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Variable reproductive success in fragmented populations

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ABSTRACT

Marine habitats are naturally patchy and anthropogenic disturbance can further fragment them. Many marine animals are sessile as adults or obligate inhabitants of particular habitats, so populations living in isolated patches of habitat are linked largely by dispersal of planktonic larvae. Theoretically, larvae are more likely to find and settle into large patches of habitat than small patches, thus small habitat patches may experience a more discontinuous supply of recruits resulting in small populations with unusual size- or age-structures or odd sex ratios — conditions where Allee effects on reproductive success are likely. We tested this hypothesis for the Caribbean spotted spiny lobster (*Panulirus guttatus*), an obligate inhabitant of coral patch reefs whose mating dynamics are size-dependent. We found that *P. guttatus* were less abundant on small reefs where their size structure and *per capita* reproductive success were significantly more variable, particularly among large females that are susceptible to sperm limitation that diminishes fertilization rates. These results are indicative of Allee effects and provide a mechanistic understanding of how size-dependent mating dynamics influence reproductive success in ways that alter population dynamics in patchy habitats.

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1. Introduction

Habitat fragmentation is a dramatic consequence of human disturbance on natural landscapes and the subject of much study in conservation biology (Lord and Norton, 1990; Fahrig, 1997; Laurance, 2008). Most landscapes are also spatially discontinuous by nature, and the degree of isolation and size of habitat patches has important repercussions for local population persistence (Fahrig and Merriam, 1985; Hansson, 1991; Hanski et al., 1996). Many studies on this subject have justifiably focused on terrestrial systems where the effects of human disturbance on habitat structure are obvious and pervasive (denBoer, 1970; Adams and Geis, 1983; Lamberson et al., 1992; Harcourt and Doherty, 2005; Duchamp and Swihart, 2008). Yet, marine habitats are also both naturally heterogeneous and subject to anthropogenic disturbance that can further fragment them (Butler et al., 1995; Hinchey et al., 2007). The spatial structure of habitats has consequences for the movement (Darcy and Eggleston, 2005), recruitment (Stockhausen and Lipcius, 2001; Butler et al., 2001, 2005), and disease dynamics (Hess, 1996; McCallum and Dobson, 2002) of marine animals among other ecological processes and it figures prominently in conservation measures in the sea as it does on land (Beck et al., 2001; Roberts et al., 2003).

The isolation imposed on marine populations and communities by the patchiness of marine habitats is often counterbalanced by high rates of dispersal in the sea. This is especially true among marine animals, the great majority of which have life cycles that include a planktonic larval stage. Movement by adults can be an important source of population connectivity in some marine species (Appledorn et al., 2003; Oremus et al., 2007; Taggart et al., 2008), but for most it is the dispersal of larvae that links spatially heterogeneous populations scattered among fragmented habitats (Gaines et al., 2007).

Larger patches of habitat are more effective at intercepting and sustaining immigrants as expressed in the "target-area" hypothesis (Lomolino, 1990) and exemplified in the dynamics described by island biogeographic theory (MacArthur and Wilson, 1967), in which communities on islands of various sizes (=habitat patches) are structured by a dynamic balance between immigration and extinction (e.g., Rieman and McIntyre, 1995; Adler, 1996; Samways, 1998; Wiggins et al., 1998). These ideas are also relevant in marine communities, many of which are dominated by sessile or philopatric species with planktonic larval dispersal and "open" population dynamics (Botsford et al., 1998; Underwood and Keough, 2001). Large patches of habitat theoretically receive a greater or more continuous supply of larvae than small patches. As a result, the density and size (or age) structure of multi-cohort populations on large patches should be more evenly distributed than on small patches of habitat where settlement is likely to be more sporadic. Infrequent larval settlement on small, isolated patches should thus lead to small populations with unusual size- or age-distributions or highly skewed sex ratios — prime conditions for Allee effects.

Allee effects, defined as reproductive failure associated with dysfunctional mating systems in small populations (Stephens et al., 1999), are more likely on small patches with small, oddly structured

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animal populations because of the unavailability of appropriately sized mates. For example, reproductive success nearly always depends on female size, but sometimes it also depends on the relative size and availability of male mates to ensure fertilization success (Adams and Paul, 1983; MacDiarmid and Butler, 1999; Kendall et al., 2001; Robertson, 2001). Thus, if population structure varies with patch size, then patch size can indirectly influence the reproductive potential of species by compromising the *per capita* fecundity of species dwelling on small patches of habitat. This relationship between habitat patch size, population structure, and reproductive success has received little attention, but it has potential consequences for our understanding of the population dynamics and management of species in isolated, patchy habitats.

We examined the relationship between patch size and the occurrence of Allee effects by comparing the population size, size structure, and fecundity of spotted spiny lobsters (*Panulirus guttatus* Latrielle, 1804) on isolated coral patch reefs in the Florida Keys (USA). The life history characteristics displayed by *P. guttatus* are representative of many marine species that dwell in patchy habitats, are relatively philopatric as adults, and whose fecundity depends on the sizes of mating males and females. Given these circumstances, we hypothesized that small reefs would have small lobster populations with heterogeneous size structures and as a consequence, individual reproductive success would vary more on small reefs than on large reefs. There were two components to our study. First, we determined lobster population density, size structure, and fecundity on 24 coral patch reefs of varying size. Second, we conducted mark-recapture studies on a subset of those reefs to evaluate whether post-settlement processes (e.g., growth, mortality/emigration, immigration) varied with reef size in ways that might confound or diminish the importance of larval supply in determining local population structure.

2. Materials and methods

2.1. Life history of P. guttatus

The spotted spiny lobster is an obligate dweller of coral and rocky reefs throughout the Caribbean, Florida, and Bermuda (Holthuis, 1991), where they occupy only shallow reefs and often coexist with their more abundant, mobile, and widespread congener − *P. argus* (Lozano-Alvarez and Briones-Fourzan, 2001; Lozano-Alvarez et al., 2007; Briones-Fourzan et al., 2006). Spiny lobsters are often targeted by large commercial and recreational fisheries (Phillips and Melville-Smith, 2006), but *P. guttatus* support only small artisanal fisheries in portions of its range because of its small size, cryptic lifestyle, and limited distribution on high-relief reefs (Losada-Tosteson et al., 2001, Guzman and Tewfik, 2004; Wynne and Cote, 2007). It is not fished in Florida (where our study took place) because the majority of adults fall below the minimum size (76 mm carapace length; CL) permitted for landing any species of spiny lobster. Also unlike many other highly motile species of spiny lobster, juvenile and adult *P. guttatus* exhibit strong site fidelity, have small home ranges (<100 m) on reefs, and typically remain on a single patch of reef for several years as shown by mark-recapture and homing studies (Sharp et al., 1997; Lozano-Alvarez et al., 2002, this study). Further evidence of this species' affinity for reef habitat comes from studies employing traps in which *P. guttatus* are only recovered from traps placed on reefs (Evans and Lockwood, 1994; Losada-Tosteson et al., 2001; Guzman and Tewfik, 2004).

P. guttatus reproduce year-round and while their fecundity is proportional to female size, it is also associated with male size (Briones-Fourzan and Contreras-Ortiz, 1999; Robertson, 2001; Negrete-Soto et al., 2002; Robertson and Butler, 2003). Female *P. guttatus* mate preferentially with larger males to minimize the potential for sperm limitation of fertilization success, which occurs when larger females mate with smaller males (Robertson, 2001). This

phenomenon is also known from other species of spiny lobster (MacDiarmid and Butler, 1999). After spawning, the planktonic larvae of *P. guttatus* spend an unknown period of time in the open sea, although the pelagic larval duration of other species of spiny lobsters is 4–24 mo (Phillips et al., 2006). Larvae metamorphose offshore into puerulus postlarvae that are transported onshore by tidal currents where they settle into small holes on the underside of rocky ledges on coral reefs and metamorphose into the benthic juvenile stage (Sharp et al., 1997). Thus, *P. guttatus* is a species demonstrating metapopulation dynamics in which juveniles and adults live in essentially isolated populations on shallow patches of coral reef and populations are linked by the dispersal of long-lived, planktonic larvae.

2.2. Population surveys

We determined lobster population density, size structure, and individual fecundity in surveys of 24 isolated patch reefs (<12 m deep, 2–6 m vertical relief) ranging in size from 20 m^2 to 8000 m^2 and haphazardly selected from thousands of shallow reefs in the Florida Keys, Florida (USA) (Fig. 1). Study reefs were spread throughout the archipelago and were separated from one another by 50 m–2 km of sand, rubble, or seagrass. Adult *P. guttatus* do not traverse open sand or seagrass (Sharp et al., 1997; Lozano-Alvarez et al., 2002, this study), thus each patch reef contained an independent isolated population. The area of each patch reef was estimated from reef dimensions determined from measurements by two divers who used a 100 m nylon transect tape to measure 4–6 cross-sections on each reef. To estimate reef volume, a better estimate of the habitat available on each reef to the crevice dwelling *P. guttatus*, we multiplied each patch reef area by its rugosity, using the standard "chain" method employed on coral reefs. Specifically, rugosity was calculated as the ratio of the non-linear, rugose measurement across the patch reef to the linear cross-section measurement made with the taut tape (Risk, 1972).

P. guttatus is a secretive species that hides by day within the crevices of the reef, but emerges at night to forage on the reef. Therefore, our surveys were conducted only at night (2100–2400 h) by 2–4 divers who searched the reef for 1 h and captured all of the *P. guttatus* that they encountered. Lobsters were collected with hand nets, placed in a mesh bag, and then brought on board a vessel where we recorded individual lobster morphometrics. The size (CL) of each lobster was recorded (± 0.1 mm), along with other metrics of reproductive development for males and females. The length of the second walking leg of males was measured to determine their size-at-maturity from a known allometric relationship between second leg length and CL (Sharp et al., 1997; Robertson and Butler, 2003). For females, we recorded reproductive status as: 1) spermatophore present (evidence of a recent mating), 2) bright orange, newly deposited eggs, 3) brown eggs with visible eye spots, 4) dark brown eggs (ready to hatch), 5) spermatophore or egg remnants (evidence of previous reproduction), or 6) no evidence of reproduction. We removed and froze all egg masses for counting in the laboratory. Lobsters were then returned unharmed to the reef. In the laboratory, each egg clutch was weighed to the nearest 0.0001 g and three samples (weighing 0.02–0.04 g) were counted. Three estimates of total eggs per clutch were calculated as:

$$\text{of eggs in clutch} = \frac{\text{total clutch mass (g)}}{\text{mass of sample (g)}} * (\text{of eggs in sample}).$$

Individual fecundity (number of eggs/clutch) was calculated as the mean of the three estimates of clutch size.

2.3. Mark-recapture studies

We conducted mark-recapture experiments on lobsters at six of the 24 patch reefs that we had surveyed earlier to determine if lobster
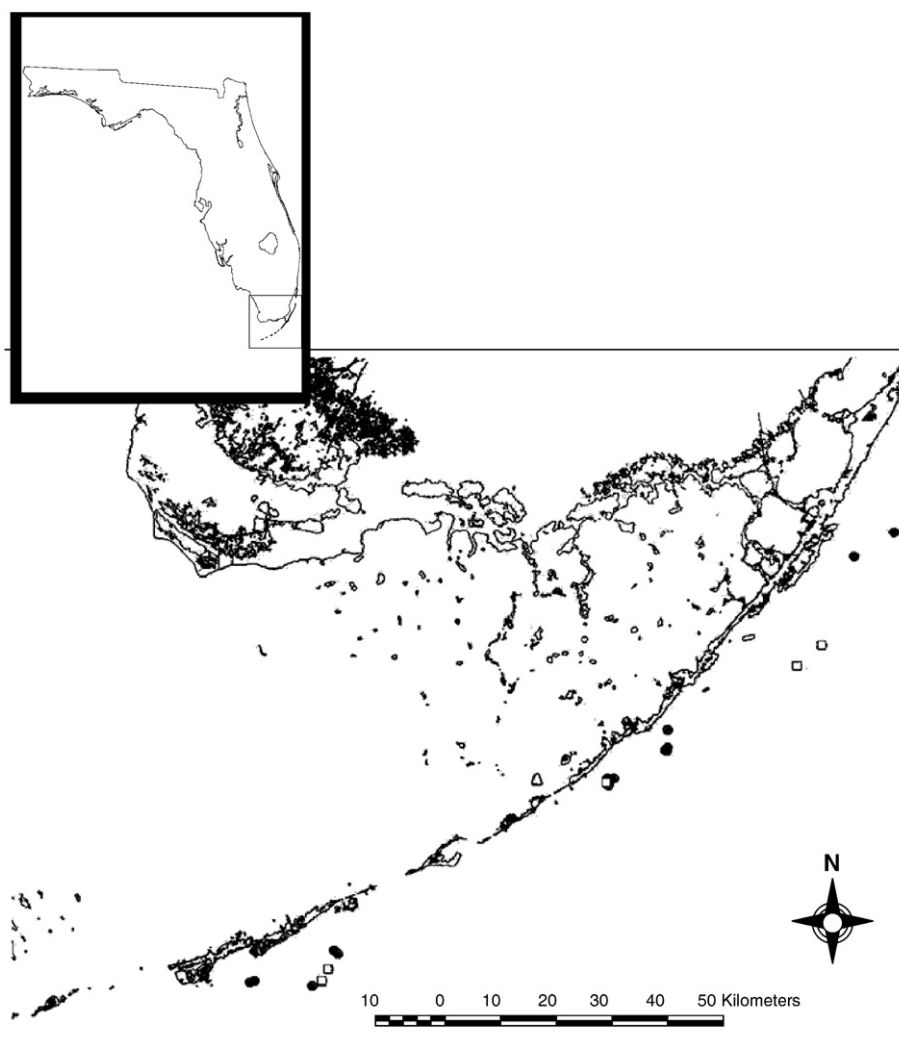
Fig. 1. Map showing the locations of field survey sites (solid circle) and mark-recapture study sites (open squares) in the Florida Keys. The Florida Keys are an island archipelago and lie at the southern tip of the state of Florida (USA), as shown in the top inset and center figure.

population parameters (e.g., growth, population addition or loss) varied with reef size. Reefs ranged in size from 152 m^2 to 8000 m^2 and were separated from one another by at least 100 m and up to several km by sand and seagrass bottom. Three reefs were sampled 3–4 times from May to August 1996 and all six reefs were surveyed 4–8 times during February through September from 1997 to 2000. During each survey, lobsters were collected by divers and data recorded as described above. Prior to release, the lobsters were tagged with an individually coded antennae tag and an internal color-coded latex tag (Northwest Marine Technologies, Shaw Island, WA). Antennal tags are lost upon molting and so were only useful for short recapture intervals. Laboratory trials conducted prior to the field study confirmed that the internal latex tags are retained after molting and neither tagging method affected growth (Robertson, 2001).

2.4. Data analyses

2.4.1. Population abundance and dynamics

Lobster population size on each patch reef we surveyed was compared using catch per unit effort (CPUE) estimates as proxies for density and was calculated as:

$$CPUE = \frac{\#\,of\,lobsters\,captured}{(\#\,of\,divers)(total\,search\,time\,(min.))}.$$

The association between lobster abundance (CPUE) and patch reef area and volume (i.e., area*rugosity) on all of the surveyed reefs was examined using Pearson correlation. On the six patch reefs where we conducted mark-recapture studies, we used a Jolly–Seber mark-recapture analysis to calculate population size, addition, and loss. Other studies of *P. guttatus* movement on reefs (Lozano-Alvarez et al., 2002) confirm the random local mixing of lobsters and our laboratory studies (see above) revealed no tag effects on growth or survival, satisfying assumptions of the mark-recapture method. We evaluated whether post-settlement population loss (mortality and emigration) and population addition (immigration) were equal across reef sizes by using a linear regression to examine the relationship between these population parameters and reef area and volume. To test for differences in lobster growth among reefs, we ran separate multiple regressions for male and female lobsters with reef area (volume) and lobster size as independent variables and growth as the dependent variable.

2.4.2. Population size structure

We tested the hypothesis that population size structure is more variable among small reefs than among large reefs using two different analyses. First we examined whether the variability of parameters that describe population size structure (mean, variance, skewness, and kurtosis) differed among reefs of three sizes (0–2000 m^2, 2000–

4000 m², 4000–8000 m²). The reef size categories were chosen arbitrarily based on an equal division of the reefs that we sampled. The parameters describing population size structure were calculated separately for males and females. This analysis was performed using a 1-factor (reef area) fixed-effect MANOVA. Second, we examined the size distribution of lobsters on each reef using a Shapiro–Wilk test of normality; both sexes were examined separately. We then used the p-values from the Shapiro–Wilk test to run a Kruskal–Wallis test for each sex to determine if size distribution varied among reefs of different sizes.

2.4.3. Reproductive dynamics

We conducted several analyses to examine whether population structure and reproductive success varied with patch reef size, particularly on small patch reefs where Allee effects might be expected. To determine if overall mate availability varied by reef size, we calculated the operational sex ratio (OSR) on each reef that we studied. The OSR was calculated using the values of size-at-maturity previously determined for male and female *P. guttatus* (Robertson and Butler, 2003). Values over 50% indicate that the population has more mature males than females. The relationship between fecundity and female size was determined using a non-linear regression on data from all reef sites. We also calculated the *per capita* number of eggs per clutch for each reef population by summing all of the fecundity values and dividing by the number of females with eggs in the population. Only the fecundity values collected during the peak reproductive period (March–June) were used in this calculation because at other times few or no females are reproductive. To determine if *per capita* fecundity varied more on small reefs than large reefs as predicted, we used Levene's test of equality of variances to determine if *per capita* fecundity varied significantly among the three size classes of patch reef.

Finally, we ran an additional set of analyses to determine if the greater variance in fecundity on smaller reefs with odd lobster size distributions was due to Allee effects (i.e., the expected sperm limitation of large female fecundity), or simply due to greater variance in female size on small patch reefs. To do so, we separated the effect of female size on fecundity from any remaining effect associated with reef size. First, we ran two regressions of female size versus fecundity; one for "large" females and one for "small" females. The cutoff for large versus small females was determined by the size at which our mating studies show that sperm limitation occurs (Robertson, 2001). Then, we plotted the residuals from the above regressions for large and small females versus reef area. If an Allee effect is present and operating primarily on large females in which sperm limitation of fertilization is most likely, we expected that residuals for large females would often be lower than average (i.e., <0) on small patch reefs. We expected no relationship between the residuals of small female fecundity and patch reef size.

3. Results

3.1. Population abundance and dynamics

We captured a total of 1235 lobsters during both the population surveys and the mark-recapture experiments and tagged 576 individuals, 272 males, and 304 females during the mark-recapture experiments. Based on size at first capture we recaptured 53 females (11 small, 22 medium, 20 large) and 46 males (15 small, 14 medium, 17 large). These numbers do not reflect multiple recaptures of which we had several, including one male initially tagged in 1997 at 31.6 mm CL and recaptured a third time in 2000 at 60.0 mm CL on a reef 2025 m² in size. The abundance of *P. guttatus*, estimated from both CPUE and Jolly–Seber techniques, was greater on patch reefs of greater area and volume (Fig. 2). The CPUE of lobster and reef area were positively correlated ($r = 0.66$, $p \leq 0.0001$), as were Jolly–Seber estimates of lobster abundance and reef area ($r = 0.515$, $p = 0.041$). The average density was

higher on smaller sites for both mark-recapture sites and population survey sites. The range of densities based on average Jolly–Seber population sizes was 25.41 to 1.06 per 100 m² of reef and based on CPUE was 0.25 to 0.0083 lobsters per 100 m² of reef. The density by area and volume was not significantly correlated for the mark-recapture sites ($r = -0.472$, $p = 0.345$ and $r = -0.356$, $p = 0.488$). However, for the population survey sites the density was significantly higher at smaller reef sizes and volumes ($r = -0.55$, $p = 0.005$ and $r = -0.53$, $p = 0.008$). Recapture rates were similar among patch reefs of different sizes ($r = -0.376$, $p = 0.085$). Approximately 36.1% of the tagged lobsters were recaptured from the study sites in 1996 (Table 1), whereas 21.3% were recaptured during the 1997–2000 study (Table 2), probably because of the change in sampling frequency (once a month in the short-term study to several times per year in the long-term study). In 1996, the average estimated survival rate for *P. guttatus* was 0.757 (S.E. = 0.1403), and the percentage of lobsters recaptured during each sample period ranged from 13% to 80%. The Jolly–Seber estimate of survival (1 − mortality + emigration) was not significantly different among the sites ($F = 0.388$, $df = 5$, $p = 0.849$) and was not related to reef size ($R^2 = 0.39$, $F = 1.89$, $p = 0.26$). Population addition (births + immigration) was also unrelated to reef size ($R^2 = 0.60$, $F = 4.44$, $p = 0.13$). The average Jolly–Seber based survival probability and population addition estimates for the mark-recapture sites studied in 1997–2000 were 0.67 and 117.6, respectively. Residence times for individual lobsters at the long-term study sites ranged from 42 to 804 days. In fact, six lobsters tagged on different reef sites remained for over 500 days on the patch reef on which they were originally tagged. None of the 576 lobsters that we tagged moved among patch reefs, even those patch reefs separated by only 50 m.

Growth of *P. guttatus* varies significantly with size and sex (Robertson and Butler, 2003), so we used a multiple regression to estimate the possible effect of reef size on lobster growth, independent of lobster size or sex. Although the two multiple regressions (one for males, the other for females) relating growth (dependent variable) to reef area and lobster size were significant, the relationship was almost entirely due to the relationship between size and growth (male: $R^2 = 0.88$, $F = 49.245$, $df = 2$, $p \leq 0.0001$; female: $R^2 = 0.72$, $F = 27.534$, $df = 2$, $p \leq 0.0001$). Growth of male and female *P. guttatus* was not related to reef area, as is demonstrated by the magnitude of the standardized coefficients for reef area (male: $\beta = -0.010$; female: $\beta = 0.081$), and by the non-significant *t*-test results for those coefficients (male: $t = 0.086$, $df = 2$, $p \leq 0.933$; female: $t = 0.666$, $df = 2$, $p \leq 0.512$). Our mark-recapture results indicate that post-settlement population dynamics (growth, mortality/emigration, immigration) did not vary significantly among reefs of varying size. Therefore, it is unlikely that they would have systematically confounded the relationship between reef size and lobster population structure or reproductive success.

3.2. Population structure

Jolly–Seber population estimates from the mark-recapture experiments indicated that population sizes of *P. guttatus* on the different patch reefs varied considerably from 12 to 690 lobsters per reef site (0.35 to 7.7 lobsters per 100 m²). Furthermore, both the abundance and size structure of *P. guttatus* populations changed with reef size as predicted. The results of the MANOVA confirmed that the size structure of male and female *P. guttatus* populations varied significantly among reefs of different sizes. Following the MANOVA, inspection of the results of univariate ANOVAs testing the independent contribution of different population parameters on the multivariate results indicate that the skewness of male lobster size frequency distributions and the variance of female lobster size frequency distributions varied most among reefs of different sizes. The results of the Kruskal–Wallis test further confirm that the size distribution of male lobsters varied significantly among different size reefs ($H = 7.27$, $df = 2$, $p = 0.026$). Specifically, male size
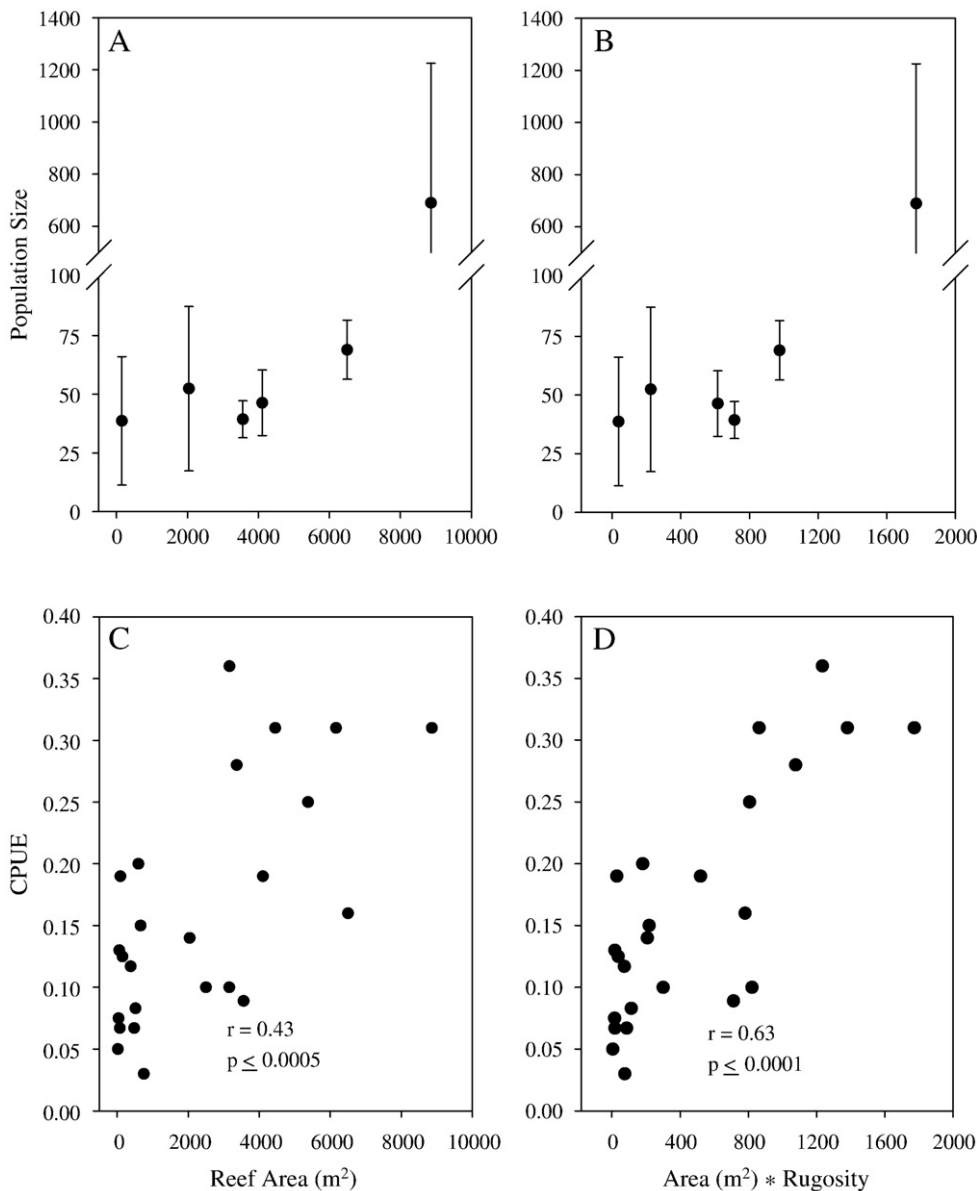
Fig. 2. The abundance of *Panulirus guttatus* in relation to patch reef characteristics in the Florida Keys, Florida (USA). Graphs (A) and (B) show Jolly–Seber estimates of population size (± 1 se) as a function of reef area and reef volume (area*rugosity). Graphs (C) and (D) are catch per unit effort (CPUE) estimates of lobster abundance as a function of reef area and reef volume (area*rugosity).

distributions on large and small reefs were different: the large reefs harbored male lobsters of all sizes, whereas many of the small reefs had no large males. Female size distributions did not differ significantly with reef size ($H = 2.87$, $df = 2$, $p = 0.238$).

3.3. Reproductive dynamics

Operational sex ratio (OSR) and reef area were not significantly related ($R^2 < 0.01$, $p = 0.972$): 73% of the *P. guttatus* populations on reefs had OSR values between 40 and 60% suggesting that reproductively competent males and females were more or less equally abundant. Reproductive activity (i.e., evidence of mating) varied among months with a peak between March and June and was similar across all lobster size classes. As expected, fecundity scaled non-linearly with female size ($F = 587.01$, $df = 1$, $p \le 0.0001$, $R^2 = 0.84$) (Fig. 3), confirming that large

Table 1
Mean Jolly–Seber population estimates for short-term mark-recapture sites.

Patch size (m²)	% Recaptured	Mean Jolly–Seber population estimates		
		Population size	Survival	Population addition
3462.80	49.8	25.2	0.82	4.9
3560.80	25	12.4	0.52	0
6500.00	20	147.3	1	0

Table 2
Mean Jolly–Seber population estimates for long-term mark-recapture sites.

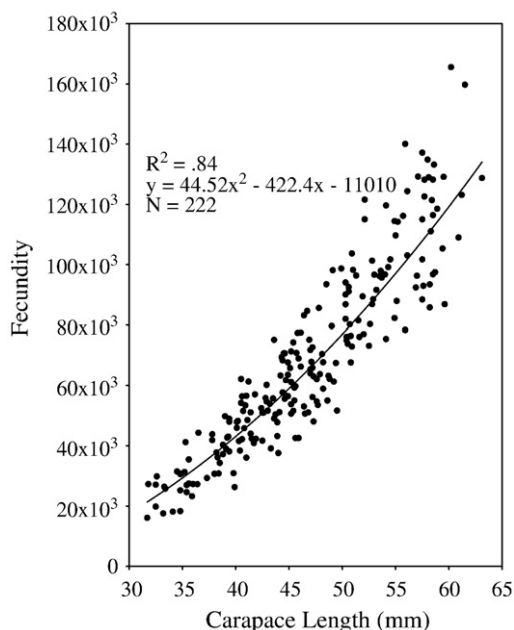| Patch size (m²)	% Recaptured	Mean Jolly–Seber population estimates		
		Population size	Survival	Population addition
152.1	16.3	39	0.57	2
1884.80	32.0	52.4	0.635	0
3462.80	32.1	30.6	0.63	28.1
3560.8	15.2	32.2	0.65	20.3
6500	21.2	69	0.63	33.2
8860.50	4.7	690	1	1070.3

Fig. 3. The relationship between female carapace length and number of eggs produced per clutch for *Panulirus guttatus*.

females produce more eggs per clutch. The individual reproductive success of female *P. guttatus* (*per capita* production of eggs per clutch) did not vary significantly with reef size ($R^2 = 0.0301$, $F = 0.5595$, $p = 0.4641$; Fig. 4). However, variability in lobster reproductive success was inversely related to reef size and significantly more variable among small reefs (i.e., those <2000 m^2 in area) than among large reefs ($F = 4.68$, $df = 2$, $p = 0.025$) (Fig. 4) — a key result indicative of an Allee effect.

If the greater variance in fecundity that we observed on small reefs (Fig. 4) is due primarily to Allee effects, caused by sperm limitation of reproductive success in large females without access to large males, then the fecundity of large females should often be lower on small
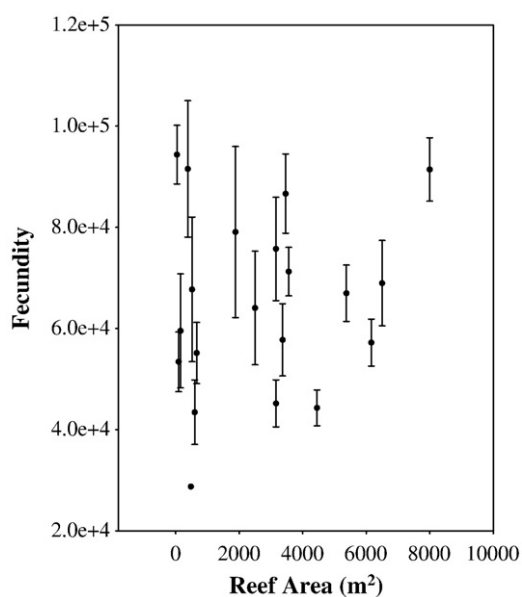
patch reefs than on large reefs. Also, there should be little or no effect on the fecundity of small females because even small males can provide them with ample sperm for fertilization. The residuals from regressions of female size versus fecundity, when plotted versus patch size, are indeed more variable for large females than small females (Fig. 5). Unfortunately, there were few large females on small patch reefs, but the fecundity of three of those four large females (75%) was lower than average (Fig. 5). These findings are consistent with our hypothesis that size-dependent mate choice combined with small local populations on small patch reefs, often results in mismatched matings and sperm limitation of fecundity in large female *P. guttatus*.

4. Discussion

Our results provide a compelling example of how the size of isolated habitat patches can influence not only the abundance of species occupying them, but also the size structure and reproductive success of those populations. We found that *P. guttatus* populations were larger and had less variable size distributions on large coral patch reefs than on small reefs. In contrast, *P. guttatus* were less abundant on small reefs where the size structure on any particular reef was highly variable. Mating is size-dependent in this species so *per capita* reproductive success was also significantly more variable on small reefs, particularly among large females that are most susceptible to diminished fertilization success due to sperm limitation when large males are absent or rare. This is a dramatic example of an Allee effect, but for reasons unlike most other documented cases in the marine realm.
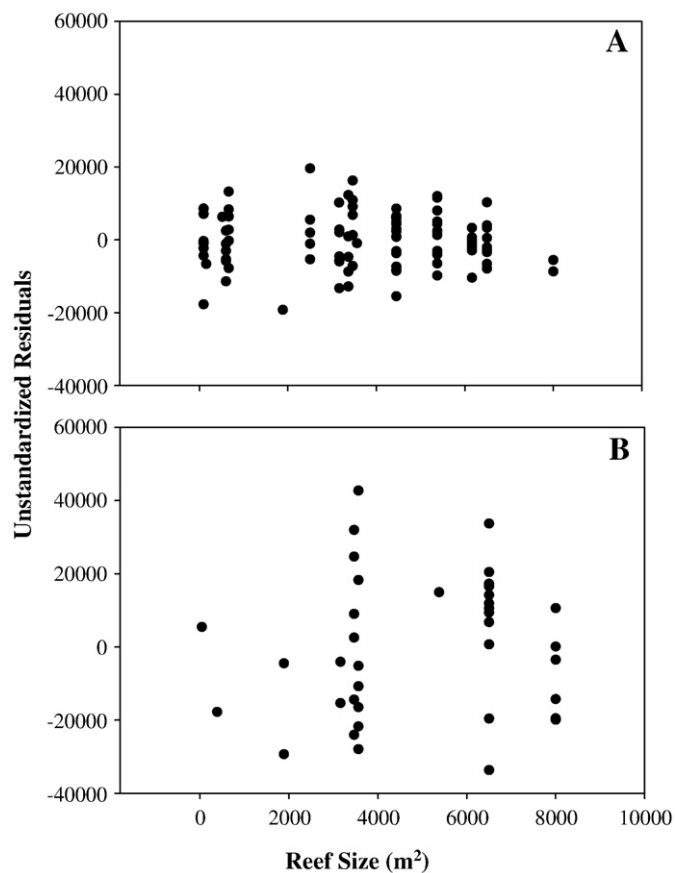

Fig. 4. The fecundity (mean *per capita* eggs per clutch +1 se) of female *Panulirus guttatus* on patch reefs of varying area (m^2).

Fig. 5. Residuals from regression analyses of fecundity by female size. Graph (A) are data for small females (30–45 mm CL) and Graph (B) for large females (55 + mm CL). The residuals are plotted against reef area to explore whether Allee effects (i.e., a preponderance of residuals <0) are present. Allee effects were expected on small reefs and primarily among large females that are most subject to sperm limitation of fertilization success.

Prior to this study, perhaps the best marine examples of Allee effects came from studies of slow moving, free spawning organisms like urchins and abalone where Allee effects are driven primarily by density-dependent fertilization success (Levitan, 1991; Pfister and Bradbury, 1996; Claereboudt, 1999; Baker and Tyler, 2001). Our results extend evidence for Allee effects to a motile marine species with complex mating dynamics whose isolation and small population size is dictated more by habitat structure, than its mobility. In this circumstance, the effect of density _per se_ is not the crucial element determining whether Allee effects are manifested or not. Instead, it is the abundance of appropriately sized mates per patch that is key. Spiny lobsters must couple to mate and they often do so based on relative size relationships, which ensures fertilization success in a mating system where a single male fertilizes a clutch of eggs and sperm is often limited (MacDiarmid and Butler 1999; MacDiarmid and St. Marie, 2006). Spiny lobsters are social and use chemical cues to quickly locate conspecifics for defensive aggregation and mating (Zimmer-Faust et al., 1985; Ratchford and Eggleston, 1998; Butler et al., 1999; Nevitt et al., 2000; Childress and Herrnkind, 2001; Raethke et al., 2004). Thus, on patches of the size we studied, lobsters could easily locate and interact with all other lobsters in the patch in a single night. For species without similar mobility, sensory capabilities, or size-dependent mating systems (e.g., abalone, urchins), population density is indeed critical for fertilization success, but our results show that density alone is not a prerequisite for Allee effects. Small populations with unusual size structures can produce the same effect (i.e., lower reproductive success) when reproductive success is size-dependent, habitats are patchy, and local populations are replenished primarily by larval recruitment.

All spiny lobsters produce pelagic larvae with long PLDs (4–24 mo) that disperse beyond their natal reefs to settle (Phillips et al., 2006). Although we and others (Sharp et al., 1997) have on rare occasions observed recently settled postlarval and early benthic juvenile _P. guttatus_ on coral reefs, no one has yet devised a method to monitor their settlement as has been done for other species of spiny lobster (Phillips and Booth, 1994). Thus, in this study we could not directly measure rates of settlement on large and small patch reefs to confirm the target-area hypothesis predictions. Namely, that small habitat patches whose populations are derived from planktonic settlement are likely to receive fewer recruits and thus be more subject to sampling artifacts than large patches.

In lieu of direct observations of settlement patterns, we assessed the population effects established at settlement indirectly with mark-recapture studies in which we estimated post-settlement population addition (recruitment, immigration), population loss (mortality, emigration), and growth of juvenile and adult _P. guttatus_ and compared those among patch reefs of different sizes. We reasoned that if post-settlement dynamics are independent of reef size, then population size structure patterns established at settlement would generally be preserved in the size structure of the resultant lobster population. The population dynamics of _P. guttatus_ did not differ with patch size in our study. Thus, we surmise that the larger, more evenly distributed population size structures of _P. guttatus_ on large patch reefs is due to more consistent larval settlement on large patches than on small ones, which is consistent with the target-area hypothesis.

Size-selective fishing is another process that can alter the size distributions of targeted species. However, these effects are not applicable in the Florida Keys as there is no fishery for _P. guttatus_. It is also hard to conceive of a scenario whereby fishing would differentially affect size distributions more on small than large reefs. Population size structure may also be influenced by the availability of appropriately scaled shelters where predation is a significant source of mortality (Beck, 1997; Kuhlmann and Walker, 1999; Eggleston et al., 1997). However, we found no relationship between reef size and rugosity (a measure of the 3D structure of the reef that roughly equates to crevice availability). Furthermore, populations of _P. guttatus_ on smaller, less rugose sites with potentially fewer shelters were not skewed toward smaller sizes, as would be expected under this scenario.

We also found no differences in estimates of population loss or addition associated with reef area that might suggest high or differential rates of adult lobster dispersal from reefs. Indeed, we recovered many tagged lobsters given the long time interval between sampling events and all marked lobsters were recovered on the same patch reef where they were initially tagged. Such results may appear incongruous for motile taxa like spiny lobsters. Indeed, many species of spiny lobster are highly mobile and exhibit complex patterns of movement associated with season and reproduction (reviewed in Butler et al., 2005) — but not _P. guttatus_. It is a reef obligate and rarely ventures off the reef, which is why we chose it as a model organism for this study. Along with our study, there are two other published studies on the movement of this species (one from Florida and one from Mexico; Sharp et al., 1997; Lozano-Alvarez et al., 2002) and all three studies report that _P. guttatus_ remain on reefs and do not venture off of them.

The key finding of our study relative to Allee effects is that the _per capita_ fecundity of female lobsters was more variable among small reefs than large reefs. In addition, an analysis of the residuals of fecundity versus female size and patch area showed that this variability is linked not only to female size, but to the size of the patch (Fig. 5). We attribute this to the fact that adult male lobster size distributions were significantly different on small versus large reefs. Indeed, operational sex ratio (based on the abundance of mature males and females) varied little with reef size, and was nearly uniform (OSR~50%) for most reefs. This suggests that the availability of mates _per se_ does not limit reproductive success — it is the availability mates of an appropriate size that is critical, as is the case generally for lobsters and decapod crustaceans (reviewed in MacDiarmid and St. Marie, 2006). For example, there were no large males (>55 mm CL) on several of the small reefs we studied, whereas large males were present on all of the large reefs (>4000 m^2). Thus, discrepancies in male and female sizes on small reefs presumably altered mate choice dynamics and thus egg production because both are size-dependent processes. Fecundity increases with size in female _P. guttatus_ (Fig. 3) (Chitty, 1973; Briones-Fourzan and Contreras-Ortiz, 1999; Robertson, 2001), but small males (<45 mm CL) produce less sperm than large males and are unable to fertilize an entire clutch of eggs produced by a large female (>55 mm CL) (Robertson, 2001). Therefore, sperm limitation in large females is more likely to arise on small patch reefs where size structure is more variable, as we have shown. Although we found relatively few large females on small reefs, it is notable that the fecundity of 75% of those large females (3 of 4) was lower than expected. This is consistent with our hypothesis that episodic recruitment into small habitat patches can create odd adult size distributions, which disrupts normal mate choice and reproductive success.

Allee effects can contribute to local population instability and extinction by decreasing individual reproductive success or by increasing its variance in small populations (Stephens et al., 1999). Yet, the potential role of Allee effects on local population stability and persistence within marine metapopulations has received relatively little attention. Metapopulation theory (Levins, 1970) suggests that populations on large habitat islands or patches are more stable, while smaller habitat patches support populations that more frequently undergo local extinction (Hanski and Gilpin, 1991). In marine systems, extinction and recolonization of local populations are generally viewed as a direct consequence of the episodic delivery of new larval recruits into suitable habitat patches. That is, periodic failures in recruitment into small habitat patches and the subsequent crash of the local population are primarily associated with the vagaries of oceanic transport of larvae (Lipicius et al., 1997; Botsford, 2001; Armsworth, 2002; Wing et al., 2003). Thus, physical factors associated with ocean currents exogenous to the population, rather than attributes of the local populations themselves, are viewed as a primary mechanism governing the extinction of local populations.

However, if habitats become increasingly fragmented and populations isolated on smaller and smaller patches, reproductive success may diminish or become more variable as our results suggest. Increased variance in the reproductive success of populations, particularly during periods of low population abundance as is now evident in marine species worldwide (Hoegh-Guldberg et al., 2006; Worm et al., 2007), is not conducive to the long-term sustainability of the species.

In summary, our results indicate that habitat patch size and the potential for Allee effects are particularly critical for species whose reproductive success depends not only on mate availability, but also mate size. Conservation strategies for species, that exhibit these characteristics must consider not only the management of adults and the factors that contribute to larval retention (e.g., hydrodynamics, larval behavior), but also the relative distribution of the population among habitat patches of varying size if the long-term persistence of local populations is to be ensured.

Acknowledgements

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