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TROPICAL AND SUBTROPICAL OSTREIDAE OF THE AMERICAN PACIFIC: TAXONOMY, BIOLOGY, ECOLOGY, AND GENETICS

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ABSTRACT Oysters have throughout history been one of the most important marine invertebrate animals used, whether as human food or as a cultural base. Today, they represent one of the most exploited natural resources, are produced by aquaculture activities, and are one of the most studied groups of shellfish. This is most evident in temperate zones, whereas studies in tropical zones have been comparatively scarce and somewhat disorganized. The present review organizes the studies of a dozen species that are grouped as oysters of the tropical and subtropical American Pacific, considering their taxonomy and identification, as well as their distribution, and establishing an identification key using the characteristics of the shell. Aspects of their biology are described, referring to general anatomy with a type species, the Cortez oyster *Crassostrea corteziensis*, as well as the life cycle, taking as reference the recent studies carried out on the rock oyster *Striostrea prismatica*. In the same way, a description of their populations and ecological interactions is provided, emphasizing the reproduction of the different species and ordering the description of the main stages in the gametogenic development of the populations in a latitudinal form. The main diseases and some uses of oysters as bioaccumulating organisms are also described, as well as phylogenetic and population genetic studies. Finally, possible future actions are discussed to provide a more comprehensive knowledge of oysters from the tropics and subtropics of the American Pacific based on the conservation and use of the resources.

KEY WORDS: oyster, bivalve, mollusc, reproduction, geographical distribution, life cycle, *Crassostrea gigas*, *Crassostrea sikamea*, *Dendostrea folium*, *Dendostrea sandvichensis*, *Undulostrea megodon*, *Saccostrea palmula*, *Ostrea angelica*, *Striostrea prismatica*, *Ostrea conchaphila*, *Crassostrea aequatorialis*, *Crassostrea columbiensis*, *Crassostrea corteziensis*

INTRODUCTION

Oysters are bivalve molluscs widely distributed globally and are considered one of the most economically important and appreciated seafoods in the world. In the tropical region of the American Pacific, they are listed as commercially important species within the invertebrates (Díaz et al. 2014, Posada et al. 2014, Ross et al. 2014). Their demand, consumption, and use today are mainly satisfied by aquaculture and are, thus, of utmost importance for the local fishing economies (Sevilla-Hernández 1993). In 2017, the world oyster production was approximately 5.9 million tons, with harvest production being 97.5% of the total production, and oysters are positioned as the fourth most important seafood group globally, by volume of production, after cyprinid fish, seaweed, and clams (FAO 2020).

In addition, to fulfilling their role as primary producers within the trophic chain, oysters are ecologically a keystone in marine ecosystems, providing ecological services as filter-feeders, calcifiers, and reef-builders, and for this last reason, they are considered bioengineers (Smaal et al. 2019); however, oyster populations have been declining because of overfishing, habitat destruction, and diseases (Beck et al. 2011), and their protection and management require a sound biological baseline.

In a taxonomic context, the shell plasticity of ostreid species has been a troublesome matter, where some "forms" of several species have been assigned different names by several authors (Harry 1985, Guo et al. 2018). Reports on the difficulty of proper species identification caused by the wide variation in body size and coloration are frequent in the literature, so the geographical distribution is somewhat uncertain. This taxonomic uncertainty affects the fishery statistics because some individuals combine multiple species as a single species, and this gives the data little analytical value with which to draw conclusions and make fisheries administrative decisions.

The present review organizes the knowledge of the Ostreidae in the tropical and subtropical American Pacific and presents an analysis of aspects of their taxonomy, classification, biology, ecology, geographic distribution, and genetics. Although there are a dozen species of oysters in the region, most of the information in this study is focused on two local species (*Crassostrea corteziensis* and *Striostrea prismatica*) and on the introduced species (*Crassostrea gigas*).

Taxonomy, Identification, and Distribution

Oysters are members of the family Ostreidae (Rafinesque-Schmaltz 1815), order Ostreida (Férussac 1821–1822), subclass

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Pteriomorphia (Beurlen 1944), and class Bivalvia (Linnaeus 1758). Sixteen living genera with about 75 species are known. Six genera are currently documented in the tropical eastern Pacific. The family occurs as early as the Triassic period.

Despite being one of the most common and economically important bivalve molluscs consumed around the world, oysters are exceptionally difficult to identify. Oyster shell shape is greatly influenced by the substratum to which they attach. They also are frequently covered with epibionts, including other oysters. That being said, there are reliable shell features that will assist in the identification of most specimens.

Some molecular studies have reorganized the taxonomy of oysters in the eastern Pacific. For instance, Polson et al. (2009) demonstrated that *Ostrea lurida* (Carpenter 1864) and *Ostrea conchaphila* (Carpenter 1857) are two distinct species despite having nearly identical shell morphology. Raith et al. (2016) have further defined the distribution of this species complex, as well as synonymizing the genus *Myrakeena* (Harry 1985), and the species *Ostrea tubifera* (Dall 1914). It is hopeful that these landmark studies will be pushed forward to all oysters in the eastern Pacific, and will also yield additional morphological characteristics to separate them.

Additional genetic studies have led to the creation of new generic and higher level names in the Ostreidae (Salvi & Mariottini 2016, Guo et al. 2018). Following suggestions by Bayne et al. (2017), the generic allocations have been maintained as outlined in Coan and Valentich-Scott (2012) and Valentich-Scott et al. (2020) until the taxa defined in these genetic studies have stabilized. A diagnostic characteristic for each species and an explanation of the current taxonomy are provided. Detailed descriptions of each species are modified from Valentich-Scott et al. (2020), Coan and Valentich-Scott (2012), and Coan et al. (2000).

In the taxonomic synonyms in the following text, we use the term "of authors." This implies that an author or authors have misapplied a species name in the literature.

Description of Shell Characteristics

Identification of oyster shells requires an understanding of a few specific terms (Fig. 1A–E). The left/right orientation of an oyster shell is not immediately apparent. The right valve is almost always the upper valve, whereas the attached valve is almost always the left valve (Fig. 1D), and the convexity is frequently a useful diagnostic characteristic. The height of the shell extends from the beaks above the hinge margin (dorsal) to the opposite (ventral) side (Fig. 1E). The length is the maximum dimension approximately 90° from the height measurement. In oysters the height is usually greater than the length. The adductor muscle scar is mostly posterior of the midline of the shell (Fig. 1E). 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 is sometimes diagnostic. Some species have only a slight area of attachment on the left valve, whereas others have extensive areas of attachment. The shell margin might be strongly undulate (Fig. 1C), or not undulate (Fig. 1D). The exterior valve sculpture can be useful in identification if not heavily eroded or encrusted with epibionts. Several species have strong radial plicae (ribs) (Fig. 5E, F, I), some have lamellate sculpture (Fig. 3H, K), and others are mostly smooth (Fig. 2A).

Internal shell characteristics are often more helpful than external ones in separating the tropical eastern Pacific oysters. The presence or absence of small denticulations (chomata) along the shell margin near the hinge can be very useful to separate genera (Fig. 1A, B); however, sometimes chomata are greatly reduced in certain specimens (e.g., *Ostrea conchaphila*). One must be careful to make an immediate or hasty identification based on a single shell character. Using the entire suite of the aforementioned characteristics leads to an accurate identification.

Crassostrea aequitorialis

Figure 2A–F
[Synonyms: *Ostrea aequatorialis* (d'Orbigny 1846: 672).]

Diagnosis

Shell usually long, narrow, attached to mangrove root; ligament groove long; shell margin not undulate; chomata absent.

Description

Shell dorsoventrally elongate, some specimens more ovate; shell thick, heavy; left valve shallowly concave; right valve flat to slightly concave; left valve usually broadly attached to mangrove roots; sculpture reduced in both valves, some with irregular commarginal lamellae; ligament groove moderately long, broad; chomata absent; exterior color cream with sporadic purple rays or blush in some; interior color cream to light brown, with darker patches in some; height to 80 mm.

Distribution

Isla Luna, Guayaquil, Ecuador (2.2° S); intertidal zone, on mangroves. Likely many other South American localities, but the distribution has been confused with *Crassostrea corteziensis*.

Remarks

This species has been confused in the literature with *Crassostrea corteziensis*. Compared with this species, *Crassostrea aequitorialis* is less inflated, has a thinner shell, a longer ligament groove, and is attached to mangrove roots. Its distribution is undoubtedly extensive, but has yet to be resolved.

Crassostrea columbiensis

Figure 2G–L
[Synonyms: *Ostrea columbiensis* (Hanley 1846: 107); *Ostrea ochracea* (Sowerby 1871: pl. 10); *Ostrea tulipa* (Lamarck, of authors, not Lamarck 1819); *Ostrea chilensis* (Philippi, of authors, not Philippi 1844).]

Diagnosis

Shell round to elongate, very thin, attached to mangrove root; ligament groove short; chomata absent.

Description

Shell irregular in shape, typically ovate–elongate, usually thin relative to other *Crassostrea*; both valves mostly flat, with slight convexity in some; broadly to moderately attached by left valve, usually to mangrove roots; left valve larger than right, frequently flared over right valve; sculpture of both valves with fine commarginal striae and growth checks; ligament groove short, broad; chomata absent; external color cream with sporadic purplish-red

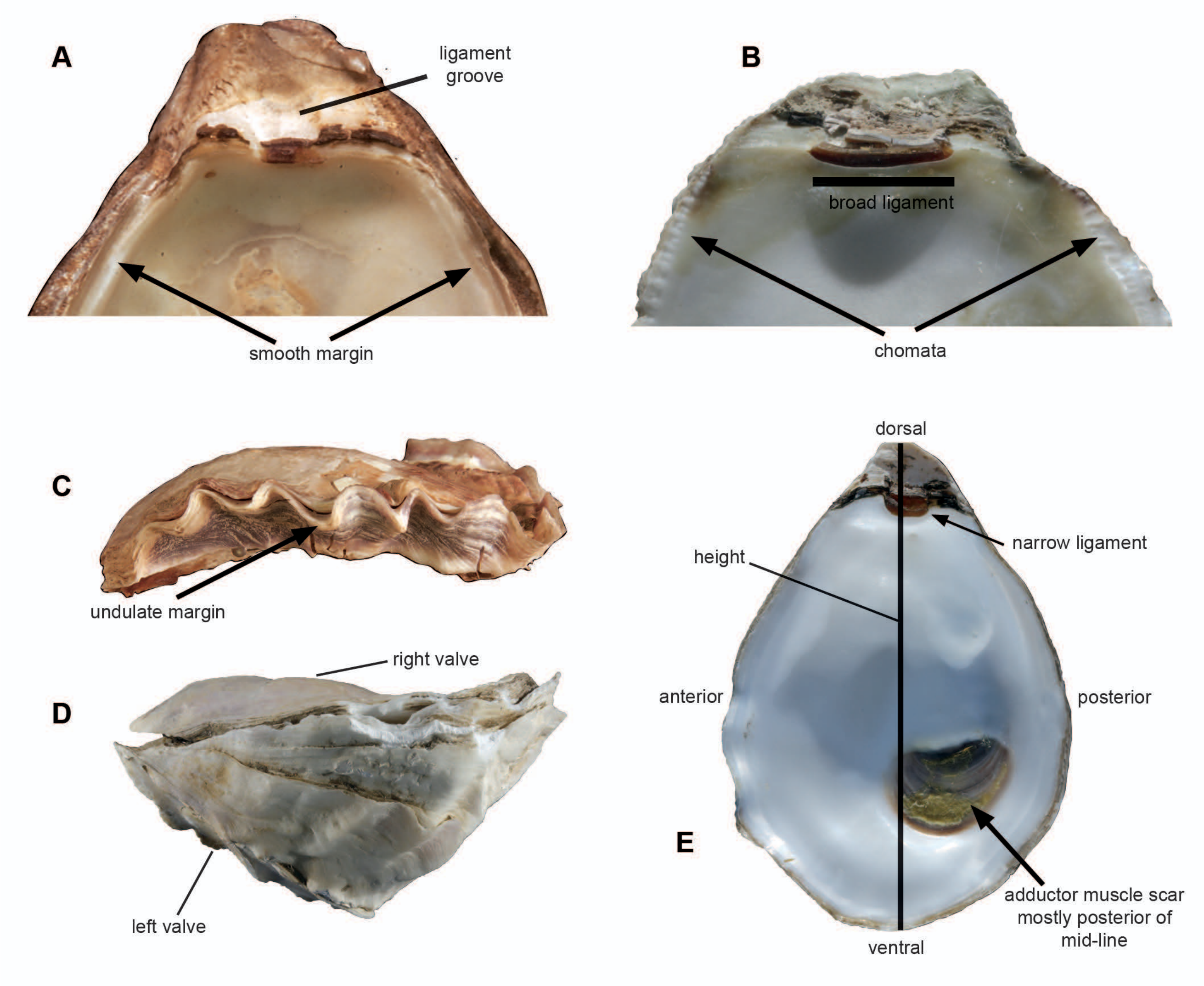

Figure 1. Shell characteristics of Ostreidae. (A) Hinge with smooth margins and long ligament groove; (B) Hinge with chomata and broad ligament; (C) Left (bottom) valve nearly flat, margin strongly undulate; (D) Left valve deeply convex, margins not undulate; (E) right (top) valve, adductor muscle scar mostly posterior of midline.

blush, and darker brown near beaks, some with rays of lighter color; exterior of right valve frequently shiny; interior color white to cream, often with dark purple margin; height to 80 mm.

Distribution

Bahía San Bartolomé, Pacific coast of Baja California Sur (27.7° N) to Colán, Piura, Peru (5.0° S); intertidal zone, particularly in mangrove swamps, attached to roots and to each other.

Remarks

The species is recorded as early as the Pliocene of California and Baja California.

Crassostrea corteziensis

Figure 3A–F

[Synonyms: *Ostrea corteziensis* (Hertlein 1951: 68); *Ostrea chilensis* (Philippi, of authors, not Philippi 1844).]

Diagnosis

Shell very heavy; left valve deeply concave, broadly attached to substratum; right valve mostly flat; chomata absent.

Description

Shell irregular in shape, from ovate to dorsoventrally elongate, some arcuate; shell very thick, heavy; left valve moderately to deeply concave; right valve flat to slightly concave; narrowly to broadly attached by left valve, more broadly attached to shells; sculpture of both valves with irregular commarginal lamellae, left valve with fluted lamellae in some; ligament groove broad, long; chomata absent; exterior color cream with sporadic brown blush in some; interior color cream to white, with purple patches in some; height to 250 mm.

Distribution

Bahía Kino, Sonora, Mexico (28.8° N), to Isla Cañas, Panama (9.0° N); intertidal zone, on rocks and shells.

Remarks

The species is recorded as early as the Pliocene of California and Baja California.

Crassostrea gigas

Figure 3G–L

Figure 2. Oyster species of the eastern Pacific: (A–F) *Crassostrea aequatorialis*, Ecuador, Guayaquil, Isla Luna. BMNH 1854.12.4.823 (holotype), length 44 mm, height 80 mm. (G–L) *Crassostrea columbiensis*, Ecuador, Guayas, Santa Elena. SBMNH 120,192 (neotype), length 62 mm, height 59 mm. (A, G) Exterior right valve; (B, H) Exterior left valve with mangrove root adhering to shell; (C, I) Interior of the right valve; (D, J) Interior of the left valve; (E, K) Lateral view of both valves; (F, L) Hinge of the left valve.

[Synonyms: *Ostrea gigas* (Thunberg 1793: 140); *Ostrea laperousii* (von Schrenck 1861: col. 411); *Ostrea talienwhanensis* (Crosse 1862: 149); *Ostrea gravitesta* (Yokoyama 1926: 388); *Ostrea posjetica* (Razin 1934: 36); *Lopha (Ostreola) posjetica beringi, posjetica zawoikoi, posjetica newelskyi* (Vialov 1946: 523).]

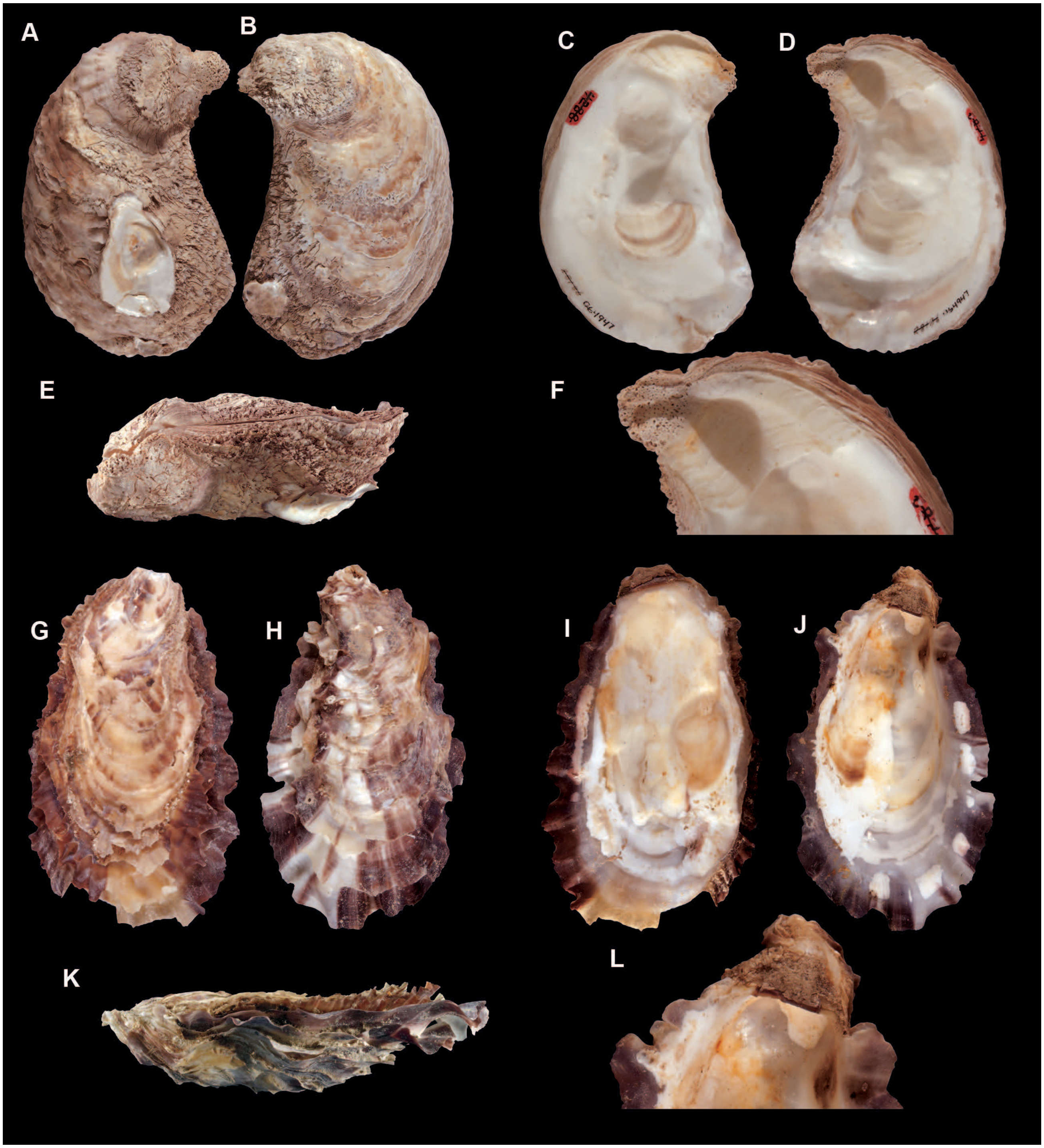

Figure 3. Oyster species of the eastern Pacific: (A–F) *Crassostrea corteziensis*, México, Sonora, Bahía Kino. CAS 064,947 (holotype), top valve length 83 mm, height 140 mm and bottom valve length 103 mm, height 152 mm. (G–L) *Crassostrea gigas*, Mexico, Sonora, Bahía la Choya, intertidal. SBMNH 359915, length 61 mm, height 119 mm. (A, G) Exterior right valve; (B, H) Exterior left valve; (C, I) Interior of the right valve; (D, J) Interior of the left valve; (E, K) Lateral view of both valves; (F, L) Hinge of the left valve.

Diagnosis

Shell height usually much greater than length; left valve deeply concave; sculpture of long thin lamellae; chomata absent.

Description

Shell irregular in shape, from ovate to more typically elliptical; left valve deeply concave; right valve flat to slightly convex; usually narrowly attached by left valve;

sculpture of commarginal frills; frills frequently abraded, but much prolonged in some habitats; ligament groove long, narrow to broad; chomata absent; external color gray to purplish, sometimes in radial bands; internal color white, generally with light-colored adductor muscle scar; height to 450 mm.

Distribution

Native to the western Pacific from Sakhalin Island, Russia, to Pakistan; introduced into Japan, Europe, and Australia. On the American Pacific coast, it has been introduced into the USA, Canada, Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, Peru, and Chile.

Remarks

Following the recommendations by Bayne et al. (2017), we are continuing to place this species in the genus *Crassostrea*.

Crassostrea sikamea

Figure 4A–F
[Synonyms: *Ostrea gigas sikamea* (Amemiya 1928: 335); *Crassostrea gigas* "kumamoto," of authors, infraspecific [ICZN Code Art. 45f (iv).]

Diagnosis

Shell height not much greater than shell length; left valve deeply concave; right valve flat; chomata absent.

Description

Shell tear-drop shaped, relatively small; left valve deeply concave; right valve flat to slightly convex; sculpture reduced, primarily of commarginal growth checks and irregular radial folds (primarily on left valve); ligament groove long, narrow; chomata absent; external color cream to dark gray; internal color white, adductor muscle scar dark purple; height to 60 mm.

Distribution

Native to the western Pacific, and brought to the West Coast from southern Japan; raised commercially from Puget Sound, WA (47.5° N), to Tomales Bay, CA (38.3° N), and also in Australia.

Remarks

Following the recommendations by Bayne et al. (2017), we are continuing to place this species in the genus *Crassostrea*.

Dendostrea folium

Figure 4G–J
[Synonyms: *Ostrea folium* (Linnaeus 1758: 699); *Ostrea serra* (Dall 1914: 2, not de Lamarck 1819); *Ostrea dalli* (Lamy 1929–1930: 252, new name for *Ostrea serra* Dall, not Lamarck); *Ostrea frons* (Linnaeus, of authors, not Linnaeus 1758); with additional synonyms in Inaba et al. (2004).]

Diagnosis

Shell height usually much greater than length; exterior surface with a few strong radial plicae; inner shell margin densely denticulate especially near hinge.

Description

Shell ovate–elongate; left valve flat to slightly convex, broadly attached; right valve convex, fitting on top of left valve; sculpture of strong radial plications that interlock; ligament groove short, narrow; weak chomata present on both sides of ligament, not present in all specimens; exterior color rose to purplish-red, sometimes eroded to cream; interior color white, light brown to rose on margins; height in the eastern Pacific to 24 mm.

Distribution

This Indo-Pacific species has a discontinuous distribution in the tropical eastern Pacific at Cabo Pulmo, Baja California Sur, Mexico (23.5° N); Bahía de Panamá, Panama; Isla del Coco, Costa Rica; Isla de Malpelo, Colombia; Isla Galápagos, Ecuador; in 8–37 m, attached to calcareous substrata, including sea urchin spines (*Eucidaris thourasii* and *Eucidaris galapagensis*), gorgonians, gastropods, and corals.

Remarks

Molecular studies are needed to understand the relationship of the two eastern Pacific species of *Dendostrea* with their Indo-Pacific analogs.

Dendostrea sandvichensis

Figure 5A–D
[Synonym: *Ostrea sandvichensis* (Sowerby 1871): pl. 27, Figure 66].

Diagnosis

Shell height usually much greater than length; exterior surface with a few weak radial plicae; inner shell margin densely denticulate over most of shell.

Description

Shell ovate to ovate–elongate; left valve attached by large area, flat to slightly concave, especially on margins; right valve flat to slightly convex, fitting on top (not inside) left valve; sculpture of numerous conspicuous sharp radial undulations or plicae, especially on margins, usually overgrown with encrusting organisms; fine crenulations often found over entire margin; ligament groove short, narrow; exterior color light brown; interior color white with green patches, margins white; height in eastern Pacific to 43 mm.

Distribution

Another Indo-Pacific species that is occasionally found in the tropical eastern Pacific. It has been reported at Bahía de los Muertos, Baja California Sur (23.9° N) and Golfo de Tehuantepec (approximately 16.0° N), Mexico; attached to coral and rocks; at a depth of 2–3 m.

Ostrea angelica

Figure 5E–J
[Synonyms: *Ostrea angelica* (Rochebrune 1895: 241); *Ostrea vespertina* (Conrad, of authors, not Conrad 1854); *Ostrea cumingiana* (Dunker, of authors, not Dunker, in Philippi 1846).]

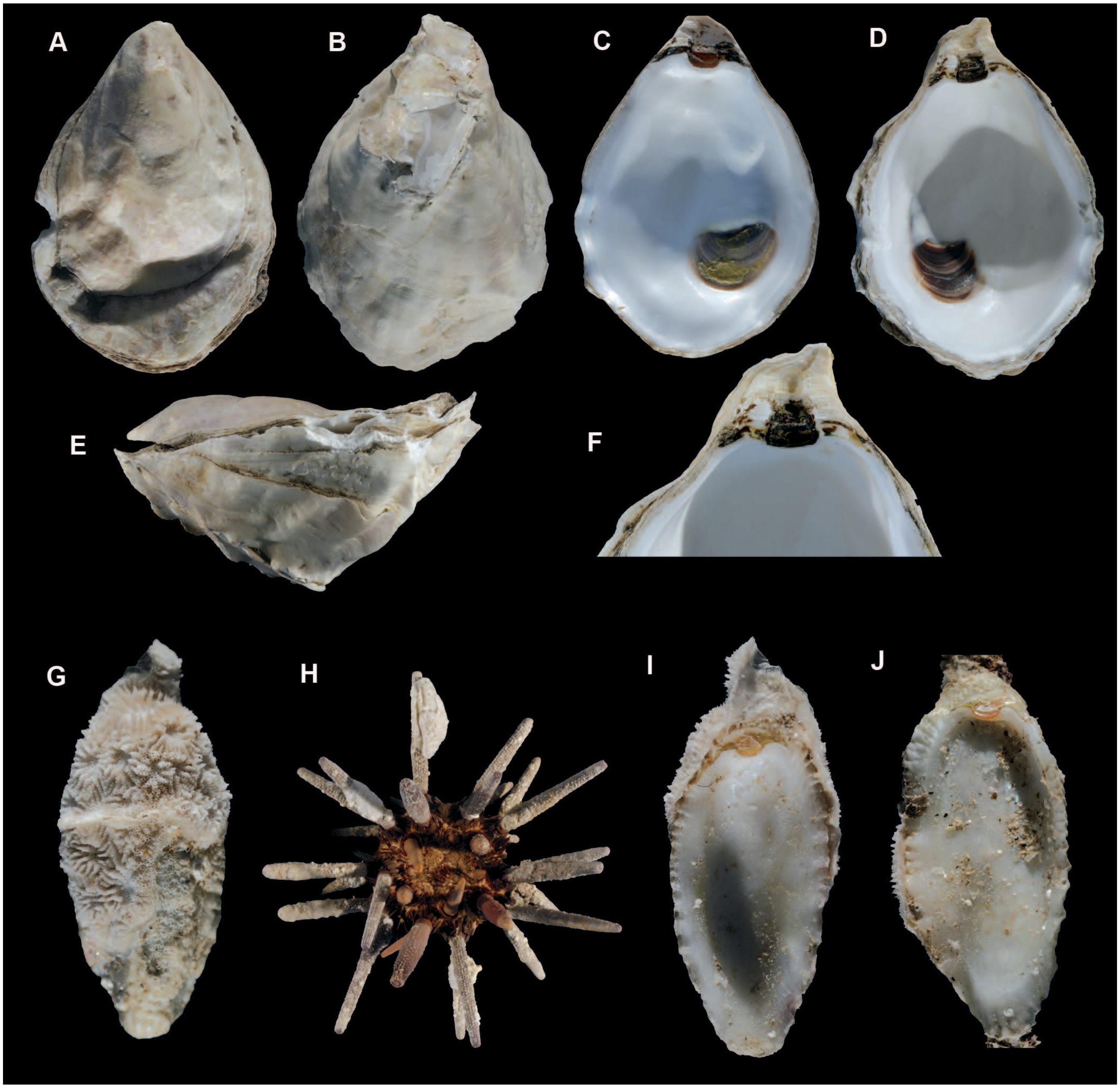

Figure 4. **Oyster species of the eastern Pacific: (A–F) *Crassostrea sikamea*, USA, OR, Lincoln County, Yaquina Bay. SBMNH 145309, length 48 mm, height 66 mm. (A) Exterior right valve; (B) Exterior left valve; (C) Interior of the right valve; (D) Interior of the left valve; (E) Lateral view of both valves; (F) Hinge of the left valve. (G–J) *Dendostrea folium*, Mexico, Baja California Sur, Punta Pescadores, attached to urchin, 3–6 m. SBMNH 83500, length 8 mm, height 17 mm. (G) Exterior right valve; (H) Urchin host with figured oyster attached to the top spine; (I) Interior of the right valve; (J) Interior of the left valve.**

Diagnosis

Shell length and height subequal in many; with weak chomata near hinge; exterior surface of both valves with many strong radial plicae; shell margin strongly undulated.

Description

Shell subovate to subcircular; left valve concave, narrowly or broadly attached; right valve flat to slightly convex, fitting slightly inside left valve; both valves with heavy radial plications, resulting in an undulating margin; ligament short to long, narrow; chomata weak to strong; exterior color grayish-white to dark brown; interior color white, frequently with large olive green regions, some with dark margins; shell height to 100 mm.

Distribution

Rocas Alijos, Pacific coast of Baja California Sur (25.0° N), to Bahía Santa Elena, Guanacaste, Costa Rica (10.9° N); low intertidal zone to 50 m. This species has been reported from as early as the late Miocene of California and the Pliocene of Baja California.

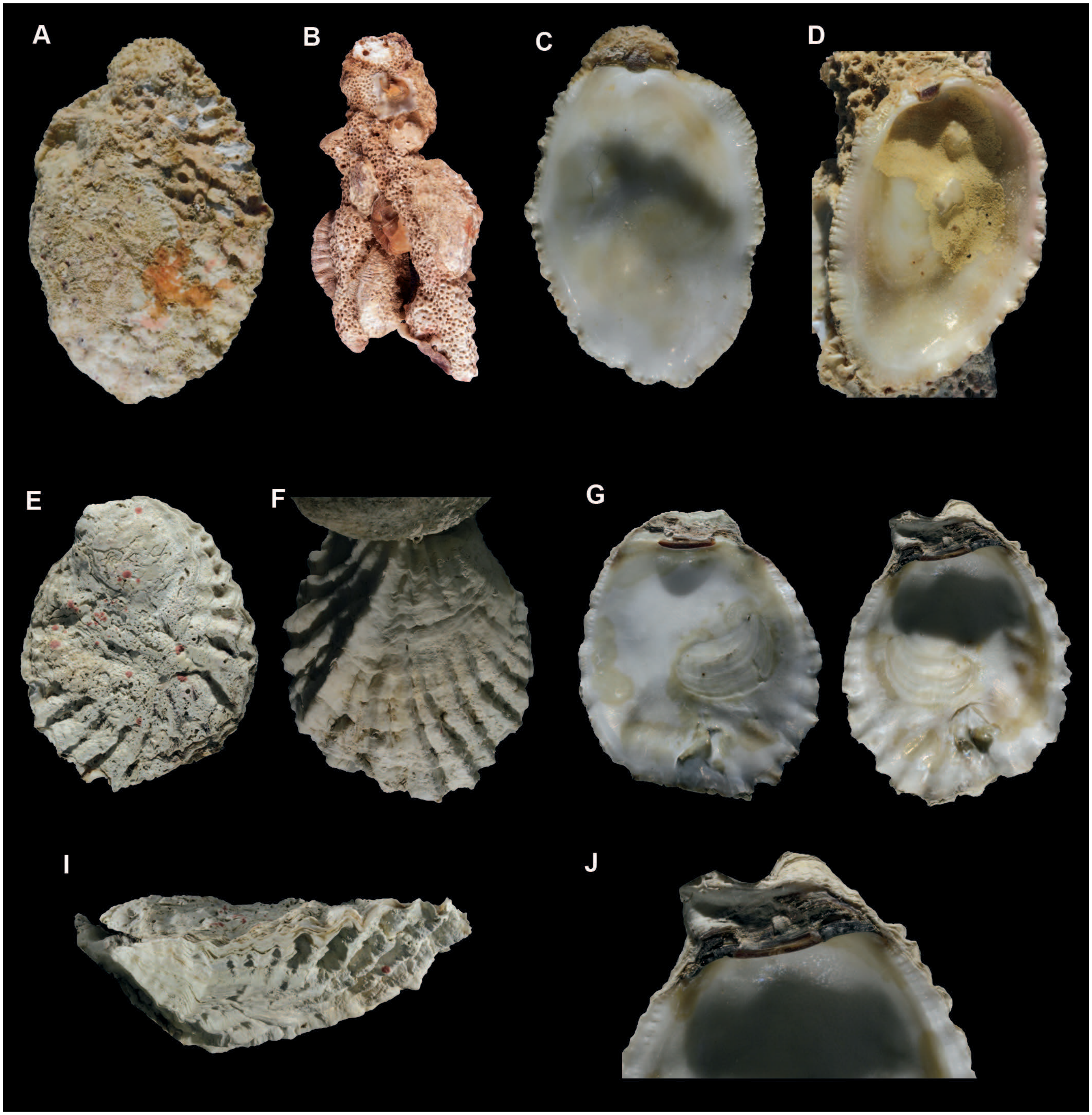

Figure 5. Oyster species of the eastern Pacific: (A–D) *Dendostrea sandvichensis*, Mexico, Baja California Sur, Bahía de los Muertos, 3–6 m. SBMNH 149691, length 18 mm, height 28 mm. (A) exterior left valve, (B) oyster attached to coral branch, (C) interior of right valve, (D) interior of left valve. (E–J) *Ostrea angelica*, Mexico, Sonora, NE of Guaymas, Bahía Batuecas, intertidal. SBMNH 135082, length 41 mm, height 42 mm. (E) exterior right valve, (F) exterior left valve attached to rock, (G) interior of right valve, (H) interior of left valve, (I) lateral view of both valves, (J) hinge of left valve.

Remarks

Harry (1985) erected a new genus, *Myrakeena*, and selected *angelica* as the type species. Raith et al. (2016) have shown that *angelica* fits well within the *Ostrea* clade and formally recognized it as *Ostrea angelica*.

Ostrea conchaphila

Figure 6A–F

[Synonyms: *Ostrea conchaphila* (Carpenter 1857: 161); *Ostrea lurida* of authors, not Carpenter (1864).]

Diagnosis

Shell usually higher than long; chomata present in most; exterior surface without strong radial plicae; interior color green to white.

Description

Shell circular to dorsoventrally elongate; left valve flat to slightly convex, frequently cemented to substratum by a broad

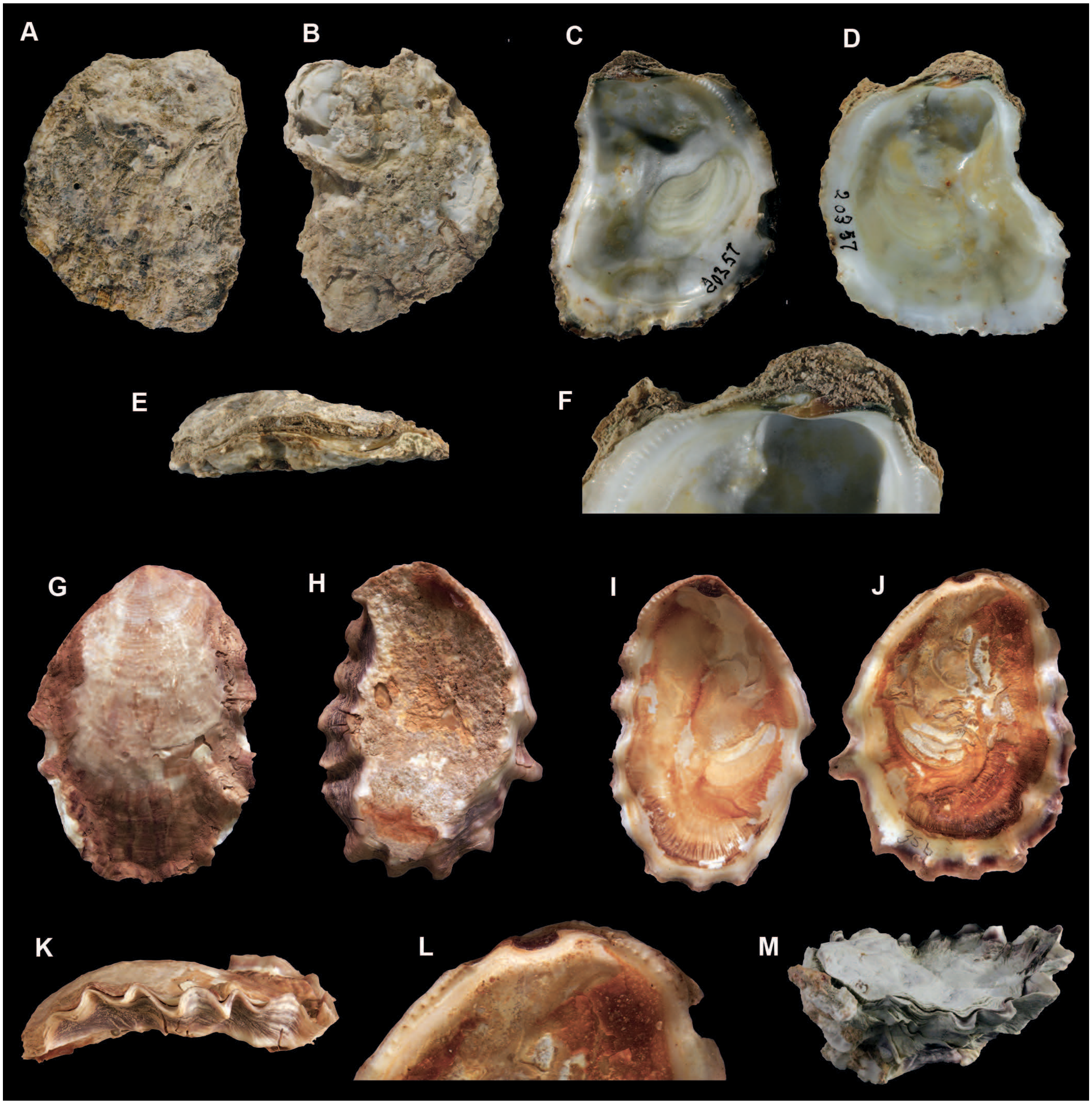

Figure 6. **Oyster species of the eastern Pacific: (A–F) *Ostrea conchaphila*, Mexico, Sonora, Estero El Soldado. SBMNH 20357, length 39 mm, height 51 mm. (G–L) *Saccostrea palmula*, Mexico, Oaxaca, Golfo de Tehuantepec. BMNH 74.12.11.260 (syntype of *Ostrea mexicana*), length 39 mm, height 51 mm. (A, G) Exterior right valve; (B, H) Exterior left valve; (C, I) Interior of the right valve; (D, J) Interior of the left valve; (E, K) Lateral view of both valves; (F, L) Hinge of the left valve. (M) *S. palmula*, Mexico, Baja California, Puertecitos. SBMNH 468301, length 52 mm, height 62 mm, depth 34 mm, lateral view depicting the deep left valve and concave right valve fitting inside left.**

area, but attachment may be smaller; right valve flat to slightly convex; ventral margin flat to slightly undulating; sculpture of obscure commarginal lamellae, frequently abraded; ligament groove very short, broad; chomata fine, not visible in some specimens; exterior color grey, purple, or white, with dark rays; interior color green to white; height to 85 mm.

Distribution

Laguna San Ignacio, Baja California Sur, Mexico (26.9° N), to Puerto Pizarro, Tumbes, Peru (3.5° S); intertidal zone with shells reported as deep as 100 m. The species has been recorded as early as the Pliocene.

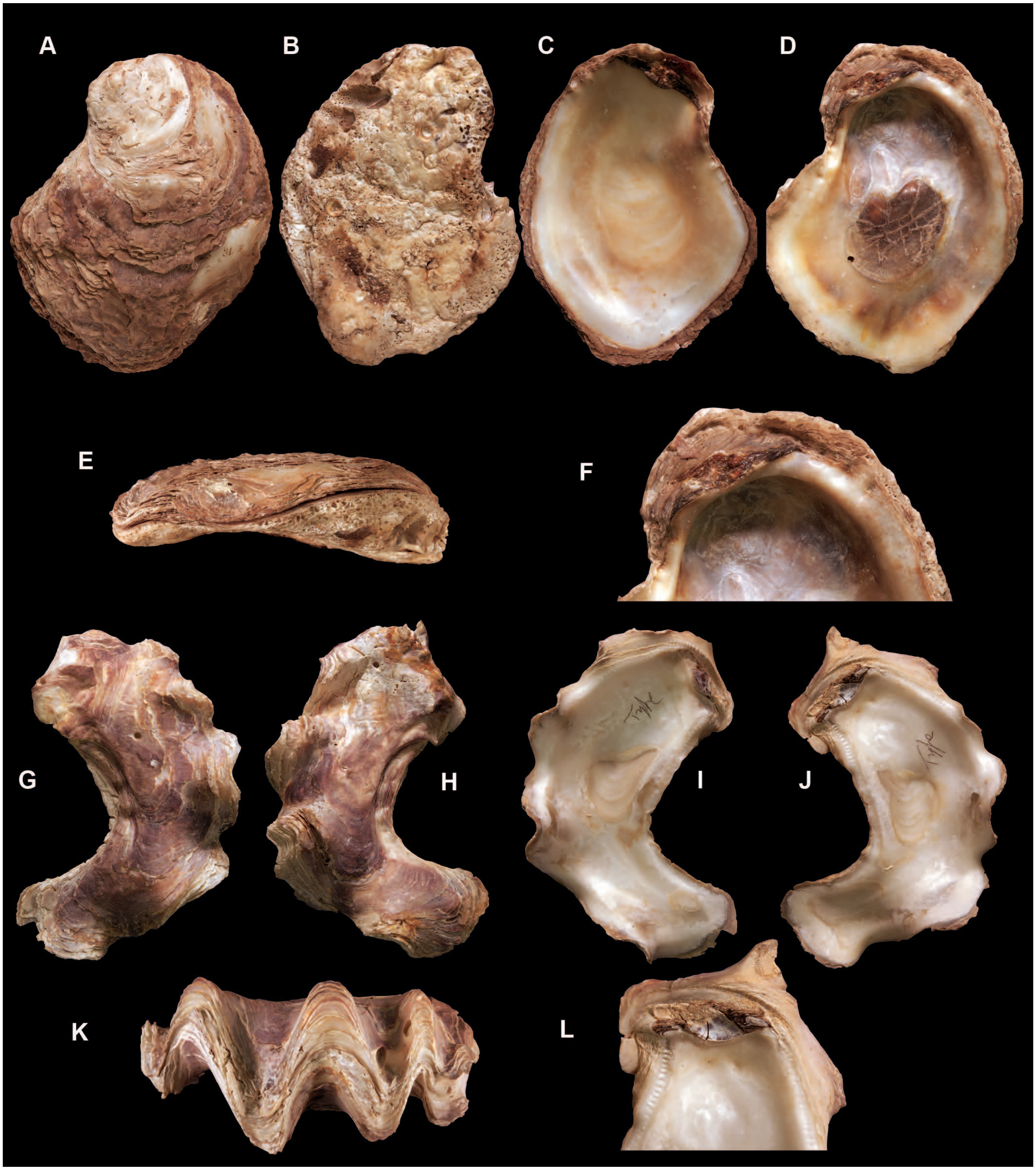

Figure 7. Oyster species of the eastern Pacific: (A–F) *Striostrea prismatica*, Panama, Veraguas, Guacamya. BMNH 1912.6.18.40 (syntype), length 63 mm, height 80 mm. (A) Exterior right valve; (B) Exterior left valve; (C) Interior of the right valve; (D) Interior of the left valve; (E) Lateral view of both valves; (F) Hinge of the left valve. (G–L) *Undulostrea megodon*, Peru (precise locality unknown). BMNH unnumbered (syntype), length 43 mm, height 102 mm. (A, G) Exterior right valve; (B, H) Exterior left valve; (C, I) Interior of the right valve; (D, J) Interior of the left valve; (E, K) Lateral view of both valves; (F, L) Hinge of the left valve.

Remarks

Genetic studies have shown that the northeastern Pacific *Ostrea lurida* (Carpenter 1864) is separable from this species, but no one has yet advanced morphological characters to tell them apart (Polson et al. 2009). Raith et al. (2016) reported that the southern limit of *Ostrea lurida* is Guerrero Negro, Baja California, Mexico, and the northern limit of *Ostrea conchaphila* is Laguna San Ignacio, Baja California Sur.

Saccostrea palmula

Figure 6G–J

[Synonyms: *Ostrea conchaphila palmula* (Carpenter 1857: 163); *Ostrea amara* (Carpenter 1864: 363); *Ostrea mexicana* (Sowerby 1871: pl. 16); *Ostrea tubulifera* (Dall 1914: 3); *Ostrea cumingiana* (Dunker, of authors, not Dunker 1847).]

Diagnosis

Shell height usually greater than length; shell margin strongly undulates; right valve exterior surface usually smooth, with strong plications on margin, frequently fitting inside left valve; chomata strong.

Description

Shell irregularly shaped; narrowly to completely attached by left valve, frequently deeply cupped, sometimes almost flat; right valve concave, flat, or somewhat convex, fitting inside left valve; shell margin slightly to strongly undulating; sculpture of a few conspicuous sharp plications, especially in left valve; ligament groove moderate to long, narrow; chomata strong; exterior color cream to purplish-brown, some with radial rays; interior color white with green or purple patches, many with purple margins; height to 80 mm.

Distribution

Laguna San Ignacio, Pacific coast of Baja California Sur (26.8° N), to Bayovar, Piura, Peru (5.9° S); also the offshore islands of Isla del Coco, Costa Rica and Islas Galápagos, Ecuador; on rocks or mangroves. The species has been recorded in the Pleistocene and Pliocene of Baja California.

Remarks

In Coan and Valentich-Scott (2012), *Ostrea tubulifera* was listed as a separate species, differentiated by its hollow (hyote) spines. Raith et al. (2016) presented genetic evidence that *O. tubulifera* is in fact a morphological variant of *Saccostrea palmula*.

Striostrea prismatica

Figure 7A–F

[Synonyms: *Ostrea prismatica* (Gray 1825: 139); *Ostrea iridescens* (Hanley, 1854: pl. 2); *Ostrea panamensis* (Carpenter 1864: 362); *Ostrea lucasiana* (Rochebrune 1895: 241); *Ostrea turturina* (Rochebrune 1895: 242); *Ostrea spathulata* (Lamarck, of authors, not de Lamarck 1819).]

Diagnosis

Shell thick, heavy; weak chomata present in most; interior iridescent, golden to dark brown; sculpture of commarginal lamellae, without radial ribs or plicae.

Description

Shell ovate to dorsoventrally elongate, heavy, thick; left valve moderately to deeply concave, often broadly attached, but with raised margin; right valve flat to moderately convex; ligament groove broad, usually short; chomata heavy, few in number; sculpture of dense commarginal lamellae, many with broad, low undulations; exterior color brownish-purple; interior iridescent gold with olive-brown patches; height to 190 mm.

Distribution

La Paz, Baja California Sur (24.2° N) [SBMNH], and Mazatlán, Sinaloa (23.2° N) [SBMNH], Mexico, to Máncora, Tumbes, Peru (4.1° S) [SBMNH]; in the intertidal zone, in exposed rocky areas. The species has been recorded in the Pleistocene of Mexico and the Pliocene of Peru.

Undulostrea megodon

Figure 7G–L

[Synonyms: *Ostrea megodon* (Hanley 1846: 106); *Ostrea gallus* (Valenciennes 1846: pl. 21); *Ostrea cerrosensis* (Gabb 1869: 35).]

Diagnosis

Shell crescent shaped; anteroventral margin of both valves with three to four strong, broad undulations; chomata present; interior color tan to dark green.

Description

Shell arcuate; both valves moderately inflated; left valve often narrowly attached; sculpture of three to four broad anteroventral undulations, each with stacked commarginal lamellae; ligament groove long, narrow, oblique; chomata strong, frequently extending well down the anterior and posterior margins; exterior color tan to purple to reddish-brown, sometimes with darker rays; interior color dark cream with green patches; height to 103 mm.

Distribution

Bahía San Bartolomé, Pacific coast of Baja California Sur (27.7° N), to Bahía de la Independencia, Ica, Peru (14.3° S); low intertidal zone to 110 m. This species has been recorded from as early as the Miocene of southern California.

Remarks

It has been followed Valentich-Scott et al. (2020) and maintaining the use of *Undulostrea* for this species until additional studies are completed that include morphometric and genetic data.

BIOLOGY AND ECOLOGY

General Anatomy

Internal anatomy of the oysters in the tropical and subtropical regions of the American Pacific is similar to that of other Ostreidae molluscs, and we take *Crassostrea corteziensis* as an oyster model. According with Chávez-Villalba et al. (2005) and Flores-Higuera (2011), two lobes forming the mantle cover the organs and shape the pallial cavity. The gills divide the space in inhalant and exhalant chambers where seawater circulation takes place. The mouth is covered by the labial palps and is oriented to the ligament, whereas the anus borders the adductor muscle. The gonad is largely diffused within the digestive gland and both surround the pericardium and part of the adductor muscle. A representative of organs and tissues of *C. corteziensis* is in Figure 8.

Life Cycle

Few studies have been conducted on the biology of oysters in the West American tropics and the subtropical eastern Pacific,

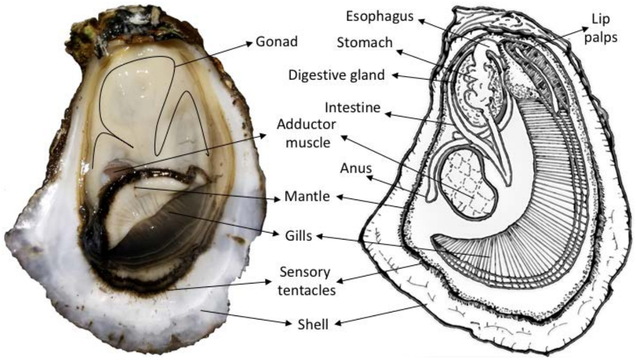

Figure 8. Main internal anatomical features of the Cortez oyster *Crassostrea corteziensis*.

and knowledge of the life cycle, particularly the early stages, is still to be determined in most native species. Embryogenesis, larval, and postlarval development of *Crassostrea corteziensis* and *Striostrea prismatica* have been described during spat production in controlled conditions (Mazón-Suástegui 2014, Lodeiros et al. 2017).

In these species, fertilization is external, and once the eggs are fertilized, the embryonic development begins quickly, reaching the trochophore larval stage in a few hours (12–18 h), resulting in ''D'' veliger mixotrophic larvae before 24 h. The planktonic life stage lasts 2 to 3 wk, during which time the larva grows and modifies its shape and behavior with very active swimming; then, the eye spot appears and the foot is developed (pediveliger larvae). At this time, the larval swimming stops, passing into a benthic phase, and then the larvae acquire a creeping displacement until obtaining an adequate substrate where they are cemented and metamorphosed to acquire their sessile lifestyle.

From this point forward (18–22 days for *Crassostrea corteziensis* and 22 days for *Striostrea prismatica*), the larva undergoes metamorphosis, loses the velum, and develops its gills. During this process, the larva chooses the substratum and cements with the left valve, thus initiating its sessile life, similar to that of the adult. Figure 9 schematically shows the life cycle details of *S. prismatica* from its fertilization, production of juveniles (in laboratory conditions), and adult stages. Although the embryonic and larval development in these oysters is similar to that of many oysters, and shows the characteristics of many bivalves, the umboned larva in *S. prismatica* has a reddish distal spot, which can be used for identification in zooplankton samples (Lodeiros et al. 2017).

Population and Ecological Interactions

Population studies and the ecological interactions of these species are intended for the evaluation of the resource for fishery and exploitation purposes, and oyster reef conservations and restoration, so they are aimed at determining their abundance and distribution by size, sex proportion, associated species, water quality, and other parameters in the systems where they are distributed naturally (Coen & Luckenbach 2000).

The rock oyster is one of the most abundant species in the coastal and subcoastal rock systems, and, in most cases, it provides the greatest fishing biomass. Ríos-González et al. (2018) performed a revision of *Striostrea prismatica* describing its biology, exploitation, and conservation. On the coasts of Mexico, the species *S. prismatica*, together with *Chama coralloides*, *Choromytilus palliopunctatus*, and *Saccostrea palmula*, accounts for almost 60% of the total abundance of species, with *S. prismatica* representing the largest biomass (Flores-Garza et al. 2014).

Unexploited stocks can have up to 175 individuals/m^2, as Campos and Fournier (1989) have reported for Curú Bay in Costa Rica; however, the stocks are generally overexploited or depleted by artisanal or commercial fisheries because of the lack of extraction regulations. Additional anthropogenic factors, such as pollution, have contributed to the decline of the fishery (Grijalva-Chon et al. 2015).

In 2000, the stocks of *Striostrea prismatica* in the rocky coast of Tumbes, Peru, showed a size range of 7–228 mm, with densities of 6–77 oysters/m^2, but in subsequent surveys (2007), the densities dropped to 0.2 oysters/m^2 (Ordinola et al. 2010, 2013). Gonzabay (2014) recorded a density of 0.7 oysters/m^2 in a rocky system of the town of Ayangue, in the El Pelao nature reserve, Santa Elena Province, Ecuador, with dominant sizes of 80.0–120.0 mm (77.1%), and García and Leones (2016) report sizes of 32.5–178.0 mm with a greater predominance of 60–90 mm, in the intertidal zone of Punta Napo and Punta Gorda, province of Manabí, Ecuador. This difference in sizes, with a shortage of large specimens, is a product of the fishing pressure that exists on the species in rocky systems.

In other species such as *Crassostrea columbiensis*, population studies are even fewer. In Punta Morales, Puntarenas, Costa Rica (years 1984–1985), individuals showed a growth that conforms to the model of Von Bertalanffy [$\mathrm{Lt} = 8.9\ (1 - e^{-0.1567}\ (t = -0.123))$], with a relationship length-weight of $P = 1.04 \times 10^{-3}$ $\mathrm{Lt} = 2.3487$ (Caballero et al. 1997), and for Magdalena Bay, Baja California Sur, Mexico, it is estimated they had a longevity of 6–7 y (García-Domínguez, unpublished data).

The palmate oyster *Saccostrea palmula* and the Arcid cockle *Anadara tuberculosa* are the most important components and the most conspicuous species in mangrove swamps of southern Baja California peninsula, Mexico. The palmate oyster can reach 50 mm in shell length at 1 y (Félix-Pico et al. 2015). Nonetheless, in the estuary Morales, Punta Morales, Puntarenas, and Costa Rica, the maximum total weight length found was 66.7 mm and 24.7 g, respectively, and the growth conforms to the von Bertalanffy model, with a relation $\mathrm{Lt} = 68.2\ (1 - e^{-0.1577t})$. In this locality, the length–weight population ratio is allometric and fits the equation $\mathrm{Pt} = 2.13 \times 10^{-2}$ Lt 1.6602 (Cabrera et al. 2001b); however, records of the biological-fishing status of their populations are not yet available.

In addition to growth studies of *Crassostrea corteziensis* during cultivation (Chávez-Villalba et al. 2005), growth in this species has been examined from two perspectives, scope of growth and use of growth models. In the first case, values of the scope for growth revealed that *C. corteziensis* is able to grow in different combinations of temperatures and salinities, but with superior results at 26°C and salinity of 20 (Guzmán-Agüero et al. 2013). In terms of growth modeling, growth data have been analyzed using the model of von Bertalanffy with the following relation: $\mathrm{Lt} = 114\ (1 - e^{-1.1t})$ (Chávez-Villalba et al. 2005). Another approach, implemented by Chávez-Villalba and Aragón-Noriega (2015), was multimodel inference by testing five different asymptotic growth models (von Bertalanffy,

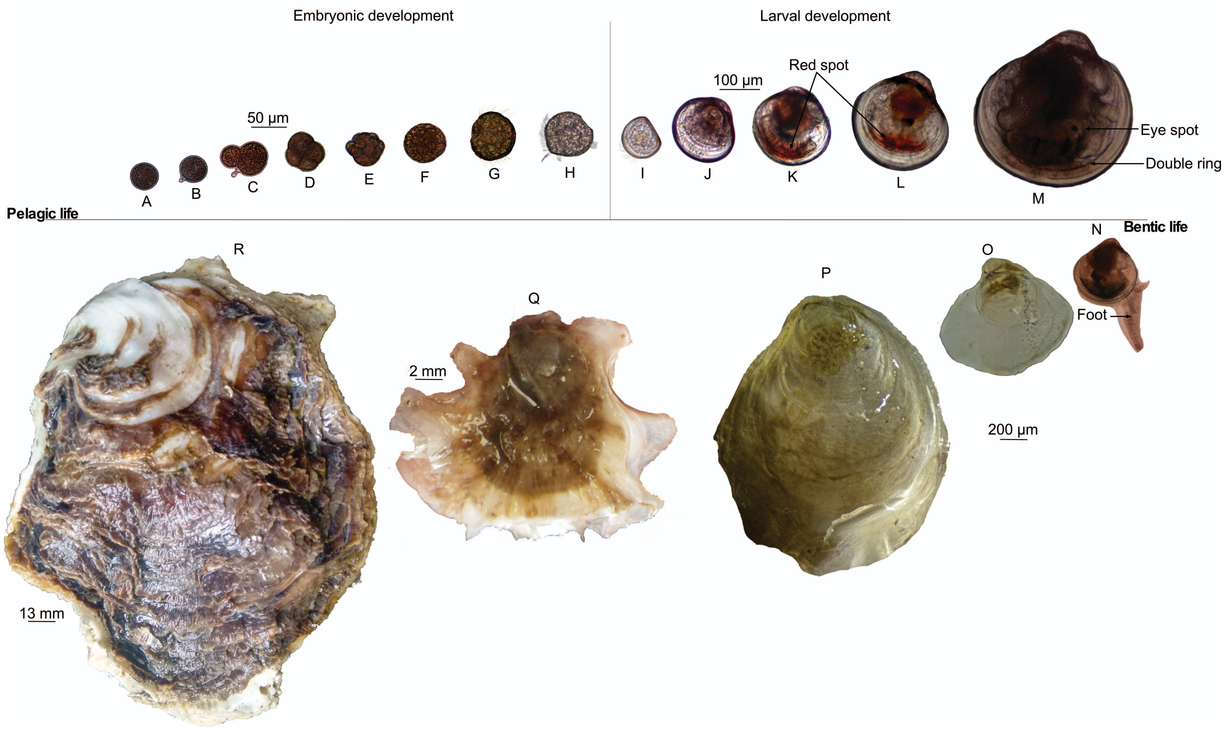

Figure 9. Life cycle of the rock oyster *Striostrea prismatica*, showing its planktonic (embryonic and larval) and benthonic (pediveliger and postlarval) development, from spat to adult stage. (A) Unfertilized oocyte; (B) First polar body indicating oocyte fertilization 15 min; (C) First cell cleavage 1 h 30 min; (D) Second cell cleavage 2 h; (E) Immobile morula 4 h; (F) Blastula 5 h; (G) Late gastrula 7 h 30 min; (H) Trochophore larvae 10 h; (I) Calcified early D-shaped larvae with prodissoconch I 20 h; (J) Veliger larvae 2 days; (K) Umboned larvae with a distal reddish-orange toward the ventral zone 9 days; (L) Umboned larvae with a more marked distal reddish-orange toward the ventral zone 12 days; (M) Large umboned larvae showed spot eye 18 days; (N) Pediveliger larvae 22 days; (O) Early postlarvae 3 days postmetamorphosis; (P) Visually observable postlarvae 9 days postmetamorphosis; (Q) Spat juvenile 90 days postmetamorphosis; and (R) adult. The images have different magnification scales delineated as horizontal bars.

logistic, Gompertz, Schnute, and Schnute–Richards). They found that the best model to describe the individual growth of the species is that of Schnute–Richards.

Considering that the Japanese oyster *Crassostrea gigas* is an exotic species on the shores of the American Pacific, it is speculated that it is highly probable that the various causative agents of epizootics may have arrived as dispersal vehicles as larvae and *C. gigas* spat from hatcheries in the United States. Many lots of oysters (spat, juveniles, and adults) were illegally introduced to Mexico, without strict sanitary controls, including the minimum required by international standards (Flores-Higuera 2011).

Although there are no reports of predators in the oyster species stocks of the tropical and subtropical American Pacific, Mazón-Suástegui (2014) points out that the main predators of *Crassostrea corteziensis* are crabs (*Callinectes* spp.), the sea urchin *Echinometra vanbrunti*, sea stars (*Heliaster kubiniji* and *Pentaceraster cuminigi*), the puffer fish *Sphoeroides annulatus*, rays, and carnivorous molluscs such as *Thais* spp.

In the oyster stocks of Tumbes, Peru, *Striostrea prismatica* serves as a substrate for a variety of benthic communities (35 species) that are predominantly molluscs, within which are the genera *Diodora* and *Crepidula*, and the drilling mussels in the genus *Lithophaga* were the most abundant. These were followed by crustaceans, echinoderms, cnidarians, annelids, and poriferans, as well as several types of macroalgae (Ordinola et al. 2013). Similarly, Mazón-Suástegui (2014) reports that the shells of *Crassostrea corteziensis* house a great diversity of species of molluscs, sponges, tunicates, bryozoans, crustaceans, scales, and some macroalgae. This high diversity of species and invertebrate epibionts that use oyster shells as habitats confers the character of bioengineers to these two species.

Oysters can harbor other organisms within their mantle cavities such as the tiny soft-bodied pea crabs of the family Pinnotheridae that live commensally in the mantle of certain bivalve molluscs. A series of adaptations have evolved to cope with their symbiotic lifestyle (Peiró et al. 2011), which makes them an interesting model to study the evolution of associations between decapods and other invertebrates. Some studies (Cabrera et al. 2001a, Salas-Moya et al. 2014) of the pea crab *Austinotheres angelicus*, living in the palmate oyster *Saccostrea palmula*, have included biometric and reproductive data, adding important information about both species (commensal: *A. angelicus* and host: *S. palmula*); however, more data are needed to get a better understanding of the interactions between population dynamics of the host and adaptive responses of the symbiotic pea crab (Salas Moya et al. 2014).

In the case of *Crassostrea gigas*, as a cultured resource in many parts of the world, particularly in temperate zones, the species can create large hard-substrate biogenic reefs, making them one of the most transformative invaders of marine ecosystems (Crooks et al. 2015). Oyster reefs may harbor invertebrate groups, support other bivalves (*Geukensia* spp., *Macoma* spp., *Ensis* spp., *Mya arenaria*, and *Mercenaria mercenaria*), and are used by many fishes as a recruitment substrate, nursery habitat, and foraging ground (Coen & Luckenbach 2000, Beck et al. 2011). These reefs may influence water quality, sediment erosion rates, and hydrodynamic patterns of water in estuaries and coastal lagoons. All of this affects the distribution and abundance of other biogenic habitats, such as seagrass beds, salt marshes, algal beds, and also influences the dynamics of disease dispersal. Despite the ecological importance of oyster reefs, the large original populations in native areas had been severely affected because of overfishing, contamination, and the construction or expansion of seaports (Beck et al. 2011). Some of the efforts aimed at reestablishing natural oyster populations have focused on finding suitable alternative substrates. In this sense, Goelz et al. (2020) make an excellent review of the use of various alternative substrates used for oyster reef restoration.

Aquaculture activities pose a risk of species introductions when oysters are transplanted or introduced into different zoogeographic regions, including the introduction of new diseases. In addition, exotic oyster introduction produces competition and displacement of congener species with the same or greater capacities of negative effects on the ecosystems to which they are introduced. Although the movements of introduced oysters as in the case of *Crassostrea gigas* along the American coasts are almost exclusively related to aquaculture practices, this activity is recognized as one of the largest potential vectors for the transport of marine invasive species (Ruesink et al. 2005, 2006). For example, the snail *Batillaria attramentaria* was introduced to the west coast of the United States with *C. gigas*, where it outcompetes and is displacing the native snail *Cerithidea californica* in several estuaries (Byers 2000).

Ecological effects of nonindigenous species when introduced in native habitats are due to not only ineffective control strategies to prevent parasite and pathogen dispersion around the world but also as a natural consequence of globalization of world commerce. Every day, substantial amounts of live fishery or aquacultural products are distributed from one country to many other countries around the world. In this overall context, the species *Crassostrea gigas* introduced by aquaculture practices may have substantial effects in terms of biodeposits, altered flow regimes, and disturbance of the substrate (see Everett et al. 1995).

Oysters remove particles from the water column during suspension feeding and produce feces and pseudo-feces, which lead to reduced particle size and increased organic content in sediments (Ruesink et al. 2005). Although this process facilitates the action of the bacterial flora of the environment and of marine floors, Villarreal (1995) argue that in Bahía San Quintín (Baja California, Mexico), biodeposits coming from oyster cultures have been associated with eutrophication.

There are two species in the genus *Dendostrea* that have been reported sporadically in the tropics and subtropics of the American Pacific (Taxonomy, Identification, and Distribution), and very little information is available for these small and regionally rare species. The few reports show *Dendostrea folium* and *Dendostrea sandvichensis* from the Indo-Pacific, as species recorded in lists of Pacific islands, such as Isla Cocos in Costa Rica and the Galapagos Islands in Ecuador (Magaña-Cubillo & Espinosa 2009, Coan & Valentich-Scott 2012). It is important to mention that *D. folium* shows a quantitatively different karyotype ($2n = 18$; Ieyama 1990) the species of the family Ostreidae ($n = 20$), and that *D. sandvichensis* is called the Hawaiian oyster.

There are only a few studies on *Ostrea angelica* (formerly *Myrakeena angelica*), dealing with taxonomy (McLean & Coan 1996, Holguin-Quiñones et al. 2008, Bastida-Zavala et al. 2013) as well as paleontological and archaeological records (Laynder et al. 2013, Rugh 2014). Marcus and Harry (1982) described the planarian *Zygantroplana ups* associated with the mantle cavity of the *Ostrea angelica*, and recently, molecular phylogenetic studies confirm its integration into the genus *Ostrea* (Raith et al. 2016).

Reproduction

Most of the reproduction studies on tropical and subtropical oysters have been carried out in natural populations (Table 1). All species whose reproductive cycle has been studied so far, including *Striostrea prismatica*, *Crassostrea columbiensis*, *Crassostrea corteziensis*, and *Saccostrea palmula*, are gonochoric organisms, and in their populations, most of the males are smaller in size (Fournier 1992, Caballero et al. 1997, Cabrera et al. 2001b, Romo-Piñera 2005, Chávez-Villalba et al. 2008, Loor & Sonnenholzner 2014). This suggests a common characteristic of protramental hermaphroditism.

In these species, the gonad is distributed throughout the visceral mass (Fig. 9), which contains large amounts of oocytes. Spawning *Striostrea prismatica* individuals of 120 mm (dorsoventral axis) induced at CENAIM-ESPOL/Ecuador hatchery indicate a fecundity of 60 million oocytes/individual. This number could be higher considering that oysters of this species may reach twice that size (Lodeiros et al. 2017). Although fecundity of *Crassostrea corteziensis* is lower (50 million oocytes/individual) than that of *S. prismatica* according to several studies at CIBNOR Mexico (Chávez-Villalba et al. 2008, Rodríguez-Jaramillo et al. 2008), both species are considered great broadcast spawners. While *C. corteziensis* has the ability to attain sexual maturity and carry out several partial spawnings during a breeding season (Mazón-Suástegui et al. 2011).

The size at the sexual maturity in 50% of *Striostrea prismatica* populations on the coasts of Nayarit, Mexico, is 87–91 mm of the dorsoventral axis (Hernández-Covarrubias et al. 2013), whereas in *Crassostrea corteziensis* in Las Guasimas, Sonora, and in Ceuta Bay, Sinaloa (Mexico), it is 50–60 mm (Chávez-Villalba et al. 2008, Mazón-Suástegui et al. 2011). For other species, such as *Saccostrea palmula* and *Crassostrea columbiensis* of Punta Morales, Puntarenas (Costa Rica), the size at sexual maturity is 10–11 mm (Cabrera et al. 2001b).

Ríos-González et al. (2018) described phases of reproduction of *Striostrea prismatica* observed in a latitudinal gradient from north to south in tropical eastern Pacific. As observed in Table 1, studies on the reproduction of *S. prismatica* cover a wide latitudinal range, from 03° S (Costa de Tumbes, Peru) to 27.5° N (Guaymas, Sonora, Mexico). With the exception of studies conducted in Curú, Gulf of Nicoya, Costa Rica, where temperatures are always high (29.0°C–32.7°C), significant changes related to high temperatures were always associated with reproductive processes, particularly the maturation and spawning of *S. prismatica*.

TABLE 1.

Studies of the reproductive cycle of populations of native Ostreidae species of the tropical and subtropical American Pacific in north-south latitudinal order.

Place	Latitude/ longitude	(°C)	Reproductive activity	Comments	Source
Striostrea prismatica					
Guaymas, Sonora, Mexico	27° 55′ N 110° 55′ W –		Gametogenesis maturation: mid-May–mid-June Spawning: mid-June–August Rest: December–February		Ramírez and Sevilla (1965)
Mazatlán Bay, Sinaloa, Mexico	23° 10′–20′ N 106° 29′–30′ W – –	23.5–31	Gametogenesis maturation: April–September Spawning: June, and October–November Rest: December–March	Macro and microscopic observation (gonadal smear)/larval abundance and spat settlement	Silva (1984)
Del Pozo and del Rey estuaries, San Blas, Nayarit, Mexico	21° 35′ N 105° 20′ W – –	24.4–31.3	Gametogenesis: February–June Maturation: June–August Rest: October–May Spawning: August–September	Histology. Spawn at high temperatures above 27.5°C	Cuevas-Guevara and Martínez-Guerrero (1979)
San Cristóbal estuary, San Blas, Nayarit, Mexico	21° 31′ N 105° 17′ W –	20.1–30.9	Gametogenesis: January–May Maturation: May Spawning: July–September	Index; gravimetric methods. Gametogenesis at 23.8°C–27.3°C Spawning at 30°C–31°C	Frías-Espericueta et al. (1997)
Lázaro Cárdenas port and Zapote de Huahua, Michoacán, Mexico	17° 57′ N 102° 12′ W – –		Gametogenesis: May–June Maturation: August Spawning: August–December Rest: January–April	Histology. Maturation and spawning in association with warm months	Meléndez-Galicia et al. (2015)
De la Ventosa bay, Salina Cruz, Oaxaca, Mexico	16° 09′ N 95° 09′ W –		Gametogenesis maturation: February–July Spawning: August–September Rest: December–February	Histology, and spawning at high temperature	Ruíz-Durá (1974)
Curú, Gulf of Nicoya, Costa Rica	09° 47′ N 84° 54′ W	29.0–32.7	Continuous reproductive activity throughout the year	Histology. Low temperature variation. Spawning with the decrease in salinity	Fournier (1992)
Ayangue Bay, Province Santa Elena, Ecuador	01° 58′ S 80° 45′ W –	23.4–28.5 –	Gametogenesis: October–December. Maturation: December–March Spawning: January–March Rest: April–September	Histology High temperatures induce maturation and spawning –	Loor and Sonnenholzner (2014)
General Villasmil, province of Guayas, Ecuador	02° 38′ S 80° 26′ W –	24.1–29.6	Gametogenesis: September–December Maturation: December–February Spawning: January–March Rest: August–September	High temperatures induce maturation and spawning	Loor and Sonnenholzner (2014)
Punta Sal Grande and Nueva Esperanza, Coast of Tumbes, Perú	03° 43′–44′ S 80°45′–47′ W –	21.3–26.3	Gametogenesis: all year Maturation: December–March mostly ripe Spawning: all year, maximum February–Mar and May.	Visual scale/recruitment. High temperatures associated with the greatest spawning Recruit all year, maximum March–May	Ordinola et al. (2013)
Saccostrea palmula					
Santo Domingo, Magdalena Bay, Mexico	24° 48′ N 112° 07′ W –	18.7–29.4	Gametogenesis maturation: all year (except February) Spawning: January, and June–October (maximum activity) Rest: February	Histology. Maturation correlated with temperature Opportunistic species	Romo-Piñera et al. (2015)
Magdalena Bay, Mexico	24° 48′ N 111° 58′ W	17–29.8	Gametogenesis maturation: September–mid-January. Spawning: November–December.		García-Pamanes (1978)
El Chisguete estuary, Magdalena Bay, Baja California Sur, Mexico	24° 48′ N 111° 58′ W	17–29.8	Reproductive activity throughout the year Highest recruitment in March to June (maximum May)	Study of spat collection	Chávez-Villalba and Cáceres-Martínez (1994)

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TABLE 1.
continued

Place	Latitude/ longitude	(°C)	Reproductive activity	Comments	Source
San Carlos port, Magdalena Bay, Baja California Sur, Mexico	24° 46′ N	18.5–31.5	Gametogenesis maturation: all year	Spawning influenced by temperature, tides, and photoperiod	Romo-Piñera (2005)
	112° 06′ W		Spawning: June–October, July, and September maximums		
	–		Rest: November–March (low reproductive activity)		
Falsa Bay, Ensenada La Paz, Baja California Sur, Mexico	24° 16′ N	18–32	Reproductive activity throughout the year	Spat collection study	Chávez-Villalba and Cáceres-Martínez (1991)
	110° 19′ W		Recruitment December–January (maximum) and April–May		
El Conchalito, Ensenada La Paz, Mexico	24° 08′ N	16.5–28	Gametogenesis: February–August	Histology	Romo-Piñera et al. (2015)
	110° 20′ W		Maturation: April–September	Maturation correlated with temperature and chlorophyll *a*.	
	–		Spawning: September–December	Conservative species	
Del Pozo and del Rey estuaries, San Blas, Nayarit, Mexico	21° 35′ N	24.5–31.3	Gametogenesis: February	Histology	Cuevas-Guevara and Martínez-Guerrero (1979)
	105° 20′ W		Maturation: March–May	Spawning related to high temperatures	
	–		Spawning: June–November	Gametogenesis with low temperatures	
Morales estuary, Punta Morales, Puntarenas, Costa Rica	10° 04′ N		Reproductive activity throughout the year	Gonad smear macro and microscopically	Cabrera et al. (2001b)
	84° 57′ W		High spawning between November and January		
Marina Papagayo (Culebra bay), Costa Rica	10° 38′ N	26.3–30.7	Gametogenesis maturation: all year (except February)	Cytology (microscopic observation)	Alvarado (2018)
	85° 39′ W		Maturation	Maturation positively correlated with phytoplanktonic biomass and low salinity. Spawning possibly related to high temperature and low salinity.	
	–		High maturity proportion from August to November	–	
Crassostrea corteziensis					
Guaymas, Sonora, Mexico	27° 55′ N	–	Gametogenesis maturation: mid-February–July	–	Ramírez and Sevilla 1965
	110° 55′ W		Spawning: August–September		
	–		Rest: mid-November–mid-February		
Las Guásimas, Sonora, Mexico	27° 53′ N	15–33.5	Gametogenesis maturation: May–November	Histology	Chávez-Villalba et al. (2008)
	110° 38′ W		Spawning: April–November	Culture	
	–		Rest: December	High association with temperature changes	
Agiabampo Bay, Sonora, Mexico	26° 22′ N	22.3–32	Gametogenesis: March–April	Histology	Mazón-Suástegui et al. (2011)
	10° 912′ W		Maturation: April–November	December–January not sampled	
	–		Spawning: August–September	–	
	–		Rest: February–half of March	–	
System lagoons of Ceuta, Gulf of California, Sinaloa, Mexico	24° 05′ N	19.5–31.5	Gametogenesis, maturation, and spawning during most of the year	Histology	Rodríguez-Jaramillo et al. (2008)
	107° 09′ W		Rest: December–February	Maturation is activated >20°C	
	–		–	Spawning >27°C	
San Cristóbal estuary, San Blas, Nayarit, Mexico	21° 35′ N	20.1–30.9	Gametogenesis: January–November	Histology and presence of larvae	Stuardo and Martiìnez (1975)
	105° 20′ W		Spawning: June–October	Spawning when temperatures are high (>25.5°C)	
	–		Rest: November–April		
Del Pozo and del Rey estuaries, San Blas, Nayarit, Mexico	21° 35′ N	24.5–31.3	Gametogenesis: February	Histology	Cuevas-Guevara and Martínez-Guerrero (1979)
	105° 20′ W		Maturation: March–May	Spawning when high temperatures	
	–		Spawning: May–November	Gametogenesis at low temperatures	
	–		Rest: January	–	

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TABLE 1.

continued

Place	Latitude/ longitude	(°C)	Reproductive activity	Comments	Source
San Cristóbal estuary, San Blas, Nayarit, México	21° 32′ N	20.1–30.9	Gametogenesis maturation: February–April and May–July	Indexes by tissue weights	Frías-Espericueta et al. (1997)
	105° 17′ W		Spawning: April–May and July–September (less intense)	Spawning when temperature rises 4°C	
	–	–	Rest: November–January	–	
La Palicienta lagoon, Boca de Camichín, Nayarit, México	21° 43′–45′ N 105° 29′–30′ W	25.5–33–0	Gametogenesis maturation: March, April, and July	Histology Temperature positively related to gametogenic development and particularly to spawning	Mena-Alcántar et al. (2017)
	–		Spawning: May, August, and October	–	
	–		Rest: December–February	–	
De la Ventosa Bay, Salina Cruz, Oaxaca, Mexico	16° 09′ N		Gametogenesis maturation: mid-February–July	Histology	Ruíz-Durá (1974)
	95° 09′ W		Spawning: August–September	Interruption of reproductive activity with lower temperatures	
	–		Rest: December–February	–	
Crassostrea columbiensis					
Los Praditos, Santo Domingo Bay, Baja California Sur, México	25° 20′ N	14.5–30	Reproduction occurs throughout the year	Histology Temperatures >22°C favor gametogenesis, 26°C–30°C maturation	Félix-Pico et al. (2011)
	112° 04′ W			Temperature decrease favors spawning	
	–				
Morales estuary, Punta Morales, Puntarenas, Costa Rica	10° 04′ N 84° 57′ W		Reproductive activity throughout the year. Maximum spawning in May and October	Gonad smear and macro and microscopic observation	Caballero et al. (1997)

Rest = undifferentiated and postrecovery reabsorption (no reproductive activity).

Loor and Sonnenholzner (2014) reported that there is no correlation between phytoplankton biomass (estimated by chlorophyll *a*) and the reproduction of *Striostrea prismatica* in the two places studied on the Santa Elena peninsula, Ecuador (General Villasmil and in Ayangue). In these locations, the chlorophyll *a* concentrations are greater than 2 μg/mL, suggesting that food availability is not a limiting factor. Similarly, other studies conducted in tropical areas such as the Gulf of Nicoya, Costa Rica, show that food availability does not appear to be a limiting factor for the reproductive processes of the species. Although Fournier (1992) did not record data on food availability in his study at the Gulf of Nicoya, it is known that the area is highly productive (León et al. 1998). In these high-productivity tropical systems, where the temperature is stable (<4°C annual variability in our analysis, Table 1), other environmental factors could be the main modulators of reproduction (Giese & Pearse 1974). Accordingly, Fournier (1992) found a negative association between spawning periods and salinity periods. In view of this, everything seems to indicate that temperature variability is the main factor in the modulation of *S. prismatica* reproduction, and, when its anual variability is minimal, salinity appears to be the main modulation factor. This agrees with the protocols established by Argüello et al. (2013) for gonadic conditioning of *S. prismatica* at high temperatures, consequently causing induction to spawning temperature changes from 28°C to 33°C accompanied by the reduction of salinity from 32 to 15.

In the southern Gulf of California, at El Verde, Sinaloa, it has been observed that *Striostrea prismatica* accumulates reserves during most of the year, which it mobilizes according to reproductive demand. Lipids decrease from October to March during the resting phase, and carbohydrates have an inverse trend in the months of April to May and June to July, whereas proteins increase in May when gametogenesis is activated and, with it, sexual maturation (Páez-Osuna et al. 1993). The aforementioned suggests that the reproductive strategy in the species is conservative.

Unlike *Striostrea prismatica*, reproduction studies in *Crassostrea corteziensis*, *Saccostrea palmula*, and *Crassostrea columbiensis* (Table 1) show in general, and regardless of latitude, a year-round reproductive activity with few periods of sexual rest. Temperature is the predominant modulating factor both for maturation (average temperatures) and spawning (high temperatures). An exception, and at the same time an interesting case, is the behavior of *S. palmula* indicated by Romo-Piñera (2005) and Romo-Piñera et al. (2015) in Santo Domingo, Magdalena Bay, and El Conchalito in La Paz Bay, Baja California Sur, Mexico. Even though these sites have similar temperature ranges and latitudes, natural populations of this species behave reproductively different, being opportunistic at the first site and conservative in the second. This difference is possibly associated with food availability, because at Santo Domingo, chlorophyll *a* has always been greater than 1 μg/L, with periods of higher production (>3 μg/L and up to 9 μg/L), whereas at El Conchalito, it was always less than 1 μg/L.

Other studies on the effect of environmental variables on gonad maturation, immunology, and genetic diversity have been carried out on *Crassostrea corteziensis*. Rodríguez-Jaramillo et al. (2008) and Chávez-Villalba et al. (2008) described the quantitative and qualitative histology and histochemistry of *C. corteziensis*. Mature organisms were found during most of the year, and there were at least two strong spawning periods, first in summer and then in autumn.

The two reproductive studies reported for *Crassostrea columbiensis* in the Bay of Santo Domingo, Mexico (Félix-Pico et al. 2011), and at Estero Morales, Costa Rica (Caballero et al. 1997), are contrasting in terms of the distance in a latitudinal order (24° and 10°, respectively); however, both populations show reproductive activity throughout the year (Table 1). In the case of Santo Domingo, where there is a greater annual temperature range, average temperatures greater than 22°C favor gametogenesis, and high temperatures (26°C–30°C) favor maturation, with a temperature decrease inducing spawning (Félix-Pico et al. 2011).

In general, the natural or harvest habitats, where the tropical and subtropical Pacific North American oysters develop, seem to provide enough phytoplankton biomass to support their reproductive processes so that the environmental modulation of reproduction is governed mainly by temperature, particularly in the maturation and spawning processes. As was indicated, in those tropical ecosystems where the temperature variability is not high, salinity also seems to be an important factor for spawning.

There are no published data to indicate the establishment of naturally reproducing populations of the Japanese or Pacific oyster *Crassostrea gigas* or the Kumamoto oyster *Crassostrea sikamea* beyond southern California, United States, or in the subtropical and tropical countries of the American Pacific Southern Hemisphere. Recently, however, the presence of the Japanese oyster has been reported outside culture sites in the Ojo de Liebre lagoon, which corresponds to the El Vizcaíno Biosphere Reserve in the Gulf of California (Carrasco & Barón 2010). Studies detailing the reproductive processes of cultivated *C. gigas* have been performed in Mexico. The species behaves as a protandrous hermaphrodite (Paniagua-Chávez & Acosta-Ruíz 1995), and depending on the region (Baja California or Sonora), the gonads are in early gametogenesis from January until June, in vitellogenesis from March to July, and mature from June to October, and partial spawning occurs from August to October (Cáceres-Martínez et al. 2004, Rodríguez-Jaramillo et al. 2017). Nevertheless, Chávez-Villalba et al. (2007) indicated that the species did not spawn in Sonoran waters, and there was evidence that oocytes were reabsorbed within the gonad. It seems that temperature regimes are the main limiting factors for the normal processes of spawning, fertilization, and larval settlement, thus preventing the establishment of feral populations. Recently, histological studies to determine the reproductive condition of *C. gigas* culture in a tropical estuary at Bahía de Caráquez, Manabí, Ecuador (0° 36′3″ S, 80° 25′23″ O), show that oysters greater than 40 mm maintain a protrandic condition with a female to male ratio of 1:2.6 with partial spawning (Lodeiros, unpublished data). This indicates limited processes for the development of *C. gigas* larvae or postlarvae in subtropical and tropical regions, restricting the establishment of feral populations.

There are no reproductive studies of the Kumamoto oyster *Crassostrea sikamea* in the tropical and South American Pacific. Nevertheless, Cáceres-Martínez et al. (2012) reported that Kumamoto oysters start gametogenesis as young as 71 days from spawning (35 days from postsettlement), with a mean shell height of 3.0 mm. This constitutes a record in age size for gametogenesis in oysters of commercial importance and adds another biological difference comparing this species with the Pacific oyster *Crassostrea gigas*.

Bioacumulators

Because of the filtering characteristics of oysters and their commercial importance, various studies have been undertaken to determine whether they bioaccumulate unwanted substances, compounds, or organisms. For instance, *Striostrea prismatica* has been used to detect organochlorine pesticides (Ponce-Vélez & Botello 2018) and heavy metals (Páez-Osuna et al. 1995, Frías-Espericueta et al. 1999a, 1999b, Soto-Jiménez et al. 2001, Osuna-López et al. 2007). Oysters also accumulate bacterial species that can cause epizootics and pathogenic agents that affect their consumption safety at harvest. In this sense, it is necessary to remember that the microbiota associated with the intestinal digestive tract of the ostreids contributes various beneficial substances to the host; it presents antibiosis or competition for space and nutrients against pathogens and their composition, and diversity varies according to the age of the mollusc and the culture site (Trabal-Fernández et al. 2014). The distribution of *S. prismatica* along the rocky coasts of the tropical and subtropical eastern Pacific suggests that the species could be used as a model in ecotoxicological studies for rocky systems. Similarly, evidence of heavy metal accumulation in conspicuous oyster species (*Crassostrea corteziensis*, *Saccostrea palmula*, and *Crassostrea columbiensis*) in the mangrove systems of the region has allowed them to be considered (particularly *C. corteziensis*) as biomarker organisms (Páez-Osuna et al. 2002, Jara-Marini et al. 2008, Bernal-Hernández et al. 2010, García-Rico et al. 2010, Páez-Osuna & Osuna-Martínez 2015). Given the direct human consumption of various molluscs, including *S. prismatica*, some studies have been carried out to advise managers on the advisability of establishing continuous monitoring programs for toxicity because of harmful algal blooms (Barraza et al. 2004, Band et al. 2010, Alonso-Rodríguez et al. 2015).

Diseases

Few diseases have been described for tropical and subtropical oysters of the American Pacific. Most reports have been for oysters (*Crassostrea gigas* and *Crassostrea sikamea*) introduced from temperate zones (Elston & Wilkinson 1985, Bower et al. 1997, Friedman et al. 1998, Burreson & Ford 2004, Friedman et al. 2005, Burge et al. 2011, Moore et al. 2011).

In a subtropical region (Baja California, México), a virus belonging to the Herpesviridae was detected after a *Crassostrea gigas* mortality event in 2000, although the role of the presumable pathogens has not been clearly defined (Vásquez-Yeomans & Cáceres-Martínez 2004, Vásquez-Yeomans et al. 2004). The OsHV-1 herpesvirus was later found in the gills of the species (Vásquez-Yeomans et al. 2010). Recently, nine genotype variants of OsHV-1 were identified in the Gulf of California, and genetic analysis suggested that linear genotypic evolution had occurred from strain JF894308 present in lagoon La Cruz (Sonora, Mexico) in 2011 (Martínez-García et al. 2020). The prevalent pathogen of oysters, *Perkinsus marinus*, causing the dermo disease or perkinsosis, has been associated with massive mortalites of *C. gigas* in culture conditions along Sonoran coasts, Mexico (Enríquez-Espinoza et al. 2010). Similarly, the protozoan *Marteilia refringens* was detected for the first time in the Gulf of California in samples of *C. gigas* (Grijalva-Chon et al. 2015). The presence of parasites including ciliates (*Ancistrocoma* and *Trichodina*), the annelid *Polydora* sp., and trematode worms has also been detected in Pacific oysters in northwestern Mexico, but they have not been associated with mortalities (see Cáceres-Martínez & Vásquez-Yeomans 2008 for more details).

In the native oyster *Crassostrea corteziensis*, a series of epizootics diseases associated with parasites, bacteria, or viruses have been recorded (Grijalva-Chon et al. 2015). This problem has been associated with the presence of *Perkinsus marinus*, *Nematopsis* sp., and some protozoa such as *Halteria grandinella*, *Hexamita* spp., *Bodo* spp., and *Marteilia refringens* during the larval and juvenile stages of the species. Reports of high mortality in larval culture associated with the presence of *Vibrio* spp. are also common and increasingly frequent (Campa-Córdova et al. 2009, 2011). Martínez-García et al. (2017) studied the possible presence of a temporary coupling of infectious events in distant cultures of *C. corteziensis* in the Gulf of California considering seasonal variation, presence, and the prevalence of *P. marinus*, *M. refringens*, and OsHV-1. Results of the molecular analysis showed a higher prevalence of *P. marinus* in the north area and *M. refringens* in the southern area. The OsHV-1 herpesvirus was only present during summer and autumn with low prevalence in the two areas. The histological analysis of the PCR-positive organisms presented alteration characteristic of infections. The presence of *M. refringens* in a new location in the Gulf of California suggests that this pathogen is already well established in the area, and the dual presence of pathogens is reported for the first time in *C. corteziensis*.

Gutiérrez-Rivera (2014) compared the immune response of the Cortez oyster *Crassostrea corteziensis* and the eastern oyster *Crassostrea virginica* after their experimental infection with the protozoan *Perkinsus marinus*. Results indicated that the protozoan caused greater mortality in the eastern oyster. This possible resistance to *Perkinsus* adds consideration of *C. corteziensis* as a good candidate for aquaculture, in addition to its better flavor and texture (Mazón-Suástegui 2014). Conversely, Bravo-Guerra (2018) showed that the parasite could be treated therapeutically because it shows a high susceptibility to silver nanoparticles at a concentration of 0.0927 mM Ag, an order of magnitude less than the concentration known to impart negative effects on *C. corteziensis*.

The parasite *Bonamia* spp. is commonly associated with oysters from temperate zones, but Hill et al. (2014) detected a *Bonamia* sp. in *Dendostrea sandvicensis* from Hawaii. This record, together with others detected in *Ostrea edulis* in Australia (Morton et al. 2003) and South Africa (Haupt et al. 2010), confirms that *Bonamia* parasites have extended their presence in tropical climates.

Bacterial infections have been little studied in the subtropical and tropical oysters of the American Pacific, and, although there is a relationship of bacterial infection when oysters are infected with the OsHV-1 virus (Cáceres-Martínez & Vázquez-Yeomans 2013), there are no specific studies that can determine the type of these infections. Luis-Villaseñor et al. (2018) conducted a study on the communities of the oysters *Crassostrea corteziensis* and *Crassostrea sikamea* from commercial oyster farms in Mexico. They found that the Kumamoto oyster *C. sikamea* presented a greater diversity of species and the highest number of pathogenic bacteria for aquatic organisms, which is a probable reflection of their poor health status in tropical culture.

POPULATION GENETICS AND PHYLOGENETIC STUDIES

Despite the fact that the Ostreidae are a conspicuous component of the coastal marine biodiversity of the tropical American Pacific, the inherent complications associated with an easy and secure identification are reflected in the paucity of studies on population genetic structure for ostreids from this region. Given the diversity of species in the family and their extended geographic ranges, relatively little has been published on the population genetics of the species in the Northern Hemisphere of the tropical American Pacific. In this sense, there are no data published on *Dendostrea folium*, *Dendostrea sandvichensis*, *Undulostrea megodon*, *Crassostrea aequatorialis*, or *Crassostrea sikamea*.

Saccostrea palmula

There are no population genetic studies for this species, but in the contribution by Cruz et al. (2007) on the microsatellite loci for *Crassostrea corteziensis*, they mention that of the 11 loci characterized for the Cortez oyster, seven can be amplified in *Saccostrea palmula*, which makes them suitable for population studies. Mazón-Suástegui et al. (2016) reported sequences of mitochondrial cytochrome c oxidase subunit 1 (*COI*) gene, the nuclear intertranscribed spacer 1 (*ITS-1*), and the nuclear *28S* ribosomal gene. By means of a phylogenetic analysis with sequences of other species of ostreids, these authors concluded that the *28S* gene was more reliable in correctly identifying species; thus, it can be used as an alternative marker. Raith et al. (2016) included *S. palmula* in a phylogenetic analysis with ostreids from the Gulf of California using *COI* and *16S* ribosomal gene sequences and mentioned a lack of genetic variation in *S. palmula*, and validated the *Saccostrea* genus.

Ostrea angelica

This species also lacks studies of population genetic diversity. The phylogenetic analysis carried out by Raith et al. (2016) confirms the closeness of this species with *Ostrea conchaphila* and *Ostrea lurida*, and placed the species within the genus *Ostrea* while invalidating the genus *Myrakeena*.

Striostrea prismatica

The levels of genetic diversity and population structure are also unknown in this species. For this species, Mazón-Suástegui et al. (2016) report sequences of *COI*, *ITS-1*, and *28S* that can be used in phylogenetic studies. In the phylogenetic study carried out by Raith et al. (2016), it is proposed that *Striostrea* is the only member of the new subfamily Striostreinae.

Ostrea conchaphila

The level of genetic diversity in this species is unknown. When analyzing *16S* and *COIII* mitochondrial markers, Polson et al. (2009) determined that this species is not a synonym for *Ostrea lurida*. Subsequently, the phylogenetic study of Raith et al. (2016) confirmed the genetic closeness with *O. lurida* and determined that there is no sympatry between them. With this molecular identification, these authors also extended its distribution range to Laguna San Ignacio, south of Punta Eugenia, Baja California Sur (Mexico).

Crassostrea columbiensis

For this species, there is only a report of the sequences of *COI*, *ITS-1*, and *28S* by Mazón-Suástegui et al. (2016).

Crassostrea corteziensis

In the tropical and subtropical eastern Pacific, *Crassostrea corteziensis* is the native ostreid species with the greatest aquaculture and fishing exploitation. Because of this, more attention has been paid to it than to the oyster species in the region. Thirty-one years ago, Rodríguez-Romero et al. (1979) described the karyotype of the species, determining that it has 20 chromosomes. Hedgecock and Okazaki (1984) carried out the first population genetics study with allozymes in organisms from Estero el Pozo, Nayarit (Mexico). These authors analyzed 17 loci, of which 58.8% were polymorphic, with an average of 2.12 alleles per locus and observed heterozygosity (*Ho*) of 13.8 and expected heterozygosity (*He*) of 19.6, outside the equilibrium of Hardy–Weinberg (HW). In the same state of Nayarit, Rodríguez-Romero et al. (1988) compared the electrophoretic profile of general proteins in organisms from two localities (Estero el Pozo and Estero Teacapan), finding statistically significant differences between the areas.

Cruz et al. (2007) reported 11 microsatellite loci for *Crassostrea corteziensis*, of which 10 proved to be polymorphic. These authors performed a test analysis with 30 wild oysters from Sinaloa and found four loci that were out of HW equilibrium, and concluded that these loci were useful for paternity tests and for population genetics studies. Later, in a study with samples from five locations within the Gulf of California, Pérez-Enríquez et al. (2008) carried out a population genetic study with allozymes and mitochondrial DNA markers. The analysis of six allozymic loci (four polymorphic) showed that *Ho* was in the range of 0.058–0.117 and the *He* was 0.089–0.129, with HW equilibrium and without evidence of a population structure because of high genetic flow. Considering the levels of diversity reported by Hedgecock and Okazaki (1984), it was concluded that diversity did not change substantially in 20 y; on the other hand, an atypical result in the genotypic frequencies of the samples taken in Topolobampo, Sinaloa (Mexico), motivated these authors to perform a sequence analysis of the *16S* mitochondrial gene, which demonstrated the presence of an unknown species, and the authors considered it to be *Crassostrea columbensis*.

Enríquez-Espinoza and Grijalva-Chon (2010) carried out an analysis of allozymes in a sample of the F1 generation descendent from a stock of breeders of wild origin from Sinaloa, Mexico. That F1 generation was cultivated in the state of Sonora. The 13 allozymic loci studied included eight polymorphic loci that were out of HW equilibrium, with an average *Ho* of 0.065 and *He* of 0.294, and with high inbreeding values.

Regarding the inclusion of this species in phylogenetic analyses, Raith et al. (2016) included it in their analyses of ostreids from the Gulf of California, so they also reported *16S* and *COI* sequences for this species. Mazón-Suástegui et al. (2016) also report sequences for *COI*, *ITS-1*, and *28S*.

Crassostrea gigas

Although some studies indicate the possibility of feral populations of *Crassostrea gigas* in Ojo de Liebre lagoon, Gulf of California, Mexico (Carrasco & Barón 2010), the population genetic studies of the species are limited to cultivated populations. Enríquez-Espinoza and Grijalva-Chon (2010) carried out an analysis with allozymes in a batch of triploid organisms that arrived as spat at Sonora. Sixteen loci were analyzed, of which 12 were polymorphic, with nine of them out of HW equilibrium, and with *Ho* and *He* averages of 0.350 and 0.309, respectively. The authors discussed the quality of these organisms because the heterozygosity values were lower than those reported for triploid oysters in the United States.

Grijalva-Chon et al. (2013) used microsatellites to analyze genetic variability in a sample from a batch of breeders that were purchased as spat from France. A second sample consisted of organisms from the F1 generation of that batch. Up to 68 alleles and 168 genotypes were detected with six microsatellite loci, with differences in the averages of the heterozygosity observed and expected in both samples ($Ho = 0.65$ and $He = 0.81$ for the parental lot; $Ho = 0.67$ and $He = 0.84$ for F1), and out of HW equilibrium in almost all loci. Finally, in the phylogenetic study reported by Raith et al. (2016), organisms of this species obtained from an oyster farm in Puerto Peñasco, Sonora, Mexico, were included.

FUTURE STUDIES

The morphological plasticity of oysters complicates their identification and, therefore, classification and taxonomy. Identification based on shell morphology has led to confusion, which has skewed production statistics, leading to an uncertain scenario for the administration of the resource, particularly in Latin America.

In recent decades, in general, efforts have been made with genetic-evolutionary studies to understand the diversity and taxonomy of oysters (Bayne 2017); however, taxonomic uncertainties still exist, and many species have not been subjected to adequate genetic analysis. There is a great need for a global survey of living oysters and a comprehensive analysis of both genetic and morphological data (Guo et al. 2018). This globally analytical need is more critical for oysters in the tropical Pacific and South American tropics, given the lack of taxonomic and genetic studies (Li et al. 2017). Therefore, it is recommended to develop studies for this purpose. A suggested focus of study is the identification and taxonomic-systematic evaluation of the endemic equatorial oyster *Crassostrea equatorialis*, whose identification characteristics are uncertain and unclear. Similarly, the taxonomic identification or reformulation of oysters with major exploitable banks is necessary even without genetic identification or clarification.

Oyster populations in the tropical and subtropical Pacific have shown signs of overexploitation for a few decades (MacKenzie & Buesa 2006), and organized research has not been carried out for these species; thus, it is essential to establish strategies for ecological protection and restoration of their populations. By contrast, there are studies on the reproduction of various commercial species that could be used to administrate their populations.

Oysters in general have a euryplastic physiology and could easily be model species to study molluscan responses to stressors as xenobiotic agents. Although there are proven studies on the consideration of oysters as model species in ecotoxicology, these studies of oysters from the American tropic and subtropical Pacific are practically nonexistent. Studies that are adequately designed to establish physiological responses, optimal ranges, and tolerance to environmental factors are necessary in these species not only to understand the physiology of tropical invertebrates but also to establish ecophysiological knowledge tool for reproduction under controlled conditions for the development of production strategies and ecological restoration.

Oysters that are filter feeders thus become systems of microbial and toxin accumulation. Few studies have been conducted on these topics. They are necessary for the development of both aquaculture and the safety of human health.

Some studies have been conducted on oyster diseases in the American Pacific subtropics, particularly in introduced oysters (*Crassostrea gigas* and *Crassostrea sikamea*) and one native oyster (*Crassostrea corteziensis*); however, it is necessary to strengthen these studies and extend them to tropical oysters, particularly those of greater commercial interest and potential for aquacultural purposes (*Striostrea prismatica* and *Crassostrea columbiensis*).

Although the nutritional benefits of oysters are known in general, mainly in temperate zones (see review of Venugopal & Gopakumar 2017, Wright et al. 2018), it is necessary to initiate nutritional studies that also include a profile of fatty acids, amino acids, and other molecules of great benefit to man for oyster species living in subtropic and tropical environments, to nutritionally enhance their consumption. It is suggested that this research should be carried out by separating cultivated oysters from those in natural populations, as well as seasonally sampling to differentiate their physiological response, particularly in relation to their reproductive state. The results of these investigations could generate information to benefit the marketable price at harvest and the overall economic profitability of the developing oyster industry in subtropical and tropical regions.

It would be useful to know the impacts of aquaculture activities with *Crassostrea corteziensis* and *Crassostrea gigas* on natural environments, especially in areas with large production volumes. It is also necessary to identify places where *C. gigas* has established feral populations, particularly in subtropics of the American Pacific, but without excluding the possible long-term adaptation of the species to tropical environments. This is needed to determine the risks to endemic oysters and other residents, and in general for the ecology of the region. In these cases, it is essential to establish management strategies to control feral populations.

The paucity of information on population genetic structure and genetic diversity of ostreids from the American Tropical Pacific is a need that must be addressed in the short term; however, this should be seen as a window of opportunity for collaboration between the academic institutions of all countries bordering the American Tropical Pacific.

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