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Research Article

Population dynamics of the rock oyster *Striostrea prismatica* in two different environments of the Mexican central Pacific

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ABSTRACT. This study aimed to determine the population dynamics (size, weight, growth, and mortality) of the rock oyster *Striostrea prismatica* (Gray, 1825) settled in two different environments: the shallow rocky sublittoral of Faro de Campos and the Cuyutlan lagoon (Colima, Mexico). The oysters from Faro de Campos (coastal site) recorded greater size and weight than in the lagoon site. Analysis of the length-frequency distribution showed five modal groups in the overall population, four in the lagoon, and only three at the coastal site. The length-weight ratio indicated negative allometric growth in the oysters at both sites. Although the asymptotic length or infinite height (H_∞) and growth coefficient (*k*) were similar in the lagoon (H_∞ = 176 mm; *k* = 1.3 yr^{-1}) and in the coastal site (H_∞ = 174 mm; k = 1.06 yr^{-1}), the lagoon oysters reach maximum length in less time than those on the coast. Mortality indicators showed signs of overexploitation on both sites, particularly in the lagoon (exploitation rate, E = 0.62), and at the upper limit of population exploitation at the coastal site (E = 0.5). This information is relevant for the sustainable management of the species in the Mexican central Pacific.

Keywords: *Striostrea prismatica*; length-weight ratio; growth; mortality; lagoon estuarine; shallow rocky sublittoral

INTRODUCTION

The rock oyster, *Striostrea prismatica*, is a filter-feeding bivalve inhabiting the first 10 m of depth along the rocky coastline, from the intertidal zone to the shallow rocky sublittoral. This species is found from La Paz, Baja California Sur (24.2°N) and Mazatlán, Sinaloa (23.2°N) in Mexico, to Mancora, Tumbes, Peru (4.1°S) (Keen 1971, Coan & Valentich-Scott 2012). It is an important fishery resource in the eastern tropical Pacific, particularly in the Mexican Pacific. Oyster fisheries in Mexico (54,964 t annually) mainly rely on three main species: the eastern oyster *Crassostrea virginica* in the Gulf of Mexico, the pleasure oyster *C. corteziensis*, and the rock oyster *S. prismatica* on the Pacific (DOF 2018). Other oyster species contribute little to commercial catches, especially those collected by local fishermen on Mexico's Pacific coast (Poutiers 1995, DOF 2018). In the Mexican Pacific, the oyster fisheries' closed season runs from June 1 to August 31 (DOF 2018). Oyster resources are mainly harvested by free diving, by boat with an outboard motor, hookah

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diving, or diving with a variable-power air compressor unit with 100 m of hose and the support of a lifeline or a person in charge of the boat. The fishing gear includes a steel rod, a knife, and collecting bags, as well as basic free-diving equipment: goggles, fins, and a weight belt.

Studies on population dynamics are necessary for proper resource management and exploitation, as they are required to estimate population size and structure, individual growth, mortality, recruitment, and maximum sustainable yield, among other population variables related to their capture and level of exploitation, which could affect survival rate, sexual maturation, and fecundity (Sparre & Venema 1997). Population dynamic studies of the rock oyster include the work of Melchor-Aragón et al. (2002), who evaluated growth and mortality in natural areas along the coast of Baja California Sur, Mexico, using the capture-recapture technique. Estimates of the abundance of this oyster have been evaluated along the southern coast of Nayarit, Mexico, by Patiño-Valencia & Ulloa (2008), where they report a fishing effort greater than the populations of this oyster can withstand, mainly due to poaching, and to the capture of juvenile organisms that have not yet reached the size of first maturity (L_{50}). Similar studies have been conducted along the coast of Peru, in the region of Tumbes, where a differential spatial distribution by size has been reported, with juvenile organisms found at shallow depths and adults at greater depths, along with an overall abundance of 0.2 ind m^{-2} (Ordinola et al. 2010).

Methods for estimating the growth of aquatic organisms are either indirect (size-based) or direct (rigid-structure-based). Indirect methods analyze length-frequency distributions. Multimodal distributions suggest similar age groups or cohorts for each mode. Direct methods examine periodically formed marks in hard structures, like otoliths and spines (Galindo-Cortes 2005). In tropical marine species, the difficulty of obtaining hard structures with periodic markings has led to indirect methods being a viable alternative for age and growth estimation. In this sense, numerous numerical approaches have been proposed to estimate growth through indirect methods. Most of these are based on parameter estimates for the von Bertalanffy (1938) growth function (VBVF). Currently, methods that account for most of the information in the size-frequency distribution are preferred over those based solely on modal length identification. Among the most frequently used methods are the Electronic Length Frequency Analysis (ELEFAN I; Pauly & David 1981) and the New Shepherd's Length Composition Analysis (NSLCA; Pauly & Arreguín-Sánchez 1995) originally proposed by Shepherd (1987). Studies using the indirect method in rock oyster populations include the work of García-Delgado & Leones-Zambrano (2016), conducted across various populations along the coast of Ecuador, and the study of Ríos-González (2021), conducted across various populations on the southern coast of Nayarit and the coast of Jalisco, Mexico.

Studying growth and biological processes is essential for fishery resource management. Organism growth each year helps maintain catches in a fishery (Pauly 1984). This study, therefore, aimed to evaluate the population structure of the rock oyster, *S. prismatica*, in two environments: the rocky sublittoral of Faro de Campos and the Cuyutlan lagoon on the Colima coast, Mexico. We estimated the length-weight relationship, growth parameters of the von Bertalanffy equation, total mortality, natural mortality, fishing mortality, exploitation rate, and survival rate.

MATERIALS AND METHODS

Sampling at the study sites

Sampling was conducted at five oyster beds along the coast of Colima, Mexico (Mexican central Pacific), divided into two site categories: coastal and lagoon. The coastal site included three oyster beds located in the rocky sublittoral adjacent to Faro de Campos (19°01'20.13"N, 104°20'11.44"W; 19°00'43.81"N, 104°19'48.25"W; and 19°02'06.21"N, 104°00'00.97"W), with depths not exceeding 10 m. The lagoon site included two oyster beds in basin two (V2) inside Cuyutlan lagoon (19°00'15.84"N, 104°15'8.64"W; and 19°01'1.39"N, 104°15'3.34"W), at depths of up to 5 m. The lagoon consists of three regulating basins: Basin 1, which is connected to the sea via the Ventanas Channel; Basin 2, which is connected to the sea via the Tepalcates Channel; and Basin 3, which has no connection to the sea, as shown in Figure 1. Oysters were collected monthly from each bed, with samples from the three beds pooled for the coastal site and samples from the two lagoon beds pooled for the lagoon site. The sampling period for both sites was from September 2018 to August 2019.

The collection was performed with the support of local fishermen using hookah or compressor diving. The number of oysters collected by fishermen varied across sites and times, but was around 200 ind per month at the lagoon site and 100 at the coastal site. Each collected oyster was cleaned with spatulas and brushes to remove the epibionts from the shell. Then, the shell

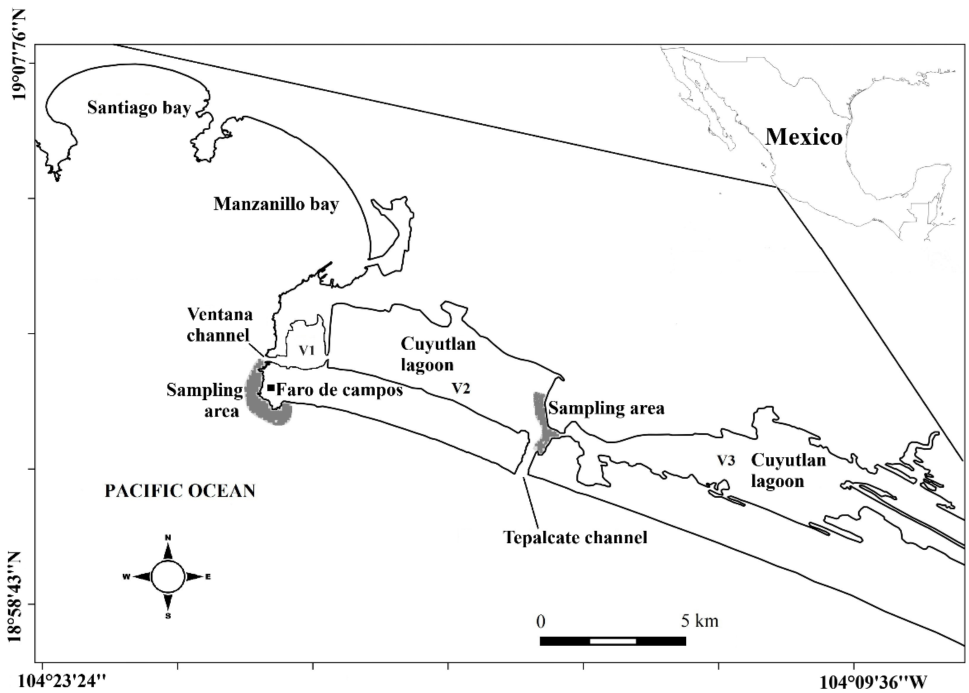

Figure 1. Map showing the collection sites of the rock oyster *Striostrea prismatica*; coastal site (Faro de Campos) and lagoon site (Cuyutlan) on the coast of Colima, Mexico. V1: regulating basins 1, V2: regulating basins 2 and V3: regulating basins 3.

height (H) from the umbo to the distal edge was measured with an electronic vernier caliper, and the total weight (W) of the organism was recorded using a scale with a capacity of 1,000 g and a sensitivity of ±1 g, removing as much moisture as possible with blotting paper. Because the oysters belonged to the fishermen, they were not opened.

Size-weight ratio

The ratio of shell height to shell weight was estimated using the equation proposed by Ricker (1975): $W = a \times H^b$, where W is the total weight (g); a is the intercept, b is the slope, and H is the shell height (mm). The isometric growth hypothesis was tested using a *t*-Student test (Zar 2010) with $\alpha = 0.05$ and the hypothesis Ho: $b = 3$ *vs*. Ha: $b \neq 3$.

Modal progression analysis (modal or age groups)

Validation of the organisms' ages was carried out using size-frequency distribution analysis and tracking of modes over time. The FISAT FAO-ICLARM Stock Assessment Tools program (Gayanilo et al. 1996), which applies the method of Bhattacharya (1967) (Pauly & Caddy 1985), was used to determine the monthly modes of the entire population at both sites and per site. At both sites, coastal and lagoon, the length distribution (height) used a range of 5 mm.

Growth

The growth estimate was analyzed using the von Bertalanffy (1938) equation:

$$\text{VBGF}: H = H_\infty\,[1 - e^{-k}(t - t_0)]$$

where H (mm) is the shell height at age t, H_∞ (mm) is the asymptotic total height, k is the growth coefficient, and t_0 is the theoretical age when its length is zero. Growth was based on size-frequency distributions with a 5 mm range, using FiSAT II software (version 1.2.2) (Gayanilo et al. 1996). First, applying the ELEFAN I routine, the H_∞ and k were estimated; second, t_0 was calculated according to the formula noted by Pauly (1979):

$$t_0 = \log_{10}(-t_0) = -0.3922 - 0.2752 \times \log_{10} H_\infty - 1.038 \times \log_{10} k$$

where t_0 is the hypothetical age at which the length is zero, H_∞ is the maximum asymptotic average total height, and k is the growth constant or curvature coefficient.

For the calculation of longevity, the Taylor (1960) equation was used:

$$A_{0.95} = t_0 + (2.996 / k)$$

where $A_{0.95}$ is the theoretical age limit or time required for the organism to reach 95% of its maximum length (A_∞).

The growth performance equation or phi prime (Ø') was applied according to the formula established by Pauly & Munro (1984):

$$Ø' = \log_{10}(k) + 2\log_{10}(H_\infty)$$

Mortality

The Beverton & Holt (1959) equation was used to estimate total mortality (Z):

$$Z = k\,(H_\infty - \bar{H}) / (\bar{H} - H')$$

where H_∞ and k are parameters of the von Bertalanffy equation, $\bar{H}$ is the average height at capture, and H' is the minimum height at capture.

Natural mortality (M) was calculated using the Taylor (1960) equation:

$$M = (2.996 / A_{0.95}) - t_0$$

where $A_{0.95}$ corresponds to the limiting age, that is, when an individual reaches a length of 95% of A_∞, and t_0 is the recruitment age of the stock. Fishing mortality (F) was calculated using the equation of Sparre & Venema (1997): F= Z - M, where Z is total mortality, and M is natural mortality. The exploitation rate (E) was calculated using the equation proposed by Gulland (1971): E = F / Z, where F is fishing mortality, and Z is total mortality. The survival rate (S) was estimated using the Ricker equation (1975): $S = e^{-Z}$.

Data analysis

A double-entry Excel database was created to record height and weight by site and sampling month. Descriptive statistics were used to obtain measures of central tendency, including the mean, minimum, and maximum, for total height and weight by site and sampling month. To compare shell height (H) and weight (W) between the coastal and lagoon sites, a Student's t-test was used. To compare the slope values of the length-weight ratio for each site, a Student's t-test was used. The height and weight data were tested for normality and equality of variance using the normality Kolmogorov-Smirnov test and homoscedasticity Bartlett's test (Zar 2010); if the assumptions were not met, nonparametric or free distribution tests were used.

Environmental conditions: temperature and chlorophyll-*a*

Monthly values of nocturnal sea surface temperature (NSST) and chlorophyll-*a* concentration (Chl-*a*) were obtained at a 4 km resolution and processed by the NASA Goddard Space Flight Center, Ocean Ecology Laboratory, Ocean Biology Processing Group (NASA 2014), using a 1-year time series (2018-2019). Broadly speaking, both SST and NSST "measure" the skin of the ocean, usually just the first millimeter of the water surface. NSST measures longwave radiation at night and includes a dust-correction algorithm. Measuring nighttime temperatures reduces the imbalance caused by sunlight reflection, providing a value more indicative of subsurface water temperature. The following is quoted from NASA's Ocean Color website (https://oceancolor.gsfc.nasa.gov/resources/atbd/sst/):

The sea surface temperature measured by MODIS and VIIRS infrared radiometers is commonly referred to as the ocean's skin temperature because the radiance measured by these instruments originates in the ocean's surface thermal skin layer, not in the water below, as measured by in situ thermometers (Donlon et al. 2007). The thermal skin layer of the ocean is less than 1 mm thick (Hanafin & Minnett 2002, Wong & Minnett 2018) and, as a rule, is cooler than the underlying water due to vertical heat flux, typically from the ocean to the atmosphere. Three distinct processes impact near-surface ocean temperature gradients: absorption of solar radiation, heat exchange with the atmosphere, and subsurface turbulence. Generally, at night or when wind speeds exceed ~6 m s^{-1}, the relationship between the skin temperature and the subsurface is often quite stable. A monthly image is the average (mean) of daily measurements, divided by the total number of days in a given month. Therefore, the value shown in the image reflects the daily average of Chl-*a* (or temperature). Using the polygon previously obtained from the regionalization of the study area (Manzanillo), information was extracted from all pixels (pxs) that coincided with the area using the SeaDAS program. Correlations of monthly mean surface temperature and Chl-*a* concentration data of the marine environment (shallow sublittoral) and the estuarine-lagoon environment (Cuyutlan lagoon) were performed using Spearman's test.

RESULTS

Height and weight composition

During the sampling period (September 2018-August 2019), a total of 3,839 oysters were collected in the two study sites, 2,575 in the lagoon site (Cuyutlan) and 1,264 in the coastal site (Faro de Campos) (Table 1).

The average height was 81.3 ± 15.6 mm at both sampling sites, with a minimum height of 36.1 mm and a maximum of 154 mm; the most frequent height range was 71-76, 76-81 and 81-86 mm (Fig. 2a). The average weight at both sites was 109.6 ± 60.8 g, with a minimum of 14 g and a maximum of 484.5 g; the

Table 1. Average height and weight of the rock oyster *Striostrea prismatica* at the lagoon site (Cuyutlan) and the coastal site (Faro de Campos), sampled from September 2018 to August 2019 on the coast of Colima, Mexico. n: sample size, Min: minimum, Max: maximum, and SD: standard deviation.

Sites	Height (mm)				Weight (g)		
	n	Min	Max	average ± SD	Min	Max	average ± SD
Both sites	3839	36.1	154	81.3 ± 15.5	14.2	484.5	109.6 ± 60.7
Cuyutlan lagoon	2575	36.1	143.9	76.9 ± 13.2	14.2	405.8	91.0 ± 41.5
Faro de Campos	1264	45.0	154	90.3 ± 16.1	21.8	484.5	147.6 ± 74.4

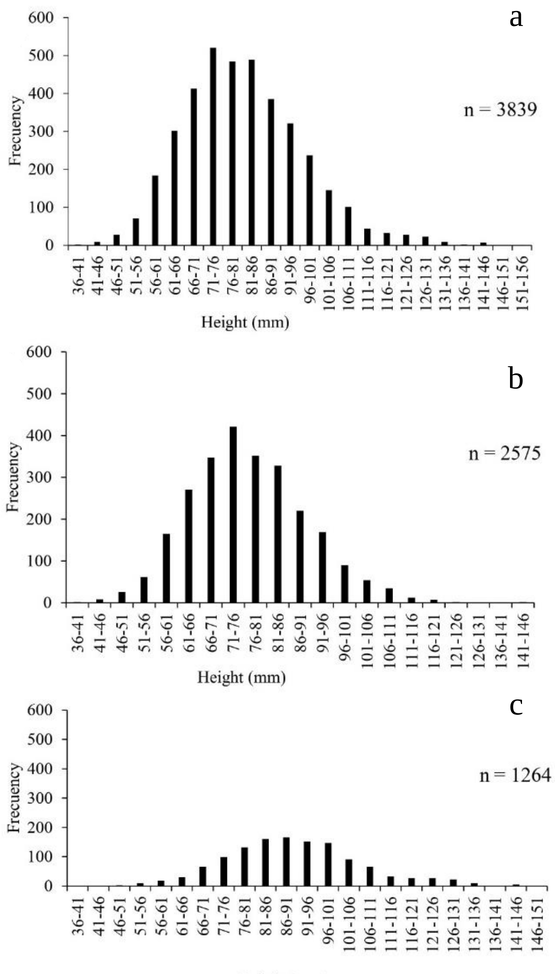

Figure 2. Height-frequency distributions of the rock oyster *Striostrea prismatica* in a) both sites, b) lagoon site (Cuyutlan), and c) coastal site (Faro de Campos) on the coast of Colima, Mexico.

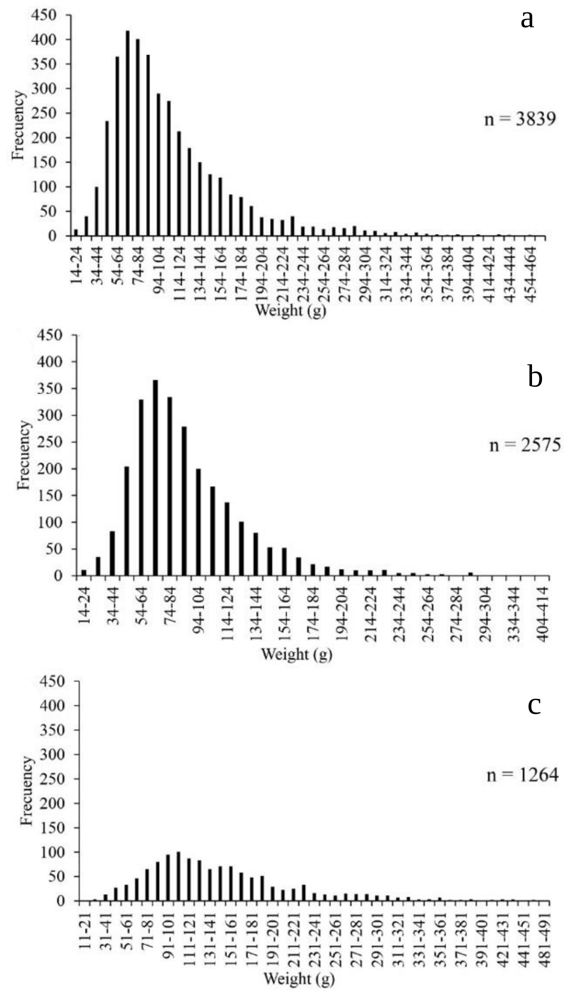

Figure 3. Weight-frequency distributions of the rock oyster *Striostrea prismatica* in a) both sites, b) lagoon site (Cuyutlan), and c) coastal site (Faro de Campos) on the coast of Colima, Mexico.

highest frequency intervals were 64-74, 74-84 and 84-94 g (Fig. 3a). The t-Student test indicated that oysters in the coastal site were significantly higher ($P < 0.05$) and heavier ($P < 0.05$) than organisms of the lagoon site. Lagoon oysters had an average height of 76.9 ± 13.2 mm with a minimum of 36.1 mm and a maximum of 143.9 mm; the most frequent range was 71-76 mm (Fig. 2b). The average weight was 91.0 ± 41.6 g with a minimum of 14.2 g and maximum of 405.8 g; the most frequent range was 64-74 g (Fig. 3b). Coastal oysters showed an average height of 90.4 ± 16.1 mm, a minimum of 45.0 mm and maximum of 154 mm; the most frequent range was 81-86 and 86-91 mm (Fig. 2c). The average weight was 147.6 ± 74.5 g, minimum 21.8 g and maximum 484.5 g; the highest frequency total weight range was 91-101 and 101-111 g (Fig. 3c).

Height-weight ratio

The height-weight ratio of the potential equation indicated that the oysters showed negative allometric growth, increasing their body volume more in height than in weight (Fig. 4a). The equation describing the height-weight ratio for lagoon oysters is $W = 0.0221H^{1.901}$ (Fig. 4b), and for coastal oysters is $W= 0.0221H^{2.1711}$ (Fig. 4c). The t-Student test indicated significant differences in the values of the growth constant '*b*' between lagoon and coastal sites ($P < 0.001$).

Modal progression analysis (modal groups or cohorts)

Length-frequency analysis of *S. prismatica* populations in both lagoon and coastal sites using the Bhattacharya method revealed the presence of seven modal groups or cohorts (Table S1); four modal groups present in populations in the lagoon site (Table S2), and only three modal groups in populations in the coastal site (Table S3). The modal groups with the highest monthly persistence or frequency at both sites were 49, 72, 93, 103, 119, and 135 mm of average height (AH). For coastal populations, the modal groups or cohorts with the highest monthly persistence were 71, 90, and 137 mm AH; at the lagoon, the modal groups or cohorts with the highest monthly persistence were 49, 68, 85, and 103 mm AH. The modal group or cohort ≤49 mm AH is considered the recruitment size, not present in coastal oysters, but present in lagoon oysters.

Growth estimation

The estimated values of the growth parameters for *S. prismatica* populations in both sites are given in Table 2: infinite height (H_∞), infinite weight (W_∞), growth coefficient (*k*), and hypothetical age at which length is zero (t_0) from the von Bertalanffy equation.

In addition, values from the growth performance equation or phi prime (Ø') and longevity values from the Taylor equation ($A_{0.95}$) are shown. The ELEFANT-I programmed routines estimated for lagoon oysters an asymptotic height (H_∞) of 176 mm and a growth coefficient k of 1.3 yr^{-1}, slightly higher than that estimated for coastal oysters, with an H_∞ of 174 mm and *k* of 1.06 yr^{-1}, indicating faster growth of lagoon oysters than in coastal oysters. The fit to the von Bertalanffy growth curve for height and weight for both sites is shown in Figure 5a, while for the lagoon is presented in Figure 5b, and for the coastal in Figure 5c. Lagoon oysters reach a shell height of 176 mm before 20 months of age, while coastal oysters, and for both sites, a little after 24 months, indicating that this oyster species reaches the commercial size of 90 mm (the official Mexican norm) before the first year of life at both study sites.

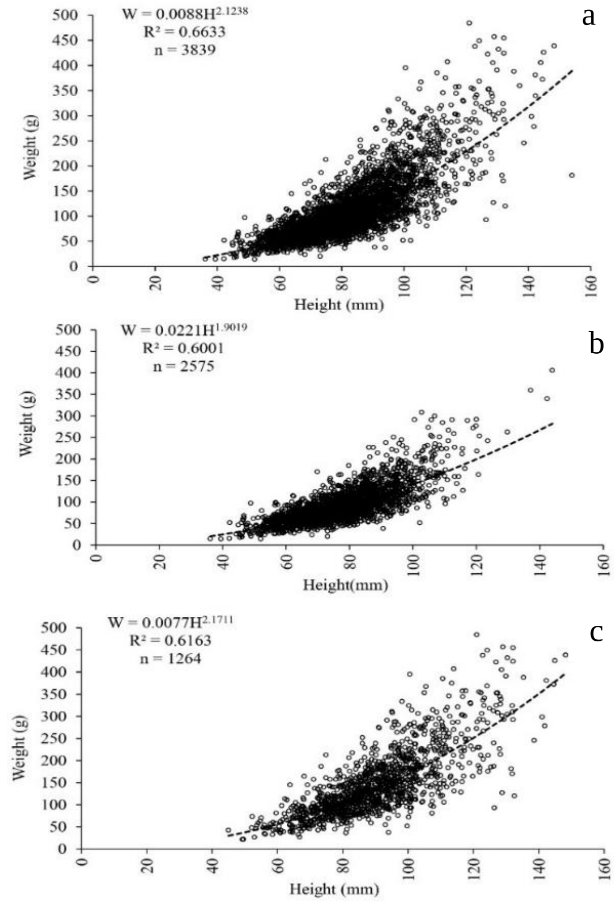

Figure 4. Dispersion of height and weight, with the adjustment to the potential equation of the height-weight ratio of the rock oyster *Striostrea prismatica* in a) both sites, b) lagoon site (Cuyutlan), and c) coastal site (Faro de Campos) on the coast of Colima, Mexico.

Mortality

The estimated values for total mortality (Z), natural mortality (M), fishing mortality (F), survival rate (S), and exploitation rate (E) at both sites are given in Table 3. The three mortality parameters (Z, M, F) and E estimated were higher in the lagoon populations than in coastal oysters. Nevertheless, S was higher in the coastal populations (15.0) than in the lagoon oysters (4.0), indicating that the higher mortality (Z) is caused by fishing (F), since the lagoon oyster resource is

Table 2. Estimated values for infinite height (H_∞), infinite weight (W_∞), growth coefficient (k) and the hypothetical age at which total height is zero (t_0), from the von Bertalanffy (1938) growth equation for the rock oyster *Striostrea primatica* in two different environments; coastal site (Faro de Campos), lagoon site (Cuyutlan), and both sites. The value of the Taylor longevity estimate ($A_{0.95}$) and the growth performance index (Ø') is given.

Parameter	Faro de Campos	Cuyutlan lagoon	Both sites
H_∞	174 mm	176 mm	192 mm
W_∞	563.5 g	410.3 g	548.8 g
k	1.06 yr^{-1}	1.30 yr^{-1}	1.01 yr^{-1}
t_0	-0.09	-0.07	-0.09
$A_{0.95}$	2.91	2.37	3.06
Ø'	4.5	4.6	4.5

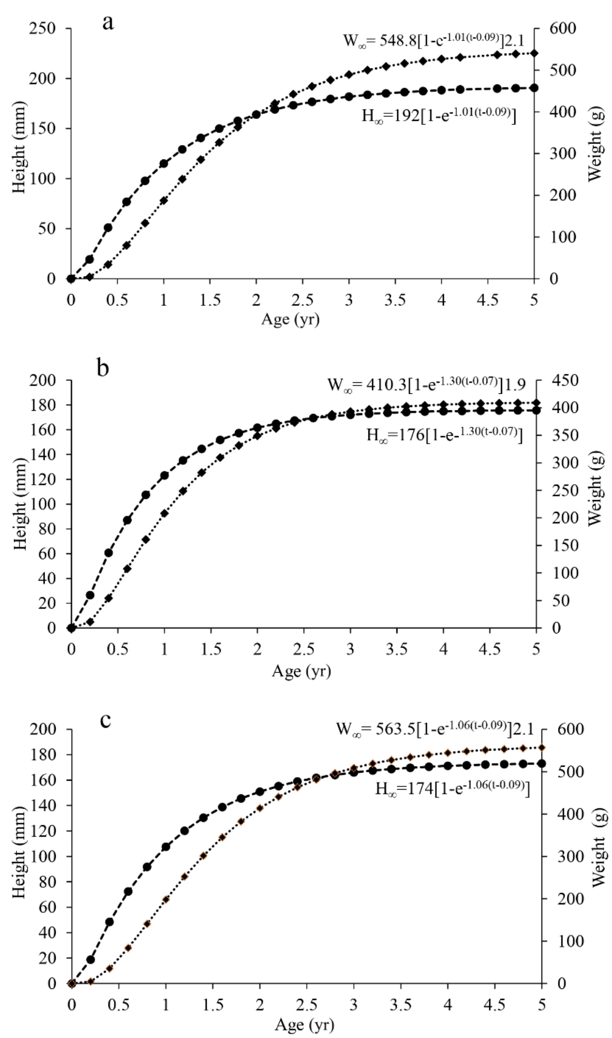

Figure 5. Height and weight growth curve fitting of the rock oyster *Striostrea prismatica* in a) both sites, b) lagoon site (Cuyutlan), and c) coastal site (Faro de Campos) on the coast of Colima, Mexico.

subject to intense capture, as indicated by the estimated values.

Sea surface temperature and chlorophyll-α concentration

The average NSST at both study sites ranged between 24 and 30°C during the annual cycle (September 2018 to August 2019) (Fig. 6). The warmest condition (30°C) was observed from June to October at both sites, and the lowest average seawater temperatures were observed from February to May. Figure 7 shows the monthly variation of the average Chl-*a* concentration in the shallow sublittoral (Fig. 7a) and in the Cuyutlan lagoon (Fig. 7b). The lagoon recorded higher average concentrations (0.12 to 4.45 mg m^{-3}) than the shallow sublittoral (0.15 to 2.2 mg m^{-3}). However, at both sites, the highest chlorophyll concentration was observed between February and May.

DISCUSSION

Populations of the rock oyster *S. prismatica* in the shallow rocky sublittoral (coastal site) and within Cuyutlan (lagoon site) showed slightly different population parameters. The average height and weight were significantly greater on the coastal oysters than on the lagoon oysters, indicating differences between the marine and lagoon environments. These environmental conditions at the entrance to the bay of Santiago and Manzanillo and inside the Cuyutlan lagoon followed the natural pattern during the annual cycle, particularly off the port of Manzanillo, where the surface temperature was warm between June and September, falling from October to May, with the lowest temperatures between March and April. While Chl-*a* concentration increased during the months of lower SST from February to May, consistent with several authors' reports (Sosa-Avalos et al. 2013, Pérez-de Silva et al. 2023). Salinity, although not recorded during the study period (September 2018-August 2019),

Table 3. Estimated values for total mortality (Z), natural mortality (M), fishing mortality (F), exploitation rate (E), and survival rate (S) for the rock oyster *Striostrea prismatica* in two different environments: the coastal site (Faro de Campos), lagoon site (Cuyutlan), and both sites.

Parameter	Campos lighthouse	Cuyutlan lagoon	Both sites
Z	1.89	3.15	2.46
M	0.93	1.18	0.88
F	0.95	1.96	1.57
E	0.50	0.62	0.64
S	15.0	4.0	8.0

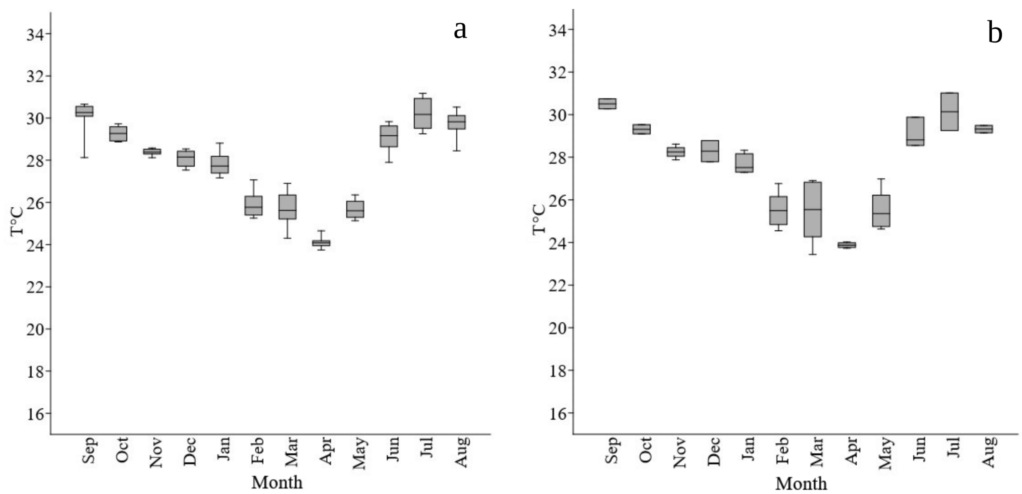

Figure 6. Monthly variation of mean (± standard error) surface water temperature (T°C) in a) the shallow sublittoral and b) Cuyutlan lagoon on the coast of Colima between September 2018 and August 2019.

used to fluctuate between 34.4 and 33.7, except when there is heavy rainfall in summer, when salinity can decrease down to 30 for short periods of only a few days and then return to an average salinity of 34 (Durand-Acosta et al. 2024). These variations in environmental conditions affect the growth, reproduction, recruitment, and mortality of sessile and filter-feeding organisms such as rock oysters (Arrieche & Prieto 2006, Crescini 2012). We know that Cuyutlan lagoon has been modified by the opening of various channels that allow seawater to enter at high tide, such as basin I (Ventanas channel) and basin II (Tepalcates channel), resulting in purely marine conditions year-round, particularly in terms of salinity. Other basic physico-chemical parameters, such as surface temperature, dissolved oxygen, and pH, are similar to those of the areas adjacent to the lagoon. Still, biological parameters, such as phytoplankton and seston concentrations, are generally higher in this estuarine-lagoon system than in the marine environment (Sosa-Avalos et al. 2006, 2013). However, the oysters from basin II inside the lagoon system did not reach similar lengths and weights to the shallow rocky sublittoral (coastal site), which suggests that fishing activity may be linked to the disappearance of larger rock oysters from the oyster beds due to heavy fishing (Table 4). That is the case in other marine areas of the eastern tropical Pacific, where intense fishing has led to a decrease in catch size, as observed along the coast of Jalisco (Ríos-González 2021). It should be noted that this study is the first report of the presence and capture of the rock oyster inside a coastal lagoon (Cuyutlan) for the Mexican Pacific, considering that this species naturally has limitations to remain in estuarine zones.

Nevertheless, Martínez-García (2024) recently reported the presence of *S. prismatica* within the El Soldado lagoon in Sonora, and that cultivation experiments of the species have been carried out in this type of water bodies (Rendón-Martínez et al. 2016, Robles et al. 2020, Rodríguez-Pesante et al. 2022). In addition, it is necessary to consider that the oyster beds within the lagoon are more easily accessible and are located in areas with reduced water circulation, compared to the access and capture conditions of this

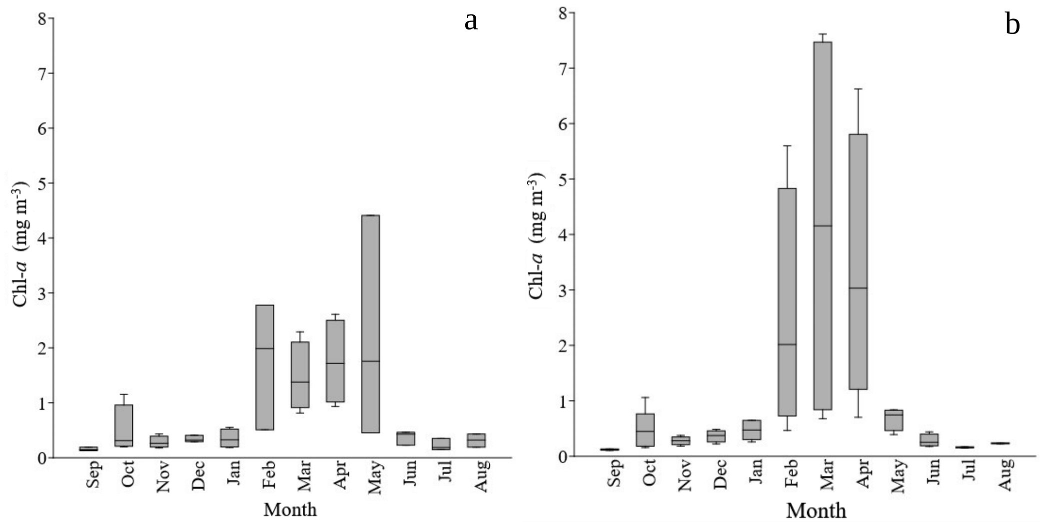

Figure 7. Monthly variation in mean (± standard error) chlorophyll-*a* (Chl-*a*) concentration in a) the shallow sublittoral and b) Cuyutlan lagoon of the coast of Colima between September 2018 and August 2019.

Table 4. Mean, minimum (Min), maximum (Max) heights and weights values of the rock oyster *Striostrea prismatica* reported by other authors and this study.

Author	Site	Height (mm)			Weight (g)		
		Mean	Min	Max	Mean	Min	Max
Present study	Both sites	81.34	36.1	154	109.6	14.2	484.5
Present study	Cuyutlan lagoon	76.9	36.1	143.9	91.01	14.2	405.8
Present study	Faro de Campos	90.34	45	154	147.5	21.8	484.5
Campos & Fournier (1990)	Curubay-Costa Rica	84.34					
Liévano-Méndez (2008)	Michoacán-Mexico	88.8	49	149			
Ordinola et al. (2010)	North-Tumbes-Peru	122.2	22	202			
	Centre-Tumbes-Peru	106.6	11	200			
	South-Tumbes-Peru	125.3	11	228			
Ordinola et al. (2013)	Tumbes-Peru		7	228			
Gonzabay-Rodríguez (2014)	La Leona-Ecuador	99.58	73	139			
	Cabuya-Ecuador	99.23	63	148			
	La Loca-Ecuador	91.06	60	118			
Meléndez-Galicia et al. (2015)	Michoacan-Mexico		50	176		50	866
García-Delgado & Leones-Zambrano (2016)	Punta Napo-San Vicente-Ecuador	79.88	32.5	160	121.3	5.4	746.6
	Punta Gorda-Sucre-Ecuador	93.36	36	178	176.3	7.9	800
Alemán-Mejía et al. (2016)	Sublittoral -Tumbes-Peru	92.4	25	210			
Rendón-Martínez et al. (2016)	Estuary Salinitas-Sinaloa	73.53			31.56		
Ríos-González et al. (2016)	Jalisco-Mexico		12	155		0.45	472
Rodríguez-Pesantes et al. (2022)	Ayangue Bay-Ecuador	75-80					

rock oyster in its natural environment at the coastal site (Faro de Campos), which evidently indicates greater movement of the water mass due to local surface currents and water circulation by swells and waves, limiting fishermen's access to capture in the oyster beds.

The length-weight relationship can be used to assess the health status of organisms within a population and to detect differences within a stock of the same species (Thejasvi et al. 2014). When the growth coefficient *b* generally falls between 2.5 and 3.5 (Carlander 1977), it indicates that the body increment (weight-length) of the organism is isometric, growing proportionally in biomass and length. Nevertheless, if the result of the length-weight relationship falls outside this range (<2.5->3.5), it indicates that the organism exhibits an allometric type of body growth, which can be positive or negative. Other authors have reported negative allometry in several populations of rock oysters in the eastern tropical Pacific, consistent with the findings of the present study (Table 5). Shell growth and shape are influenced by abiotic (exogenous or environmental) and biotic (endogenous/physiological) factors, which, in several bivalve species, cause shells to become taller and wider during growth to counteract involuntary dislodgement by turbulence and currents (Gaspar et al. 2002). In *S. prismatica*, several authors have reported negative allometry (Table 5), indicating that body length increases more than body weight. Our results are particularly consistent with those reported by Melchor-Aragón et al. (2002) and García-Delgado & Leones-Zambrano (2016).

The modal progression analysis used to estimate modal groups (cohorts) in rock oyster populations at both study sites identified up to five cohorts. However, studies in which the species has been cultivated in marine and estuarine environments have shown that it can reach marketable size (90-100 mm shell height or 90-120 g) in 12 months (Rodríguez-Pesante et al. 2022), which means that the identified cohorts comprise oysters in their spat phase and juvenile and adult stages, including mature organisms, i.e. the entire life cycle between 12 and 24 months of age, consistent with the results obtained in the present work (Tables S1-S3), both in the lagoon populations and in the coastal oyster beds.

The estimated values of the infinite height (H_∞) and growth coefficient k (1.3 yr^{-1}) at the lagoon (H_∞ = 176 mm) and at the coastal site (H_∞ = 174 mm; 1.06 yr^{-1} respectively), are consistent with those reported by other authors at various sites in the geographical distribution of *S. prismatica* in the eastern tropical Pacific (Table 5). In populations of this oyster from the coast of Ecuador, García-Delgado & Leones-Zambrano (2016) report H_∞ = 168 mm and a growth coefficient of k = 1.1 yr^{-1}, similar to that recorded at both sites on the coast of Colima. It is also similar to that reported for sites on the coast of Sinaloa, Mexico by Melchor-Aragón et al. (2002), with an estimated infinite height of H_∞ = 155 mm and a growth coefficient of 0.066 $month^{-1}$. Converted to the annual cycle, this is estimated at k = 0.83 yr^{-1}. According to Pauly & Munro (1984), if the results of the growth performance index or premium Ø 'are similar, it indicates that the H_∞ and k were adequately estimated. Our results from the present study for *S. prismatica* in the lagoon (Ø' = 4.6) and the coastal site (Ø' = 4.5) were very similar. The values of k suggest that the organisms in the lagoon (k = 1.3) have a higher growth rate than the organisms in the coast, reaching A_∞ in approximately 38 months, and probably reaching the official commercial size for this species at 90 mm in average height after approximately nine months (DOF 2018), which coincides with what was reported by Rodríguez-Pesante et al. (2022), who reported that this species reaches an average height of 85 mm from a larva with an average height of 1.4 mm in 12 months in a suspension culture system in Ayangue Bay on the coast of Ecuador, making it a candidate species for cultivation in natural areas such as coastal lagoons (Cuyutlan) and the shallow rocky sublittoral (Faro de Campos) of the Mexican Pacific and at other latitudes in southern Mexico.

Estimation of growth and mortality values for exploited stocks is undoubtedly an important parameter in the construction of models for designing management strategies for fishery resources (Wright-López et al. 2009). If the calculated values of fishing mortality (F) exceed those of natural mortality (M), it indicates that fishing pressure exceeds natural causes of mortality, suggesting that the resource is in a state of overexploitation (Borda & Cruz 2004). In the present study, the rock oyster populations in the lagoon showed this trend (F = 1.96 *vs.* M = 1.18), supported by the value of the exploitation rate (E = 0.65) above the optimum exploitation value ($E \leq 0.5$) (Gulland 1971), indicating intense harvesting of oysters inside the lagoon. A different situation is in the oyster beds at the coastal site, where F and M recorded similar values (F = 0.95 *vs.* M = 0.93), again supported by the exploitation rate value (E = 0.5), indicating that the oyster populations during the study period are still under fishing pressure at the optimum. The total mortality rate (Z) of rock oysters was higher (Z = 3.15 yr^{-1}, E = 0.62) in the lagoon, compared to the shallow sublittoral of the coastal site (Z = 1.89 yr^{-1}, E = 0.50), which is probably related to high predation (natural and fished), as well as the persistence of higher monthly water temperatures, which accelerate biological processes as established by Pauly (1979), when he describes M as a function of k, L_∞ and the thermal condition of the environment where organisms live. It is also suggested that the same species may have different mortality rates (Z, M, F) across areas, depending on predator and competitor densities, which are directly affected by fishing activities (Sparre & Venema 1997). Likewise, Crescini (2012) suggests that

Table 5. Growth parameters of the von Bertalanffy (1938) and Ricker (1975) equations for the rock oyster *Striostrea prismatica,* from different authors and this study. H_∞: infinite height, *k*: growth coefficient, t_0: hypothetical age at which total height is zero, Ø': growth performance index, a: is the intercept, *b*: the slope or growth constant, and R^2: determination coefficient.

Author	Site	H_∞	*k*	t_0	Ø'	a	b	R^2
Present study	Cuyutlan lagoon	176	1.3	-0.07	4.6	0.0221	1.9	0.60
Present study	Faro de Campos	174	1.06	-0.09	4.5	0.0077	2.17	0.63
Present study	Both sites	192	1.01	-0.09	4.5	0.0088	2.12	0.66
Melchor-Aragón et al. (2002)	San Ignacio-Sinaloa	134	0.069	-0.66		0.00629	2.18	
	San Ignacio-Sinaloa	155	0.098	-0.399		0.00111	2.61	
Ordinola et al. (2010)	Tumbes-Peru					0.0008	3.17	
García-Delgado & Leones-Zambrano (2016)	Punta Napo-Ecuador	168	1.11	0.089	4.49	0.0003	2.87	0.77
	Punta Gorda- Ecuador	199.5	1.91	-0.048	4.88	0.0004	2.8	0.81

variations in mortality (Z, M, F) are a consequence of changes in environmental conditions (Arrieche & Prieto 2006), the intense fishing activity of the resource and/or intraspecific and interspecific relationships, such as predation, competition for space and food, which directly affect growth and mortality.

The results of the present study provide the first insight into the population dynamics of the rock oyster, *S. prismatica*, in the shallow rocky sublittoral and within a coastal lagoon off the coast of Colima, Mexico. The organisms in the rocky sublittoral zone had greater shell height (H) and weight (W) than the organisms inside the Cuyutlan lagoon. The rock oyster populations in both environments exhibited negative allometric growth. Estimates of total asymptotic height, growth coefficient, and theoretical indicate that organisms in the Cuyutlan lagoon could reach asymptotic size in less time than organisms in the rocky sublittoral zone. Rock oyster populations show signs of overexploitation, particularly within the Cuyutlan lagoon and at the optimum limit in rocky sublittoral populations. The latter would suggest further studies of oyster resources in estuarine-lagoon environments and in the rocky sublittoral environment of the Colima coast, and the identification of catch quotas to allow for a more accurate determination of the level of exploitation. The management measure for this oyster fishery in the Mexican Pacific is the closed season, from June to August (DOF 2018). However, for the Cuyutlan lagoon, it could be suggested that some temporary fishing areas be restricted to increase size and weight, at least similar to those recorded in the shallow rocky sublittoral zone off the coast of Colima, as is done with other species of fishing interest.

Author contribution credits

J. Palacios Valdes: conceptualization, validation, methodology, formal analysis and writing-original draft; E. López Uriarte: conceptualization, funding acquisition, project administration, supervision, analysis performed, review and editing; J. Chávez Villalba: supervision, analysis performed, review and editing; E. López Uriarte wrote the first draft of the manuscript, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Conflict of interest

The authors have no relevant financial or non-financial interests to disclose.

Data availability

Data are available on request from the authors.

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SUPPLEMENTARY MATERIAL

Table S1. Monthly modal groups of *Striostrea prismatica* in Faro de Campos and Cuyutlan lagoon of the coast of Colima, Mexico. n: sample size, AH: average height, SD: standard deviation, SI: separation index.

Month	n	AH	SD	SI
Sep	60	83.2	5.42	
	70	97.07	7.81	2.01
	6	118.5	3.96	2.18
Oct	269	64.27	8.42	
	101	92.18	7.30	2.34
	30	116	7.18	2.19
Nov	32	49.49	6.25	
	253	71.02	8.62	2.24
	115	91.18	9.68	2.05
	18	122.1	11.6	2.19
Dec	98	71.41	8.21	
	132	87.03	5.32	2.05
	65	101.3	6.21	2.06
	6	124.1	5.69	2.20
Jan	378	71.11	8.59	
	83	94.27	10.7	2.1
Feb	378	72.14	11.4	
	27	106.3	23.3	1.98
Mar	36	56.07	5.02	
	219	77.88	9.7	2.23
	15	101.67	4.17	2.23
Apr	366	79.90	10.6	
May	409	74.88	11.3	
	19	102.7	6.26	2.24
	5	117.6	8.84	2.00
Jun	22	78.96	4.44	
	40	99.19	7.0	2.21
	3	124	5.01	2.24
Jul	382	83.96	9.91	
	13	119	5.74	2.42
Aug	248	72.07	9.12	
	42	92.48	6.56	2.12
	8	103	4.38	2.00
	19	119	8.12	2.07
	4	135	6.83	2.01

Table S2. Monthly modal groups of *Striostrea prismatica* in Cuyutlan lagoon, Colima, Mexico. n: sample size, AH: average height, SD: standard deviation, SI: separation index.

Month	n	AH	SD	SI
Sep	17	81	5.55	
	19	87.27	8.77	1.81
Oct	252	63.6	8.19	
	24	81.33	3.48	2.06
	4	93.5	6.8	2.17
Nov	31	49.25	5.95	
	94	62.90	4.70	2.11
	17	89.81	6.32	2.47
Dec	62	68.43	5.66	
	154	86.12	6.77	2.14
	27	102.9	2.84	2.16
	14	113.8	3.61	2.08
Jan	108	62.73	5.41	
	106	82.22	7.21	2.2
Feb	21	49.10	3.67	
	263	67.49	10	2.18
	2	103	2.89	2.61
Mar	28	59.68	4.53	
	365	79.5	10.1	2.16
Apr	28	59.68	4.53	
	369	81.18	10.6	2.2
May	211	75.73	10.7	
	42	108.2	8.54	2.31
Jun	34	95.56	9.94	
Jul	63	68.25	5.16	
	180	82.77	6.87	2.07
	15	103.3	3.84	2.22
Aug	175	65.99	6.57	
	13	78.50	5.14	2.02

Table S3. Monthly modal groups of *Striostrea prismatica* in Faro de Campos, Colima, Mexico. n: sample size, AH: average height, SD: standard deviation, SI: separation index.

Month	n	AH	SD	SI
Sep	90	93.07	10.5	
	5	117.5	3.87	3.39
Oct	84	94.79	7.43	
	34	114.4	7.42	2.09
Nov	177	86.60	13.1	
	14	132.5	13.5	2.39
Dec	43	97.69	11.5	
	3	122.5	6.47	2.12
Jan	32	71.45	6.47	
	46	93.29	10.2	2.13
Feb	130	81.01	10.7	
	9	119.4	7.36	2.44
Mar	18	83.89	4.35	
	12	100.7	3.28	2.21
Apr	38	75	13.9	
	10	116.8	12.3	2.35
May	181	74.45	12.1	
	25	117.9	13.8	2.40
Jun	32	79.51	7.28	
	11	104.5	7.28	2.25
Jul	140	86.42	12.1	
Aug	107	90.78	9.84	
	14	125.1	3.49	2.42
	4	137.5	4.77	2.06