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Distribution and abundance of Caribbean spiny lobsters in the Key West National Wildlife Refuge: relationship to habitat features and impact of an intensive recreational fishery

David B. Eggleston[A] *and Craig P. Dahlgren*[B]

[A]North Carolina State University, Department of Marine, Earth and Atmospheric Sciences, Raleigh, North Carolina 27695-8208, USA

[B]The Ocean Conservancy, 1725 DeSales St, NW, Suite 600, Washington, D.C. 20036, USA; present address: Caribbean Marine Research Center, 250 Tequesta Dr., Suite 304, Tequesta, Florida 33469, USA

Abstract. During 1999 we determined abundance and size frequency of the Caribbean spiny lobster, *Panulirus argus*, in various habitats within the 'Lakes' and 'Marquesas' regions (122 km^2) of the Key West National Wildlife Refuge (KWNWR), USA, using visual surveys. We also assessed the relationship between lobster abundance and habitat characteristics. During July–August 2000, we quantified the impact of a two-day recreational fishing 'miniseason' in fished and nonfished areas within the KWNWR. Lobster density was highest in channels, followed by hard bottom and patch reefs. *P. argus* was rarely observed in sea-grass and never in mangrove prop-roots. Its density was related to density and volume of large sponges in channel habitats. Although channels represent only 0.06% of the study area, they provide abundant refuges and a likely corridor for migrating juveniles. The two-day fishing season reduced density of lobsters >7 cm CL by an average of 80% across several habitats, including three marine protected areas closed to fishing. The observed decline was probably due to fishing, because percent change in density was related to number of recreational boats anchored at a given site. Relatively small marine protected areas (30–150 ha) may therefore be too small to protect the population structure of *P. argus* adequately within the KWNWR.

Introduction

Marine protected areas (MPAs) are currently being touted as one of the most powerful tools for promoting recovery and sustainability of the world's fisheries (Agardy 1994; Allison *et al.* 1998; McManus 1998; Guénette *et al.* 1998). Wise use of MPAs will require both understanding of the ecological roles and economic values of specific nursery habitats (Costanza *et al.* 1997; Beck *et al.* 2001) and rigorous tests of the efficacy of specific marine reserve designs (Allison *et al.* 1998; Lauck *et al.* 1998). Only assessing the MPA efficacy will reveal whether or not a MPA is large enough and located appropriately to achieve management goals. Optimal MPA placement requires identification of the range of habitats used by species of concern and determination of demographic rates in various habitats, so initially, a comparison is needed of organism abundance over a broad range of possible habitats.

The Florida Keys marine ecosystem in the USA supports important commercial and recreational fisheries for both fish and invertebrates (*e.g.*, Caribbean spiny lobster; stone crab, *Menippe mercenaria*; snapper, Lutjanidae; grouper, Serranidae), as well as a marine-based tourism industry. Despite the ecological and economic significance of the Florida Keys coral reef ecosystem, it is faced with a growing number of threats including water-quality degradation (Lapoint and Clark 1992), habitat loss (Robblee *et al.* 1991; Durako 1994, Herrnkind *et al.* 1997), and overfishing (see, *e.g.*, Ault *et al.* 1998). Because of these multiple insults, the Florida Keys coral-reef ecosystem has been classified an 'ecosystem-at-risk' (NMFS 1996). A network of protected areas is being established to conserve this threatened ecosystem and to safeguard its living resources.

The first protected area in the Florida Keys was the Key West National Wildlife Refuge (KWNWR), established in 1908. Marine habitats within the KWNWR include mangroves, sea-grass beds, hard bottom, macroalgal beds, sand flats, and coral reefs. Both recreational and commercial fishing are allowed within a majority of the KWNWR. Although most of the refuge consists of shallow bank and sea-grass habitats interspersed with mangrove islands, it also contains numerous patch reefs within Hawk Channel to the south and in the Gulf of Mexico to the north. Within the KWNWR are two smaller areas, referred to as the 'Lakes' and 'Marquesas' (122 km^2) (Fig. 1), that contain a complex mosaic of habitat types including sea-grass, channels, macroalgal meadows, hard bottoms, mangroves, and patch

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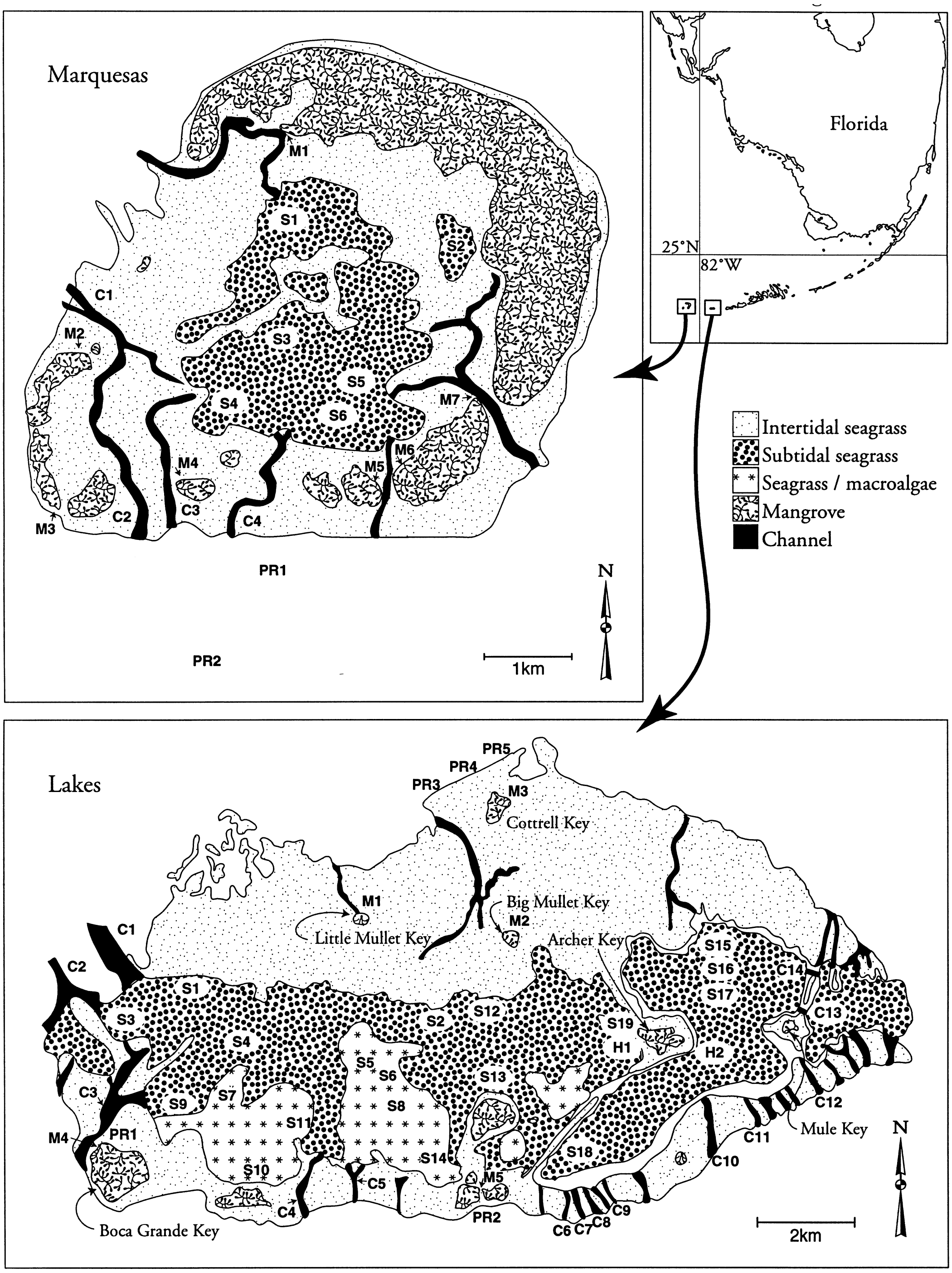

Fig. 1. Schematic of habitat types and locations of sampling stations within the Lakes and Marquesas regions within the Key West National Wildlife Refuge, Florida, USA. Habitat maps were generated with ground-truthed, geo-referenced, and digitized aerial photographs (1:48 000 scale obtained from the National Ocean Services, NOAA). C = channel habitats, S = sea-grass habitats, M = mangrove habitats, and PR = patch reefs. See text for details regarding the sampling approach.

reefs. In the present study, we gathered information on distribution and abundance patterns of the Caribbean spiny lobster (*Panulirus argus*) across the mosaic of five habitats described above, as an initial step toward identification of the nursery role (*sensu* Beck *et al.* 2001) of these habitats. We also quantified the relationship between lobster abundance and specific habitat features and describe the impact of an exclusively recreational fishery on spiny lobsters in a series of small marine protected areas as well as areas open to fishing.

Materials and methods

Sites and habitats

The KWNWR is a rectangular area (24°40' to 24°27'N,82°10' to 81°49'W) measuring 766.9 km^2. We conducted initial site and habitat reconnaissance during July 1999 by ground-truthing aerial photographs (1:48 000; obtained from the National Ocean Service, NOAA) of the Lakes (24°35'N,82°55'W) and Marquesas (24°36'N,82°8'W) regions with a small (7-m) boat and by snorkeling and SCUBA (Eggleston *et al.* 2000). We identified six habitats within which to measure the density and size frequency of Caribbean spiny lobsters: submerged mangrove (*Rhizophora mangle*) prop roots, channels bisecting mangrove islands or sea-grass shoals, subtidal sea-grass beds, inshore hard bottoms, inshore patch reefs, and offshore reefs (Fig. 1). We did not sample shallow, intertidal sea-grass beds that were often exposed during spring low tides (Fig. 1).

Design and general approach for surveys of lobster density and habitat features

We used standardized visual survey techniques for rapid assessment of lobster distribution and abundance patterns in the Lakes and Marquesas regions over a three-month period in the six marine habitats listed above. All surveys were conducted during the day when underwater visibility exceeded 10 m, and during a seven-day window bracketing the new moon each month so as not to confound lobster counts with possible variation in abundance due to diel and lunar variation in migration behaviour (Herrnkind *et al.* 1975).

We used a stratified random survey procedure for lobsters in subtidal sea-grass beds (areas with and without macroalgal meadows; Fig. 1) and randomly chose channels, mangroves, hard-bottoms, patch reefs and offshore reefs. The areal cover of sea-grass and channels was approximately three times greater in the Lakes than in the Marquesas (Eggleston *et al.* 2000), so our sample size for each habitat was about three times higher in the Lakes than in the Marquesas. Lobster counts were conducted with two general approaches, each using SCUBA divers: visual band transects, which provided density estimates; and 10-min surveys with visual estimates of area searched, which provided another measure of density.

Habitat-specific surveys

Sea-grass

To sample lobsters in sea-grass, we superimposed a grid system containing cells measuring ~200 × 200 m over sea-grass in each region. We then randomly chose 19 cells at the Lakes and 6 cells at the Marquesas and used SCUBA divers to determine lobster density and size frequency, as well as habitat characteristics in each cell. If a randomly chosen cell corresponded to an intertidal sea-grass bed, we randomly chose another cell until a subtidal sea-grass site was selected. Two parallel band transects (60 × 2m) were then haphazardly placed beginning at the downstream edge of each cell such that divers began their survey by swimming against the current. Transects were located approximately 100 m apart and identified with floats at the ends. All counts were made during the day (0900–1600 hours) when water visibility exceeded 8–10 m. All counts within a single band were made by two divers; the first diver counted lobsters, and the second quantified habitat characteristics. Divers estimated spiny-lobster carapace length (CL) in centimetres by comparing lobsters to a ruler attached perpendicular to the far end of a 70-cm rod (Eggleston and Lipcius 1992, Eggleston *et al.* 1997). This device helped avoid underwater magnification problems in estimating lobster sizes and aided in delineating the 2-m band width. Lobster CL was measured to the nearest 1 cm. The response variable produced from the band transects was the density (number/120 m^2) of *P. argus*.

Because macrophyte structural complexity (*e.g.*, sea-grass shoot density and biomass) is often positively related to crustacean density in macroalgal and sea-grass systems (*e.g.*, Stoner 1983, Orth *et al.* 1984), we measured sea-grass habitat characteristics (mean shoot density and blade height) at each band transect within a grid cell ($n = 2$ per cell). We quantified sea-grass shoot density by tossing a 0.07-m^2 quadrat haphazardly near the starting point of each band transect. Individual sea-grass shoots and mean blade height (mean of 10 haphazardly chosen shoots) within a quadrat were counted by SCUBA divers. Blade height (cm) was measured with a ruler. After sea-grass characteristics were measured within a quadrat, percentage cover of the different sea-grass species (*Thalassia testudinum*, *Syringodium filiforme*, *Halodule* sp.) and microhabitats (*Laurencia* sp.; 'other' macroalgae such as *Penicillus* sp., *Udotea* sp., and *Halimeda* sp.; sponges; coral rubble; sand) within a transect (120 m^2) was estimated to the nearest 5% visually by divers.

After a band transect was completed, divers continued to swim upcurrent and initiated a timed (10-min) visual survey for spiny lobsters. We started the timed transect approximately 30 m from the end of the band transect in an attempt to keep the two surveys independent. At the end of the 10-min survey, the diver surfaced, visually estimated the distance back to the band-transect float, and subtracted 30 m to estimate the total distance travelled. The distance travelled averaged 120 m. The width of the 10-min transect was determined by underwater visibility, which averaged 10 m. Thus, the 10-min survey in sea-grass covered an average area of 1200 m^2. Although this method of estimating distance travelled was crude, it provided an estimate of lobster densities and variance that could be used to estimate required sample sizes for future studies, to make relative comparisons of density across structurally complex habitat types that did not lend themselves to band-transect methods (*e.g.*, mangrove prop roots, patch reefs), and to compare lobster densities measured by band-transect and timed-swim survey methods. The mean of the values arrived at by the two surveys within a sea-grass cell served as a single replicate ($n = 19$ at the Lakes and 6 at the Marquesas).

Channel habitats

Channel habitats measuring 2–4 m deep that bisected mangrove islands and shallow sea-grass and sand shoals (Fig. 1) probably serve as important conduits for organisms undergoing ontogenetic migrations from nursery habitats within the Lakes and Marquesas to offshore reefs. We determined the density and relative abundance of spiny lobsters and habitat characteristics as described above for sea-grass habitats, and in addition quantified sponge habitat characteristics. A total of 14 were randomly chosen from available channels at the Lakes and 4 from the Marquesas (Fig. 1). Two separate band transects and 10-min surveys were conducted within each channel as described above for sea-grass. The mean of the values for lobster and habitat characteristics from the two surveys within a channel served as a single replicate ($n = 14$ at the Lakes; $n = 4$ at the Marquesas, respectively). The average area searched during 10-min surveys in channel habitats was 1000 m^2.

Relatively large loggerhead sponges (*Speciospongia vesparia*) serve as important habitat for Caribbean spiny lobster (Herrnkind *et al.* 1997; pers. observation). Large sponges were a relatively common feature of channel bottoms probably because of high tidal current speeds (1–1.5 m s^{-1}), which scoured the bottom, providing a hard substrate for sponge attachment, and delivered suspended food for these suspension-feeders. The number of sponges and sponge volume per transect (120 m^2) were estimated by divers. We estimated sponge volume by measuring (in centimetres) the radius (r) and height of each sponge with a ruler and multiplying height by πr^2.

Hard-bottom habitats

Within sea-grass beds in the Lakes region, we observed hard-bottom areas, typically 1–4 ha in area, that were devoid of sea-grass but contained solution holes, sponges, and coral rubble.. These hard-bottom areas were absent for the most part in the Marquesas and relatively uncommon in the Lakes (located east and west of Archer Key; Fig. 1). Nevertheless, hard-bottom habitats provided some of the few crevices available for spiny lobsters within large sea-grass beds and so were included in our Lakes surveys during September ($n = 2$ hard-bottom sites). Lobster abundance and habitat features were measured by both band-transect and timed-survey methods, as described above for sea-grass habitats. The average area searched during 10-min surveys in hard-bottom areas was 400 m^2.

Mangroves

We applied a replicable, relatively rapid, and quantitative estimate of lobster abundance that avoided destructive sampling techniques such as rotenone or trawling. Divers conducted standardized 10-min surveys for lobsters in mangrove prop-root habitats as described but did not use a line transect of predetermined length (see, *e.g.*, Rooker and Dennis 1991). Instead, the survey transect followed the perimeter of the because mangrove fringe. Because the perimeter varied from place to place in degree of convolution, and because the mangrove-fringe understorey varied in its accessibility to divers (see below), search time along a linear transect of fixed length would have varied widely and would probably have biased our counts in favour of higher relative abundances in more convoluted mangrove fringes. Each mangrove survey at a given site was conducted by two divers, and the mean of the values they arrived at was used in statistical analyses ($n = 5$ in the Lakes and 7 in the Marquesas). We estimated the area covered during a 10-min search by recording the distance that we could see within the prop root canopy (~2–17 m) and by placing floats at the beginning and end of each survey. After a particular survey was completed, we retraced the transect in a boat and visually estimated the linear distance covered, taking into account indentations along the mangrove fringe. Our estimates of linear distance covered during a 10-min search ranged from 10 m to 80 m and averaged 38 m. The average area covered during 10-min surveys in mangrove prop-root habitats was 152 m^2. Although we randomly chose seven out of all available mangrove habitats to sample at the Marquesas, we were restricted to five mangrove sites in the Lakes (Fig. 1) because all of the other mangrove areas were too shallow for boat access, particularly during low tides.

Nearshore patch reefs and offshore reefs

We counted lobsters at all patch-reef sites that we could locate near the Lakes ($n = 5$) and Marquesas ($n = 2$) (Fig. 1) with the 10-min survey method. We also used this method to determine the abundance of lobsters at four randomly chosen offshore reefs within the KWNWR: Sand Key, Western Dry Rocks, Coalbin Rocks, and the eastern portion of Cosgrove Shoals. These reefs are not shown in Fig. 1 but were located 12–15 km south of the Lakes and Marquesas along the southern boundary of the KWNWR. Lobster counts and sizes were estimated as described above for sea-grass habitats. We used the mean counts from 4 divers per reef in statistical analyses. The mean areas searched per diver during 10-min surveys ranged from 300 to 700 m^2 and averaged 600 m^2. The mean areas searched per diver during 10-min surveys ranged from 1000 m^2 to 1700 m^2 and averaged 1500 m^2.

In summary, the band transect and 10-min survey methods were used in sea-grass, channel, and hard-bottom habitats, whereas only the 10-min-survey method was used in mangrove prop roots, patch reefs, and offshore reefs.

Impact of miniseason

The spiny-lobster fishery in Florida, USA, is closed during the spawning season (March–July) except for a two-day recreational 'miniseason' for sport divers at the end of July, just before the opening of the fishing season in August. This miniseason presents a unique opportunity to assess the sole impact of a recreational fishery on a fishery resource. Three days before the opening of the miniseason in July 2000, we determined the density of *P. argus* in habitats where we had identified relatively high lobster densities in 1999 (in, *e.g.*, channel, hard-bottom, patch reef, and offshore reef habitats). We also surveyed nine small (~2 m^2) solution holes in hard-bottom areas near Archer Key in the Lakes (Lakes sites H1 and H2 on Fig. 1). We then resampled these same sites over a three-day period immediately after the close of the miniseason. The offshore reef sites we surveyed were somewhat different from those sampled in 1999 and included three reefs that were closed to fishing as a part of the Florida Keys Marine Sanctuary Program (Eastern Dry Rocks, Sand Key, Rock Key) and three that were open to fishing (Satin Shoal, Vestal Shoal, Western Dry Rocks). In an attempt to improve assignment of causes to changes in lobster density after the fishing season, we counted the recreational dive boats anchored at each of our lobster survey sites on each day of the miniseason. The order in which we checked sites for dive boats varied from day to day.

Statistical analyses

Surveys of lobsters and habitats

We examined the effects of region (Lakes, Marquesas) on the mean density of spiny lobsters in sea-grass, channel, and patch-reef habitats with separate *t*-tests. We used separate *t*-tests, rather than an ANOVA approach that would include habitat type as a factor, because we did not know the equivalence of our visual-survey technique in different habitat types and because habitat types differed widely in area searched (from 152 m^2 for mangroves to 1200 m^2 for sea-grass). The data were log of $(x + 1)$ transformed when necessary to meet the assumptions of normality (tested with a Kolmogorov-Smirnov test) and homogeneity of variances (tested with Levene's test). We calculated the mean density of *P. argus* in hard-bottom and offshore reef habitats but did test these data statistically for regional differences because hard-bottoms were only sampled in the Lakes, and offshore reefs were located well outside of the Lakes and Marquesas. We did not include lobster density in mangrove prop roots in statistical analyses because *P. argus* was never observed there (see below).

A forward, stepwise multiple-regression model was used to examine the relationship between habitat characteristics and lobster density measured during band transects in sea-grass and channel habitats. For sea-grass, the regression model included as independent variables sea-grass shoot density, mean sea-grass blade height, and percentage cover of *Thalassia*, *Syringodium*, *Halodule*, *Laurencia*, other macroalgae, sponges, coral rubble, and sand. For channel habitats, the independent variables were similar to those for sea-grass, with the addition of sponge density and mean sponge volume. Habitat characteristics were described by Eggleston *et al.* (2000). Alpha to enter and remove factors from the model was 0.10.

Impact of miniseason

We assessed the effects of fishing season on the mean density of *P. argus* in channel, hole, hard-bottom, and patch-reef habitats within the Lakes and Marquesas with separate, paired *t*-tests. We also used a replicated Before-After-Control-Impact (BACI) experimental design (Underwood 1994) to determine the main and interactive effects of location (closed to fishing: Eastern Dry Rocks, Sand Key, Rock Key; open to fishing: Satin Shoal, Vestal Shoal, Western Dry Rocks) and fishing season (Before and After) on the mean density of *P. argus* residing in offshore reefs. In this case a two-way ANOVA model was employed (Underwood 1994). The data were log of (x + 1) transformed when necessary to meet the assumptions of normality (tested with a Kolmogorov-Smirnov test) and homogeneity of variances (tested with Levene's test), as described above. We examined the relationship between the percentage change in lobster density from before to after fishing, and the number of recreational boats observed at a specific site with a linear least-squares regression model.

Results

We conducted 248 diver surveys (band transects and 10-min surveys combined) during August–October 1999 in the KWNWR and recorded distribution, abundance, and size frequencies of Caribbean spiny lobsters. Our surveys covered an area of approximately 0.15 km^2 (Eggleston *et al.* 2000).

Effects of habitat type and region on lobster density

We measured primarily juvenile (4.1–7.0 cm CL) *P. argus* at the Lakes and primarily larger juveniles (4.1–5 cm) and adults (7.1–8 cm CL) at the Marquesas (Fig. 2). No juvenile lobsters below 3.1 cm CL were observed at the Marquesas (Fig. 2*b*). Although more large lobsters were observed at the Marquesas than at the Lakes (Fig. 2), mean carapace lengths in the two regions did not differ significantly (Lakes: mean = 5.5 cm CL, SE = 1.3, *n* = 17 sites; Marquesas: mean = 5 cm CL, SE = 3.7, *n* = 4 sites, *t*-test, *P* = 0.89). Both sea-grass and hard-bottom habitats harboured primarily juvenile lobsters less than 7 cm CL, whereas offshore reefs harboured primarily adults greater than 7 cm CL (Fig. 3). Channel and patch-reef habitats harboured a broad size range of lobsters but mainly juveniles less than 6 cm CL (Fig. 3).

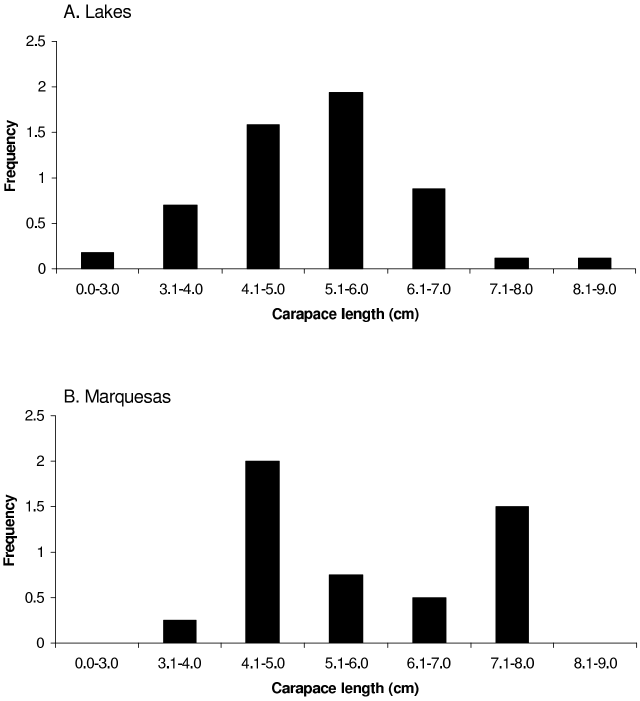

Fig. 2. The size–frequency distribution of Caribbean spiny lobster (Palinuridae, *Panulirus argus*) estimated from a combination of band-transect and 10-min survey methods in sea-grass, channel, hard-bottom, and patch-reef habitats in the (*A*) Lakes and (*B*) Marquesas regions of the Key West National Wildlife Refuge. See text for the results of statistical analyses.

The density of *P. argus*, as measured with band transects, was greatest in channel and hard-bottom habitats; almost no lobsters were observed in sea-grass (mean = 0.001/m^2) and none at all in mangrove prop-root habitats (Fig. 4*a*). Densities of *P. argus* were significantly higher in channels at the Lakes than the Marquesas (*t*-test; *P* = 0.03), and no lobsters were observed in sea-grass habitats in the Marquesas (Fig. 4*a*). Habitat-specific patterns of lobster density measured with 10-min surveys were similar to those measured with band transects (Fig. 3). For example, channel, patch-reef, and hard-bottom habitats showed the highest densities of *P. argus*; almost no lobsters greater than 3 cm CL were observed in sea-grass, and none at all in mangrove prop-root habitats (Fig. 3*b*). Densities of *P. argus* in sea-grass and patch-reef habitats were significantly higher at the Lakes than the Marquesas (*t*-test: both $P < 0.01$) (Fig. 3*b*). Lobsters observed in sea-grass were typically residing beneath detrital sea-grass that had accumulated in small depressions on the sea floor. Densities of *P. argus* in channel habitats were significantly higher at the Marquesas than the Lakes (*t*-test; *P* = 0.04) (Fig. 4*b*).

We found no relationship between the density of *P. argus* and sea-grass habitat characteristics such as shoot density and blade height (all $P > 0.05$), not surprising given that lobsters were essentially absent from sea-grass. We did, however, find a significant positive relationship between the density of *P. argus* and both sponge count and sponge volume in channel habitats (Fig. 5). The condition index from the multiple regression indicated mild collinearity (value of 9), which did not require alternative analyses (Philippi 1993). The multiple-regression model indicated that sponge count had the highest partial R^2 value; the model R^2 value increased by 27% when sponge volume was added. Nonlinear functions did not improve the fit of the lobster density and sponge data over linear functions.

Impact of miniseason

The mean density of *P. argus* declined in all habitats and sites examined from before to after the 2-day recreational fishing season (Figs 6 and 7). The percentage decline ranged from 22% in channels to 100% in hard-bottom

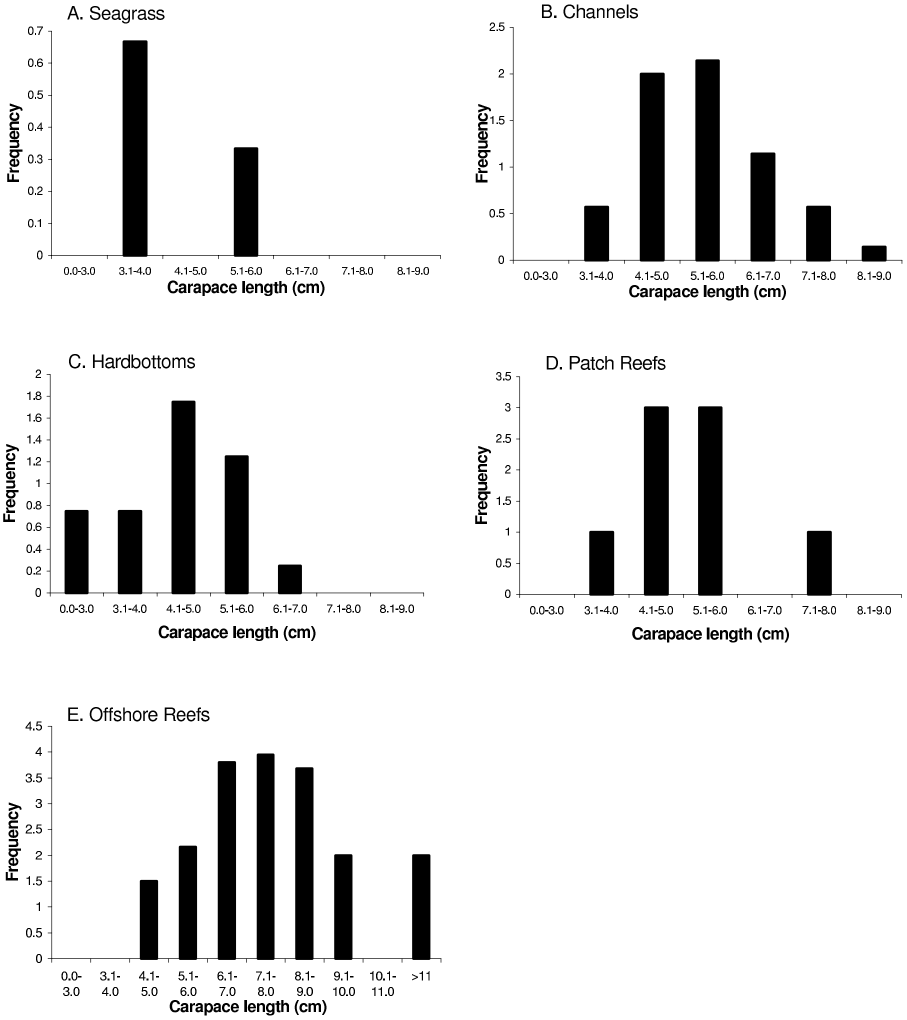

Fig. 3. The size–frequency distribution of Caribbean spiny lobster (Palinuridae, *Panulirus argus*) estimated from a combination of band-transect and 10-min survey methods in (*A*) sea-grass (*B*) channel (*C*) hard-bottom (*D*) patch-reef, and (*E*) offshore habitats in the Key West National Wildlife Refuge (Lakes and Marquesas regions pooled). Statistical comparisons of size–frequencies in different habitats were not conducted because the accuracy of visual survey methods was unknown and area searched differed in different habitats.

habitats. It was significant for hard-bottom and patch-reef habitats in the Lakes and Marquesas (paired *t*-test; both $P < 0.01$). Density did not decline significantly, however, in channel and hole habitats (paired *t*-test; both $P > 0.10$) (Fig. 6*a*). The mean density of *P. argus* >7 cm CL (log + x transformed) at offshore reefs was significantly affected by site and fishing period (two-way ANOVA; Site: df = 5, 12, $F = 5.31$, $P = 0.001$; Period: df = 1, 12, $F = 14.5$, $P = 0.001$; Fig. 6); the interaction effect was not significant ($P = 0.63$). The mean density of *P. argus* was significantly higher at Eastern Dry Rocks than at Sand Key or Rock Key, which, in turn, had significantly higher lobster densities than Satin Shoal or Vestal Shoal, followed by Western Dry Rocks (Fig. 6; Ryan's Q multiple-comparisons test). The mean density of *P. argus* >7.0 cm CL declined from before to after fishing at all sites, including those closed to fishing (lower-level ANOVA with fishing season as a 2-level factor; $P > 0.05$; Fig. 7). Finally, percentage change in the mean density of *P. argus* was significantly positively related to the number of recreational boats observed at specific sites during the miniseason (Fig. 8).

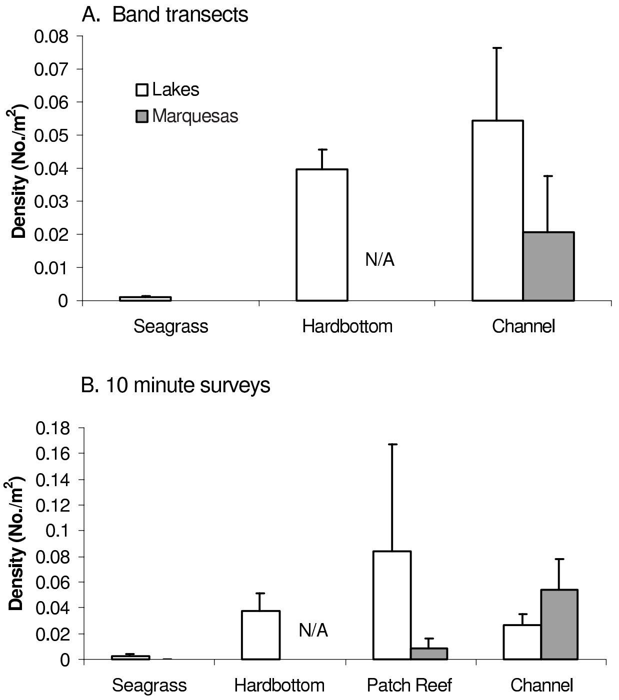

Fig. 4. The effects of region (Lakes, Marquesas) and habitat (seagrass, hard bottom, patch reef, channel) on the mean (+ 1 SE) density of *Panulirus argus* measured with (*A*) band transects and (*B*) 10-min surveys. See text for significance levels.

Discussion

Our key findings are (1) that the Lakes harboured primarily juvenile *P. argus*, whereas the Marquesas harboured both juveniles and adults; (2) that channel, hard-bottom, and patch-reef habitats contained the highest densities of *P. argus* and that extremely low densities were observed in sea-grass and none in mangrove prop roots; (3) that seagrass, channels, hard bottoms, and patch reefs harboured primarily juvenile lobsters less than 6 cm CL; (4) that the density of *P. argus* was significantly positively related to both number and volume of large sponges; (5) that the density of *P. argus* declined in all habitats from before to after a two-day recreational fishing season (significantly in hard-bottom, patch-reef, and offshore reef habitats, the latter of which included three reefs closed to fishing); and (6) that the percentage decline in *P. argus* density was significantly positively related to the number of recreational fishing boats observed at specific sites during the 2-day fishery.

Potential sampling biases

We recognize that some of the differences in lobster density among the habitats we surveyed may be due to differences in the efficiency of our visual-survey methods in different habitats. Poor underwater visibility and the cryptic nature of small juvenile *P. argus* in complex benthic habitats can reduce the accuracy and precision of visual survey techniques. We tried to reduce habitat- and observer-

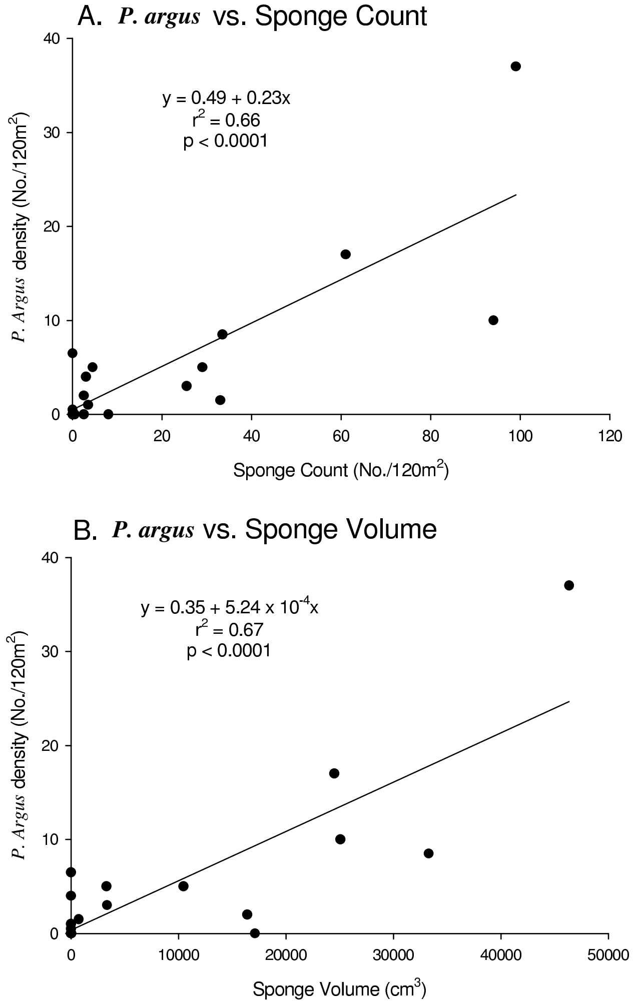

Fig. 5. The relationship between the density of *Panulirus argus* and (*A*) sponge count and (*B*) sponge volume estimated during band transects. Sponge volume was estimated as height × πr^2.

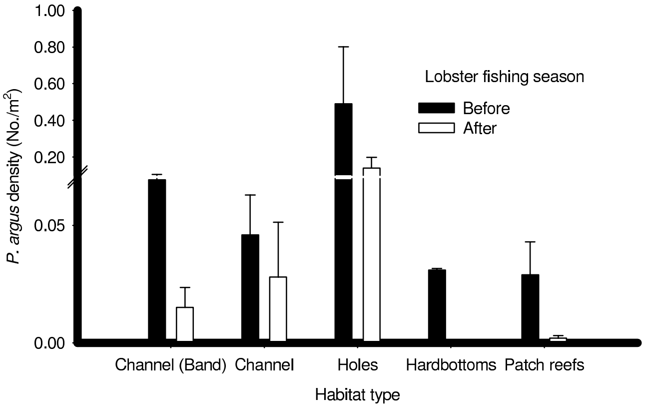

Fig. 6. The effects of a two-day recreational lobster fishing season (before, after) and habitat type (channels, holes, hard bottoms, patch reefs) on the mean (+ 1 SE) density of *Panulirus argus* >70 mm carapace length. Lobster density was estimated from 10-min diver surveys except as noted for channels, in which both band-transect and 10-min survey methods were used. See text for significance levels.

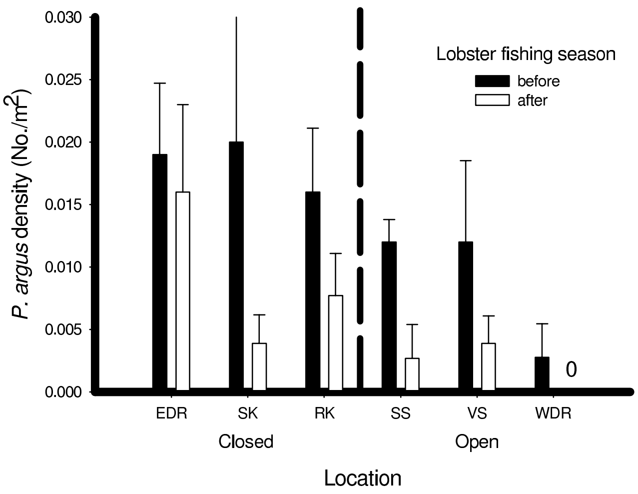

Fig 7. The effects of a two-day recreational lobster fishing season (before, after), Marine Protected Area status (open, closed to fishing), and offshore reef site (EDR, Eastern Dry Rocks; SK, Sand Key: RK, Rock Key: SS, Satin Shoal; VS, Vestal Shoal; WDR, Western Dry Rocks) on the mean (+ 1 SE) density of *Panulirus argus*>70 mm carapace length. Lobster density was estimated from 10-min diver surveys. See text for significance levels.

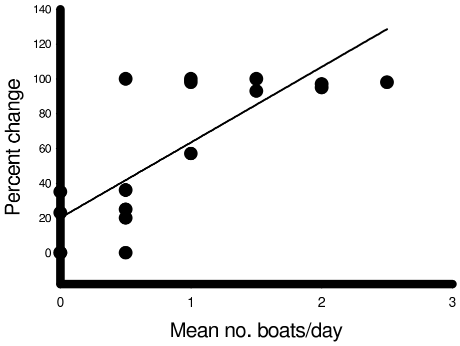

Fig. 8. The relationship between the percent change in the density of *Panulirus argus* >70 mm carapace length and the mean number of boats observed at specific sampling sites over the two-day recreational fishing season.

specific biases in our visual survey techniques by using divers with experience in quantifying distribution and abundance patterns of *P. argus* in offshore reef, patch-reef and macroalgal habitats; replicate surveys within a given sampling cell or site; slow and methodical searches in complex benthic habitats; a complementary combination of band transect and timed surveys in many habitat types; and restricting visual surveys to periods when visibility was high (>10 m).

Distribution and abundance patterns of Panulirus argus

Of the mosaic of important fishery habitats in the Key West National Wildlife Refuge, one of the most important for *P. argus* was channels. Channel habitats provide a corridor for postlarvae transported into the Lakes and Marquesas areas from offshore (Dahlgren and Eggleston unpubl. data.), and for organisms migrating from sea-grass and mangrove habitats to patch reefs and offshore reefs. Nearly half of the channels we surveyed contained relatively large stands of sponges, as well as numerous small patch corals, solution holes, and other crevice shelters. The availability of crevice shelters is thought to limit early bethic stages of *P. argus* in certain ecosystems, thereby representing a population bottleneck (Butler and Herrnkind 1997).

Before 1992, in the middle Florida Keys portion of southern Florida Bay, large sponges (primarily *Speciospongia vesparia*) were the most commonly used refuge for postalgal-phase *P. argus*, the first stage that seeks crevice shelters rather than vegetation (Marx and Herrnkind 1985). An especially productive nursery site in Florida Bay, with a mean density that exceeded 450 juveniles ha^{-1} (Forcucci *et al.* 1994), was located in an area where >80% of the lobster dens were in large loggerhead sponges (Childress 1995). In 1991 and 1992, cyanobacterial blooms killed virtually all sponges in 20% of the spiny lobster nursery (~500 km^2) in Florida Bay, suggesting the possibility of a shortage of shelter for juvenile *P. argus* and consequent decline in juvenile lobster numbers (Butler *et al.* 1995). Although refuge and lobster abundance declined on previously sponge-rich sites without alternative shelter, the local population of spiny lobster was relatively unaffected by the sponge die-off because lobsters in areas of alternative shelter switched to residing in previously underused shelter (solution holes, coral heads, etc.) (Butler *et al.* 1995). In addition, throughout the period of sponge die-off, postlarval supply was fortuitously high (Herrnkind *et al.* 1997).

In the present study, channel habitats contained extremely high densities of mainly juvenile *P. argus* (247–642 lobsters ha^{-1}). Moreover we demonstrated what we believe to be the first positive, significant relationship between sponge density and volume in channel habitats and lobster density. Sponge habitat is therefore probably very important for spiny lobsters in the Lakes and Marquesas regions of the KWNWR. In fact, we found very little alternative habitat for spiny lobsters in this region. A sponge die-off in the KWNWR would probably have an extremely detrimental effect on lobster populations because of the general lack of alternative shelters.

In contrast, the role of mangrove prop roots and sea-grass as habitat for juvenile and adult *P. argus* is less clear. For example, in Belize, *P. argus* preferred the crevice shelter of stony corals, but their use of mangrove prop roots or undercut peat banks increased wherever coral cover was sparse near mangrove island margins (Acosta and Butler 1997). In contrast, we never observed *P. argus* in mangrove prop roots in the Lakes or Marquesas in this study, despite slow methodical searches for antennae protruding from acroalgae that colonized prop roots, as well as searches within the prop-root canopy. Several explanations might account for the discrepancy (Acosta and Butler 1997). First, alternative shelter in the form of large sponges in nearby channel habitats was available to lobsters in our study. Second, we observed extremely high densities of piscine predators among mangrove prop roots (Eggleston *et al.* 2000), so predation pressure, particularly on relatively small juvenile lobsters, was probably very high. Although *P. argus* have been occasionally observed residing in sea-grass in the upper portion of Florida Bay, USA (M. Butler, Old Dominion University, pers. comm.), we rarely saw any *P. argus* in sea-grass off of Key West. When we did observe spiny lobsters in sea-grass, they were typically residing beneath sea-grass detritus that had accumulated in small depressions on the seafloor. These observations suggest that sea-grass is probably not widely used as habitat by postalgal and juvenile *P. argus* greater than 3.0 cm CL.

Impact of recreational fishery

The results from this study indicate recreational SCUBA divers can have considerable impact on the local abundance of *Panulirus argus* in only two days. The mean density of *P. argus* declined by an average of 80% from before to after the two-day recreational miniseason. The percentage decline in lobster abundance observed in this study is higher than that observed for Looe Key, Florida, in 1987, when abundance of *P. argus* decreased by 55% immediately after the miniseason (Blonder *et al.* 1988). Similarly, Davis (1977*a*) observed a 58% decline in the abundance of *P. argus* after the entire 8-month fishing season in the sport-harvest area of the Fort Jefferson National Monument, Dry Tortugas, Florida, a result that prompted the U.S. National Park Service to halt all fishing for *P. argus* in 1974 (Davis 1977*b*). The relatively large decline we observed is probably due to the relatively close proximity of the KWNWR to Key West, Florida, and the increasing popularity of sport SCUBA diving.

A major concern is the significant decline in mean lobster densities in areas closed to fishing during the miniseason. The Eastern Dry Rocks, Rock Key, and Sand Key are located approximately 10 km south-west of Key West, Florida, and measure 30 ha, 30 ha, and 150 ha, respectively. The significant impact of fishing in these closed areas may result from poaching, emigration of lobsters as a result of disturbance, the relatively small size of the protected areas, or all of the above. Although lobsters may have been taken illegally from the closed areas, the number was probably small, as we observed only large sailing and dive-charter vessels in these areas during our recreational boat surveys, and these vessels would probably not have allowed customers to harvest lobsters in the closed areas. Moreover, the Florida Marine Patrol surveyed these closed areas during the miniseason. The most likely explanation for the decline in closed areas is that lobsters dispersed from closed areas during night-time foraging or because of diver handling (Herrnkind *et al.* 1975), or during general nomadic movement, and were harvested by sport divers just outside of these relatively small closed areas. Our results suggest that the ability of the relatively small Eastern Dry Rocks, Rock Key, and Sand Key MPAs (which total only 0.001% of the area of the KWNWR) to preserve relatively large and highly fecund *P. argus* will be minimal.

Conclusions

Although channels containing large sponges represent only 0.06% of the total area of the Lakes and Marquesas, they provide abundant refuges and a likely corridor for migrating *P. argus*. Hard-bottom habitats containing crevices and solution holes also contained high densities of *P. argus* and occupied even less area than channels, only 0.0001% of the total in the Lakes and Marquesas. Patch reefs also contained high densities of *P. argus* but were located primarily outside of the Lakes and Marquesas, although within the KWNWR. Solely on the basis of relative lobster abundance, patch reefs, channels, and hard-bottom habitats appear to be key habitats for *P. argus* for most of the juvenile period and their inclusion in future studies of lobster growth, survival, and emigration should produce a more complete picture of their nursery role (*sensu* Beck *et al.* 2001). Our results also bear on the efficacy of MPAs. The recreational miniseason reduced *P. argus* densities by an average of 80%, even in areas closed to fishing as a part of the Florida Keys Marine Sanctuary Program. The three closed areas constitute only 0.001% of the total area of the KWNWR and may be too small to preserve the abundance and size-at-age structure of *P. argus* from fishing pressure.

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