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The phytoplankton of the ria of Vigo from January 1953 to March 1954

by R. Margalef, M. Duran, and F. Saiz

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# THE PHYTOPLANKTON OF THE RIA OF VIGO FROM JANUARY 1953 TO MARCH 1954 by R. Margalef, M. Duran & F. Saiz $FRG \rightarrow CST$

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THE PHYTOPLANKTON OF THE RIA OF VIGO /p. 85

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### I. INTRODUCTION

In a previous publication (MARGALEF & DURAN, 1953), the microplankton of the Ria was studied from September 1951 to the same month in 1952. This work is fairly complete from a taxonomic point of view; however it is not sufficient to give us an idea of the dynamism of the plankton community. The research which we are now reporting, though not offering definite descriptions, enables us to recognize the basic trends of the yearly cycle, while posing a series of new problems of broad general interest. It may be useful to comment on some of these problems, now that a ship from the Vigo laboratory has gone into service, making it possible to prepare a more ambitious programme for the future.

In the pages which follow, the data obtained are first of all reported, after which an attempt is made to classify the variations making up the yearly cycle and, lastly, different aspects of the dynamics of the plankton populations are considered in a very partial manner, so that their detailed examination could be undertaken in future studies. It is likely

that a pattern similar to the present one will be found in other Galician rias, with detail variations resulting mainly from a different ratio between length and width at the mouth, average depth and size of the catchment area.

#### II. METHODS USED AND DATA OBTAINED

The characteristics of the plankton of the Ria of Vigo are such that their study requires great assiduity. As a general rule, samples were taken daily in surface waters of the port of Vigo, in the locality marked with a cross on the map of figure 11. Occasional observations at other points on the Ria have shown that the series of samples offers a general qualitative picture of what occurs in the Ria; however, a precise evaluation of said series is not possible, since phytoplankton distribution shows considerable local heterogeneity, qualitatively and quantitatively, and we shall speak about this later. For the study of the phytoplankton, samples of four liters of water were taken daily at the same time.

a) <u>Pigments</u>.- Four liters of surface water were filtered on "Albet" number 242 paper. Concerning the vertical distribution of the phytoplankton, see chapter V, section d. The filter with the residue was extracted for 12 hours or more using cold acetone. For certain studies on heterogeneity of distribution, we began using a suction and filtering device, which will be described elsewhere, installed on board the "Lampadena", the laboratory boat; in this case, volumes of close to 10 liters were filtered. The pigment was assessed in units according to HARVEY (UPH), comparing them visually with a series of controls, or else with a colorimeter, and

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## TABLE I

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## Phytoplankton from the surface waters of the port of Vigo

December 1952 to March 1954

· ··	Date	uph/in³	Date	UPH/m <sup>3</sup>	Date	UPH/m <sup>3</sup>
December	11	6 000	28	50 750		. 19 050
	22	5 250	March 2	35 750	25	7 600
	31	7 900	3	49 000	27	9 500
January	18	40 000	4	5 <b>7</b> 500	29	6 500
	19	13500	5	23800	30	. 10 500
	20	$24\ 300$	6	<b>27 0</b> 00	Mow 1	. 13 100
	21	58 000	7	25 000	2	. 16 900
	21	71 000	9	10 000	4	. 5 500
	22	82 500	10	10 000	5	. 13 200
	23	47 500	11	13 500	6	. 11 800
	24	32500	12	9 025	7	. 9 250
	26	16 000	13	92 600	8	. 12 375
	27	$15\ 625$	14	33 000	9	. 18 000
	28	5 500	16	25500	10	. 11 500
	29	9 450	17	22000	11	. 12 250
	30	16150	18	19125	. 12	. 9350
	31	12750	20	10850	13	. 14 000
Robruary	2	4 855	23	7 800	15	15.750
rebruary	3	3 375	24	17 500	16	. 6 000
	4	3750	25	9 500	18	. 15 625
	5	5 625	26	2 060	• 19	. 17 900 1
• •	6	3 412	27	2 000	21	. 4 600
	9	7250	28	3.000	23	. 10.000
	10	9 800	30	4 800	25	. 13.650
	11	21.259	April ?	5 5 5 5	26	. 10 450
	12	13 300	9	8 769	27	. 7250
	13	7 187	10	7 500	June 1	. 7660
	16	12.750	13	6 250	2	. 9.750
	17	9 250	14	6 700	3	. 20 000
	18	12 500	15	6 300	5	. 58 500
	19	12750	16	3 730	6	. 91/250
	20	10 125	17	3 000	8	. 36 700
	23	20 125	20	27150	• 9	.52500
	24	25(29)	21	33750	10	. 30.690
	25	21,060	22	19 125	. 11	. 1 20 625
	27	31 500	23	23100	12	. 13 500

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TABLE I (cont'd)

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	D	ate	uph mi		Date	LPH m <sup>3</sup>	Date	UPII m <sup>a</sup>
June	(cont'd)	13	11 150		22	401.000	9	000 3
0	(,	15	18375		23	$140\ 690$	10	<b>5</b> 300
		16	20.000		24	100,000	11	6 000
		18	12800		25	127 009	12	6 000
•		19	8 300		26	70000	14	10 800
		20	S 000		28	54.000	15	9 750
		22	12000		29	28500	16	0.000
		23	3750		30	33.000	17	7 200
		24	5.125	Oct.	1	20.250	18	6 250
		25	3.000		2	10.725	19	5 2 8 0
		26	5 625		3	11 750	<b>9</b> .9	5 500
	.4111 v	1	9 900		5	48 750	. 23	5 000
	oury	3	3 800		6	20,000	28	7 000
		4	4 000		7	123750	29	4 500
		7	10450		8	$112\;500$	30	5 800
	• .	9	18 550		ÿ <b>.</b>	62500	31	5 000
		20	\$ 500		10	75 000	Jan. 2	7 500
		11	14 250		13	$63\ 000$	4	7 750
		13	12 600		14	47 500	5	7 500
		1.5	13 000		15	32 625	7	6 000
		15	19 375		16	26250	8	6 000
		16	39 375		17	15 000	9	6 000
		17	68 750		19	14 850	<b>i1</b>	11 500
•		20	54 000		20	$26\ 625$	12	10 800
		20	50 250		22	57 750	13	16 250
		21	41 250		24	87 500	14	16 000
		22 99	45 000		26	41 875	16	14 000
		·23	26 500		27	30 000	. 19	36 500
		27 97	10 200		28	30 000	22	27 000
1		40	21 000		29	18 200	25	22 275
		20 90	11 000		30	17 800	26	23 000
		28	12 530		31	18 000	28	17 500
•		au	13 200	Nov.	. 3	9 000	Feb. 2	11 000
• 2	August	5	36,000		4	22 000	5	13 000
	-	<i>J</i>	27 000		5	$22\ 500$	6	11 000
		7	26 000		6	$24\ 000$	17	8 000
		10	36 200		7	27 500	18	8 800
. •	• •	10	57 750		9	15 000	19	8 000
		19	48 800		11	5 000	22	7 000
,		12	28 400		12	13 750	23	5 500
1		14	46 000		13	11 250	25	6 75
1		19	50 600		16	11 000	26	10 000
		10	66 020		17	8 700	27	12 00
i i		10	87 400		18	10 250	March 1	13 25
1		21	80 380 01 400		19	29 000	2	25 37
			114 200		20	11 900	3	25 00
1		27 95	118 600		23	13 500	4	25 50
}		20	195 000		24	9 750	8	49 00
i		20	96 200		26	9 000	9	23 00
ł		20	86 200		27	8 000	10	26 25
i		00 91	120 025		28	10 625	11	18 00
:	a . 1	۰۰۰۰۰۰ لټ	80 205		30	13 500	12	18 50
	September	1	40 200	Dec	1	15 400	13	18 00
		4	47 200	Dec.	2	15 000	15	24 00
		3	50 000		4	11 500	16	26 25
		4	000 UG		5	9 000	17	28 50
		7	41 300	•	6	9 000	29	33 75
		-						



FIG. 1. — Fitoplanaton (norde superior del gráfico) y algunas condiciones ambientales en la ria de Vigo, de diciembre de 1952 a marzo de 1953.

Fig. 1- Phytoplankton (upper portion of the graph) and some environmental conditions in the ria of Vigo, from December 1952 to March 1953.

Key to Figure 1 -

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1 - AVERAGE DAILY VALUES OF RANGE OF VARIATION OF THE TIDE

2 - TEMPERATURE OF THE SURFACE WATER

3 - AVERAGE DAILY WIND SPEED

the results are generally given to the nearest cubic meter. Table 1 shows the data obtained: the experimental error may be calculated if the observer does not know its origin - from the results of double determinations shown in table IX, and generally it is below 10%. The colour of the acetone extract is generally comparable with the Harvey control, except when there are many dinoflagellates, in which case it is somewhat redder, the same colour found in plankton at a certain depth (10 to 20 m, March 1954), and in this case it is due to a high proportion of dead cells and detritus, in which the chlorophylls are destroyed more rapidly than the carotenes.

**PERSON** 

In order to reduce the pigment units to total phytoplankton weight, we must keep in mind the following. The ratio between pigment and dry weight is about 1 UPH =0.013 mg, though it varies widely depending on the conditions under which the algae develop (MARGALEF, 1954 a). The dinoflagellates are definitely poorer in pigments; a determination on the plankton collected on September 22, 1953 (dominance of Ceratium furca, see table II) showed 1 UPH =0.037 mg (SAIZ). According to GILLBRICHT (1952), the diatoms contain 2.9 times more chlorophyll per unit of dry weight without ashes than the dinoflagellates, ratio which coincides with our own findings. Thus, considering table I or figures 1 to 4, if we wish to represent the plankton weight corresponding to the values tabulated, we must keep in mind that the overall conversion factor will be greater when dinoflagellates predominate. In table III, this difference has been taken into account when calculating present production figures. Even using this precaution, the pigment maximums give an exaggerated idea of the weight, because the cells which multiply rapidly contain a

higher proportion of chlorophyll, and also because of the error represented by the chlorophyll contained in detritus suspended in the water, which is more abundant during periods of maximum agitation. In some periods, especially during the winter plankton minimums, the detritus, though not being quantitatively very abundant, perhaps forms the greater portion of the seston. The effects of light and temperature on the ratio between pigment units and dry weight are probably compensated.

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Fig. 2- Phytoplankton (upper portion of the graph) and some environmental conditions in the ria of Vigo, from April to July 1953. The vertical lines show the moments of greatest floristic discontinuity.

Key to Figure 2 -

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- 1 INDEX OF DIVERSITY
- 2 INDEX OF DISCONTINUITY
- 3 MEAN DAILY VALUES OF RANGE OF TIDAL VARIATION
- 4 TEMPERATURE OF THE SURFACE WATER
- 5 SURFACE SALINITY
- 6 AVERAGE DAILY WIND SPEED

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Microplancton de la ria de Vigo, desde abril de 1953 hasta marzo de de los símbolos se indica en el texto. Los momentos de mayor disc

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1954, según muestras obtenidas en el puerto pesquero. La equivalencia ontinuidad florística se indican por medio de un espacio en blanco.

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b) Qualitative study and indices of diversity.- Another sample of surface water, also weighing four liters, was filtered on paper in the same way and, when little liquid remained, it was shaken with the residue, and immediately fixed with neutralized Formol, for the qualitative study. This method ensures conservation of the tiniest elements of the plankton. Their study consisted in the examination of a few preparations from each tube, so that some of the less represented species may have gone unnoticed. In given cases, the cells were counted, to determine the exact numerical representation of the different species; however, normally, we limited ourselves to using the empirical scale constituted by the symbols 5,4,3,2,1 and +, proportional, respectively, to 100 (or more), 60,30,10,1 and an isolated specimen. In any case, the figures of table II refer to the number of cells and not to the number of colonies. Of necessity, the small, naked flagellates have been ignored; also indicated in the corresponding tables is the quantity of detritus, which sometimes appears in considerable amounts, being relatively more apparent when plankton is scarce. Tintinnids have been recorded; however, other animal microplankton no.

In figures 1-4 we have calculated the indices of diversity for each sample, using the formula.

 $d' = \frac{\text{number of species}}{\log_{10} \text{ of UPH per m}^3}$ 

This equation is open to criticism, because we certainly did not see all the species present in a cubic meter of water, of which the total number of individuals is proportionate to the pigment content: however

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the figures obtained by this means remain proportionate to the true diversity of the aggregates, because a similar effort was put forth in the study of each sample. In order to ensure this, for a series of samples from May to June of 1953, two indices of diversity were simultaneously calculated that indicated (d'), and that used on other occasions and apparently more correct

> d - number of species minus one log<sub>e</sub> of the number of individuals

very good correspondence being found between the different pairs of values using the conversion factor

d' = 2.14d

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The limit values of the coefficient were 1.74 and 2.73. This formula permits the comparison of aggregates in which different indices of diversity are used (d and d').

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Fig. 3.- Phytoplankton (upper portion of the graph) and some environmental conditions in the ria of Vigo, from August to November of 1953.

Key\_to Figure 3 -

1 - INDEX OF DIVERSITY

2 - INDEX OF DISCONTINUITY

3 - AVERAGE DAILY VALUES OF RANGE OF TIDAL VARIATION

4 - TEMPERATURE OF THE SURFACE WATER

5 - SURFACE SALINITY

6 - AVERAGE DAILY WIND SPEED

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Heterogeneity between successive samples has been estimated using another index called the index of discontinuity, obtained by dividing the difference between the index of discontinuity. obtained to dividing the difference between the index of diversity of the aggregate formed by combining the two successive samples - and the index of diversity of the first sample, by the number of days which elapsed diversity of the first sample, by the number of days which elapsed between the taking of the two samples being compared (generally one), according to a method of analysis of population dynamics introduced in a recent work (MARGALEF, 1954 b). The equivalence between our index V' and the V used in said work (referring to the tintinnids of the plankton of Castellón) is found to be:

v' = d'1, 2 - d'1	$V = \frac{d_{1} \cdot 2}{c_{1} \cdot 2} - \frac{d_{1}}{c_{1} \cdot 2}$
Ę	<del>t/5</del>
if d' = 2.14 d,	V = 0.428 V

One limitation of the index of discontinuity V' is that it is based on the presence or absence of the species, and does not reflect their ratios of The maximum values of this index, which exceed a certain dominance. arbitrarily fixed value, have been used as limits to break down the cycle leen deer se lomine to treas coun the prove into a series of periods, thus facilitating analysis. The examination of Secol Terrari atlaumsi P. The engineerich of the succession, as outlined in table II, forces us to recognize these same limits and in addition, perhaps another two which the index of STR GRAT IN THE MALE AND ADDRESS OF diversity does not clearly indicate, in the middle of September and white, it is then of September and November, respectively. We feel that it is much more natural to use this المركز breakdown instead of the artificial division by months. ---- altis, --

If d' and V' are calculated, not on single samples, but rather on groups of two, three, etc. consecutive samples, the result is that all the variations are reduced, without eliminating the variations which are presumably "parasitic" or statistical.

12 1? c) Other data.- Data relating to temperature and salinity were obtained on the surface waters where the plankton was collected, from 8 to 10 o'clock in the morning. Some observations made in March 1954 with a "Thermistor" show that variations in surface temperature may be considerable due to the effect of insolation, winds and perhaps other factors. The range of variation of the tide has been calculated using the tables of the Hydrographic Institute, which take into account a tide guage installed in the same port of Vigo. The meteorological data were provided by the Vigo Observatory of the National Meteorological Service, and we wish to extend our thanks to the Observatory personnel.

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Fig. 4.- Phytoplankton (upper portion of the graph) and some environmental conditions in the ria of Vigo, from December 1953 to March 1954.

Key to Figure 4 -

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1 - INDEX OF DIVERSITY

2 - INDEX OF DISCONTINUITY

3 - AVERAGE DAILY VALUES OF RANGE OF TIDAL VARIATIONS

4 - TEMPERATURE OF THE SURFACE WATER

5 - SURFACE SALINITY

III. NOTES ON SOME SPECIES

Schyzophyta, Flagellatae, etc.

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Beggiatoa sp. - Filaments 5.8 µ in diameter (March 4, 1954)

Torula? sp. - A chain of cells, resembling yeast, on a <u>Noctiluca</u> (June 22, 1953).

<u>Chrysophyceae Undet</u>. -(Fig. 5, a). Cells with chromatophores and bilateral symmetry, inside dense envelopes  $37-45 \times 13.5 \mu$ 

<u>Rhodomonas</u> sp. - (Fig. 5, b). A species measuring  $18 \times 10 \mu$ , very compressed and asymmetrical; with chromatophores.

<u>Acicular cells</u>. - (Fig. 6, q). Detail of <u>Ankistrodesmus</u>, membrane apparently without structure; with chromatophores. Dimensions: 68-146 x 1.5-3.5 µ.

# Dinoflagellatae

Dinophysis hastata Stein. - (Fig. 5, c). Longtitudinal dimension, 66  $\mu$ ; sagittal dimension, 49  $\mu$ ; antiapical spine, 12  $\mu$ .

<u>Noctiluca scintillans</u> (Macar) Kof. & Swezy. - (Fig. 5, d). Organisms enclosed: <u>Chaetoceros curvisetus</u>, <u>Thalassiosira rotula</u>, <u>Ceratium fusus</u>, <u>Helicostomella</u>, <u>Favella</u>, a metanauplius measuring 220 µ, fragments of apendicularia (observed twice, figure on the right).

<u>Peridinium americanum</u> (?) Gran & Braarud. - (Fig. 5, e). Cells 37 x 37 x 35  $\mu$ , slightly depressed. Membrane thick, though the plates are not defined, so that the determination is uncertain.

P. brevipes Paulsen. - (Fig. 5, f). 27 x 27 µ.

P. cerasus Paulsen, quarnerense (br. Schr.) Broch. - (Fig. 5, g).

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Some cells of a shape intermediate between those of the two species mentioned, length  $45 \cdot 51 + 4 - 6 \mu$ ; cross diameter  $48 - 51 \mu$ . The similarity of <u>cerasus</u> and <u>quarnerense</u> has been discussed (PAULSEN, SCHILLER, etc.); the presence of intermediate types is not sufficient reason for maintaining that they are one and the same, but it does make a thorough study of the entire group desirable.

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P. (Minuscula) minusculum Pavillard. - Length 19-27 + 6-7 μ; cross diameter 1.7-19.5 μ.

P. minutum Kofoid (P. monospinum Paulsen). - (Fig. 5, i and j). Cross diameter 37-46 u; length 39-50 u.

<u>P. nudum</u> Meunier. - Partitioned like <u>P. trochoideum</u>, however of smaller average size (17.5-19 x 17.5-19  $\mu$ ) and shorter, with the epitheca more rounded.

<u>P. cf. Paulseni</u> (?) Pavill. - (Fig. 5, k). Cross diameter 44-57 µ; total length 62.5-78 µ. It is a <u>Peridinium</u> not fully studied which we associate with <u>Paulseni</u> simply because this was done in the 1953 work; it shows a certain resemblance to <u>P. solidicorne</u>, although it is meta and not para, like the former.

P. styliferum (?) Schiller. - (Fig. 5, 1). Length 35 + 6.5 μ; cross diameter 27 μ. One specimen June 20, 1953.

Goniaulax diacantha (Meunier) Schiller. - (Fig. 5, m). Cross diameter 23.3-29.5 u; length 43-46.5 + 11-19.5 µ.

<u>C. polyedra</u> Stein. - (Fig. 5, n). Spherical cysts measuring 48-59  $\mu$  in diameter, membrane quite thin and <u>smooth</u> (unlike what was observed by NORDLI, 1951, who describes cysts of spiny membrane in a population of this

species coming from a Norwegian fjord). These cysts were abundant and loose, in September.



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FIG. 5. — a. Crisoficca indeterminada; b. Rhodomonas sp.; c. Dirophysis hastata;
d. Noetilaca scintillans, el ejemplar de la derecha con una cola de aperdicularia;
e. Perdilalum conscionant ?; f. Peridiabas brevipes: d. Peridibium constant/quaracterist n. Peridiabum constant ?; j. Peridibium constant ?; peridibium constant ?; peridibium constant ?; j. Peridibium constant ?; peridibium styliferum ?; m. Goniaular diactatia; n. Goniaular polycdra, con caste; o. Goniendar tumarcusis, de Vico; p. Goniaular tumarcusis, de In behia de Fandy, q. Pyrocipitis lucada; r, Dirodonalization indeterminada (a); s. U. collagelada indeterminada (b).

Fig. 5 - a, undetermined Chrysophicea; b, <u>Rhodomonas sp.; c, Dinophysis</u> <u>hastata; d, Noctiluca scintillans</u>, the specimen on the right with a tail of appendicularia; e, <u>Peridinuim americanum</u> ?; f, <u>Peridinium brevipes</u>; g, <u>Peridinium cerasus/quarnerense</u>; h, <u>Peridinium conicum</u>; i,j, <u>Peridinium</u> <u>minutum</u>; k, <u>Peridinium cf. Paulseni</u> ? 1, <u>Peridinium styliferum</u> ?; m, <u>Goniaulax diacantha; n, Goniaulax polvedra</u>, with cyst; o, <u>Goniaulax tamarensis</u>, from Vigo; p, <u>Goniaulax tamerensis</u>, from the Bay of Fundy; <u>q</u>, <u>Pvrocvstis lunula</u>; r, undetermined Dinoflagellata (a); s, undetermined Dinoflagellata (b). During red water, this and other species of peridinians have very thick membranes. This fact ties in with an observation made in the waters of Castellon: a given sample (no. 640, March 24, 1953) showed a dominance of dinoflagellates, and these were characterized by exceptionally thick membranes in all species of <u>Ceratia</u>. In both cases, the dominance of the group is associated with the particular development of the cell envelopes.

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<u>G. tamarensis</u> Lebour. - (Fig. 5, o). Cross diameter. 28.5-29  $\mu$ ; length 33-38  $\mu$ . When fixed, they open at the cingulum, and the protoplast becomes globous; the two mamelons of the hypotheca are very characteristic. It has been compared with specimens from Canadian coasts (Bay of Fundy, July 15, 1949, courtesy of Dr. WILLIAM R. MARTIN), and found to be identical (fig. 5, p; 35-38 by 35-38  $\mu$ ). The presence of this species in the Ria of Vigo is of interest, since toxic properties have been attributed to it (NEEDLER, 1949). In the western part of the Bay of Fundy, it is abundant in summer (maximum August, T = 12-15°C.), somewhat later than in Vigo (June-August, T = 15-18°), where it still has not been seen in quantity. Toxicity remains in mollusks for almost a month after the dinoflagellates have disappeared from the plankton. In Portugal, there have been intoxications of the type produced by <u>Goniaulax</u> from mollusks (PINTO, 1953). The worst species seems to be <u>G. catenella</u>; perhaps <u>G. polyedra</u> is also somewhat toxic. It is a topic which merits further study.

<u>Goniaulax sp</u>. - Very small cells, 18 µ in length, with the hypotheca typically angular due to the presence of three keels approximately parallel to the sagittal plane (August 18, 1953).

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Pyrocystis lunula Schuett. - (Fig. 5, q). Maximum dimension, about 100 µ. Shape of the cell quite variable, more or less curved.

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Dinoflagellata (a) (Fig. 5, r). Length 19-21.5 µ; cross diameter 13-15 µ; largest diameter 15-21 µ.

Dinoflagellata (b). - (Fig. 5, s). Length 33-35  $\mu$ ; cross diameter 20  $\mu$ ; maximum diameter 25  $\mu$ . Membrane thick as in the preceding species; larger, higher and with the apical pole more pointed.

# Bacillariophyta

<u>Sceletonema costatum</u> (Grev.) Cleve - Diam. 1.5-11.7 μ; pervalvar axis 6-20 μ.

<u>Thalassiosira hispanica</u> Paulsen. - (Fig. 6, a). Diameter 12.5-17 μ. The cells are joined by a central filament. It could be considered as a slightly silicified form of <u>Th. Nordenskioeldi</u> with the mucilaginous cushions more apparent.

<u>Th. rotula</u> Meunier. - (Fig. 6, b). Auxospores on October 25, 1953, January 4,11 and 14, 1951. The diameter of the cells varies from 35-39 μ to 56-59 μ.

Coscinodiscus Granii Gough. - The diameter attains 300 µ.

<u>Corethron criophilum</u> Castracane. - (Fig. 6, d). Diam. 13-13.5  $\mu$ . pervalvar axis 57-82  $\mu$ . Corresponds to the <u>criophilum</u>, or typical, phase of HENDEY. We take this opportunity to mention the presence of this species for the first time in the plankton of the coasts of Castellón; sample number 350, December 28, 1950, <u>pelagicum</u> phase, 73  $\mu$  in diameter.

Leptocylindrus. - (Fig. 6, e and f). The specimens observed in Vigo, where the genus is common, permit the identification of two main

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types, though it is not possible to establish a clear line of separation. The most typical form, recorded in table II under the name of L. danicus, measures 2 to 9 µ in diameter, and its cells have chromatophores which are elongated in shape and relatively scarce in number. (Fig. 6, e). The other type is entered in table II under the name of L. adriaticus (?) Schroeder, its diameter is similar  $(2-8 \mu)$  and it is characterized by a larger number of chromatophores, which are more rounded in shape (Fig. 6, f) and more dispersed throughout the cell. The character constituted by the shape of the chromatophores is uncertain, since it may be due to fixation, for live cells of both types were not compared; another character which manifests itself following fixation is a certain twisting of the protoplasts of "adriaticus", which become contracted at the extremities of the fixed cells following a helicoidal plane (fig. 6, f). Leptocylindrus adriaticus Schroeder is an insufficiently described species which supposedly differs from the common species L. danicus in that it has many small chromatophores (15-25 according to the figure of SCHROEDER) and in that the cells, generally, are narrower and longer than in the former species, which is not the case in Vigo populations (fig. 6, f, left, shows abnormally short cells; generally their degree of elongation does not differ from the typical L. danicus).

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Rhizosolenia fragilissima Bergon. - (Fig. 6, g and h). Diam. 9.8-29 µ.

Chaetoceros compressus Laudes. - Ap#ical axis 11.5-29 µ; 6-9 chromatophores.



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FIG. 6. — a, Thalassiosira hispanica; b, Thalassiosira rotula, con auxósporas; c, Thalassiosira subtilis, con Nitzschia ? epífita; d, Corethron criophilum; e, Leptocylindrus danicus; f, Leptocylindrus, forma de clasificación dudosa, referible quizás a L. adriaticus; g, h, Rhizosolenia fragilissima; i, Rhizosolenia styliformis; j, k, Chaetoccros Lorenzianus, con endósporas; l, Chaetoceros socialis, con Nitzschia ? epífita; m, Chaetoceros teres; n, Hemiaulus sp; o, Navicula membranacea; p, Nitzschia ?; q, células aciculares indeterminadas.

Fig. 6. - a, <u>Thalassiosira hispanica</u>; b, <u>Thalassiosira rotula</u>, with auxospores; c, <u>Thalassiosira subtilis</u>, with <u>Nitzschia</u>? as epiphyte; d, <u>Corethron criophilum</u>; e, <u>Leptocylindrus danicus</u>; f, <u>Leptocylindrus</u> form of doubtful classification, asc ribable perhaps to <u>L. adriaticus</u>; g.h, <u>Rhizosolenia fragilissima</u>; i, <u>Rhizosolenia styliformis</u>; j,k, <u>Chaetoceros</u> <u>Lorenzianus</u>, with endospores; 1, <u>Chaetoceros socialis</u>, with <u>Nitzschia</u>? as epiphyte; m, <u>Chaetoceros teres</u>; n, <u>Hemiaulus sp</u>.; o, <u>Navicula membranacea</u>; p, <u>Nitzschia</u>?; q, undetermined acicular cells.

<u>Ch. cf. fragilis</u> Meunier. - Apical axis 6-12 µ, values rounded, <u>/p.100</u> one chromatophore. Chains at times twisted and frequently curved, fragile and irregular, enveloped in mucilaginous cushions.

Ch. Lorenzianus Grun. - (Fig. 6, j and k). Endocysts on January 25 and 28, 1954.

<u>Ch. teres</u> Cleve. - (Fig. 6, m). Apical axis 25 µ. It is possible that the form doubtfully classified as <u>Ch. Lauderi</u> in MARGALEF & DURAN, 1953, p. 48, should actually be ascribed to this species.

<u>Ch. socialis</u> Lauder. - (Fig. 6, 1). It is not possible to separate this species from <u>Ch. radians</u>, though we suspect that most if not all of the specimens found in the Ria of Vigo should be designated by the former name. The few spores observed were from smooth valves, as is consistent with socialis.

<u>Hemiaulus sp</u>. - (Fig. 6, n). Apical axis 19.5  $\mu$ ; valves only slightly convex, without visible structure; pervalvar axis long with short appendices. A single chain which because of its characters, is of doubtful classification. Although it is close to <u>H. Hauckii</u> in structure, it is in no way typical as regards the other characters.

<u>Fragilaria sp.</u> - Apical axis 29  $\mu$ . Very fine striae. Long bands Navicula membranacea Cleve. - (Fig. 6, o). Apical axis 35-43  $\mu$ .

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<u>Nitzschia delicatissima</u> Cleve. - Cells sometimes classed as <u>N</u>. <u>seriata</u> should be <u>N. delicatissima</u> or another still unidentified species, since it has been noted that in certain chains, cells of the size of <u>N</u>. <u>seriata</u> have a sculpture which, because of its fineness, is more consistent with <u>N. delicatissima</u>. The distinction between the two species, in table II, has generally been made on the sole basis of the size of the

valves, so that errors may have resulted.

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<u>Nitzschia (?) sp</u>. - (Fig. 6, a 1 and p). Cells  $17.5-23 \mu$  in length, isolated, joined in pairs at one end, or in series like those of <u>N. seriata</u>, and <u>always</u> in the mucilage or between the filaments of Chaetoceros socialis, Thalassiosira subtilis and Thalassiosira rotula.

#### Heterocontae

<u>Pelagocystis (?) sp</u>. - Cells approximately 10 x 20  $\mu$ , isolated, in pairs or in groups of four, in small nests of mucilage. August 18-24, 1953. It is very similar to a species which appears quite frequently in the waters of Castellón, although the dimensions of the cells are, on the average, smaller.

### Tintinnoinea

<u>Tintinnopsis karajacensis</u> Brandt. - (Fig. 7, b). The specimens usually mentioned for the Ria of Vigo belong to the var. <u>rotundata</u> Joerg; however, that of the figure (49 x 33.5  $\mu$ ) seems to belong to the typical form, given the thickness of the walls of the lorica, which are whorled towards the oral portion, although the aboral extremity is slightly acuminate.

<u>T. nana</u> Lohmann. - (Fig. 7, a). 37 x 21  $\mu$ ; aboral extremity hemi-shperical.

<u>Tintinnopsis</u> sp. - (Fig. 7, c). On June 11, 1953, a cylindrical lorica ended in an open aboral appendix, 99  $\mu$  in length and 34  $\mu$  in diameter which, because of its shape and the fact that the aboral end is open, recalls <u>T. kofoidi</u> Hada, though it is too short to be ascribed with certainty to this species. Figure 16 of the work of DURAN (1953) shows a specimen

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from Castellon, with clear signs of fragmentation, which probably belongs to the aforesaid T. kofoidi.

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FIG. 7. — a, Tintinnopsis nana; b, Tintinnopsis karajacensis;
c, Tintinnopsis sp.; d, Helicostomella longa; e, Helicostomella fusiformis; f. g. formas de Helicostomella; h, Protorhabdonella ? sp.

Fig. 7. - a, <u>Tintinnopsis nana;</u> b, <u>Tintinnopsis karajacensis;</u> c, <u>Tintinnopsis sp; Helicostomella longa;</u> e, <u>Helicostomella</u> <u>fusiformis;</u> f,g. forms of <u>Helicostomella</u>; h, <u>Protorhabdonella</u> <u>? sp.</u>

Helicostomella longa Brandt. - (Fig. 7, d). In a previous work (MARGALEF & DURAN, 1953), there is mention of loricae ascribable to this species with the whorls extending over the entire lorica, which together with other considerations, led us to question the validity of the systematic characters considered for this genus. Figure 7, d, shows another specimen of the same type: length 99  $\mu$ ; oral diameter 28  $\mu$ ; June 8, 1953.

<u>H. fusiformis</u> (Meunier) Joerg. - (Fig. 7, e). A single lorica, with no visible whorl. Length 127  $\mu$ ; oral diameter 19 u; largest diameter 25  $\mu$ . <u>Helicostomella sp</u>. - (Fig. 7, f and g). These irregular forms probably could be ascribed to <u>H. subulata</u>. We even suspect that the specimen described as <u>H. fusiformis</u> may be merely an abnormal form of <u>H. subulata</u>. See discussion of the genus in MARGALEF & DURAN, 1953, p. 62.

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Favella ehrenbergii (Clap. & Lachm.) Joerg. - On April 25, 1953, an individual that had ingested cysts of <u>Peridinium</u> cf. <u>diabolus</u>.

<u>F. serrata</u> (Moebius) Joerg. - Observed individuals parasited by a dinoflagellate, probably Duboscquella tintinnicola.

<u>Protorhabdonella</u> (?) sp. - (Fig. 7, h). With reservations, we ascribe to this genus a bell-shaped lorica, with conical aboral extremity, perhaps slightly crushed, with very thin walls and no apparent structure. May 25, 1953. Length 29  $\mu$ .

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# IV. PLANKTON SUCCESSION

a) <u>General Remarks</u>. - Research on the plankton cycle in eastern Spanish waters (Castellon) has shown that the yearly succession is regulated there by the upwelling, in given months of the year, of deep waters which are probably very rich in nutritive salts, when temperatures even out vertically and the wind and currents establish suitable conditions. This type of cycle is characterized by a winter period of relatively high production, frequently broken down into a series of consecutive pulsations, and a summer stabilization period, during which phytoplankton is poor and contains a high ratio of organisms which are totally or partially heterotrophic.

The picture offered by the Ria of Vigo is entirely different. In addition to the qualitative differences, which may be seen upon comparing the tables published on the plankton of both waters (examples: Thalassiothrix Frauenfeldi, Asterionella japonica, A. mediterranea, typical of Castellon; Stephanopyxis, Thalassiosira, Chaetoceros socialis, typical of Vigo, and even greater differences in the dinoflagellates), the quantitative differences are enormous. In Vigo, there is a large quantity of phytoplankton all year round, though the difference between the maximum and minimum figures (in UPH) may reach a quotient of one thousand, exceeding the maximum variations in the waters of Castellon. The variations in the plankton of Vigo do not show the regularity observed in Eastern Spain; the fluctuations cover a much shorter period, so much so that it was necessary to carry out daily determinations to get an approximate idea of what happens; a somewhat confused idea, however, because of the strong heterogeneity of distribution. It is logical to suppose that the general rhythm of phytoplankton

production in the Ria must be governed by other factors.

The quantity of nutritive salts can never be a serious limiting factor, since the plankton is never scarce, as is shown by the following comparison.

Minimum <sub>3</sub> Values		Average <sub>3</sub> Values	Maximum Yalues
UPH/m		UPH/m <sup>3</sup>	UPH/m <sup>3</sup>
- Castellón Ria of Vigo	250300 2,000	1,500-3,000 30,000	5,000-15,000 400,000

It is not suprising that this occurs since, due to the shallowness of the Ria (maximum depth about 50 meters), the tidal currents and the action of the wind can alone bring about the vertical agitation of its waters. The basin of the Ria of Vigo is very small, about six times the area of the ria itself, so that additions of fresh water are only of limited importance, as may be seen from the salinity values, which only fall below normal during heavy rain (fig.s 3 and 4, months of October to December, 1953).

We know of no study which describes a plankton cycle of the same type as that of the Ria. We first thought of comparing it with the Norwegian fjords; however, at the outset, these offer two important differences: 1) the greater depth and the existence of a threshold ? (umbral), as a result of their glacial origin, which affect the stagnation of deep waters; and 2) a much greater inflow of fresh water. The great abundance of coccolithophorales in Norwegian fjords, in contrast with the scarcity of same in Gallician rias, could be the result of a different calcium content of the waters, which it is necessary to verify.

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The careful study of the succession of plankton communities in the Ria of Vigo reveals a slight tendency towards higher values of phytoplankton with more intense light and higher temperatures. Aside from this yearly wave (fig. 8), another two types of regularities of a shorter cycle may be recognized. On the one hand, there is clearly a rapid succession of variations, of which the minimums, generally speaking, coincide with the moments of maximum discontinuity in the quantitative evolution of the population. Given the shape and low volume of the Ria, this pulsation revealed by the examination of the samples definitely corresponds to a biotic succession and only in a very limited manner to a sequence of populations resulting from the movement of water masses. On the other hand, the composition of each of the successive proliferations and, as a character which is easily observable, the ratios of diatoms and dinoflagellates in same, permit us to identify broader systems or complexes, each of which includes from two to five of the variations mentioned previously. The inherent complexity of all natural communities and the deficiencies in the original data exclude a priori the possibility or the hope of finding clear manifestations of all these cycles and, with it, the possibility of using some simple mathematical equation in their analysis. In fact, the variations in the phytoplankton reflect the interference of numerous factors, a large number of which are either unknown or their intensity could not be evaluated. With these cautionary remarks, we shall proceed to examine the various aspects of the cycles which have been best identified.

b) <u>Annual cycle</u>. - The examination of figures 1-4 reveals a certain relationship between surface temperature and quantity of phytoplankton.

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#### TABLA 111

5.5

Ciclo del fitoplancton en la ría de Vigo, esquematizado con el uso de medias para los distintos períodos en que se ha subdividido la sucesió tomando como límites los momentos de discontinuidad mayor en la composición florística de las comunidades, momentos indicados por media de líneas de trazos en las figuras 1 a 4. Los valores ponderales se dan solamente a título orientador y con referencia a las aguas superficiale por ser numerosos los errores que se acumulan en su cómputo; se ha considerado 1 UPH = 0.018 mg de peso seco para las diatomeas 1 UPH = 0.037 mg de peso seco para las dinofngeladas. Se da el tanto por mil de células de las especies más importantes, imprimiendo  $\epsilon$  negritas los valores que exceden del 10 % y que corresponden a las especies de mayor importancia en la producción de cada período. La cifras menos exactas se han encerrado entre parentesis. Las distintas sucesiones parciales se han separado por espacios verticales más an chos. Las especies se han distribuido en tres grupos, atendiendo a su importancia relativa en las consecutivas etapas de cada sucesión para cial. ×, presencia inferior al uno por mil.

Fecha	2	5-1V	a 3-V	'1I		4.	-VII a	ı 29-l	x			17	7-X a	29-3	XII	30	)- <b>X</b> II	a 31-	-III-1	95-
Número de dias	31	17	9	13	26	10	13	11	9	19	17	13	39	8	12	17	33	14	9	2
Temperatura	15,6	14.8	15.8	17,3	16,9	17.0	17,7	17.7	1	7.6	15,8	14.7	14,7	14.9	15,4	13,8	12,1	11,9	12,3	15
UPH/litro	11,5	32.2	13.2	6.2	26,5	25.6	52.6	99.1	6	1.5	52.7	35,7	13,6	7,4	5.6	8,8	18.6	8,9	29,9	2:
Relación entre núm. células diatomeas/dinoflageladas	8.4	7	9.9	0.07	1,6	0,5	1,6	1	0	.15	0,9	7,3	0.8	0,1	0,7	50	202	(3,4)	21	1
, Diatomeas, mg m³	133	366	167	5	212	107	420	642	1	105	320	408	85	8	29	112	241	90	370	2
Dinoflageladas. mg/m <sup>3</sup>	-46	150	48	214	377	620	750	1830	) 2	030	1001	159	274	250	118	1	1	74	51	ļ
Total. diats. más dinoflag	179	516	215	219	589	727	1170	2472	2	135	1321	567	369	258	147	113	241	164	421	3
<b>G 1 1 1 1</b>	·								• ~	÷							110			
Sceletonema costatum	97	550	18	17	65		61	×	•	•	193	37	13	•	(21)	231	110	(90)	1 551	F
Chaetoceros sociale + radians	114	60	172	2	339	187	90	×	2	×	89	255	43	•	٠	43	187	(20)	991	อ
rium	9	12	2	3	13	13	19			×	34	13	11	3	(21)	69	12		12	
					••															
Chaetoceros densus	118	•	1	1	47	1	4	٠	•	•	1	•	1	•	•	•	•	(10)	3	
Rhizosolenia Stolterfothi	127	74	6	•	1	2	1	×	•	•	1	13	1	•	•	×	×	•	2	
Leptocylindrus danicus	312	9	110	2	83	73	374	459	23	•	16	166	135	5	(10)	32	11	(61)	45	
Thalassiosira rotula	1	•	6		•.			×	1	×	1.	142	62			123	137	(20)	34	
Lauderia borealis	8	1	187	2	×	•	x		•	2	<b>2</b> 9	62	3	•	(10)	121	13	(20)	5	:
Schroederella delicatuia	×	1	х			18	19	28	36		•	×	1	•	•	8	3	(20)	97	]
Bacteriastrum hyalinum			4		•	•	•	•	•	3	31	7	•	•	(5)	107	55	•	•	
Chaetoceros curvisetus, pseu- docurvisetus, decipiens, di-	10	3	- 1	4	1	19	.,		1		45	108	30	8	(12)	174	386	(123)	155	ų
dymus	12	-3	11	Т	1	 2	ì	•	Т		-10	9	2	0	(14)		000	(1.00)	3	~
Eucampia zooaiacus	40	10	51	•	•	J	1	-	•		U	. 0	-	•	•	•	•	•	Ū	
sima	25	10	85	1	34	1	8	<b>2</b>	1		10	33	41	•		$^{2}$	1	•		
Coscinodiscus Granii									•	1	2	9	8		(15)	•	1	(61)	3	
Rhizosolenia alata	51	12	86	26	×	1	11	13	205	1	×	×			•		1	•	•	
Rhizosolenia delicatula	<b>26</b>	23	64	2	2	1			•	•	1	×						•		
Thalassionema nitzschioides .	25	76	75		6			2	23	•	1	17	33	10	(15)	28	2	(31)	3	
Otras diatomeas	29	26	21	30	23	14	28	5	2	3	6	11	66	6	(200)	37	63	(510)	·10	1
Prorocentrum micans	11	13	28	164	35	35	26	38	64	72	168	31	34	100	(325)	3	1	(20)	15	
Peridinium pl. sp	35	49	18	115	93	87	50	72	102	178	121	27	59	82	(36)	5	2	(51)	6	J
Divophysis pl. sp	24	23	11	114	24	62	41	35	47	155	135	42	208	168		1	×	(51)	•	;
Goniaular pl, sp	2	5	ĩ	17	2	1	5	5	153	10	×	×	×	•	•	•	•	•	×	
Noctilucu scintillans	×	1	5	278	17		5	3	1		<	x				•		•	•	
Ceratium fusus	18	20	16	280	117	238	30	93	16	121	26	11	<b>7</b> 0	5	(9)	•	•			1
Ceratium furca	4	6	5	223	95	238	227	240	318	420	82	C	11	59	•	10	1	(71)	21	2
Ceratium tripos, buccros, can-											~	~		10						
delabrum, etc	1	1	•	4	×	•		*	•	22	5	2	176	81		•	•	•		>
Otras dinoflageladas	3	5	1	9	1	13	2	2	5	5	2	•	206	427	(216)	×.	۰.	(20)	T	-

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### Table III

Phytoplankton cycle in the ria of Vigo, diagramed using the averages for the different periods into which the succession has been subdivided, taking as limits the moments of greatest discontinuity in the floristic composition of the communities, moments indicated by means of dash lines in figures 1 to 4. The ponderal values are given only as a guideline and refer to surface waters, since numerous errors occur in their calculation: we have taken 1 UPH = 0.013 mg of dry weight for the diatoms and 1 UPH = 0.037 mg of dry weight for the dinoflagellates. The per thousand value of cells of the most important species is given, the values exceeding 10% and corresponding to the most important species in the production of each period being pinted in black. The less precise figures have been shown in brackets. The different partial successions have been separated by wider vertical spaces. The species are broken down into three groups, according to their relative importance in the consecutive phases of each succession. x, less than one per thousand.

Key to Table III -

1 - Date

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- 2 Number of days
- 3 Temperature
- 4 UPH-liter
- 5 Ratio between number of cells diatoms/dinoflagellates

- $6 \text{Diatoms, mg/m}^3$
- 7 Dinoflagellates,  $mg/m^3$
- 8 Total of diatoms plus dinoflagellates
- 9 <u>Scel. costatum</u>, etc.
- 10 Other diatoms
- 11 Prorocentrum micans, etc.
- 12 Other dinoflagellates

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FtG. 8. — Esquema simplificado para el estudio de las posibles relaciones entre la agitación del agua (curva central), la producción actual de fitoplaneton (curva superior, escala logaritmica) y los indices de discontinuidad florística entre muestras succeivas (curva inferior). Las posibles relaciones de causa a efecto se indican por medio de rectas. La curva de acitación se ha computado sumando para cada día la oscilación máxima de la marca en decimetros y el doble de la velocidad media del viento en kilómetros por hora.

Fig. 8. - Simplified diagram for the study of possible relations between agitation of the water (central curve), production of phytoplankton (upper curve, logarithmic scale) and indices of floristic discontinuity between successive samples (lower curve). The possibile relations of cause and effect are indicated by means of straight lines. The agitation curve has been calculated by adding the maximum daily tidal variation in decimeters to twice the average daily wind speed in kilometers per hour.

Key to Fig. 8. -

1 - Production

-

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2 - Agitation

4 - Production

5 - Agitation

3 - Discontinuity

6 - Discontinuity

This coincidence can only be evaluated in a general way and a more detailed analysis, like that offered in table III, again referring to surface plankton, does not enable us to establish a clear correlation. This should not surprise us, since the data we have on the development of phytoplankton tend to discount any simple relationship between phytoplankton and temperature; the winter temperature values are amply sufficient for the development of most of the algae species. More certain is the relationship between temperature and quantity of dinoflagellates, or between temperature and relative mass of same in the total plankton (fig. 9), which may be clearly seen, in comparison with the behavior of the diatoms.

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FIG. 9. — Relación entre la temperatura media de cada uno de los periodos en que se ha dividido la sucesión para su estudio y la producción o masa actual media de diatomeas (circulos blancos) y de dinoflageladas (circulos negros). Datos de la tabla III.

Fig. 9. - Relationship between the average temperature of each of the periods into which the succession has been divided for its study and the production or present average mass of diatoms (white circles) and of dinoflagellates (black circles). Data of table III.

Dinoflagellates

。 Diatoms

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We lack data on the intensity of irradiation in Vigo and its penetration in the waters of the Ria. The Secchi disk disappears rapidly; in various series of observations made during the month of March 1954, we obtained values generally ranging from 4 to 7 meters (maximum 9) for a white disk 30 cm. in diameter, which corresponds to values of the extinction coefficient ( $\mathcal{K}$ ) of about 0.2 to 0.3. Figure 11 shows the /p. 108 reduced transparency of the water as one moves towards the bottom of the Ria; we would need to know the annual variations.

There are very few species in the Ria of Vigo which show a periodicity in their development observable above and beyond the shorter cycles we shall be commenting on. With the help of the data published in previous works, we may divide those showing such periodicity into three groups. Type I, from September to January: Thalassiosira rotula, Coscinodiscus Grani, Rhizosolenia robusta, Ceratium tripos. Type II, from April to October: Rhizosolenia alata, Eucampia zoodiacus, Goniaulax polyedra. Type III, from August to December: this group includes oceanic species, that is to say, species normally scarce in the Ria, though common in outside waters, so that their regular presence could indicate greater intensity of mixing with the outside or greater influence of Atlantic waters; however, it would be hazardous to say so at this time, since the observations for the years 1951 and 1952 do not, in truth, enable us to break down the species as characteristic of the Ria or of outside waters. In future, it will be necessary to determine the relationship between Ria populations and those of outside waters, defining the periods with optimum conditions for an exchange of organisms, as well as the interannual variations in said periods, which may be very important in

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the study of populations of certain species of fishes. In group III, we may include, for the time being: <u>Pyrophacus horologium</u>, <u>Coscinodiscus radiatus</u>, <u>Peridinium crassipes</u>, <u>Ceratium candelabrum</u>, <u>Asteromphalus heptactis</u>, <u>Ceratium massiliense</u>, <u>Ceratium macroceros</u> and species of <u>Hemiaulus</u>, <u>Oxytoxum</u>, <u>Goniodoma</u> and <u>Eutintinnus</u> (ciliate).

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c) Cycles related to vertical agitation. - It is advisable to deal first with the shortest period after the annual period. In figure 8, we have combined: 1) a curve (central) representing an arbitrary sum of the range of tidal and wind speed variation, to give an approximate idea of the degree of agitation and mixing in the waters of the Ria; 2) another curve (upper) representing surface phytoplankton, in which the maximums shown are in relation to an arbitrary line representing the annual component which could be attributed to variations in solar intensity; ;and 3) a third curve (lower) indicating the values of the index of floristic heterogeneity between each two consecutive samples. The overall graph is a bit confused, as may well be expected, given the complexity of the natural cycles; however, we cannot deny a certain coincidence between moments of maximum mixing and moments of highest production, and between moments of greatest calm in the water and the occurrence of changes in the composition of populations. To correctly interpret the relationship between agitation and quantity of plankton, we must keep in mind that at times of great turbulence, the plankton shows greater vertical homogeneity in its distribution (fig. 11), so that /p. 109 the data relating to surface plankton are unsuitable for purposes of comparison with moments when the plankton is accumulated on the surface days of minimum agitation -. The greater abundance of detritus and

higher ratio of diatoms in the agitated water are other unknown elements which act in the opposite sense to that just mentioned. A statistical study of the correspondence between the different series of values has not be feasible, since it is a question of historical series of which the dependence on the values of the independent series (vertical mixing) would show a certain unspecified, variable delay, and probably also autoregression, that is to say, dependence on the values preceding the same series (obviously the present mass of plankton depends, not only on past agitation, but also on the quantity of plankton which existed previously). The simplest manner of explaining the relation's observed is the following:

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MAXIMUM	MINIMUM
Rising of algae (Rhabdonema, Stria tella, Pleurosigma) and detritus from the bottom and presence of repro- duction cells of littoral algae. Continuous produc- tion due to the inflow of nutritive salts and the sepa- ration of cells to- wards lower layers.	Depletion of nutritive salts and reduction in light penetration because of the population con-Sedimen- centration on tation the surface.
Agitation and vertical mixing	Stagnation and stratification
Homogeneization of plank- ton populations Constancy in time and space of the phytoplankton compo- sition	Conditions favo- Low population rable to the density favors segregation of random differ- heterogeneous ation communities Heterogeneity in space with subsequent development of one of the differentiated communities, with as a con- sequence discontinuity in time
Qualitatively	· · · · · · · · · · · · · · · · · · ·

Fig. 10. - Diagram illustrating the relationship between characteristics of phytoplankton populations and intensity of turbulence in the water.

According to the diagram of figure 10, the population is very /p. 110 dense and uniformly distributed in depth at times of maximum agitation; it later decreases, concentrates more on the surface, and it may be supposed that is when the heterogeneous nuclei appear or develop more fully at different points in the Ria, forming independent, locally segregated populations. The following phase of the succession occurs when one of these populations, more specifcally that for which the conditions becoming generalized in the Ria environment are more favourable, ousts the others and gives rise to a new maximum. Some last-minute observations (fig. 11) definitely indicate greater vertical heterogeneity in the distribution of plankton at times of greater tidal amplitude; however, we have not yet obtained qualitative data showing in what way floristic discontinuity in moments of calm could be caused by a presumed horizontal heterogeneity in the distribution of the plankton species. Further on, we shall comment on various secondary aspects of this continuous oscillation between two opposite situations. The tide lends its rhythm to the action of the wind, as is demonstrated by the more or less bi-weekly periodicity of this rhythm.

d) <u>Cycles related to the biotic determination of the succession.</u>-We discovered another type of regularity upon studying the succession of communities represented in the pulsations described, of which the moments of greatest floristic discontinuity coincide, generally speaking, with the minimums of present production. Each one of the successive populations shows a distinct personality, as may be seen from the simple examination of table II. In table III, the succession has been broken down into phases, taking as limits the moments of maximum discontinuity; the data thus

summarized and simplified enable us to better identify and more briefly describe the course of the succession. Its regularity takes the form of a repetition of segments of same - or partial successions, which cover about three months, each one thus including three or more of the simple pulsations studied in the preceding paragraph. The successive phases - each ordinarily represented by one or two biweekly pulsations which characterize each of the typical partial successions, are the following:

1. Clear dominance of diatoms over dinoflagellates, the former being represented by species, (measuring about 10 µ in diameter), showing rapid proliferation and having few requirements, as is demonstrated by their ability to live in acquariums. <u>Sceletonema costatum</u>, <u>Chaetoceros</u> <u>socialis</u> and <u>Leptocylindrus danicus</u> are the species most characteristic of this group, all of them able to multiply so rapidly that the population may be doubled and even tripled in 24 hours.

2. Gradual increase in the ratio of dinoflagellates. The diatoms, which continue to show a slight dominance, include, as the most typical species, <u>Lauderia borealis</u>, <u>Rhizosolenia alata</u>, <u>Thalassiosira rotula</u>, <u>Thalassionema nitzschioides</u> and various <u>Chaetoceros</u>, all of them having larger dimensions than the species of the preceding group. When the waters do not permit huge daily increases, the species of this group gradually eliminate those of the preceding phase. Some of them, like <u>Rhizosolenia alata</u>, are comparable to those of the first group as regards their high potential for multiplication. Frequently, the diatoms form endocysts at the end of this second phase.

3. The final phase may be so prolonged that there is an impoverishment

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of the plankton and, throughout its entire duration, the mass the dinoflagellates exceeds that of the diatoms. The dominance of the dinoflagellates is also dependent on temperature, since it is more manifest in summer (fig. 9). Species of <u>Ceratium</u>, <u>Dinophysis</u> and <u>Peridium</u> dominate the plankton population. These are species with a lower ratio of pigments than the diatoms and some of them are partially heterotrophic. This is also the case of <u>Noctiluca</u>.

The most probable explanation for the regular repetition of these partial successions would be that the development of each of the consecutive communities transmits given properties to the water, or else ambients it or places it under conditions/this concept is widely used today in ecology and is sometimes expressed using terms deriving from the Latin condio, season, temper; eg. "Environmental conditioning", in ALLEE, etc., 1950, p. 352) which will favour the establishment of certain communities in preference to others. The three periods mentioned generally follow each other with considerable, though not with absolute, regularity, since it may happen that one of them is shortened or appears sporadically - perhaps developing locally, in which case it appears as a sequence of populations in a water which is being displaced. We leave to the reader the task of interpreting table III according to the principles outlines. Table IV shows the different types of partial successions observed.

The wide variations in the ratio of dinoflagellates in Vigo have a different explanation than those occurring in Eastern Spain. In the Mediterranean, the density of dinoflagellates could be considered

practically constant throughout the year, because the periods in which they dominate coincide with those of low total production. This empirical rule is consistent with reality, so that the total number of algae cells, in relation to a constant number of dinoflagellates (100 to 1000) is a reliable index of the density of the total phytoplankton population, since it corresponds closely to the quantity of pigment contained in the plankton.

#### TABLA IV

### ·Sucesiones bióticas en el fitoplancton de la ría de Vigo

Sus etapas van indicadas por los mismos números que encabezan los párrafos del texto (capítulo IV, apartado d) en que han sido descritas. En las tablas II y III del presente trabajo y en las I y II de uno anterior (MARGALEF & DURÁN, 1953) puede verse la composición de las comunidades que aquí se han reducido a unos pocos tipos

1951-1952	1952	1953-1954
	13-IV-52	25-IV-53
	· 1	1
		. 2
	2	3
•	20-VI-52	3-VII-53
	1	1
		3
	2	1
	3 .	2
	5-1X-52	3 red water 30-IX-53
3	2	transition
15-XI-51		15-X-03
1		1-2
2		3
<b>28-I-5</b> 2	·	· 29-XII-53
1-2		1
3	•	2
3		2-3
13-IV-52		31-III-54

# Table IV

Biotic successions in the phytoplankton of the Ria of Vigo

The phases are indicated using the same numbers which begin the paragraphs of the text (chapter IV, section d) in which they have been described. Tables II and III of the present work and I and II of a previous work (MARGALEF & DURAN, 1953) show the composition of the communities which here have been reduced to a few types.

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This procedure cannot be used for Vigo, so that a table included in a preceding work becomes worthless (MARGALEF & DURAN, 1953, table II), and, for the same reason, in table III the rates per thousand are given in relation to the total number of cells. The variations in the representation of the two most important groups of planktonic algae, mean that we must take into account their ratio to give a ponderal expression of the quantity of pigment, as has been done in table III for the averages of the different phases of the succession and as is discussed in chapter II, section a). These considerations may be ignored when the pigment mass is taken as a simple index of productivity. The other groups of planktonic algae are always poorly represented and particularly noticeable is the scarcity of coccolithophorales which, since the filtering was only done (illegible) .....

e) <u>Hematothalassia</u>. - Frequently, the mass of dinoflagellates exceeds that of the diatoms, even at moments of maximum production, such as the so-called "red water"; (however, we prefer the term <u>hematothalassia</u> introduced by SOBRINO (1918), the first Spanish author who wrote about it knowledgeably), which appears frequently, though not necessarily every year, in the Ria, as well as in other Galician rias. In 1952, it did not occur in Vigo, though it appeared in 1953 (September), terminating one of the partial successions which led to the accumulation of a huge quantity of dinoflagellates. Possibly these organisms are concentrated in the top layers, which would explain the sudden decreases in their density, occurring either following a strong tide or due to the action of the wind. SOBRINO observed the phenomenon in the Ria of Pontevedra during the months of June-July (1916) and July-August (1917). Red water

/p.113

is, therefore, a summer phenomenon, its intensity and the date on which it appears at full force varying from year to year.

The red water in the Ria of Vigo - at least that of 1953 - was not an exceptional or chaotic event, but rather the culmination of a perfectly normal development of the population. Though on different occasions, both here and in other waters, the dominant species in the red water was <u>Goniaulax polyedra</u>, in 1953, the largest production recorded was of <u>Ceratium furea</u>.

In table V, there is a comparison of various cases of hematothalassia in peninsular waters and - because of the high interest offered by the similarity of composition - in the Oslo fjord. In August -and September of 1952, a similar population was developing, however due to unknown causes, it did not reach the level needed for the water to visibly change colour; in spite of this, we have included the corresponding data in table V. We lack precise data for a comparative analysis of the years 1952 and 1953; perhaps the rain had something to do with the difference. In 1952, the strongest tides of the equinox occurred with the full moon /p. 114 on September 4; the rain which fell during the last ten days of August was 23.7 liters/m<sup>2</sup>; during the first ten days of September, nil; during the second ten days of this same month 6  $1/m^2$ .

Statistics Statistics In 1953, the full moon occurred on September 23 and 37 and 113 liters/m<sup>2</sup> of rain were collected during the last ten days of August and the first three weeks of September. Wind intensity was approximately the same during the corresponding periods of the two years compared.

Obviously, the high plankton production needed in order for its concentration to become visibly perceptible can only occur in restricted

#### TABLA V

:	Pontevedra	Vigo	Vigo	Areia Branca	Fiordo de Oslo
	VIII-17 Sobrino	9-IX-52	21-IX-53	IX-1944 Dos Santos	6-IX-50 Nordli
	(1918)			(1949)	(1951)
Ceratium furca	+	20 %	81 %	*3 %	45 %
Goniaulax polyedra.	en masa	40 %	+	85 %	43 %
Prorocentrum micans	+	+	2 1/2 %	4 %	8 %
Peridinium sp. pl	+	+	3 %	6 %	2 %
Ceratium fusus	+	+	5 %	•	1 %
Dinophysis sp. pl	•	· + ·	5 %	1 %	1/2 %
Ceratium tripos	•	+	1 %	•	÷

Composición del fitoplancton, en tanto por ciento de individuos, en varios ejemplos de hematotalasia. +, presencia escasa o indeterminada.

(\*) Ceratium lineatum.

#### Table V

Composition of the phytoplankton, by percentage of individuals, in various cases of hematothalassia. +, low or undetermined quantities.

areas which combine favorable circumstances. The low depth and the inland nature of the water are the most essential. For SLOBODKIN condition for) (1953), the initial cause of hematothalassia along the coast of Florida is the presence of a mass of low water, with salinity lower than that normal in the Gulf of Mexico. In any case, a certain discontinuity with neighbouring waters is important. In other localities, hematothalassia Large is frequently associated with the death of layer quantities of fishes and other marine animals, including mammals, and sometimes with an irritation of human respiratory tracts. The damage is more strongly felt when known toxic species appear in the plankton (Goniaulax catennela, Gymnodinium brevis). See GUNTER & al. (1948, WOODCOCK (1948) and HAYES & AUSTIN (1951).

#### V. FRAGMENTARY OBSERVATIONS ON OTHER ASPECTS OF THE DYNAMISM

a) <u>Reason for the increase in the species</u>. - Minimum estimates of the net increase have been obtained - disregarding sedimentation and consumption by animals - by comparing the population density of a given species during successive days of <u>normal</u> increase in phytoplankton, estimated in the portion representing the total population measured in units of pigment. The figures obtained include the error represented by the uneven density of pigment in the cells of the different species, the essential regularity being provided by data referring to species which multiply rapidly, since it is only with these species that periods of a few days can offer usable data, for they are the only ones which can  $\frac{\Delta m}{\Delta m}$  use sufficient homogeneity in the changing picture of the Ria plankton.

Table VI gives the values found, expressed in different units, as reason for increase (r), number of divisions in 24 hours (n) and percentage of daily increase (a). The area/volume ratio has been calculated approximately using geometric models.

The values of this table are comparable with the figures published by other authors (GRAN, 1933: <u>Rhizosolenia alata</u>, 1,2 divisions per day; BRAARUD, 1937: <u>Sceletonema costatum</u>, 0.9-1.2 divisions per day at 10-12<sup>o</sup>C, etc.). It should be noted that all the species showing rapid increases have small cells and a relatively large area. They are "acquarium" species, which generally achieve their maximum production rapidly in wild plankton crops. They may compared with ruderal plants and, like them, they become rapidly established under altered conditions; however, over a long period, they are replaced in the natural succession by other larger-

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#### TABLA VI

Incrementes notos de varias especies del altoplancion, deducido del aurento observado en poblaciones naturales de la ría de Vista, e, racón de incrementor o, numero de divisiones en 25 horas; a, fundo por ciento de aumento diado.

1 2 · 3 ESPECIE, FECHAS Y TEMPERATURAS	$\mathbf{r} \\ (\mathbf{N}_i = \mathbf{N}_0 \mathbf{e}^{i\mathbf{t}})$	n (n = 1.44r)	a [a=100(er=1) =100(2n=1)]	RFLACIÓN SUPENE./VOL. p°/p3
Chactoceros socialis 4 a 7-X1-53, 13 a 17° C	0.6 - 1,3	1-2	80-270 %	1,2 - 1.8
Sceletorena costatua 26-V a 6-VI-53, 14 a 14.5° C. 1 a 8-X-53, 16 C.	0.6 - 1,2	1-2	80 - 230 %	0.7 - 1,6
Rhizosolenia alata 1 a 10-X-53, 16° C.	0.45 - 0.7	0.6 - 1	55 - 95 %	0.4 - 1
Leptocylindrus danicus 5 a 15-V-53. 15.5 a 16,4° C. 4 a 26-VIII-53. 16.8 a 17.8° C.	0,4 - 0,5	0.5 - 0.7	50 - 65 %	0.5 - 1
Ceratium furca 4 a 21-1X-53, 16 a 18.3° C	0.12 - 0.25	0,2 - 0,4	12 - 30 %	0.2 - 0,3

#### Table VI

Net increases in various species of phytoplankton, assumed from the increase observed in natural populations of the Ria of Vigo. r. reason for increase; n, number of divisions in 24 hours; a. percent of daily increase.

Key to Table VI -

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1 - Species 2 - Dates 3 - Temperatures

sized species with a smaller relative area. This becomes obvious from the comparison of phases 1 and 2 of the succession described in chapter IV, paragraph d).

Species capable of high increases achieve sudden maximums (diatoms); they also cause heterogenous distribution. For example, the 42,000 UPH/,<sup>3</sup> "bank" of figure 11, lower right (station II, 10 m depth), was made up mainly of <u>Chaetoceros socialis</u>, of which the colonies may be observed at
a glance as thin flakes floating on the water sample.

The downward lines in the upper right-hand corner of graphs 1 to 4 give us an idea of the increases normally occurring in mixed plankton populations. If the representation semilogarithmic (logarithms of UPH), a given rise corresponds to each value of r. The maximums are usually slightly above r = 0.5 for populations with a dominance of diatoms, and r = 0.1 for those with dominance of dinoflagellates. The values found in the plankton of Castellon are much lower, perhaps they do not exceed r = 0.25. It is worthwhile mentioning that the "optimum" for a given species or mixed population is not the cusp or maximum of the curve indicating its present production or mass, but rather the maximum value of r, that is to say, the moment in which its population increases with greatest intensity.

b) <u>Importance of losses due to exchange with the outside, sed-</u> <u>imentation and the action of animals</u>. - If we consider the Ria as a plankton-producing system communicating with a sea which lacks plankton, so that the plankton going out with the tidal currents later disperses and does not return with the incoming tide, we may calculate a maximum limit for plankton loss due to the alternate flow of the tides.

In this hypothesis, the value to which a unit population is reduced through the action of the tide may be estimated at

 $(1 - \frac{h}{Z})$  2t h - range of tidal variation Z - average depth of the Ria t - time in days

This equation gives 0.72 approximately, for one day, in the case of high  $f_{\mathcal{M}}$  tides, and 0.9 in those of lesser amplitude. A more manageable equation

would be:

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$$N_t = N_{oe} mt$$

in which m (always negative) is a reason for "emigration", such that

$$m = \log_e \left(1 - \frac{h}{Z}\right) 2$$

m equals -0.33 for tides of maximum amplitude and -0.1 for lower ones. In reality, this picture is extremely confused, since we do not have detailed knowledge of the tidal currents and we have disregarded the return of plankton from the sea to the Ria. We also disregarded the circulation between the sea and the Ria due to differences in density, of which the importance is still unknown (x). The decrease in surface plankton at moments of maximum amplitude of the tides (fig. 11: stations I and II on April 3, 1951 and 6 and 5 on March 30, 1954) may be partly due to the higher speed of the currents on the surface. In any case, these limit estimates give us a basic for discussion. Any value of r higher than m ensures the maintenance of an endemic population in the Ria; in truth a lower value would suffice, since our estimate of m is exaggerated. Phytoplankton maximums usually coincide with spring tides, so that during these times, the increase more than compensates the population loss in the Ria, which is also greater on these same dates. The effects of tidal currents on the distribution of plankton inside the Ria should studied as a premise for the exact comparison of samples taken at different points in the tidal cycle.

A portion of the cells produced in the phytoplankton becomes sedimented. Their ratio is difficult to assess. It is possible that a  $\overline{(x)}$  KETCHUM (1954) in a recent work, develops similar ideas.

future study of the successive aspects of the "clouds" of plankton will give us a general idea of their importance. The data of GILLBRICHT (1952), aside from being open to question, are difficult to apply to our Ria. Estimating on the basis of literature published on fresh or marine waters, we must accept a sedimentation reason S of about s = -0.3 to -0.45.

We must also take into account a reason - also negative - constituted by consumption on the part of animals ("grazing"), which we shall call <u>f</u>. We still lack data on the development of zooplankton in the Ria, though our first impression is that it must be quite irregular. Certainly, there must be very high values of <u>f</u> at some periods; for example, when there is a sudden appearance of large quantities of brachyuran larvae, etc. We might consider attributing some of these decreases in the phytoplankton population mainly to the action of animals, however the speed and irregularity with which the entire plankton community develops in our case prevents the use of the equations of FLEMING (1939) and other similar ones assumed for a plant population on the increase, of which the increment causes a progressive rise in the animal population which lives at its expense, to the point of hindering the multiplication of algae.

In view of all that has been said, the net increase in the phytoplankton population should be made equal to

$$N_t = N_{oe}(r-m-s-f)t$$

and consider a net reason

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r' = r-m-s-f

which may be positive or negative, depending on the circumstances of the moment. Certainly the sum of the absolute values of m+s+f may be about 0.8 or even as high as 1. If this sum exceeds the multiplication potential of phytoplankton populations, the present mass of phytoplankton is diminishing. It is understood, therefore, that decreases in the <u>/p.118</u> plankton mass may, depending on circumstances, be due to a reduction in the rate of increase of the algae, which can no longer compensate "normal" losses, or else to an unusual increase in emigration, sedimentation or

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grazing ., even though the rate of multiplication of algae remains very high. The difference is considerable, even from a practical point of view, because in the second case, the productivity of the water remains higher.

c) <u>Competition and its relation to the index of diversity</u>. -The example given in table VII covers a short period (from May 6 to 16, 1953) during which the population mass varied little, however with a gradual alteration in the quantitative ratios between the different species. Certainly many other similar examples could be found, however we have chosen this one because it covers a period in which the plankton varied little and in which exact counts of the number of cells were made.

In the course of the ten days covered in the example, we note a regression of <u>Rhizosolenia Stolterfothii</u>, <u>Eucampia zoodiacus</u> and <u>Sceleto-nema costatum</u> - this latter being a small-celled species - as a result of growing pressure from <u>Leptocylindrus danicus</u> and <u>Rhizosolenia alata</u>.

Ejemplo de competencia en la sucesión de las comunidades planctónicas de la ría de Vigo. Representación, en tantos por ciento, de diversas especies de algas en el número total de células del plancton. Mayo de 1953.

1	Date JPH/liter	6 11,8	7 9,3	8 12.4	9 18	11 12.3	12 9.4	15 15,7	1 16 6	RAZÓN DE INCRE- MENTO NETO, SU- PONIENDO CONS- TANTE EL PLINC- TON TOTAL (1')
2	Leptocylindrus danicus Rhizosolenia Stolterfothi Rhizosolenia alata	48.5 14.8 1,2	57.4 14.3 3.2	63,5 19,7 1.5	74.6 9,4 6,3	62.1 9,3 6.3	86,1 6.1 1,5	78.8 4,1 10,3	79,8 2.2 3.2	+ 0.057 - 0.19 + 0.23
	Eucampia zoodiacus	3,5	5,6	5,4	1	0.4	0,7	0,2	0,6	- 0,39
	Sceletonema costatum	5	1,7	0.9	0	1.9	0,5	1 06	0.3	- 0.281 indeterminable
	Chaetoceros pl. sp.	17.6	10.4	5.4	4.3	11.7	1.1	0	3.5	indeterminable
3 <sup>.</sup>	Total especies citadas	96,0	92.6	97,5	96,7	94.8	97,2	95,0	95.7	0

## Table VII

Example of competition in the succession of plankton communities of the Ria of Vigo. Representation, in percentages, of the different species of algae in the total number of plankton cells. May 1953.

Key to Table VII -

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1 - Reason for net increase	2 - Leptocylindrus danicus,
supposing the total	etc. etc.
plankton remains	
constant (r')	3 - Total of species mentioned

Supposing the total phytoplankton mass to be constant and equal to K - the amounts of pigment remain similar - and <u>p</u> being a reason which includes losses due to sedimentation, emigration, consumption by animals and natural mortality (p = m + s + f ...; immigration must be negligible), we may write:

$$N_{1oe}(r_1-p)t + N_{2oe}(r_2-p)t + N_{3oe}(r_3-p)t + N_{moe}(r_m-p)t = K$$

where  $r_1$ ,  $r_2$ ,  $r_3$ ,  $\dots$ ,  $r_m$  are the reasons for the increase in the different species and <u>p</u> a reason for loss which, in an initial approximation, is assumed to be equal for all the algae of the community, even though in

reality this cannot be entirely true since, although they all run the same risk of being carried out to sea on the tidal currents, all species do not have the same probability of becoming sedimented or of being eaten by the animals which are most abundant at that moment. The analysis of this factor must be left for the future: however, it is still useful to continue the discussion, because it can give us a general idea of the magnitude of the parameters which come into play, and this is important in the planning of new research: in absolute values, p cannot be less than the maximum negative values of  $r'_m = r_m - p$ , because <u>r</u> can never be negative. For Eucampia, the table gives  $r^2$ 0.4; because of what has been said in the preceding paragraph, p must fall between this value and -0.8. A value of p = -0.45 would give us r values of 0.7 and 0.5 respectively for Rhizosolenia alata and Leptocylindrus danicus, similar to those which appear in table VI, however those of this table are closer to  $\underline{r}^{I}$  than to  $\underline{r}$ , given the circumstances . under which they were obtained, so that it is reasonable to make p equal to at least -0.6.

If <u>p</u> were equal for all species, the values of <u>r</u> in the specific conditions under which competition develops would determine its future trend (\*). If the total population does not vary, the differences  $\underline{r} - \underline{p}$ must constantly diminish, until <u>p</u> is equal to the value of <u>r</u> of the species which, in the end, is the sole survivor, having successfully eliminated all the others. It may happen that <u>p</u> actually increases, however we must also recognize the effect of over-population (depletion of nutritive salts, intoxication by ectocrine substances) which reduce the values

(\*) Experiments under way show that in mixed algae populations, there is an interaction which obliges us to modify this initial hypothesis, which is overly simplistic.

of <u>r</u>. The fact is that the differences  $r_m - p$  tend progressively towards zero. In our case, the ultimate survivor would in theory be <u>Rhizosolenia alata</u>. In reality, the successions can never be defined this clearly, because environmental conditions are constantly changing. This is why analyses of this type are still useless in the study of natural communities, serving only to illustrate some aspect of their dynamism. The problem dealt with by VOLTERRA (1926) of the "association between two species which compete for the same food" is similar and leads to the same results: elimination of one species by another, except for improbable cases of very special values of the constants.

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Let us arrange, in descending order, for two successive dates, the quantities of the different species of the community analyzed, including /p.120the rare ones not included in table VII (Table VIII). The regularity noted in both progressions lets us see immediately that the average reason / between two consecutive terms is greater in the latter than in the former. From the ratios studied elsewhere (MARGALEF, 1954 b), it appears that the index of diversity of the community shows a negative correlation with the mean quotient between the number of individuals of species occupying neighbouring localities, when they are arranged in descending order of abundance.

The normal dynamism of any community or, better stated, the manifestation of competition among species, should in theory lead to a reduction in the index of diversity (MARGALEF, 1954 b) and this fact increases the tendency (seen in graphs 1, to 4) following each moment of

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### TABLA VIII

Sucesiones formadas por los números de individuos de las distintas especies presentes en cada muestra, ordenadas de más a menos abundantes, en dos momentos del desarrollo de una comunidad de fitoplancton en la ría de Vigo. Se dan también los indices de diversidad.  $d=(S-1)/\log_c N y d'=S/\log_{10} UPH$  (d' calculado por duplicado, según las especies de este recuento y según todas las vistas en la muestra).

Date (1953)	INDIVIDUOS CONTADOS DE LAS DIFERENTES ESPECIES	d	ď
Мау б	500:152:109:87:61:51:12:12:9:8:8:4:4:2:2:2:2:1:1:1	2,9	5,2 - 6,5
May 16	$\bigcirc \bigcirc \bigcirc \bigcirc$ 504:52:15:14:10:7:7:4:4:3:3:2:2:1:1:1:1:1	2,6	4,7 - 6,2

## Table VIII

Successions formed by the numbers of individuals of the different species present in each sample, in descending order, at two moments in the development of a phytoplankton community in the ria of Vigo. The indices of diversity are also given.  $d = (S-1)/\log N$  and  $d' = S/\log_{10}$  UPH (d' calculated twice, according to the species in this count and according to all those seen in the sample).

Key to Table VIII -

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1 - INDIVIDUALS COUNTED FOR THE DIFFERENT SPECIES

intense floristic change, when the situation is normalized, towards an arrangement by decreasing values of the aforesaid indices, tendency which we have attempted to emphasize - sometimes a bit arbitrarily - by drawing, lines.

d) <u>Heterogenous distribution of plankton in the Ria in relation</u> to the intensity of water mixing.. - SVERDRUP (1953), basing his comments on the studies of GRAN & BRAARUD (1935, p. 423), according to whom the spring increase in phytoplankton can only occur if the vertical turbulence does not cause an excessive loss of cells from the layers where assimilation is possible, poses, as a necessary condition for the increase in phytoplankton, a minimum value of the ratio between the agitated surface layer (top mixing layer) and the depth of compensation of the phytoplankton. This ratio could not exceed 5-10 times. These ideas are open to broader generalization, assimilating them with those of KIERSTEAD & SLOBODKIN (1953), who assign a minimum horizontal dimension to the water mass surrounded by others with different conditions or conditions unsuitable for the species considered, so that the population cannot be preserved or increased in it. A finite population can only resist /p. 121 dispersion if its rate of multiplication exceeds the losses, of which the order of magnitude is the ratio of the "diffusivity" to the square of the dimension of the region in the zone of maximum diffusion (K & S, 1953, p. 146).

Both principles mean impossibility of growth (when the neighbouring waters are empty) or of maintenance of biotic independence if the diffusion or dispersion of the individuals exceeds their production. In a preceding section (chapter V, section b), we have applied this. principle in evaluating the maximum loss which could be caused by the tidal currents, coming to the conclusion that the value of  $\underline{r}$  more than exceeded it, permitting the conservation of a native population in the Ria.

Having established the independence of the Ria with respect to outside waters, since the increase values are much higher than the loss of plankton, we must determine whether these same conditions can bring about heterogeneity within the Ria. Following KIERSTEAD & SLOBODKIN, however, without any need to apply the final formulae obtained by them, we shall suppose that the square root of the quotient between the ratio of loss or diffusivity and the ratio of multiplication

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is in proportion to the dimension along which a given population maintains a balance or remains independent. If multiplication compensates emigration in a 20 km ria, if this distance is increased four times, it will be possible to maintain distinct populations separated by 10 km, or nine times to ensure heterogeneity of the same type between distances of 6.6 km. Hence we assume that under productivity conditions which are frequently repeated, where the net increase is two to ten times greater than the loss or mixing of individuals through the tidal currents, within the Ria heterogeneous populations may be produced and maintained, and even more easily when the growth rate of the plankton is higher and the tides less violent.

In the Bay of Kiel and in the North Sea, BILLBRICHT (1952, p. 178) and KREY (1954, p. 12), studying samples obtained during successive periods at short distances, bring to light notable differences in the composition of the phytoplankton, even between distances of 2 km. Even before we became acquainted with these works, the foregoing considerations had already led us to the conviction that there was considerable heterogeneity in phytoplankton distribution. The first positive data were obtained in March of 1954, upon studying the pigment content of 10 liter samples obtained at different points in the Ria. These initial studies must be supplemented by research on the distribution of the different species. The samples were taken successively in pairs: for example, first surface and 20 meters, then 10 meters and 20 meters, later 10 meters and surface, in such a way that a pair of samples from the same point was collected within an interval of an hour to an hour and a half,

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so that the variance between points (table X) not only measures the experimental error, but also that of possible drifting of the water mass during that time, as may be seen from the existence of the odd high deviation (table IX, April 3, station I, surface). Tables IX and X and figures 11 show the results obtained.

Between points separated by only 3 km, one already notices considerable heterogeneity in the phytoplankton distribution. Horizontal heterogeneity may be expressed as a gradient referring to one kilometer of distance from the unit density. Thus, from the data published, we may assume values ranging from 1.15 to 1.3 and around station II on April 3, 1954, at a depth of 10 meters, a maximum value of 1.77, that is to say, a 77% increase over 1 kilometer. The analysis variance has also been used by CUSHING (1952) in studying of discontinuity between patches of plankton; in our case, the value of z measures heterogeneity well and it is especially useful for comparing vertical and horizontal heterogeneity and interaction (diversification of types of vertical distribution according to localities, or viceversa); however there is the disadvantage that it may be obtained independent of distances. It should be possible to express the tendency of plankton to differentiate or segregate into heterogeneous communities in a simplier way. It is to be hoped that future studies will enable us to make it a function of the square of the distance between the points being compared and the growth rate of the plankton (in turn related to the difference between the present population and the maximum under those conditions), as factors favoring diversification, and of the

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### TABLA IX

Heterogeneidad en la distribución cuantitativa del fitoplancton en la ría de Vigo. Unidades Harvey de pigmento contenidas en series de muestras de 10 litros obtenidas el mismo día en distintos puntos de la ría. Localización de las estaciones indicada en la fig. 11; profundidades: 0. 10 y 20 metros. Muestras duplicadas para cada punto. Horas, huso 0.

March 26,	1	954. Pleamar:	6 h. 40 min., 2,6 m	i; 19 h., 2.7 m.	
		2 Bajamar:	12 h. 45 min., 1,2 i	m.	
		Station I	Station IJ	Station III	Station IV
		12 h. 30 - 13 h.	9 h. 45 - 11 h. 20	18 h 19 h. 10	15 h. 15 - 16 h. 10
Cumfaco		76,7	142	119	117,5
Surrace		•	175 .	123,5	168.5
10 meters		81.1	49	<b>59.2</b>	57,5
			32,8	65,6	66
20 meters		41.5	58.7	54	42,7
		•	66.7	58.5	49
					•

April 3, 1954. Pleanar: 14 h. 55 min., 3.7 m. 4 Enjamor: 8 h. 50 min. y 21 h. 10 min., 0.1 m.

	Station I 14 h. 15 - 16 h.	Station II 16 h. 30 - 18 h.	Station III 10 h12 h.	Station IV 12 h. 40 - 14 h.
Surface	. 65	76	137	122
bullado	133	93	157	144
10 meters	. 66	400	1.5.4	129
To merero	83	490	157	. 158
20 meters	. 256	164	140	16社
20 Hecci 5	270	171	147	187

### Table IX

Heterogeneity in the quantitative distribution of phytoplankton in the ria of Vigo. Harvey units of pigment contained in series of 10 liter samples obtained on the same day at different points in the Ria. Location of the stations indicated in fig. 11; depths: 0, 10 and 20 meters. Double samples for each point. Hours, zone 0

Key to Table IX -

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1 - High tide: 6 h. 40 min., 2.6 m; 19 h., 2.7 m 2 - Ebb tide: 12 h. 45 min., 1.2 m.

3 - High tide: 14 h. 55 min., 3.7 m.
4 - Ebb tide: 8 h. 50 min., & 21 h. 10 min., 0.1 m.

#### TABLA N

A server en la distración constitutiva del inteplanetos en la ría de Vigo.
 Anori a los la contará a de los resultados con nandos en la cola VII.

March 26, 1954

	1 MILLING 2	SUMD 3	GRAPOS 4	CP VDR VDO MEDIO	F	2	р
567 89 10	Futre protondidades Varie estaciones Esteracción Totar entre pandos Toror entre duplicados Total	26 114 1 2%, 4 7.4 22 1 7 1 909 24 034	2 3 5 11 9 20	13 057 413 792 2 918 220	59,35 1.87 3.6 13.26	2,04 0,31 0.64 1.29	< 0 001 0.2 0.05 < 0.001
67 89 10	Varia estacionas Esteracción Tatat entre pandos Tator entre duplicados Yatat	1 2% 4 1% 22 1 7 1 900 34 0%	3 15 11 9 20	413 792 2 918 220	1.87 36 13.26	0,31 0.64 1.29	0 < 0

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	12 VARIANCIA	13 SUMA CUADRADOS	L4 GRADOS 1 LIET RTAD	5 MI 100	F	2	р
16	Vet a profundidades .	39 911	2	19 955	67,18	2.10	< 0.001
17	the estacienes	42 597	3	14 1:06	47.76	1.93	< 0.001
18	Interacción	184 255	6	30 709	103.39	2.31	< 0.001
19	Total entre munios .	266 753	11	24 259	81.65	2,20	< 0,001
$\overline{20}$	T'mor entre duplicade	os 3 564	12	297			
21	Total	270 317	23				

# Table X

Heterogeneity in the quantitative distribution of phytoplankton in the ria of Vigo. Analysis of variance of the results given in table VII.

Key to Table X -

1 - VARIANCE	2 - SUM OF	3 - DEGREES OF	4 - MEAN
	SQUARES	FREEDOM	SQUARE

- 5 Between depths
- 6 Between stations
- 7 Interaction
- 8 Total between points
- 9 Error between duplicate samples
- 10 Total

11 - April 3

12 - VAR	IANCE 13	- SUM OF	14 - DEGREES	OF	15 - MEAN
		SQUARES	FREEDOM		SQUARE

- 16 Between depths
- 17 Between stations
- 18 Interaction
- 19 Total between points
- 20 Error between duplicate samples
- 21 Total

intensity of mixing of the water - dependent on the winds and tide and of the square root of the population density (since the probability of random heterogeneous distributions, which may serve as a basis for further differentiation, is related to the relative error  $\sqrt{N/N} = 1/\sqrt{N}$ ) as factors which oppose that segregation. The qualitative heterogeneity in space must manifest itself in a sequence of distinct populations which may correspond to swarms of plankton wandering through the Ria. In fact, when tidal amplitude is lowest, the indices of floristic discontinuity between consecutive samples attain their highest values, which could be attributed to a manifestation in time - due to circulation of the water - of that segregation in space.

Another aspect of research on heterogeneity is the attempt to relate accumulation or rarefaction of plankton to special configurations in the distribution of given properties of the water. In a couple of cases (table XI) the concentration of plankton corresponds to thermal anomalies and we consider it of highest importance to properly explore this point. In this regard, it is worthwhile calling attention to the works of ROUBAULT (1946) and SARGENT & WALKER (1948), the former referring to smooth "patches" which are seen on the surface of the water, at somewhat lower temperature (by 0.2°C) and with more plankton in the upper layers, and the latter associate the presence of whirlwinds with the accumulation of diatoms.

In spite of the shallowness of the Ria, vertical heterogeneity is considerable. The stagnation following an agitation which has vertically mixed phytoplankton must in turn be followed by a more intense growth of algae in surface waters. If  $\underline{r}$  varies in direct relation to light intensity,

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Fig. 11. - Quantitative heterogeneity of phytoplankton distribution in the ria of Vigo. In the upper portion, location of the stations with indication of where samples were taken. In the other graphs, the numbers indicate UPH in 10 liters of water; the stations are marked with arabic numerals (centre) or roman numerals (below). See tables IX and X.

# Key to figure 11. -

2 - Heterogeneity 3 - Tidal amplitude 1.95 m 4 - vertical 1 - March 307 - March 26 8 - Tidal amplitude 5 - horizontal 6 - Secchi disk ·9 - vertical 10 - interaction 11 - horizontal 12 - Heterogeneity 13 - March 24 14 - interaction 15 - April 3 17 - vertical 18 - interaction 19 - horizontal 20 - Heterogeneity

### TABLA XI

con respecto a la media de estaciones inmediatas.								
	March	30,	1954			April	3, 1954	
Stations		6	5	4	Stations	I	II	III

181

UPH .....

Temperature (°C.)

256

13.1

354

(+136)

(--- 0.25)

12.9

Distribución de fitoplancton, en UPH por 10 litros, a 10 metros de profundidad, en relación con las temperaturas del agua al mismo nivel. Entre paréntesis, diferencias con respecto a la media de estaciones inmediatas.

' UPH .....

13,2 Temperature<sup>C.)</sup>

Table XI	

Phytoplankton distribution, in UPH per 10 liters, at a depth of 10 meters, in relation to water temperatures at the same level. In brackets, differences with respect to the average of neighbouring stations.

for the normal values of  $\underline{r}$  (about 1) and the absorption of light in the Ria ( $\kappa$  - 0.2), we would find that a surface layer which represents one fifth of the depth of the Ria, and which, supposing uniform vertical distribution initially, would contain 20% of the population, will have to lodge more than 50% four days later, and about 85% eight days later. In the lower graphs of figure 11 we see that the phytoplankton accumulates on the surface when tidal amplitude is low. At such times a sudden agitation wind - may cause the surface plankton to descend rapidly, and to become uniformly distributed in a vertical column. It is to this phenomenon and to the reverse of accumulation that we must undoubtedly attribute some of the extreme short-term variations in the series of phytoplankton determinations in surface waters. Since the vertical mixing does not eliminate much plankton from the region where photosynthesis is possible,

490

(+ 246)

12.7

(----0.7)

13,4

156

13,5

given the shallowness of the Ria, but rather it even leads to a better utilization of light by the plankton - as in a waving crop, and the same circulation favours the distribution of nutritive salts, there is an optimum degree of turbulence- sufficiently above the minimum for maximum total productivity, which it will be necessary to study. This is why moments of agitation of the water correspond to absolute maximums, and at times of greater stagnation, the occasional accumulation of plankton on the surface generally does not dissimulate the minimum production which then occurs. In the figure last mentioned, it may be seen that on April 3, the surface plankton is no more abundant than a week earlier; on the other hand, the total mass of phytoplankton is much higher, as a result of the more violent agitation to which the water has been subjected. The problem posed by GRAN & BRAARUD and SVERDRUP concerning the need for a proper ratio between the top mixing laver for the production of phytoplankton, does and depth of compensation not occur here; however, in its place we have the problem already outlined: to determine the degree of turbulence which, under given conditions of light penetration ensures maximum productivity in the plankton community. GENERAL CONCLUSIONS, POSITION OF THE RIA AND SUGGESTIONS FOR FUTURE VI. WORKS.

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The idea we have formed of the plankton cycle in the Ria of Vigo may be properly expressed by referring to an example of a cycle dominated by the upwelling of deep waters, such as that of Castellon. In the East, over equal periods, at least three systems of determinant causes of the

annual rythm are superimposed: intensity of irradiation, which may affect the summer dominance of dinoflagellates; "upwelling" which characterizes moments of maximum production, limited in this case to a small part of the year; and the biotic succession due to conditioning of the water, in reason of which we may explain the successive development of diatoms, which appear as the deep water begins to rise, followed by other species, the formation of endocysts, the appearance and growing dominance of dinoflagellates and lastly, the proliferation of dinoflagellates so characteristic of the last weeks of autumn. In Vigo, the three systems are also superimposed, however each one of them is characterized by a different rythm. The heat and radiation cycle is the only one which also remains annual and which may explain the relative scarcity of plankton in winter and the growing dominance of thermophile dinoflagellates as the water temperature rises. The cycles of agitation are not one per year or several concentrated in a short season, but rather they succeed each other constantly and, naturally, according to the intensity of the agents which move the water: winds and tides. The decisive importance of these last is shown in the succession of small maximums, the jagged lines of the phytoplankton curve follow the springtides with close approximation. The biotic succession is dependent on the two preceding cycles. The extreme dynamism of the community enables it to develop the complete succession in less than a year; however, for its total realization, the half-month periods corresponding to the tides are insufficient. Therefore, the biotic succession follows these lesser variations and includes the maximum production of

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dinoflagellates during the hottest period. It is easily seen that an unusual situation occurs, with successions of quite different total duration (2 to 4 months) and which vary from year to year, with a changeability which indicates that propers in research will be difficult. It is pointed out that this breakdown of the cycle of the Ria into the superimposition of a triple system: annual cycle, cycle of agitation of the water - tides - and cycle determined by biotic factors, opens up new prospects for the analysis of the dynamism of plankton communities in places where the three cycles are superimposed and where this independent analysis is therefore difficult (Castellón).

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The study of the Ria of Vigo requires great assiduity because of the rapidity of its dynamism. It is necessary to confirm its richness of nutritive salts and obtain the hydrographical data needed to situate plankton observations. As regards phytoplankton, it would be advisable to carry out quantitative determinations of carotids and dry weight. Research on zooplankton should give us an idea of the role of same in the regulation of phytoplankton populations. Possibly the topic of greatest interest which this work suggests is the study of the heterogeneity and diversification of plankton within the Ria, as well as its possible relationship with the waters outside of same.

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## SUMMARY

A survey of the phytoplankton and Tintinnoinea of the Ria of Vigo, from April 1953 to March 1954. Duplicate 4 1. samples of superficial water were collected near the pier marked by a cross in fig. 11, and filtered through paper. One of the samples served for the extraction of plant pigments (expressed as Harvey units [UPH] per m<sup>4</sup> in the table I and figs. 1-4); the other was resuspended in a small volume of water and microscopically examined. The results are reported in table II, rating the abundance of every species from + to 5. The standing crop is always important, around a mean of about  $30\ 000\ UPH/m^3$ . Coccolithcphorales are scarce. In figs. 1-4 are gathered different data on pigment units, diversity and discontinuity indices and some ambiental factors.

Annual succession may be explained as a result of the interplay of three separate cycles. 1) The annual cycle dependent on radiation, determining a major production (chiefly of dinoflagellatae) in the warmer and brighter months. 2) The approximatively biweekly cycle dependent on tides and winds; stronger mixing increases the production, since practically no phytoplankton escapes the photosynthetic layer (the Ria is only 20-50 m deep); in calmer water phytoplankton develops specially near the surface and then occur the major floristic discontinuities (vertical broken lines in figures 1-4) Influence of fresh water is unimportant, since the basin of the Ria is small. 3) Biotic successions lasting in full 2-4 months and embracing a number of minor pulsations. Their typical phases are: a) bloom of small cellcd diatoms; b) other diatoms and increasing number of dinoflagellatae; c) dominance of dinoflagellatae (table III). Summer successions may lead, almost every year, to a final discolouring of water; in 1953 the dominant species in the red water was *Ceratium furca*, other years was *Goniaulax polyedra*.

Discussion of a number of fragmentary observations allow a better understanding of the dynamics of phytoplankton populations. Minimum values for the rate of increase of some fast growing species have been computed (table VI); the species having a greater surface/volume ratio show the higher values. As a result of concurrence (exemplified in table VII), in undisturbed populations, the trend of the ratios between numbers of cells of different species is to become higher (table VIII), so that diversity indices generally drop along the «normal» segments of succession (figures 1-4, «indice de diversidad»). An estimate for the maximum leakage of plankton through tidal currents may be obtained, but our data give no measure of sedimentation and grazing. Rate of increase of phytoplankton in the Ria is high enough, not only to maintain independence of the interior populations towards the Atlantic ones, but also to create a certain amount of horizontal heterogeneity in the distribution of phytoplankton along the Ria. A small number of data gathered in marchapril 1954 afford full evidence of an heterogeneity greater than previously suspected ttables IX, X; fig. 1D, with gradients up to 77 % per km. In two instances, patches of diatoms have been found associated with thermical anomalies (colder batches of water, table NID.

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