Journal of Shellfish Research, Vol. 27, No. 4, 691–700, 2008.

HARVEST HISTORY AND CURRENT DENSITIES OF THE PEARL OYSTER *PINCTADA MAZATLANICA* (BIVALVIA: PTERIIDAE) IN LAS PERLAS AND COIBA ARCHIPELAGOS, PANAMA

ROBERTO CIPRIANI,[1,2] HECTOR M. GUZMAN[2]* AND MELINA LOPEZ[3]

[1]*Departamento de Estudios Ambientales, Universidad Simón Bolivar, A.P. 89000, Caracas 1080, Venezuela;* [2]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama;* [3]*Department of Chemistry, Geosciences and Environmental Science, Tarleton State University, Box T-0540, Stephenville, Texas 76402*

ABSTRACT Four hundred years of commercial harvest of the oyster *Pinctada mazatlanica* in Pacific Panama were characterized by historical collapses and recoveries that finally ended in the 1940s; oyster populations have not recovered since then. This study provides a baseline and meta-analysis of current *P. mazatlanica* densities in Las Perlas and Coiba Archipelagos. We compared the oyster densities in relation to substrates and depths at 103 sampled sites using randomization techniques. Mean oyster density per site ranged from 2.8–238.9 ind·ha^{-1} in Las Perlas and 6.0–263.9 ind·ha^{-1} in Coiba. These values are one to three orders of magnitude lower than those reported for La Paz, Baja California (3,000–12,000 ind·ha^{-1}) and Costa Rica (24,200 ind·ha^{-1}) in recent times. Substrates within the archipelagos were diverse. We found an increasing trend of density variance when regressing log-transformed densities against substrates ordered according their increasing availability of hard surfaces. In Coiba, densities in substrates including rocks plus corals and sand were statistically lower in shallow than in deep waters, probably caused by harvest. The highest densities in Las Perlas occurred southeast of Del Rey and western Saboga islands. In Coiba, we found the highest densities in Ranchería Island and on the westernmost side of Coiba and Jicarón Islands. These data will help to define the environmental framework within which future research on this important species must be conducted and can be used to improve plans to address its management and conservation.

KEY WORDS: historical ecology, pearl oyster harvest, *Pinctada mazatlanica*, Las Perlas, Coiba, Panama

INTRODUCTION

In September of 1513, Spaniards commanded by Vasco Nuñez de Balboa became the first Europeans to set eyes upon the Eastern Pacific Ocean. Within a few days of their arrival on the shores of Bahia de San Miguel in Panama, Balboa visited a group of islands about 20 nautical miles to the west in today's Gulf of Panama. There, local tribes greeted him with pounds of pearls (Camargo 1983). The great abundance and large size of these pearls prompted Spaniards to name the islands therein as *Islas de las Perlas*, which is Spanish for the Pearl Islands (Galtsoff 1950, Camargo 1983, Castillero 2004).

Pearls also were abundant and large on the coast of Veraguas and in other islands in the Gulf of Chiriquí, especially in Coiba Archipelago. Described to Spaniards for the first time by Francisco Carreño ca. 1562, Coiba Archipelago became an important pearl fishing ground when oysters declined in the Gulf of Panama at the turn of the sixteenth century (Camargo 1983). This area was heavily exploited for pearls until the dawn of the twentieth century.

The periodic and drastic declines and slow recoveries that characterized the population dynamics of the pearl oyster, *Pinctada mazatlanica* (Hanley 1856), along the Pacific Coast of Panama (Galtsoff 1950, Camargo 1983, MacKenzie 1999) because the 1600s seem to explain the low haplotype, nucleotide, and gene diversities recently measured for these populations (Arnaud et al. 2000, Arnaud-Haond et al. 2003). Since the last population collapse recorded in Las Perlas and Coiba Archipelagos in 1948 (Galtsoff 1950), densities of *P. mazatlanica* have never recovered to the levels that existed before World War II. However, oysters remain one of the many species still sought by local divers.

Pinctada mazatlanica is closely related to the Pacific ''black lip pearl oyster,'' *Pinctada margaritifera* (Linnaeus 1758) (Hertlein & Strong 1955, Arnaud et al. 1999, Arnaud-Haond et al. 2003). Some authors and worldwide databases refer to *P. mazatlanica* either as a subspecies or a junior synonym of the latter (e.g., Jameson 1901, Lamy 1909, Gervis & Sims 1992, MacKenzie 1999, Jiuan-Jiuan & Okutani 2003). Growing on rocks from below the intertidal zone to an average of depth of 22 m, *P. mazatlanica* was easily harvested throughout its geographical range, which extends from Sonora, Baja California, Mexico south to Paita, Peru and west to Isla del Coco, Costa Rica, and the Galapagos Islands, Ecuador (Hertlein 1937, Coan et al. 2000). Its common names—Panama shell (Hertlein & Strong 1955), Panamanian pearl oyster (Hickman & Finet 1999), and Calafia pearl oyster (Arnaud et al. 2000, Monteforte 2003; this one honors the mythological Queen of California)—are reminders of the regions in which exploitation of *P. mazatlanica* was the most intense over the course of 400 y.

The Republic of Panama designated Coiba and Las Perlas Archipelagos as protected areas in 2004 and 2007, respectively. These designations do not regulate the use and exploitation of oysters, or their meat, shells, or pearls, but they do prohibit the use of certain fishing methods; they also vow to regulate fisheries within these protected areas using the best scientific evidence available. Unfortunately, scientific information about the status of the oyster populations in these areas is meager. The first and last oyster survey on the Pacific coast of Panama, occurred in 1948 (Galtsoff 1950), and MacKenzie (1999), provides the only recent report describing the overall status of the pearl oyster fishery in Las Perlas Archipelago. Clearly, to

*Corresponding author: E-mail: guzmanh@si.edu

achieve the goals to protect local populations and avoid overfishing of these protected areas, managers will need baseline information that describes the status of the oyster pearl population in both archipelagos. In addition, a comparison of the oyster populations from both archipelagos will allow the assessment of contrasting regions in which the intensity of harvest has differed; oyster fishing in the seasonal upwelling area of Las Perlas historically was more intense than in the nonupwelling area of Coiba.

In this study, we assessed and compared the status of the pearl oyster population in Las Perlas and Coiba Archipelagos by: (1) describing the historical framework within which the fisheries of *P. mazatlanica* developed in these two regions and (2) reporting the results of an extensive oyster survey of the shallow water habitats surrounding both archipelagos. We characterized the substrates of the areas in which the oysters live and quantitatively compared current oyster densities in relation to the substrates and depths of our sampling sites. We also projected overall estimates of the standing pearl oyster population size in the waters of both archipelagos.

MATERIALS AND METHODS

History of Harvesting Pearl Oysters

We reviewed key contributions in English and Spanish on the history of pearl oyster harvest in Pacific Panama (Galtsoff 1950, Camargo 1983, Villaláz & Gómez 1997, MacKenzie 1999, Castillero 2004).

Study Area

Las Perlas Archipelago is perhaps the most important shell fishing area of Panama (Villaláz & Gómez 1997). It consists of ca. 255 islands and islets (Campbell 2005) with a total coastline of ca. 318,460 km. Its largest island, El Rey (8°22′54.64″N, 78°54′20.16″W), lies in the Gulf of Panama 38 km southwest of the mainland. The marine special management zone that encloses the archipelago protects an area of 168,771 ha, including 33,153 ha of land, and two additional geographically isolated satellite zones, Roca Trollope and Isla Galera.

Coiba National Park includes an archipelago consisting of 30 islands and islets in the Gulf of Chiriquí and has a surface area of ca. 270,125 ha. The largest island, Coiba (7°28′00.72″N, 81°46′53.27″W), sits approximately 24 km southwest of the mainland.

The marine environments of Las Perlas are most productive from January through April when cold water and nutrients arrive in the region caused by seasonal upwelling (Glynn & Stewart 1973). In contrast, the effects of upwelling seem to be small or negligible in Coiba National Park (D'Croz & O'Dea 2007). Both archipelagos are subject to stresses of varying magnitudes caused by El Niño Southern Oscillation (ENSO) events that occur approximately every 4 y (McNiven 2003). Nevertheless, both archipelagos are biologically diverse and harbor a number of coastal and shallow water ecosystems ranging from sandy, rodolith, and mangrove environments to rocky shores and coral reefs and coral communities (Guzman et al. 2008).

Sampling Locales

Following the mapping methodology described in Guzman and Guevara (2002) and in Guzman and Tewfik (2004), we used the software program ArcGIS V9.1 (Environmental System Research Institute) with topographic maps at a scale of 1:50,000 and LANSAT-7 ETM satellite images from the year 2000 to select the sampling area of our study. The vertices of irregular polygons of ca. 2 × 2 km delimited our sampling sites in the field. Polygons were arbitrarily positioned, mostly one adjacent to another, in such a way that they covered all of the shallow water surface areas immediately surrounding the islands within each archipelago (*sensu* Guzman et al. 2008). To characterize both regions, we randomly selected 68 out of the 108 polygons (108 sites = 28,891 ha; 68 sites = 63%) from the waters of Las Perlas and 35 out of 84 polygons (84 sites = 29,326 ha; 35 sites = 42%) from the waters around Coiba. Each site was separated into two levels according to their depth. We set an imaginary boundary at ca, 10 m to separate shallow waters from deep waters, but the actual ranges varied according to the bottom geomorphology of each site. In each level, we haphazardly selected three geographical positions (totaling 6 per site), and in each of these we surveyed one bottom belt-transect of 6 × 100 m that ran parallel to the shore (total surface area surveyed at each site = 3,600 m^2). The effects of tidal variations were included in the data during the analyses. Scuba divers performed the surveys between June 2 and July 11, 2006 in Las Perlas and between October 6, 2006 and February 1, 2007 in Coiba.

Gauged depths varied from 1.50–18.3 m in Las Perlas and from 1.20–14.0 m in Coiba. The corresponding average differences in depth between shallow and deep sets of transects within each site (mean ± SD) were 4.6 ± 2.6 m and 5.7 ± 1.5 m, respectively. Despite tidal amplitudes of 4.85 m and 5.67 m at the two sites, respectively, differences between corrected depths from shallow and deep sites were still significant in 40% of transects. Hence, we treated depth levels as separate treatments.

Substrate Characterization

Because *P. mazatlanica* requires hard substrates to recruit and grow, the availability of hard surfaces on the sea floor plays an important role in their distribution. We found that a combination of seven different types of substrates, or substrate categories, qualitatively described the dominant substrates in each transect during visual surveys. The seven substrates were: (1) rocks (R) was used to described volcanic and sedimentary substrate; (2) hard carbonate substrates (H) was used only when reef frameworks, dead corals, and coralline rubble, which were hard to the touch, were present; these might serve as a substrate for growing oysters; (3) coral communities (C) was assigned to transects in which living coral colonies were abundant; (4) seagrasses (G); (5) algae (A) was used to describe aggregations of nonencrusting coralline algae and macroalgae that covered substantial areas of the substrate underneath; (6) sand (S) was used to describe a wide variety of substrates, including silica and coralline sand; and (7) mud (M). Hence, we used SR to describe a transect dominated by sand and rocks, CH to describe one with abundant corals and hard carbonate substrates, M to describe another dominated by mud, and so on. One substrate category was assigned to every transect.

Density of **Pinctada mazatlanica**

We estimated the density of *P. mazatlanica* by counting the number of living individuals in each transect along the different categories of substrates. Densities per transect were estimated by dividing the abundance per transect by 600 m^2, whereas densities per substrate category were estimated by dividing the sum of all oyster individuals (abundance) found in transects within that category to their corresponding surface area. We used mean densities from all six transects from a site to describe the overall mean density of each sampling site, and we scaled all density values to hectares (ha). Estimations of densities in sites that we did not survey were obtained by interpolating density values of transects from neighboring polygons to produce final maps.

Statistical Analyses

The data in our study consist of absolute frequencies of oysters within transects and of oyster density values. We used standard methods of linear regression model fitting (LRM) and log-transformations to fit exponential and power-law abundance distributions in bins of five units each and to test the relationship between oyster densities (all data, not means) and substrate categories (Sokal & Rohlf 1995).

We used statistical analyses based on randomization techniques (Manly 1997) developed in Microsoft Visual Basic (2005). In all tests we used $\alpha = 0.05$, and tests were run at $i = 5{,}000$ iterations. Sample means (mean), sample standard deviations (SD), and 95% confidence intervals (CI) were calculated in all procedure tests, analyses. We corrected CIs using Bonferroni method to allow for multiple comparisons, such that $\alpha_{\text{Bonf.}} = \alpha \cdot c^{-1}$, where c was the number of groups to be simultaneously compared. NS indicated nonsignificant results.

We used three basic types of randomization tests: resampling (RES test), permutation (PER test), and rarefaction (RAR test). We used RES to: (1) compare oyster density between substrate categories within each archipelago; (2) compare mean density values within archipelagos in substrate classes resulting from pooling categories with similar availability of hard substrates; and (3) test for trends in the mean values of oyster density along depth by comparing samples from selected transects pooled by depth level. Within each archipelago, we tested those categories found in the largest number of transects and spanning the widest depth range. We used PER to compare the number of substrates types (S, R, C, H, A, G, and M) between archipelagos and RAR to test if the differences in the substrate categories shared between Las Perlas and Coiba resulted only from the unequal amount of sampling effort exerted in each archipelago. In both analyses, the number of transects in Las Perlas ($N_{\text{Perlas}} =$ 347 in comparable categories) was rarefied to 204, Coiba's smaller total sample size. Las Perlas mean values and Coiba's original frequencies were compared within each corresponding substrate category using the CIs.

RESULTS

History of Oyster Harvesting in Pacific Panama

In 1513 Spaniards began exploiting the native people and resources in Panama. Taxation records filed between 1514 and 1521 suggest that confiscating pearls from Amerindians was a commercial endeavor. Organized activities to obtain pearls from collected oysters probably did not start before 1522, which was the year in which the first official records of extraction were dated. Pearls from Las Perlas Archipelago were large, ranging from 31–60 karats, and highly valuable (Castillero 2004). The Crown requested a 20% tax of the product's value (Camargo 1983).

A reduction in productivity caused by a decline in the work force followed the initial pearl bonanza. Spaniards had always depended on Amerindians to dive and extract the oyster shells (Camargo 1983), but disease swiftly killed thousands of native people. Native Indian slaves continued to be the main work force of the pearl industry until 1585–1609, when royal decrees banned them from extracting pearls. From then on, African slaves were the only ones allowed to dive and collect oysters (Castillero 2004), an activity in which they were involved from the 1560s and onward (Camargo 1983).

The first pearl industry crisis on record, which was caused by the decline of natural populations of Panamanian oysters, occurred about 50 years after the exploitation began in the Bay of Panama. By the 1570s, oyster densities were sharply declining, pearls were becoming too small for the market, and several fishing regulations were issued to reduce oyster harvesting. The Crown prohibited diving for pearls for almost a decade to allow oyster banks to recover. In 1573, four harvest zones in the Gulf of Panama were suggested; every zone was to be harvested every 4 y, whereas the others were left unexploited so that the oysters could recover. Unfortunately, this plan was never put in place (Camargo 1983, Castillero 2004).

At the turn of the seventeenth century, oyster densities in the Gulf of Panama were so low that the Crown decreased the tax to 8.3%. The oyster fisheries moved north into Coiba Archipelago during the summer and as far south as Manta in Ecuador (Camargo 1983). At this time, causes other than oscillations in natural oyster populations also affected the pearl industry. The industry was driven at the time by about 30 boats and over 500 slaves, but by 1610 the supply of slaves from Portugal declined and by 1619 measles and smallpox ravaged their population in Panama. Venetian glass pearls took over the European markets, whereas most Venetian and Genoese merchants in the Gulf of Panama increasingly avoided paying taxes to the Spaniards for the pearls they sold (Camargo 1983, Castillero 2004). The reduction of the Panamanian pearl business led to a reduction in harvest, which in turn led to the recovery of local populations of oysters. By the 1700s, the pearl business in the region had recovered, with a fleet of up to 230 boats and 400 divers. As the black market grew, the Crown shifted taxation from revenue to fishing effort and regardless of the revenue (Camargo 1983).

At least 500 people were involved in the Panamanian oyster fisheries between 1812 and 1837, which was a period in which the pearl production briefly soared. It declined again in the 1840s, probably because of the new economic opportunities offered by the trans-Isthmian railroad business (Camargo 1983). The reduction of natural oyster populations likely also played a role in the industry's decline, because by 1853 most oyster fisheries had moved from the Gulf of Panama to the coast and islands south of Veraguas and Chiriquí. At this time, the oyster fleet for the islands of Coiba and Coibita consisted of only 15 boats (Camargo 1983).

Pearl production in the Gulf of Panama recovered in the 1860s and 1870s, but collapsed again soon after. By the end of the 1880s, well-established local pearl companies received permission from the Government of Colombia to extract

TABLE 1.

Results of the rarefaction test on the number of transects per substrate category (RAR test, 13 groups). Significance at $\alpha = 0.05$. The Las Perlas column shows averages resulting from rarefaction, (CI), and [original number of transects in category]. *Significant difference. [nc]Noncomparable values. Substrate categories: R: rocks; H: hard carbonate substrates; C: corals; G: seagrasses; A: algae; S: sand; M: mud. Substrate classes include categories from hardest (1) to softest (4).

Substrates		Substrates Between Archipelagos Mean (CI) [N° transects]		Substrates		Substrates Between Archipelagos Mean (CI)	
Class	Category	Las Perlas	Coiba	Class	Category	Las Perlas	Coiba
1	R	53.5 (6.0) [93]*	7	3	SR	27.2 (4.8) [48]	23
	H	4.8 (2.0) [10][nc]	0		SH	3.3 (1.6) [6]	2
	RH	3.6 (2.0) [7][nc]	0		SRH	0.3 (0.4) [1][nc]	0
	RC	8.7 (2.2) [17]*	38		SRC	0	3
	CH	0.9 (0.3) [1][nc]	0		SRA	2.4 (1.3) [4]*	4
	C	4.5 (1.2) [9]*	32		SC	4.5 (1.6) [6]*	9
					SCA	2.0 (0.9) [3]	2
2	RA	16.0 (6.2) [30]*	2	4	SG	2.2 (1.6) [4][nc]	0
	HA	0.6 (0.5) [1][nc]	0		SA	2.0 (0.9) [3]*	12
	RCA	3.5 (1.8) [7][nc]	0		A	1.3 (0.8) [2]*	3
	CA	0	3		S	66.6 (5.8) [120]	64
					M	2.1 (1.6) [6]*	6

oysters in Veraguas and the Gulf of Chiriquí using diving gear (helmet and suit). Oyster densities in the Gulf of Panama were dismal because of previous illegal diving operations. In the following years, more permits to dive for pearls were granted, and taxes and laws to control the productivity followed. Unfortunately, industrial abuse, illegal exploitation, and the spread of the pearl's black market (Camargo 1983).

Economically, by the 1900s the pearl oyster industry in Panama was very well developed and most of its production came from Veraguas and Coiba Archipelago. Since 1913, Government regulations included biological information based on meager landing records to define fishing seasons and minimum shell sizes. Fisheries inspectors enforced compliance to these rules by companies extracting pearls in Coiba by quantifying

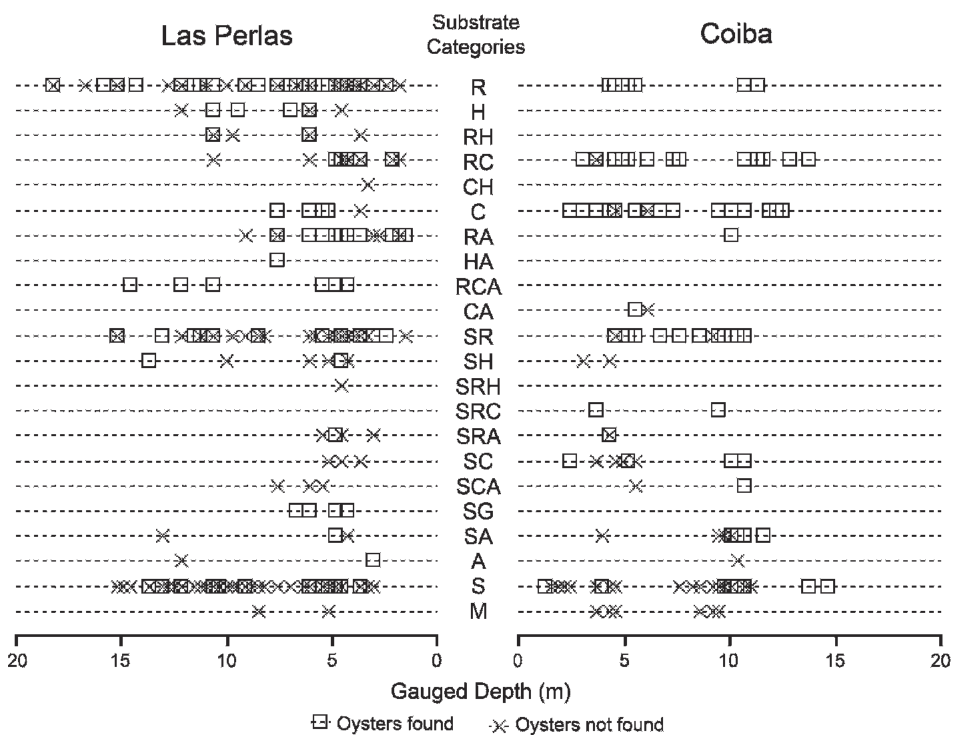

Figure 1. Presence-absence of oysters on transects in Las Perlas (left) and Coiba (right) Archipelagos according to substrate category and gauged depth. Open white squares represent transects with oysters; Xs represent transects without oysters. Substrate categories consist of combinations of the seven types of substrate: R: rocks; H: hard carbonate substrates; C: corals; G: seagrasses; A: macroalgae; S: sand; and M: mud.

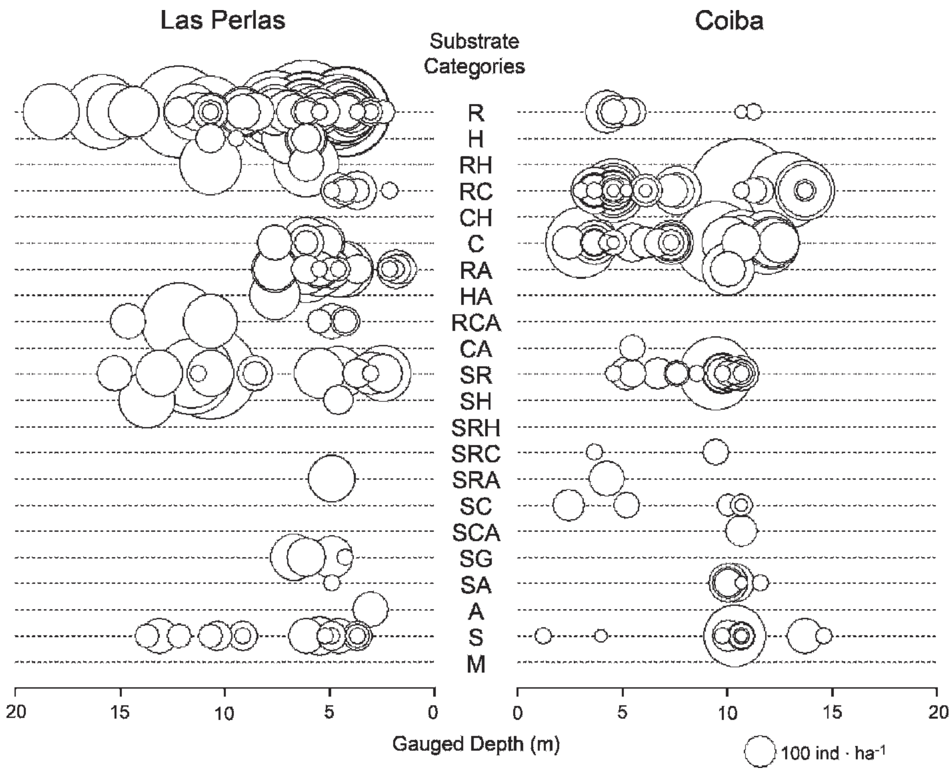

Figure 2. Distribution of oyster density per transect (ind·ha^{-1}) in Las Perlas (left) and Coiba (right) Archipelagos according to substrate category and gauged depth. The area of the circles is proportional to oyster density. Substrate categories consist of combinations of the seven types of substrate: R: rocks; H: hard carbonate substrates; C: corals; G: seagrasses; A: macroalgae; S: sand; and M: mud.

the production onboard the vessels in which oysters were gathered before pearls were extracted.

By 1916, Panamanian pearl oysters were famous in China, Geneva, and Venice; and more countries were eager to exploit the resource. As pearl oyster populations recovered, some companies moved back to the Gulf of Panama, particularly after a penitentiary facility began operations in Coiba Island in 1919. Many companies at the time harvested oysters for 6 mo in Coiba and 6 mo in Las Perlas (Camargo 1983).

Harvesting records from the Panamanian Government show that production boomed from 1905–1925, with a harvest topping 1,200 metric tons of oysters per year. However, a significant decrease occurred in the 1930s, when production floundered at 200 tons per year. Despite the entrance of cultivated Japanese pearls into the international market in the 1930s, production of Panamanian pearls continued. Fisheries in both archipelagos nearly collapsed between 1940 and 1945. Although production continued until 1960 (Galtsoff 1950, Villaláz & Gómez 1997), the pearl industry in Panama never again recovered.

The first oyster survey in Las Perlas and Coiba Archipelagos, which occurred in 1948 as part of a report to the United States Department of the Interior, described diminished oyster populations in both regions (Galtsoff 1950). In 1998, old residents of Las Perlas confirmed that by 1948, the oyster fishery had collapsed and pearl fishing practically ceased until the 1970s (MacKenzie 1999). This hiatus in harvest activities allowed the oysters to recover partially, and since the 1970s, the Las Perlas and Coiba populations have supported harvesting at a small scale, mostly for subsistence. By 1999, restaurants, tourists, and the button industry were the main markets for the oyster's meat, pearls, and shells, respectively, collected in Las Perlas.

Substrate Characterization

We visually surveyed 618 transects that totaled ~37.1 ha. In Las Perlas ($N_{Perlas} = 408$), transects contained substrate types in the following proportions: R 51%, H 6%, C 11%, G 1%, A 12%, S 48%, and M 1%. Within Coiba ($N_{Coiba} = 210$), substrate types were distributed as follows: R 37%, C 41%, H 1%, A 12%, S 57%, and M 1%. Transects with substrates dominated by G were not found in Coiba. The percentages do not add up to 100%, as most substrates were categorized using more than a single substrate type. The distributions of substrate types at the two archipelagos were significantly different (PER test, 7 groups, $P < 0.05$).

Twenty-two possible combinations of substrates categories were described in both archipelagos (Table 1). Categories were ordered accordingly to reflect a decreasing gradient of availability of hard substrates.

The substrate composition was qualitatively different between archipelagos, as only 13 of the 22 substrate combinations were found in both regions. Missing in Las Perlas were categories CA and SRC, whereas categories H, RH, CH, HA, RCA, SRH, and SG were missing in Coiba (Table 1).

When comparing the frequency of the 13 shared substrate categories between both archipelagos using rarefaction, differences in all comparable categories except SR, SH, SCA, and S were significant (RAR test, 13 groups, $P < 0.05$) (Table 1). This means that the larger sampling effort in Las Perlas cannot explain all of the differences found in the distribution of substrates between archipelagos. This result also is congruent with the existence of a substrate composition specific to each of the regions.

Densities of **Pinctada mazatlanica**

We found living oysters in only 152 of 408 (39%) transects in Las Perlas and in 125 of 210 (60%) transects in Coiba (Fig. 1). The total number of oysters counted in Las Perlas was 1079 and in Coiba was 983. Living oyster abundances per transect oscillated from 1–32 in Las Perlas and from 1–62 in Coiba. The distribution of oyster abundances per transect in Las Perlas followed an exponential function of the form:

$$y = 168.7 \cdot e^{-0.1498x}, \qquad (1)$$

whereas in Coiba, the same distribution followed a power law relation:

$$y = 1,586.05 \cdot x^{-0.18987}, \qquad (2)$$

where y represents oyster abundance and x represents histogram classes of bin size 5 (both tests: LRM, $R^2_{\mathrm{Perlas}} = 0.99$, $R^2_{\mathrm{Coiba}} = 0.90$, $P < 0.05$).

Our results suggest that ca. 1,279,000 individuals constitute the standing population size of pearl oysters Las Perlas Archipelago. In Coiba, the estimated standing population size was of ca. 2,288,000 oysters. These sizes are probably underestimates, as small postlarval individuals usually are overlooked in visual surveys. However, these are the most robust population estimates available and, to our knowledge, the first estimations of total oyster abundance in these regions.

Mean densities of living oysters in transects varied from 16.7–533.3 ind·ha^{-1} in Las Perlas and from 16.7–1,033 ind·ha^{-1} in Coiba. Per substrate category, densities oscillated from (mean ± SD) 16.7 ind·ha^{-1} (SA) to 161.9 ± 57 ind·ha^{-1} (RH) in Las Perlas and from 44.5 ± 13 ind·ha^{-1} (SRC) to 201 ± 46 ind·ha^{-1} (RA) in Coiba (Fig. 2). Oyster densities differed between some substrate categories within Las Perlas (RES test, 15 groups, $P <$ 0.05) and within Coiba (RES test, 12 groups, $P < 0.05$) (Table 2). However, some of the statistical inferences probably are not very robust because all differences except those resulting from comparing categories R-[RC, S] and S-RH in Las Perlas, and categories SRC-[RC,C,RA] and SC-[C,RA] in Coiba involved at least one category assigned to a single transect.

We found significant differences in mean densities of oysters from Las Perlas in relation to the four classes of substrates classified by hardness. In Las Perlas, oysters grew at higher densities in the substrate class containing the hardest substrates (class 1) compared with that containing the softest substrates (class 4) (RES test, 4 groups, $P < 0.05$) (Table 2: pooled mean densities). In contrast, we did not find significant differences in mean densities among the four-substrate classes in Coiba (RES test, NS) (Table 2). However, we did find slopes that were statistically different from zero when we regressed log-transformed oyster densities per transect against substrate categories ordered from the hardest to the softest in both archipelagos (LRM, slope = –0.0424, a = 4.62, $R^2_{\mathrm{Perlas}} = 0.1$, $P < 0.0001$; slope = –0.0336, a = 4.77, $R^2_{\mathrm{Coiba}} = 0.05$, $P < 0.02$).

We selected substrate categories R and S to test the association of densities with depth because they were the categories with the largest number of oyster observations and occurred at both depth levels in Las Perlas. We performed the same analysis for Coiba using categories RC, C, SR, and S. In Las Perlas, mean densities in each depth level did not differ significantly (RES test, NS). In Coiba, however, densities (mean ± CI) in substrates categories RC [shallow: 113.7 (33.1) – deep: 279.9 (199.6)] and S [shallow: 25.0 (9.2) – deep: 91.5 (53.5)] were statistically different (REST, 2 groups, $P < 0.05$).

Mean densities of living oysters per site (mean ± SD) oscillated from 2.8 ± 6.8 ind·ha^{-1} to 239 ± 161 ind·ha^{-1} in Las

TABLE 2.

Mean densities (ind·ha^{-1}) per substrate category (RES test) in Las Perlas and Coiba Archipelagos. The pooled mean density (PMD) values were obtained from independent RES tests, not directly from the averages shown in the columns. Substrate categories: R: rocks; H: hard carbonate substrates; C: corals; G: seagrasses; A: macroalgae; S: sand; M: mud. Substrate classes include categories from hardest (1) to softest (4). PMD with * is statistically different from that marked with ** (RES test, 4 groups, $P < 0.05$). Other significant differences not marked.

Substrates		Mean densities per substrate category Mean (CI)		Substrates		Mean densities per substrate category Mean (CI)	
Class	Category	Las Perlas	Coiba	Class	Category	Las Perlas	Coiba
1	R	156.0 (46.5)	83.0 (53.0)	3	SR	134.3 (81.5)	108.8 (59.3)
	H	72.6 (44.3)			SH	108.0 (87.7)	0
	RH	161.9 (96.1)			SRH	0	
	RC	45.8 (23.7)	154.2 (85.7)		SRC		44.5 (21.6)
	CH	0			SRA	116.7 (0.0)	133.3 (0.0)
	C	70.8 (39.1)	182.9 (81.8)		SC	0	56.8 (32.6)
					SCA	0	100.0 (0.0)
PMD Class 1:		130.4 (35.6)*	158.2 (56.0)	PMD Class 3:		130.2 (69.5)	94.5 (42.7)
2	RA	79.3 (35.8)	200.8 (92.5)	4	SG	79.3 (50.4)	
	HA	133.3 (0.0)			SA	16.7 (0.0)	88.7 (58.8)
	RCA	99.6 (90.8)			A	66.7 (0.0)	0
	CA		66.7 (0.0)		S	42.8 (14.8)	80.8 (67.7)
					M	0	0
PMD Class 2:		86.2 (35.4)	154.7 (120.9)	PMD Class 4:		49.3 (17.8)**	83.2 (51.1)

Perlas and from 6.0 ± 14 ind·ha^{-1} to 264 ± 136 ind·ha^{-1} in Coiba. In Las Perlas, 22 (20%, 7,147 ha) of all 108 sites (based on interpolation) contained no living oysters, whereas 69 (64%, 17,418 ha), 14 (13%, 3,942 ha), and 3 (3%, 384 ha) sites had low (1–88 ind·ha^{-1}), medium (89–176 ind·ha^{-1}), and high (177–264 ind·ha^{-1}) relative densities, respectively. Medium densities were found on the southwest coast of San Jose Island, southeast of El Rey (including Bajo Trollope and Galera), and in a shoal south to Saboga. High densities were only found at three sites in a shoal southeast of Del Rey and on the west coast of Saboga (Fig. 3A).

In Coiba, 12 (14%, 4,415 ha) of the 84 sites contained no living oysters, whereas 44 (52%, 17,599 ha), 20 (24%, 5,147 ha), and 8 (10%, 2,165 ha) sites had low, medium, and high relative oyster densities, respectively. Medium densities were found scattered around Ranchería Island, Coibita Islet, Coiba, and Jicarón. High densities were found on the northern, eastern, and southern coasts of Ranchería, on the westernmost extreme of Coiba (including Ensenada de Playa Hermosa), and the northern half of the western coast of Jicarón (Fig. 3B). Overall mean densities were 44.1 ± 60 ind·ha^{-1} for Las Perlas and 78 ± 80 ind·ha^{-1} for Coiba.

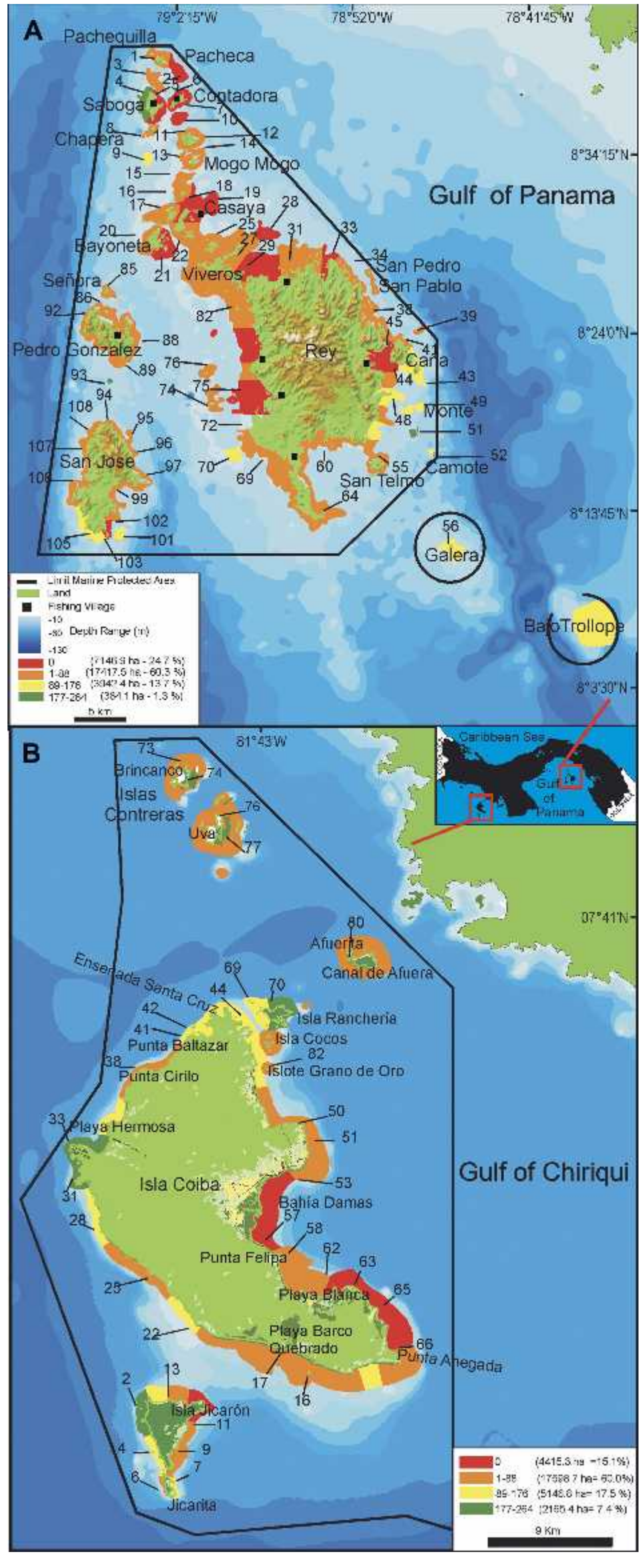

Figure 3. Maps of Las Perlas (A, top) and Coiba (B, bottom) Archipelagos showing the distribution of low (yellow), medium (orange), and high (green) relative densities (ind·ha^{-1}) of oysters in the region. Red indicates harvest areas with no oysters. Sampling sites are labeled in roman numerals. The large polygon and circles represent the limits of the protected areas. The insert in map B shows the relative positions of the archipelagos in Pacific Panama.

DISCUSSION

This study reports the results of the most extensive survey to date of the population of *Pinctada mazatlanica* inhabiting Las Perlas and Coiba Archipelagos in Pacific Panama. Oyster abundances in both archipelagos were low when compared with a number of historical and modern records. By 1925, the maximum production of oysters reported by the government of Panama topped 1,200 metric tons per year, or 1,200,000 kg of shelled oysters. If a single pearl oyster weighed on average between 0.4 and 0.7 kg (MacKenzie 1999; data estimated using weight-length relation in *P. margaritifera* from Pouvreau et al. 2000), this production represented a harvesting rate of approximately 1.7–3.0 million oysters per year. This value is almost equivalent to the total number of individuals existing today in the combined shallow water populations of Las Perlas and Coiba Archipelagos. Other localities along the eastern Pacific that were subject to considerable harvest pressures in the past also have low population sizes. For example, Díaz-Garcés (1974) reported a population size of 2 million oysters in Canal de La Paz, Mexico and 8 million individuals living in protected localities of Espíritu Santo Island, north of the Panama Canal. Twenty years later the population in Bahía de la Paz was estimated to be no greater than 500,000 individuals (Monteforte & Cariño 1992, Monteforte 2003).

Changes in the effort required to collect oysters also reflect changes in their abundance. In 1998, an experienced diver using mask, snorkel, and fins needed about 1 h to collect five oysters at depths to 5.5 m (MacKenzie 1999), whereas in the 1940s, a diver with helmet and heavy gear required on average almost 2 h to find a single living oyster in Las Perlas. In Coiba, a similar diver needed on average 3 h to find one live oyster (Galtsoff 1950). In 1925, a diver with gear in the Gulf of Panama could collect from 11–45 kg of shells during an average day of work. In contrast, a diver under the same conditions in the same locality but using less refined underwater gear could occasionally collect more than 300 kg of shells per day in Las Perlas in 1905 (Camargo 1983). In 1513, at the dawn of the pearl oyster exploitation by Europeans, the inexperienced men of Balboa needed only 4 days to collect more than 2.5 kg of pearls from oysters growing in the shallow waters of the Bay of Panama (Galtsoff 1950).

Historical documents are not the only evidence of centuries-long harvesting and repeated collapses and recoveries of the pearl oyster populations in the region. Arnaud et al. (2000) reported evidence that the genetic differentiation of populations of *P. mazatlanica* from Mexico to Panama followed a pattern of isolation by distance. Their data showed low levels of differentiation at scales of 10–100 km but significant genetic structure at larger geographic scales. The Panamanian oyster population also was monomorphic (haplotype diversity = 0), in contrast to populations from northern and southern Mexico. All of these results are congruent with a relatively recent reduction of population sizes. Mitochondrial and nuclear gene variability of oysters decreased from northern to southern populations (Arnaud-Haond et al. 2003). Arnaud-Haond et al. (2003) also reported a significant correlation between distances obtained from mtDNA and geographical distances, which led them to suggest a recent recolonization of oysters in the southern areas of their sample range, mostly corresponding to Panama.

Current densities of pearl oysters in different locales in the eastern Pacific contrast to the status of the Panamanian populations. Densities of *P. mazatlanica* have been measured at localities in and close to La Paz, in Baja California Sur (Monteforte & Cariño 1992, Monteforte 2003, González-Medina et al. 2006) and from the Gulf of Nicoya in Costa Rica (Solano-López et al. 1998) (Table 3). Densities from Baja California (3,000–12,000 ind·ha^{-1}) are one to four orders of magnitude greater than those reported in this study (3–264 ind·ha^{-1}). Densities from the Gulf of Nicoya also are staggeringly high in relation to those from Panama, as they reached more than 24,000 ind·ha^{-1} (Table 3). In contrast, the density value reported from Espíritu Santo Island was only 100 ind·ha^{-1} (González-Medina et al. 2006).

Analysis of substrate availability allowed us to test hypotheses about pearl oyster–environment associations and provided a means to compare two ecologically distinct archipelagos. Substrate categorization was based on substrate types, or their combinations, that were most frequently observed in transects. However, hard substrates such as rocks and rubble, could still be present in transects with predominantly soft substrates, such as those categorized as S.

The composition of substrates within each archipelago was diverse. Categories R, SR, RA, and S were the most common in Las Perlas (71%), whereas RC, C, SR, and S dominated Coiba (75%). These differences between regions did not depend on the number of transects sampled in each archipelago, but rather on the composition of substrates itself (Table 1).

In Las Perlas and Coiba, we observed a significant increasing trend of the log-transformed values of density when they were regressed against categories ordered according to the hardness of their substrate. This trend means that the density average increases passively, as the density's variance is the parameter that actually increases (Table 2).

The availability of a mechanically suitable site for anchorage is not the only trigger that a bivalve larva requires to metamorphose; other environmental and chemical cues also are necessary to initiate the process (Hadfield et al. 2001, Zhao et al. 2003). However, different qualities of hard substrates seem to play an important role in the distribution of oyster populations in both archipelagos. Indeed, the most robust statistical comparisons were those involving density values with magnitudes that significantly related to each other as follows: R > RC, R > S and RH > S in Las Perlas and RC > SRC, C > SRC, RA > SRC, C > SC, and RA > SC in Coiba. All of these significant differences are congruent with the association of oysters to harder substrates (Table 2). Oyster densities also were statistically

TABLE 3.

Densities (ind·ha^{-1} and standard deviation in parentheses) of *Pinctada mazatlanica* reported along the eastern Pacific. ^{1}Maximum density under particular habitat; ^{2}Population density; ^{3}Density in oyster banks; ^{4}Average density; ^{5}Density at location; ^{6}Densities per transect; ^{7}Density per sites calculated using 3600 m^2.

Region	Locality	Density	Reference
La Paz, Baja California Sur, Mexico	Gaviota Island	3,600 (1,800)^1	Monteforte and Cariño (1992)
	El Merito Bay	7,000 (2,000)^1–9,700^2	
	El Sargento Bay	8,500 (4,300)^1	
	Port Balandra (?)	4,000 (1,000)^1	
	El Gallo Island	8,000^2	
	Gaviota Creek	7,400^2	
	San Gabriel Bay	6,700^2	
Gulf of Nicoya, Costa Rica	Isla Pan de Azucar	24,200 (8,000)	Solano-López et al. (1997)
La Paz, Baja California Sur, Mexico	Bahía de La Paz	8,000–12,000^3 3,000–5,000^4	Monteforte (2003)
Baja California Sur, Mexico	Espíritu Santo Archipelago	100^5	González-Medina et al. (2006)
Gulf of Panama, Panama	Las Perlas Archipelago	16.7–533.3^6 2.8 (6.8) – 238.9 (160.8)^7	This study
Gulf of Chiriquí, Panama	Coiba Archipelago	16.7–1033^6 6.0 (14) – 263.9 (136.4)^7	

lower in shallow than in deep waters within substrate categories RC and S in Coiba. As our sampling depth range lies well within the reported habitat of *P. mazatlanica* (Galtsoff 1950, Coan et al. 2000) and RC and S are the most abundant substrates in the archipelago, we speculate that this depth distribution pattern might be produced by harvesting the bivalve.

In the future, changes in oyster resources in both archipelagos could be monitored by comparison with our baseline abundance distribution presented in equations 1 and 2. As human pressure increases on Las Perlas and Coiba Archipelagos, the results of regular monitoring of their natural resources will become more valuable. The first rational steps to manage the marine resources in these two regions of Pacific Panama already occurred when the regions were classified as areas under special management. The next step—a common and effective one to protect resources that experience strong harvesting pressure—is to identify the areas in which the highest abundances of the species exists and designate them as No Take Areas (NTAs). The underlying assumption of this procedure is that the most abundant population might be the one that contributes more free-swimming larvae to other, more depauperate populations. Identifying actual donor populations may require more than just looking for abundances and could involve the use of genetic markers. However, guaranteeing the existence of the resource is the first step to take. If identifying NTAs is to be used in Las Perlas, the preferred locales would be the shoals southeast of El Rey, the southern coast of Isla San Jose, and the west coast of Saboga. In Coiba, they would be the northern, eastern, and southern coasts of Ranchería, the westernmost extreme end of Coiba, and the northern half of the western coast of Jicarón.

Recognizing the substrates used by oysters to recruit and grow and protecting those habitats might be another useful approach. Indeed, the oyster-preferred substrates with the largest distribution in Las Perlas seem to be R and SR, whereas in Coiba they are RC and C (Tables 1 and 2). We suggest that these habitats and those sites with the largest densities should be targeted for conservation to protect and monitor pearl oyster populations in Pacific Panama.

ACKNOWLEDGMENT

The authors thank C. Guevara, A. Lam, C. Vega, C. Pimiento, and F. Torres for providing invaluable assistance in the field and E. Coan and A. Crawford for their contributions to early versions of this manuscript. The Government of Panama provided permits to work and collect in the area. The International Community Foundation, the Smithsonian Tropical Research Institute, Universidad Simon Bolivar, DEFRA's Darwin Initiative, the United Nations Foundation/UNESCO/ Conservation International Project (243RLA4000) partially sponsored this project.

LITERATURE CITED

Arnaud, S., F. Bonhomme & F. Blanc. 1999. Phylogeography of two pearl oysters *Pinctada margaritifera* and *P. mazatlanica* using mitochondrial markers. Meeting volume and abstracts of Biology & Evolution of the Bivalvia, from September 14 to 17. Geological Society Publishing House.

Arnaud-Haond, S., M. Monteforte, F. Blanc & F. Bonhomme. 2003. Evidence for male-biased effective sex ratio and recent step-by-step colonization in the bivalve *Pinctada mazatlanica*. *J. Evol. Biol.* 16: 790–796.

Arnaud, S., M. Monteforte, N. Galtier, F. Bonhomme & F. Blanc. 2000. Population structure and genetic variability of pearl oyster *Pinctada mazatlanica* along Pacific coasts from Mexico to Panama. *Conserv. Genet.* 1:299–308.

Camargo, M. 1983. Las pesquerías de perlas y conchas madre perla en Panamá. *Loteria (Panama)* 326–327:32–72.

Campbell, I. 2005. The role of local communities in the designation of a marine protected area in Las Perlas Archipelago. MSc Thesis, School of Life Sciences, Heriot-Watt University, Edinburgh.

Castillero, A. 2004. El oro y las perlas en la economía colonial. In: A. Castillero (ed), Historia General de Panamá. Comité Nacional del Centenario de la República, Panamá, pp. 431–456.

Coan, E. V., P. V. Scout & F. R. Bernard. 2000. Bivalve seashells of Western North America. Marine Bivalve Mollusks from Baja California to Arctic Alaska. Santa Barbara Museum of Natural History Monographs.

D'Croz, L. & A. O'Dea. 2007. Variability in upwelling along the Pacific shelf of Panama and implications for the distribution of nutrients and chlorophyll. *Estuar. Coast. Shelf Sci.* 73:325–340.

Díaz-Garcés, J. J. 1974. Estructura, densidad y tasa de crecimiento de la población de *Pincatada mazatlánica* en la Bahía de La Paz, Baja California. Resumen. V. Congreso Nacional de Oceanografia, Guaymas, Sonora, Mexico. pp. 45.

Galtsoff, P. S. 1950. The pearl oyster resources of Panama. *US Dep. Inter. Fish Wildl. Serv. Spec. Sci. Rep.* 23:1–52.

Gervis, M. H. & N. A. Sims. 1992. The biology and culture of pearl oysters (Bivalvia: Pteriidae). ICLARM Studies and reviews 21. Manila, Philippines. pp. 49.

Glynn, P. W. & R. H. Stewart. 1973. Distribution of coral reefs in the pearl islands (Gulf of Panama) in relation to the thermal conditions. *Limnol. Oceanogr.* 18:367–379.

González-Medina, F. J., O. E. Olguín-Quiñones & G. De La Cruz Agüero. 2006. Variación espacio-temporal de algunos macroinvertebrados (Gasteropoda, Bivalvia y Echinodermata) de fondos someros del Archipiélago Espíritu Santo, Baja California Sur, Mexico. *Cienc. Mar.* 32:33–44.

Guzman, H. M. & C. A. Guevara. 2002. Population structure, distribution and abundance of three commercial species of sea cucumber (Echinodermata) in Panama. *Caribb. J. Sci.* 38:230–238.

Guzman, H. M. & A. Tewfik. 2004. Population characteristics and co-occurrence of three exploited decapods (*Panulirus argus, P. guttatus*, and *Mithrax spinosissimus*) in Bocas del Toro, Panama. *J. Shellfish Res.* 23:575–580.

Guzman, H. M., S. Benfield, O. Breedy & J. M. Mair. 2008. Broadening reef conservation across the Tropical Eastern Pacific Seascape: Distribution and diversity of reefs in Las Perlas Archipelago, Panama. *Environ. Conserv.* 35:1–9.

Hadfield, M. G., E. J. Carpizo-Ituarte, K. Del Carmen & B. T. Nedved. 2001. Metamorphic Competence, a major adaptive convergence in marine invertebrate larvae. *Am. Zool.* 41:1123–1131.

Hertlein, L. G. 1937. A note on some species of marine mollusks occurring in both Polynesia and the Western Americas. *Proc. Am. Philos. Soc.* 78:303–312.

Hertlein, L. G. & A. M. Strong. 1955. Marine mollusks collected during the ''Askoy'' expedition to Panama, Colombia, and Ecuador in 1941. *Bull. Am. Mus. Nat. Hist.* 107:1–317.

Hickman, C. P. & Y. Finet. 1999. A field guide to marine molluscs of Galapagos. Sugar Spring Press.

Jameson, H. L. 1901. On the identity and distribution of the mother-of-pearl oysters; with a revision of the subgenus *Margaritifera*. *Proc. Zool. Soc. London* 1:372–394.

Jiuan-Jiuan, H. & T. Okutani. 2003. Taxonomy and distribution of the genera *Pteria* and *Pinctada* (Bivalvia: Pteriidae) in Taiwan. *J. Fish. Soc. Taiwan* 30:199–216.

Lamy, E. 1909. Pelecypodes recueillis par M. L. Diguet dans le Golfe de Californie. *J. Conch.* 57:207–254.

MacKenzie, C. L. 1999. A history of the pearl oyster fishery in the Archipelago de Las Perlas, Panama. *Mar. Fish. Rev.* 61:58–65.

Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall.

McNiven, G. 2003. An assessment of the Pearl Islands Archipelago Pacific Panama. School of Life Sciences, Heriot-Watt University, Edinburgh.

Microsoft Visual Basic. 2005. Microsoft Visual Studio 2005 Professional. Microsoft Corporation.

Monteforte, M. 2003. Aprovechamiento racional de las ostras perleras (*Pinctada mazatlanica* y *Pteria sterna*) en Bahía de La Paz, Baja California Sur, México: cultivo, repoblamiento y perlicultura. Informe Final Proyecto Q008-CONABIO.

Monteforte, M. & M. Cariño. 1992. Exploration and evaluation of natural stocks of pearl oysters *Pinctada mazatlanic*a and *Pteria sterna* (Bivalvia: Pteriidae): La Paz, South Baja California, Mexico. *Ambio* 21:314–320.

Pouvreau, S., J. Tiapari, A. Gangnery, F. Lagarde, M. Garnier, H. Teissier, G. Haumani, D. Buestel & A. Bodoy. 2000. Growth of the black-lip pearl oyster, *Pinctada margaritifera*, in suspended culture under hydrobiological conditions of Takapoto Lagoon (French Polynesia). *Aquaculture* 184:133–154.

Sokal, R. R. & F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. 3rd edition. W.H. Freeman and Co.

Solano-López, Y. H., J. C. Cabrera, R. A. Cruz & J. A. Palacios. 1998. Estructura de la población y crecimiento de *Pinctada mazatlanica* (Pterioida: Pteriidae), Golfo de Nicoya, Costa Rica. *Rev. Biol. Trop.* 45:1055–1060.

Villaláz, J. R. & J. A. Gómez. 1997. History, present condition, and future of the molluscan fisheries in Panama. *NOAA Technical Report NMSF* 128:33–40.

Zhao, B., S. Zhang & P.-Y. Qian. 2003. Larval settlement of the silver- or goldlip pearl oyster *Pinctada maxima* (Jameson) in response to natural biofilms and chemical cues. *Aquaculture* 220:883–901.