JOURNAL OF SHELLFISH RESEARCH

SPONDYLIDS OF EASTERN PACIFIC OCEAN

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ABSTRACT Members of the bivalve molluscan family Spondylidae were very important elements in the world view of pre-Hispanic cultures of America, and today remain as symbols of culture heritage in contemporary society. In recent decades, given the importance they have for crafts and jewelry, as well as for fisheries and gastronomy, their exploitation has caused a drastic decrease in natural populations leading to restrictions in fishing. In the present review, data about *Spondylus* species of eastern Pacific Ocean, describing the symbolism, taxonomy, distribution, biology, and ecology, their status as exploitable resources, the advances in aquaculture of these species, as well as management experiences and conservation efforts are presented.

KEY WORDS: *Spondylus*, Andean culture, taxonomy, invertebrate fisheries, aquaculture, marine conservation

INTRODUCTION

Along the eastern Pacific Ocean, there are four spondylid species (Mollusca: Bivalvia); two of them are commercially exploited, *Spondylus crassisquama* Lamarck, 1819 and *Spondylus limbatus* Sowerby, 1847, whereas *Spondylus gloriosus* Dall, Bartsch & Rehder, 1938 and *Spondylus leucacanthus* Broderip, 1833 are harvested occasionally. These species have played an important role since prehistorical times, not only as economic resources but also in political, cultural, and religious affairs in the population of America, in particular for the Mesoamerican and Andean cultures. They also been the focus for poetic inspiration:

> …*Saqué del mar, abriendo las arenas,*
> *la ostra erizada de coral sangriento,*
> *Spondylus, cerrando en sus mitades*
> *la luz de su tesoro sumergido,*
> *cofre envuelto en agujas escarlatas,*
> *o nieve con espinas agresoras*…
> Mollusca Gongorina, Pablo Neruda, 1950

Currently, spondylids are commercially harvested, principally for its adductor muscle and their ornamented shells, throughout most of their geographical distribution. Although modern fishing of spondylids started around the end of 1970s, most natural populations are overfished and local populations have been depleted in many regions. For this reason, spondylids are listed under threatened status in most of the countries and subjected to special regulations for their harvesting, in particular in Mexico

and Ecuador. Given the concern about the declining stocks of natural populations, there have been research-oriented studies to support the eventual development of spondylid aquaculture and stock enhancement initiatives. A summary of the results from the research efforts about members of the Spondylidae from the Eastern Pacific Ocean covering their role for the people of Mesoamerican and Andean cultures, a review of its taxonomy, distribution range, biology and ecology, fisheries management, aquaculture research activities, and conservation efforts is presented in the following sections.

SYMBOLISM AND USE

The shells of the bivalve *Spondylus* became very important elements in the pre-Hispanic cultures of the American Pacific Ocean and the Andes (Paulsen 1974, Marcos 2005). Its valves were used in rituals and offerings (Fig. 1) and served as raw materials for crafting religious and personal decorative objects such as necklaces, bracelets, and pectorals. They were also used by pre-Hispanic elites in their clothing to express social status (Fig. 2) and as grave goods of important persons (Melgar-Tísoc 2007, Paz-Bautista & Zúñiga-Arellano 2007, Carter 2011).

The most widespread hypothesis about its symbolic character derives from its association with fertility, considering the coincidence of the periodic increase in sea water temperature, the onset of the rainy season, and the noticeable abundance of spondylids in the coasts of the Pacific Ocean (Marcos 1977, 2005). These phenomena are probably associated with El Niño southern oscillation events, particularly in places with little precipitation like the northern coast of Peru (Sandweiss 1999). Likewise, its increase in a particular time of the year could serve as an indicator in the agricultural calendar, marking the onset of

Figure 1. Mesoamerican shaman with *Spondylus* shells. Source: Donkin (1998).

crop time (Marcos 1977). In the indigenous Mesoamerican and Andean cultures the symbolic value of spondylids probably derives from its red and orange colors because these colours are linked to the power of blood and vitality (Hocquenghem 1983, 1987, 2009).

Archaeological evidence and written sources of Spanish colonizers show that all pre-Hispanic cultures invested a great amount of resources and effort to obtain spondylids shells (Donkin 1998). These shells are present in places far beyond the territory of natural distribution of the species, from the southern border of the United States and into southern Peru and northern Chile (Donkin 1998), as a consequence of the transmission of its symbolism through commerce and exchange among cultures (Stothert 2003).

Spondylids and the objects crafted with their shells represented some of the most important goods in the commerce between the high Andean lands and the American Pacific Coast (Paulsen 1974, Blower 1995, Carter 2011). In the Chimú culture of Peru, there existed a long-distance exchange network where the shells of *Spondylus* had a prevailing role (Pillsbury 1996). There is also evidence of the exchange of spondylids between the Ecuadorian Coast and the western region of Mexico (Marcos 2005). On the site Punta Mita in Nayarit, Mexico, diving weights and stone anchors were found which were very similar to those widely known in the Manteño-Huancavilca culture of the southwestern coast of Ecuador (Beltrán-Medina 1997).
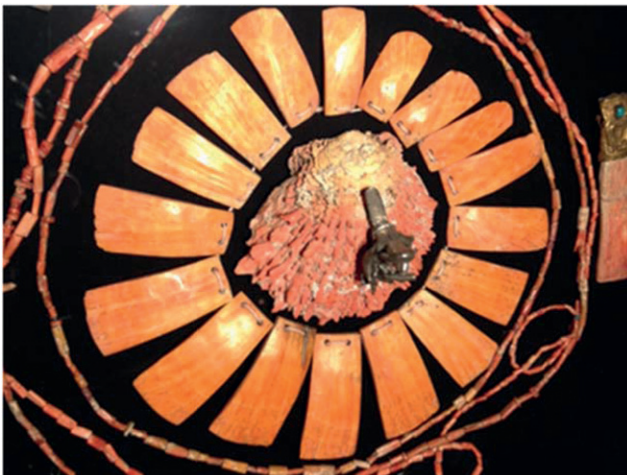

Figure 2. *Spondylus* necklace of the Nazca culture. Pre-Columbian Art Museum of Cusco, Lima, Peru. Photo by César Lodeiros.

Currently, spondylids maintain an important position as cultural identity in many countries that keeps communities linked to their ancient past (Cordy-Collins & Giannoni 1999, Sandweiss 1999, Bauer 2007). Unfortunately, since the 1980s to 1990s, several species of *Spondylus* gained a gastronomic fame, becoming one of the most coveted and in-demand items from the sea along the coasts of the Pacific Ocean in Mexico, Ecuador, and Peru. This intensified demand has triggered the overexploitation of these resources. The shells of *Spondylus* are still used to craft jewels, figures, and their symbolism remains rooted in the coasts of the American Pacific Ocean, particularly in the Province of Santa Elena, Ecuador, where they are marketed as objects of cultural and touristic desirability (Fabara 2003, Bauer 2007, Mackensen 2013) (Fig. 3).

TAXONOMY, IDENTIFICATION, AND DISTRIBUTION

Spondylids are members of the family Spondylidae (J. E. Gray, 1826); order Pectinoidea (Rafinesque, 1815); subclass Pteriomorphia (Beurlen, 1944) within the class Bivalvia (Linnaeus, 1758). In spite of being an economically important group of bivalve molluscs, the taxonomy of Spondylidae has been chaotic since the mid-1990s. Although the genus is not exceedingly diverse in the eastern Pacific Ocean, the taxonomic and biological literature has been exceedingly disparate in the use of names for a given species. In the studies of Skoglund and Mulliner (1996) and Coan and Valentich-Scott (2012), members of this family have been well documented, as well as in more general works (Keen 1971, Lamprell 2006, Huber 2010). Coan and Valentich-Scott (2008) and Huber (2009) recognized previously misunderstood *Spondylus* names in the Panamic Province [coastal area of the Tropical Eastern Pacific Ocean, from Magdalena Bay on Baja California (24.8° N) to Punta Aguja, Peru (5.9° S) Robertson and Cramer (2009) and Coan and Valentich-Scott 2012] leading to significant name changes among the common species in the region. These newly applied names have been embraced by some (Coan & Valentich-Scott 2012, Mackensen et al. 2012), but overlooked by others (Martínez-Tovar 2010, Cota-Hernández 2011).

A diagnostic characteristic for each species and an explanation of the current taxonomy is provided. Detailed descriptions of each species are modified from Coan and Valentich-Scott (2012).

Description of Shell Characteristics

Identification of *Spondylus* shells requires an understanding of a few specific terms, (Fig. 4A–D. Various types of spines are highlighted, including broad, spathate spines (shovel like) and fine interstitial spines (Fig. 4A) that are in the space between the major spines, and needle-like spines (Fig. 4B).

The left/right orientation of a *Spondylus* shell is not immediately apparent. The left valve is almost always the upper valve. The adductor muscle scar is mostly posterior of the midline of the shell (Fig. 4C). Thus, the left valve has the adductor muscle scar mostly to the left of the midline, and the right valve has a scar mostly to the right of the midline.

The amount of shell attachment to the substratum can be very diagnostic. Some species are free living or only have a slight area of attachment on the right valve, whereas others have extensive areas of attachment.

Figure 3. Current symbolism of spondylids in the Province of Santa Elena, Ecuador.

Internal shell characteristics are most helpful in separating these challenging species. The size and color of the hinge teeth in the left valve (upper valve) is very important (Fig. 4C and D). Similarly, the marginal color band around the circumference of the inner margin of the shell (Fig. 4C and D) is helpful in separating some species.

Few shell characteristics are absolute in a single species. For instance, there are some specimens of *Spondylus leucacanthus* that have a color band around the entire shell margin,
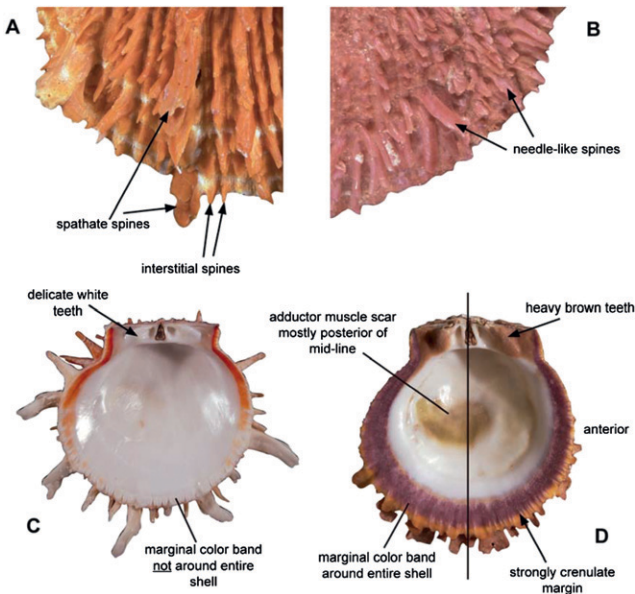

Figure 4. Shell characteristics of *Spondylus*. (A) Spathate (shovel-like) and interstitial spines, (B) needle-like spines, (C) white hinge and incomplete marginal color band, and (D) brown hinge and complete marginal color band, adductor muscle scar mostly of midline.

instead of the more common partial color band. Each specimen must be examined for all characteristics to form an accurate identification.

Key to the Eastern Pacific Spondylids

1a. Attachment area of right (bottom) valve absent or small ……………………………………………………...2
1b. Attachment area of right valve extensive…………….……3
2a. Left valve hinge teeth white; spines wide, long…………… ………....................................*Spondylus leucacanthus*
2b. Left valve hinge teeth brown; spines of medium length, spathate ……......................................*Spondylus crassisquama*
2c. Hinge teeth light brown to white; spines needle-like……… ……...*Spondylus gloriosus* (in part)
3a. Hinge teeth large, brown; spines short, spathate………… ……………………...........................*Spondylus limbatus*
3b. Hinge teeth light brown to white; spines needle-like……… ……...*Spondylus gloriosus* (in part)

Spondylus crassisquama

[Synonyms: *Spondylus princeps* Broderip, 1833: 4, not Schreibers, 1793; *Spondylus dubius* Broderip, 1833: 4; *Spondylus basilicus* Reeve, 1856: pl. 11; *Spondylus princeps unicolor* G. B. Sowerby II, of authors, not *Spondylus unicolor* G. B. Sowerby II, 1847, and *Spondylus pictorum* "Chemnitz," of authors, not Schreibers, 1793, ex Chemnitz manuscript] (Fig. 5A–C).

Diagnosis:

Hinge teeth in left valve brown; inner color band usually around entire margin; primary spines spathate with many interstitial rows; attachment area of right valve small. Description: left valve with six primary rows of spathate spines;
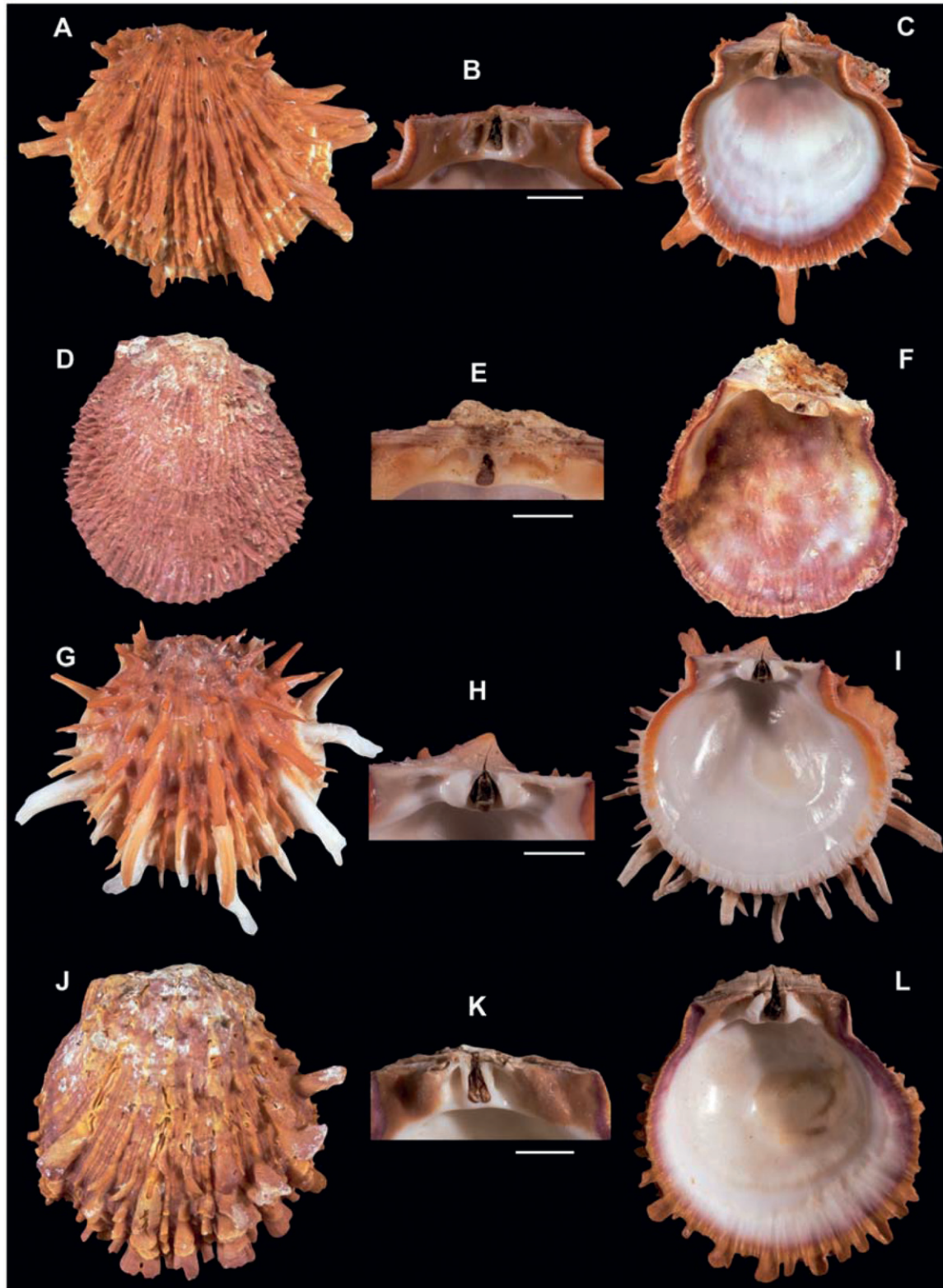
Figure 5. *Spondylus* species of the eastern Pacific. *Spondylus crassisquama*, México, Baja California, Isla Danzante, 13–32 m depth. SBMNH 83225, length 113 mm, height 117 mm. (A) Exterior left valve, (B) hinge of left valve, and (C) interior of right valve. *Spondylus gloriosus*, Costa Rica, Puntarenas, Isla del Coco, 10–25 m depth. SBMNH 359609, length 47 mm, height 54 mm. (D) Exterior left valve, (E) hinge of left valve, and (F) interior of right valve. *Spondylus leucacanthus*, México, Baja California Sur, Loreto, 30–45 m depth. SBMNH 359622, length 91 mm, height 85 mm. (G) Exterior left valve, (H) hinge of left valve, and (I) interior of right valve. *Spondylus limbatus*, México, Baja California Sur, Playa Santispac, depth unknown. SBMNH 138092, length 142 mm, height 153 mm (J) exterior left valve, (K) hinge of left valve, and (L) interior of right valve. Scale bar = 1 cm.

1–6 rows of short, usually pointed interstitial spines on distinct radial ribs; right valve with frilly commarginal ribs near attachment area, unattached area with spathate spines; attachment area small; exterior color orange, red, or purple, commonly dusty rose and purple with orange spines; color rarely white; interior margin with broad band matching exterior color; hinge teeth in left valve brown, diagonal to perpendicular to hinge line; adductor muscle scar shallow; interior margin with numerous fine to coarse crenulations and length up to 145 mm.

Distribution:

Isla Cedros, Pacific Coast of Baja California (28.2° N), into the Golfo de California as far north as Bahía de Los Ángeles, Baja California (28.9° N), and Bahía San Carlos, Sonora (27.9° N), México, to Isla la Plata, Manabí, Ecuador (1.3° S) (Santa Barbara Museum of Natural History—SBMNH, British Museum of Natural History); a few records from near Chiclayo, Lambayeque, Perú (6.7° S), and L'Île Clipperton, France; occurring in depths from 5 to 90 m.

Remarks:

This species has largely been known as *Spondylus princeps* in the taxonomic and biological literature prior to 2009. Huber (2009) details finding a type specimen of *Spondylus crassisquama* in the Musee d'Histoire Naturelle, Geneva, Switzerland. This specimen was mistakenly labeled from the Indian Ocean, but it was quickly understood to be from the Panamic Province, and the type locality was changed to Ecuador (Huber 2009). Given the ''Principle of Priority'' in the International Code of Zoological Nomenclature (http://iczn.org/iczn/index.jsp), the earlier name, *S. crassisquama* as proposed by Lamarck in 1819, should be used upon the later name of *S. princeps* Broderip 1833.

Spondylus gloriosus

[Synonyms: *Spondylus nicobaricus* Schreibers, of authors, not Schreibers, 1793; *Spondylus tenebrosus* Reeve, of authors, not Reeve, 1856, and *Spondylus linguaefelis* G. B. Sowerby II, of authors, not G. B. Sowerby II, 1847] (Fig. 5D–F).

Diagnosis:

Hinge teeth of both valves light brown; inner color band usually around entire margin; spines numerous and needle like; attachment area of the right valve from small to very large.

Description:

Left valve (upper) with many rows of narrow, needle-like spines; right valve with large lamellar ruffles and sharp spines; right valve attachment area from small to very large; exterior color dusty rose to orange, some small specimens with maculations of yellow or orange on right valve; interior marginal band matching exterior color; hinge with pale brown color; left valve with teeth parallel to hinge line; small specimens with bifid teeth in right valve; adductor muscle scar shallow, with slight ventral callus; interior margin with numerous fine crenulations and length up to 130 mm.

Distribution:

Mostly distributed on the offshore islands of the Panamic Province: Roca Partida and others of the Islas Revillagigedo, México (19.0° N); Isla del Coco, Costa Rica; L'Île Clipperton, France; Isla Jicarita, Panamá (7.2° N); Isla de Malpelo, Colombia; Isla San Salvador and Isla Pinta (0.6° S), Islas Galápagos, Ecuador; also in the western Indo-Pacific to Hawaii; occurring in depths from 4 to 80 m.

Remarks:

In the eastern Pacific, this fine-spined species has been misreported as *Spondylus tenebrosus* Reeve 1856, and *Spondylus linguaefelis* G. B. Sowerby II, 1847 (Huber 2009).

Spondylus leucacanthus

[Synonyms: *Spondylus ursipes* S. S. Berry, 1959: 107; *Spondylus pictorum* ''Chemnitz,'' of authors, not *S. pictorum* Schreibers, 1793, ex Chemnitz manuscript; *Spondylus princeps* Broderip, of authors, not Broderip, 1833; *S. victoriae* G. B. Sowerby II, of authors, not G. B. Sowerby II, 1859] (Fig. 5G–I).

Diagnosis:

Hinge teeth in left valve white; inner color band usually only near the hinge and beaks, only rarely around entire margin; primary spines long, straight, with many interstitial rows; without attachment area on right valve, or only very small attachment.

Description:

Left valve with six primary rows of long, straight, narrow spines; 1–5 rows of interstitial spines between the primary rows; right valve with frilly commarginal ribs around the small attachment area; exterior color white, orange, or coral, more uncommonly red-brown or peach; internal marginal color band usually near hinge only, occasionally around entire margin; hinge teeth white, diagonal to hinge line in left valve (except in large and old specimens, that have more perpendicular teeth); adductor muscle scar shallow to deep; internal marginal crenulations coarse and length up to 156 mm.

Distribution:

Isla Cedros, Pacific Coast of Baja California (28.2° N), into the Gulf of California as far north as Bahía de Los Ángeles, Baja California (28.9° N), and Isla Tiburón, Sonora (28.7° N), México, to Isla la Plata, Manabí, Ecuador (1.3° S); occurring at depths from 10 to 90 m.

Spondylus limbatus

[Synonyms: *Spondylus calcifer* Carpenter, 1857: 152; *Spondylus radula* Reeve, 1856: pl. 4, not Lamarck, 1806; *Spondylus smithi* Fulton, 1915: 357, new name for *Spondylus radula* Reeve, not Lamarck and *Spondylus lamarckii* Chenu (as ''Hanley manuscript'') of authors, not Chenu, 1845] (Fig. 5J–L).

Diagnosis:

Hinge teeth in left valve brown; inner color band usually around entire margin; spines irregular, spathate; some large

specimens without spines, some small specimens are more spiny; attachment area of right valve moderate to large.

Description:

Left valve with irregular spathate spines. These spines may be reduced to coarse threads on some specimens; young specimens with many rows of short, spathate spines in major and minor rows; some large, thick specimens with only traces of spines; spines on new growth of larger specimens short, broad; right valve with sharp spines on unattached portion; right valve with moderate to wide attachment area, fitting to substratum; exterior color red-purple, yellow-orange, never white; interior marginal color band matching exterior color; hinge teeth heavy, those of left valve brown, teeth diagonal to hinge line and length to 250 mm.

Distribution:

Rocas Alijos, Pacific Coast of Baja California Sur (25.0° N), into the Gulf of California as far north as near its head at Bahía la Choya, Sonora (31.4° N), México, to Caleta Mero, Tumbes, Perú (3.9° S); occurring in depths from the low intertidal zone to 55 m.

Remarks:

As pointed out by Coan and Valentich-Scott (2008), the well-known *Spondylus calcifer* is now regarded as a synonym of the earlier named *Spondylus limbatus*.

BIOLOGY AND ECOLOGY

The rock scallop *Spondylus limbatus* (also commonly referred to as "spiny oyster" or "donkey thorny oyster") has received significantly more attention than its congeneric species, *Spondylus crassisquama*, *Spondylus leucacanthus*, and *Spondylus gloriosus*. In this section, knowledge about biology, ecology, and population structure, mostly concerning *S. limbatus*, is reviewed, and complemented with information about the other lesser species.

Adults of *Spondylus limbatus* are sessile and inhabit rocky reef areas from the intertidal to 55 m in depth (Poutiers 1995). In *S. limbatus*, shell growth rings (validated by oxygen isotope analysis) are formed annually (Cudney-Bueno & Rowell 2008). Annual growth rings (white bands) are readable in cross section of the shell, hinge teeth, and umbo. Reading in cross-section shell can be misleading in older individuals because of damage of the shell caused by burrowing organisms (Cudney-Bueno & Rowell 2008, Cota-Hernández 2011). White bands, corresponding to periods of slow growth, are formed during winter and spring months, whereas opaque bands are formed when shell growth accelerates during warmer months (Cudney-Bueno & Rowell 2008, Cota-Hernández 2011). Maximum age estimated from growth rings is 14 y (hinge teeth) and 10–12 y (cross-section shell) for populations of the Gulf of California (Cudney-Bueno & Rowell 2008, Cota-Hernández 2011) and 22 y for individuals of Ayangue, Ecuador (Mackensen 2013). Estimated parameter values of the von Bertalanffy model (H^∞ and k) have been estimated for a population in the Gulf of California. The estimated asymptotic shell height (H^∞) is 180.7 mm, and the growth rate (k) is 0.15/y (Cota-Hernández 2011). Adults may attain 250 mm in shell height (Poutiers 1995, Skoglund & Mulliner 1996).

The rock scallop is a gonochoric species with an estimated sex ratio of 1:1 (Villalejo-Fuerte et al. 2002, Cudney-Bueno & Rowell 2008), but simultaneous hermaphroditism may occur in a small fraction of the population (Cota-Hernández 2011, Mackensen et al. 2011). First spawning occurs at a size of 86–113 mm in shell height (Villalejo-Fuerte et al. 2002), estimated to be between 2.5 and 4 y of age (Cudney-Bueno & Rowell 2008). In the Gulf of California, Mexico, the spawning events occur from June to October when seawater temperature is at least 29°C. Spawning is followed by a protracted period of gonad recovery during autumn and winter seasons (Villalejo-Fuerte et al. 2002, Cudney-Bueno & Rowell 2008). In temperate waters of Ecuador, spawning takes place throughout the year with a peak in October–December when the temperature is low and primary productivity is high (Mackensen et al. 2011). Energetic resources for gonadal maturation are allocated on the adductor muscle throughout winter and spring (Villalejo-Fuerte et al. 2002, Cudney-Bueno & Rowell 2008). This is a broadcast spawner and its early life cycle was described under laboratory conditions (Soria et al. 2010, Loor et al. 2016). The fecundity, estimated by counting oocytes (60 μm) after spawning induction, varies between 1.5 and 72×10^6 oocytes, depending on size and reproductive condition of the individual (Soria et al. 2010). The first polar body appears 10–15 min postfertilization of oocytes, and embryogenesis takes place to trochophore (80 μm) 18 h afterward. At 26 h, a calcified D-shaped veliger larva with the prodissoconch-I is completely developed (100 μm in shell length). A provinculum is highly noticeable at 3-day-old larvae sizing 120 μm, when the veliger larvae turned markedly umboned (150 μm/day 8). The eyespots are formed when the larvae reach 165 μm (day 10) and crawling pediveligers with a double ring on the shell edges appear on day 12 in larger sized larvae (185 μm), when the pelagic phase is finished (Soria et al. 2010, Loor et al. 2016) (Fig. 6). Metamorphosis occurs during the subsequent days since postlarvae are observed on day 16 (>190 μm). During these processes, the byssal attachment was not observed. Postlarval stages may remain as free-living benthonic organism until final cementation on hard substrates when shell size is 2–3 mm (2–3 mo). The cemented postlarvae continued their growing, reaching a 14 mm after 6 mo from the postlarvae settlement (Loor et al. 2016) (Fig. 7).

In the congeneric species *Spondylus leucacanthus*, from the Gulf of California, spawning occurs during early autumn followed by rapid phagocytosis of the residual material and an inactive period that last over the entire winter (Villalejo-Fuerte & García-Domínguez 1998, Rodríguez-Astudillo et al. 2002). Energy for reproductive cycle seems to come directly from feeding and from reserves stored in the adductor muscle, digestive gland, and gonads (Rodríguez-Astudillo et al. 2002).

Off the coast of Ecuador, 71 epibiont and endobiont taxa were identified on *Spondylus crassisquama* shells, representing 10 phyla and 2 divisions. Epibionts includes bivalves, polychaete worms, ascidians, echinoderms, cirripeds, bryozoans, cnidarians, sponges, and algae among other species. The substrate provided by *S. crassisquama* contributes to increasing benthic species biodiversity (Mackensen et al. 2012).

Spondylid populations are structured in metapopulations where subpopulations of sessile juveniles and adults are connected exclusively through larval dispersal during the pelagic stage. Our understanding of metapopulation dynamics has improved recently by combining coupled biological oceanographic
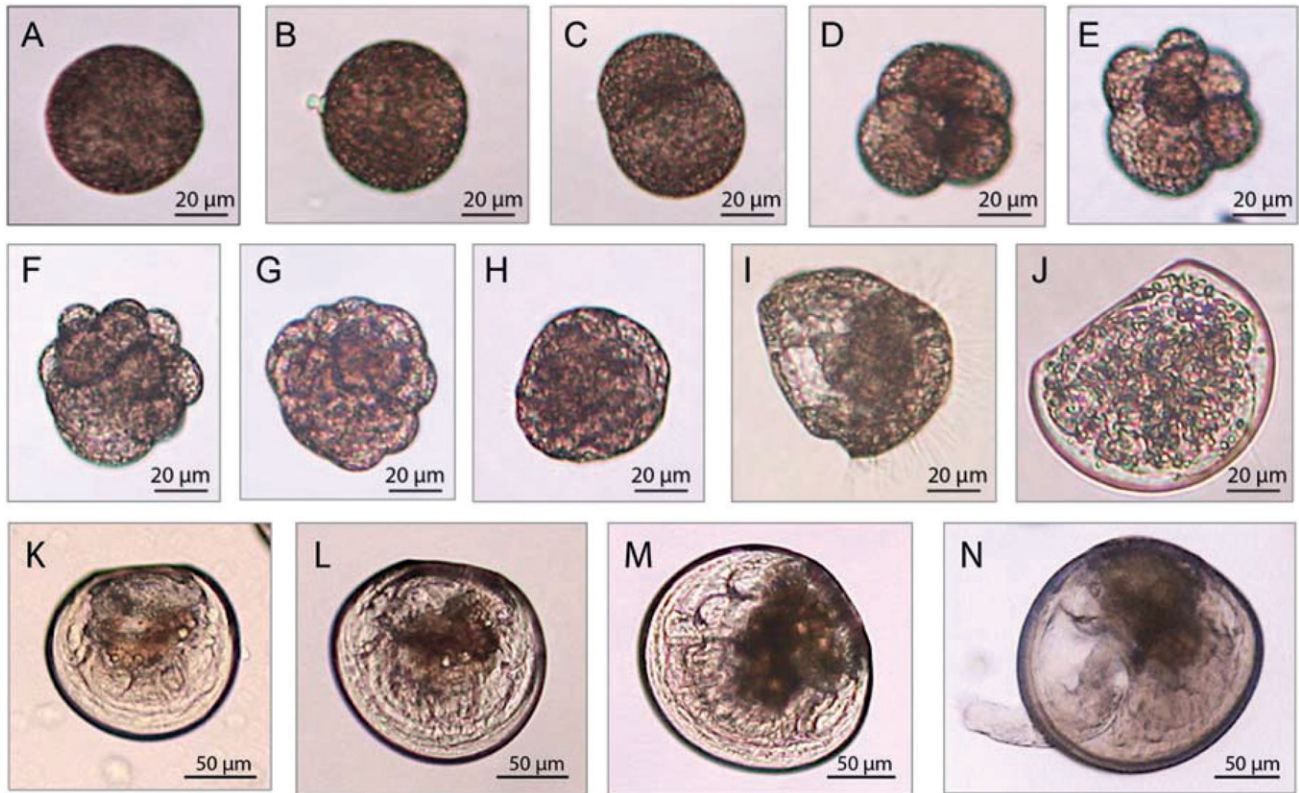
Figure 6. Embryogenesis and larval stages of *Spondylus limbatus*: (A) oocyte, (B) oocyte and polar bodies, (C) first cleavage, (D) second cleavage, (E) third cleavage, (F) fourth cleavage, (G) morula, (H) ciliated gastrula, (I) trochophore larva, (J) straight-hinge D-larva, (K) veliger, (L) umboned veliger, (M) eyed veliger, (N) pediveliger.

models (CBOM) and population genetic studies. Coupled biological oceanographic models describe patterns of ocean circulation and transport of particles (virtual larvae) during the planktonic phase to generate connectivity hypotheses about the direction, scale, and magnitude of larval dispersal between sites. Genetic studies of individuals collected at various field sites and screened at multiple polymorphic genetic markers (e.g., microsatellites, mitochondrial DNA) allow to measures empirically the observed levels of gene flow and genetic structure between sites (Soria et al. 2012). The Gulf of California, Mexico, is a narrow (~100 km), long (~1,300 km), and deep (>3,000 m) gulf, has strong (e.g., 30–70 cm/s), unidirectional currents driven by oceanic gyres that consistently change direction twice a year (Marinone 2012). During the spawning period of *Spondylus limbatus* (summer), larval dispersal in the northern Gulf of California is not symmetrical but follows a cyclonic gyre along the mainland coast (Fig. 8A), where larvae are transported downstream 82–102 km on average (Soria et al. 2012). In this unidirectional system, larval sources are located upstream relative to the predominant flow (e.g., sites 1–3), and larval sinks are located downstream (e.g., sites 9–11). A consequence of such asymmetrical arrangement is that geographic distance is a poor predictor of genetic connectivity between populations. For example, levels of genetic structure from 8 microsatellite loci (Munguía-Vega et al. 2010, Soria et al. 2012) using the standardized genetic differentiation measure D (Jost 2008) among 11 subpopulations in the NGC (Fig. 8A) are not correlated with geographic distance ($R^2 = 0.035$, $P = 0.991$). In contrast to geographic distance, graph distance in a larval connectivity network (Fig. 8A), predicts about half of the variation in pairwise comparisons of microsatellite genetic structure between *S. limbatus* populations (Fig. 8B) as suggested by a CBOM (Soria et al. 2012) and considering the strength and direction of the connectivity links (Munguia-Vega et al. 2014). By taking into account ocean currents, the spawning period, and the planktonic larval duration, those sites farther apart oceanographically according to the direction of the predominant flow (e.g., sites 1–3 versus 9–11) show larger levels of population structure.

Metapopulation dynamics are driven by ocean currents and also influence levels of genetic diversity found within *Spondylus limbatus* populations. By considering larval dispersal among sites, downstream sink sites showing low centrality (e.g., sites 9–11) show higher levels of allelic diversity because they accumulate larvae and genetic variants from multiple upstream larval sources (Kool et al. 2011). Eigen vector centrality, a measure of the stepping-stone connections between sites calculated from a larval connectivity network derived from a CBOM (Fig. 8A), explains about half of the differences observed in the number of microsatellite alleles within each site (corrected by difference in sample sizes among sites, i.e., effective alleles) (Fig. 8C). In conclusion, seemingly chaotic patterns of subtle genetic structure among *S. limbatus* subpopulations (e.g., global $F_{ST} = 0.006$, $P = 0.001$ for nuclear microsatellites; global $\Phi st = 0.006$, $P = 0.139$ for 583 base pairs from the mitochondrial DNA gene COI) and small variations in levels of genetic diversity (range of effective alleles 3.893–4.828 for microsatellites; 0.1% intraspecific sequence divergence for COI) (Soria et al. 2012,
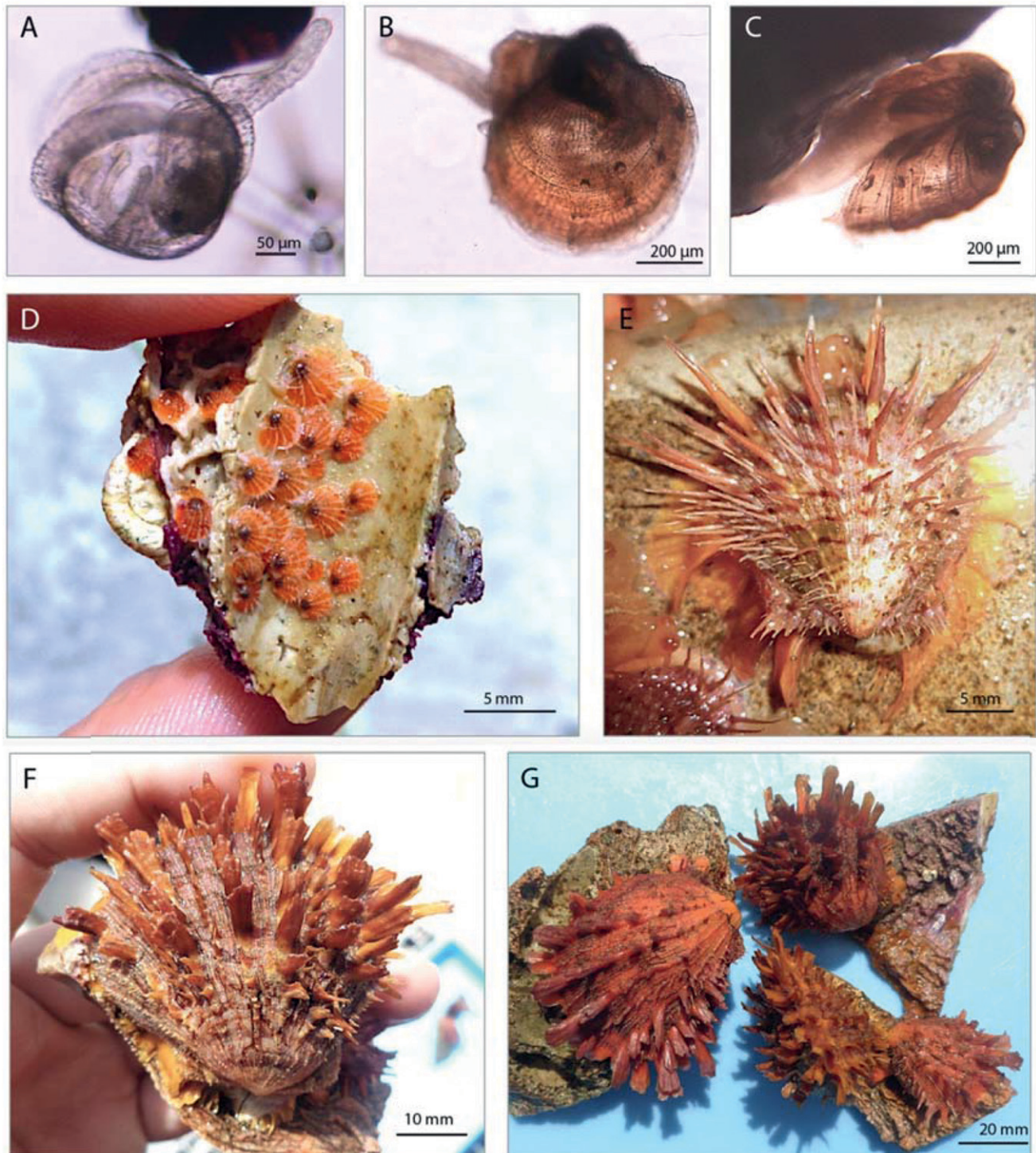
Figure 7. Postlarval and juveniles *Spondylus limbatus*: **(A)** unattached postlarva, **(B)** unattached juvenile, **(C)** unattached juvenile on hard substrate, **(D–G)** attached juveniles.

Medina-Espinoza 2013) are nevertheless the result of patterns of larval dispersal.

FISHERIES

Spondylid resource exploitation in the eastern Pacific has a long fishing tradition. Their catch goes back to the years 2600 to 2000 BC (Shady 2005); however, after the countries of the tropical and subtropical Pacific became independent from the Spaniard domain, spondylids lost the economic, political, and religious value, and their extraction became sporadic, mainly for local consumption. Their exploitation was limited to relatively shallow waters, but could be extended to some deeper water areas with wooden bells and diving suits. In the late 1970s
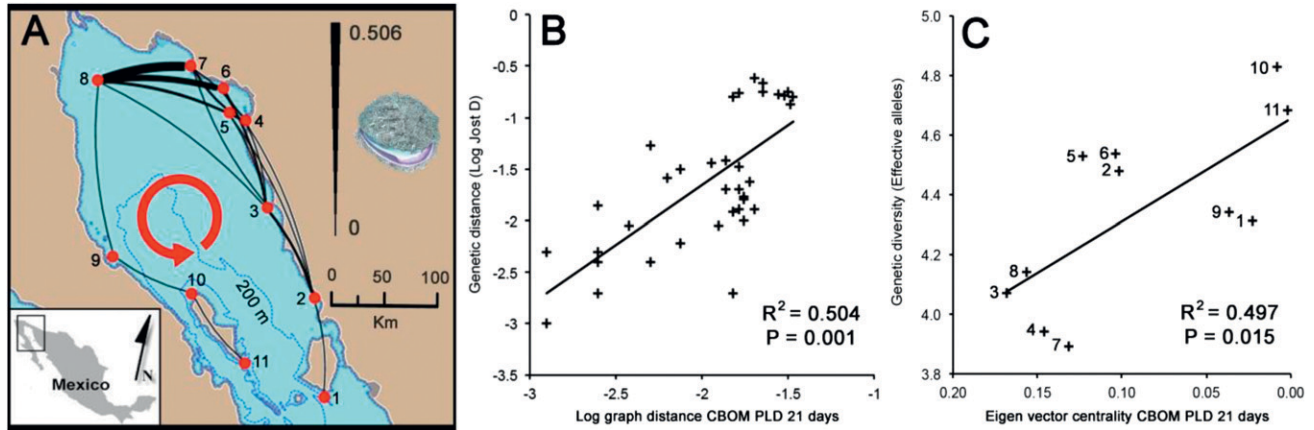
Figure 8. (A) Map showing the location of 11 populations of *Spondylus limbatus* in the Northern Gulf of California, Mexico, and a larval connectivity spatial network showing the probability of larval dispersal (links) between rocky reef sites (nodes) as suggested by a CBOM (Soria et al. 2012) for a planktonic larval duration of 21 days. The weights of the links represent probability according to the scale on the upper right. The 200-m isobath is shown. Note that all links are directed, asymmetric, and follow a cyclonic gyre (counter clockwise, indicated by a curved arrow in the center). **(B)** Scatter plot between log graph distances estimated from the larval connectivity network and empirical pairwise genetic structure measured by log Jost D distance based on eight microsatellite loci. **(C)** Scatter plot between the Eigen vector centrality of each site calculated from the larval connectivity network and empirical levels of genetic diversity measured by the average number of effective alleles at eight microsatellite loci. Numbers to the left of each data point refer to sites shown in A.

and early 1980s spondylids became again objects of direct exploitation, when the catch was extended to deeper areas, and for longer periods, prompted by the use of "SCUBA" and "hookah" (narghile) systems. Currently, although exploitation of spondylid shells is still carried out in some places, for the manufacture of jewelry, their main use is for consumption of the adductor muscle or "callus" (Fig. 9) as a foodstuff with high commercial value.

Spondylids are captured from the Gulf of California along the eastern central Pacific to the seashores of southern Peru. The activities of the artisanal fisheries sector have gone under little or no management control and are mostly harvested under an open access regimen. Fisheries data are limited to specific regions, particularly the Gulf of California, in Mexico (Baqueiro-Cárdenas et al. 1982, Cudney-Bueno & Rowell 2008) and the coasts of the provinces of Santa Elena, Manabi, and Esmeraldas, in Ecuador (Mackensen et al. 2011).

Figure 9. Adductor muscle or "callus" from *Spondylus limbatus*.

The cause of the renewed demand of spondylids in Ecuador is unknown, although after being practically forgotten for a long time, an American archaeologist was responsible for "restoring" the traditional use of *Spondylus* species, according to reports of local divers in Salango, Manabi Province (Bauer & Lunniss 2010, Mackensen et al. 2011). In the 1980s, dishes based on spondylids already appeared in the menus of restaurants in the province of Manabi. Its value was rediscovered giving it a reputation as a "delicacy," possibly as a result of its colloquial name "food of the gods" because of the ancestral use that was given in ceremonial offerings (Mackensen et al. 2011). Before long, *Spondylus* exploitation accelerated with drastic consequences to their population's stocks. In the province of Manabi, catches of 150 kg of adductor muscles by 3–4 divers were common in 1990. By 2002, a similar effort produced a maximum of 5 kg (Fabara 2003). A similar decline was observed 5–8 y later, when the fishery was expanded to Esmeraldas province (Northern Ecuador), given the demand for spondylids, not only for consumption but also for the production of jewelry. For example, in 2000, commercial divers began collecting shells of *Spondylus crassisquama* in Esmeraldas, largely caused by the demand of Peruvian artisans who reported that catches in Peru had already caused a collapse of local fisheries. By that period, a diver could collect 300 individuals in 1 day. Only 7 y later, the catch was not profitable because of their low abundance (Mackensen et al. 2011). Unfortunately, in Ecuador, no formal records of catches were taken, but it was evident that spondylids had been under high levels of exploitation that threatened the viability of the fishery and the sustainability of the species.

The evolution of the spondylid fishery in the Mexican Pacific Coast has followed a similar pattern to that in Ecuador. Both *Spondylus limbatus* and *Spondylus crassisquama* have been collected for hundreds of years. It was not until the end of the 1970s and early 1980s that an intensive fishing started, given the local and regional demand of the adductor muscle. This, in turn, coincides with a marked increase in commercial diving activities

in Mexico, primarily using "hookah-"type diving. Most of this effort focused on the extraction of *S. limbatus* in the northern Gulf of California. In this region, the fishing of spondylids mainly started in the community of Bahia de Kino, where shrimp boats (during the closure of shrimp season) made trips to explore the Islands of Las Cinturas and La Encantada. Subsequent to these trips, some large *Spondylus* beds, along with other molluscs, were discovered in rocky reefs surrounding the upper Gulf of California, next to the town of Puerto Peñasco (Cudney-Bueno 2000). Although the extensive reefs in this region represented an incentive for the development of diving activities, strong tidal currents and poor visibility limited its exploitation. Few divers settled in the area of Puerto Peñasco, and many of the divers who arrived in the 1970s to 1980s or their sons, are still collecting spondylids in the region (Cudney-Bueno 2007).

Currently, spondylid extraction uses "hookah" systems made of air compressors with 100-m-long hoses, with an adapted air regulator mouthpiece. A fishing trip normally involves two divers and a deckhand (Cudney-Bueno 2007). The fishing is usually performed at depths of 10–20 m, although the extraction can be performed up to 30–45 m. This has been more common as the resource has been overexploited in the nearshore beds.

The few population studies available have reported low densities for spondylids in Mexico; in Baja California Sur, for example, average individual densities of $1/100 \text{ m}^2$ of *Spondylus limbatus* were estimated (Villalejo-Fuerte et al. 2002). In the upper Gulf of California, populations appear to be healthier than in other regions of the Gulf and the Mexican Pacific, in general, reaching densities of up to 70–80 individuals/100 m^2. On the other, areas near the coast that once were considered rich for collecting spondylids have been virtually forgotten by the near absence of the resource, driving the extraction of spondylids to more remote and deeper areas (Cudney-Bueno 2007).

AQUACULTURE

Experimental studies were mainly focused on broodstock maintenance and spawning induction, larvae culture, and juvenile production under laboratory conditions, and natural spat collection. Although intermediate and grow-out phases have not been scaled up yet, in this section, knowledge about species of *Spondylus* and experimental results that may have significance for the development of aquaculture and repopulation initiatives of spondylids is reviewed.

Natural Spat Collection

The spat of *Spondylus limbatus* and *Spondylus crassisquama* can be obtained using polyethylene monofilament and Netlon nets, though reported yields of spat per collector are low (few individuals per collector) (Ruiz-Verdugo & Cáceres-Martínez 1990, Soria 2010, Soria et al. 2012). Postlarval stages are cemented to hard substrates making natural collection of spat or juveniles impractical.

Parental Conditioning and Spawning Induction

Reproductive animals can be dislodged from the rocks by SCUBA diving and transported in insulated boxes. The dislodging of the animal should be done with caution to avoid fractures of the cemented shell. Usually, visual inspection of gonad stages, as it is in most pectinid species, is impractical in spondylids because the narrowness of the opening of the shells. Spondylids are generally highly overloaded with epibionts and shell-boring organisms. Removal of such organisms is laborious, time consuming, and unnecessary. Adult animals can be maintained in flow-through or batch systems during the acclimation, reproductive conditioning, and spawning induction process (Soria et al. 2010, Loor et al. 2016).

In general, spondylids are large individuals (*ca*. 200 mm in shell length), in particular *Spondylus limbatus*, and thus require a proper design of tank capacity to allow good maintenance of the animals. Spondylids can withstand maintenance and husbandry without mortality. These animals have been reared at density of one adult per 25 l in a flow-through system with an exchange rate of 2 l/min (partial exchange of 6.4 times per day) (Soria et al. 2010) and fed on *Tisochrysis lutea* (T-ISO) and *Chaetoceros calcitrans* (clone C-CAL) at an average algae concentration of 150 cells/ml (ratio: 1:1). Loor et al. (2016) reared 1 adult per 100 l with a 25% of daily water exchange and fed on an algal mixture of *Chaetoceros gracilis* and *T. lutea* (ratio: 2:1 in cells number) provided daily at a mass dry algal weight equivalent to a 5% of broodstock dry meat weight in tanks.

Mature individuals responded positively to spawning induction by means of thermal shocks (thermal range: 20–30°C) (Soria et al. 2010), combination of intramuscular serotonin injection (a neurotransmitter), and warm-water thermal shocks (26–35°C) (Parnell 2002), and to other stimulus such as stripping of gonads, the addition of food or gametes, and 30 min of desiccation (Loor et al. 2016). Spawning response depends mainly on the gonadal development. Usually, individuals spawn shortly after induction, frequently within 1–2 h.

Larval Culture and Spat Production

A ratio of 10 sperm to 1 oocyte yielded >95% success of fertilization rate (Loor et al. 2016). Fertilized eggs had a diameter of 60 μm. First straight-hinge larvae can be observed within 24 h after fertilization (Soria et al. 2010, Loor et al. 2016) (Table 1). Soria et al. (2010) reared *Spondylus limbatus* larvae in a 15-l batch system at a density of 3 larvae/ml at 30°C, and renewed 100% of the water culture every 48 h. Larvae grew faster (12.4 μm/day) when fed a combination (1:1) of *Tisochrysis lutea* and *Chaetoceros calcitrans* at a concentration of 50 cells/μl. At lower rearing temperatures, minor larval growth rates could be obtained (Table 2). In about 2 wk, larvae of *S. limbatus* and *Spondylus gloriosus* may begin the settlement, though plantigrade stages can be observed up to 3 mo after fertilization (Table 1) (Parnell 2002, Soria et al. 2010, Loor et al. 2016). The size of the pediveliger larvae at settlement was 185–190 μm.

Under laboratory conditions, pediveliger larvae settled on scallop shell fragments. The capacity to form a byssus during settlement was not observed suggesting that the byssus production may be absent during this stage. Postsettled organisms are able to remain unattached for at least 3 mo and perform crawling movements before cementation (Parnell 2002, Loor et al. 2016) (Table 2). The cemented postlarvae continue growing, reaching a mean shell length of 6 mm after 3 mo and 14 mm after 6 mo (Loor et al. 2016).

TABLE 1.

Summary of time to appear the spondylids larval stages reared in batch cultures.

	Species		
Larvae stage	*Spondylus gloriosus**	*Spondylus limbatus*†	*S. limbatus*‡
Throchophore	11 h	7 h	9 h
D-larvae	21 h	17 h	26 h
Pediveliger	12 days	14 days	12 days
Postlarvae	21 days	–	16 days
Plantigrade	2 mo	–	3 mo

Source: * Parnell (2002), † Soria et al. (2010) and ‡ Loor et al. (2016).

Preliminary studies with laboratory-produced juveniles of *Spondylus limbatus* (anterior–posterior shell length = 12.7 ± 3.13 mm) transferred to the sea and cultivated in plastic cages at El Pelado, Ecuador, showed a high growth rate reaching 44 mm after in almost a year (Fig. 10), but low survival rate (70%). Density of animals was 50 individuals/m². On the other, juveniles reared under laboratory nursery conditions, fed on mix diet of *Chaetoceros calcitrans*–*Tisochrysis lutea* (160,000 cells/ml/day) and kept at the same density conditions reached a lower shell size (30 mm) but with a higher survival rate (86%). After 1.5–2 y, juveniles of *S. limbatus* can reach first maturity in culture condition in the sea (70–80 mm).

MANAGEMENT AND CONSERVATION

Spondylid species have been overexploited throughout their geographic ranges, although most fishing activities have been done without formal fishing permits and, in general, there are no reliable records of fishery landings (Cudney-Bueno & Turk-Boyer 1998). Moreover, spondylids rarely appear in official records because their landings are reported along with catches of other bivalve species (Fig. 11), thus they are frequently misreported (Moreno et al. 2008). The local depletion of *Spondylus* species affects also benthic biodiversity given the relevance of spondylids species as substratum for both epibionts and shell-drilling endobiont species (Mackensen et al. 2012). Fishing of spondylids is banned in most countries; however, it can be legally fished under special permits, and there are few cases where total allowable catches are estimated. Prohibition of fishing is also poorly enforced generally, whereas, conservation initiatives are rare.

In Mexico and Ecuador, *Spondylus limbatus* is listed under a threatened status. In Mexico, the fishery is regulated by the Secretary of the Environment through the issue of special permit with strict restrictions (SEMARNAT 2001). The fishing of species under special protection is managed independently from the Secretary of Agriculture, Livestock, Rural Development, Fisheries and Food in charge of the management of most fisheries through National Commission of Aquaculture and Fishery, the fisheries authority (Cinti et al. 2014). Under this scenario, the General Division of Wildlife may grant exclusive access rights to exploit resources listed under special protection status (NOM-059-ECOL-1994) within areas designated as "predios" (short for Predios Federales Sujetos a Manejo para la Conservación y Aprovechamiento Sustentable de Vida Silvestre) (SEMARNAT 2001, Orensanz & Seijo 2012, Cinti

TABLE 2.

Summary of *Spondylus* batch larvae culture, including culture conditions and biological parameters.

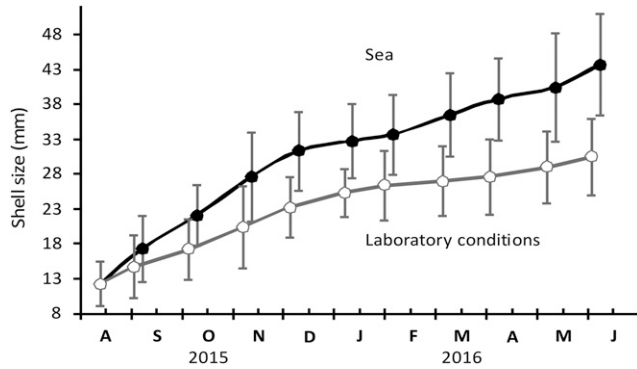| Species	Density (larvae/ml)	Temperature (°C) salinity (g/l)	Algal species (ratio)	Algae ration (cell/µl)	Growth rate (µm/day)	Pediveliger size (mean, µm)	Final survival (%)	Source
Spondylus gloriosus	0.6	22 34	*Tisochrysis lutea + Skeletonema costatum*	N/A	11.4	260	N/A	(Parnell 2002)
Spondylus limbatus	3	30 35	*T. lutea + Chaetoceros calcitrans* (1:1)	50 30 75	12.42 10.6 11.7	234.01 210.48 221.81	32.1 29.4 11.1	(Soria et al. 2010)
S. limbatus	4	25 34	*T. lutea* *Chaetoceros gracilis* *T. lutea + C. gracilis* (3:1) *T. lutea + C. gracilis* (1:1) *T. lutea + C. gracilis* (1:3)	10–40 10–40 10–40 10–40 10–40	3.12 3.19 3.67 4.73 5.5	135.5 136.5 142.2 154.1 164.0	0.7 18.8 1.1 5.4 5.7	(Loor et al. 2016)

Figure 10. Growth in anterior–posterior shell length of the *Spondylus limbatus* juveniles in baskets at El Pelado bed, Santa Elena Province, Ecuador and in the nursery laboratory conditions.

et al. 2014). Permit holders are required to prepare a regional management plan that may include a harvest season, total allowable catches, and size limits (Orensanz & Seijo 2012).

Most fishermen are not aware of the special regulations to obtain specific fishing permits for such species, making the implementation of such management strategies very problematic. In spite of this, in the northern and central region of the Gulf of California, there is one fishing cooperative from Puerto Peñasco, Sonora, which obtained fishing permits to harvest *Spondylus limbatus* in 2006 (Vásquez-Amaya 2014).

In retrospect, after the implementation of this kind of special fishing permits, there have been several achievements toward the management of the species. For the first time there are records of the fishery landing, stock assessments, and comanagement initiatives that came with the implementation of the *predio* system (Vásquez-Amaya 2014). Nevertheless, lack of government support and enforcement at local and state levels, and continuous pressure to fulfill the burden of requirements to maintain fishing permits, undermines this originally well-implemented initiative (Cudney-Bueno & Basurto 2009, Orensanz & Seijo 2012).

Along the Ecuadorian Coast, the fisheries of the several spondylids species operated under an open access regimen without formal fishing regulations. In 2009 by petition of the Salango community, Manabi Province, through its scuba

fisher's association, which has detected low densities of *Spondylus* spp., the subsecretary of fishery resources under the Ministry of Agriculture, Livestock, Aquaculture and Fisheries (MAGAP), decreed a fishing closure of *Spondylus* spp. (Acuerdo Ministerial 136). Under this decree, the harvesting, transport, trading, and consumption of these species were banned until the current state of the population was evaluated and fisheries and management information were available to elaborate sustainable fishing practices (Viceministerio de Acuacultura y Pesca 2009).

The Fishery National Institute started a research-oriented study to evaluate the resource and found an average abundance of 0.02 individuals in 100 m^2, showing no sign of stock recovery of traditional beds located in Santa Elena Province (Viceministerio de Acuacultura y Pesca 2010). Currently, the National Center of Aquaculture and Marine Research (CENAIM) of Escuela Superior Politécnica del Litoral (ESPOL), in a more exhaustive prospection in 2015 at El Pelado bed, found an average abundance of 3 individuals in 100 m^2 (Sacha Esteiner, CENAIM-ESPOL, personal communication, 2016), suggesting an incipient recovery. However, illegal fishing still persists (Fig. 12). In addition, CENAIM-ESPOL and MAGAP are developing a repopulation program of *Spondylus limbatus* based on hatchery-produced juveniles, allowing the seeding of the former natural population at El Pelado, a well-known *Spondylus* spp. bed (see Aquaculture section).

OVERVIEW AND PROSPECTS

Social and historical aspects of the species of spondylids have received much general interest from academics. In relative terms, this situation constitutes a paramount scenario in comparison with the sparse biological information. Besides the broad distribution of the species of spondylids, scarce information is available for the populations distributed along this range, in particular within the Panamic Province. In spite of the efforts in Mexico and Ecuador to study spondylids, there are no research studies or baseline information in most countries.

Figure 11. *Spondylus limbatus* specimens collected with mother-of-pearl (*Pinctada mazatlanica*) in the Gulf of California, Mexico. Photo by Richard Cudney-Bueno.
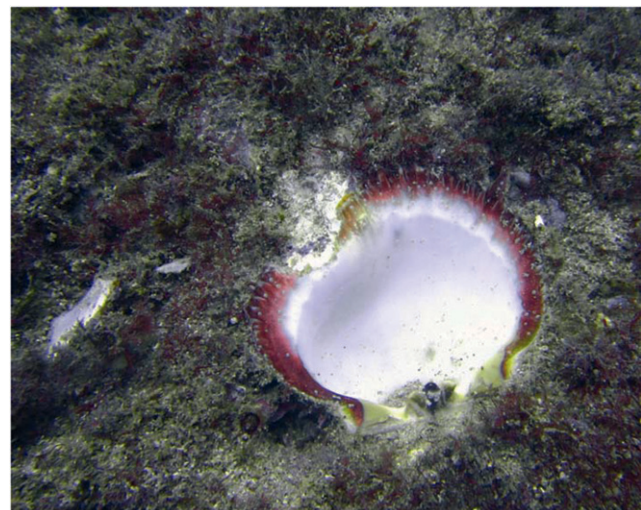

Figure 12. *Spondylus limbatus* without left shell in the El Pelado bed, Santa Elena Province, Ecuador, showing evidence of the uncontrolled poaching activities. Photo by Adrián Márquez, June 2016.

This situation undermines the management and conservation of *Spondylus* species. The *predio* system, a form of Territorial Use Privilege implemented in Mexico, served to revert the absence of information. The *predio* system give the necessary incentives, through legal instruments, to exploit the resource. Implementation of fishing and management strategies require the integration of the complex factors involved in the biological and physical environment, as well as social conditions. In this context, projections of possible studies to restore and conserve these resources are discussed.

The exploitation of most natural beds throughout the eastern Pacific has been poorly controlled and/or under an open-access system. Unfortunately, there are several pieces of information suggesting that natural stocks are not recovering to preharvest conditions. Spondylids are structured as meta-populations where discrete subpopulations of sessile individuals are connected to each other by exchange of planktonic larvae. Thus, the development of robust management and conservation tools require knowledge about the spatial and temporal dynamic of connectivity patterns, in particular, information about the potential sources of larvae that can populate a region. It is also important to develop other location-based tools that specifically acknowledge the spatial structure of benthic resources to avoid the dispensation mechanisms (such as allele effects) that might reduce the overall reproductive success.

In an exclusive manner, divers perform the fishing operation of spondylids. The use of other fishing methods seems to be impracticable given the environmental conditions where spondylids live, attached to hard substrates. Such characteristics must be capitalized in the sense that fishermen can only harvest them manually, and thus fishermen must be encouraged to participate in the monitoring and surveillance process. Similarly, the presence of spondylids in clearly defined areas could sustain a management system, as the *predio* system in Mexico, by implementing territorial use privileges. The high reproductive potential of spondylids species (e.g., *Spondylus limbatus* might spawn more than 70 million eggs), can facilitate the repopulation of exploited areas by establishing marine reserves, seasonal closures, rotation of areas and other placed-based tools aimed to protected sessile juveniles and adults.

The use of aquaculture techniques in the sense of the development of restoration and stock enhancement programs of the natural population are promising alternatives for the recovery of spondylid species. Significant success in the hatchery production of larvae and spat has been achieved recently in Mexico and particularly in Ecuador. Hatchery achievements must encourage the creation of conservation programs. For this, stock enhancement programs need to be designed carefully as to not compromise the viability or evolutionary potential of natural populations, for example, through the release of highly inbreed individuals in natural habitats.

Throughout their geographical distribution, spondylids species are considered a valuable resource in high demand. The significance of spondylids might lead to the creation of preferential markets that value the sustainability of the resource in the whole sense, as a fishing and aquaculture resource, giving them political, archeological, and social value.

Governmental or nongovernmental institutions should take actions to develop management and conservation methods and to implement restoration and stock enhancement programs for spondylids species of eastern Pacific Ocean.

ACKNOWLEDGMENTS

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