mottled slate grey if a calf	*Delphinapterus leucas* (Beluga, or White whale)
—	Whale or dolphin with distinct dorsal fin present	9

9 (8) Flukes lacking a central notch between them. Head bulbous, teeth few in number, or lacking, snout rather distinct .... Family Ziphiidae, beaked whales

Hyperoodon ampullatus (bottlenosed whale), and *Mesoplodon bidens* (Sowerby's beaked whale), are the two species most likely to be encountered in the Bay of Fundy. Beaked whales, especially females and immatures of both sexes, are very difficult to identify. Since material is rare in scientific collections, every effort should be made to contact a specialist should a stranded specimen be encountered.

— Whale or dolphin with a distinct notch between the tail flukes 10

10 (9) Small whale, less than 4.5 m, having a small mouth with curved teeth set well back beneath the head. Flippers pointed, dorsal fin present. General appearance rather shark-like, except of course, for the presence of a blowhole and the absence of gills! .... *Kogia breviceps* (Pigmy sperm whale)

— Small or medium-sized whale, or dolphin, not fitting this description 11

11 (10) Small peg-like teeth, confined to front part of jaw, head bulbous, flippers long and distinctly "elbowed", dorsal fin very prominent. Body blackish brown with a white belly streak, and other white patches may be present above and behind the eye, or behind the fin. ..... *Globicephala melaena* (Pilot or Pothead whale)

— Teeth not so restricted in distribution in the mouth, not peg-like, but pointed or spatulate at apices, head and body porpoise or dolphin-like, head not markedly bulbous 12

12 (11) Teeth spatulate at apex, animal less than 2 m in length, blackish brown above, greyish shading on flanks, white beneath, with rather small and broadly triangular dorsal fin .... *Phocoena phocoena* (Harbour porpoise)

— Teeth bluntly or sharply pointed at apex. Specimen likely to be more than 2 m in length 13

13 (12) Body distinctly grey, rather uniformly pigmented, beak of snout a few inches in length .... *Tursiops truncatus* (Bottlenose dolphin)

— Body quite strikingly patterned, either brown and white or blackish and white, often with distinct, segregated pale patches behind head or on flanks 14

14 (13) Flippers distinctly paddle-shaped, head with a distinct and characteristic white oval above and behind the eye. Animal rather large, even calves being about 2 m at least. Adult male with very high, narrow dorsal fin .... *Orcinus orca* (Killer whale)

— Flippers tapering to blunt point, head lacking such a discrete lateral patch 15

15 (14) Animal with rather prominent beak, back brownish before death, with yellowish shading on the flanks, whitish beneath .... *Delphinus delphis* (Common dolphin)

— Animal with wedge-shaped head in profile, lacking a distinct beak 16

16 (15) Large dolphin (2 — 4.5 m), with pale patch around the blowhole, the short beak region pale-pigmented, and a white patch on the flanks extending well forward of the dorsal fin, as seen in profile .... *Lagenorhynchus albirostris* (White-beaked dolphin)

— Large dolphin, lacking pale patch around blowhole, with a dark beak, a fine "eye-stripe" running from the eye to the top of the flipper through an extensive area of white *above* the flipper. White area on flank just about extending to the anterior line of the dorsal fin, but not curving up to meet it. White area on posterior flank limited to a rather narrow stripe and not rising to meet back of dorsal fin as in the other species .... *Lagenorhynchus acutus* (White-sided dolphin)

17 (1) Pelt bluish-grey on the back, with overlying scattering of whitish rings, whirls and loops, and blackish spots and irregularly-shaped marks .... *Phoca vitulina* (Harbour seal)

— Pelt dark grey, almost blackish in males, lighter in females, with small patches of light grey in flanks. Females may be whitish on the belly, but back and flanks have dark grey or blackish blotches. Head characteristically horse-like in profile .... *Halichoerus grypus* (Grey seal)

Dissection of the stranded small cetacean (based on the harbour porpoise *Phocoena phocoena*, unless otherwise stated) — Under normal circumstances, the specimen will be lying on its belly, and since you will soon discover that even relatively small dolphins and porpoises are heavy for their size and difficult to manoeuvre, it is convenient to carry out a lateral dissection.

You will require the following items:

1. Sharp hunting knife, with at least a 5″ (13 cm) blade.
2. Surgical scalpels, scissors, forceps, all of medium size; an additional *large* pair of long forceps is often very useful.
3. Plastic freezer bags, 32-oz (1L) bottles, and a supply of neutral buffered formalin made up to a 10% standard. Use a phosphate buffer.
4. Recording book or pad, and several soft pencils.
5. Bag ties.
6. Sturdy manilla, reinforced, baggage labels.
7. Access to a deep freeze.
8. Plastic pail for washing out body cavity with large volumes of water.
9. Pair of strong cutters, or even better, surgical, stainless steel bone snips.
10. A supply of water.
11. Plastic or latex surgical gloves, and an overall or laboratory coat which can be washed. The danger of catching the stubborn dermatological condition known as "seal finger" from a small cetacean is not particularly high, but there is no point in taking chances. The ability of the characteristic oily odor of porpoise blood to cling to clothing and skin is almost lengendary.

The student cannot be too strongly advised to write out all the labels which will be required *in advance*, and to bag and label anatomical specimens *as you go*. If you deposit your tissues in a bloody heap and then try to sort them out, you will find that fragments of organs are not quite as easy to recognize as you think. Tissues for histological preparations should generally be taken within half an hour of death. The maximum permissible postmortem time varies from tissue to tissue: the retina undergoes critical changes after one minute, but muscle tissue is fairly robust. The fibers may in fact stay alive for some hours after the death of the organism.

The key to success in dissecting a small cetacean is realizing that the organs are "packed" slightly differently from those of terrestrial mammals with which you are more familiar, and so to be systematic in your approach.

Removal of the blubber — After the external measurements and observations have been made, and any desired photographs taken, remove enough of the flank blubber to expose a substantial working area. On a porpoise or dolphin, the thickness of the blubber varies from 0.5 to about 2 cm, depending on species and location on the body surface. Make two cuts, as shown in Fig. 25, and, starting from the tail end of the body in the dorsal cut, work the blubber away from the underlying muscle, alternately using the front and back edges of the knife. Under normal circumstances, the blubber is removed with little difficulty. Repeat for the ventral cut, and then work to separate the middle flank area from the tail end forward, peeling the section forward as you go, and cutting it free when the base of the rib line is reached. There is no reason why the panel cannot, at this stage, be removed all the way back to the base of the flipper. If the flap is not severed, it will tend to keep folding back and be in your way. Examine the severed piece of blubber: note the sparse occurrence of major blood vessels and the texture of the blubber (while the fat content can be as high as 95%, there is a significant connective tissue structure). You may find small waxy cysts, which may be of more than one species. Little is known about these parasites. Lamprey scars may penetrate deeply into the blubber. Necrosis may be present, with secondary and hypodermal pathology in cetaceans. Very rarely, the stalk of a *Penella* barnacle may penetrate the skin, with a holdfast embedded in the blubber.

not have great mobility. Cutting away the blubber surrounding the blowhole reveals the complex pattern of NASAL SACS, which are characteristically black and leathery. They certainly control the opening of the blowhole, and have been implicated by many researchers in the production of some, if not all, sounds made by these animals. Anterior to the blowhole is the fatty MELON, again believed to be involved in the acoustic system of the odontocete.

If a saw is available, the top of the cranium can be removed. The CEREBRUM is typically mammalian, except that the temporal lobes are disproportionately large; this is believed to be associated with the relative high importance of sound to these animals and the need for cortical surface for handling and storage of acoustical information. The CEREBELLUM can be seen by reflecting the cerebrum anteriorly. Composed of a median and a pair of lateral lobes, it is quite typically mammalian. If the skull is flensed (stripped) of blubber and removed from the carcass, the characteristic form of the TYMPANIC and PERIOTIC BONES can be observed.

Observation of Whales at Sea (Fig. 27)

OBJECTIVES

By careful and reptitious study of cetaceans at sea, the skilled observer can accrue information on general,

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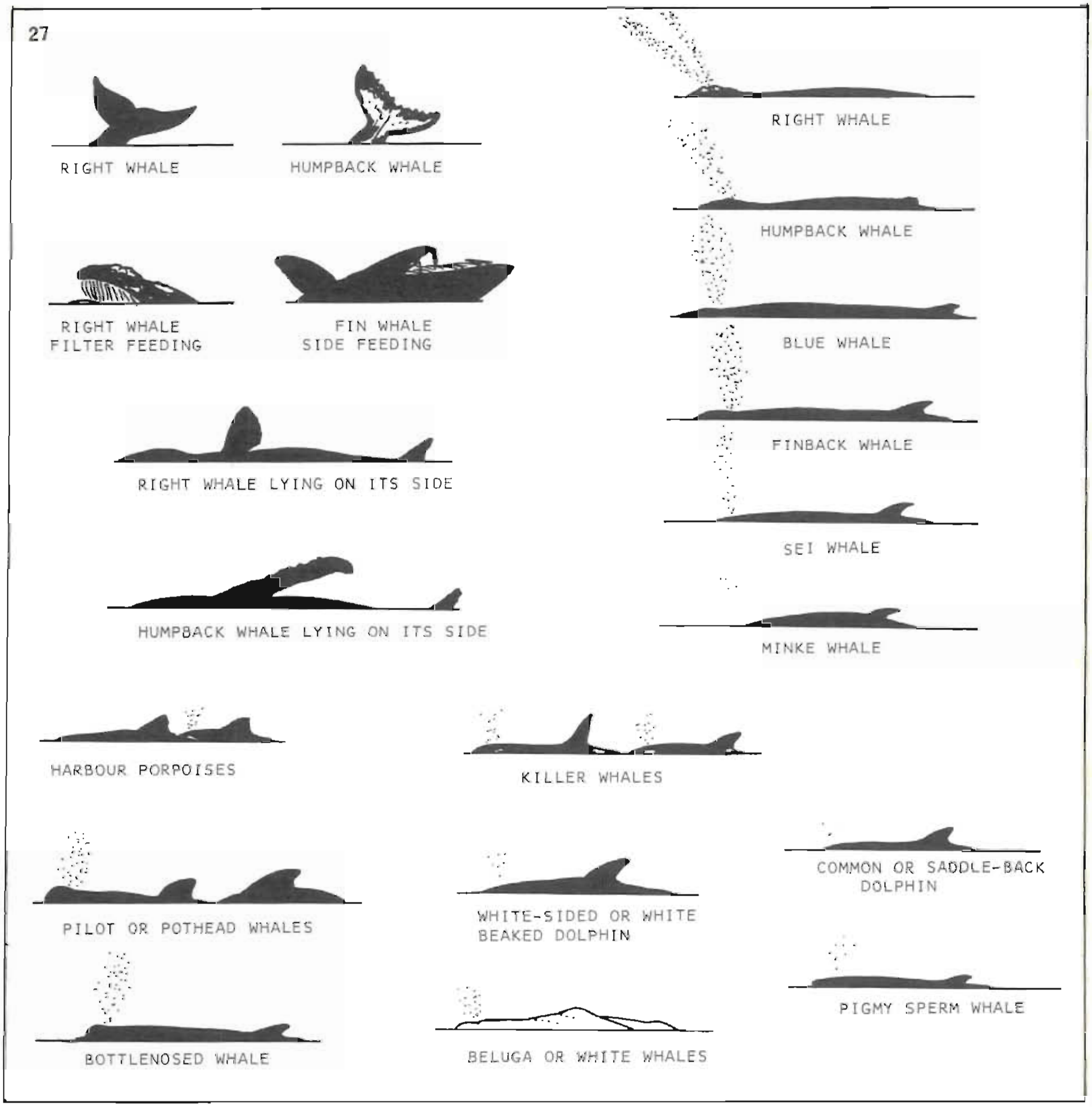

FIG. 27. Some useful silhouettes of whales and dolphins seen at sea.

feeding, and sexual behavior, daily and seasonal movements, size and composition of population, respiration cycles; he can even, by cataloguing recognizable scars or similar natural markings, keep track of the comings and goings of particular individuals over extended periods of time. The relationship of feeding areas to current boundaries, subsurface topography, and tide phase can be determined by concurrent use of charts and oceanographic equipment.

The method of observation selected depends on locality, species, weather conditions, and last but far from least, funding available to the observers. The charter cost of a medium-sized boat for a day rose from $40 to $300, between 1970 and 1982, and shows every likelihood of continuing to rise. Needless to say, increases in fuel and operating costs now render the use of light aircraft or helicopters impossible to all amateurs except those with independent means, or excellent, tolerant, and free-spending connections.

Whales and porpoises can be adequately observed from large or small vessels in these inshore waters. Vessel size should match the size of the party of observers. Crowded gunwales are dangerous gunwales. If money is no particular object, opt for a medium-sized vessel, say 12–15 m, with a low frequency, slow revolution, inboard engine.

APPROACHING MARINE MAMMALS

Close approach to a ledge by a vessel under power will invariably cause hauled-out seals to go into the water; they will not return to the ledge until the intrusion ends. It is much wiser to stop the engine while some 200–300 m upcurrent from the ledge and drift slowly down towards the animals; they will consider this much less threatening and you will be able to get correspondingly closer for photographs, detailed observation, and counts.

Harbour porpoises almost invariably avoid a boat under power. About the only satisfactory way of photographing these wary animals is to drift for several hours in areas where they concentrate to feed. Other species, such as humpback and finback whales, sometimes seem oblivious to the presence of a boat, although they will turn away from a small craft with a noisy outboard engine. Minke and pilot (pothead) whales and the nomadic white-sided dolphins, however, exhibit considerable curiosity towards boats, and will sometimes approach them very closely. None of the dolphins normally renowned for "bow-riding" commonly occur in the Bay of Fundy. If you think it necessary to make an active effort to get closer to cetaceans, do so with the engine at *low* and *constant* revolutions. Sudden changes in revolutions almost invariably startles the animals, as they are constantly alert for possible threats manifested by changes in the acoustical background of their environment.

Above all, when observations are in progress *keep quiet.* This usually means keeping still as well, and not constantly moving from spot to spot for a slightly better angle from which to photograph. Establish observation positions, and then keep to them. The sharper sounds, such as those created by cameras or binoculars tapping against the side of the wheelhouse or hardsoled boots on deck planking, carry far more efficiently through water than air. A painstaking half-hour drift into a favorable position can be negated by a single sharp noise or loud comment.

OBSERVATION EQUIPMENT

Photography — Regrettably, cetaceans in the water are uncompromisingly unphotogenic objects; to obtain good results you need all the help that your equipment can give you. The cheaper type of "Instant" camera usually has a semi-wide angle lens suitable for photographing groups or landscapes, but is usually quite useless for cetaceans. Even a transparency or print taken with an SLR 50 mm standard lens is usually quite disappointing. Some kind of telephoto lens of at least 135 mm, and preferably 200 or 300 mm, is essential. At longer focal lengths, hand-holding results in blurred pictures, except at the very highest shutter speeds. Other problems are the behavior of the animals, and the great differences in light readings obtained at sea with the angle of the sun and its position relative to the object being photographed: you are photographing fleetingly visible objects under varying light conditions. During a single breathing roll, a porpoise is usually above the surface for less than a second, although it may seem longer until you try to photograph it. Since human reaction time is at the very least 0.2 sec, this leaves little time for aiming, focussing, adjusting the "f" stop and speed, and taking the actual photograph. A fully automatic lens really comes into its own in such a situation, and some kind of motor drive unit greatly reduces the number of chances lost by the time taken to manually transport the film from frame to frame.

Binoculars — During the course of a day, you will spend several hours peering through binoculars searching for animals. It is a good idea to use glasses which are completely suited to the task.

First, they should be light. You might construct a T-shaped handle which can be comfortably grasped with both hands in front of the chest or at waist level, with the binoculars strapped to the top of the "T". Remember that you will be making the observations at sea, not from the land, so that little is gained by obtaining glasses with the highest possible magnification: these only magnify the movements, and if you have any tendency to seasickness, aggravate that as well. Binoculars of 7 × 35 or 7 × 50 power are quite adequate. It is a good idea to have at least one pair of wide angle glasses in the group. A pair of 7 × 50 angle lenses will allow you to observe a zone 150–200 m (165–220 yards) wide at 1000 m.

Recording observations — The two enemies of written recordings at sea are gusts of wind and showers of spray; damaging visitations of either come without warning. It is worth an extra dollar or two to cover your notebooks or pads in a closing clipboard folder with a vinyl coating. Most inks, even of marking pens and ballpoint, run when drenched with salt water spray, so a soft pencil is recommended for all writing.

Many observers prefer to tape their behavioral observations and transcribe them later. Many incidental notes that would otherwise not find their way on to paper can be salvaged this way. Two observations on this method: (1) the time and effort needed to transcribe is always much

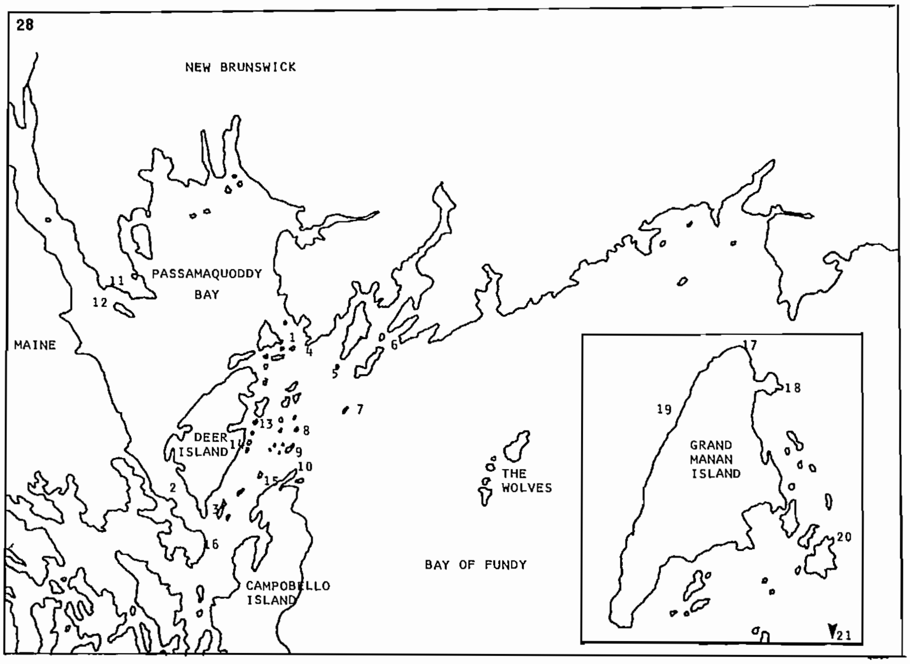

FIG. 28. Place names mentioned in the text with respect to spotting cruises for whales, dolphins and seals. 1) Letite Passage; 2) Western Passage; 3) Deer Island Point; 4) Green's Point (Letite) Lighthouse; 7) Whitehorse Island; 8) White Island; 9) Spruce Island; 10) East Quoddy Lighthouse; 11) St. Andrews township; 12) Niger Reef, Navy Island; 13) Mink Island ledges; 14) Leonardville township; 15) Head Harbour Passage; 16) Eastport town; 17) Northern (& Ashburton) Heads; 18) Swallowtail Head; 19) Dark Harbour; 20) Sheep Rock Head; 21) Brazil Shoal and Old Proprietor Shoal (off map).

longer than you expect it to be, and (2) a missing key point in an observation, i.e. the time of contact or the date, are easily seen to be missing in a notebook simply by quickly scanning the pages for pertinent points, but a missing reference is not so easily noticed on a tape until the notes are transcribed, or sometimes much later. If you use a tape, develop a standard format of identification that you review each time you are about to start a series of observations.

Amateur observers are frequently tempted to make a temporary waterproof cap for their microphone and to lower it into the water to try to obtain underwater whale or dolphin noises. This is invariably a total waste of time and tape, although it does provide a rather interesting recording of boots clomping on planks, distorted voices, and the sound of water slopping against the hull of the boat, which can provide a splendid acoustic background to the right kind of party.

Specific Localities for Observing Marine Mammals (Fig. 28, 29)

One is likely to see some marine mammals from almost any vantage point on the shores of the lower Bay of Fundy if sufficient hours of observation are expended. Prime localities in which they can be *expected* to be seen are, however, at a premium.

Harbour seals are almost always found in small numbers around the Niger Reef, just outside Navy Island, near St. Andrews township. They are also commonly seen[2] near Minke Island, just north of Leonardville on the seaward coast of Deer Island and near Cummings Cove on the Western Passage shore of Deer Island.

If a sea-going boat is available, cruise across Passamaquoddy Bay and out through Letite Passage, towards Black's Harbour, then turn to pass Whitehorse Island with its bird colonies, and head towards the East Quoddy light on the northern tip of Campobello Island; in summer you will almost invariably see a few schools of harbour porpoises and, with luck, a minke and finback whale or two. If the sea is calm, numbers of harbour porpoises (which are rather difficult animals to see at any distance) should be seen from late July to the end of September. Finback whales are not likely to be seen much before mid-July, but will stay until the end of September.

Vantage points on shore are not numerous; Green's Point (Letite) lighthouse at the outer end of Letite Passage can be approached by road, and gives a good view across the outer approaches to the passage. Northern Head, Swallowtail Head, and Dark Harbour on Grand Manan are sites from which finback whales, sometimes in company with other species, and almost certainly plenty of harbour porpoises might be seen. Deer Island Point camp ground, on the southern tip of Deer Island, is a good place from which to observe Harbour porpoises moving up and down the Western Passage between Deer Island

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[2] But totally absent in 1979, perhaps because of disturbance by weir fishermen.

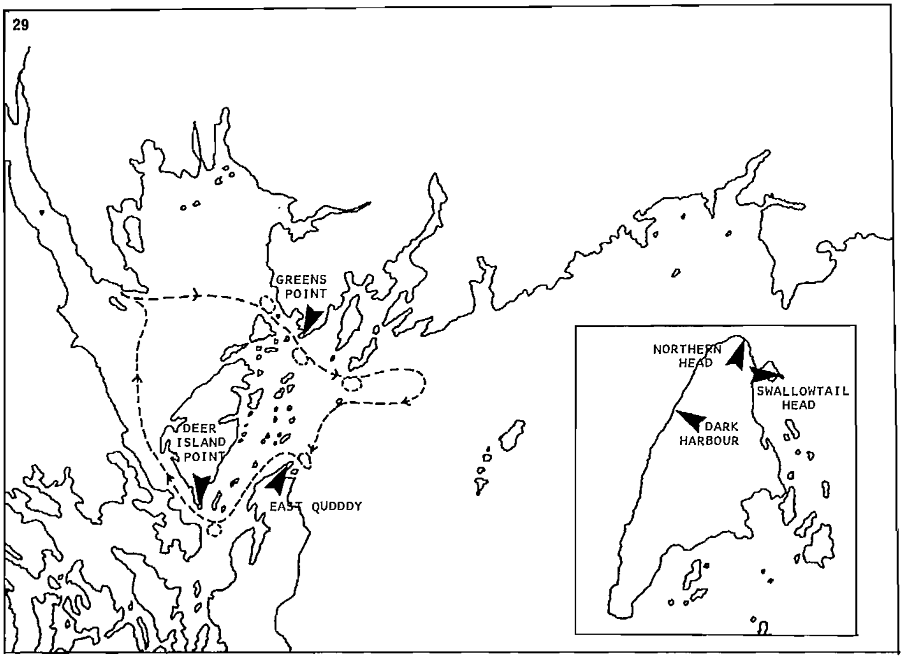

FIG. 29. Suitable vantage points from which cetaceans may be observed with naked eye or binoculars, circumstances permitting.

and Eastport on the coast of Maine. The common occurrence of porpoises in any numbers is virtually limited to June–October; as previously stated, a few overwinter (we have records for all months of the year from the Deer Island area).

Finback whales sometimes occur in the approaches to Head Harbour Passage, where they may be seen from East Quoddy light, which can be approached by land. Look towards White and Spruce Islands and out towards the Wolves. Minke may turn up anywhere in the outer part of the Quoddy region and, less frequently, in Passamaquoddy Bay itself. Finback whales occasionally move into the Western Passage. In recent years Right whales have been seen near the Wolves and, more rarely, in the approaches to Head Harbour Passage. Together with finback whales and probably humpback whales, they have been reported in 1975–77 from the vicinity of the Old Proprietor Shoal off southeastern Grand Manan. This is a dangerous area to approach without local knowledge. When passing through this area, stay well on the seaward side of the line from the bell off Sheep Rock Head and the bell marking Old Proprietor. Heavy ebb rips in this area can be severe in certain wind conditions and can be hazardous for small boats.

Warning to Observers

SAFETY

The over-riding consideration when selecting a boat for this kind of work should be its seaworthiness and its suitability for the size of observer party going out. *Always check all the life-saving gear before going out to sea. Do it every time, not just once a week. The time someone removes the life jackets to dry them, without telling other people, could be the only time you'll ever need one.*

Always engage the services of someone who knows the Quoddy region intimately if venturing far from St. Andrews. The weather changes can be savage even in summer, and the non-local will frequently fail to see or heed the warning signs developing. The whole outer Quoddy area can be enveloped in fog within half an hour after a wind change to the east. The Deer Island, Campobello Island, and Grand Manan Island regions are a maze of channels and submerged reefs, not all of which are unambiguously marked. The great tide range must not be forgotton; a reef easily visible at low water may be out of sight and out of mind at half-flood.

Danger of a collision with a large whale is minimal under normal circumstances. Be assured that they have a better idea of your position at any given moment than you do of theirs while they are under the surface. Even a curious animal will rarely venture much within two or three body lengths of a boat.

But they are, after all, *very* heavy animals. If you are in the vicinity of humpbacks and right whales and they begin to show signs of breaching behavior (jumping partly or completely out of the water), get well clear. Also, if you are in a small or medium-sized boat, keep a good distance away from a humpback or right whale female with a calf: there is always the chance that the mother will resent your intrusion in no uncertain manner. Also avoid humpbacks which appear to be engaged in mating behavior. Apart from these rather infrequent occurrences, there is no doubt that large baleen whales are among the safest of all large mammals, from the point of view of the naturalist observer at close hand.

INTERFERENCE WITH SCIENTIFIC PROGRAMS

A final plea. There have been active scientific whale and porpoise observational and experimental programs going on in the Bay of Fundy since 1969. Before setting out on an observation and photographic cruise which involves close approaching a cetacean closely, please enquire first to see if an official program is operating at that particular time. If your boat turns up unannounced, piloted by someone with only a nodding acquaintance with marine mammals — and that includes most local fishermen, regardless of what they might say to the contrary (although there are one or two very notable exceptions) — you may seriously disrupt a series of observations or recordings with your boat noise or by disturbing the animals. Research groups working in the Bay of Fundy include those from the University of Guelph, the Grand Manan Research Station and Ocean Search (contact Dr. Gaskin), the New England Aquarium, Boston (contact Dr. Prescott or S. Kraus), the University of New Brunswick in Saint John (contact Dr. Terhune), and the University of Maine (contact Dr. Gilbert). They will be pleased to assist you.

HARASSMENT OF MARINE MAMMALS

Continued disturbances will seriously disrupt feeding behavior of marine mammals. Experimentation or dead or live capture is strictly controlled in Canada by a permit system operated by the Fisheries and Marine Service under the Fisheries Act sections pertaining to mammals. Only such permits, and even then only when the aims, objectives, and necessities of the program have been discussed and approved allow experimentation and/or capture.

While there is no specific law (as in the United States) covering harassment of marine mammals, there are nevertheless a number of routes by which a person or persons so doing could be brought before the courts by the Humane Society or the police, to face possible imprisonment or fines. While no one interested in these animals is remotely likely to deliberately harass them, inadvertent harassment, such as by making repetitious close passes in a small boat with a high-powered, very noisy outboard, can easily occur.

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CHAPTER 17

The Coastal Forest of the Passamaquoddy Bay Area

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Introduction

The coastal forest in the Quoddy Bay area is a highly variable product of both maritime and terrestrial processes. It is here defined as the forest or dominant vegetation above the high-tide mark of all tides and extending inland to the point where marine influences and the biotic communities associated with these become negligible components in the ecosystem (Dickinson 1977). It is a transition zone between tidal and terrestrial characterized in its entirety by a great diversity of species, a reflection of less extreme ecological conditions and a variety of niches.

The vegetation of the Quoddy Bay Region of southwestern New Brunswick is the result of many factors including glacial, climatic, geological, and human historical, and has been affected by fire, disease, drought, wind, salt spray, plant migration rates, and the availability of a seed source. Chance is also involved in the distribution of plants.

Postglacial History

Palynological studies of lake sediments in the region reveal that the vegetation has changed markedly since the last glacial maximum approximately 15 000 yr B.P. The sequence of vegetational types began with a treeless tundra with many shrubs and herbs probably closely related to present arctic tundra taxa. This condition lasted approximately 600 yr, after which birch and poplar became dominant. The vegetation then went through periods when spruce was dominant. Later, pine, birch, and other hardwoods, including oak, ironwood, ash, and maple, became more important. About 6600 yr B.P. hemlock increased and pine decreased until about 5100 yr B.P., when beech dominated the forest along with other hardwoods. By about 2000 yr B.P., hemlock again became important with the hardwoods and some pine. Finally, spruce became more dominant again and hemlock declined considerably (Mott 1974).

Climate

The present climate is characterized by late, cool springs, moist summers with frequent periods of fog, and moderated winters (Chapter 2). This creates a coastal habitat similar in many ways to that of boreal and montane areas and the vegetation reflects this to a remarkable extent. Long-term effects of storms are great and their importance as ecological factors is considerable. Wind-carried salt spray, with an accumulation of ions from sodium chloride, is not considered a problem in most coastal communities because of leaching by the relatively high rainfall (Chapman 1977) and the protected nature of Quoddy Bay. The bay is relatively sheltered from the open waters of the Bay of Fundy by Deer and Campobello islands as well as the Mascarene Peninsula. The maritime influence decreases with distance from the sea in a manner which is exponential rather than linear (Dickinson 1977).

Other Factors

Fires have been an important factor in shaping the present vegetation, especially in the adjacent uplands. In the fog zone, close to the coast, fires have not been as important (Wein and Moore 1977).

There has been considerable pressure on the habitat by man for nearly 200 yr. Much of the marketable lumber was harvested early. According to Wicklund and Langmaid (1953), this is poor agricultural land because of the excessively acid and stony soil, yet a high percentage of the more level or gently sloping land was cleared for pasture, hay meadow, and grain crops by early settlers. Some pasture is still utilized and a few blueberry plantations are maintained, but since the late 1930's much of the land has been reverting back to red or white spruce and alder forest. Glacial tills cover much of the area and the soil material is therefore often unrelated to the underlying rocks. In many places, these outwash gravels are coarse-textured and several feet deep. Rock outcrops are common in the area.

Forest Types

In their classification of the forests of the Quoddy Bay area, Loucks (1961) and Rowe (1972) used different terminology for similar forest divisions. Rowe's Fundy Coast section of the Acadian Forest Region (Louck's Musquash District of the Fundy Bay Ecoregion) includes the outer St. Andrews Peninsula, the Quoddy Islands, and the Mascarene Peninsula. It is an area dominated by red spruce (*Picea rubens*) on the relatively undisturbed sites, with an admixture of yellow birch (*Betula lutea*), mountain ash (*Sorbus americana*), and red maple (*Acer rubrum*). Red spruce is the common species repopulating abandoned farm land. Eastern hemlock (*Tsuga canadensis*), eastern white cedar (*Thuja occidentalis*), and white pine (*Pinus strobus*) are rare in this section. On the uplands, sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) are present but sparse. Immediately adjacent to the shore is a mixed forest of white spruce (*Picea glauca*), black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), and tamarack (*Larix laricina*). Raised sphagnum bogs are also characteristic of this section but are sparse in the Quoddy Bay area. Trembling aspen (*Populus tremuloides*) and white (*Betula papyrifera*) and gray birches (*Betula populifolia*) are repopulating old burns, with red maple found on the wetter sites.

The remainder of the Quoddy Bay area is included in Rowe's Southern Uplands section of the Acadian Forest

Region (Louck's Mt. Pleasant District of the Magaguadavic–Hillsborough Ecoregion). The vegetation is transitional, with elements of the Fundy Coastal forest intermingled with sugar maple, beech, and yellow birch on the uplands and red maple, white birch, balsam fir, red spruce, white pine, and eastern hemlock at lower elevations. Much of the area is marked by a long fire history, which favors the maintenance of the pioneer hardwoods such as trembling and bigtoothed aspen (*Populus grandidentata*), white and gray birches, and red maple. Black ash (*Fraxinus nigra*), red spruce, white cedar, and red maple occur commonly in swamps and black spruce and tamarack dominate in the bogs.

Throughout much of the area the undergrowth includes many ferns and other herbaceous plants showing affinities with the boreal forests farther north and with the vegetation of north-facing mountain slopes in New Brunswick's central highlands. The most common nonarboreal vascular plants are bunchberry (*Cornus canadensis*), Canada mayflower (*Marianthemum canadense*), goldthread (*Coptis groenlandica*), wild sarsaparilla (*Aralia nudicaulis*), white woodland aster (*Aster acuminatus*), wood sorrel (*Oxalis montana*), and twinflower (*Linnaea borealis*). Shrubby species of importance are withe-rod (*Viburnum cassinoides*), mountain holly (*Nemopanthus murcronata*), low-bush blueberries (*Vaccinium angustifolium*, *V. myrtilloides*), and sheep laurel (*Kalmia angustifolia*). Fireweed (*Epilobium angustifolium*) and bracken fern (*Pteridium aquilinum*) become dominant following fires, along with species of *Rubus*, *Aster*, and *Solidago*.

Specific Sites

KILMARNOCK HEAD

General — This peninsula jutting into Quoddy Bay is situated opposite Ministers Island from the St. Andrews Peninsula. It is one of the best examples of coastal forest in the vicinity of Quoddy Bay and has not been heavily lumbered for over 50 yr.

To get to Kilmarnock, take the road off N.B. Route 127 by the Salmon Research Institute weir on Chamcook River and continue on this road past the weir for about 3 km until it becomes gravel and flat open rock appears on the left side. Near the bottom is the bay. Taking the road to the right, one approaches the beach from an abandoned farm site with many apple trees in the vicinity. Remnants of cultivation near a former house site include daylilies (*Hemerocallis* sp.) and hops (*Humulus lupulus*). The large colony of salt-spray rose (*Rosa rugosa*) may have been planted or may have escaped from cultivation from plants in the vicinity.

This location is on the east side of the headland, the top of which faces south (Chapter 1, Fig. 1). From the beach, one faces due east towards Anderson Mountain (175 m) on the mainland. To the right is Hardwood Island and another nearly unforested island, behind which lies the Mascarene Peninsula, and, finally, Deer Island as one sights off the edge of the head.

The visit should be planned to coincide with low tide, so one can skirt the cliff on the beach and climb the rocks into the woods where the cliff dips to meet the shore (Fig. 1). The general aspect of the entire forested headland is

FIG. 1 Kilmarnock Head: the shore.

FIG. 5 Ovenhead: a conglomerate cliff.

The land slowly rises from the causeway to a high point approximately 30 m high on a cliff of conglomerate rock of Upper Silurian and Lower Devonian (Ruitenberg 1968). The area appears to have been used for some time as an open camping area and there are remnants of an old farm and graveyard on the head. The grassland is perhaps partly maintained by mowing and partly by the effects of wind and salt spray. The backside (north) of the headland appears to be somewhat protected and here occur red spruce, white and yellow birch, pin cherry (*Prunus pensylvania*), and apple (*Pyrus malus*), with an understory of mountain maple, red elder (*Sambucus pubens*), speckled alder (*Alnus rugosa*), and shadbush (*Amelanchier* spp.). Staghorn sumac (*Rhus typhina*), fireweed, hawkweeds, and species of *Rosa*, *Carex*, *Solidago* and *Aster*, as well as several grasses occur in the open areas. Common juniper (*Juniperus communis var. depressa*) is also a part of this assemblage. There is an interesting gradation between salt marsh plants and woodland species on the steep bank where the base of the headland meets the barrier beach/salt marsh (Fig. 7).

Attached to the headland and jutting into the bay is a small promontory of special interest because of the persistence of a remnant of the coastal forest (Fig. 8). It is dominated by red spruce and eastern white cedar, many individuals of which have been blown over and suffer the effects of wind and salt spray. Other typical coastal plants include shadbush, mountain ash, balsam fir, speckled alder, withe-rod, and many herbaceous plants such as New York aster (*Aster novi-belgii*), rattlesnake root (*Prenanthes trifoliolata*), wood-rush, (*Luzula multiflora*), wild sarsaparilla, Canada mayflower, starflower, downy goldenrod, and twinflower. These species are mixed with invading halophytes such as arrow-grass, seaside goldenrod, red fescue grass, mountain cranberry, and goosetongue.

The white cedars especially show the effects of wind-blown salt spray and other species show various degrees of stress due to the continuous erosion of their habitat and the opening of the forest floor to the drying effects of wind and the increased concentrations of salt ions. Red raspberry (*Rubus idaeus var. canadensis*) has invaded the openings created by the disturbance.

Cliff aspects — The conglomerate cliffs of Ovenhead are sparsely vegetated because of the friable nature of the substrate (Fig. 5). Where the cliff is more gradually sloping, some vegetation has secured a roothold. The most prevalent species are yarrow, harebell, red fescue grass, sheep sorrel, (*Rumex acetosella*), prostrate knotweed (*Polygonum arenastrum*), and evening primrose. Goosetongue occurs near the lower reaches.

Suggestions for Study

The coastal forest is a convenient and compact site for study of ecological factors such as plant community patterns, soil development, role of drainage as a component of various habitats, influence of soil pH, and the results of concentration of certain ions, namely, those derived from sodium chloride. When planning a study of coastal vegetation, the following factors should be considered: field surveys, evaluation of existing sources of data, aim of the study, logistical resources, and time constraints.

As a scientific resource, the coastal forest can be studied from the standpoint of basic inventories of organisms, seeking to provide information on distribution rather than to provide explanations. Studies can also be undertaken relating to the dynamics of plant communities or to the ecology of certain critical plant species.

FIG. 6 Ovenhead: the shore.

With the possibility of large oil tankers traversing Quoddy Bay waters, environmental impact studies should be undertaken to ascertain the probable damage to coastal vegetation in the event of a major oil spill. Similarly useful would be environmental impact studies investigating the effect of man's recreational activities on the cliffs of the Quoddy Region.

Another study approach would be to map the spatial distribution of minor morphological features, including factors such as slope, elevation, exposure, and stability of surface and substrate, which exert a major influence on the communities.

The most important ecological gradients run from the shore inland. Line transect sampling is useful in providing maximum information about habitat and community change when following such gradients (see Andrews 1974: 155–159 for methods).

An important research project that should be undertaken along the coast is the study of the successional pattern imposed on the headland vegetation where it meets the erosional force of the sea. What are the dynamics of forest disruption and plant distribution as the coast is cut back, bringing such factors as salt spray, wind, and increased sunlight progressively farther into the forest? Permanent plot markers and photographs would be useful here.

In studies dealing with cliff vegetation, analysis is difficult with random sampling because of the isolated nature of certain niches or their being confined to a limited area of the cliff face. The cliff top can be treated as a normal terrestrial habitat, keeping in mind its lack of windbreaks.

In any study of cliff vegetation, cliff-face aspect is important in determining the temperature of foliage, rate of photosynthesis, and rate at which the soils warm up or dry out. The stability of the cliff face is related to the angle of slope and the geological substrate. For the most part, on the lower spray-washed cliff faces, the influence of geology and soil pH are not detectable because of the overriding influence of soil salinity. On most cliffs there is a gradient of species from cliff base to cliff top, which parallels soil salinity. However, there is often a better correlation between salinity and aspect than either salinity and height above or distance from the sea (Goldsmith 1973). Goldsmith also found that competition was an important factor for occurrence of perennial, slow-growing maritime species on seacliffs. They cannot compete with faster-growing inland species. One project worth undertaking would be to ascertain how much the vegetation of the sea-cliffs reflects what falls from the brink above.

FIG. 2 Kilmarnock Head: the herbaceous layer in the woods.

reminiscent of a mountain forest on the mid-slopes of the northern New England or central New Brunswick mountains. It has a distinctly boreal aspect, with trees of medium height looking somewhat battered near the shore and dominated by red spruce, balsam fir, and white birch, with scattered white cedar and yellow birch. The understory is mountain maple (*Acer spicatum*), moosewood (*Acer pensylvanicum*), mountain holly, and withe-rod. Near the edge of the cliff, mountain ash and mountain alder (*Alnus crispa*) become more common. The herbaceous layer in the woods, back from the edge of the cliff, is composed of carpets of mosses and lichens (Fig. 2), bunch-berry, starflower (*Trientalis borealis*), white woodland aster, wild sarsaparilla, creeping snowberry (*Gaultheria hispidula*), twinflower, ground-cedar clubmoss (*Lycopodium complanatum*) and white violet (*Viola* sp.). In the fall, many species of basidiomyceous fungi are evident throughout. There are numerous windthrown spruce and fir lying with their tops pointing mostly in a westerly or southwesterly direction, an indication of prevailing wind direction.

Cliff aspects — The cliffs of Kilmarnock Head become higher towards the tip, where they reach a height of about 20 m (Fig. 3). Near the tip is an interesting unconformity between quartz latite and andesite towards the east and red sandstone and conglomerates overlying towards the west (Fig. 4). The metamorphic rock has more vegetation cover than the sedimentary rock. This appears to be correlated with the friable nature of the sedimentary rock, which disintegrates quickly when exposed to weathering agents. The harder metamorphic rock provides numerous stable crevices where soil accumulates and plants can gain a foothold. In the tension zone at the top of the cliff are found meadow-sweet spiraea (*Spiraea latifolia*),

FIG. 3 The cliffs of Kilmarnock Head.

FIG. 4 Kilmarnock Head: an unconformity near the cliffs.

white-topped aster, New York aster (*Aster novi-belgii*), bush honeysuckle (*Diervilla lonicera*), red fescue (*Festuca rubra*), wavy hairgrass (*Deschampsia caespitosa*), wild oat grass (*Danthonia spicata*), harebell (*Campanula rotundifolia*), yarrow (*Achillea lanulosa*), downy goldenrod (*Solidago puberula*), silverrod (*Solidago bicolor*), hawkweeds (*Hieracium* spp.), and mountain cranberry (*Vaccinium vitis-idaea*). Here, mountain ash and mountain alder dominate the canopy.

On the cliff surface itself occur large patches of rock tripe lichen (*Umbilicaria papulosa*) and other foliose lichens, silverrod, rock polypody fern (*Polypodium virginianum*), harebell, hairycap moss (*Polytrichum* sp.), meadowsweet, and bush honeysuckle, with stunted trees of white cedar, red spruce, white birch, and mountain ash. This assemblage of plants emphasizes the protected nature of this headland. On similar rocks in a less protected situation, such as on Barnaby Head about 40 km east, very little vegetation is found on the cliffs, probably because of the effect of windblown salt spray. One notable plant, black crowberry (*Empetrum nigrum*), which is an indicator of windswept, extreme environmental conditions, is absent from the Kilmarnock cliffs but plentiful just a few kilometers away near the Letite lighthouse and very common at Barnaby Head. Also, there are only a few salt-adapted plants at the base of the Kilmarnock cliffs. These are not common and include goosetongue (*Plantago maritima*), arrowgrass (*Triglochin martima*), and seaside goldenrod (*Solidago sempervirens*).

There is an interesting vegetational change where the rock substrate changes from the acidic metamorphic rock to the more basic sedimentary rock. On the sandstone and conglomerate there is a great increase in heart-leaved aster, harebell, yarrow, and downy goldenrod and a decrease in conifers, except white cedar. Certain species such as willow-herb (*Epilobium watsonii*) and evening primrose (*Oenothera parviflora*) first appear along this area of the cliff. The open wood at the top is dominated by white birch and moosewood, with occasional white cedar, balsam fir, and mountain maple. Mountain ash and mountain alder are rare. The herbaceous layer includes white woodland aster, white-topped aster (*Aster umbellatus*), bunchberry, one-sided pyrola (*Pyrola secunda*), wild sarsaparilla, hay-scented fern (*Dennstaedtia punctilobula*), and seedlings of maple and balsam fir. The pH of soil samples made on the east and west sides of the unconformity should prove instructive.

Johnson and Skutch (1928) have described the vegetation of an exposed headland on Mt. Desert Island, ME. Their zonations and component vegetation would compare more favorably with a headland such as North Head on Grand Manan Island or Barnaby Head on the mainland. However, many of the plants mentioned by Johnson and Skutch occur on Kilmarnock. A comparison of the two areas would be an instructive exercise for an interested student.

OVENHEAD

General— At Ovenhead several communities can be studied within a relatively small area. There are good examples of barrier beach, salt marsh, coastal forest, old field, and cliff habitats (Fig. 5, 6). This small headland is northeast of St. Andrews in Digdiguash Harbour. It is approached along a dirt road out of Bethel off N.B. Route 1. The head is mostly open shrub and grassland, with scattered areas of medium-sized deciduous and coniferous trees. A narrow gravel causeway separates Ovenhead from the mainland, giving it an insular aspect. There is open bay on one side and salt marsh on the other.

FIG. 7 Ovenhead: saltmarsh/barrier beach and woodland.

FIG. 8 Ovenhead: remnant of a coastal forest.

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Taxonomic Index

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