Journal of Shellfish Research, Vol. 27, No. 4, 889–896, 2008.

POPULATION ASSESSMENT OF THE CONCH *STROMBUS GALEATUS* (GASTROPODA, STROMBIDAE) IN PACIFIC PANAMA

ROBERTO CIPRIANI,[1,2] HECTOR M. GUZMAN,[1]* ANGEL J. VEGA[3] AND MELINA LOPEZ[4]
[1]*Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama;* [2]*Departamento de Estudios Ambientales, Universidad Simón Bolivar, A.P. 89000, Caracas 1080, Venezuela;* [3]*Departamento de Biología Marina y Limnología, Escuela de Biología, Universidad de Panamá-Sede Veraguas, Apartado 0923-00173, Panamá;* [4]*Department of Chemistry, Geosciences and Environmental Science, Tarleton State University, Box T-0540, Stephenville, Texas 76402*

ABSTRACT Populations of *Strombus galeatus* Swainson 1823 have been severely overfished in Pacific Panama. In this study, we assessed the status of the *S. galeatus* population in Las Perlas and Coiba Archipelagos. Average densities per site were dismal: 0.45 ± 3.8 $\text{ind}\cdot\text{ha}^{-1}$ and 6.0 ± 18 $\text{ind}\cdot\text{ha}^{-1}$ in Las Perlas and Coiba, respectively. In Las Perlas, low densities occurred on the southwest coast of Del Rey, the south coast of Chaperas, and Bolaños, whereas intermediate densities were found on the eastern coast of Saboga. In Coiba, high relative densities occurred only on the west coast of Coiba Island and at the north and south of Bahía Damas. Environmental variability and depth did not explain the differences found between densities nor the low abundances in the archipelagos. Shell length of *S. galeatus* from Coiba ranged from 91.0–213.3 mm (156 ± 22.2 mm). We fitted a von Bertalanffy growth model to juvenile data using the following parameters: $L_\infty = 315$ mm, $K = 0.029\ \text{mo}^{-1}$, and $t_o = 0.5$ mo. The model suggests that 27–28 mo are required (on average) before the outer lip begins to form. Two years after the enactment of Decree No. 159 in September 2004, which banned the *Strombus* fisheries in Panama for five years, the conch populations in Las Perlas and Coiba have not recovered. The Las Perlas population is recruitment limited and we recommend that a program of law enforcement and monitoring should be implemented immediately to protect this species, conducive to increase spawning and settlement in nursery grounds.

KEY WORDS: conch, *Strombus galeatus*, overfishing, Las Perlas, Coiba, Panama

INTRODUCTION

The giant conch, *Strombus galeatus* Swainson 1823 inhabits the coastal waters of the Eastern Pacific, ranging from the Gulf of California to Ecuador, the Galapagos Islands, and Peru (Keen 1958, Arroyo-Mora 2003). The giant conch, *S. galeatus*, is popularly known in Panama, Costa Rica, and Nicargaua as *cambute* and in Mexico as *caracol burro* and the Cortez conch. It lives on sandy bottoms with rocks (Arroyo-Mora 2003) and adjacent to mangrove areas (González 1997) from the low tide mark to 15 m deep, but it has been found as deep as 30 m. *S. galeatus* feeds primarily on macroalgae and is preyed upon by octopi, rays (Myliobatidae), triggerfish (Balistidae), and snappers (Lutjanidae). It spends part of the time partially buried in the sand, but it also is capable of moving long distances (on the scale of km; Arroyo-Mora 2003) over the course of months. During the early months of the year, *S. galeatus* forms large aggregations in shallow waters where mating and oviposition takes place. Females lay egg masses directly on the sand and on dead shells (Arroyo-Mora 1998, Arroyo-Mora 2003).

Strombus galeatus, *Melongena patula* Broderip & Sowerby 1829, *Pleuroploca princeps* Sowerby 1825, and *Malea ringens* Swainson 1822 are all gastropod species important for subsistence and small commercial fisheries on the Pacific coast of Panama. The largest conch production in Panama comes from San Blas and Bocas del Toro on the Caribbean coast (Martans 1997). There, and throughout the Caribbean Sea, the exploitation pressure on *S. gigas* and *S. costatus* has been driven by the high demand for their meat and their increasing market values (Tewfik 1997).

Coiba and Las Perlas Archipelagos in Pacific Panama were designated as protected areas in 2004 and 2007, respectively. These designations prohibit the use of particular fishing methods and guarantee the regulation of fisheries using the best scientific evidence available. However, very little is known about the biology, ecology, and distribution of *S. galeatus* in Pacific Panama. No formal studies on the giant conch in Las Perlas have ever been conducted, and only one report is available in the literature for Coiba (Vega & Pérez 2003), although anecdotal information is available from local people. Fishermen from the Ensenada community on Las Perlas have informally reported their catches for the past 4 y. Their reports show an average catch of nonspecified gastropods of about 949 kg per year, with harvest peaks in September and November. Panama's Marine Authority has also recorded national totals annually, and according to these records, catches of conch have been declining rapidly. In 1998, the annual catch was 116 metric tons, declined in 1999 to 17 metric tons, and collapsed in 2000 and 2001 when only 1 metric ton was reported. Pinpointing the source of conch decline is impossible, however, as the data from Panama's Marine Authority comes from catch values pooled from both Pacific and Caribbean conch species. Decree No. 159 by the Government of Panama, which went into effect in September 2004, established a 5-y fishing ban for all species of *Strombus* in Panama. It was enacted because *S. costatus* and *S. gigas* were overexploited throughout the Caribbean, but it was not based on any specific knowledge about the potential overfishing of *S. galeatus* in the Pacific.

In this study, we assessed the status of the *S. galeatus* population in Las Perlas and Coiba Archipelagos, quantified this species' abundance and density, and documented its geographical distribution in these regions. We also fit a growth

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*Corresponding author. E-mail: guzmanh@si.edu model to juvenile and subadult conchs from Coiba to estimate their age at maturity. Finally, we suggested candidate areas in both archipelagos for population monitoring. Further studies on the ecology and growth of this species will certainly improve the management plans necessary for the rational exploitation and protection of the giant conch resource in the years to come.

MATERIALS AND METHODS

Study Areas

The Las Perlas Archipelago lies in the Gulf of Panama 60 km southeast of Panama City. It consists of approximately 255 islands with ca. 318,460 km of coastline (Campbell 2005). The largest island, Del Rey, (8°22′54.64″ N, 78°54′20.16″ W), sits approximately 38 km southwest of the mainland. The Las Perlas Archipelago, which is enclosed in a marine special management zone, is Panama's most important fishing area (Villalaz & Gómez 1997). This zone covers a core area of 1688 km^2, as well as two small satellite areas, Roca Trollope and Isla Galera, that are located to the southeast. Upwelling, produced by northerly winds, occurs along the Gulf of Panama between January and April and strongly affects the water temperature and salinity of the region (Glynn & Stewart 1973).

Coiba National Park, located in the Gulf of Chiriquí, contains 30 islands and islets and has a surface area of ca. 270,125 ha. The largest island is Coiba (7°28′00.72″ N, 81°46′53.27″ W), which lies approximately 24 km southwest of the mainland. The upwelling that occurs in the Gulf of Panama does not seem to strongly affect Coiba National Park, but every 4 y both archipelagos experience El Niño Southern Oscillation (McNiven 2003, D'Croz & O'Dea 2007) which has severely affected coral reef ecosystems and related fisheries in 1982/83 and slightly in 1997/98.

Both archipelagos contain rich and biodiverse coastal and shallow water ecosystems, ranging from sandy bottoms and rocky shores to mangroves, seagrasses, and coral reefs (Guzman et al. 2004, 2008).

Sampling Design

We selected the sampling localities of our study using the ArcGIS V9.1 software (Environmental System Research Institute) with LANSAT-7 ETM satellite images (2000) and topographic maps (1:50,000) following the methodology described in Guzman and Guevara (2002) and Guzman and Tewfik (2004). Irregular polygons of ca. 2 × 2 km arbitrarily positioned one adjacent to another delimited our sampling sites. They covered the waters surrounding each archipelago (*sensu* Guzman et al. 2004, Cipriani et al. in review).

In Las Perlas, we randomly selected 68 out of the 108 available polygons (108 sites = 28,891 ha; 68 sites = 63%) and in Coiba, 35 out of 84 polygons (84 sites = 29,326 ha; 35 sites = 42%). We designated an imaginary boundary at ~10 m deep to divide each sampling site into two depth levels, although depth ranges varied according to local geomorphology. In each of the two depth levels, we randomly selected three bottom transects of 6 × 100 m (totaling 6 per site), which covered a surface area of 3600 m^2 per site. Gauged depths varied from 1.50–18.3 m in Las Perlas and from 1.20–14.0 m in Coiba. Depth levels were considered separate treatments, as depth differences between levels were still significant in 40% of transects after corresponding tidal amplitudes of 4.85 m (Las Perlas) and 5.67 m (Coiba) were added to the gauged data. Scuba divers conducted visual surveys between June 2 and July 11, 2006 in Las Perlas and between October 6, 2006 and February 1, 2007 in Coiba.

Substrates

Substrate characterization followed Cipriani et al. (in review), which describes substrates by considering the presence of rocks (R); hard carbonate substrates (H); coral communities (C); seagrasses (G); algae (A); sand (S); and mud (M), and their combinations. Using this nomenclature, for example, category SA described any transect dominated by sand and algae and CH any transect with abundant corals and hard carbonate substrates. Substrates differ between the archipelagos, but both have a large proportion of substrates categorized as S (48% of transects in Las Perlas and 57% in Coiba) (Benfield 2005, Cipriani et al. in review). Such substrates are known to be preferred by conchs (Arroyo-Mora 1998, 2003).

Densities

We estimated the abundances of *S. galeatus* by directly counting the number of living individuals found in each transect. Densities per transect were estimated by dividing the abundance per transect by 600 m^2 and scaling it to hectares (ha). The overall mean density of each sampling site was obtained by averaging the density of all six transects. Transect densities from neighboring polygons were used to interpolate conch densities in polygon areas that were not surveyed (i.e., for 40 of the polygons at Las Perlas and 49 in Coiba). All averaged values and their corresponding standard deviations are reported as mean ± s.d.

We used a chi-square (χ^2) test based on permutations implemented in Microsoft Visual Basic® (2005) (PER test) to compare the frequency of conchs per substrate and the proportion of substrates in Coiba Archipelago, but not in Las Perlas due to small sample size. We used significant differences between these parameters to pinpoint habitat preferences in conchs. Differences in densities were tested by depth level using statistical analyses based on resampling tests (RES test) (Manly 1997) and implemented in Microsoft Visual Basic® (2005). For these tests, we used 5000 iterations and set significance at $\alpha = 0.05$. We used Bonferroni's method to calculate and correct confidence intervals (CIs), which allowed for multiple comparisons, such that $\alpha_{\text{Bonf.}} = \alpha \cdot c^{-1}$, where c was the number of groups to be simultaneously compared. Results are reported as mean ± CI.

Information shared by fishermen from Las Perlas about the distribution of sites in which adult conchs were abundant was geo-referenced and compared with the distribution of conch densities resulting from our survey.

Biometrics and Juvenile Growth

Because densities of *S. galeatus* in Las Perlas and Coiba were very low, we performed a growth analysis on 88 tagged conchs from Coiba Archipelago that were followed between 1999 and 2000 (data partially analyzed in Vega & Pérez 2003). These data consist of 510 values of *S. galeatus* shell length (i.e., distance from the apex to the siphon opening) collected over the course of 9 mo (April through January, excluding December) and measured to the nearest millimeter. The modes of the age groups of juveniles and subadults (following Arroyo-Mora 1998) identified on the shell length frequency histograms were assumed to be representative of *S. galeatus* age groups in Coiba Archipelago and were used to fit a von Bertalanffy growth model (Hilborn & Walters 1992, Essington et al. 2001). In the Caribbean queen conch (*S. gigas*), shell length is a relatively good predictor of relative age only before sexual maturity. After that, the thickness of the recently formed outer lip becomes the best proxy of relative age (e.g., Appeldoorn 1988). In Vega and Perez's 2003 data set, the thickness of the outer lip of *S. galeatus* was measured to the nearest millimeter in a subset of 40. Here, the relation between lip thickness and shell length in these individuals of *S. galeatus* was compared with that in 191 individuals of *S. gigas* collected in the similarly exploited area of Los Roques Archipelago, Venezuela (data from Cipriani & Posada 2003) as both species are closely related (Latiolais 2003).

RESULTS

Densities

We found *S. galeatus* in only 7 of the 408 transects (24.5 ha) surveyed in Las Perlas, and only 11 individuals were observed (1–3, 1.6 ± 0.8 per inhabited transect). Substrates in these transects included 5 of the 20 categories present in the archipelago (substrate category, abundance of *S. galeatus*): H, 2; SH, 1; SA, 2; A, 3; and S, 3. No robust statistical inferences about the association of conchs with different substrates could be obtained because the number of conchs was too low.

We found living conchs in only 32 of the 210 transects surveyed (12.6 ha) in Coiba, and the total conch abundance was 70 (1–10, 2.1 ± 1.8 per inhabited transect). Relative abundances varied according to the substrate category assigned to transects. Conchs were found in 8 of 15 categories of substrates present in Coiba (proportion of transects in that category, abundance of *S. galeatus*): RC 1, C 15, SH 1, SRA 2, SC 4, SCA 1, SA 6, and S 30). The corresponding relative abundances found in these substrate categories were statistically different from those expected at random (PER test, $\chi^2 = 32.9$, d.f. = 7, $P < 0.0001$). The highest proportion of individuals was found in transects with substrate category S, but conchs were more abundant than expected in substrates SRA and SA.

The density in transects with living conchs in Las Perlas varied considerably, ranging from 16.7–50 ind. ha^{-1} and averaging 26.2 ± 13.1 ind·ha^{-1}. Density in all four surveyed sites with conchs ranged from 2.8 and 13.9 ind·ha^{-1} and averaged 7.6 ± 4.7 ind·ha^{-1} per site.

In Coiba, the densities in transects with living conchs were greater than those recorded in Las Perlas, varying from 16.7–167 ind·ha^{-1} and averaging 35.4 ± 30.6 ind·ha^{-1}. Density in all 16 surveyed sites with conchs ranged from 2.8–38.9 ind·ha^{-1} and averaged 12.2 ± 11.1 ind·ha^{-1} per site.

In Las Perlas, abundances were too low to make any statistical inference about the distribution of density by depth level per transect, and in Coiba, statistical differences were not found (average ± CI) (shallow level 38.0 ± 10.2; deep level 32.2 ± 16.0; RES test, NS).

Average densities per sampling site (considering all sites in each archipelago, even those not sampled) were low for both archipelagos. In Las Perlas, the estimated density was 0.45 ± 3.8 ind·ha^{-1}, and in Coiba, 6.0 ± 18 ind·ha^{-1}. Estimates of population sizes based on these values are ~13,000 conchs in Las Perlas and ~176,000 conchs in Coiba. Because visual surveys are not the best method to account for recruits and small juveniles, these values are probably underestimates.

In both archipelagos, we categorized sites as having low (1–16 ind·ha^{-1}), intermediate (17–32 ind·ha^{-1}), and high relative densities (33–48 ind·ha^{-1}) of conchs. In Las Perlas, 104 of 108 sites (27,801 ha, 96% of the total area surveyed in this archipelago) had no conchs, whereas 3 sites (815 ha, 3%) had relative low densities and 1 site (275 ha, 1%) had an intermediate density of *S. galeatus*. Low densities occurred on the southwest coast of Del Rey, the south coast of Chaperas, and Bolaños Island. An intermediate density was found only on the eastern coast of Saboga (Fig. 1A).

Fishermen reported usually collecting adult *S. galeatus* in several areas around Las Perlas Archipelago, mostly on Galera Island, on the coast and shoals located south and southeast of Del Rey, in several localities around San Jose, and in shoals located west of Pedro Gonzalez (Fig. 1B). Other collecting areas extend to the north of the archipelago and include the islands of Mina, Bayoneta, Casaya, Mogogo, Chapera, Contadora, and Pacheca (Fig. 1B). Few of these shoals pointed out by fishermen, relatively far from land, were not surveyed in our study.

In Coiba, conchs were absent in 47 of 84 sites (16,502 ha, 56%). In 27 sites (8541 ha, 29%) density was relatively low, in 7 sites (2816 ha, 10%) density was intermediate, and in 3 sites (1467 ha, 5%) density was relatively high (Fig. 2). High densities were found on the west coast of Coiba Island, north of Bahía Damas (Punta Damasi), and on the southern extreme of the same bay (Fig. 2).

Biometrics and Juvenile Growth

Shell length of *S. galeatus* from Coiba ranged from 91.0–213.3 mm (156 ± 22.2 mm). We pooled shell length values by month (from April to November 1999, and January 2000) and used their frequency distributions to identify 17 shell length modes that allegedly represented different age groups (Fig. 3). Following the recruitment that occurred in November, we used 10 modes belonging to juveniles and subadults (with shells ≤ 175 mm in shell length) to fit a von Bertalanffy growth model of the form:

$$L(t) = L_\infty \cdot \left(1 - e^{-K\cdot(t-t_o)}\right) = 315 \cdot \left(1 - e^{-0.029\cdot(t-0.5)}\right), \qquad (1)$$

where $L(t)$ is shell length at time t, $L_\infty = 315$ mm is the hypothetical maximum length that shells can attain, $K = 0.029\ \text{y}^{-1}$, is the rate of growth, and $t_o = 0.5$ is the time at which growth described by a convex curve starts (Fig. 4).

In smaller *S. galeatus*, lip thickness remains approximately constant as shell length increases. When the shell reaches approximately 170 mm in length, the lip starts to thicken (values at bottom of Figure 5). In conchs larger than 170 mm, lip thickness varies from 5 mm to more than 27 mm (values at center of Figure 5). When we compared shell length and lip thickness, to relate age of two exploited *Strombus* congeners with similar growth (Arroyo-Mora 1998), for 40 *S. galeatus* individuals from

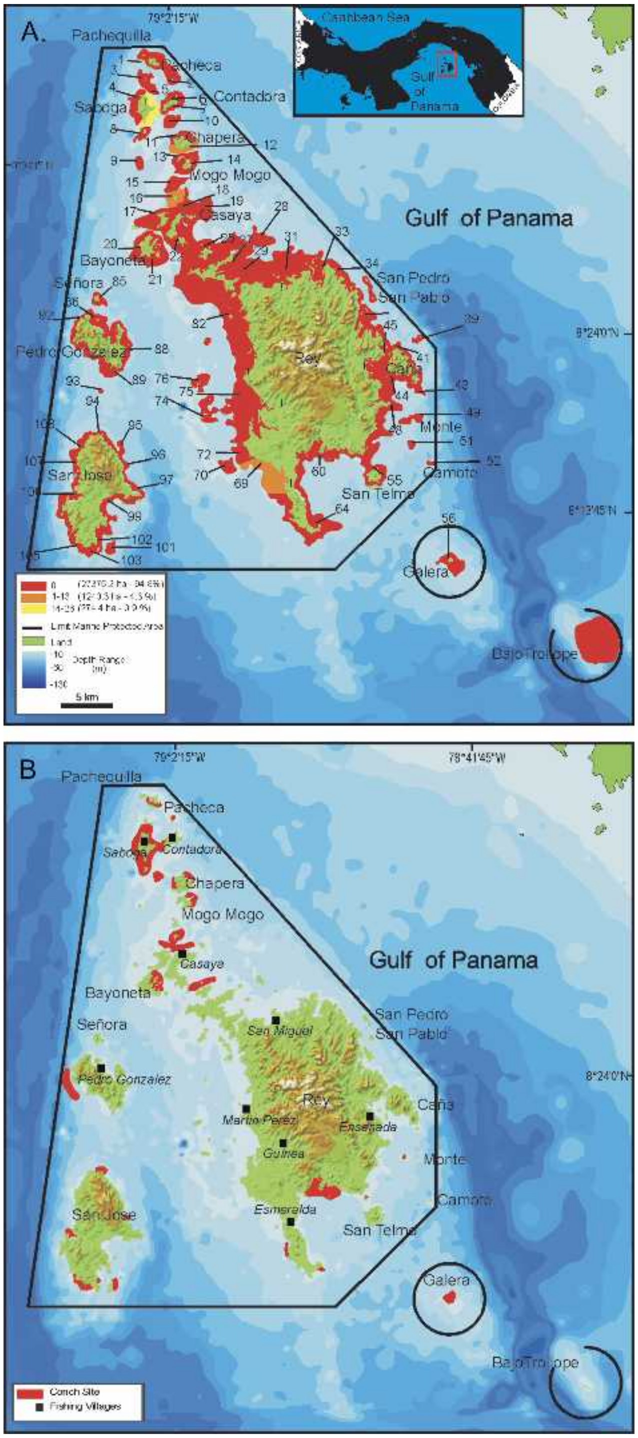

Figure 1. Maps of Las Perlas Archipelago showing the distribution of conch *S. galeatus*. (A) Map from survey showing the distribution of low (orange) and medium (yellow) relative densities (ind·ha^{-1}) of conchs in the region. (B) Map made with information from fishermen showing distribution of adult conchs. Insert shows relative position of the archipelago in Pacific Panama. Red indicates areas with no conchs. Sampling sites are labeled with numbers. The large polygon and circles represent the limits of the protected areas.

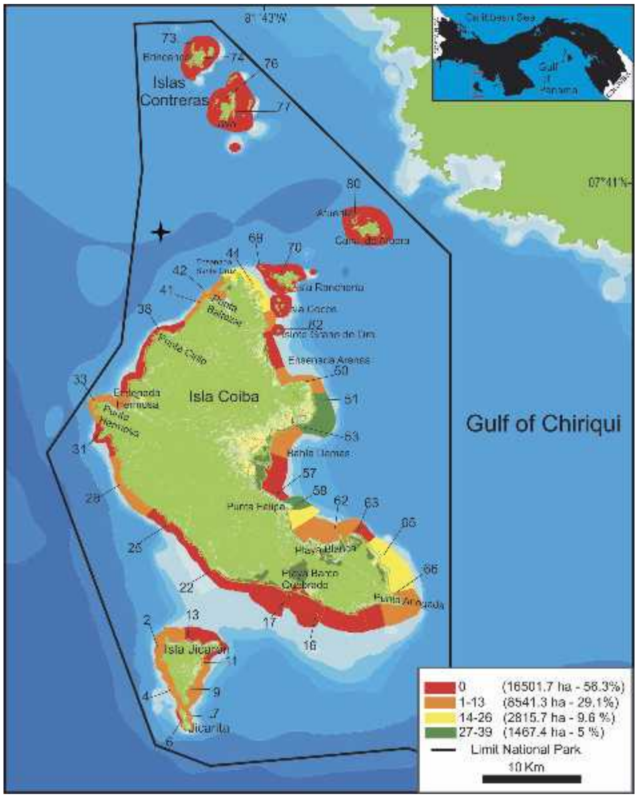

Figure 2. Map of Coiba Archipelago showing the distribution [low (orange), medium (yellow), and high (green) relative densities (ind·ha^{-1})] of the conch *S. galeatus*. Red indicates areas with no conchs. Sampling sites are labeled with numbers. The large polygon represents the limits of the national park.

Coiba (data used in Vega & Pérez 2003) (shell length = 111–213 mm, 172 ± 26 mm; lip thickness = 0.5–27 mm, 10.1 ± 10.3 mm) with those of 191 individuals of *S. gigas* from Los Roques Archipelago, Venezuela (Cipriani & Posada 2003) (shell length = 165–215 mm, 202 ± 11.3 mm; lip thickness = 1–34 mm, 17.6 ± 9.5 mm), we found that the shape of the relationship between these two variables was similar in both species (Fig. 5).

DISCUSSION

In this extensive survey, we assessed the population status, abundance, density, and distribution of *S. galeatus* in Las Perlas and Coiba Archipelagos in Pacific Panama. The abundance of the giant conch in both archipelagos was very low: In our surveys, we found only 11 living individuals in Las Perlas and 70 in Coiba.

Densities per transect in Las Perlas varied, averaging 26.2 ± 13.1 ind·ha^{-1} in the 7 transects that contained living conchs. In the 32 transects from Coiba in which conchs were found, densities were one order of magnitude higher, 35.4 ± 30.6 ind·ha^{-1}, but these values are still low when compared with those reported for transects from Laguna de San Miguel, Reserva Natural Absoluta de Cabo Blanco, in Costa Rica (500 ind·ha^{-1}) between 1993 and 1997 (Arroyo-Mora 1998, 2003).

Estimations of population sizes obtained from average site densities — 0.45 ± 3.8 ind·ha^{-1} in Las Perlas and 6.0 ± 18 ind·ha^{-1} in Coiba—also were extremely low: approximately 13,000 conchs in Las Perlas and 176,000 in Coiba. In Las Perlas, this population size barely surpasses the lowest production of conch of Panama (Caribbean and Pacific) in 1999: 11,300 shells

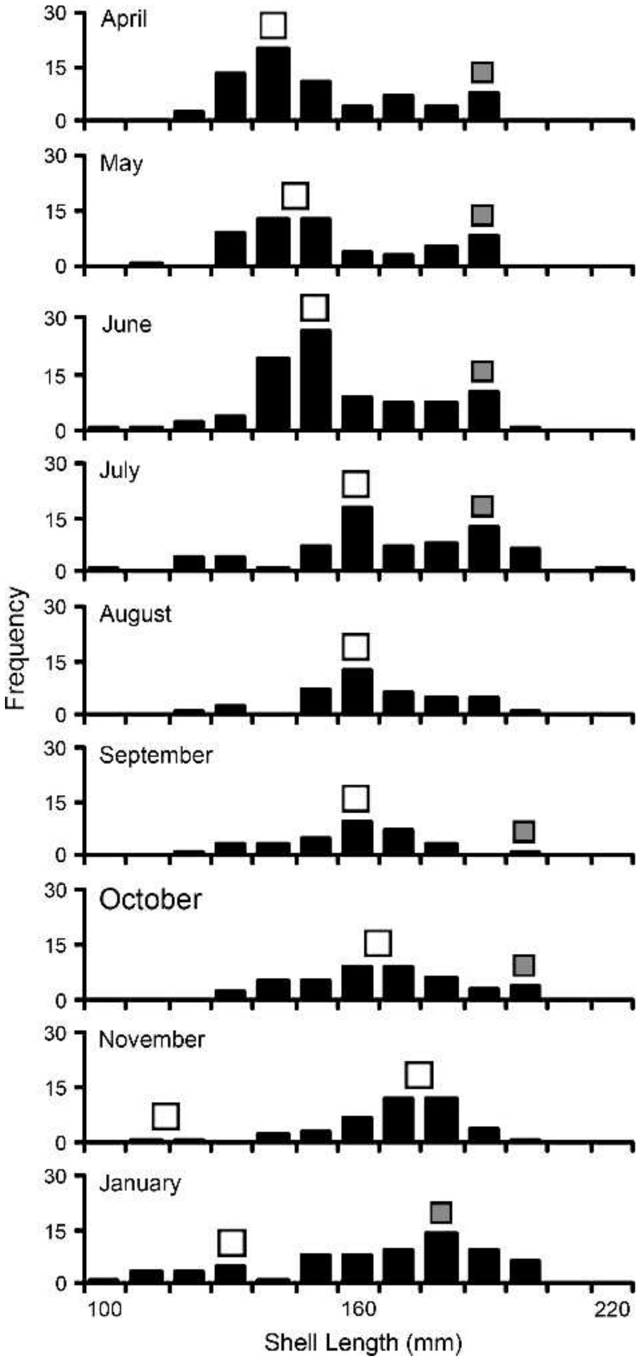

Figure 3. Size frequency histograms of *S. galeatus* shell length of from April 1999 to January 2000 in Coiba Archipelago. Large white squares represent juveniles and subadults. These modes were used to fit the Von Bertalanffy growth model. Small gray squares on bars represent adults.

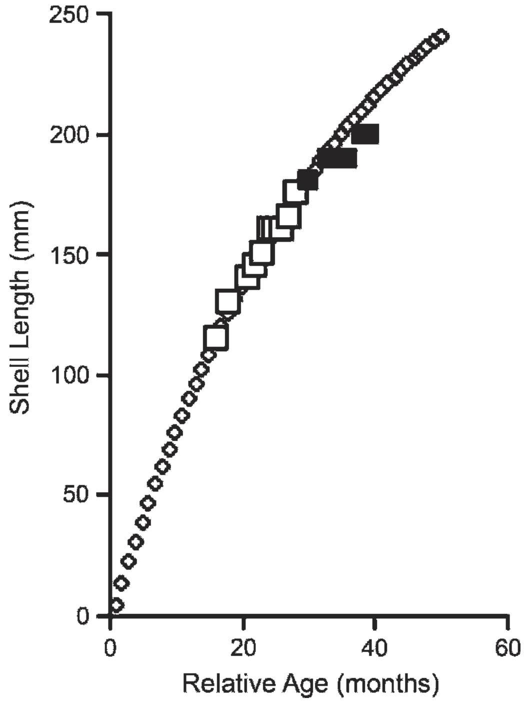

Figure 4. Von Bertalanffy growth model (small white circles) fit to shell length modes (white squares) of juvenile and subadults of *S. galeatus*. Small gray squares represent adults (data from Vega & Pérez 2003. Model parameters: $L_\infty = 315$ mm, $K = 0.029\ y^{-1}$, $t_o = 0.5$.

or 17 tons at 1.5 kg per adult conch (Arroyo-Mora 2003), according to the Panama's Marine Authority. These average densities and population sizes of *S. galeatus* in Pacific Panama are low compared with those of exploited populations of *S. gigas* in the Caribbean. For example, in Cayo Cochinos, Honduras, the overall density of queen conch was 14.6 ± 36 ind·ha^{-1} (Tewfik et al. 1998). In Los Roques Archipelago National Park, Venezuela, the actual population of *S. gigas* had average densities of 17.5 ind·ha^{-1} (Schweizer & Posada 2006) and population size (considering only subadults and adults) was estimated to be 1,278,415 (Schweizer & Posada 2006, Cipriani & Antczak in review). These values suggest that *S. galeatus* is under strong harvesting pressure in Pacific

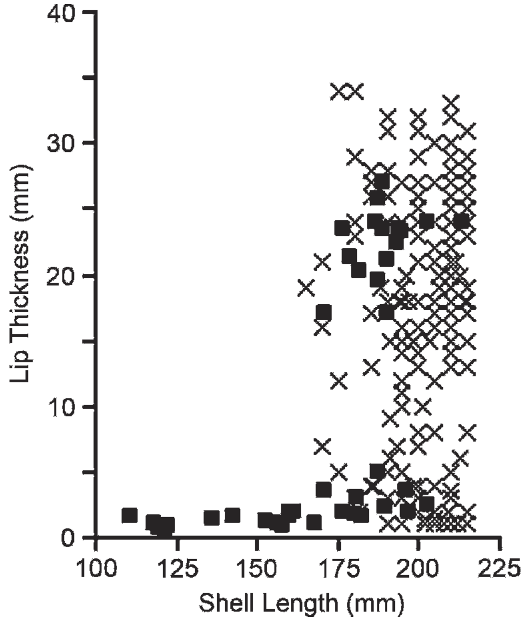

Figure 5. Relationship between shell length and lip thickness of the Pacific giant conch, *S. galeatus* (black squares, this study) and the Caribbean queen conch, *S. gigas* (gray crosses) (data from Cipriani & Posada 2003).

Panama, assuming that unexploited populations for both species were similar.

The effects of overfishing were most clearly seen in Las Perlas Archipelago. Overall, 96% of the sites in Las Perlas were devoid of conchs (Fig. 1, Fig. 2). As the distribution of fishing grounds of adult conchs reported by fishermen in Las Perlas was mostly covered in our survey (Figs. 1A, B), we could extrapolate that the fishermen's catch of 949 kg of giant conch meat per year (4.8 tons of living animal), approximately 2791 shells (at 1.7 kg per adult conch; *sensu* Arroyo-Mora 2003), represented ~22% of the standing population size. We found the population of *S. galeatus* in Las Perlas to be dangerously reduced, and under these conditions, even a 22% catch might lead to the regional collapse of its population in few years. For example, low densities are known to hinder or even prevent reproduction in some species. This process, also known as the Allee effect, seems to play an important role in the dynamics of *S. gigas* in the Bahamas. There, queen conchs seem unable to find a mate at densities lower than 56 ind ha^{-1} (Stoner & Ray-Culp 2000).

The conch population in Coiba Archipelago, even if larger than that in Las Perlas, is also very reduced compared with Costa Rica; 56% of all sites in Coiba had no conchs, and the west coast of Coiba Island and the northern and southern extremes of Bahía Damas were the only localities with the highest relative densities of conch in Pacific Panama (Fig. 2). Historical evidence also suggests that conchs in Coiba have been under fishing pressure for at least a decade. The maximum and average shell length values for conchs collected in Coiba Archipelago National Park between 1999 and 2000 (91.0–213.3 mm, 156 ± 22.2 mm) were smaller, respectively, than those found in conchs from Reserva Absoluta Natural Cabo Blanco, Costa Rica between 1993 and 1997 (87.0 mm to 293.5 mm, average 183 mm) (Arroyo-Mora 2003; Arroyo-Mora & Mena 1998).

The giant conch also has been exploited or depleted in Nicaragua (González 1997, Anonymous 2006), Costa Rica (Arroyo-Mora 2003), and the Gulf of California (Saenz-Arroyo et al. 2005). In Mexico in 2004, the price of 1 kg of its meat was US$4.6 (Anonymous 2004). In Costa Rica between 1993 and 1997, the average number of conchs surveyed by divers was 4–8 conchs $hour^{-1}$ in localities in which *S. galeatus* was exploited, such as Lagarto and San Juanillo in Guanastes. In Reserva Natural Cabo Blanco, the rate obtained during the same period of time was 14–40 conchs $hour^{-1}$ (Arroyo-Mora 1998) or 500 $ind{\cdot}ha^{-1}$ (Arroyo-Mora & Mena 1998, Arroyo-Mora 2003), considerably high for a previously exploited population under protection because 1963.

Environmental variability did not explain the differences between conch densities in Las Perlas and Coiba archipelagos or the low abundances. The substrate composition was qualitatively different between them (Cipriani et al. in review), but this variability was minimal when considering only those substrates in which *S. galeatus* was more likely to be found. The substrates in which we found living conchs in Las Perlas (H, SH, SA, A and S occurred in 141 transects (8.5 ha), and those in Coiba (RC, C, SH, SRA, SC, SCA, SA, and S) in 154 transects (9.2 ha) (Cipriani et al. in review). These results do not differ from those previously reported for *S. galeatus* in Coiba, where juveniles were found buried in sand, close to corals, and on substrates with algae, whereas adults crawled on sandy bottoms (Vega & Pérez 2003), or from those reported in Laguna de San Miguel, Costa Rica, where individuals were found living on sand and rocks (Arroyo-Mora 1998).

Variation in the distribution of conchs with depth did not explain our results either. Previous literature on the vertical distribution of *S. galeatus* in Costa Rica and Coiba indicated that small conchs live in shallow water (from 0.5–4 m deep) and large conchs live in deeper waters (Arroyo-Mora 1998, Arroyo-Mora 2003, Vega & Pérez 2003). However, our survey in Coiba Archipelago did not reveal any statistical difference between conch densities at different depth levels (estimated in those transects that contained living conchs).

The distribution of length data on the monthly histograms suggests that every year juveniles recruited to the conch population of Coiba Archipelago at least twice (Fig. 3). The first recruitment occurred during the months of April, May, and June, and the second started in November and continued at least until January. Results of a similar analysis in Costa Rica using tagged giant conchs suggested that recruitment in Cabo Blanco occurred over the course of several months, indicating that reproduction was constant throughout the year (Arroyo-Mora & Mena 1998). In a study from two decades ago, Weil and Laughlin (1984) reported that *S. gigas* in Los Roques Archipelago, Venezuela, reproduced throughout the year, with a peak in intensity between April and November.

We fitted a Von Bertalanffy model to the modes of shell lengths of juveniles and subadults, considering the limitations of the model itself (Roff 1980, Hilborn & Walters 1992, Day & Taylor 1997) and those of using it on conchs (Appeldoorn 1990, Appeldoorn 1992, Glazer & Berg 1992) (Figs. 3 & 4). Particularly in *S. gigas*, the Von Bertalanffy model seems to describe shell growth in juveniles reasonably well, until the outer lip begins to form and thicken (Appeldoorn 1988, Appeldoorn 1990). The lip thickness of the giant conch changes slowly whereas the shell grows, but after maturity the shell stops growing and the outer lip becomes thicker (Fig. 5). Thus, using a Von Bertalanffy model based on shell length categories, to describe growth for the conch's entire life span results in biological interpretations that are misleading (Appeldoorn 1990). This model is not recommended for application to adult conchs for another reason: in old *S. gigas* specimens, erosion by epibionts and borers reduces the shell's length, completely obliterating the age structure signal of the shell length modes. We assumed that *S. galeatus* suffers a similar process, as epibionts and signs of erosion are common on adult shells (Arroyo-Mora 1998, 2003).

As growth in different isolated groups of conchs of the same stock can be heterogeneous (Glazer & Berg 1992), in this study we used the growth model to determine a rough estimate of the amount of time (in months) *S. galeatus* juveniles from Coiba must grow before the outer lip develops and thicken. According to Arroyo-Mora (1998), in *S. galeatus* this occurs at shell lengths of 170 mm. In our data, the outer lip began to thicken at a shell length interval including this value, 170–175 mm (Fig. 5). The Von Bertalanffy model suggested that a conch would need 27–28 mo (on average) to begin forming its outer lip, or 2.3–2.4 y. *Strombus gigas* requires longer times to reach maturity than *S. galeatus*: 3.19–3.22 y in La Parguera, PR (Appeldoorn 1992) and 3.5–4.0 y in the Florida Keys (Glazer & Berg 1992).

Notice that the value of $L_\infty = 315$ mm is larger than any available *S. galeatus* shell length. To our knowledge, the maximum shell length reported in the region is 293.5 mm (Arroyo-Mora 2003). As we only worked with juvenile and subadult conchs, $L_\infty = 315$ mm should be interpreted as the maximum hypothetical size the giant conch would attain if it did not mature and invest its energy in reproduction (Appeldoorn 1990).

A positive value of $t_o = 0.5$ was indicative of the existence of a very early inflexion point in the growth curve (Appeldoorn 1990). The average rate of growth in shells from 110–120 mm long was 8.21 mm month^{-1} in Vega and Pérez's (2003) study, but in our model the same interval of sizes showed a smaller average rate of 5.91 mm month^{-1}. This difference also suggests that the actual growth curve of *S. galeatus* possesses an early inflexion point. However, our sample size was too small to study it further. Indeed, the results obtained from the Von Bertalanffy model should be considered preliminary rather than definitive, as more data and work are necessary to understand the growth of this species in this region.

Future studies of the growth of the giant conch must include a complete record of paired values of shell length and lip thickness to study growth in juveniles and subadults and in adults, respectively. Different models for males and females also should be considered. In addition, to identify the adequate shell biometrics to regulate harvesting, it is necessary first to establish a precise relationship between shell morphology and sexual maturity. *Strombus galeatus* is considered to be sexually mature when it reaches 170 mm in length and begins to grow its shell's outer lip (Arroyo-Mora 1998, Arroyo-Mora & Mena 1998, Arroyo-Mora 2003). We know that *S. gigas* is mature only when its lip is completely formed and its thickness reaches 5 mm (Egan 1985, Appeldoorn 1988, Glazer & Berg 1992, but see Avila-Poveda & Baqueiro-Cárdenas 2006). However, the appearance of a thin shell lip is considered a poor criterion for sexual maturity and a lip of 13.5 mm or greater is recommended to protect stocks under heavy fishing pressure (Avila-Poveda & Baqueiro-Cárdenas 2006). The differences between these two closely related species (Latiolais 2003) and the little knowledge we have about the biology and ecology of *S. galeatus* warrant a closer and better look at the gonadal development and the reproductive cycle of the giant conch.

Two years after the enactment of Decree No. 159 in September 2004, which banned the *Strombus* fisheries in Panama for five years, the populations of *S. galeatus* in Las Perlas and Coiba Archipelagos have not recovered. On the contrary, the giant conch population from Las Perlas seems to be in critical condition or near collapse. Inasmuch as Decree No. 159 is a sensible measure taken at the right time, its enforcement is fundamental to achieving its goal: the recovery of the conch resources in Panama.

The Las Perlas giant conch population is in such meager condition that we recommend that a program of monitoring begin at once. The progress of the population can be evaluated and potentially restored by transplanting adults to increase spawning stocks into nursery grounds (*sensu* Glazer & Delgado 2003). The areas in the archipelago that should be monitored immediately are those in which conchs are still alive; the southwest coast of Del Rey, the south coast of Chaperas, Bolaños Island, and the eastern coast of Saboga. *Strombus galeatus* stocks can be successfully restored under protected areas (Arroyo-Mora & Mena 1998, Arroyo-Mora 2003) and the suggested creation of a marine reserves network within the archipelago may contribute to increase nursery grounds (Guzman et al. in rev.). For instance, a Costa Rican small reserve (18 km^2 marine area) has reached over 500 ind·ha^{-1} in almost 45 y of protection (see Arroyo-Mora & Mena 1998). Education, training, and involvement of local fishermen in the management and restoration efforts of the giant conch in Las Perlas and Coiba Archipelagos are actions that should be considered without delay, as the experience and knowledge of local peoples about the resource will undoubtedly be helpful in designing future programs for conserving and harvesting of *S. galeatus* in Pacific Panama.

ACKNOWLEDGMENTS

The authors thank C. Guevara, A. Lam, C. Vega, C. Pimiento, and F. Torres for providing invaluable assistance in the field and to all the fishermen who kindly provided information about the distribution of conchs in Las Perlas. The Government of Panama provided permits to work in the area. This research was partially sponsored by the International Community Foundation, the Smithsonian Tropical Research Institute, the United Nations Foundation–Global Conservation Fund, the UNESCO, Conservation International, the Universidad Simon Bolivar, and DEFRA's Darwin Initiative Fund (UK).

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