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POPULATION ASSESSMENT OF THE PACIFIC GREEN SPINY LOBSTER *PANULIRUS GRACILIS* IN PACIFIC PANAMA

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ABSTRACT Populations of the green spiny lobster *Panulirus gracilis* (Streets 1871) have sustained increasing harvesting pressure in Pacific Panama for decades, but basic information about their biology and ecology in the region is scarce. This study provides baseline data for the densities and biometrics of *P. gracilis* in Las Perlas and Coiba Archipelagos. The number of surveyed lobsters in both archipelagos was surprisingly low (85 in Las Perlas and 67 in Coiba), and average densities were dismal (4.1 ± 8.8 ind. ha^{-1} and 5.3 ± 7.6 ind. ha^{-1}, respectively). Saboga and San Jose Islands had the highest relative densities of *P. gracilis* in Las Perlas, whereas intermediate relative densities were found only on Coiba Island in the Coiba Archipelago. Lobster density was not associated with either substrate or depth. In Las Perlas, female carapace length (CL) was 40–95 mm and that of males was 25–100 mm; in Coiba, female CL was 45–124 mm and male CL was 45–121 mm. In Las Perlas, the smallest lobster with eggs had a CL = 65 mm and a tail length (TL) = 120 mm, whereas the smallest in Coiba had a CL = 60 mm and a TL = 81–115 mm. We recommend implementing: (1) the minimum capture CL as the average carapace length at which half of the lobster population from Coiba is adult (CL = 84 mm; TL = 112–155 mm); (2) a fishing season no longer than 6 mo; (3) management decisions involving local fishermen and native peoples; (4) marine reserves or no-take areas (NTA); and (5) long-term monitoring plans, as the best current options to insure the survival of *P. gracilis* in the region.

KEY WORDS: green spiny lobster, *Panulirus gracilis*, overfishing, fishery management, Las Perlas, Coiba, Panama

INTRODUCTION

The green spiny lobster, *Panulirus gracilis* (Streets 1871), inhabits marine substrates composed of rocks and gravel down to waters deeper than 30 m along eastern Pacific continental shelf (Gracía & Kensler 1980). Large solitary individuals and subadults living in aggregations (Heydorn 1969, Hindley 1977) prey on a variety of sessile organisms and on molluscs, worms, small crustaceans, and algae. Seasonally, green lobsters migrate between deep and shallow waters either looking for food, refuge, and optimum conditions to reproduce or in response to disturbances such as hurricanes and storms (Herrnkind 1977). In the northern hemisphere, they migrate to coastal shallow waters in November and December and remain there until May (Briones & Lozano 1977, Weinborn 1977). In Mexico, *P. gracilis* reproduces for at least 10 mo (Weinborn 1977), whereas in Ecuador it reproduces year-round (Loesch & López 1966) and spawns at least twice per year (Briones & Lozano 1977).

Because of its great economic value, the green spiny lobster has experienced harvesting pressure throughout its geographic range, from Baja California south to Peru (Holthuis 1991, Pérez-González et al. 1992, Hickman & Zimmerman 2000). In Panama, lobster harvest records are scarce. Records from the Official Controller's Office from 1951–1959 consist of pooled production values of lobsters, molluscs, and other crustaceans. Records starting in 1991 reveal a production of lobsters that oscillates between 25,000–950,000 kg per year, with an overall increase in production since 1997. Records from the Panama Maritime Authority begin in 1995 and show a similar increasing trend (Guzman & Tewfik 2004). However, all data corresponding to 2000–2004 are actually pooled production values of the Pacific green spiny lobster, *Panulirus gracilis*, and the Caribbean spiny lobster, *P. argus*.

Locals and Kuna indigenous people using hooks and spears exploit green lobster in the Las Perlas and Coiba Archipelagos for commercial and subsistence purposes. Despite the increase in production, basic information about the biology and ecology of the green spiny lobster populations in Pacific Panama that is required for making rational management decisions never has been obtained. This fact has not deterred the enactment of laws governing this resource. Executive Decree No. 15, released in March of 1981, established an arbitrarily minimum capture length for harvested lobsters in Panama (from the Caribbean and Pacific coasts); this minimum carapace length (CL) of 60 mm and corresponding minimum tail length (TL) of 120 mm were the lengths allegedly attained by individuals that had reproduced at least once during their lifetime. However, a recent study of Caribbean spiny lobsters, *Panulirus argus*, showed that all individuals with a CL = 60 mm were immature and that their corresponding TL values were very different from the 120 mm established in the Decree (Guzman & Tewfik 2004). This law therefore provides no spawning protection to Caribbean or Pacific lobsters in Panama. In Pacific Mexico, Briones & Lozano (1977) reported that *P. gracilis* reaches sexual maturity at carapace lengths between 47.5 and 53.0 mm but also that they grow at different rates according to their sex (i.e., males grow

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faster than females), locality, season, and food availability (Briones-Fourzán & Lozano-Alvarez 2003).

In this study, we estimated the density, spatial distribution, and population sex ratio of *Panulirus gracilis* in Pacific Panama, and we used simple linear models to quantify the relationship between carapace and tail lengths of individuals grouped by sex and locality. Our study also describes the distribution of lobsters according to local fishermen, who kindly contributed by pointing out where they find lobsters in their daily work and recognized the near depletion of the populations in both archipelagos. Because official records do not provide production information from specific localities, we decided to focus our study in Las Perlas and Coiba, the biggest archipelagos in Pacific Panama, both areas declared as protected areas in 2007 and 2004, respectively. The laws established in these declarations define a seasonal regimen for the lobster fishery in Las Perlas and vow to regulate fisheries within these protected areas using the best scientific evidence available.

MATERIALS AND METHODS

Study Areas

The Las Perlas Archipelago lies in the Gulf of Panama 60 km southeast of Panama City and it is composed of approximately 255 islands with ca. 318,460 km of coastline. It is a main fishing resource area for the country (Villalaz & Gómez 1997). Del Rey, the largest island (8°22′54.64″N, 78°54′20.16″W), is located 38 km southwest of the mainland. The Marine Special Management Zone that encloses the archipelago covers an area of 168,771 ha, including 33,153 ha of land as well as Roca Trollope and Isla Galera, two satellite zones located to the southeast (Guzman et al. 2008).

Coiba National Park encompasses an archipelago of 30 islands and an islet located in the Gulf of Chiriquí and has a surface area of ca. 270,125 ha. Coiba is the largest island (7°28′00.72″N, 81°46′53.27″W) and is located approximately 24 km southwest of the mainland. Between January and April, the northerly winds create upwelling along the Gulf of Panama, which strongly affects the water temperature and salinity of this area (Glynn & Stewart 1973). Whereas the effects of upwelling seem to be small or negligible in Coiba National Park, periodically both archipelagos experience the effects of El Niño Southern Oscillation (e.g., McNiven 2003, D'Croz & O'Dea 2007).

Sampling Design

We used ArcGIS V9.1 software with topographic maps (1:50,000) and LANSAT-7 ETM satellite images from 2000 to select the sampling locations for our study, following the methodology introduced by Guzman and Guevara (2002) and Guzman and Tewfik (2004). Sampling sites were irregular polygons of ca. 2 × 2 km arbitrarily positioned one adjacent to another in such a way that they covered all of the waters surrounding each archipelago (*sensu* Guzman et al. 2004, Guzman et al. 2008, Cipriani et al. in review). Of the 108 polygons (28,891 ha) covering the waters of Las Perlas, we randomly selected 68 (18,201 ha, 63% of total area). Of the 84 polygons (29,326 ha) covering Coiba we selected 35 (12,317 ha, 42% of total area). Within each sampled polygon, we divide the site into two depth levels at ca. 10 m, but actual depth ranges varied according to the geomorphology of each site. Three transects of 6 × 100 m were haphazardly within each depth level (totaling 6 per site), constituting a survey surface area of 3,600 m^2 per site. Transects were visually surveyed counting all lobsters in crevices and under rocks by two divers at two depths. Using a 6-m long PVC pole as reference, each diver surveyed a half of each transect (a 3-m width strip). Gauged depths varied from 1.50–18.3 m in Las Perlas and from 1.20–14.0 m in Coiba. After depth data were corrected by the corresponding maximum tidal amplitudes of 4.85 m and 5.67 m, depth differences between levels were still significant in 40% of transects. Hence, depth levels were considered separate treatments. Scuba divers conducted the surveys between June 2 and July 11, 2006, in Las Perlas and between October 6, 2006 and February 1, 2007, in Coiba.

Substrates

The coastal and shallow water ecosystems that are home to the rich biodiversity of both archipelagos range from sandy bottoms and rocky shores to mangroves, seagrasses, and coral reefs (Guzman et al. 2004, 2008). In this study, we used Cipriani et al.'s (2008) substrate characterization of Las Perlas and Coiba Archipelagos. It contains the following categories: rocks (R); hard carbonate substrates (H); coral communities (C); sea grasses (G); algae (A); sand (S); and mud (M); and their combinations. For example, using this nomenclature, any transect dominated by sand and rocks fell into the category SR, and any transect with abundant corals and hard carbonate substrates fell into CH. The composition of substrates differs between archipelagos, but both contain a large proportion of substrates with R (51% of transects in Las Perlas and 37% of transects in Coiba), C (11% and 41%), A (12% and 12%), and S (48% and 57%) (Benfield et al. 2007, Cipriani et al. in review), all of which offer habitats known to be preferred by lobsters (Briones et al. 1981, Pérez-González et al. 1992, Hickman & Zimmerman 2000).

Densities of **P. gracilis**

We conducted our surveys during two different periods of the year: June 2 to July 11, 2006 (Las Perlas) and October 6, 2006 to February 1, 2007 (Coiba). We estimated the abundances of *P. gracilis* by counting the number of live individuals found in each transect. Densities per transect were estimated by dividing the abundance per transect by 600 m^2. Mean densities in all six transects were used to describe the overall mean density at each sampling site. All density values were scaled to hectares (ha). Density values of transects from neighboring polygons were used to interpolate lobster densities in sites that were not surveyed (i.e., 40 in Las Perlas and 49 in Coiba). We tested the differences in densities between depth levels estimating intervals of 95% confidence (CI) using a resampling procedure (5,000 iterations) (e.g., Manly 1997) implemented in Microsoft Visual Basic (2005) (RES test). We used Spearman rank order (SPEAR test) and a Kendall Tau (KENT test) correlation analyses to measure the dependence between the total number of lobsters per substrate category and the number of transects per category within each archipelago. Low or negative correlations would indicate potential habitat preferences of lobsters.

Total abundances in Las Perlas and Coiba were obtained by multiplying the average density per site with the total surface area covered by all sites and assuming either that lobsters could inhabit all type of substrates or only those on which they were found alive.

We also interviewed a number of fishermen in Las Perlas and obtained information about the distribution of sites in which lobsters were abundant, based in the fishermen's daily search. This information was geo-referenced and compared with the distribution of lobster densities in this archipelago obtained in our survey.

Biometrics

We measured the green lobster's cephalothorax or carapace length (CL) and abdomen or tail length (TL) to the nearest millimeter. CL was measured from the base of the rostral horns to the posterior end of the carapace, and TL was measured from the anterior edge of the tail to the posterior end of the telson while keeping the tail straight. A RES test was used to estimate the CIs of CL and TL. These CIs were corrected using Bonferroni method to allow for multiple comparisons between sexes and localities. Sex was determined by the presence of biramous pleopods in females and uniramous pleopods in males (Morgan 1980). The presence of eggs on the underside of the abdomen was used as a condition for maturity (Chubb 1994). However, not all mature lobster had eggs. Hence, we determined the smallest CL of female lobsters with eggs (SCLE) from both archipelagos and considered those having a CL smaller than the SCLE to be immature. To estimate the CL value at which half of the populations we sampled was mature, we fitted a logit regression to a pooled sample of length data from Las Perlas and Coiba (CLM). The CL corresponding to the 50th percentile of the cumulative distribution of carapace lengths of the adult population of lobsters (LC50) from Coiba and Veraguas was estimated using a simple logistic regression and suggested as a candidate value for minimum capture size. Because densities in Las Perlas and Coiba were low, we used several fishermen's catches in each region to increase the number of individuals measured for the biometric analysis. Some of these catches included lobsters fished in the coastal area of Veraguas and other adjacent areas in the Gulf of Chiriquí.

We regressed log-transformed values (log base = 10) of TL from lobster individuals within the archipelagos and grouped by sex against those of CL using reduced major axis models implemented in Microsoft Visual Basic (2005). CIs of regression parameters were estimated using standard parametric methods (Sokal & Rohlf 1995).

RESULTS

In Las Perlas, the total number of lobsters observed was 85. They were present in only 29 of the 408 surveyed transects (or 21 of 68 sampled sites). The number of lobsters per substrate category oscillated between 1 and 41, and was significantly correlated to the number of transects with lobsters within each category (1–14) (SPEAR test: $r = 0.9$, $n = 9$, $P \leq 0.005$; KENT test: $Tau = 0.85$, $n = 9$, $P \leq 0.005$). Lobsters were found on the following substrates (category & relative abundance): C 2%, H 1%, HS 2%, R 48%, RA 20%, RC 5%, RCA 2%, RS 14%, and S 5%.

In Coiba, a total of 67 lobsters were found in 31 of the 210 sampled transects (in 19 of 35 samples sites). As in Las Perlas, the number of lobsters per substrate category, varying from 1–18 was significantly correlated to the number of transects within each category (1–8) (SPEAR test: $r = 0.97$, $n = 7$, $P \leq 0.0003$; KENT test: $\tau = 0.93$, $n = 7$, $P \leq 0.004$). Lobsters were found on the following substrates (category & relative abundance): R 16%, RC 27%, C 25%, CA 1%, RS 18%, CS 9%, and S 3%.

Statistical differences in lobster densities from transects surveyed at the two different depth levels were found neither in Las Perlas nor in Coiba (RES test, NS).

Overall, average densities per sampling site were low for both archipelagos. In Las Perlas, lobster density was 4.1 ± 8.8 ind. ha^{-1} and in Coiba, 5.3 ± 7.6 ind. ha^{-1} (Table 1). Using these values, rough extrapolations of populations sizes resulted in approximately 100,300 lobsters for Las Perlas and approximately 156,000 lobsters for Coiba. These estimations were further reduced to approximately 90,200 and 130,700 lobsters, respectively, when considering the substrates on which lobsters were found. However, all these abundances are probably underestimates, as new recruits are usually not well accounted for in visual surveys on reefs and rocky areas.

After interpolating lobster density to all 108 sites in Las Perlas, 66 (17,840 ha, 61.7% of the total area) had no lobsters, whereas density was low (1–16 ind. ha^{-1}) in 35 sites (9853 ha, 34.1%), intermediate (17–32 ind. ha^{-1}) in 5 sites (746 ha, 1.2%), and relatively high (33–48 ind. ha^{-1}) in 2 sites (451 ha, 2.6%). The highest densities of *P. gracilis* occurred on the western coast of Saboga Island and in the westernmost peninsula of San Jose Island. Intermediate densities occurred in few sites, including those on the western coast of San Jose Island, the westernmost coast of Pedro Gonzalez Island, and a shoal on the southwest coast of Del Rey (Fig. 1A).

The distribution of lobsters in the archipelago according to fishermen (Fig. 1B) perfectly matched that of our study; their observations even extended to other sites not included in our random survey. Sites in which juvenile lobsters were found are scattered around San Jose Island, the south coast of Del Rey, the northern and western coast of Caña, the northern coast of Pedro Gonzalez, and in at least three other localities on the north side of the archipelago, including one on the southern coast of Saboga Island and two close to Casaya Island (Fig. 1B).

After interpolating lobster density to all 84 sites in Coiba, lobsters were absent in 39 (14,877 ha, 50.7%) whereas density was low (1–16 ind. ha^{-1}) in 36 sites (11,494 ha, 39.2%) and intermediate (17–32 ind. ha^{-1}) in 9 sites (2955 ha, 10.1%). We

TABLE 1.

Lobster densities (individuals · ha^{-1}) in Las Perlas and Coiba Archipelagos. Averages ± SD. N, sample size.

Archipelago	Sampling Unit	Transects and Sites with Lobsters: Range (N)	Transects and Sites with Lobsters: Average	All sites Average
Las Perlas	Transects	16.7–217 (21)	48.9 ± 48.5	—
	Sites	5.6–47.2 (29)	17.7 ± 13.6	4.1 ± 8.8
Coiba	Transects	16.7–100 (31)	36.0 ± 25.1	—
	Sites	2.8–27.8 (19)	14.2 ± 9.2	5.3 ± 7.6

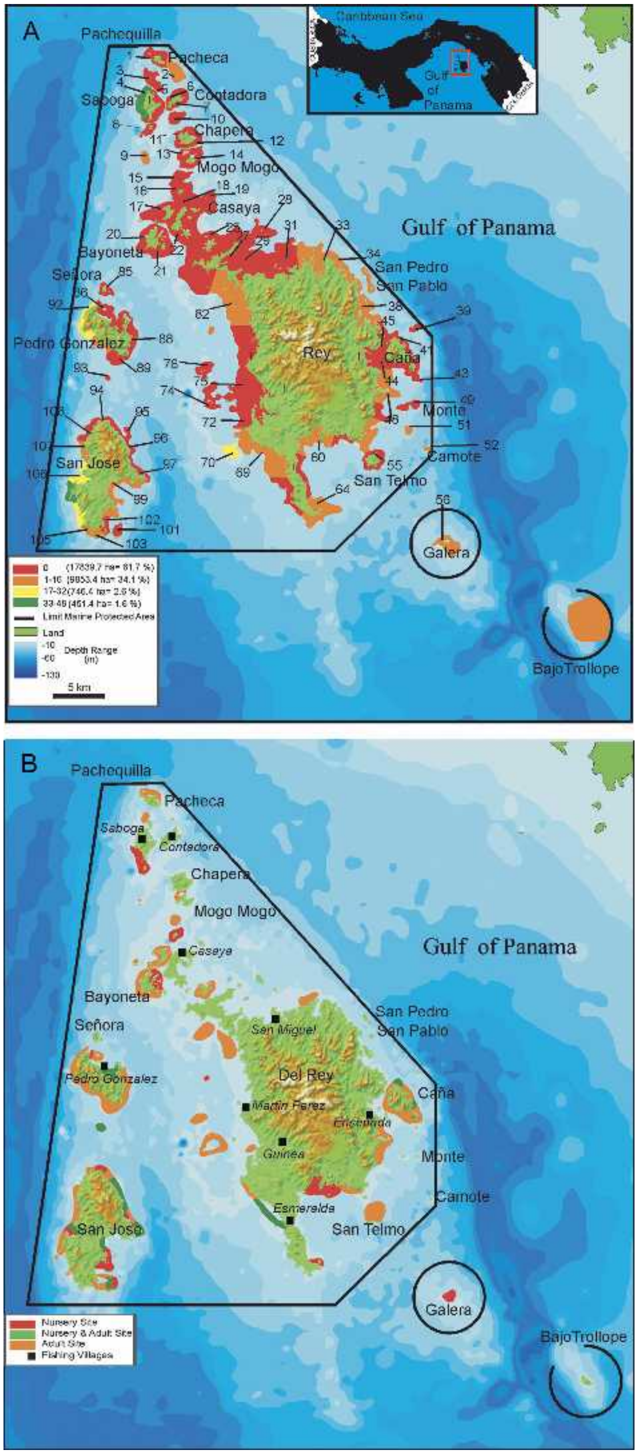

Figure 1. Maps of Las Perlas Archipelago showing the distribution of lobsters (*Panulirus gracilis*). (A) Map from survey showing the distribution of low (orange), medium (yellow), and high (green) relative densities (ind. ha^{-1}) of lobsters in the region. Red indicates areas with no lobsters. Sampling sites are labeled with numbers. (B) Map made with secondary information from fishermen: red, nursery; yellow, nursery and adults; green, adults. Insert shows relative position of the archipelago in Pacific Panama. The large polygon and circles represent the limits of the protected areas.

did not find sites with high relative densities in this archipelago. Intermediate densities occurred only at Coiba Island on the westernmost and south coast from Punta Hermosa (Fig. 2).

In Las Perlas, we were able to measure only 177 lobsters (fishermen catch and survey): 69 were females and only 5 of them (7%) had eggs. The ratio of males to females was 1.57:1. In lobsters from both sexes, the CL was always significantly shorter than the TL, but significant differences were not found between CLs and between TLs (Table 2, Fig. 3A, B). SCLE was 65 mm (corresponding TL = 120 mm) and only 22 lobsters were found to be immature in this sample (Fig. 4A). The CLM value from the pooled sample was very similar, CLM = 66 mm (logit regression, $P < 10^{-3}$). We could not estimate the CL50, because too few individuals with eggs were found. The relationship between TL and CL for each gender was described by the following equations (Table 2; Fig. 4A, B):

$$\log_{10}\text{TL} = \log_{10}\text{CL} \times 0.9532\ (\pm 0.1728) + 0.3089\ (\pm 0.3026),\quad R^2 = 0.58\ ♀ \qquad (1)$$

$$\log_{10}\text{TL} = \log_{10}\text{CL} \times 0.9679\ (\pm 0.1503) + 0.2598\ (\pm 0.2770),\quad R^2 = 0.76\ ♂ \qquad (2)$$

In Coiba, lobsters were larger on average than in Las Perlas. Of the 679 lobsters measured (fishermen catch and survey), 297 were females and 175 of them (59%) had eggs. The ratio of

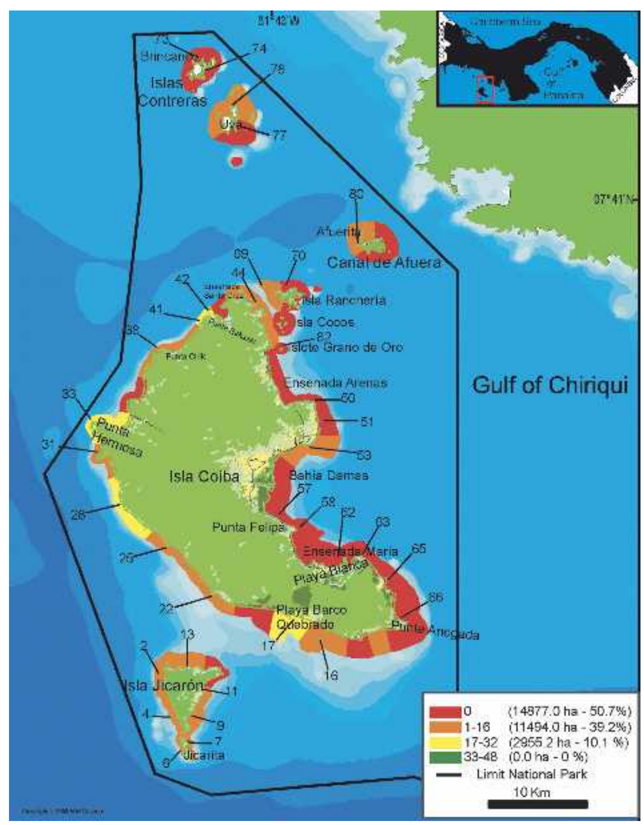

Figure 2. Map of Coiba Archipelago showing the distribution of lobsters (*Panulirus gracilis*): low (orange), medium (yellow), and high (green) relative densities (ind. ha^{-1}). Red indicates areas with no lobsters. Sampling sites are labeled with numbers. The large polygon represents the limits of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

TABLE 2.

Carapace (CL) and tail length (TL) of lobsters from Las Perlas and Coiba Archipelagos. Lengths in millimeters, averages ± SD (CI, Bonferroni corrected intervals of 95% confidence).

			CL		TL	
Archipelago	Sex	N	Range	Average (CI)	Range	Average (CI)
Las Perlas	F	69	40–95	67 ± 10 (3)	70–168	111 ± 16 (5)
	M	108	25–100	67 ± 14 (3)	40–145	106 ± 19 (5)
Coiba	F	296	45–124	85 ± 14 (2)	81–180	137 ± 16 (2)
	M	384	45–121	79 ± 15 (2)	81–170	116 ± 15 (2)

males to females was 1.29:1. As in Las Perlas, CL was always significantly shorter than the TL in both sexes. However, male lobsters from Coiba are smaller than females (in CL and TL), and female tails were significantly larger than male tales (Table 2, Fig. 3C, D). SCLE was 60 mm (corresponding TL = 115–119 mm) (Fig. 4C), and only 6 immature lobsters were found. The CL50 was 84 mm (corresponding TL = 112–155 mm) (Fig. 5). The relationship between TL and CL in each gender was described by the following equations (Table 2; Fig. 4C, D):

$$\log_{10}\text{TL} = \log_{10}\text{CL} \times 0.7747\ (\pm 0.0686) + 0.6442\ (\pm 0.1324),\quad R^2 = 0.49\ ♀ \tag{3}$$

$$\log_{10}\text{TL} = \log_{10}\text{CL} \times 0.6614\ (\pm 0.0377) + 0.8099\ (\pm 0.0715),\quad R^2 = 0.58\ ♂ \tag{4}$$

Slopes in Eqs. (1) and (2) (females and males from Las Perlas) were not statistically different from a value of 1, whereas those in Eqs. (3) and (4) (females and males from Coiba) were significantly different. As expected, variables TL and CL were significantly correlated in all these linear models. CIs are shown between parentheses.

DISCUSSION

This study reports the results of the most extensive survey to date of the populations of the green spiny lobster *Panulirus gracilis* inhabiting Las Perlas and Coiba Archipelagos in Pacific Panama. The abundance of lobsters in both archipelagos was shockingly low. In our surveys we counted only 85 lobsters in Las Perlas and 67 in Coiba. Overall site average densities were also dismal: 4.1 ± 8.8 ind. ha^{-1} in Las Perlas and 5.3 ± 7.6 ind. ha^{-1} in Coiba. These values were very similar to those recorded for the overexploited Caribbean spiny lobster, *P. argus*, in the Bocas del Toro region in Caribbean Panama (3.85 ind. ha^{-1}) (Guzman & Tewfik 2004). They were also similar to the lowest values reported for Guerrero (6.6–43.1 ind. ha^{-1}), a Mexican state that supported 23.4% of the total combined national production of *P. gracilis* and *P. inflatus* between 1985 and 1997 (Briones-Fourzán & Lozano-Alvarez 2000). These maximum density values from Mexico are close to the maximum site value reported for Las Perlas (47.2 ind. ha^{-1}), but they are more than one-third greater than the maximum site density reported for Coiba (27.8 ind. ha^{-1}).

Our population size estimates—approximately 100,300 lobsters for Las Perlas and 156,000 lobsters for Coiba—amount to only about 27% of the total production of lobsters from both coasts of Panama in 2005 (data from the Panama Official Controller Office), assuming each lobster weighs on average 1 kg. This percentage is reduced to 23–24% when considering lobster densities estimated from selected substrates. These data

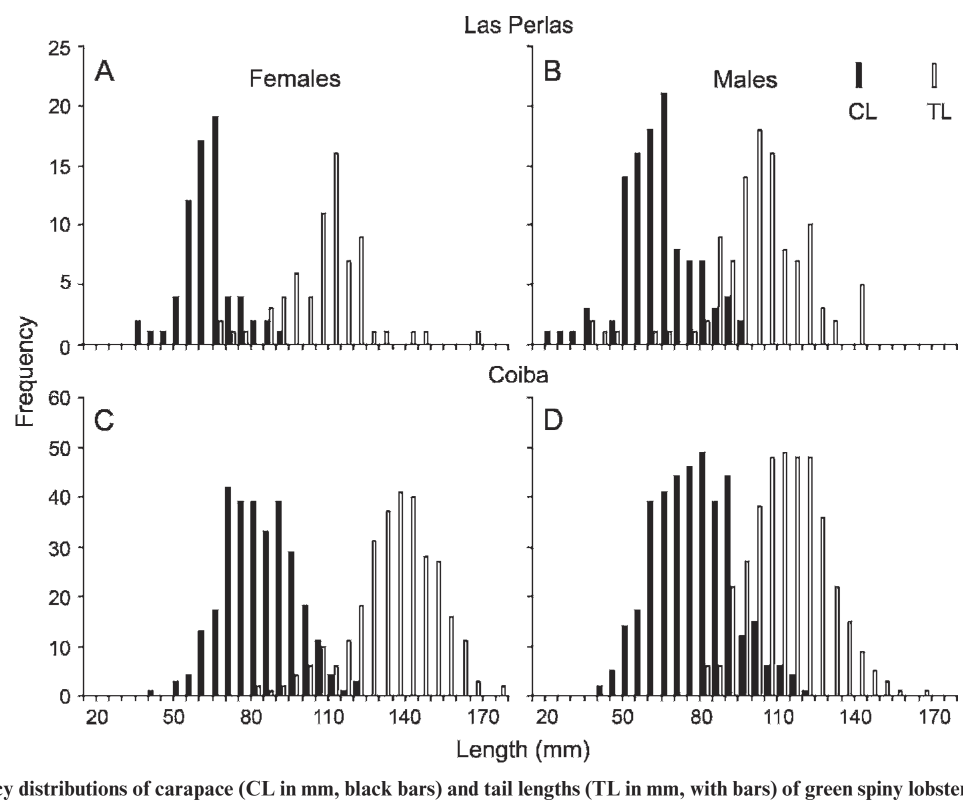

Figure 3. Frequency distributions of carapace (CL in mm, black bars) and tail lengths (TL in mm, with bars) of green spiny lobsters. (A) Females from Las Perlas; (B) Males from Las Perlas; (C) Females from Coiba and Veraguas; (D) Males from Coiba and Veraguas.

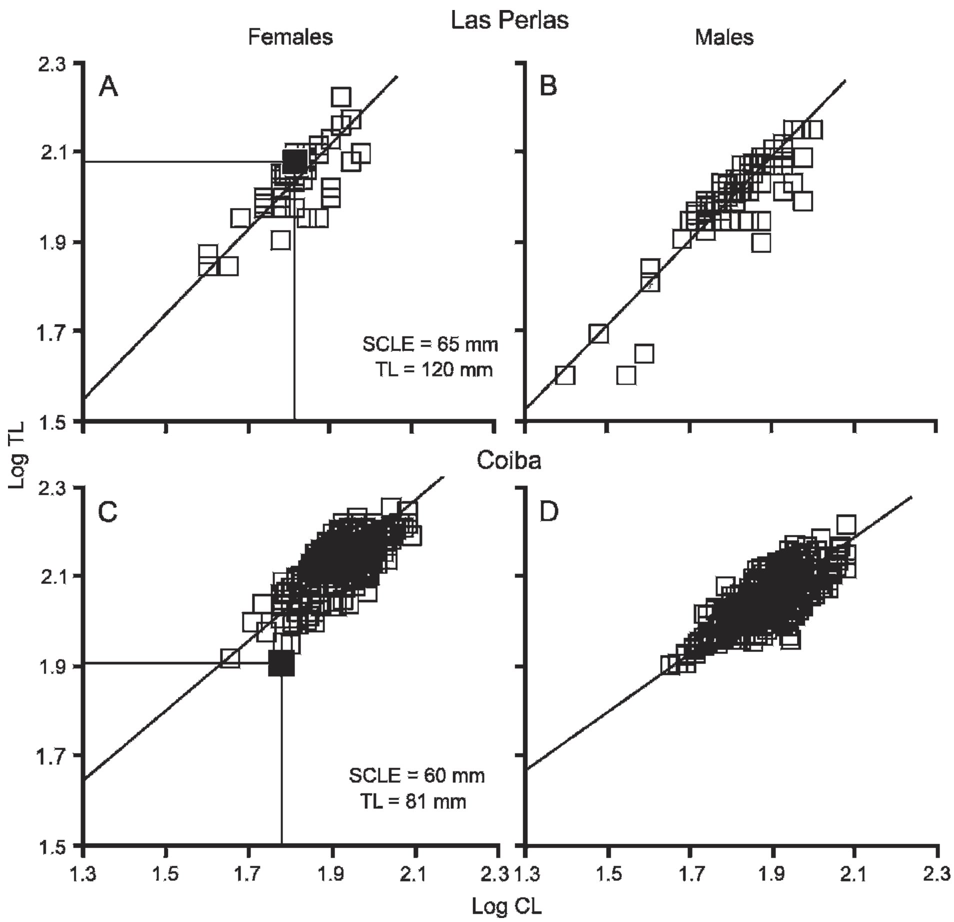

Figure 4. Relationship between logarithmic transformation (base 10) of the variables carapace length (CL in mm) and tail length (TL in mm) of green spiny lobsters collected by fishermen in Las Perlas and in Coiba and Veraguas, Panama. Regression lines were generated using the reduced major axis model [see Eqs. (1) to (4)]. (A) Females from Las Perlas. Large black square represents coordinates of lobster having eggs with the smallest CL, SCLE = 65 mm, TL = 120 mm; (B) Males from Las Perlas; (C) Females from Coiba and Veraguas. Large black square represents coordinates of lobster having eggs with the smallest CL, SCLE = 60 mm, TL = 81 mm; (D) Males from Coiba and Veraguas.

suggest a very strong fishing pressure even for a species spawning all year round (Briones-Fourzán & Lozano-Alvarez 1992, Toral et al. 2002, A.J. Vega, unpublished data). Other evidence that this resource is being overexploited is the scarcity of sites or refuges in the archipelagos in which lobsters can be found (Figs. 1 & 2). The western coasts of Saboga and San Jose islands are the only places in Las Perlas with high relative densities of *P. gracilis* (Fig. 1A), whereas Coiba Archipelago has only intermediate relative densities, and they are scattered around the main island (Fig. 2).

Because lobsters migrate to coastal shallow waters from November to May (Briones & Lozano 1977, Weinborn 1977), we should have observed larger densities in Coiba than in Las Perlas. However, lobster abundances and densities in both archipelagos were very small and those from Coiba were smaller than those from Las Perlas. Indeed, in our interviews, fishermen recognized that fishing lobsters was becoming difficult and their size and numbers were reduced considerably. All these findings suggest that *P. gracilis* is strongly harvested in Pacific Panama. However, as sampling months differed, seasonal effects probably explain why fishermen's catches from Coiba, Veraguas, and other adjacent areas that we used for the biometric analyses contained more lobsters than did those from Las Perlas.

Green spiny lobsters are known to prefer habitats with sand, rocks, corals, and algae (Briones et al. 1981, Pérez-González et al. 1992, Hickman & Zimmerman, 2000). The composition of substrates between archipelagos differs, as R, SR, RA, and S constitute 71% of all categories in Las Perlas and RC, C, SR, and S compose 75% of all categories in Coiba (Cipriani et al. 2008). However, the small numbers of lobsters observed in the field likely prevented us from determining any preference lobsters had for particular substrates. Possibly, this is the same reason why we were unable to find any statistical difference in lobster density between depth levels.

At both sites, the sex ratio was biased towards males (1.57:1 in Las Perlas and 1.29:1 in Coiba). These values are very similar to those reported for *Panulirus gracilis* in Mazatlan (1.52:1; Salazar-Navarro et al. 2006) and from other locations in Pacific Mexico (Briones-Fourzán & Lozano-Alvarez 1992) but are slightly larger than those reported in Galapagos Islands (1.02:1–1.48:1; Toral et al. 2002). However, the ratios in our study are far less skewed toward males than those reported for *P. gracilis* in the state of Guerrero, Mexico (3.6:1; Briones-Fourzán & Lozano-Alvarez 2003). Sometimes, ratios become less biased during reproductive seasons as the local female abundance increases (Salazar-Navarro et al. 2006).

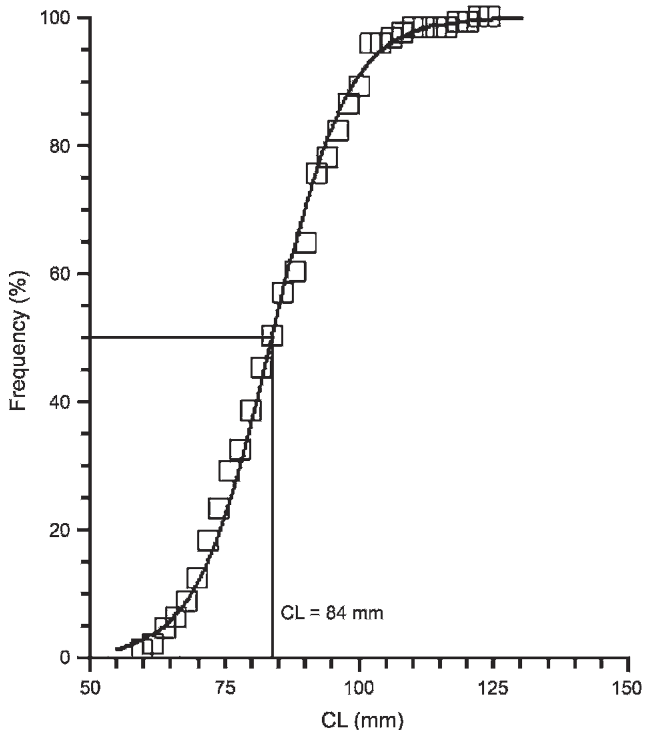

Figure 5. Cumulative frequency of carapace length (CL) of adult female green spiny lobsters from Coiba and Veraguas, with a logistic regression fitted to the data. The carapace length at the 50th percentile of the distribution is CL50 = 84 mm.

Because of its rigidity and relatively small variability, the cephalothorax is the preferred structure to measure the length of lobsters. However, for management and law enforcement purposes the length of the abdomen is also an important measure to consider, because lobster tails are the parts of the body that are marketed (e.g., Briones-Fourzán & Lozano-Alvarez 2000). This is why some countries in which lobsters are an important resource include both CL and TL in the wording of their laws.

Female lobsters from fishermen's catches in Las Perlas were smaller than males. Female CL oscillated between 40 and 95 mm, whereas that of males varied between 25 and 100 mm. In contrast, female and male CL values from Coiba were very similar (female CL 45–124 mm; male CL 45–121 mm) (Table 2). These size intervals are comparable to those of green spiny lobsters from other localities on the Pacific coast of Mexico, such as those from Guerrero (female CL 56.3–88.9 mm; male CL 48–107.5 mm) (Briones-Fourzán & Lozano-Alvarez 2003) and Mazatlan (CL 50–125 mm, both sexes) (Salazar-Navarro et al. 2006).

Panamanian Executive Decree No. 15 established a minimum capture CL of 60 mm and TL of 120 mm for all lobster species inhabiting Pacific and Caribbean Panama. The overall objective of this law was to guarantee the protection of the resource and its rational exploitation. However, a major flaw has made this law ineffective in controlling the exploitation of this natural resource. First, *Panulirus gracilis* inhabits Pacific Panama and *P. argus* inhabits Caribbean Panama, and they are different species. Thus, any biological parameter used as a mean to control their harvest ideally must be species specific. Indeed, the minimum size at maturity of *P. argus* in Bocas del Toro that corresponds to a TL of 120 mm is actually 88 mm, not 60 mm as this decree assumes (Guzman & Tewfik 2004).

Equations (1) to (4) illustrate the relationship between CL and TL for lobsters in Pacific Panama. These equations can be used to estimate appropriate average values of TL from values of CL for management purposes. For example, a CL equal to 84 mm in Las Perlas corresponds to an average TL of 138 mm in females and 133 mm in males, whereas in Coiba it corresponds to an average TL of 136 mm in females and 121 mm in males.

The sample size from Coiba was larger than that from Las Perlas and individuals from Las Perlas were on average smaller, and probably younger, than their counterparts (Table 2). These differences are congruent with the fact that the regression slopes obtained from Coiba's lobsters [Eqs. (3) and (4)] were significantly smaller than those from Las Perlas's (Eqs. 1 and 2) and smaller than 1, as differences caused by allometric growth are most conspicuous when comparing large and relatively old adults among themselves. Also, sexual dimorphism in allometric growth is better observed in relatively old adults than in young adults. Indeed, Eqs. (3) and (4) suggest that lobsters from Coiba are sexually dimorphic, because the rate in which TL grows in relation to CL in females, is larger than that in males.

In Las Perlas, the SCLE of *P. gracilis* was 65 mm (Fig. 4A) with a TL of 120 mm, whereas the SCLE in Coiba was 60 mm (Fig. 4C) with a TL between 81 and 115 mm. Recently, a reproductive analysis on green spiny lobsters from Golfo de Montijo, Panama, revealed that the smallest lobster with mature gonads had a CL = 63 mm and a TL = 89 mm (A. J. Vega, unpublished data), suggesting that the presence of eggs in this species is a good proxy for sexual maturity. The CL of egg-bearing *P. gracilis* females has been reported to vary between 47 and 82.5 mm (Weinborn 1977), between 49 and 100 mm in Mexico (Briones-Fourzán & Lozano-Alvarez 1992), and 73 mm in Galapagos Islands (Toral et al. 2002). The maximum CL of egg-bearing females was 90 mm in Las Perlas and 121 mm in Coiba. This last value is larger than those reported from lobster populations in Mexico.

The CLM from both Las Perlas and Coiba pooled length samples was 66 mm, and is very similar to the SCLE values estimated from both archipelagos. Size at maturity also has been reported at CLs ranging from 45–50 mm in Mexico (Briones-Fourzán & Lozano-Alvarez 2003) and at 94 mm in the Galapagos Islands (Toral et al. 2002).

Obviously, the minimum legal CL and TL cannot be set to the smallest size at which lobsters first attain maturity, because they must have a chance to reproduce before being harvested. There are several approaches to estimate rational average values to be used as minimum capture sizes, and the most commonly used is the average age at first maturity, which is obtained by fitting a logistic regression to data with and without mature individuals. The significant midpoint of this regression estimates the average size at which lobsters mature. Collecting lobsters larger than the midpoint size guarantees that the population remaining alive is made up by young adults and immature lobsters. As our proxy of maturity was the presence of eggs, we used the SCLE to roughly estimate an absolute minimum size at first maturity. Then, considering that lobsters are overexploited in this region, we preferred using the CL value corresponding to the 50th percentile of the distribution of carapace lengths in the population of mature females (CL50) as a proxy of minimum capture size (e.g., Salazar-Navarro et al. 2006). We were able to calculate the CL50 only in samples from Coiba and Veraguas as the fishermen's catch coming from this region was large enough (Coiba = 296). This is a more conservative approach to defining legal capture sizes as it guarantees that on average, half of the adults living in the population are the target of fisheries. The CL50 was 84 mm (Fig. 5), with a corresponding TL that oscillated between 112 and 155 mm. These values are very similar to those used to regulate *P. gracilis* fisheries in Mexico, where the minimum capture legal size (CL) varies between 75 and 82.5 mm according to the region (e.g., Briones-Fourzán & Lozano-Alvarez 2000, Salazar-Navarro et al. 2006), but are lower than those used in Galapagos Islands, ca. CL = 95 mm (estimated from TL using Eq. 3) (Toral et al. 2002). Our TL values are also similar to those recommended in Nicaragua as the minimum capture size of *P. gracilis*, 114–120 mm (Velasquez & Gutierrez 2006) but again are lower than those used in Galápagos Islands, TL = 150 mm (Toral et al. 2002).

Differences in SCLE and CLM values between lobsters from Pacific Panama and Mexico, and those from the Galapagos Islands, could be explained in part by biological and environmental factors varying between populations and localities, but also by the effects of lobster fishery regulations. In Galapagos, a 4 mo fishing season extends from September to December (Toral et al. 2002), whereas in Mexico the fishing seasons vary from 5–7 mo depending on the region (Briones-Fourzán & Lozano-Alvarez 1992), and in Panama the fishing season is open all year long but recently in Las Perlas and Coiba Archipelagos. Fishing egg-bearing lobsters is forbidden in all these areas. If the SCLE and the CLM are reflecting the fishing status of the lobster resource, these comparisons suggest that the implementation of a fishing season (6 mo), combined with other basic regulations such as minimum capture size and marine reserves, is an effective tool for a sustainable management of the green spiny lobster fishery. The frequency of females with mature gonads in the population from the Gulf of Chiriquí increases between October and March, with one large peak occurring between October and March followed by a second small peak between July and September (A. J. Vega unpublished data). Similarly, frequencies of females with eggs were higher between October to January, March, and July. Therefore, it seems reasonable to suggest a six-month fishing season, from April to September and a closure season from October to March of each year.

The distribution of lobsters described by local fishermen (Fig. 1B) illustrates two important aspects of lobster harvesting in Las Perlas. First, harvesting of adult lobsters occurs in almost all areas of the archipelago, matching most of our sampling sites but also including localities not originally included during our random survey, such as the shallow waters between San Jose, Del Rey, and Pedro Gonzalez, close to Cocos and Aposentros islands. Second, fishermen recognize the places in which small growing lobsters occur, referred to here as nursery grounds. This suggests that management strategies involving local fishermen and native peoples could benefit from their experience and biological knowledge of the resource. For example, the Comcaác, a native community from California (also known as the Seri), manage their coastal resources by choosing the best seasons in which to harvest them. These resources include *P. gracilis*, which they only collect between October and March (Nabhan 2007).

The establishment of marine reserves or no-take areas (NTA) in selected zones of Las Perlas and Coiba Archipelagos is also an alternative to insure the survival of *P. gracilis* and other commercial species in the region (sensu Guzman et al. 2008). For example, *Jasus edwarsii*, a lobster from New Zealand, increased its abundance and biomass 11 and 25 times, respectively, after NTAs were declared (Shears et al. 2006). If NTAs were to be used in Las Perlas, then the priority locales would be those in which juveniles are present, because they probably are zones of lobster recruitment or juvenile gathering. These areas are scattered around San Jose, Del Rey, Caña, Pedro Gonzalez, Saboga, and close to Casaya islands (Fig. 1B). However, further studies are needed to confirm the distribution of nursery grounds in Coiba Archipelago.

Our results suggest that (1) implementing a size limit of CL = 84 mm in Pacific Panama as the minimum legal capture size of *P. gracilis*, (2) implementing, maintaining, and enforcing a fishing season spanning no longer than 6 mo, from April to September, (3) designing management strategies involving local fishermen and native peoples; (4) establishing marine reserves or NTAs in particular vulnerable zones, such as those in which juvenile lobsters grow; and (5) implementing long-term monitoring plans, will further guarantee the recovery and maintenance of the lobster resource for years to come. Finally, we are confident that the results of this study will improve the management decisions made for this resource in Pacific Panama and encourage better management plans for this species in other parts of the eastern Pacific.

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