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High population density enhances recruitment and survival of a harvested coral reef fish

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ABSTRACT

A negative relationship between population growth and population density (direct density dependence) is necessary for population regulation and is assumed in most models of harvested populations. Experimental tests for density dependence are lacking for large-bodied, harvested fish because of the difficulty of manipulating population density over large areas. We studied a harvested coral reef fish, *Lutjanus apodus* (schoolmaster snapper) using eight large isolated natural reefs (0.4-1.6 ha) in the Bahamas as replicates. An initial observational test for density dependence was followed by a manipulation of population density. The manipulation weakened an association between density and shelter-providing habitat features, and revealed a positive effect of population density on recruitment and survival (inverse density dependence), but no effect of density on somatic growth. The snappers on an individual reef were organized into a few shoals, and we hypothesize that large shoals on high-density reefs were less vulnerable to large piscivores (groupers and barracudas) than the small shoals on low-density reefs. Reductions in predation risk for individuals in large social groups are well documented but, because snapper shoals occupied reefs the size of small marine reserves, these ecological interactions may influence the outcome of management actions.

KEYWORDS: coral reef fish, critical habitat, demographic rate, density dependence, inverse density dependence, large-scale experiment, marine protected area, recruitment, survival.
INTRODUCTION

Density dependence is central to population dynamics and is required for population regulation (Murdoch 1994). Most models for harvested populations assume that per-capita population growth rates will increase when and where harvesting reduces population density by increases in rates of growth, reproductive output, or survival (Sissenwine 1984, Rose et al. 2001). This direct density-dependent feedback is expected because unharvested populations are assumed to be at their carrying capacity set by limited resources (Rose et al. 2001). This assumption may, however, be false in situations where unharvested populations are kept below carrying capacity by predators, disturbance, or changing environmental conditions.

Evidence for direct density dependence in harvested marine species is limited because testing is difficult for several reasons. Firstly, many stocks have been so depleted that there are simply no high-density populations to study (Myers and Cadigan 1993). Secondly, it is sometimes difficult to isolate effects of density using observational studies because population density often covaries with other variables (Shima and Osenberg 2003). For example, animals tend to select better quality habitats and so they are often naturally more crowded in better quality habitat. Experimental manipulation of population density can mitigate these difficulties, but it is logistically challenging with harvested species, and so has only been done using small juveniles (reviewed in White et al. 2010). In contrast, density-manipulations have been performed many times using small-bodied reef fishes because they are abundant, have small home ranges, and can be stocked on small experimental habitat replicates to create gradients of density (Hixon and Webster 2002, Osenberg et al. 2002). It is hoped that insights into density dependence learned from these “model species” apply to larger harvested species that are more difficult to work with, but there is no empirical basis to conclude that they do.
Studies on “model species”, like small coral-reef fishes, have revealed that direct
density dependence is common (Hixon and Webster 2002), but not universal. Some studies
have revealed no effects of density (e.g., Doherty 1983), and others have revealed inverse
density dependence (e.g., Booth 1995, Sandin and Pacala 2005, White and Warner 2007).
White et al. (2010) hypothesized that inverse density dependence was more likely in
schooling species, which benefit from group living, whereas direct density dependence might
be more prevalent in solitary species. Extrapolating to harvested fishes, we might expect that
species living in schools are more likely to experience inverse density dependence (Clark
1974, Murphy 1980).

Because density-dependent interactions determine how populations respond to
thinning or crowding, a better understanding of their effects is necessary for successful
management and conservation. For example, the relative efficacy of marine reserves versus
more traditional fisheries regulations in maximizing harvest hinges on the form and intensity
of density dependence (Hastings and Botsford 1999). The crowding that follows the build-up
of harvested fish populations within no-take reserves (Halpern 2003, Lester et al. 2009) is
predicted to induce direct density dependence (Sanchez Lizaso et al. 2000), which in turn
should decrease the fisheries yield from reserves via the export of young to fished areas
(Hastings and Botsford 1999, Gerber et al. 2003). If, instead, the steady build-up inside
reserves leads to increased survival or reproductive rates (inverse density dependence) this
may increase fisheries production in surrounding areas through reproductive export. With
inverse density dependence, a network of marine reserves might produce higher overall
yields than more traditional management tools, such as catch limits.

Here we report the results of an observational test for density dependence in a
harvested coral reef fish, followed immediately by a field manipulation of population density.
We used a set of large isolated natural reefs as replicates, each of which was comparable in
size to a small marine reserve. By working in a lightly fished area, we were able to create a
gradient of density that spanned most of the natural range for the study species. Specifically,
our goals were to (1) perform a correlational test for density dependence under natural
conditions, 2) test the relationship between density and habitat attributes, and 3) manipulate
density to reduce its correlation with habitat attributes to get a stronger test for density
dependence.

METHODS

Study populations

The study species, *Lutjanus apodus* Walbaum (the schoolmaster snapper) is one of the
most abundant large generalist carnivores on reefs in the Caribbean and subtropical Atlantic.
*L. apodus* is harvested from coral reefs throughout the region (Anderson 2002) and is found
in schools of several to hundreds of individuals. We studied populations of *L. apodus* on 8
natural reefs in the Bahamas (23°46’ N, 76°10’ W) that were spread over a 25-km long area
and sufficiently isolated to serve as natural replicates (Appendix A). Each study reef was
separated from other suitable habitat for *L. apodus* by at least hundreds of meters of sand
plains or seagrass beds, and from other study reefs by 1 – 6 km (Appendix A). Other small
fragments of suitable back-reef habitat existed in the study area, but our study sites contained
the largest expanses and the majority of suitable habitat for *L. apodus* in the area. Individual
reefs contained between 0.4 and 1.6 hectares of suitable habitat for our study species, and so
were comparable in size to small marine reserves (IUCN and UNEP 2010). The study reefs
were all back reefs in shallow water (1-10 m), and were primarily composed of coral heads,
soft corals and sponges on sand, rubble or pavement substrata. They ranged in shape from
rings of reef habitat surrounding small islands, to long, isolated patch reefs, to large expanses
of reef off the shores of islands. The study populations are fished infrequently, because human population densities are low in this area and fishers still target higher value fisheries for conch, lobster and Nassau grouper, which are no longer viable in much of the Caribbean (Chiappone et al. 2000).

Study design

Our study was conducted in two phases: an observational phase and an experimental phase. The 2-year observational phase (June 2002 – June 2004) mimicked the typical design of tests for density dependence in harvested species. In the third year (July 2004 – August 2005), densities of L. apodus were manipulated to provide a stronger test of density-dependent feedbacks (detailed below). During both phases, survival and growth were measured by standard mark-recapture methods (described later). Recruitment was measured with underwater visual censuses (described below) only during the experimental phase. We tested for density dependence by correlating per-capita vital rates (survival, recruitment and somatic growth) with spatio-temporal fluctuations in snapper density.

Estimating population density of L. apodus

Population density and size structure (standard length (SL)) of L. apodus, were assessed by underwater visual census along 3–7 permanent 50 x 10 m band transects at each site. Transects were counted by a single observer (the first author) on 18 occasions between June 2002 and August 2005. A pilot study showed that underwater visual estimates of fish length were quite accurate. The first author visually estimated the SL of individually recognizable (externally tagged) L. apodus during a census and the same fish were then captured and measured. The mean difference between estimated and actual SL was 0.7 cm, and paired measurements were statistically indistinguishable (paired t-test, n = 44, t = 1.5, df = 43, P = 0.14; Wormald and Steele 2008).
Quantifying habitat quality

Structural attributes of the habitat were quantified to assess the influence of the physical environment on *L. apodus* density. Preliminary observations revealed that this species congregated near large coral heads or limestone boulders (lithified carbonate sediments fallen from adjacent islands). Coral and limestone boulders were distinguished because coral boulders usually include a larger number of internal voids than similarly sized limestone boulders and our observations suggested they provide more shelter space for *L. apodus*. The height, width and breadth of all coral heads and limestone boulders larger than 0.5 m in any dimension was measured on each of the permanent 50 x 10 m band transects surveyed for *L. apodus*. These habitat features were surveyed only once because they did not change perceptibly over the study period. Since we did not know beforehand which specific features of the coral heads and boulders *L. apodus* might be responding to, we evaluated a number of metrics: total number of coral and limestone boulders per m$^2$, the sum of coral and limestone boulder heights per m$^2$, sum of coral and limestone boulder volume per m$^2$, total number of coral boulders per m$^2$, sum of coral boulder heights per m$^2$, and the sum of coral boulder volume per m$^2$. Models including only limestone boulders and not coral boulders were not evaluated because limestone boulders were relatively rare and present at only 3 of the 8 sites. Each metric was related to the density of *L. apodus* using linear regression and the best metric was defined as the one that explained most variation in density (highest $r^2$ value) and had the highest model likelihood (lowest corrected Akaike Information Criterion (AICc) value; Burnham and Anderson 2002).

Recruitment to the study reefs

*L. apodus* juveniles occupy mangroves and shallow inshore areas nursery areas before recruiting to coral reefs. Most recruitment to the study reefs occurred between July and November and recruits are between 8-14 cm SL when they first appear (Nagelkerken et al.,
Operationally, we defined all *L. apodus* less than 14 cm SL counted during the underwater visual transects as recruits. Our analysis of recruitment used data only from 2004 and 2005 (after the density manipulation), because we did not collect data in autumn of the previous two years.

General linear models were used to test whether recruit density was a function of post-recruit (*L. apodus* ≥ 14 cm SL) density, habitat quality (coral boulder volume m$^{-2}$) or differed among years (2004 and 2005). Site means each year were replicates for the analysis (8 sites x 2 years; *n* = 16). Different combinations of independent variables were tested, and the best model was chosen based on relative model likelihood (AICc values) and variance explained (*r*² values).

**Mark-recapture sampling for growth and survival**

Capture-mark-recapture (CMR) methods were used to measure growth and estimate survival throughout the study (Lebreton et al. 1992). Twelve CMR sessions were conducted between June 2002 and August 2005, each lasting between 1 and 4 weeks. During each session, fish were sampled using unbaited 2.5-cm square-mesh fish traps with a 24-hour soak time and all *L. apodus* captured were given unique passive integrated transponder (PIT) tags (12 mm, 125kHz; Allflex USA Inc., Dallas, Texas). Captured *L. apodus* were first anaesthetized in a 200 mg/L solution of tricane methanesulfonate (MS-222) in seawater buffered with sodium bicarbonate. Once anaesthetized, they were measured (SL) and scanned for a PIT tag. A PIT tag was injected into the abdominal cavity of all untagged fish. In a previous double-tagging study (*n* = 376), PIT tag loss was < 6% in the first week and 0% in the subsequent year, so we assumed loss of PIT tags was negligible (Wormald and Steele 2008). After processing, each fish was placed into a holding tank with fresh seawater for 10 to 20 minutes. The fish were then released by placing them in an opened trap near a coral head at the capture site. This method was developed during a 2001 pilot study and, based on
our observations, ensured that *L. apodus* were able to safely rejoin their school upon release.

A total of 1,863 *L. apodus* were tagged, ranging in size from 10-40 cm SL. Seven hundred and sixty nine individuals were recaptured at least once, and the interval between recaptures ranged from 1-809 days.

Experimental phase: density manipulation

In the initial observational phase of the study, *L. apodus* populations were denser at sites with abundant shelter (Fig. 1) so we manipulated population densities to reduce the correlation between fish density and habitat. The 8 study sites were divided into 4 pairs that had similar densities and habitat characteristics. One member of each pair was randomly assigned for reduction of density and the other for density-elevation (Appendix A). We moved fish from reduction to elevation reefs 4 times over a span of 12 months to maintain differences between the treatments (a press manipulation, sensu Bender et al. 1994).

Fish were moved among reefs during trapping sessions. At reduced density sites, a subset of captured *L. apodus* was haphazardly selected for relocation. Selected fish were placed in holding tanks in the boat and driven to the designated density-elevation reef. At the elevation reef, the fish were placed in a closed fish trap near to coral heads harboring other schoolmasters and allowed to acclimate for 20 minutes before being released by a freediver. In a separate analysis, we detected no difference in growth and survival of PIT tagged fish that were relocated from those remaining at their home site (Wormald 2007).

Based on the 18 underwater visual censuses (7 before the manipulation and 11 after it), we succeeded in altering densities at the study sites, as indicated by a significant interaction between treatment (density elevation or reduction) and time period (pre- or post-manipulation) (ANOVA: $F_{1,123} = 19.92, P<0.001$) (Appendix B); and in weakening the correlation between density and habitat attributes (Fig. 1).
Estimating somatic growth rates

Growth was estimated using PIT tagged individuals that were recaptured at least once. Daily growth was calculated as the change in SL divided by the number of days at liberty. To test the precision of SL measurements made in the boat, we compared repeated measurements of fish recaptured after less than 7 days at liberty (based on the conservative assumption that, over such a short time, differences reflect only measurement error). Repeated measurements of the same fish differed by 0.14 cm SL on average ($n = 61$). To minimize the influence of this slight measurement error, we only analyzed growth for individuals at liberty for more than 38 days (mean growth after 38 days = 0.37 cm). Growth estimates were obtained from 299 individuals in the pre-manipulation period and 187 in the post-manipulation period. For individuals recaptured more than once, we used a single growth estimate derived from the change in length over the longest at-liberty span. Average growth was 1.66 cm, considerably more than our measurement error.

To test the effect of density on growth rate, it was necessary to correct for the effect of a fish’s initial size on its daily growth rate because growth declined with size. To remove this effect of size, rather than analyze absolute growth in mm/day, we used residuals from the relationship between daily growth and initial size. These residuals were not normally distributed and so to meet this assumption they were log transformed (after adding 0.002 to each residual to make them all positive). We used linear regression to test for an effect of density and habitat (coral boulder volume m$^2$) on growth rate. Separate regressions were run for the pre- and post-density manipulation periods, and mean growth rates per reef were used as replicates ($n = 8$ per period). We tested models that included terms for adult density, habitat, and both factors.
Estimating survival rates

Per-capita rates of apparent survival ($\Phi$) were estimated using the recapture histories of the 1863 PIT-tagged fish (Lebreton et al. 1992). We refer to $\Phi$ as apparent survival, since the permanent disappearance of tagged fish could represent either mortality or emigration.

Because there were 12 recapture sessions and some fish were recaptured more than once (maximum = 9 recaptures), we were able to model both $\Phi$ and the probability that a fish would be captured if present ($p$) using the Cormack-Jolly-Seber (CJS) model (White and Burnham 1999). The time step for the CJS models was one month (i.e., $\Phi$ and $p$ are probabilities measured over 30 days).

The CJS model assumes $p$ is a function of site and time. Preliminary modeling of recapture histories revealed that $L. apodus$ captured in the preceding trapping session had a slightly higher capture probability in the next session than other individuals (i.e., they were “trap-happy”) (Wormald and Steele 2008). To account for this bias in capture probability, $p$ was modeled as a function of $m$ (whether a fish was captured in the preceding session) (following Pradel 1993). Tests of model fit showed that $p$ was well described as an additive function of site, time, and $m$ (Wormald 2007); and $p$ was modeled as such in all analyses of factors affecting $\Phi$.

We assessed effects of density and habitat on $\Phi$ over the entire study period by constructing a candidate set of plausible CJS models for $\Phi$ that incorporated different combinations of covariates (density and habitat) plus relevant grouping variables (site and time). Relative fit of the models to the data was assessed using AICc, which is particularly useful when comparing models with varying numbers of parameters because it reflects both model fit to the data and simplicity (few parameters) (Burnham and Anderson 2002).
RESULTS

During the initial observational phase, the density of *L. apodus* was positively associated with various metrics quantifying the availability of large coral boulders on a reef (Fig. 1, Appendix C). The volume of coral boulders per m² was a slightly better predictor of *L. apodus* density than either the height or number of boulders per m², suggesting that *L. apodus* responds to the three-dimensional structure of the corals (Appendix C). Coral boulders were common at all 8 sites, whereas terrigenous limestone boulders occurred at only 3 sites and were relatively rare. Adding the availability of limestone boulders to regression models for *L. apodus* density always weakened the prediction (lower $r^2$, Appendix C). *L. apodus* was thus more strongly associated with coral boulders, which contain internal voids suitable as shelter, than with terrigenous solid limestone boulders. Our manipulation of density succeeded in weakening the relationship between habitat (coral boulders) and density (Fig. 1), and broadened the range of *L. apodus* densities on the reefs to span the range reported throughout the Caribbean (Appendix B, Appendix D). The manipulation was thus successful in creating a stronger test of the effect of density, and isolating the relative effects of density and habitat.

Recruitment of small *L. apodus* (< 14 cm SL) after the density manipulation was positively related to the density of larger *L. apodus* ($F_{1,13} = 7.37, P = 0.018$; Fig. 2), and this relationship was consistent across the two years studied (2004 and 2005) ($F_{1,12} = 2.0, P = 0.19$). There was no compelling evidence that habitat availability (volume of coral boulders) affected recruitment (Appendix E). Models to predict recruit density that included a term for the effect of habitat in addition to, or instead of, a term for the density of larger *L. apodus* were less well supported (model likelihood 0.11 and 0.13, respectively) than the model including only density. In addition, the term for the effect of habitat was not significant in either model (model with habitat only: $F_{1,12} = 0.01, P = 0.95$; model with habitat and density $F_{1,13} = 2.82, P = 0.12$, respectively).
Growth of 486 *L. apodus* was measured over intervals from 38-809 days (mean = 214 days) and growth rates ranged from -0.01 to 0.05 cm SL/day (mean = 0.01 cm SL/day). We found no evidence that daily growth was density-dependent. Growth rates in the observational phase of the study, and after the density manipulation, were unrelated to population density, habitat (coral volume per m$^2$) or these two factors combined, ($t < 1.12, P > 0.12$) (Appendix F).

Although we cannot completely rule out the possibility that disappearance of tagged fish from the 8 study reefs was due to emigration, three observations suggest that $\Phi$ is primarily a measure of survival. First, none of the 769 recaptured PIT tagged fish moved among the 8 study sites. Second, in a pilot mark-recapture study from 2001-2002, 199 of 376 visually tagged *L. apodus* were resighted, but no resightings occurred in thorough searches of other reef habitat in the study region. Third, repeated recaptures of PIT tagged individuals at the same site over 4 years, coupled with repeated observations of other recognizable individuals (identified based on scars or other unique visual marks) suggested that site fidelity was high.

Comparison of candidate models for $\Phi$ revealed the strongest support for a model in which $\Phi$ was a simple function of density (Appendix G). The model that included only the covariate density was almost three times better supported than the model that included terms for site and time (to capture unmeasured sources of spatio-temporal variation in $\Phi$); and more than thirty times better supported than a model where $\Phi$ was constant (the simplest possible model). Substituting the term for density with a term for habitat (volume of coral boulders per m$^2$) markedly reduced model support (Appendix G). Models including terms for both habitat and density, in additive or multiplicative combinations, produced no improvements in fit over the model just containing density (Appendix G). Reconstituting estimates of $\Phi$ across a gradient of *L. apodus* density revealed that $\Phi$ increased at higher densities (i.e., was inversely
density dependent) (Fig. 3). The apparent monthly survival of *L. apodus* was thus higher at sites and/or during months when their population was dense (Fig. 3).

**DISCUSSION**

We found positive effects of conspecific density on the demography of *L. apodus*. Our density manipulation weakened the association between *L. apodus* density and habitat availability (volume of large coral boulders) with the result that, over the entire study period, spatio-temporal fluctuations in apparent survival were better described as a simple function of density than as a function of habitat availability. Model selection analysis, which rewards increased model fit but penalizes increased model complexity, indicated that the improvement in model fit by including a term for the effect of habitat was not sufficient to outweigh the “cost” of increasing model complexity. Although we routinely observed *L. apodus* congregating near coral boulders, our results suggest that any density-independent effect of this habitat feature on apparent survival is relatively weak compared to the influence of conspecific density. *L. apodus* is a long-lived fish and small, positive effects of habitat quality on survival of this species might accumulate over several years to generate the correlation between density and coral boulders that we detected.

Although we did not quantify the causes of loss of *L. apodus* during our study, we suggest predation by larger fish as a simple and plausible agent of the inversely density-dependent survival we observed. Circumstantial evidence supporting this hypothesis is as follows. Firstly, the fact that apparent survival was density-dependent, whereas somatic growth was not, is consistent with predation as the main agent of mortality rather than factors with an obvious energetic component to their effect, such as food supply or infection with pathogens. Second, although a systematic study of *L. apodus* behavior was not our intent, observations amassed over more than 3000 hours on SCUBA during the study revealed that
L. apodus were grouped into a few schools, which appeared to function as coherent social groups when avoiding or escaping attacks from barracudas and large groupers, which were the predators most frequently observed attacking L. apodus in the area. Larger predatory fishes such as reef sharks (Carcharhinus perezii) and lemon sharks (Negaprion brevirostris) though occasionally sighted on these reefs were relatively rare, as is the case in most of the Caribbean (Stallings 2009, Ward-Paige et al. 2010). Barracuda and large grouper densities at our sites were relatively lightly impacted by fishing. Although their densities were not as high as found in some marine reserves (Chiappone and Sealey 2000), they were similar to those at other lightly fished sites in the Caribbean (Appendix D), and these predatory fishes should have the potential to control L. apodus populations. The density of these predators was not correlated with density of L. apodus on the study reefs (Appendix D), which is expected because barracuda and large groupers consume a variety of fish species. Lastly, alternate mechanisms known to generate inverse density dependence are not consistent with our results. Cooperative feeding can generate inverse density dependence but is not consistent with the density-independent growth we observed (Courchamp et al. 1999). Demographic stochasticity, genetic inbreeding and reduced heterozygosity can also generate inverse density dependence in very small populations, but are unlikely to be expressed across the wide range of densities we studied (Lande 1998).

We also observed a positive association between the densities of new recruits and older individuals. One possible mechanism is recruitment facilitation, a common phenomenon in other group-living reef fishes, in which juveniles select sites with high adult density when they first colonize the reef habitat (reviewed in Hixon and Webster 2002). Alternatively, early survival of recruits (from the time of arrival at a reef to the time of census) might be inversely density-dependent, as shown for larger L. apodus.
It is well known that some vertebrates forming social groups survive better in large groups because they detect predators earlier, recognize and assess predator intent more effectively, are better able to inhibit predator attacks, or are more confusing to attacking predators than their counterparts in small groups (Pulliam 1973, Bertram 1978, Crawley 1992, Pitcher and Parrish 1993). A rich array of these social behaviors have been linked to population level dynamics for small reef fishes and other vertebrates whose behaviors are readily observable (Sutherland 1996). Recent studies have indicated that large, harvested fishes also have complex and varying social organization (Rowe and Hutchings 2003, Egli and Babcock 2004). *L. apodus* may thus be an example of a harvested species whose antipredator strategies become more effective in large groups.

Inverse density dependence expressed only at very low densities, the Allee effect, occurs in many taxa (Courchamp et al. 1999) but is rarely detected in harvested fish (Myers et al. 1995). Models of the Allee effect typically assume that per capita population growth rate is positive below a carrying capacity (set by limited resources) until density drops to a threshold, below which per capita growth becomes negative. An important implication of the Allee effect is that populations dropping below the threshold are less likely to recover, and more likely to go extinct (Dennis 1989, Lande 1998). Inverse density dependence spanning the normal density range, as observed in *L. apodus*, has been reported relatively infrequently (Courchamp et al. 1999) and has different implications for management.

Because many small, no-take reserves are similar in size to our study reefs, our results suggest that a reduction in fishing mortality within reserves should allow *L. apodus* densities to increase, which may in turn produce increased natural survival. This synergistic effect should magnify the build-up of fish within reserves beyond that expected if natural mortality is either density-independent or directly density-dependent (Sanchez Lizaso et al. 2000). Our finding of a strong correlation of density with coral boulder volume, emphasizes the need to
include high-quality habitat within reserves (e.g., Parnell et al. 2006). Ultimately, of course, the benefit to *L. apodus* of being in larger schools within reserves depends on the biological mechanism for inverse density dependence. If, as we hypothesize, interactions between *L. apodus* and their predators are the cause, reserve effects on *L. apodus* will depend on whether reserves promote recovery of top predators that consume *L. apodus* (Abrams et al. 2011). Although logistically challenging, further experimental and behavioral studies to identify the biological mechanisms creating density-dependent feedbacks will thus help predict the response of harvested fishes to alternate management actions.
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APPENDICES

Appendix A
A table and a figure showing the location and approximate size of the 8 study reefs in the central Exuma Cays, Bahamas.

Appendix B
A figure showing that the manipulation of *L. apodus* density succeeded in increasing density at density elevation sites and reducing density at density reduction sites.

Appendix C
A table showing relationships between *L. apodus* density and habitat features used as shelter.

Appendix D
A table documenting densities of *L. apodus* and two of their predators at sites throughout the Caribbean and tropical Atlantic.

Appendix E
Comparison of general linear models relating recruit density of *L. apodus* to density of older conspecifics or habitat features used as shelter.

Appendix F
A figure showing that growth in standard length was unrelated to *L. apodus* density across the natural range of densities and across a broader range of experimentally established densities.

Appendix G
A table showing mark-recapture models testing the effects of *L. apodus* density, habitat, site, and time on survival probability.
FIGURES

Fig. 1. Relationship between *L. apodus* density and coral boulder volume at $n = 8$ study sites. Mean densities (number of individuals per m$^2$ ± SE) of *L. apodus* and coral boulder volume (per m$^2$) are shown for the (a) pre-manipulation period of the study, based on 7 visual censuses between June 2002 and June 2004 ($r^2 = 0.78$, $P = 0.002$) and the (b) post-manipulation period based on 11 visual censuses from August 2004 to August 2005 ($r^2 = 0.52$, $P = 0.05$). Coral volume (per m$^2$) is based on a single survey (see Methods). The manipulation weakened the relationship between *L. apodus* density and coral volume, allowing isolation of the effects of population density and habitat quality on survival rates.

Fig. 2. Relationship between density of recruit and adult *L. apodus* (number of individuals per m$^2$ ± SE) ($r^2 = 0.34$ and $P = 0.02$) at $n = 8$ study sites. There was no significant difference in the relationship between the years 2004 (open circles) and 2005 (closed circles) (ANCOVA: $F_{1,12} = 2.0$, $P = 0.19$).

Fig. 3. Relationship between survival and density of *L. apodus*. Survival values ($\Phi$) were reconstituted from parameters estimated by Program MARK, from the model $\Phi(\text{density})$, $p(\text{site} + \text{m} + \text{time})$ fit to the recapture histories of 1863 tagged *L. apodus* (see Methods). Parameter m represents a short-term trap response in capture probability (p). Survival is the probability of survival over a one-month time period. Broken lines represent the 95% confidence interval of the survival estimate.
Fig. 1.

- (a) All sites pre-manipulation
- (b) All sites post-manipulation
Fig. 2.

Mean recruit density (m$^{-2}$) vs. Mean adult density (m$^{-2}$).
Fig. 3.