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Comparative spatial ecology of fished spiny lobsters *Panulirus argus* and an unfished congener *P. guttatus* in an isolated marine reserve at Glover's Reef atoll, Belize

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Abstract Palinurid lobsters are being exploited with increasing intensity in coral reef ecosystems, but marine protected areas may play a key role in preventing overfishing and local extinctions. In order to define the spatial requirements for protection, we compared the spatial and temporal patterns in distribution, density, biomass, size structure, and reproductive seasonality of Caribbean spiny lobsters *Panulirus argus* and the congeneric spotted lobsters *P. guttatus* on coral patch reef, forereef, and deep reef habitat at Glover's Reef, Belize. The relative impact of fishing on *P. argus* was also examined in an isolated marine reserve and adjacent fished habitats, in comparison with the relatively unfished distribution of *P. guttatus*. Over a 5-year period, both species co-occurred in all major reef habitats, but aspects of their population dynamics differed markedly due to both habitat and fishing effects. All size classes of spiny lobsters *P. argus* occupied shallow patch reefs, but large adults were predominant on the deep wall reef. *Panulirus guttatus* also occupied patch reefs in the lagoon, but spur-and-groove forereef appeared to be the primary habitat of this species. Density and exploitable (adult) biomass of *P. argus* increased significantly over time in the protected patch reef habitat of the lagoon but remained stable on deep reef habitat. The biomass of spotted lobsters *P. guttatus* in all habitats was at least an order of magnitude less than that of exploitable *P. argus*. Reproductive activity by both species was evident most of the year in all habitats, but breeding *P. argus* females were concentrated on the deep reef. Commercial fisheries

for spotted lobsters *P. guttatus* are currently being considered for development, but data from this and other studies suggest that such a fishery may be relatively unproductive and may lead to rapid localized extinctions. Spiny lobsters *P. argus* used a variety of coral reef habitats, but spotted lobsters *P. guttatus* were habitat specialists restricted to shallow reef habitat. The protection needs of both species are similar in one aspect: large protected areas. However, *P. argus* required large areas with heterogeneous habitats including coral reefs and seagrass beds, whereas *P. guttatus* required large areas of coral reef habitat.

Keywords Spiny lobster · *Panulirus argus* · *Panulirus guttatus* · Marine reserves · Reef fisheries

Introduction

Overfishing has resulted in precipitous declines in many exploited populations in coastal habitats (Dayton et al. 1995). Because current fishery regulations appear to be inadequate to protect many exploited populations and maintain sustainable fisheries, researchers and managers have suggested that marine reserves in which fishing is prohibited may be necessary to prevent local extinctions (Ballantine 1991; Bohnsack 1993; Lauck et al. 1998). A marine reserve that functions as an effective harvest refuge has the potential for increasing local population size, mean individual size, and, consequently, reproductive output, compared to fully exploited populations (Dugan and Davis 1993). These effects may result in increased regional larval supply, as well as net movement of adults from the reserve to adjacent fishing grounds as densities build up in the reserve (Polacheck 1990; Carr and Reed 1993; DeMartini 1993). However, a number of factors may impact the efficacy of marine reserves as functional harvest refuges, and the comparative effects on species with different life histories are largely unknown.

The fishery for the spiny lobster *Panulirus argus* is the largest and most economically valuable in many

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Caribbean countries. Many regional populations of spiny lobsters are fully capitalized or over-fished as indicated by declining catch-per-unit effort in local fisheries (e.g., Ehrhardt 1994; Fonteles-Filho 1994). The Caribbean spiny lobster *P. argus* is a long-lived palinurid species with a complex life history typical of many wide-ranging tropical marine species. The postlarval recruits settle in shallow vegetated habitats with abundant macroalgae and seagrass (Butler et al. 1997). Increased movement activity coincides with decreasing natural mortality and ontogenetic habitat shifts as subadults move from vegetation to crevice shelters under large sponges, mangrove prop roots, and coral reefs (Childress and Herrnkind 1996; Acosta and Butler 1997; Butler and Herrnkind 1997; Acosta 1999). With the onset of maturity, adults are believed to migrate to deeper offshore reefs to breed (Cruz et al. 1986; Davis and Dodrill 1989).

On Caribbean coral reefs, *P. argus* co-occurs with the congeneric spotted lobster *P. guttatus*. The life history of the spotted lobster is markedly different in that all benthic stages from postlarval settler to adult appear to occupy coral reef habitat (Sharp et al. 1997). Their growth and reproductive dynamics are also very different from that of *P. argus* (Robertson 2001). Fisheries for spotted lobsters are currently conducted with limited regulations in Bermuda and Martinique (Evans and Lockwood 1994; Luckhurst et al. 2001), and efforts are underway to create new fisheries for this species in other countries. No fishery regulations currently exist for this species in most Caribbean countries, due in part to the limited availability of life history information.

We addressed questions of how these co-occurring species use coral reef habitat and how these spatial requirements impact the efficacy of marine reserves as harvest refuges. We studied the comparative spatial ecology of spiny lobsters *P. argus* and spotted lobsters *P. guttatus* on an isolated coral atoll off Belize. Effective protection in a no-fishing zone of a large marine reserve allowed for comparisons of an unfished population of the spiny lobster *P. argus*. There is currently no commercial fishery for *P. guttatus* here, although these lobsters are taken incidentally in the *P. argus* fishery. We compared spatio-temporal patterns in distribution, density, population size structure, biomass, and reproductive seasonality in representative coral reef habitats over a 5-year period. We discuss the implications of these patterns for protecting palinurid lobster populations on coral reefs.

Methods

Site characteristics

We conducted surveys of all lobster species in the Glover's Reef Marine Reserve, Belize. Glover's Reef is a coral atoll that is isolated by deep water (400–2,000 m depth less than 2 km from the reef crest), located 45 km off the coast of Belize. The atoll is ringed by an emergent reef crest with few large breaks (Fig. 1). The outer forereef slopes 30–45° from the surface down 15–20 m

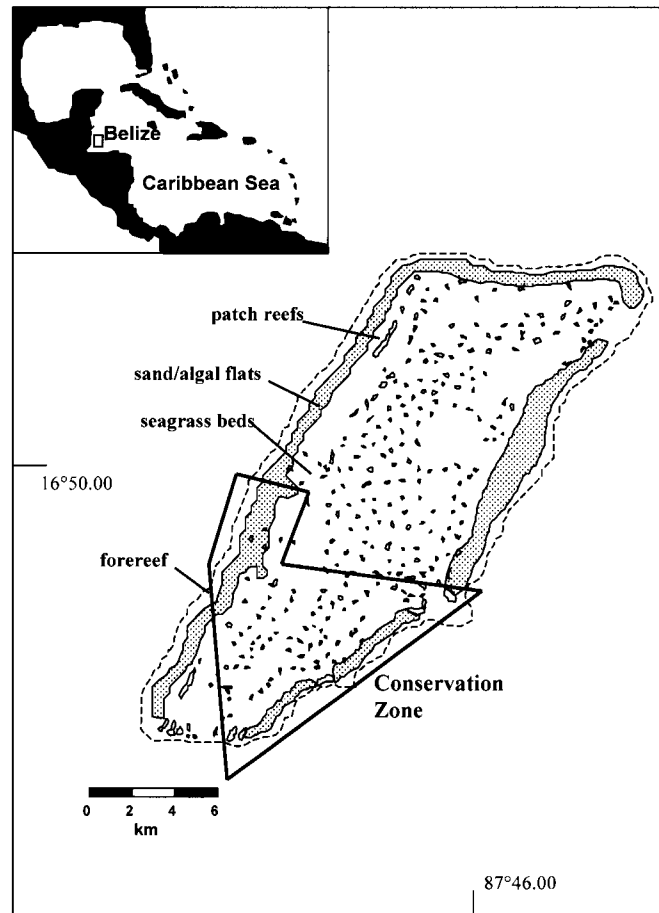


Fig. 1 Map of Glover's Reef atoll, Belize, showing distribution of habitats inside and outside the conservation (no-fishing) zone of the marine reserve. The contour boundary of the forereef and wall reef at 15–20 m is shown as a dashed line. Inset shows location of study area in the western Caribbean

where the vertical wall reef drops off abruptly. The coral community at our forereef sampling sites was well developed, dominated by *Agaricia agaricites* and *A. tenuifolia* spur-and-groove formations on the west slope and large mound corals (*Montastrea annularis*, *Dendrogyra cylindrus*, and *Diploria* spp.) on the east slope (Stoddart 1962). The deep wall reef sites contained numerous crevices with calcareous algal cover. Within the shallow lagoon, the benthic habitat grades from sand-algal flats to seagrass beds interspersed with numerous (> 700) discrete coral patch reefs of varying sizes, dominated by *M. annularis*, *M. cavernosa*, and *Siderastrea siderea*. Coral reef habitat is considered here only as lobster shelter, and all primary habitats were represented inside and outside the protected area.

The atoll was designated as a marine reserve in 1993 and was zoned for various purposes with a conservation zone (74 km²) where all commercial fishing is prohibited and a general use zone (300 km²) where artisanal fishing is allowed (Fig. 1) (Government of Belize 1993). The conservation zone encompasses all representative habitats of the forereef, the wall reef to the 100-fathom depth contour, and the lagoon containing seagrass beds, sand-algal flats, and patch reefs. Prior to 1999, enforcement of the conservation zone of the reserve was minimal and ineffective, as evidenced by no change in fished populations (Acosta 2001). Fishing activity is concentrated on spiny lobsters *P. argus* and strombid gastropods *Strombus gigas* in shallow habitats that are accessible to free-diving fishers. Trap fishing is prohibited, so the fishery is largely restricted to habitats < 10 m deep in the lagoon.

Lobster population surveys

Fishery-independent surveys for spiny lobsters *P. argus* and spotted lobsters *P. guttatus* were conducted from 1996 to 2001 in three representative reef habitats in the atoll: coral patch reefs (depth 1–3 m) in the lagoon, spur-and-groove formations on the forereef (depth 5–7 m), and crevices of the wall reef (depth 20–25 m). Sampling sites were selected as lobster habitat if coral cover exceeded 80% surface area and if vertical relief was ≥ 2 m (range 2–4 m). In the lagoon, eight patch reefs (mean surface area 0.2 ha; range 0.07–0.5 ha) were surveyed in the conservation zone, and eight patch reefs of similar total area were surveyed in the fishing zone. Patch reef size was estimated by measuring the perimeter using fiberglass tapes fitted around the edge, average width was estimated from three across-reef measurements, and the area was approximated as a circle because patch formations were mostly circular or elliptical. Surveys on the forereef and wall reef were conducted on five replicate 50×10 m transects in each habitat (total 0.25 ha per habitat). Sites were located using global positioning satellite (GPS) coordinates and sampled on a quarterly basis. Four surveys of the forereef and wall reef could not be conducted due to inclement weather conditions.

During surveys, two divers systematically searched all crevices for lobsters using hand-held lights when necessary. Lobsters were measured [to 5 mm carapace length (CL)] by placing a marked ruler over the carapace, and the sex of adults was identified visually from external dimorphic characters. Mature females were also inspected for the presence of egg masses on the ventral abdomen. Lobsters were not captured or further disturbed. Small lobsters, particularly early post-settlement juveniles, were most likely undersampled by this visual method, and so the data represent conservative estimates of density of small size classes.

The spatial distribution of density of *P. argus* and *P. guttatus* was analyzed using a repeated measures analysis of variance (RMANOVA) with month (quarter) as the between-subjects factor and habitat (patch reef, forereef, and wall reef) as the within-subjects factor. In the analysis for *P. argus*, only the density of the unfished population on patch reefs in the conservation (no-fishing) zone of the lagoon was compared with unfished forereef and wall reef habitat (Fig. 1). There is currently no targeted fishing activity in these habitats. Data were log-transformed (count + 1) for variance homogeneity. Mauchly's test of sphericity was used to inspect the error covariance matrix of the dependent variable, and Levene's equal variance test was used to confirm homogeneity of error variances. Bonferroni tests were used for post-hoc comparisons between habitats.

To compare population size structure, we separated lobsters into 10-mm CL size class intervals (10–20, 21–30, ...). The mean annual frequencies of size classes were calculated as 3-month (quarterly) moving averages. Two-sample Kolmogorov-Smirnov tests using the D_{mn} statistic were used to compare size frequency distributions between habitats. Biomass was calculated using the median weights of each size class during a sample period in the different habitats. The weight-at-length relationship for *P. guttatus* was determined from data in Caillouet et al. (1971). Weight-at-length for *P. argus* was calculated using the power equation $W_t = 0.00158(CL^{2.871})$ ($R^2 = 0.99$; residual $df = 314$) (M.J. Butler IV, Old Dominion University, Norfolk, Virginia, USA, unpublished data). The adult or exploitable biomass (ExB) for each habitat was then calculated as:

$$ExB_t = \sum_{i=x_c}^{\infty} N_i(x)w(x) \quad \text{for all } x \geq x_c$$

where B_t is mean biomass per hectare in year t , $w(x)$ is the mean weight of size class x , and x_c is the size at first maturity (spiny lobsters *P. argus* ≥ 76 mm CL; spotted lobsters *P. guttatus* ≥ 35 mm CL). $N_i(x)$ is the number of lobsters in size class x during year t [see Kirkwood et al. (1997) for derivation of exploitable biomass from the Beverton and Holt (1957) equilibrium equation]. The short-term natural mortality rate is thus incorporated into observed densities of each size class. The use of mean values instead of cohort functions is appropriate if natural mortality is relatively

low at larger size classes (e.g., lobsters), as opposed to semelparous species (e.g., squid) (Kirkwood et al. 1997).

We then compared temporal trends in density and biomass of both species across habitats and in the fishing and conservation zones of the marine reserve. To determine whether density and biomass increased, decreased, or remained stable over time, we conducted simple least-squares trend analyses and F-tests on the null hypothesis that slopes are not significantly different from 0. To assess the reliability of the density and biomass indices, we estimated the power and the coefficients of variation (CV) of each time series. Power was estimated by conducting Monte-Carlo simulations of linear trends using means and variances of survey counts (Gerrodette 1987; Gibbs 2000; <http://www.mpl-pwrc.usgs.gov/powcase/monitor.html>; accessed May 2002). The CVs were calculated by dividing the means of survey counts by the detrended standard deviations obtained from the standardized residuals of linear regressions of counts against time. The overall CV of a time series was calculated as an annual moving CV (analogous to a moving average).

Results

The density of unfished spiny lobsters *P. argus* was significantly higher on patch reef habitat (mean \pm SE per hectare: 91.2 ± 11.7) in the conservation zone of the marine reserve, compared to wall reef (38.3 ± 4.5) or forereef habitat (15.2 ± 4.1) (Table 1). Over 5 years, annual mean density of *P. argus* increased significantly on patch reef habitat in the protected conservation zone, from 45.7 ± 3.4 in 1996 to 146.7 ± 6.3 in 2001 (Fig. 2); this buildup occurred mainly in the density of adults (Table 2). The density of juvenile spiny lobsters *P. argus* on patch reefs was slightly higher in the conservation zone (55.9 ± 5.1) than in the fishing zone (32.1 ± 3.1), but mean adult density was substantially higher in the conservation zone (35.4 ± 6.5) than in the fished area (8.2 ± 1.5). Results of the RMANOVA also indicated that fluctuations in density occurred over sampling months (Table 1), but this was largely confined to lagoon patch reef habitat (Fig. 2). Density remained stable over time on the forereef and the wall reef (Fig. 3). Spiny

Table 1 Results of repeated measures analysis of variance (RMANOVA) on unfished lobster density at Glover's Reef, Belize, with month (quarterly 1996–2000) as the within-subjects factor and habitat (patch reefs, forereef, wall reef) as the between-subjects factor. Density estimates for patch reef habitats were from the no-fishing conservation zone of the marine reserve. Bonferroni post-hoc tests among habitat means revealed that densities differed significantly among all three habitats for both species of lobster

Source	MS	df	F	P
<i>P. argus</i>				
Month	0.432	17	4.316	0.05
Interaction	0.074	34	0.742	0.84
Error	0.100	357		
Habitat	10.674	2	34.907	0.001
Error	0.306	22		
<i>P. guttatus</i>				
Month	0.081	17	1.564	0.14
Interaction	0.043	34	0.839	0.72
Error	0.052	357		
Habitat	5.026	2	39.831	0.001
Error	0.126	22		

Fig. 2 Densities of spiny lobsters *Panulirus argus* and spotted lobsters *P. guttatus* on patch reefs in the lagoon of Glover's Reef, Belize, from 1996 to 2001. Comparative densities of juveniles and adults are shown separately for the protected (conservation zone of the marine reserve) and fished areas

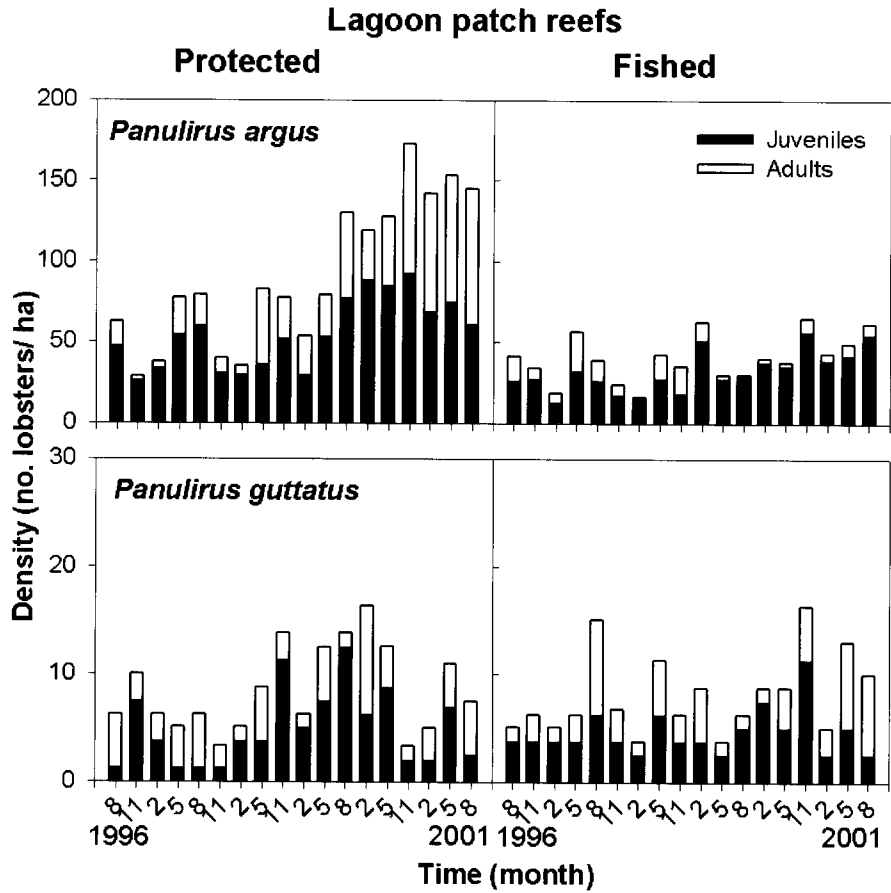


Table 2 Least-squares trend analyses for lobster density and adult biomass on primary reef habitats at Glover's Reef, Belize. Counts from the forereef and wall reef (FR/WR) are combined for each species because of the highly localized distribution in these habitats. PR_C : Patch reefs in conservation zone of lagoon; PR_F : patch reefs in fished area. (Slope significant from 0: * $P < 0.05$; ** $P < 0.01$)

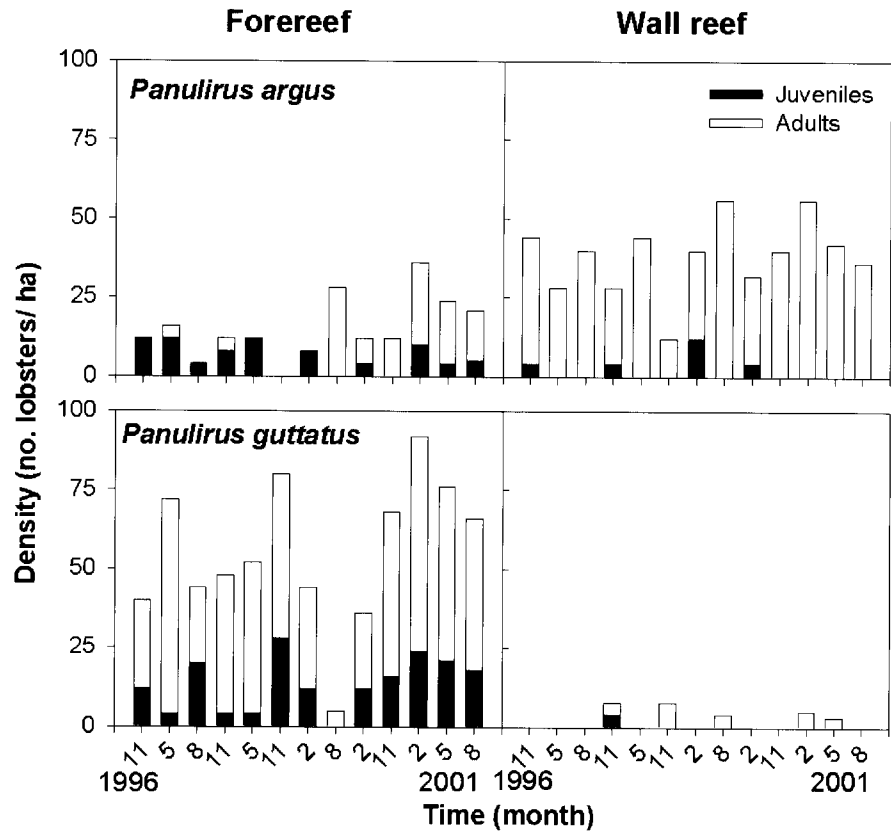
	F	R_2	Power	CV
Density				
<i>P. argus</i>				
PR_C				
Juveniles $y = 29.1 + 2.8x$	4.46	0.48	0.73	0.43
Adults $y = -7.48 + 4.5x$	50.39**	0.76	0.84	0.35
PR_F				
Juveniles $y = 16.9 + 1.6x$	6.52	0.48	0.92	0.35
Adults $y = 12.9 - 0.5x$	3.50	0.42	0.72	0.40
FR/WR				
All $y = 38.4 + 2.2x$	2.35	0.41	0.64	0.50
<i>P. guttatus</i>				
PR				
Juveniles $y = 7.4 + 0.2x$	1.66	0.31	0.63	0.28
Adults $y = 5.1 + 0.2x$	2.14	0.34	0.61	0.29
FR/WR				
All $y = 45.5 + 1.7x$	0.90	0.46	0.76	0.36
Adult biomass				
<i>P. argus</i>				
PR_C $y = -22.9 + 6.2x$	31.54**	0.66	0.91	0.24
PR_F $y = 6.1 - 0.2x$	2.79	0.39	0.78	0.33
FR/WR $y = 21.8 - 27.7x$	4.80*	0.55	0.82	0.23
<i>P. guttatus</i>				
PR $y = -16.8 + 5.9x$	28.1*	0.64	0.72	0.34
FR/WR $y = 5.3 - 5.9x$	0.13	0.40	0.71	0.28

lobsters occupying the forereef and wall reef were mostly large adults.

In contrast to the spatial distribution of *P. argus*, the density of spotted lobsters *P. guttatus* was highest on the forereef (55.6 ± 7.5 ; Fig. 3), secondarily on patch reefs (8.3 ± 1.3 ; Fig. 2), and very low on the deep wall reef (2.2 ± 1.1 ; Fig. 3). Densities were relatively stable over sampling months in all habitats (Table 1). There were no significant differences in the density of juvenile and adult *P. guttatus* on patch reefs in the lagoon (Table 2). Both juvenile and adult spotted lobsters also occupied spur-and-groove formations on the forereef.

Adult female *P. argus* carried egg masses on the forereef and wall reef year round, with proportions ranging from 100% in May to 20% in November (Fig. 4). Female *P. argus* also carried egg masses on shallow patch reefs < 1 m deep in the lagoon. Adult female *P. guttatus* carried egg masses year round, in similar proportions on both forereef and patch reef habitats (Fig. 4). The distribution of breeding female *P. argus* was also associated with the habitat-specific size-frequency distribution. All sizes of spiny lobsters (mean \pm SE: 59.4 ± 0.9 mm CL; range 10–180 mm CL) were found on patch reefs in the lagoon, but large, mostly adult, lobsters (89.7 ± 1.7 mm CL; range 70–180 mm CL) occupied the forereef and the wall reef (Fig. 5) ($D_{mn} = 1.379$; $P < 0.05$). Over time, large adult *P. argus* were increasingly common on shallow patch reefs in the

Fig. 3 Densities of juvenile and adult spiny lobsters *Panulirus argus* and spotted lobsters *P. guttatus* on forereef and wall reef habitat of Glover's Reef atoll, Belize, 1996 to 2001



conservation zone. In contrast, all size classes of *P. guttatus* were found on forereef and patch reef habitat (Fig. 5) ($D_{mn} = 1.051$; $P = 0.10$).

The patterns of density and population size structure impacted the spatial and temporal distribution of biomass. Because the density, and consequently biomass, of juvenile lobsters did not fluctuate significantly in space and time, only adult (exploitable) biomass was considered further. The mean exploitable biomass of spiny lobsters *P. argus* on the deep reefs increased slightly in 2001 but was relatively stable over time, averaging 40.4 ± 5.2 kg/ha (Table 2; Fig. 6). However, biomass of *P. argus* increased 20-fold on patch reefs in the conservation zone by 2001 over that on fished patch reefs of the lagoon, from 15.1 ± 2.3 kg/ha in 1996 to 320.1 ± 7.4 kg/ha in 2001. A single pulse in spiny lobster biomass was observed in the shallow lagoon during late 1998, and a corresponding large decrease in biomass occurred on the deep reefs (Fig. 6). The mean biomass of spotted lobsters *P. guttatus* was stable on the forereef (4.9 ± 0.6 kg/ha) and was substantially greater than on lagoonal patch reefs (0.8 ± 0.1 kg/ha) (Table 2).

Discussion

Translating the effects of habitat protection in marine reserves to population-level impacts on exploited species generally involves a prohibitive number of assumptions. Primary among these is whether the areal extent and

types of critical habitats in the reserve are adequate to protect a substantial proportion of the population for a substantial period of time. For example, a large number of studies have indicated that density and biomass of coral reef fishes increased significantly in marine reserves (e.g., Russ and Alcala 1989; Polunin and Roberts 1993; McClanahan and Kaunda-Arara 1996; Wantiez et al. 1997). However, distinguishing between the effects of habitat variation and reserve protection is difficult and often overlooked (Paddock and Estes 2000). The spatial distribution of habitats and the habitat requirements of target species may ultimately determine whether population increase in a refuge is sustained over time.

Young juvenile spiny lobsters *P. argus* exclusively used shallow patch reefs near vegetated nursery habitats in the lagoon of the Glover's Reef atoll. Adults occupied all reef habitats, but density and biomass were variable between the lagoon and the forereef. The impact of habitat heterogeneity on population size structure is well known for palinurid lobster species that use multiple essential habitats (*P. marginatus*, Parrish and Polovina 1994; *P. argus*, Butler and Herrnkind 1997). In Florida marine protected areas, low abundance of adult spiny lobsters in the protected area of Florida Bay, Everglades National Park, was related to the paucity of reef habitat (Davis and Dodrill 1989), in contrast to high adult abundance in the Dry Tortugas, Fort Jefferson National Park, which contained abundant coral reef habitat (Davis 1977). In several marine reserves in New Zealand, significant annual increases in density and biomass were

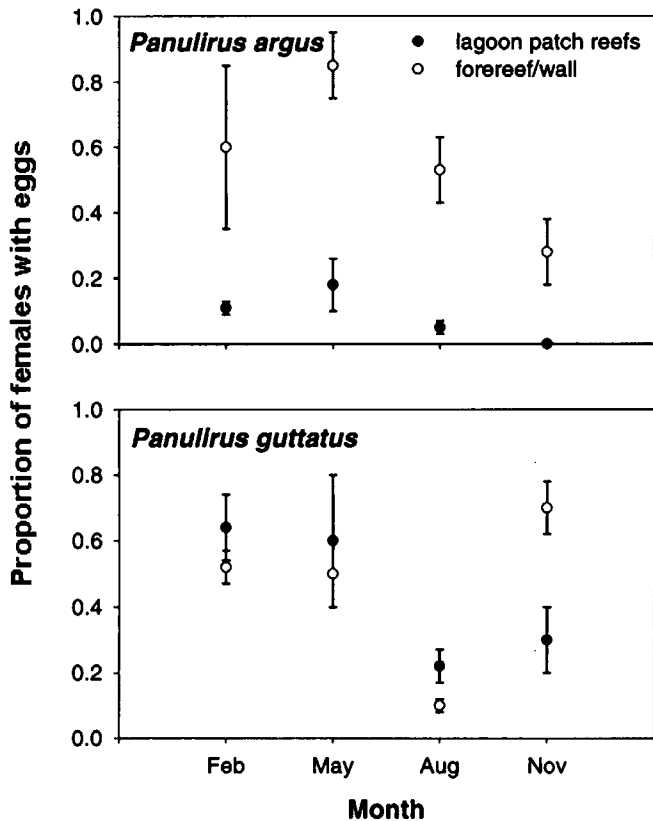


Fig. 4 Reproductive activity of adult female spiny lobsters *Panulirus argus* and spotted lobsters *P. guttatus* on patch reefs in the lagoon and forereef/wall reef of Glover's Reef atoll. Bars represent standard errors of proportion of females with egg masses during quarterly surveys from 1996 to 2001

observed for lobsters *Jasus edwardsii*, and the magnitude of these increases were related to habitat depth (Kelly et al. 2000).

On patch reef habitat in the conservation zone of the Glover's Reef Marine Reserve, the mean annual density of spiny lobsters *P. argus* increased by 300% over 5 years of protection, but the magnitude of increase in adult biomass in this habitat was almost 2,000%. By 2001, the density of adult *P. argus* on fished patch reefs in the lagoon was nine-fold lower than in the conservation zone. The density of small juvenile spiny lobsters did not differ significantly between fished and protected areas or fluctuate substantially over time. This demonstrates the substantial impact of a relatively low-technology, artisanal fishery on this lobster population, even though deep habitats are not fished. Deep reef habitats in the Glover's Reef atoll may supply adult lobsters to the fishing area, and may currently represent a larger, albeit temporary, refuge for a proportion of the breeding stock. The current inability of the local artisanal fishery to exploit lobsters on deep reefs may rapidly change in the near future with increased fishing technology. Therefore, the real protection afforded by this reserve to the spiny lobster population is based not only on the amount of protected habitat in the shallow lagoon, but

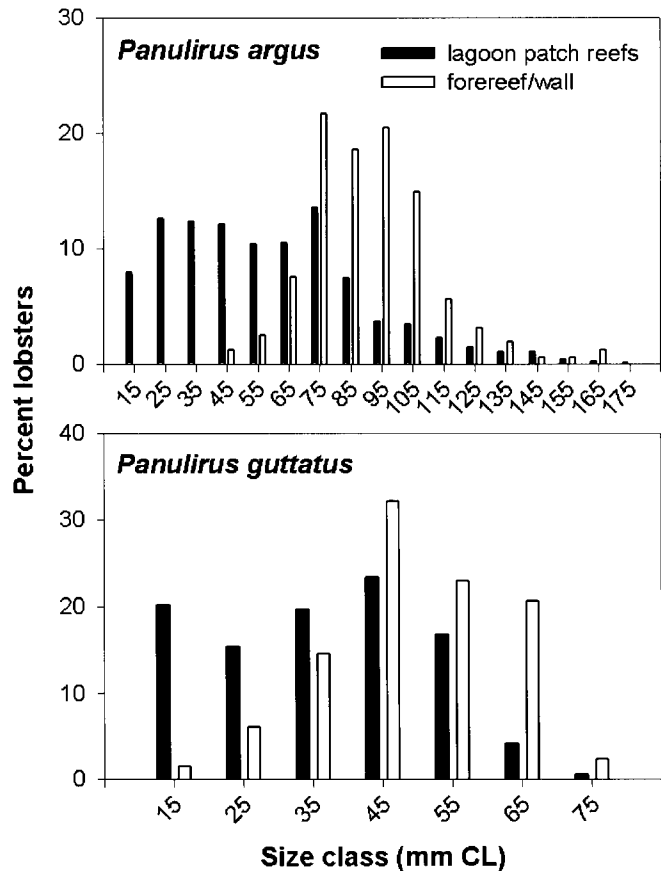


Fig. 5 Population size structure of spiny lobsters *Panulirus argus* and spotted lobsters *P. guttatus* on lagoon patch reefs and forereef/wall reef habitats of the Glover's Reef Marine Reserve. Annual frequencies (per hectare) were estimated from densities in size classes observed during quarterly surveys. Size classes indicate the median value of 10 mm CL groups

also on the amount of forereef and deep reef habitat included in the reserve.

Migratory movement of breeding female spiny lobsters to deep reefs has been associated with seasonal mating and spawning in *P. argus* (Kanciruk and Herrnkind 1973; Davis 1977; Cruz et al. 1986) and other palinurids (Phillips 1983; MacDiarmid 1991). However, a strongly seasonal distribution pattern associated with reproductive activity was not documented at Glover's Reef during this study. This pattern may be absent because reproductive activity occurred throughout most of the year. Breeding female spiny lobsters were most abundant on the forereef and wall reef, but females with egg masses were also found on shallow patch reefs in the lagoon. Furthermore, tracking studies have shown that adult spiny lobsters moved randomly between the shallow lagoon and the deep reef habitats at Glover's Reef throughout the year (Acosta 1999, 2002). The only indication of a mass movement event by adults from the deeper reefs to lagoon patch reefs occurred after the passing of Hurricane Mitch (category 5 on the Safir-Simpson scale) in November 1998 (inferred from Fig. 6), which resulted in extensive wave damage to shallow

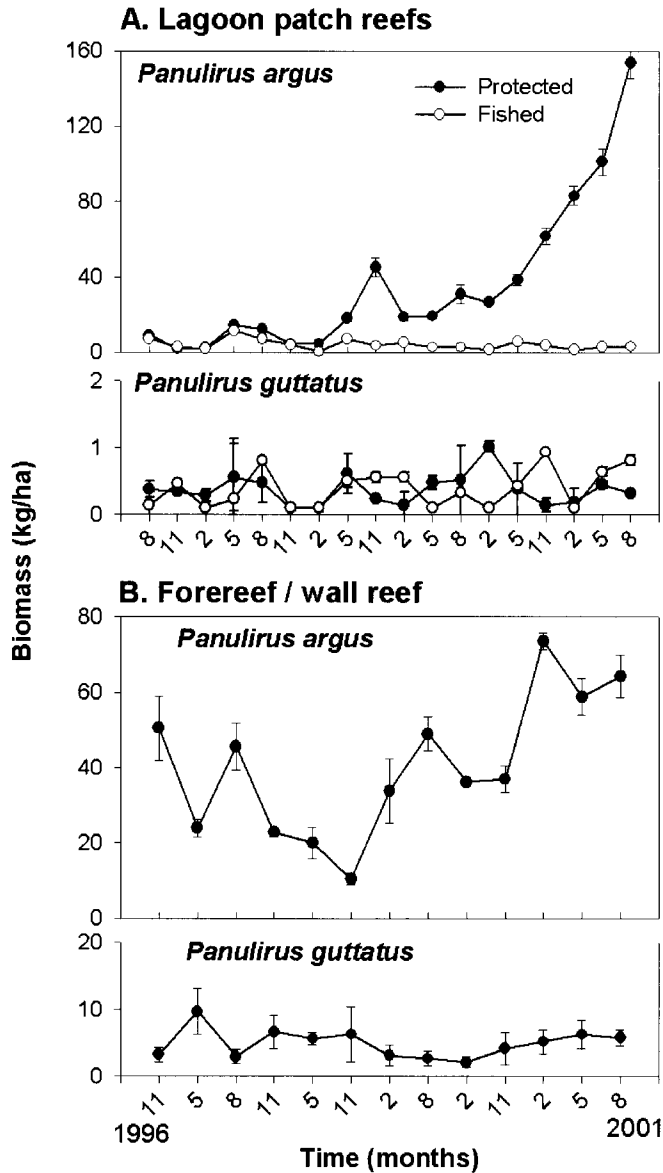


Fig. 6 Exploitable (adult) biomass per hectare of reef habitat for spiny lobsters *Panulirus argus* and spotted lobsters *P. guttatus* in the Glover's Reef Marine Reserve from 1996 to 2001. X-axis scales of the two panels of the graph are not aligned because of missed surveys due to inclement weather in the deep reefs. **a** Protected and fished patch reefs in the lagoon; **b** forereef and wall reef

coral reefs off Belize. Spiny lobsters *P. argus* are known to migrate to deeper water in response to the approach of large storms (Herrnkind 1969). Mass movement back into the lagoon may have been associated with foraging to exploit accessible food resources on shallow reefs that were damaged.

The density and biomass of spotted lobsters *P. guttatus* in shallow reef habitats at Glover's Reef were stable but low over time, compared to those of *P. argus*. The primary habitat for *P. guttatus* was the forereef where the adult biomass was about five times greater than that on lagoonal patch reefs. Density and biomass of *P. guttatus* was highest on the forereef but was an order

of magnitude lower on lagoon patch reefs. In contrast to *P. argus* in equivalent habitats, adult biomass of spotted lobsters *P. guttatus* was nine times lower on the forereef and 20 times lower on patch reefs than the exploitable biomass of *P. argus*. These estimates (≈ 59 lobsters/ha over all reef habitats; 6 kg/ha exploitable biomass) were substantially higher than that reported for a fished population (1.72 lobsters/ha; 0.34 kg/ha) in Bermuda (Evans and Lockwood 1994). The mean size of spotted lobsters in all surveys was 55 mm CL, well within the adult size class.

Reproductive activity of *P. guttatus* occurred in all habitats throughout most of the year, similar to that in Mexico (Padilla-Ramos and Briones-Fourzán 1997) and Florida (Sharp et al. 1997) but in contrast to the seasonality observed in Bermuda (Evans and Lockwood 1994). Evans and Lockwood (1994) suggested that female spotted lobsters may undertake seasonal migrations from shallow to deep reefs associated with breeding in Bermuda, similar to that observed in *P. argus*. However, recent population studies and mark-recapture experiments (Sharp et al. 1997; D.N. Robertson and M.J. Butler, unpublished data) on unfished populations found no evidence of migratory movement, but rather that benthic dispersal between coral reef patches may be highly restricted in this species.

Summary and recommendations

The comparative spatial ecology of these two species provided some insights into habitat use, fishery impacts, and the implications for management of lobster populations in marine reserves. All post-settlement size classes of spiny lobsters *P. argus* occupied shallow patch reefs in the lagoon, whereas mainly adults were found on the forereef and wall reef. The artisanal fishery at Glover's Reef kept densities on fished reefs at less than 10% of that on protected shallow reef habitat. All size classes of spotted lobsters *P. guttatus* used the shallow forereef and patch reef habitats. However, density and exploitable biomass of *P. argus* were substantially greater than those of *P. guttatus* in equivalent habitats. These results, combined with life history differences in dispersal and reproductive dynamics, indicate that the functional benefits of marine reserves may be very different for these species.

First, the fishery regulations for *P. argus* provide minimal protection for the population. For example, the closed season does not protect breeding activity that occurs year round but may only provide for recolonization of shallow habitats by lobsters from deeper reefs. Any increase in fishing technology (e.g., mechanized trap hauls) may rapidly reduce adult lobster density and biomass in deep reef habitats to low levels seen on shallow reefs, putting the reproductive population at risk. Both shallow and deep reefs, as well as vegetated nursery habitats, are essential habitats that must be included in harvest refuges for *P. argus*.

Second, increases in density and biomass in a marine reserve are directly linked to the carrying capacity of that area, in terms of areal size and types of habitats. The *P. argus* population in this reserve may already have reached these limits (Acosta 2002). The Glover's Reef Marine Reserve is currently one of the larger no-take marine reserves in the Caribbean. Our results suggest that smaller reserves may be marginal or ineffective for protecting populations of spiny lobster *P. argus*.

Third, the density and biomass patterns of the spotted lobster *P. guttatus* suggest that a commercial fishery for this species may have low yields per fishing effort. Additionally, fishery pressure can potentially result in rapid local extinctions on isolated coral reefs. Clearly, an effective marine reserve for the conservation of spiny lobsters *P. argus* must incorporate large areas of heterogeneous habitats, whereas an effective marine reserve for spotted lobsters *P. guttatus* must protect large areas of shallow coral reef habitat.

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