Journal of Shellfish Research, Vol. 23, No. 2, 575–580, 2004.

POPULATION CHARACTERISTICS AND CO-OCCURRENCE OF THREE EXPLOITED DECAPODS (*PANULIRUS ARGUS, P. GUTTATUS* and *MITHRAX SPINOSISSIMUS*) IN BOCAS DEL TORO, PANAMA

HECTOR M. GUZMAN[1]* AND ALEXANDER TEWFIK[2]

[1]*Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002,* [2]*Department of Biology, McGill University, 1205 Ave. Dr. Penfield, Montreal, Canada, H3A 1B1*

ABSTRACT Spiny lobster populations within the Bocas del Toro archipelago appear to be overexploited. Extensive visual surveys over a wide area of reef habitat down to 20 m in depth indicate mean lobster abundance, sizes, and percent maturity levels for both *Panulirus argus* and *P. guttatus* below other areas in the region. The almost complete absence of egg-bearing female lobsters may have serious implications for local production and recruitment and emphasizes the need for revision of management strategies for these populations, which are critical to the socio-economic wellbeing of local artisanal fishers and their dependent communities. An increase in the minimum carapace length for *P. argus* from 60–88 mm may allow protection for most juveniles. The implementation of a closed season or total fishing ban for lobster may also be considered to rebuild the spawning stock biomass to sustainable levels. The extensive pressure likely being exerted on lobster resources may spill over to co-occurring but poorly studied species, such as the large West Indian spider crab, *Mithrax spinosissimus*. This study presents the first data collected on a wild population of *M. spinosissimus*. More importantly, it illustrates the poor understanding we have of the inter-relationships between co-occurring species and the need to understand communities of populations that should be co-managed for the preservation of resources and biodiversity.

KEY WORDS: spiny lobster, *Panulirus*, spider crab, *Mithrax*, stock assessment, overfishing, Panama, shelter, dens

INTRODUCTION

The shallow water environments of the Panamanian coast provide important habitats for a wide variety of animal populations that support a number of important commercial and subsistence fisheries (Cruz 2000, Castillo & Lessios 2001, Guzman & Guevara 2002, Tewfik & Guzman 2003). Throughout these areas and the wider Caribbean region 3 large decapod crustaceans, *Panulirus argus* (Caribbean spiny lobster), *P. guttatus* (spotted spiny lobster), and *Mithrax spinosissimus* (West Indian spider crab) appear to coexist over reef habitats. Humans, to some lesser or greater extent, have attempted to exploit all three species with a particular focus on *P. argus* (Cochrane & Chakalall 2001). *P. guttatus* may be caught incidentally throughout the region but directed fisheries appear to exist only in Bermuda and Martinique (Evans & Lockwood 1994, Evans & Evans 1995). *M. spinosissimus* appears to have the most restricted use with incidental catches in some areas, namely the Panama Canal area, and limited efforts directed at experimental culture of the species (Wilber & Wilber 1991).

Our knowledge of the biology and ecology of these three organisms seems in approximate proportion to their level of exploitation. All three are nocturnal omnivores with varying diurnal den-dwelling preferences (Hazlett & Rittschof 1975, Lozano-Alvarez & Briones-Fourzan 2001). An extensive literature exists for the large *P. argus* and subsequently most lobster resource management in the Caribbean is based on experience with this species (Briones-Fourzan 1995). *P. argus* undergoes a number of ontogenetic habitat shifts, including the use of reef environments, and is highly migratory (Kanciruk & Herrinkind 1978, Butler & Hernkind 1997). In contrast, the smaller *P. guttatus* appears to be an obligate, shallow-water reef dweller and is not migratory (Sutcliffe 1953, Sharp et al. 1997). Finally, very little is known about *M. spinosissimus* in the wild with limited observations being conducted in semi-natural and culture environments (Hazlett & Rittschof 1975, Wilber & Wilber 1991).

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

Given the significant role these decapods likely serve as intermediate consumers in reef and associated habitats and the socio-economic importance they have to local free-diving fishers, operating almost exclusively from small canoes (dugout cayucos), an extensive visual survey was conducted for these three species in the Panamanian archipelago of Bocas del Toro. The following paper is the first report of abundance, population structure, morphology, and spatial distribution of *P. argus* and *P. guttatus* in the study area. This work is also the first documented survey of a wild population of *M. spinosissimus* in the wider Caribbean.

MATERIAL AND METHODS

The survey was conducted over approximately 62,533 hectares of shallow water (<20 m) coral reef habitats in the Bocas del Toro archipelago between April and September 2002 (Fig. 1). A comprehensive description of the sea bottom topography, climate, geology, and reef distribution of the archipelago are available in several other publications (Rodriguez et al. 1993, Greb et al. 1996, Guzman & Guevara 1998). A total of 110 sites were randomly selected and surveyed. Within each site three replicate belt transects (100 × 6 m), randomly placed, were surveyed by two divers (3-meter width each) at four different depth strata (0–5 m, 5–10 m, 10–15 m, 15–20 m) when they occurred.

All individual lobsters encountered during the surveys were measured for carapace length (CL) and tail length (TL) to the nearest millimeter and sex was determined. Carapace length was measured from the base of the rostral horns to the posterior edge of the carapace and tail length was measured from the anterior edge of the tail to the posterior tip of the telson. Sex was determined by the presence of biramous pleopods for females and uniramous pleopopds for males (Morgan 1980). The presence of a whole or remant eggmass on the ventral abdominal segments was used to determine female maturity (Chubb 1994). All observed *M. spinosissimus* had carapace width (maximum distance between lateral margins) measured to the nearest millimeter as well as determination of sex again by the presence of biramous or uniramous pleopopds. Maturity of females also was assessed based

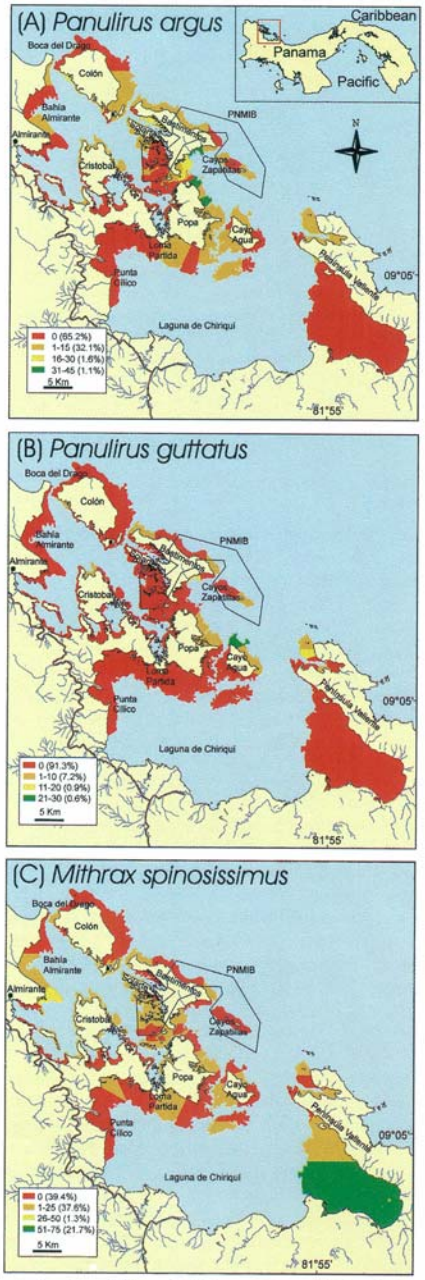

Figure 1. Location of the archipelago of Bocas del Toro in Panama (upper right). Density range distributions (individual ha^{-1}) of *Panulirus argus* (A), *P. guttatus* (B), and *Mithrax spinosissimus* (C) over shallow water reef habitats (<20 m).

on presence of a whole or remnant eggmass (Hernandez-Reyes et al. 2001).

The density distribution of all three species was calculated as mean number of individuals per hectare by site and depth strata. Site data was mapped using Geographical Information System (GIS). A digital classification for the area of study was based on topographic maps at scale 1:50,000. Density data were integrated using the programs MIP V3.1 (Map and Image Processing System) and ArcView V3.0. All data sets for morphologic correlations and abundance were analyzed using SYSTAT V10.2. Parametric techniques were used for correlations and non-parametric (Kruskal-Wallis one-way analysis of variance by ranks and the two-sample Kolmogorov-Smirnov test between pairs) techniques for differences in abundances between species and depth strata given the non-normal distribution of the data due to high numbers of zero values and the poor success of transforming such data.

RESULTS

A total of 496,800 m^2 (49.6 ha), using 828 transects, were surveyed down to 20 m during the course of the study. A total of 180 *Panulirus argus*, 41 *P. guttatus* and 189 *Mithrax spinosissimus* were found.

Highest densities for *P. argus* (31–45 lobster ha^{-1}) occurred at the North-east side of Popa and the southern edge of Bastimentos (see Fig. 1A). *P. guttatus* was most abundant (21–30 lobster ha^{-1}) at the northern tip of Cayo Agua, the southern edge of Bastimentos, and at the tip of the Peninsula Valiente (see Fig. 1B). All of these areas are associated with complex patch reef habitats. Maximum *M. spinosissimus* densities were found in areas of low visibility south of Peninsula Valiente (51–76 crab ha^{-1}) and at the southern tip of Bahía Almirante (26–50 crab ha^{-1}) (see Fig. 1C).

M. spinosissimus had the highest overall percent occurrence (55.5%) and *P. guttatus* the lowest (13.6%) with *P. argus* appearing at 50.0% of the 110 sites examined. The highest percent occurrence for each species by depth was; *P. argus*, 40.6% at 5–10 m; *P. guttatus*, 10.4% at 10–15 m; and *M. spinosissimus*, 34.0% at 5–10 m. The co-occurrence of species at sites was as follows: the 2 lobster species, 11.8%; *P. argus* and *M. spinosissimus*, 23.6%; *P. guttatus* and *M. spinosissimus*, 7.3%; and all 3 species, 6.4%. At no time was any individual den occupied by more than one species. None of the three species occurred in 22.7% of the sites.

Overall density values (mean individual ha^{-1} ± SE) for the 3 decapod species, *P. argus*, 3.85 ± 0.66; *P. guttatus*, 0.91 ± 0.30; and *M. spinosissimus*, 4.11 ± 0.87, did vary significantly (Kruskal-Wallis, H = 43.17, df = 2, $P < 0.0001$). Both *P. argus* (Kolmogorov-Smirnov 2 sample differences, $P < 0.0001$) and *M. spinosissimus* ($P < 0.0001$) overall densities were higher than *P. guttatus*. Analysis of variance (Kruskal-Wallis) by depth revealed significant differences within the 0–5 m strata (H = 29.55, df = 2, $P < 0.0001$) and the 5–10 m strata (H = 30.83, df = 2, $P < 0.0001$) between *P. guttatus* and the other two species (Fig. 2). None of the three species individually varied significantly across the four depth strata. However, no *P. guttatus* were found below 15 m.

Carapace length (width for *M. spinosissimus*) frequency distributions were constructed for males and females and showed a unimodal distribution for all species over the range of individuals measured (Fig. 3). Carapace statistics (mean and standard error) for *P. argus*, *P. guttatus*, and *M. spinosissimus* were 52.0 mm ± 1.2 (±SE), 39.7 mm ± 1.6, and 91.7 mm ± 2.1 respectively. Significant correlations were made between CL and TL for both lobster spe-

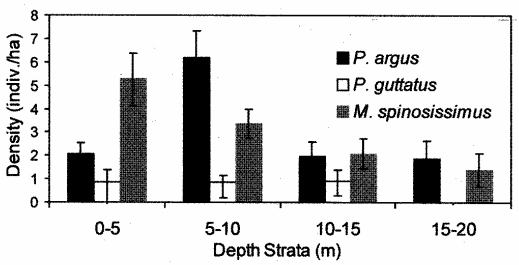

Figure 2. Density distributions across depth strata for *Panulirus argus*, *Panulirus guttatus*, and *Mithrax spinosissimus* populations in Bocas del Toro, Panama. Error bars represent standard error.

cies (*P. argus*, $y = 1.4178x - 5.1383$, $R^2 = 0.76$, $P < 0.05$; *P. guttatus*, $y = 1.6794x - 15.773$, $R^2 = 0.83$, $P < 0.05$) (Fig. 4). Male to female sex ratios for all species were: *P. argus*, 1:1.2; *P. guttatus*, 1.6: 1; *M. spinosissimus*, 1.2:1. No *P. argus* females were found to be eggmass-bearing and only a single eggmass-bearing female *P. guttatus* (65-mm carapace) was encountered. The 50% maturity level for *M. spinosissimus* females, based on presence of eggmasses only, was found to be in the 81–90 mm carapace size class (Fig. 5).

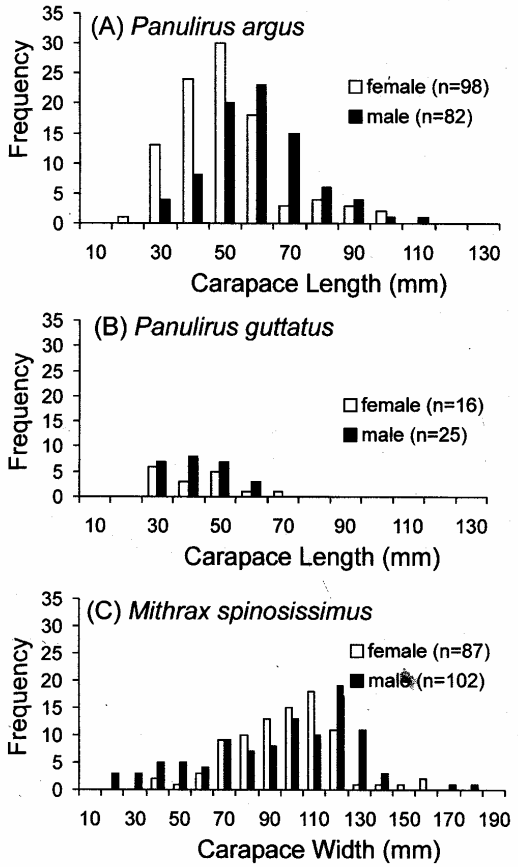

Figure 3. Frequency distributions of female and male (A) *Panulirus argus*, (B) *Panulirus guttatus*, and (C) *Mithrax spinosissimus* in Bocas del Toro, Panama.

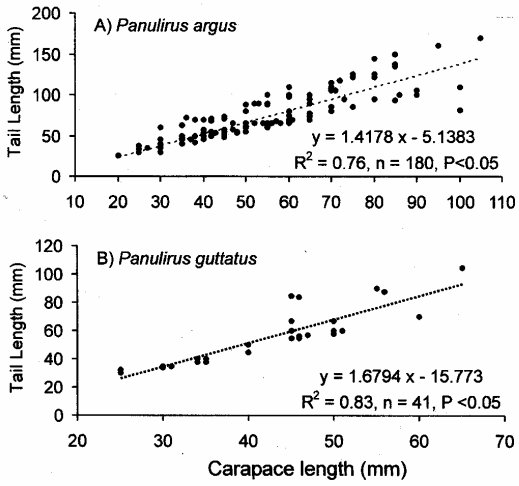

Figure 4. Tail length plotted against carapace length for female and male (A) *Panulirus argus* and (B) *Panulirus guttatus*, in Bocas del Toro, Panama.

DISCUSSION

The demand for spiny lobster resources throughout the Caribbean region over the last 50 years has resulted in depleted populations and an increase in the harvest of undersized and immature lobsters (King 1997, Cochrane & Chakalall 2001). This pattern may now be apparent in Panama with continual increases in landings (Fig. 6) and the documentation of removals of small lobsters in the San Blas archipelago (Castillo & Lessios 2001). This study may provide additional insights into depletions of *Panulirus argus* and *P. guttatus* populations in the Bocas del Toro through details on population abundance and distribution. This research also provides details on a poorly studied species, the West Indian spider crab (*Mithrax spinosissimus*), which may become a target of increased exploitation as a consequence of the depletion of other

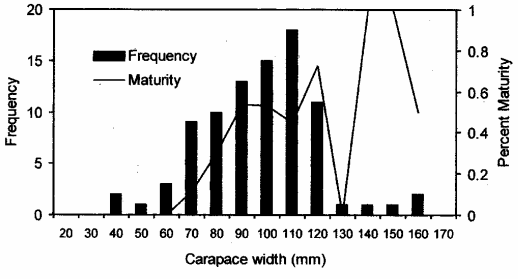

Figure 5. Frequency distributions and percent maturity of female *Mithrax spinosissimus* ($n = 87$) in Bocas del Toro, Panama.

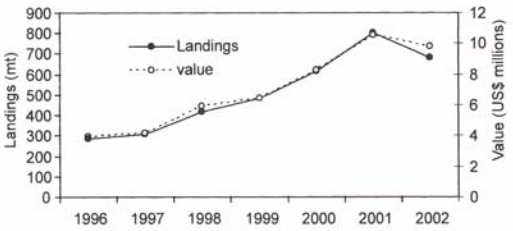

Figure 6. Total lobster landings (mt) and value (US$ millions) of those landings in Panama (1996–2002). No detailed species composition is available (Cruz 2002).

more commercially preferred targets including lobster and conch (Tewfik & Guzman 2003) species.

The mean CL of both *P. argus* (52 mm) and *P. guttatus* (40 mm) are well below those reported in other areas of the Caribbean, including the San Blas archipelago (Yallondaro et al. 2001, Castillo & Lessios 2001, Losada-Tosteson et al. 2001). Even amongst fishery independent studies, the mean sizes in Bocas del Toro are small (Sharp et al. 1997, Tewfik et al. 1998). When examining size at sexual maturity and percent maturity of female lobsters, substantial depletions may be inferred when only a single egg-bearing *P. guttatus* (65 mm) was found in a total of 114 female lobsters examined of both species. Although our study was only conducted between April and September, it is generally considered that tropical species of *Panulirus* breed year around (Chubb 1994) with a significant proportion of egg-bearing females being identified over the period from February until November (Sharp et al. 1997, Castillo & Lessios 2001, Acosta & Robertson 2003). The small sizes and lack of mature individuals strongly suggest an over exploitation of the population as seen in other decapod fisheries (Abbe 2002). The importance of decreases in mean size and size at maturity is directly related to annual and lifetime egg production within a population (Pollock 1995) and ultimately levels of local recruitment. These links are known from other areas with simultaneous declines in spawning stock, recruitment, and individual size of adults (Lipcius & Stockhausen 2002). The skewed sex ratio towards males (1.6:1) in *P. guttatus* was as reported elsewhere (Sutcliffe 1953, Evans & Lockwood. 1994, Sharp et al. 1997, Losada-Tosteson et al. 2001). This skeweness has been variably attributed to sex differences in survival, catchability, movement related to reproductive activity, and other behaviors (e.g., den guarding) and should be investigated further (Losada-Tosteson et al. 2001).

In contrast, morphological information obtained for *M. spinosissimus* including the large mean carapace width (92 mm) and high percentage of egg-bearing females, 45% with 50% maturity at approximately 85 mm, indicates that adults do exist. However, absolute comparisons of this *M. spinosissimus* population to others are difficult due to a shortage of other studies for this species in particular. Suggestions of a large literature base, and therefore understanding, on *Mithrax spp.* should be met with caution, as studies of the much larger *M. spinosissimus* are extremely limited.

Low overall density values for *P. argus* and *P. guttatus* compared with other fishery independent studies again suggest overexploitation (Tewfik et al. 1998, Acosta & Robertson 2003). It is possible that *P. guttatus* was underestimated compared with *P. argus* due to its preference for dens that conceal the whole body and behaviors that include retreating back as far into the den as possible to deter attacks from predators (Loranzo-Alvarez & Briones-Fourzan 2001). The absence of *P. guttatus* below 15 m conforms to the findings of other studies that this species is indeed a shallow water reef specialist (Sharp et al. 1997, Tewfik et al. 1998, Acosta & Robertson 2003). Absolute comparisons for *M. spinosissimus* are again impossible. The distribution of the three decapod species by depth (see Fig. 2) and area (see Fig. 1) are likely due to 2 main factors: resources and catchability. High densities may be facilitated by an abundance of shelter resources (complex reef habitats) or low catchability of targets due to low visibility for free-diving and/or rough surface conditions for the majority (87.5%) of fishers operating from small canoes. It is believed that a combination of both factors is responsible for the variability in density over the study area.

On the shelter resource, it is known that these three crustaceans do contend for occupancy of suitable den or crevice space. *P. argus* and *P. guttatus* may use the same dens, with *P. argus* on the floor and *P. guttatus* on the ceiling, but rarely simultaneously (Sharp et al. 1997). Observations of *P. argus* and *M. spinosissimus* indicate that the lobster can bar co-occupation by the crab but the crab cannot prevent the lobster from co-occupying a den (Hazlett & Rittschof 1975).The recruitment of juvenile Panulirids may also be limited by the availability of den or crevice space (Lipcius & Cobb 1994). Given the low densities of all three species and the observation that no more than one of the three species was seen occupying a single den it must be assumed that shelter resources are not limiting in Bocas del Toro at this time. However, the limitation of shelter resources among sympatric species in such systems may be of interest in the context of marine protected areas or fisheries reserves when ambient densities are increased through management.

In summary, it seems that the Panulirid populations of Bocas del Toro are in an overexploited state especially given the wide extent of the surveys throughout the archipelago. Recent interviews with the 192 lobster fishers within the area indicate that 55% are in favor of a ban on lobster with only 22% opposed. A further 18.5% would support a ban if other fishing possibilities existed (Cruz 2002). The strong support for management amongst resource users lends further credence to the view that lobsters are in short supply but also potentially bodes well for the rapid implementation of new protective legislation. Slight decreases in landings over the last 3 years within Bocas del Toro (18.63 mt in 1999, 17.95 mt in 2000, and 17.31 mt in 2001), in the context of national increases (see Fig. 6), may also reflect the difficulties that experienced fishers have locating lobsters.

A portion of Executive Decree No. 15 (March 30, 1981) describing size regulations for the harvest of lobster in Panama as a minimum CL of 60 mm and minimum TL of 120 mm seems inadequate and puzzling. Given the morphometric analyses conducted for *P. argus* in this study a 60-mm CL corresponds to an 80-mm TL. However, a 120-mm TL, by the same regression equation ($y = 1.4178x - 5.1383$), corresponds to an 88 mm CL. It seems obvious that a 60 mm minimum CL does not allow sufficient protection of juvenile *P. argus* because no mature individuals can be found at that size as well as the fact that the minimum CL and TL do not match. Furthermore, the average mean size of *P. argus* at maturity in the region ranges between 70–109 mm CL (Yallonardo et al. 2001). The existing minimum CL cannot be used for *P. guttatus* as virtually all individuals harvested would be illegal as is the case in Morrocoy National Park, Venezuela (Losada-Tosteson et al. 2001). It seems reasonable to raise the

minimum CL for *P. argus* to 88 mm to correspond to the existing and reasonable TL of 120 mm. This would allow many *P. argus* to become mature before being harvested and therefore increase the potential for contribution to future recruitment. Separate minimum sizes should be established for *P. guttatus* given their much smaller size. The suggestion that morphometric relationships established for either species in other parts of its range should be used for management is extremely dangerous and rejects the potential differences that may exist between populations. The exact minimum size for both lobster species should be based on more detailed local population CL when 50% of females are mature (egg-bearing) (Chubb 1994).

Further modifications to existing regulations could include a seasonal closure during reproductive peaks to allow undisturbed mating and spawning (Villegas et al. 1982). Alternatively, given the extremely low densities, a fishing ban could be implemented for several years to protect all lobsters allowing a rebuilding of the spawning stock, which presently seems to be low (Chiappone & Sealy 2000, Goni et al. 2001). The exact nature of the management strategy for *M. spinosissimus* seems more difficult, given the extremely limited understanding we have of the species. The existence of mature crabs is a positive point. However, given the high pressure on many of the shallow-water marine resources of the archipelago further study is urgently required.

ACKNOWLEDGMENTS

The authors thank C. Guevara, A. Castillo, and W. Pomaire for providing invaluable assistance in the field and Z. Batista, I. Candanedo, M. Caswell, M. Endara, and G. Martinez for administrative support. J.M. Guevara developed the map in GIS. The Government of Panama provided all necessary permits to work in the country. This research was partially funded by The Nature Conservancy (35%) through the Therodney Johnson and Katherine Ordway Stewardship Endowments and the Smithsonian Tropical Research Institute (65%).

LITERATURED CITED

Abbe, G. R. 2002. Decline in size of male blue crabs (*Callinectes sapidus*) from 1968 to 2000 near Calvert Cliffs, Maryland. *Estuaries* 25:105–114.

Acosta, C. A. & D. N. Robertson. 2003. Comparative spatial ecology of fished spiny lobster *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize. *Coral Reefs* 22:1–9.

Briones-Fourzan, P. 1995. Diferencias y similitudes entre *Panulirus argus* y *P. guttatus*, dos especies de langosta comunes en el Caribe Mexicano. *Revista Cubana de investigaciones Pesqueras* 19:14–20.

Butler, M. J. & W. F. Hernkind. 1997. A test of recruitment limitation and the potential for artificial enhancement of spiny lobster (*Panulirus argus*) populations in Florida. *Canadian Journal of Fisheries and Aquatic Sciences* 4:452–463.

Castillo, A. & H. A. Lessios. 2001. Lobster fishery by the Kuna Indians in the San Blas region of Panama (Kuna Yula). *Crustaceana* 74:459–475.

Chiappone, M. & K. M. S. Sealey. 2000. Marine reserve design criteria and measures of success: Lessons learned from Exuma Cays Land and Sea Park, Bahamas. *Bull. Mar. Sci.* 66:631–705.

Chubb, C. F. 1994. Reproductive biology: Issues for management. In: B.F. Phillips, J.S. Cobb & J. Kittaka, editors. Spiny Lobster Management. Oxford: Blackwell Scientific Publications. pp. 181–211.

Cochrane, K. L. & B. Chakalall. 2001. The spiny lobster fishery in the WECAFC region—an approach to responsible fisheries management. *Mar. Fresh. Res.* 52:1623–1631.

Cruz, L. G. 2000. Campaña de educación ambiental para la conservación y protección del pepino de mar (Echinodermata: Holothuroidea) en 15 comunidades del Archipiélago de Bocas del Toro y Península Valiente. MSc. Thesis, Universidad Santa Maria La Antigua, Panamá. 145 pp.

Cruz, L. G. 2002. Diagnóstico de la situación de la pesca de langosta en 9 comunidades del Archipiélago de Bocas del Toro. Final Report to The Nature Conservancy, Panama. 33 pp.

Evans, C. R. & A. P. M. Lockwood. 1994. Population field studies of the guinea chick lobster *Panulirus guttatus* (Latreille) at Bermuda: abundance, catchability, and behaviour. *J. Shellfish Res.* 13:393–415.

Evans, C. R. & A. J. Evans. 1995. Fisheries ecology of the spiny lobsters *Panulirus argus* (Latreille) and *Panulirus guttatus* (Latreille) on the Bermuda platform: Estimates of sustainable yields and observations on trends in abundance. *Fisheries Res.* 24:113–128.

Goni, R., O. Renones & A. Quetglas. 2001. Dynamics of a protected Western Mediterranean population of the European spiny lobster *Palinurus elephas* (Fabricius, 1787) assessed by trap surveys. *Mar. Fresh. Res.* 52:1577–1587.

Greb, L., B. Saric, H. Seyfried, T. Broszonn, S. Brauch, G. Gugau, C. Wiltschko & R. Leinfelder. 1996. Ökologie ind sedimentologie eines rezenten rampensystem an der Karibikküste von Panama. Profil, Band 10, Universität Stuttgart, Germany. 168 pp.

Guzman, H. M. & C. A. Guevara. 1998. Arrecifes coralinos de Bocas del Toro, Panamá: I. Distribución, estructura y estado de conservación de los arrecifes continentales de la Laguna de Chiriquí y la Bahía Almirante. *Rev. Biol. Trop.* 46:601–622.

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

Hazlett, B. & D. Rittschof. 1975. Daily movements and home range in *Mithrax spinosissimus* (Majidae, Decapoda). *Mar. Behav. Physiol.* 3: 101–118.

Hernandez-Reyes, I. M., J. L. Palazon-Fernandez, J. A. Bolanos-Curvelo & J. E. Hernandez. 2001. Reproductive biology of *Mithrax forceps* (A. Milne-Edwards, 1875) (Crustacea: decapoda: Majidae). *Ciencias Marinas* 27:21–34.

Kanciruk, P. & W. F. Herrinkind. 1978. Mass migration of spiny lobster, *Panulirus argus* (Crustacea: Palinuridae): behaviour and environmental correlates. *Bull. Mar. Sci.* 28:601–623.

King, T. D. 1997. Folk amangement among Belizean lobster fishermen: success and resilience or decline and depletion. *Human Organization* 56:418–426.

Lipcius, R. N. & J. S. Cobb. 1994. Introduction: ecology and fishery biology of spiny lobsters. In: B.F. Phillips, J.S. Cobb & J. Kittaka, eds. Spiny lobster management. Blackwell Scientific Publications, Oxford. pp. 1–24.

Lipcius, R. N. & W. T. Stockhausen. 2002. Concurrent decline of the spawning stock, recruitment, larval abundance, and size of the blue crab *Callinectes sapidus* in Chesapeake Bay. *Mar. Ecol. Prog. Ser* 226:45–61.

Loranzo-Alvarez, E. & P. Briones-Fourzan. 2001. Den choice and occupation patterns by two sympatric lobster species, *Panulirus argus* and *Panulirus guttatus*, under experimental conditions. *Mar. Fresh. Res.* 52:1145–1155.

Losada-Tosteson, V., J. M. Posada & F. Losada. 2001. Size and reproductive status of fished spiny lobster, *Panulirus gutatus*, in Morrocoy National Park, Venezuela: a preliminary report. *Mar. Fresh. Res* 52: 1599–1603.

Morgan, G. R. 1980. Population dynamics of spiny lobsters. In: J.S. Cobb & B.F. Phillips, eds. The biology and management of lobsters, vol. 2: Ecology and management. New York: Academic Press. pp. 189–217.

Pollock, D. E. 1995. Changes in maturation ages and sizes in crustacean and fish populations. *S. African J. Mar. Sci.* 15:99–103.

Rodríguez, E., R. Almanza & R. Alvarado. 1993. Situación biofísica y ambiental de la Provincia de Bocas del Toro. In: S. Heckadon-Moreno, ed. Agenda Ecológica y Social para Bocas del Toro. S.A. Panamá: Impresora Continental. pp. 55–72.

Sharp, W. C., J. H. Hunt & W. G. Lyons. 1997. Life history of the spotted spiny lobster, *Panulirus guttatus*, an obligate reef-dweller. *Mar. Fresh. Res.* 48:687–698.

Sutcliffe, W. H., Jr. 1953. Notes on the biology of a spiny lobster, *Panulirus guttatus*, in Bermuda. *Ecology* 34:794–796.

Tewfik, A., H. M. Guzman & G. Jacome. 1998. Distribution and abundance of spiny lobster populations (*Panulirus argus* and *Panulirus guttatus*) in Cayos Cochinos, Honduras. *Rev. Biol. Trop.* 46:125–136.

Tewfik, A. & H. M. Guzman. 2003. Shallow-water distribution and population characteristics of *Strombus gigas* and *Strombus costatus* (Gastropod: Strombidae) in Bocas del Toro, Panama. *J. Shellfish Res.* 22: 789–794.

Villegas, L., A. C. Jones & R. F. Labisky. 1982. Management strategies for spiny lobster resources in the Western Central Atlantic: A cooperative approach. *North American J. Fish. Manag.* 2:216–223.

Wilber, D. H. & T. P. Wilber, Jr. 1991. Environmental influences on the growth and survival of West Indian spider crabs *Mithrax Spinosissimus* (Lamark) in culture. *J. Exp. Mar. Biol. Ecol.* 146:27–38.

Yallonardo, M., J. M. Posada & D. M. Schweizer. 2001. Current status of the spiny lobster, *Panulirus argus*, fishery in the Los Roques Archipelago National Park, Venezuela. *Mar. Fresh. Res.* 52:1615–1622.