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Cover Photo: Adult bicolor damselfish (*Stegastes partitus*) on a Caribbean coral reef. An eight-year field study in the Bahamas showed that, on reefs with appropriate habitat structure, local populations of this species are regulated by density-dependent survival despite highly fluctuating recruitment (see Hixon et al., pp. 467-489). Fecundity is also density dependent in these populations, and combined mechanisms may regulate the broader marine metapopulation. Photo credit: David Nasser.

Density dependence and population regulation in marine fish: a large-scale, long-term field manipulation

MARK A. HIXON,^{1,3} TODD W. ANDERSON,^{1,4} KEVIN L. BUCH,^{2,5} DARREN W. JOHNSON,^{1,6} J. BROCK MCLEOD,^{1,7} AND
CHRISTOPHER D. STALLINGS^{1,8}

¹Department of Zoology, Oregon State University, Corvallis, Oregon 97331-2914 USA

²Perry Institute for Marine Science, Caribbean Marine Research Center, Lee Stocking Island, Bahamas

Abstract. Do small-scale experiments showing spatial density dependence in marine fishes scale-up to temporal density dependence and regulation of relatively large local populations? If so, what are the causative mechanisms and their implications? We conducted an eight-year multigeneration study of population dynamics of bicolor damselfish (*Stegastes partitus*) inhabiting four large coral reefs in the Bahamas. After a four-year baseline period, it was clear that two populations naturally received very few settlement-stage larvae, so recruitment of recently settled fish was artificially enhanced at one low-settlement reef and reduced at one high-settlement reef to ensure a broad range of population sizes over which to test for regulation. Over all eight years, populations on the two naturally high-settlement reefs experienced temporal density dependence in multiple per capita demographic rates: mortality, survival to adulthood, and fecundity. These local populations also displayed components of regulation: persistence, boundedness, and return tendency. Reefs supporting regulated populations were structurally complex, providing sufficient prey refuges that ensured high survival at low densities. In contrast, populations at low-settlement reefs experienced either density-independent or slightly inversely density-dependent demographic rates, even though recruitment was artificially augmented to high levels at one reef. There was no evidence of regulation at these reefs, and indeed, one local population suffered temporary extirpation. Here, habitat complexity was relatively low, increasing the risk of predation, especially at low population densities when fish would have to travel longer distances when finding mates or home sites inhabited by conspecifics. Among all demographic parameters, density dependence in individual growth (an indicator of within-species competition for food) was least correlated with the presence or absence of local population regulation. We conclude that, for systems like these, the environmental context of a local population, especially predation risk and the distribution and abundance of spatial refuges, is more important than the magnitude of larval supply alone in determining the existence of regulating density dependence. At the broader metapopulation scale, density dependence in both survival and fecundity exogenously caused by predation may provide regulation for the entire stock, even when endogenous within-species competition (assumed to be important in most fisheries models) is weak.

Key words: competition; coral-reef fish; fecundity; fisheries; growth; marine metapopulation; mortality; population dynamics; predation; recruitment; scaling.

INTRODUCTION

Population regulation and its underlying density-dependent mechanisms are key concepts in both

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³ E-mail: hixonm@science.oregonstate.edu

⁴ Present address: Department of Biology and Coastal & Marine Institute, San Diego State University, San Diego, California 92182-4614 USA.

⁵ Present address: Research Office, Oregon State University, Corvallis, Oregon 97331-2140 USA.

⁶ Present address: National Center for Ecological Analysis and Synthesis, Santa Barbara, California 93101 USA.

⁷ Present address: Biology Program, Oregon State University, Corvallis, Oregon 97331-2911 USA.

⁸ Present address: College of Marine Science, University of South Florida, St. Petersburg, Florida 33701-5016 USA.

conservation biology, in terms of management preventing extinctions (Morris and Doak 2002), and fisheries biology, in terms of sustaining catches (Walters and Martell 2004). Regulated populations exhibit three closely related characteristics: (1) persistence, where a population survives for many generations in the absence of a random walk, (2) boundedness, where a population remains between some upper and non-zero lower limits, and (3) return tendency, where a population decreases when above a certain size and increases when below a certain size (Murdoch 1994, Turchin 1995). In a regulated population, at least one per capita (proportional) demographic rate is directly density-dependent (e.g., the birth rate decreasing or the death rate increasing as density increases). The two possible mechanisms that cause density dependence are competition, and in special circumstances, predation, including

the threat of predation causing competition for prey refuges (review by Hixon et al. 2002). To be regulating, density dependence must operate temporally (demonstrated through time within populations, rather than merely observed among populations at the same time) in a way that causes the population growth rate to be positive at low population sizes and vice versa at high densities (Murdoch 1994, Turchin 1999, Hixon et al. 2002). In contrast, inversely density-dependent demographic rates may push a population toward extinction, a phenomenon known as the Allee effect (Courchamp et al. 1999, Stephens and Sutherland 1999).

Empirically testing for density dependence and population regulation is problematic enough in demographically closed, typically terrestrial and freshwater populations (review by Cappuccino and Price 1995). In the sea, an added challenge is that most demersal (seafloor-oriented) fish and invertebrate populations exist as "marine metapopulations," defined as spatially patchy and at least partially demographically open local populations linked by dispersal of larvae (Kritzer and Sale 2004, 2006). In local populations, recruitment of newly settled larvae is analogous to the local birth rate (Hixon et al. 2002), and such recruitment is often highly variable and typically independent of local population size (reviews by Doherty 1991, 2002, Caley et al. 1996, Houde 2009). Although per capita recruitment necessarily declines with increasing local density as new recruits accumulate through time, such quasi-density-dependent "recruitment regulation" (sensu Hughes 1990) cannot regulate entire metapopulations (Caley et al. 1996, Armsworth 2002). Rather, recruitment variability may possibly affect the presence and strength of density dependence in other demographic rates (Houde 1987, Doherty and Williams 1988, Myers 2002). Nonetheless, true density dependence in mortality and/or fecundity within substantial local populations is sufficient to regulate an entire marine metapopulation (Armsworth 2002). Thus, the search for demographically meaningful density dependence in marine fishes typically focuses on mortality and factors that affect survival, such as growth, which can also eventually translate to fecundity.

To date, there have been preciously few empirical demonstrations of population regulation in marine fishes at sufficiently large spatial and temporal scales that characterize substantial local populations. Numerous field experiments, mostly on tropical coral reefs but also including temperate rocky reefs, have demonstrated that early post-settlement mortality at small scales is typically directly density dependent, and often involves predation (reviews by Hixon and Webster 2002, Osenberg et al. 2002, Hixon and Jones 2005). These results corroborate patterns found in broad-scale observations of a wide variety of demersal fishery species, mostly on temperate continental shelves (reviews by Houde 1987, Myers and Cadigan 1993, Bailey 1994). While there are examples of inverse

density dependence at small scales in reef fishes (reviews by Hixon and Webster 2002, Osenberg et al. 2002, White et al. 2010), Allee effects have seldom been detected in marine fishery species at the scale of entire stocks (Myers et al. 1995).

In a few cases, patterns of density dependence have been compared at both small and large spatial scales for the same species. Steele and Forrester (2005) demonstrated for the annual coral-reef fish, bridled goby (*Coryphopterus glaucofraenum*), that the strength of density-dependent mortality detected experimentally on small habitat patches was similar to that observed both among large reefs within years and among years within reefs (i.e., large-scale mortality was both spatially and temporally density dependent). Similarly, Johnson (2006) detected density-dependent mortality in the temperate kelp rockfish (*Sebastes atrovirens*) in both small-scale experiments within years and large-scale observations among years. In contrast, an observational study by White and Warner (2007) reported inversely density-dependent mortality at small scales and direct density dependence only at large scales in the tropical bluehead wrasse (*Thalassoma bifasciatum*). Finally, Forrester et al. (2008) found that small-scale experiments on the goldspot goby (*Gnatholepis thompsoni*) accurately scaled up to predict spatial but not temporal density dependence in mortality observed on large coral reefs.

Clearly needed to understand population regulation in demersal marine fishes more fully are long-term, large-scale, field studies that (1) include a broad and natural range of recruitment, (2) test for both temporal density dependence and regulation of substantial local populations in species with multiyear life spans over multiple generations, (3) examine multiple demographic rates, and (4) correlate these broad-scale patterns with possible causative factors. Here, we report such a labor-intensive study.

Study species, prior tests for density dependence, and hypotheses

Our model species was the bicolor damselfish (*Stegastes partitus*, family Pomacentridae), a common planktivore/benthivore on tropical Western Atlantic and Caribbean coral reefs (Emery 1973). Bicolors are semi-social, living in loose groups of up to about 20 fish inhabiting the same patch of coral heads (Myrberg 1972, Stevenson 1972). They are highly reef associated because holes in living or dead coral provide both shelter from predators (Nemeth 1998) and sites for egg nests (Knapp and Warner 1991). Bicolors are ideal fish for demographic studies because, although they can live for several years, they have high site fidelity within reefs, are easy to mark and recapture repeatedly, and their demersal eggs can be easily quantified. Bicolors in our study region settle in and near adult habitats at about 1.5 cm total length (TL; Nemeth 2005) after about a 30-day larval

duration (Sponaugle and Cowen 1996, Nemeth 2005), and mature at about 6 cm TL (Schmale 1981; M.C. Schmale, *personal communication*), which corresponds to about 1 year of age in our system (M. A. Hixon, *personal observation*). Some individuals reach 10 cm TL and live a maximum of about 4 years in our study region (see *Results*). Spawning on a lunar cycle mostly during the summer months, males defend reef holes where females deposit clutches of demersal eggs that hatch into larvae in 3.5 days in our study region (Schmale 1981, Cole and Sadovy 1995, Robertson et al. 1998, Johnson et al. 2010; M. A. Hixon, *personal observation*).

In prior small-scale, short-term experiments in the Bahamas near two of the study reefs reported here (Normans Pond and Windsock Reefs), Samhuri (2009) showed that growth and fecundity of bicolors were spatially density dependent. Carr et al. (2002) and Johnson (2008) demonstrated that early post-settlement mortality of bicolors on both patch reefs and continuous reefs was also spatially density dependent. This density dependence was caused by predation interacting with interference competition, given that the experimental removal of predators and/or aggressively dominant territorial damselfish resulted in density-independent mortality. A combination of mechanisms likely explained these patterns (Carr et al. 2002; see also Holbrook and Schmitt 2002, Figueira et al. 2008a, Samhuri 2009). First, because recruit bicolors and adults of more aggressive damselfish of the same and different species compete for the same shelter from predation, the presence of dominants increased per capita displacement of bicolor recruits from reef shelters (e.g., Robertson 1996), exposing them to predation. Second, agonistic interactions between recruits and adult damselfish increased susceptibility of recruits to predators through distraction and/or reduced vigilance. Third, increases in activity owing to increased aggressive interactions drew greater attention of predators.

Although prior experiments demonstrated the importance of multispecies interactions in causing early post-settlement density dependence at small scales, many important questions remained, which provided the hypotheses for this study. Is density dependence also evident at the broader spatial scales and longer temporal scales characteristic of large local populations? If so, does that density dependence translate to local population regulation? Does substantial variation in recruitment alone determine the presence and strength of density dependence? Besides previously documented density-dependent mortality, is there evidence for density dependence in individual growth and fecundity? Finally, what are the broader ramifications of these patterns for conservation biology and fisheries biology of ecologically similar species in the context of metapopulation dynamics?

METHODS

Study sites

Our study sites were four shallow coral reefs on the Great Bahama Bank in the vicinity of Lee Stocking Island, Bahamas (Fig. 1). Normans Pond and Windsock Reefs are located adjacent to the deepwater Exuma Sound, the source of settlement-staged larvae carried onto the Great Bahama Bank by tidal currents (Fig. 1; see also Shenker et al. 1993, Thorrold et al. 1994a, b, c). The Barracuda Reefs are located about 15 km from the Exuma Sound, and consequently experienced far lower recruitment rates and population sizes (see *Results*).

Typical of larger reefs in this region, each was approximately 100 m in diameter. Normans Pond and Windsock Reefs were dominated by star coral (*Montastrea annularis*), and NW and SE Barracuda Reefs were dominated by mustard hill coral (*Porites astreoides*), both as living heads and as dead rubble. Highly site attached, bicolors inhabited mostly highly complex branching corals where available: lettuce coral (*Agaricia agaricites*) at Normans Pond and Windsock Reefs, and finger coral (*Porites porites*) at the Barracuda Reefs (see Nemeth 1998). During this study, we documented that overall habitat complexity was greater at Normans Pond and Windsock Reefs compared to the Barracuda Reefs (see *Results*).

Demographic monitoring

From 1998 to 2006, we periodically sampled demographic parameters of bicolors at all four study reefs. Each reef was surveyed in 22 plots, each 2×2 m and centered on a group of bicolors, which encompassed the home range of that group (Emery 1973). The 22 plots at each reef included virtually all bicolors inhabiting the low-recruitment, low-density reefs (NW and SE Barracuda), and well over two-thirds of the bicolors at the high-recruitment, high-density reefs (Normans Pond and Windsock). Visual overviews of the high-density reefs indicated that the study plots were representative of the total bicolor population in terms of fish size structure and adult sex ratio (based on male courtship and nest-defense behavior; see Myrberg [1972]), justifying use of that large subsample as an index of total population size.

Each reef was surrounded by sand and seagrass, where bicolors were never seen, so both emigration and immigration were nonexistent or negligible (see also Figueira et al. 2008b), and the disappearance of a fish from a reef could safely be attributed to mortality.

Tagging.—At the start of the study, and thereafter as new recruits appeared on study plots, divers captured each individual using the fish anesthetic quinaldine and hand nets, transferred the fish to a seawater-filled plastic bag, recorded its total length (TL), and individually tagged it by small injections of colored elastomer pigment (Beukers et al. 1995) just under the skin in the lightly pigmented posterior half of the body. To

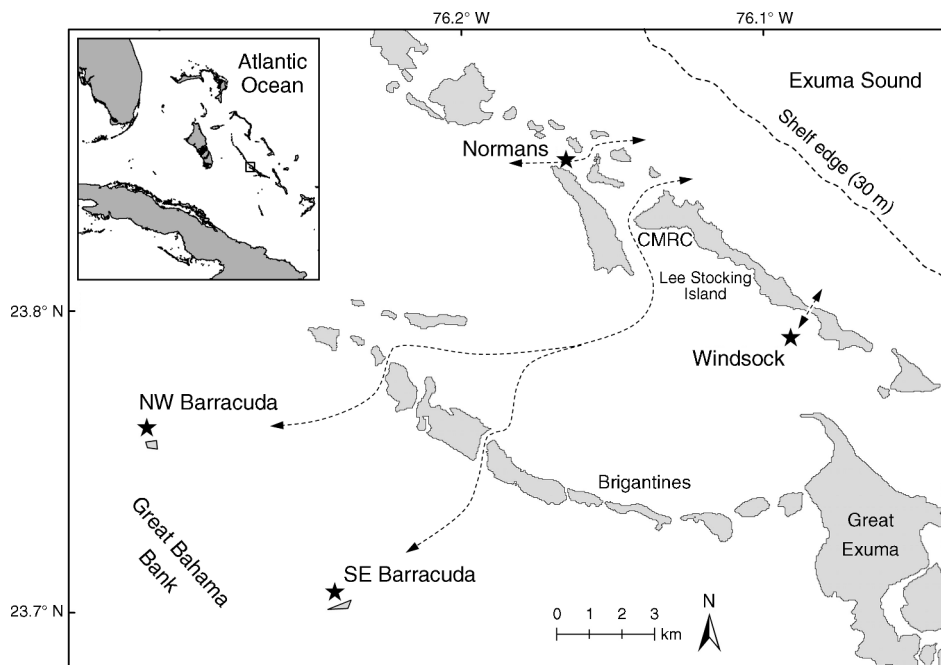


FIG. 1. Study region near Lee Stocking Island and the Caribbean Marine Research Center (CMRC) showing the locations of the four study reefs (stars). The Great Bahama Bank on which these reefs grow averages about 3 m deep. Arrows indicate the path and direction of tidal currents that deliver settlement-stage larvae from the Exuma Sound (>1500 m deep). Notice that Normans Pond Reef and Windsock Reef are immediately adjacent to the Sound, whereas the Barracuda Reefs are about 15 km from this source of larvae. Recruitment manipulation treatments (see following figures): Normans Pond Reef, high-recruitment reference site (hi R r); Windsock Reef, high-recruitment removal site (hi R -); NW Barracuda Reef, low-recruitment reference site (lo R r); SE Barracuda, low-recruitment addition site (lo R +).

minimize stress, all handling and release of each fish occurred exactly where captured underwater, and each fish was handled for less than a minute.

Previous studies showed that colored injections do not affect the mortality of small reef fishes substantially (Beukers et al. 1995, Frederick 1997, Malone et al. 1999, Hoey and McCormick 2006), and indeed, tagged fish in our study lived for years. Nonetheless, to test whether tagging artificially increased mortality of small bicolors, we conducted a supplemental field experiment. In 1999, we transplanted 120 new recruits captured far from our study reefs to 30 isolated coral-rubble plots on a sand flat near Normans Pond Reef. Each plot included approximately 100 L of coral rubble (common settlement habitat of bicolors) spread in a uniform 0.75×0.75 m area, with 10 m between adjacent plots. At these isolation distances, fish did not emigrate during the month-long experiment, yet predators of various species regularly visited from nearby reefs. All four recruits transplanted to each of 10 plots were randomly assigned to one of three treatments: orange elastomer tag, blue elastomer tag, or no tag. Survival and any movements were subsequently monitored for 30 days and then compared among treatments by one-way ANOVA.

Parameters.—For the main experiment, from 1998 to 2006, demographic censuses were conducted at each of the four large study reefs weekly during the summer

recruitment season (June to September), and at least once each winter (usually January to February). During each census, divers recorded the following parameters: (1) total population size at each reef based on the cumulative number of fish in all study plots, (2) the tag and approximate length of each fish, adding new tags as needed (including new recruits), and (3) starting in 2000, the number and areas of all clutches of eggs laid in artificial nests. To distinguish local movements in and out of study plots from mortality, each reef was also searched completely for any tagged fish living outside of study plots (which were negligibly rare events). Those few fish that did move were tracked as part of the total population. During the first and last censuses of the summer (at a minimum), as well as during the winter, all fish were recaptured, remeasured, and released to provide data on individual growth rates.

To test whether weekly censuses adequately measured recruitment, that is, whether a substantial number of new settlers died less than a week after appearing on the reef, we monitored recruitment intensively at two reefs (Normans Pond and Windsock) during the summer of 1997. At each site, one-half of the study plots were caged to prevent access to predators. Cages measured $1 \times 1 \times 0.5$ m and were made of rebar frames covered by 1.5-cm vexas plastic mesh. Each plot was then checked daily for new settlers for a full month, given that damselfish settle

in lunar cycles (Robertson et al. 1988, Sponaugle and Cowen 1996, Paris and Cowen 2004). Of 17 new recruits that settled in the uncaged plots at least a week before the end of the 30-day study, 15, or 88%, survived at least a week, indicating that weekly recruitment surveys were reasonably representative. Only six new recruits appeared on the caged plots, and all survived at least a week, yet the relatively poor recruitment to cages indicated that this was not a viable approach for measuring recruitment in general, so caging was discontinued.

Egg production.—Starting in 2000 at all four study reefs, egg production was monitored by attaching an artificial nest to the seafloor in each study plot inhabited by adult fish. The nest was a 15 cm long \times 5 cm diameter tube of PVC plastic, capped at one end. The interior of the tube was lined with a lightly sanded, transparent, acetate plastic sheet (14 \times 16 cm of exposed surface), on which females readily deposited clutches of eggs in preference to natural surfaces (Knapp and Kovach 1991, Knapp and Warner 1991, Knapp 1993, 1995, Cole and Sadovy 1995, Knapp et al. 1995, Johnson et al. 2010). Because fertilized eggs changed color with developmental time, it was easy to identify individual clutches (Knapp et al. 1995). Removing and unrolling the acetate sheet underwater allowed divers to trace the area of each clutch, then replace the eggs into the nest nondestructively. Because the eggs were laid in monolayers, the area of each clutch was proportional to the number of eggs (Knapp and Warner 1991, Knapp et al. 1995). No acetate sheet was ever completely covered in eggs. Because hatching occurred 3.5 days after spawning (M. A. Hixon, *personal observation*; see also Robertson et al. 1988, Johnson et al. 2010), egg masses measured during one weekly sample of fecundity were not present in subsequent samples, precluding redundant data.

Counts of eggs laid in these artificial nests provided a reasonable estimate of fecundity for several reasons. First, male bicolors guard nests and exhibit conspicuous reproductive behaviors, including courtship displays and vigorous defense against potential egg predators (Thresher 1984). When multiple reproductive males were observed within study plots, additional artificial nests were placed in the vicinity of the identified males. All such males defended those nests, and were never observed defending natural nesting sites. Females do not lay eggs without a male to defend the clutch because mortality of unguarded eggs is extremely high due to predation and lack of aeration and cleaning (Thresher 1984). Second, molecular genetic evidence suggests that the vast majority of matings are between bicolors whose home territories are less than 4 m apart (D. W. Johnson, *unpublished data*; also see Cole and Sadovy [1995] for similar results based on spawning observations). Third, because our study plots were a haphazard sample of the surrounding reef, we reasoned that the effect of any females that did leave the study plots and spawn elsewhere would be balanced by non-study females

spawning in the nests we monitored, such that our estimates of fecundity would be representative of the local population.

Recruitment manipulations

After monitoring demographic parameters on each reef for four years (summer 1998 to summer 2001), it was evident that, first, bicolor recruitment and population sizes were an order of magnitude greater at the two reefs near the Exuma Sound source of larvae (Normans Pond and Windsock) compared to the two isolated reefs (SE and NW Barracuda), and second, the natural range of bicolor recruitment within each reef was often too narrow to test for density dependence effectively (see *Results*). Therefore, for the next four years of demographic monitoring (summer 2002 to summer 2005), we artificially increased recruitment at one low-recruitment reef (lo R + treatment at SE Barracuda Reef), decreased recruitment at one high-recruitment reef (hi R – treatment at Windsock Reef), and left one of each kind of reef as unmanipulated reference sites (lo R r treatment at NW Barracuda Reef and hi R r treatment at Normans Pond Reef). The intention was to broaden the range of recruitment at two reefs within natural limits observed among reefs. Site replication at the scale of this manipulation was not possible due to logistic constraints, similar to whole-lake manipulations (Carpenter et al. 2001).

Recruitment was reduced at Windsock Reef by simply capturing and removing new recruits (<2 cm TL) as soon as they were detected within each study plot (i.e., recruits were not removed from the entire reef). Recruitment was enhanced at SE Barracuda Reef each summer by capturing and tagging new recruits at a site far from all study reefs, transporting them in insulated containers in sealed, seawater-filled plastic bags, and releasing them within study plots in known settlement habitat: small reef holes and coral rubble in the vicinity of adult habitat. New recruits were added at a density of 4 recruits/m² of settlement habitat. To avoid the possibility of artificially high mortality rates of transplants contaminating our demographic monitoring, we counted transplants as being successful (i.e., subsequently gathered demographic data on them) only if they survived at least 24 hours after being released. With this conservative approach, measured recruitment was bolstered by a total of 362 successful recruit transplants: 112 in 2002, 82 in 2003, 96 in 2004, and 72 in 2005. In comparison, we counted 31 natural recruits over this same period, demonstrating that we had artificially bolstered recruitment by an order of magnitude.

Tests for density dependence

Because the logistic constraints of demographically monitoring four large reefs precluded site replication during our manipulations of recruitment, we could not use reefs as replicates in our analyses. Additionally, four years turned out to be an insufficient “before” period to

design a true before-after-control-impact experiment (sensu Green 1979) because of the narrow range of recruitment and population sizes observed at some reefs (see *Results*). Instead, we examined demographic patterns of mortality, growth, and fecundity within each reef over all eight years of the study. Our analyses of mortality and growth proceeded in two stages. First, we examined these parameters separately with the goal of explicitly testing for density dependence in demographic rates while accounting for the complex relationships between body size and these rates. We then combined estimates of mortality and growth to examine whether among-year variation in survival to maturity exhibited patterns of density dependence that would be consistent with regulation of local population size.

Mortality.—Within each study reef, we analyzed mortality by examining the relationship between survival time and two predictor variables: body size (length at capture) and population density (total number of fish within the 22 study plots). Survival times were assumed to follow a Weibull distribution, which is often used to describe time-to-event data (such as survival) and provides a convenient parametric description of mortality rates (review by Fox 2001). Moreover, a Weibull survival model allows per capita mortality to increase or decrease over time as fish grow and age, a pattern expected for bicolors (Figueira et al. 2008b, Johnson and Hixon 2010). Based on the Weibull distribution, the probability density of survival times, $f(t)$, can be described as

$$f(t) = \frac{a}{b} \left(\frac{t}{b}\right)^{a-1} e^{-(t/b)^a} \quad (1)$$

where t is time, a is a shape parameter, and b is a scale parameter. We modeled both the shape and scale of the distribution as functions of body size and population density. Specifically,

$$a = \exp(\alpha_1 + \beta_1 \times \text{size} + \beta_2 \times \text{density}) \quad (2)$$

and

$$b = \exp(\alpha_2 + \beta_3 \times \text{size} + \beta_4 \times \text{density}) \quad (3)$$

where α and β are scaling coefficients. We used maximum likelihood to estimate parameters describing the shape and scale of the distribution of survival times. Because an individual's survival time was never known exactly (disappearances occurred between censuses), in order to fit the data and estimate parameter values, we calculated likelihoods of surviving at least as long as the census prior to disappearing and no longer than the first census after the fish had disappeared (i.e., survival times were treated as interval censored, e.g., Bolker [2008]). We used likelihood ratio tests to evaluate whether density-dependent models significantly explained variation in survival time better than models without the density terms. The strength and direction of density-dependent effects were inferred from the magnitude and sign of the estimated coefficients relating density to the

shape and scale of the survival-time distribution. Analyses were conducted using the *bbmle* package in R (Bolker 2008, R Development Core Team 2010).

Growth.—We measured growth as change in total length. Typical of many fishes, growth rate of bicolors is relatively rapid during the juvenile phase, then slows and approaches zero at the oldest ages, resulting in an asymptotic pattern of size-at-age. Obviously, measured growth also depends on the amount of time elapsed between release and recapture. We used measurements of change in length to estimate parameters of a Richards function, L_t , describing size-at-age:

$$L_t = L_\infty(1 - Be^{-kt})^{-n} \quad (4)$$

where L_∞ is asymptotic size, k is a growth rate constant, n is a shape parameter, and B is a scaling parameter equal to $(L_\infty^{(-1/n)} - L_0^{(-1/n)})/L_\infty^{(-1/n)}$, where L_0 is size at settlement (estimated to be 1.5 cm TL). Although individual growth can be described well by slightly simpler models, which also display asymptotic growth (e.g., a Von Bertalanffy growth function [Johnson and Hixon 2010]), the Richards function allowed greater flexibility to model average growth within each population and to examine density-dependent responses, particularly if the shape of the growth curve was density dependent. Following Ebert (1980), we estimated parameters of the Richards equation as follows:

$$L_{t+T} = [L_\infty^{(-1/n)}(1 - e^{kT}) + L_t^{(-1/n)}e^{-kT}]^{-n} \quad (5)$$

where L_{t+T} is length at recapture after T days at liberty, L_t is length at initial tag-and-release, and other variables are as described for Eq. 4. We used generalized nonlinear least squares to estimate parameter values. Because residual variation in L_{t+T} decreased sharply with L_t , we modeled the variation in L_{t+T} as a power function of L_t . To test for density dependence, each of the three growth parameters was expressed as a linear function of density (note that residual plots did not indicate any justification for more complex relationships between parameter values and density). We used likelihood ratio tests to evaluate whether density-dependent models significantly explained variation in growth better than models without the density terms.

Survival to maturity.—We combined estimates of survival and growth to estimate survival to maturity. For each year of the study, we estimated survival parameters as described in *Methods: Tests for density dependence: Mortality*, except that we did not include a parameter describing the effects of density. Similarly, we estimated growth parameters for each year using Eq. 5 without terms for density effects. Because the growth data were somewhat sparse during some years of the study (i.e., during low-recruitment years and recruitment-removal years), we used mixed-effects models to estimate growth parameters for each year (see Helser and Lai [2004] and Weisberg et al. [2010] for detailed examples of mixed-effects models of growth in fishes).

This approach combined information on variation in growth both among and within years, and provided robust estimates of growth even when within-year sample sizes were relatively low. We used a single model for each study reef. “Year” was treated as a random effect and all three growth parameters were allowed to vary among years. We used the predicted values of the random effects (growth parameters that varied among years) to estimate a growth function for each year of the study.

For each year, expected age at maturity was estimated from the growth function and calculated as the time (in days) it would take for a fish to reach 6 cm TL, a minimal size at maturity established by earlier histological studies (Schmale 1981). Specifically, time to reach 6 cm (t_6) was calculated as

$$t_6 = -\ln \left(\frac{1 - \left(\frac{6}{L_\infty} \right)^{\left(\frac{-1}{-n} \right)}}{B} \right) \Bigg/ k \quad (6)$$

where the growth parameters are as already described. Survival to maturity (S_{t_6}) was then calculated by combining the size-dependent mortality function with the growth function:

$$S_{t_6} = \exp \left[- \int_0^{t_6} \frac{a}{b} \left(\frac{t}{b} \right)^{a-1} dt \right]. \quad (7)$$

Here, the integrand describes daily per capita mortality. For these calculations, mortality is a function of time because both a and b are functions of body size (i.e., Eqs. 2 and 3 without density effects) and the growth function for each year (Eq. 4) describes body size (L_t) as a function of time. Variability in each yearly estimate of survival to maturity was calculated with a resampling procedure. For each of 100 iterations, parameters defining the growth and mortality function were drawn at random from a multivariate normal distribution using the estimated mean and covariance values (*MASS* package in R). Survival to maturity was calculated as described in Eq. 7, and we used the 2.5th and the 97.5th quantiles of the distribution to generate 95% confidence intervals about the expected survival to maturity. To explore among-year variation in survival to maturity and temporal patterns of density dependence, we plotted expected survival to maturity vs. average population density in each year. Values of r^2 were calculated based on a linear regression of logit-transformed survival data.

Fecundity.—To examine density dependence in fecundity, we tested whether per capita egg production (total egg area per artificial nest) varied with local population density. Bicolors spawn on a lunar cycle and egg production also varies seasonally (Schmale 1981, Robertson et al. 1988, 1990), especially in the Bahamas (Johnson and Hixon 2011). We therefore modeled egg production as a function of season (summer high vs. winter low), lunar day, and density. To meet the

assumption of normality in our analyses, we used the square root of egg area per nest as our measure of fecundity. The expected value of fecundity for a given season, \hat{F} , was modeled as

$$\hat{F} = \beta_0 + \beta_1(s) + \beta_2(d) + A \left(\cos \left[\left(\frac{2\pi}{29.5} \right) (D_L - D_{\max}) \right] \right) \quad (8)$$

where β_0 describes baseline fecundity, β_1 and β_2 describe deviation in fecundity due to season and density, respectively, s is a season indicator variable coded as 1 for summer and 0 for winter, d is density as local population size, A is the amplitude of lunar variation, D_L is the lunar phase day (1 = new moon), and D_{\max} is a location parameter indicating the lunar day on which average fecundity was maximum. The last term in Eq. 8 describes the lunar spawning cycle as sinusoidal variation in spawning activity. To visually display patterns of density dependence in fecundity, we plotted relationships between density and residual fecundity (i.e., residual values from \hat{F} predicted by Eq. 8 with no density term).

Tests for local population regulation

Typical of demersal marine fishes, our four study populations were demographically open systems in which input occurs via recruitment of dispersive larvae spawned from external sources, perhaps as well as internal sources (review by Caley et al. [1996], see Christie et al. [2010] for bicolors). In such open systems, local populations are expected to fluctuate around an equilibrium value determined by the balance of recruitment and post-settlement mortality, a phenomenon called “recruitment regulation” (Hughes 1990). Although this phenomenon may contribute to apparent regulation of local populations, external recruitment is typically highly variable and independent of population size (reviews by Doherty and Williams 1988, Doherty 1991, 2002), so the degree to which local populations are regulated by density-dependent processes in the face of variable external recruitment is critical to the broader regulation of marine metapopulations (Armsworth 2002, Figueira 2009).

Our approach was tailored to open populations, so we tested whether the local density of adults exhibited components of regulation (persistence, boundedness, and return tendency) *given the observed variation in recruitment*. These tests and their interpretation are somewhat different than tests of regulation in closed populations. Our tests focused on regulation as effected by density dependence in post-settlement mortality and growth, and provide a means of assessing whether individual demographic rates (i.e., the size-dependent patterns of mortality and growth described in previous subsections) combined to produce a signature of regulation in adult population densities among years.

Given the context of open local populations, examining persistence was a simple one-sided test: if any population was extirpated during the study, then that population obviously lacked persistence. Testing long-term persistence over many generations was clearly beyond the scope of this study. To test for boundedness and return tendency in each of the four study populations, we examined whether interannual variation in adult population size during the eight years of the study was significantly less than what would be expected if actual recruitment rates were as observed, yet demographic rates were density independent. For boundedness, our test statistic was the coefficient of variation in adult population size, measured at the first census of the year (i.e., just prior to each summer recruitment season). For return tendency, we calculated the correlation between $\ln(N_t)$ and $\ln(N_{t+1}/N_t)$, where N = number of adults at the first annual census and t = year. A negative correlation indicated that years with relatively high densities tended to experience lower population growth (or greater declines in population size), with stronger negative correlations indicating stronger regulation (Pollard et al. 1987).

For both boundedness and return tendency, we compared the actual value calculated from the observed data to a distribution of expected values generated by a density-independent randomization procedure. Test statistics significantly lower than the distribution of values generated by randomized data provided evidence of regulation. Each iteration of the randomization procedure produced a simulated eight-year time series of adult population abundances. Starting with the observed number of adults in the first year of the study, adult population sizes in subsequent years were predicted from observed recruitment during the previous year and observed demographic rates (survivorship and growth). For each iteration, demographic rates based on observed values during the eight-year study were randomly shuffled (i.e., density independent) among years to predict adult population sizes. Shuffling demographic rates from each year destroyed any underlying density dependence, yet preserved the observed covariance among survival, growth, and migration. The coefficient of variation in adult abundance and estimated return tendency were calculated for the time series generated by each iteration. This procedure was repeated 1000 times for each study reef. P values were calculated as the number of randomizations that produced a test statistic equal to or lower than the observed value. Because such tests for population regulation can be affected by autocorrelation in demographic rates and sampling error (e.g., Holyoak and Lawton 1993, Fox and Ridsdill-Smith 1996), a simulation-based evaluation of Type I error rates in these regulation tests is provided in Appendix A. This evaluation indicated that our tests were robust.

Reef structure and interspecific interactions

It is well documented that a synergistic combination of habitat structure, heterospecific competitors, and predators can affect the presence and intensity of local density dependence in reef fishes (review by Hixon and Jones 2005). Therefore, at each of the four study reefs, we characterized habitat structure and periodically censused the density of interference competitors that interact with bicolor damselfish and resident predatory fishes likely to consume bicolors. We also conducted a supplemental experiment that assessed the intensity of predation on bicolors by transient piscivores, which constantly swim among reefs, typically in schools.

Reef structure.—The availability of prey refuges provided by the physical structure of a reef strongly affects the survival of reef fishes (review by Beukers and Jones 1997), including bicolor damselfish (Nemeth 1998). We therefore characterized the structure of each study reef relevant to bicolor survival both within and among study plots. Within each plot, habitat complexity was measured by combining two independent measures into a single index. First, the coral heads in each plot were assigned a rugosity score from 1 to 5, where 1 is massive coral or flat reef bench with only a single shelter hole (e.g., massive *Porites*), 2 is a mixture of 1 and 3, 3 is convoluted corals with a moderate number of holes (e.g., *Montastrea*), 4 is a mixture of 3 and 5, and 5 is highly branched corals with many holes (e.g., *Agaricia*). Photographs of each plot facilitated between-plot comparisons to ensure accurate relative scoring. In cases where the complexity of a plot changed through time due to storm damage, the time-weighted mean score before and after that damage was used. Second, given that coral heads inhabited by bicolors were roughly the same size, the approximate area covered by coral heads in each plot in 1-m² increments was multiplied by the rugosity score to produce a composite habitat complexity index. Habitat complexity index values were compared among the four reefs by Kruskal-Wallis nonparametric one-way ANOVA with Tukey pairwise multiple comparisons.

Among study plots, adult bicolors occasionally and briefly leave their home coral heads and visit other corals inhabited by conspecifics, especially when courting and spawning (Myrberg 1972, Knapp and Kovach 1991, Knapp and Warner 1991, Knapp 1993, 1995, Cole and Sadovy 1995, Knapp et al. 1995). Therefore, the spatial distribution of coral heads inhabited by adult bicolors will influence how far fish must swim during such visits, and the greater the distance between occupied corals, the greater the exposure to predation. This situation manifests a common trade-off in fishes between avoiding predation and engaging in other activities (e.g., Cerri and Fraser 1983, Werner et al. 1983, Dill and Fraser 1984).

On each reef, we used a combination of direct underwater tape measurements and high-resolution GPS to map the distribution of all 22 study plots and

the nearest neighboring corals occupied by adult bicolors (be they study plots or not), calculating the distance from each study plot inhabited by adults to its five nearest neighbors. Because some plots never supported adult fish (yet did support recruits and/or juveniles), sample sizes were unequal among reefs: all 22 plots were inhabited by adult bicolors at both Normans Pond Reef and Windsock Reef vs. 14 plots at NW Barracuda Reef and 10 plots at SE Barracuda Reef. The four reefs were compared by Kruskal-Wallis nonparametric one-way ANOVA with Dunn pairwise multiple comparisons.

Interference competitors and resident predators.—Several species of territorial damselfish (mostly genus *Stegastes*) are known to be aggressively dominant over bicolors (Robertson 1996). At least once each summer, these species were censused in each study plot, as were mid-sized reef-resident predatory fishes (moray eels, groupers, and snappers). Whereas territorial damselfish were resident within or lived immediately adjacent to each plot, the home ranges of the predators were often much larger than the study plots, so their censuses reflected only relative visitation frequencies. Damselfish and resident predator counts were pooled among plots, averaged by reef each summer, and annual means and standard errors calculated for eight years each. Because the level of population turnover for territorial damselfishes and resident predators was unknown, there was no guarantee that annual means were independent, so no inferential statistics were applied.

Transient predators.—Bicolors were attacked by both resident and transient predators (Emery 1973, Carr et al. 2002). The intensity of predation by transient piscivores was determined independent of habitat complexity and other interacting fishes during a separate short-term field experiment near the end of the baseline period in 2001. Two patch reefs were constructed in sand and seagrass habitat about 50 m off each of the four study reefs, separated from each other by at least 50 m. Each circular reef measured 4 m in diameter, and consisted of a core of three heads of lettuce coral (*Agaricia agaricites*) ringed by four heads of mustard hill coral (*Porites astreoides*) and five heads of star coral (*Montastrea annularis*). All coral heads were living, measured about 40 cm in diameter, and were translocated from unconsolidated reefs far from the study reefs. An outer ring of 100 empty shells of queen conch (*Strombus gigas*) with their holes facing upward lined the perimeter of each patch reef. This combination of natural substrata provided a wide range of shelter-hole sizes of equivalent abundances among the eight experimental patch reefs.

Each empty reef was then seeded with 20 recent bicolor recruits (<2 cm TL), and their survival monitored weekly for two months. The transplanted recruits were given distinct elastomer tags (different from natural recruits on the main study reefs) to test for any movement of fish between the main reefs and the patch reefs. No such movement was detected, indicating

that this short-term experiment did not contaminate observations on the main study reefs. Any natural recruits were removed during the experiment, so that, given the absence of resident predators, bicolor mortality was due solely to visiting transient predators (mostly jacks; see Emery 1973, Hixon and Carr 1997, Carr et al. 2002). Due to low sample sizes (two experimental patch reefs per main study reef), results were not analyzed by inferential statistics.

RESULTS

Population dynamics

Over the course of the eight-year study, the dynamics of local populations of bicolor damselfish at the four study reefs were somewhat complex. As expected and especially evident during the first four years, there was a general annual cycle of population increase during the summer recruitment season followed by decrease during the winter, when mortality exceeded larval recruitment (Fig. 2A). Occasional general disturbances affected these populations, especially the coral bleaching event during the summer of 1998 (Aronson et al. 2000) that killed lettuce coral occupied by bicolors on two of 22 study plots at Normans Pond Reef and eight of 22 plots at Windsock Reef. Passing Hurricane Floyd removed some of the dead coral heads in September 1999, but more importantly, bicolors were displaced from the dead heads by more aggressive damselfish that defended and consumed the algae that grew on the dead coral, especially at Windsock Reef (M. A. Hixon, *unpublished manuscript*). Thus, the bleaching and mortality of lettuce coral likely contributed to a regional two-year decline in bicolor abundance (Fig. 2A), including temporary extirpation at SE Barracuda Reef from September 2000 to January 2001 (Fig. 2D). Populations at all reefs began to recover in 2001, and the effects of subsequent passing hurricanes and storms were negligible (Fig. 2).

During the four-year pre-manipulation baseline period (1998–2002), bicolor population sizes were always greater at the two reefs close to the Exuma Sound source of larvae (Normans Pond and Windsock) compared to the two relatively isolated reefs (NW and SE Barracuda, Figs. 1 and 2A). The two unmanipulated reference reefs showed complementary patterns of abundance over the eight years of the study, including similar population sizes for about a year from mid 2002 to mid 2003: the population at Normans Pond Reef steadily declined from 1998 to early 2003, then subsequently recovered, whereas the population at NW Barracuda Reef peaked in late 2002, then slowly declined (Fig. 2B).

As expected, during artificial reduction of recruitment at Windsock Reef from 2002 to 2006, the population declined and remained low (Fig. 2C). The population persisted because not all settling larvae were detected and removed. In contrast, following annual pulses of artificial recruitment at SE Barracuda Reef during the same four consecutive summer recruitment seasons, the local population briefly reached sizes slightly greater

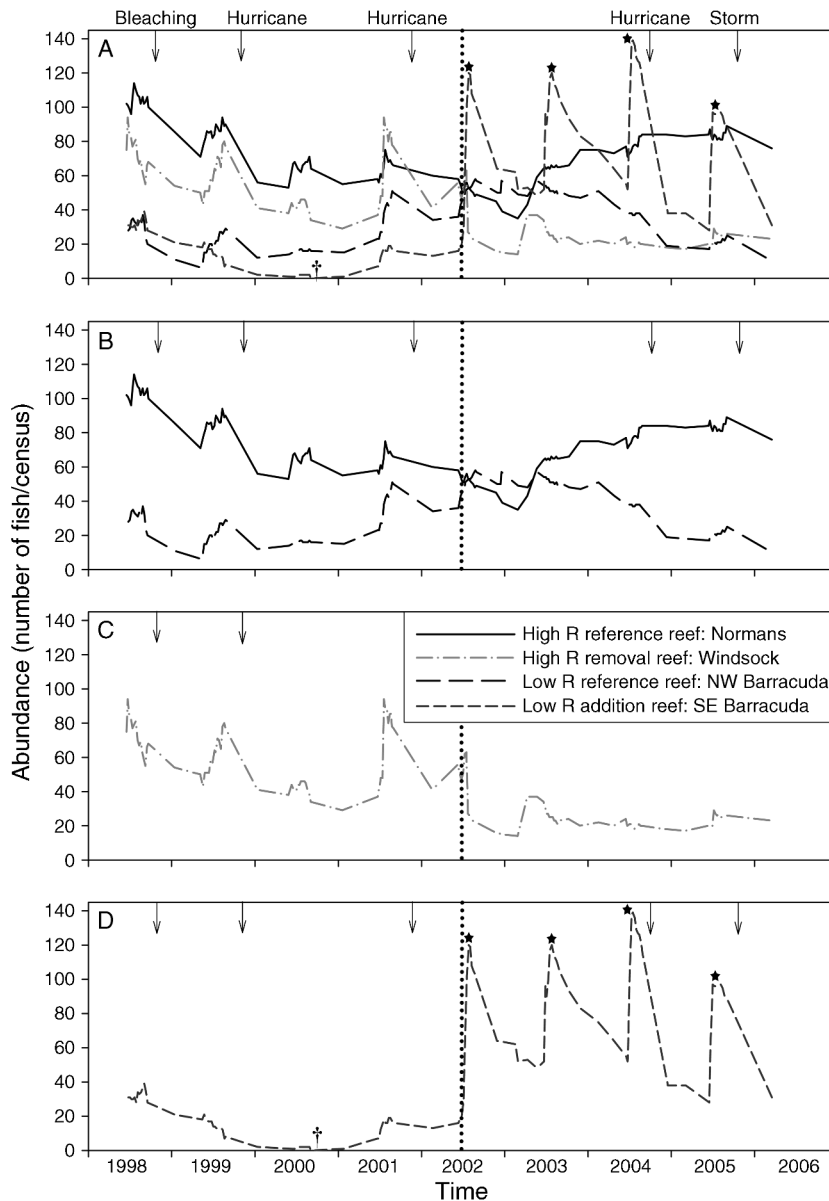


FIG. 2. Population time series at the four study reefs over eight years. The vertical dotted line in mid-2002 separates baseline and manipulation periods, and the vertical arrows denote natural disturbances. (A) All sites combined. (B) Naturally high- and low-recruitment reference reefs. (C) High-recruitment reef where new recruits were removed. (D) Low-recruitment reef where new recruits were added. The dagger indicates a brief period when this population naturally was extirpated in 2000, and the stars denote the four artificially induced peaks in recruitment during the four-year manipulation period.

than those observed at any unmanipulated reef (Fig. 2D). However, subsequent mortality soon brought the population back to levels similar to the mean size among reefs, although still greater than the baseline period at that particular reef (Fig. 2A).

Recruitment dynamics

Unmanipulated natural larval recruitment was an order of magnitude greater at Normans Pond and Windsock Reefs (Fig. 3A and B), which are relatively

close to the Exuma Sound source of settlement-stage larvae, compared to the two relatively remote and larvae-starved Barracuda Reefs (Fig. 3C and D). Over eight years, excluding the manipulations of recruitment at Windsock Reef (removals) and SE Barracuda Reef (additions), the mean (\pm SEM) number of natural recruits per census was 2.64 ± 0.26 at Normans Pond Reef, 3.02 ± 0.26 at Windsock Reef, 0.67 ± 0.13 at Normans Pond Reef, and 0.46 ± 0.10 at Normans Pond Reef. Nonetheless, at Windsock Reef, which was

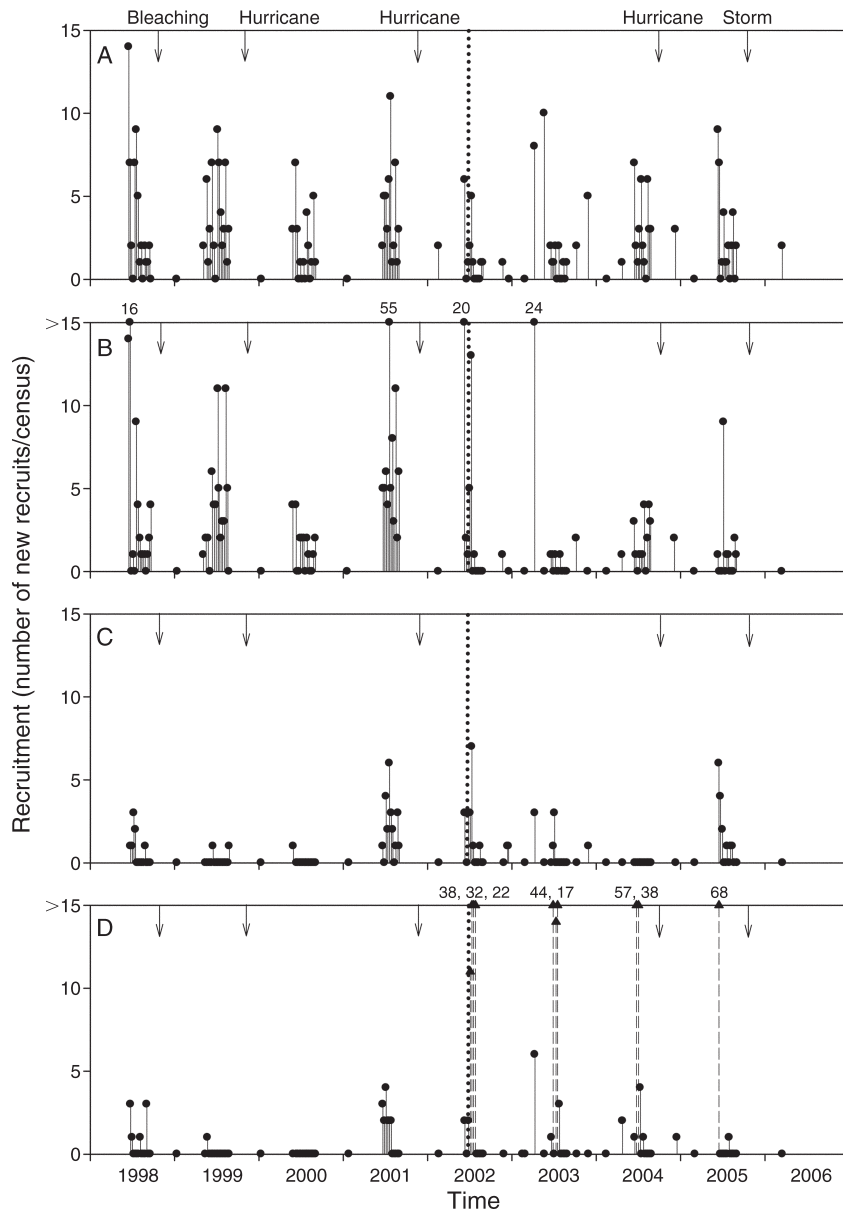


FIG. 3. Recruitment time series at the four study reefs over eight years. The vertical dotted line in mid-2002 separates baseline and manipulation periods, and the vertical arrows denote the same natural disturbances as in Fig. 2. (A) Naturally high-recruitment reference reef (Normans Pond Reef). (B) High-recruitment reef where new recruits were removed (Windsock Reef), values shown before removals. (C) Naturally low-recruitment reference reef (NW Barracuda Reef). (D) Low-recruitment reef where new recruits were added (SE Barracuda Reef), triangles illustrating artificially enhanced recruitment. In plots (B) and (D), recruitment values above 15 fish per census are shown as numbers.

affected more than the other reefs by the bleaching and death of *Agaricia* corals in 1998, natural recruitment was relatively low during the second half of the study, even before recruits were removed (Fig. 3B).

Tests for density dependence

Mortality.—The tagging-effects experiment demonstrated that tagged new recruits suffered no greater mortality than untagged fish of the same size in the same habitat, and that tag color did not differentially affect

mortality (one-way ANOVA $F_{2,27} = 0.91$, $P = 0.41$). Mean 30-day per capita mortalities (\pm SEM) were 0.40 ± 0.06 for untagged fish, 0.30 ± 0.10 for orange-tagged fish, and 0.45 ± 0.07 for blue-tagged fish.

Per capita mortality rates during the main study varied strongly with body size and were significantly density dependent (increased with density) at both Normans Pond Reef (likelihood ratio test, $\chi^2 = 11.53$, $df = 2$, $P = 0.003$; Fig. 4A) and Windsock Reef ($\chi^2 = 15.67$, $df = 2$, $P < 0.001$; Fig. 4B). Density dependence

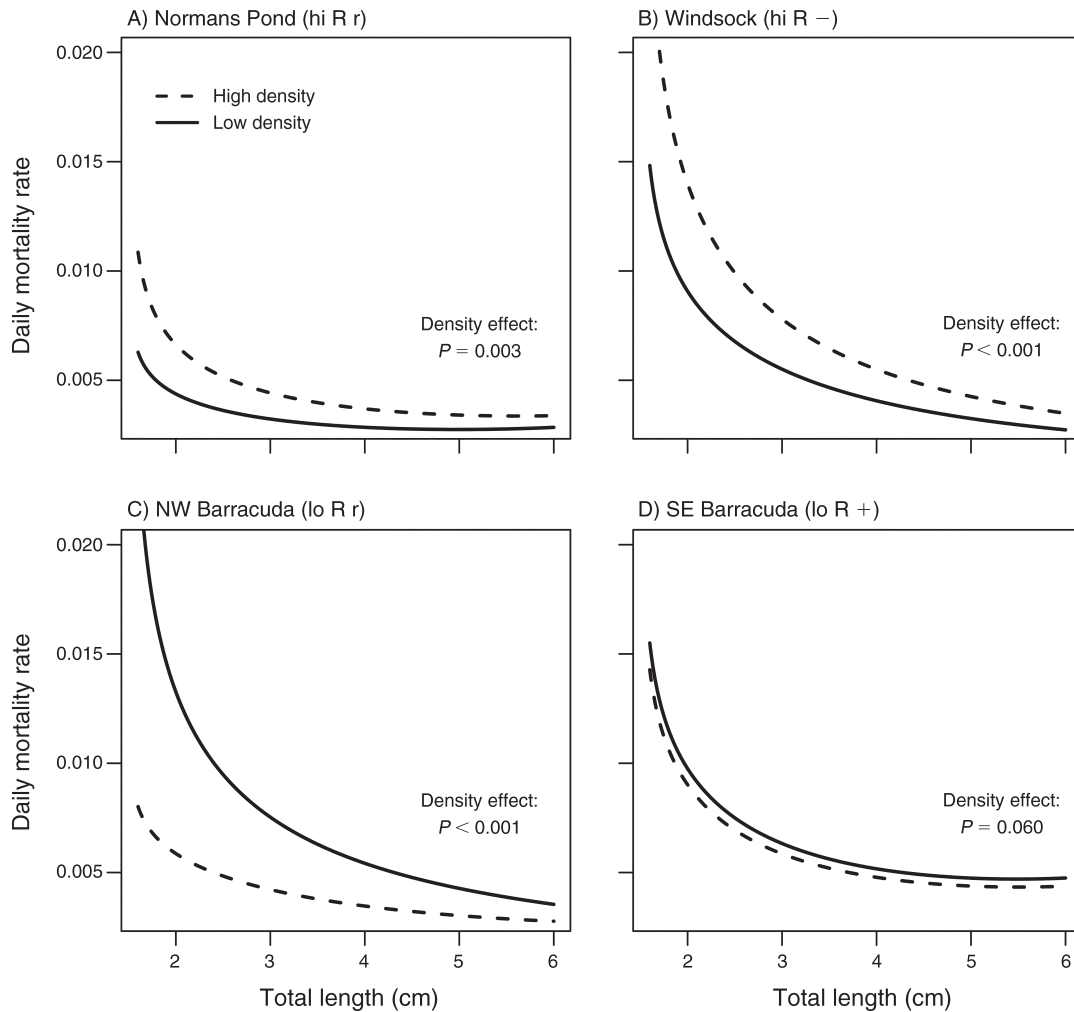


FIG. 4. Average size- and density-dependent per capita mortality rates at the four study reefs over eight years. Solid curves show size-dependent patterns of mortality at low densities (the lowest yearly average for each site), and dashed curves show size-dependent patterns of mortality at high densities (the highest yearly average for each site), such that the area between each pair of curves spans the full range of observed densities among years. Yearly averages were calculated as the total number of fish within the 22 study plots, averaged across all censuses within the year. The relative positions of these curves illustrate direct density dependence (high-density mortality > low-density mortality), inverse density dependence (high-density mortality < low-density mortality), or density independence (high-density mortality = low-density mortality). (A) Density dependence at the naturally high-recruitment reference reef (Normans Pond, hi R r). (B) Density dependence at the naturally high-recruitment reef where new recruits were removed (Windsock, hi R -). (C) Inverse density dependence at the naturally low-recruitment reference reef (NW Barracuda, lo R r). (D) Density independence at the naturally low-recruitment reef where new recruits were added (SE Barracuda, lo R +). P values give significance of likelihood ratio tests comparing the fit of full models (i.e., mortality both density- and size-dependent) to the fit of reduced models (mortality size-dependent only).

was evident across body sizes at both sites, yet least evident for larger fish (>4 cm TL) at Normans Pond Reef. In contrast, mortality was inversely density dependent at NW Barracuda Reef (likelihood ratio test, $\chi^2 = 26.58$, $df = 2$, $P < 0.001$; Fig. 4C), where the mortality of small fish was the highest observed. Mortality was density independent at SE Barracuda Reef, despite the large enhancement of recruitment at this site ($\chi^2 = 5.62$, $df = 2$, $P = 0.060$; Fig. 4D). Overall mortality rates (evaluated at average densities) were greatest at Windsock Reef and lowest at Normans Pond Reef, which were the two sites where density dependence

was clearly evident (Fig. 4). Parameter values associated with these tests for density dependence are provided in Appendix B.

Growth.—Individual growth at Normans Pond Reef was independent of density (likelihood ratio test, $\chi^2 = 6.01$, $df = 3$, $P = 0.111$; Fig. 5A), whereas growth at Windsock Reef was strongly density dependent, decreasing as density increased ($\chi^2 = 45.52$, $df = 3$, $P < 0.001$; Fig. 5B). Density-dependent growth was particularly strong during the juvenile phase (0–200 days post-settlement) and growth during later ages did not exhibit any compensating response. This pattern resulted in

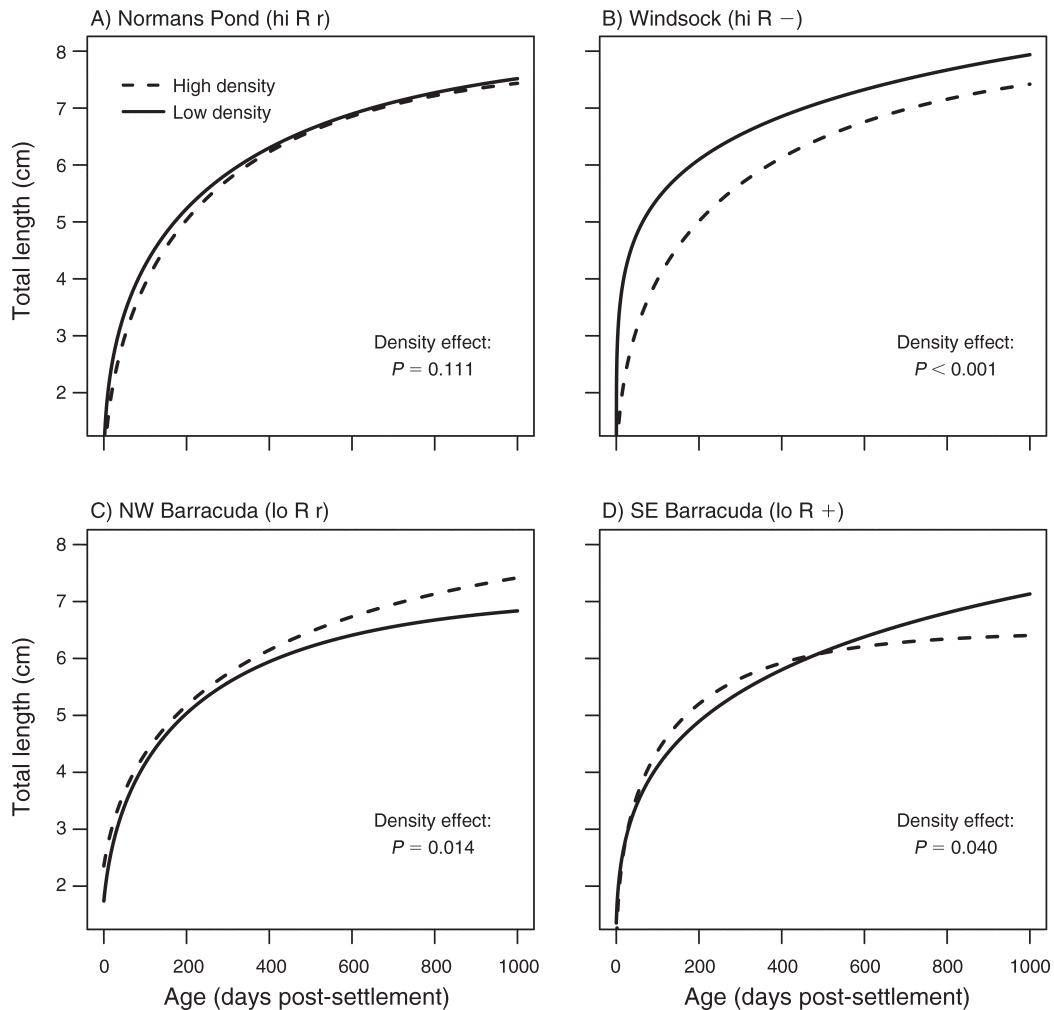


FIG. 5. Average individual growth rates at the four study reefs over eight years expressed as growth curves showing body size (total length) as a function of age (days post-settlement). Solid curves show size-dependent patterns of mortality at low densities (the lowest yearly average for each site), and dashed curves show size-dependent patterns of mortality at high densities (the highest yearly average for each site), such that the area between each pair of curves spans the full range of observed densities among years. Yearly averages were calculated as the total number of fish within the 22 study plots, averaged across all censuses within the year. The relative positions of these curves illustrate direct density dependence (high-density growth < low-density growth), inverse density dependence (high-density growth > low-density growth), or density independence (high-density growth = low-density growth). (A) Density independence at the naturally high-recruitment reference reef (Normans Pond, hi R r). (B) Density dependence at the naturally high-recruitment reef where new recruits were removed (Windssock, hi R -). (C) Inverse density dependence at the naturally low-recruitment reference reef (NW Barracuda, lo R r). (D) Density dependence at the naturally low-recruitment reef where new recruits were added (SE Barracuda, lo R +). P values give significance of likelihood ratio tests comparing density-dependent growth models to their nested density-independent counterparts.

consistently lower size-at-age when densities were high (Fig. 5B). Growth at NW Barracuda Reef was inversely density dependent overall ($\chi^2 = 10.62$, $df = 3$, $P = 0.014$; Fig. 5C), particularly at the adult stage (>600 days post-settlement), with juveniles less than 1 year old exhibiting density-independent growth. Growth at SE Barracuda Reef was density dependent overall ($\chi^2 = 8.289$, $df = 3$, $P = 0.040$; Fig. 5D), yet the response to density was relatively complex. Growth during the juvenile phase (50–400 days post-settlement) was weakly inversely density-dependent, but growth during adult ages (>500 days post-settlement) was directly density-depen-

dent. Overall growth rates were higher at the two sites located closer to Exuma Sound, with maximum growth occurring at Windssock Reef (Fig. 5). Parameter values associated with these tests for density dependence are provided in Appendix C.

Survival to maturity.— The mean (\pm SEM, $n = 4$ reefs) post-settlement life span of bicolors monitored during this study was 0.88 ± 0.10 yr, although those fish that survived at least 1 yr lived an average of 1.59 ± 0.14 yr. The maximum life span recorded was 3.6 yr.

Over all eight years of the study, comparing the two reference reefs (Fig. 6A and C) with the two manipu-

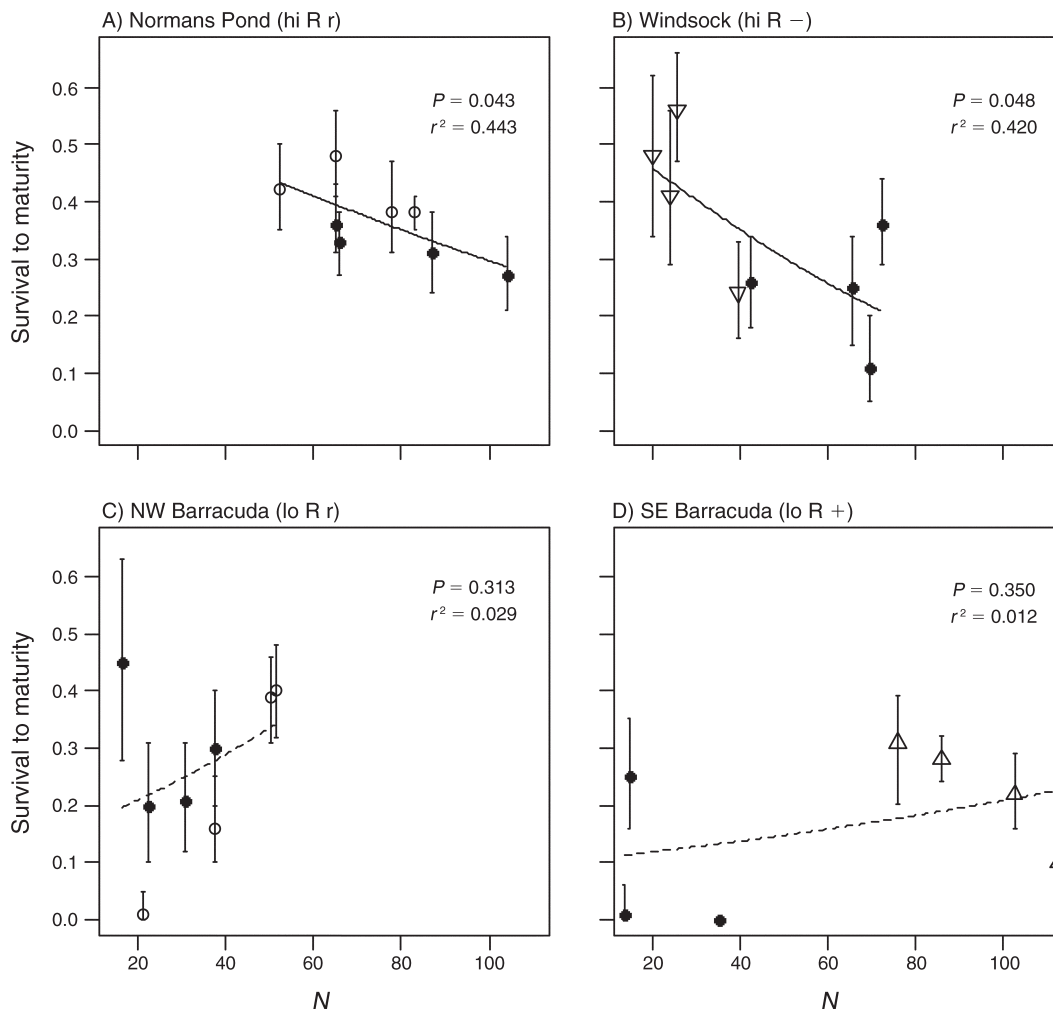


FIG. 6. Annual post-settlement per capita survival to adulthood (when fish reach 6 cm total length) at the four study reefs over eight years (mean \pm 95% CI). On all reefs, filled circles represent the four baseline years. On the two unmanipulated reference reefs, open circles represent the four years recruitment was manipulated at the other two reefs. (A) Density dependence at the naturally high-recruitment reference reef (Normans Pond, hi R r). (B) Density dependence at the naturally high-recruitment reef where new recruits were removed (Windsock, hi R -) for four years (inverted triangles). (C) Density independence on the naturally low-recruitment reference reef (NW Barracuda, lo R r). (D) Density independence on the naturally low-recruitment reef where new recruits were added (SE Barracuda, lo R +) for four years (triangles). Curves and summary statistics show logistic regressions describing the relationship between mean survival to maturity and mean population size (N).

lated reefs (Fig. 6B and D) revealed that recruit manipulations generated sufficient ranges of population size to provide robust tests for density dependence.

Annual post-settlement per capita survival to adulthood was significantly density dependent (decreasing as density increased) at the two reefs receiving high natural recruitment ($r^2 = 0.443$, $P = 0.043$ at Normans Pond; $r^2 = 0.420$, $P = 0.048$ at Windsock), even after the latter reef was artificially starved of recruits (Fig. 6A and B). At the two reefs receiving low natural recruitment (NW and SE Barracuda), survival was density independent among years ($r^2 = 0.029$, $P = 0.313$ at NW Barracuda; $r^2 = 0.012$, $P = 0.350$ at SE Barracuda; Fig. 6C and D). (Note that, at NW Barracuda in 2000, population densities were low and survival to maturity was

unusually high. If this year is excluded from the analysis, then the pattern becomes significantly inversely density dependent ($r^2 = 0.44$, $P = 0.030$), but we had no a priori reason to exclude this year as an outlier, so we based our conclusions on analysis of the entire data set.)

Overall, populations at the naturally low-recruitment reefs never showed direct density dependence in survival to maturity, even after recruitment was artificially augmented at one reef. The differences among the reefs were primarily due to strongly differential survival at the lowest observed population sizes: below approximately 30–40 fish (Fig. 6). Despite manipulations of recruitment, at the lowest population densities observed, average survival to maturity at the naturally high-recruitment reefs exceeded 0.4, whereas survival at the

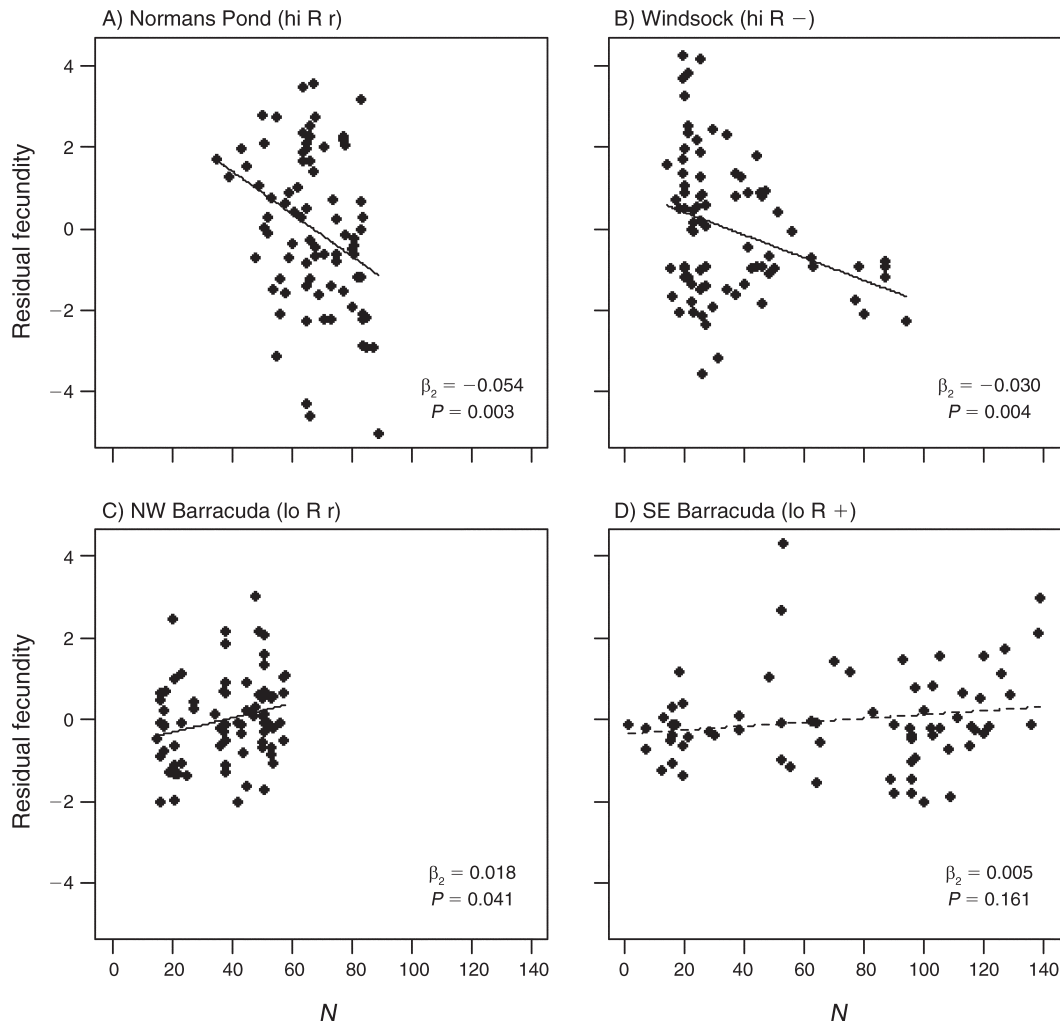


FIG. 7. Residual fecundity as a function of population size (N) at the four study reefs over all weekly surveys during the six summers that nests were monitored (2000–2005). (A) Density dependence at the naturally high-recruitment reference reef (Normans Pond, hi R r). (B) Density dependence at the naturally high-recruitment reef where new recruits were removed (Windsock, hi R -). (C) Inverse density dependence at the naturally low-recruitment reference reef (NW Barracuda, lo R r). (D) Density independence at the low-recruitment reef where new recruits were added (SE Barracuda, lo R +). Regressions are illustrated as solid lines if $P < 0.05$, and dashed lines otherwise. β_2 is the deviation in fecundity due to density.

naturally low-recruitment reefs remained less than 0.3 (with the sole exception of the lowest population size at NW Barracuda Reef in 2000, Fig. 6C).

Fecundity.—Fecundity measured as square-root transformed egg production per nest was density dependent (declining as density increased) at both Normans Pond Reef ($\beta_2 = -0.054$, $SE = 0.018$, $P = 0.003$, Fig. 7A) and Windsock Reef ($\beta_2 = -0.030$, $SE = 0.010$, $P = 0.004$, Fig. 7B, where variance was best modeled as a power function of density). Fecundity was slightly yet significantly inversely density-dependent at NW Barracuda Reef ($\beta_2 = 0.018$, $SE = 0.009$, $P = 0.041$, Fig. 7C), and density-independent at SE Barracuda Reef ($\beta_2 = 0.005$, $SE = 0.004$, $P = 0.161$, Fig. 7D), despite the wide range of densities that occurred throughout the eight years. Note that Fig. 7 displays residual fecundity

values. Gross fecundity (mean area of egg masses \pm SEM) was higher at the two reefs located closest to Exuma Sound (Normans Pond, 19.4 ± 0.70 cm²; Windsock, 22.1 ± 0.90 cm²) and substantially lower at the two more isolated Barracuda Reefs (NW Barracuda: 12.4 ± 1.0 cm²; SE Barracuda: 13.2 ± 1.1 cm²).

Tests for local population regulation

Local populations of bicolor damselfish at the two reefs with the highest natural levels of recruitment (Normans Pond and Windsock) exhibited clear regulation over eight years (several generations): both persisted and both exhibited significant boundedness and return tendency (Table 1). This outcome was despite the fact that Windsock Reef experienced order-of-magnitude artificial reductions in recruitment for half

TABLE 1. Three measures of population regulation at four study reefs over eight years.

Reef (treatment)	Persistence?	Boundedness			Return tendency		
		Obs CV	DI CV	<i>P</i>	Obs <i>r</i>	DI <i>r</i>	<i>P</i>
Normans Pond Reef (hi R r)	yes	0.176	0.346 ± 0.003	0.001***	-0.682	0.151 ± 0.087	0.001***
Windsock Reef (hi R -)	yes	0.455	0.795 ± 0.042	0.030*	-0.673	-0.193 ± 0.066	0.024*
NW Barracuda Reef (lo R r)	yes	0.637	0.781 ± 0.030	0.183 ns	-0.421	-0.437 ± 0.044	0.541 ns
SE Barracuda Reef (lo R +)	no	0.615	0.835 ± 0.020	0.080 ns	-0.242	-0.462 ± 0.044	0.854 ns

Notes: Persistence is a yes/no measure of whether that population was extirpated during the study. Boundedness is the observed coefficient of variation (CV) of N relative to the CV expected if dynamics were density-independent (DI CV). Return tendency is the correlation (r) between $\ln(N_t)$ and $\ln(N_{t+1}/N_t)$ relative the correlation expected if dynamics were density independent (DI r). For the latter two measures, density-independent variation was generated by randomizing actual annual demographic rates 1000 times each. Thus, "Obs" is the actual observed value, "DI" is the expected density-independent value (mean ± variance), and P is the proportion of 1000 trials that the expected DI value was less than the observed value. Note that tests at SE Barracuda Reef excluded the 2000–2001 period when the local population of bicolors at that site went extinct temporarily. Treatments are as follows: hi R r, high-recruitment reference reef (Normans Pond); hi R -, high-recruitment removal reef (Windsock); lo R r, low-recruitment reference reef (NW Barracuda); lo R +, low-recruitment addition reef (SE Barracuda).

* $P < 0.05$; *** $P < 0.001$; ns, not significant.

the study period. In contrast, populations at the two reefs receiving the lowest natural recruitment (NW and SE Barracuda) showed no signs of regulation, except in the simplest and ambiguous sense that bicolors at NW Barracuda Reef persisted throughout the study (Table 1). This outcome was despite the fact that SE Barracuda experienced artificially enhanced recruitment over four years. Thus, the existence of population regulation was clearly not a simple function of variation in larval recruitment per se.

Reef structure and interspecific interactions

Reef structure.—Within study plots, there was a gradient in habitat complexity among the four study reefs, being greatest at the two reefs with the highest natural recruitment (hi R), Normans Pond and Windsock, and least at the two Barracuda Reefs with the lowest natural recruitment (lo R) (Fig. 8A; Kruskal-Wallis test $P < 0.001$, Tukey multiple comparisons $P < 0.05$, $n = 22$ plots per reef). Among study plots, the distance between coral heads inhabited by adult fish was low at the two high-recruitment reefs, and significantly much greater at the two low-recruitment reefs (Fig. 8B, Kruskal-Wallis test $P < 0.001$, Dunn multiple comparisons $P > 0.05$, $n = 10$ –22 plots per reef).

Interference competitors.—The abundance of heterospecific territorial damselfish within study plots was not substantially different among three of the four reefs, with Windsock Reef being the outlier at about triple the density of other sites (Fig. 8C). This discrepancy was correlated with the bleaching and death of many *Agaricia* corals at this reef in 1998 (see Aronson et al. 2000), resulting in high colonization of herbivorous territorial damselfishes that prefer dead coral surfaces (M. A. Hixon, unpublished manuscript). Territorial damselfishes included mostly *Stegastes dorsopunicans*, *S. leucostictus*, *S. planifrons*, and *S. variabilis*, all four of which have been shown to be competitively dominant over bicolors (Robertson 1996).

Resident and transient predators.—In contrast to territorial damselfishes, the abundance of resident

predatory fish in study plots was not significantly different among reefs, although mean values roughly followed the same pattern as habitat complexity (Fig. 8D; Kruskal-Wallis test $P > 0.05$, $n = 8$ years per reef). Resident predators included spotted moray eel (*Gymnothorax moringa*), small groupers (*Cephalopholis cruentatus*, *C. fulvus*, *Epinephelus guttatus*, *E. striatus*), and small snappers (*Lutjanus* spp.). Mortality caused by transient predators was comparable among three of the four reefs, the exception being NW Barracuda Reef, where such predators were relatively seldom seen (Fig. 8E). Based on gut contents (Randall 1967) and field observations of attacks, transient predators capable of consuming bicolors observed at the experimental patch reefs included small nurse sharks (*Ginglymostoma cirratum*), juvenile great barracuda (*Sphyraena barracuda*), and schooling jacks (*Caranx ruber* and *C. bartholomaei*).

DISCUSSION

Over an eight-year period spanning multiple generations, local populations of bicolor damselfish inhabiting four large Bahamian reefs underwent variable dynamics (summarized in Table 2). Populations at Normans Pond and Windsock Reefs were clearly regulated via direct density dependence in multiple demographic parameters. Mortality, growth, survival to adulthood (combining mortality and growth), and fecundity were all density dependent in both populations, with a single exception: individual growth was density independent at Normans Pond Reef. In contrast, two other local populations inhabiting the Barracuda Reefs were unregulated and showed no evidence of direct density dependence in any demographic rate, again with a single exception: growth of adults (but not juveniles) was density dependent at SE Barracuda Reef. Thus, density dependence in individual growth was the demographic rate least well correlated with local population regulation.

The results at Normans Pond and Windsock Reefs demonstrated that density-dependent mortality of re-

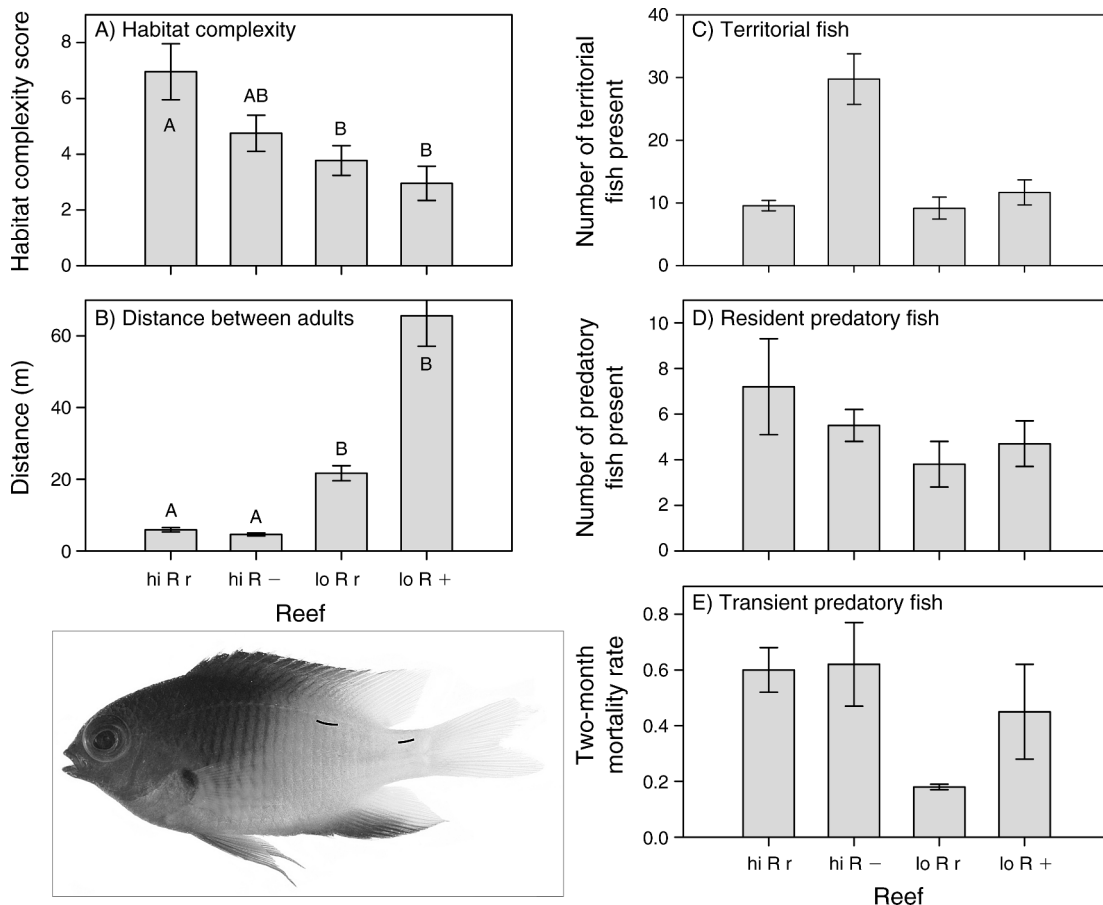


FIG. 8. Comparisons among the four study reefs of (A) within-plot habitat complexity, (B) among-plot distance to nearest coral heads with adult bicolors, (C) within-plot territorial damselfish abundance, (D) within-plot resident predatory fish abundance, and (E) mortality due to transient predatory fishes. Codes are as follows: hi R r, high-recruitment reference reef (Normans Pond); hi R -, high-recruitment removal reef (Windsock); lo R r, low-recruitment reference reef (NW Barracuda); lo R +, low-recruitment addition reef (SE Barracuda). Each bar gives the mean \pm SE of (A) 22 plots, (B) 10–22 plots (see *Methods* for explanation), (C, D) eight years, and (E) two patch reefs. In panels A and B, bars labeled with the same letters are not significantly different (Kruskal-Wallis tests followed by Tukey multiple comparisons in panel A, and by Dunn multiple comparisons in panel B).

cruit bicolors detected by short-term experiments on both patch reefs and continuous reefs near these large reefs (Carr et al. 2002, Johnson 2008) scaled-up to regulation at intergenerational time scales on entire large reefs. Among other fishes, temporal density dependence had previously been documented for several species (Webster 2003, Steele and Forrester 2005, Johnson 2006, Schmitt and Holbrook 2007), yet scaling-up of experimental demonstrations of density dependence had previously been demonstrated only for mortality of annual gobies in the same Bahamian system (Steele and Forrester 2005, Forrester et al. 2008).

Manipulating recruitment from high to low levels in our study did not shift dynamics from density dependent to density independent, or vice versa. Rather, manipulating recruitment generated broader ranges of population sizes over which density-dependent mechanisms could or could not act, and demonstrated that factors other than recruitment alone determined the presence

and strength of density dependence and subsequent regulation. Examining environmental differences among reefs provides insight on the causative mechanisms underlying these patterns.

Regulated local populations

The environments and bicolor populations at Normans Pond Reef (unmanipulated reference site) and Windsock Reef (recruitment reduction site) suggest both similarities and differences in the mechanisms of regulation. Both reefs are located near the Exuma Sound source of settlement-stage larvae, explaining naturally high recruitment levels (Shenker et al. 1993, Thorrold et al. 1994a, b, c). The biotic and abiotic environments were quite similar at these reefs, with one major difference: highly territorial heterospecific damselfishes, known to be superior interference competitors relative to bicolors (Robertson 1996), were three times more abundant at Windsock Reef, probably attracted

TABLE 2. Summary of results, comparing bicolor damselfish populations on unmanipulated reference reefs (hi R r and lo R r) to manipulated reefs where recruitment was artificially reduced (hi R -) or enhanced (lo R +).

Parameter	Reef			
	Normans Pond (hi R r)	Windsock (hi R -)	NW Barracuda (lo R r)	SE Barracuda (lo R +)
Relative recruitment				
Baseline period (natural)	high	high	low	low
Manipulation period	to high (natural)	to low (removal)	to low (natural)	to high (addition)
Density dependence				
Mortality	DD	DD	idd	di
Growth	juv di, ad di	juv DD, ad DD	juv di, ad idd	juv idd, ad DD
Survival to maturity	DD	DD	di	di
Fecundity	DD	DD	idd	di
Population regulation				
Persistence	yes	yes	yes	no
Boundedness	yes	yes	no	no
Return tendency	yes	yes	no	no
Environment				
Habitat complexity	high	medium high	medium low	low
Distance between adults	low	low	moderate	high
Territorial competitors	low	high	low	low
Resident predators	ns	ns	ns	ns
Transient predators†	high	high	low	high

Notes: Abbreviations are: DD, directly density dependent; di, density independent; idd, inversely density-dependent; juv, juvenile; ad, adult; ns = no significant differences among reefs. Manipulation period descriptions are natural (unmanipulated), removal (recruits removed), addition (recruits added), high vs. low (high vs. low parameter values) and yes vs. no (yes vs. no regarding the presence of significant components of population regulation).

† Based on simple comparison of means; inferential tests not run because $n = 2$ experimental plots per reef.

by the abundance of dead lettuce coral (due to the 1998 bleaching event) on which they established their territories (M. A. Hixon, *unpublished manuscript*). Prior field experiments near these two reefs had demonstrated that such interspecific interference competition interacted synergistically with predation in causing spatially density-dependent mortality in bicolor recruits over small spatial and temporal scales (Carr et al. 2002, Johnson 2008). Correlated with high densities of heterospecific territorial damselfishes, overall rates of mortality were highest at Windsock Reef, though the effects of increased mortality on survival to maturity were somewhat mitigated by rapid individual growth at this site. Windsock was the only study reef with strong currents on both incoming and outgoing tides. Because feeding rates of bicolors are known to increase with current speed (Stevenson 1972), it is therefore not surprising that growth rates were the highest at this reef. Besides mortality being directly density dependent, growth and fecundity were also density dependent at this reef, apparently as a result of energy being diverted to agonistic interactions with abundant territorial competitors (Figueira et al. 2008b, Johnson 2008, Samhoury 2009; see also Warner and Hoffman 1980).

In contrast, with lower levels of interspecific competition from territorial damselfishes, overall mortality rates were lower at Normans Pond Reef and directly density-dependent mortality was most evident for new recruits and juveniles. The outcome was that this population reached the highest abundances of all four

study reefs. We hypothesize that, because interspecific competition was relatively low, density-dependent fecundity evident at this reef was caused more by intraspecific competition for food. Consistent with this hypothesis, planktonic food may be limiting for bicolors in other regions (Nemeth 1997), as well as for other species of damselfish (e.g., Jones 1986, Forrester 1990, Booth 1995). Inconsistent with this hypothesis, feeding experiments near our study reefs indicated that density dependence in bicolors was not influenced by food supply (Samhoury 2009), and in the Florida Keys, local variation in demographic rates of bicolors was not correlated with the availability of planktonic prey (Figueira et al. 2008b). Alternatively, high densities at this site could have resulted in substantial intraspecific competition for mates.

Unregulated local populations

Almost no evidence of direct density dependence was detected at the two Barracuda Reefs, and the local populations at these reefs failed all tests for regulation, except for the ambiguous result that the population inhabiting NW Barracuda persisted over all eight years (an insufficient period to distinguish true persistence from a random walk). In a two-year demographic study in the Florida Keys, Figueira et al. (2008b) also detected no density dependence in bicolors.

Bicolor populations at the Barracuda Reefs were naturally and severely starved of recruits, being located relatively far from the Exuma Sound source of larvae.

Such recruitment-limited populations have long been predicted to have density-independent dynamics (Doherty 1981, 1998). Mechanistically, recruitment-limited population sizes could have been so low that both competition and density-dependent predation were precluded, and indeed, the integrated measure of survival to maturity was density independent at both these reefs. However, we artificially enhanced recruitment at SE Barracuda Reef to high levels, yet no density dependence in any demographic rate was subsequently detected in this population, with a single exception: inversely density-dependent growth of juveniles later compensated by directly density-dependent growth of adults. At NW Barracuda Reef, most demographic rates were slightly inversely density dependent.

Regulated vs. unregulated local populations

What explains the lack of local population regulation at the Barracuda Reefs? Further, what was the source of inverse density dependence in these populations? The most consistent difference between regulated populations (at Normans Pond and Windsock Reefs) and unregulated populations (at the Barracuda Reefs) involved survival to maturity (which integrates mortality-at-size and size-at-age): such survival was directly density dependent in both regulated populations and density independent in both unregulated populations. Survival to maturity was similar among all four reefs at higher densities ($N > 50$ fish). However, at the lowest densities observed, the regulated populations typically showed much higher survival (i.e., density dependence) than the unregulated populations. Thus, the key mechanistic differences between regulated and unregulated populations operated at low densities.

The major environmental difference between the environments of regulated and unregulated populations was reef structure: at the reefs with unregulated populations, coral habitat complexity within plots occupied by bicolors was somewhat lower, yet more obviously, the distance between coral heads inhabited by adult bicolors was much greater than at reefs with regulated populations. Thus, fish in unregulated populations faced potential prey-refuge constraints at two spatial scales: within patch and between patch. Within suitable patches, less habitat complexity would normally mean greater competition for prey refuges (i.e., density dependence). However, habitat complexity differed a maximum of only about twofold between regulated and unregulated populations, whereas recruitment naturally differed by an order of magnitude. Thus, even within patches of suitable habitat, prey refuges were likely less scarce in the more recruitment-limited unregulated populations than in the more saturated regulated populations. Indeed, only about half the 22 study plots at each of the unregulated populations ever supported adult bicolors (though they frequently supported juveniles). In contrast, all 22 plots at both regulated populations supported adults.

We believe that the key difference between regulated and unregulated populations was the much larger between-patch distances in the latter, and that the demographic importance of inter-patch spacing was manifested primarily at lower population densities. When densities are sufficiently high that each patch is inhabited by multiple individuals, social and mating interactions can occur within that patch with relatively little exposure to predation, explaining the comparable survival rates among all four reefs at higher population sizes. However, at lower population sizes, especially when there is only a single individual per patch, we hypothesize that between-patch visits become more common, with an associated increase in exposure to predation (e.g., Dill and Fraser 1984), which may have effects that are both lethal (increased mortality) and sublethal (reduced growth and fecundity). It is well documented that bicolors regularly visit neighboring fish in adjacent coral habitat patches (Myrberg 1972, Knapp and Kovach 1991, Knapp and Warner 1991, Knapp 1993, 1995, Cole and Sadovy 1995, Knapp et al. 1995). This activity occurs mostly at dawn, which precluded such observations at some of our study reefs. We hypothesize that, in the unregulated populations (relative to the regulated populations) at lower population sizes, higher between-patch distances led to longer time in transit during visitations, and thus greater exposure to predators, explaining not only the absence of density dependence, but also the occasional occurrence of weak inverse density dependence in mortality, growth, and fecundity. This effect could possibly be exacerbated by a phenomenon previously documented in our study system whereby predators tend to focus on relatively rare prey species, which would characterize bicolors at their lowest densities (Almany and Webster 2004).

These among-reef differences placed bicolors at the Barracuda Reefs at greater risk from predation due to lower availability of physical shelter both within and between plots (a pattern also suggested in the Florida Keys by Figueira et al. 2008b). At home coral heads within plots, less physical shelter providing fewer prey refuges means fewer individuals survive to adulthood, as has been previously documented for bicolors (Nemeth 1997, Almany 2004) and numerous others reef fishes (e.g., Roberts and Ormond 1987, Jones 1988, Beukers and Jones 1997; review by Gratwicke and Speight 2005). Consistent with the importance of predation, male bicolor damselfish are known to court females less frequently in the presence of piscivores (Figueira and Lyman 2007), and where bicolors inhabit gorgonian fields that limit the field of view (unlike our study), predation risk is substantial (Rilov et al. 2007). All told, habitat structure interacting with predation was the most parsimonious explanation for the lack of direct density dependence at the Barracuda Reefs and the resulting lack of local population regulation.

Implications for metapopulation regulation

Marine metapopulations differ somewhat from more restrictive concepts of metapopulations developed for terrestrial species in that dispersal among isolated local populations is more common and extirpation is less common (Kritzer and Sale 2004, 2006). Demersal marine fishes and invertebrates form such metapopulations, commonly called “stocks” in fisheries biology (Frank and Leggett 1994). Entire marine metapopulations are regulated when they include some local source populations that are both substantial in size and locally regulated, “source” in this sense occurring where the self-recruitment rate exceeds the death rate (Armsworth 2002). In our study region, local populations of bicolors similar to those where we documented regulation are in fact self-recruiting, as shown by genetic studies that have detected parents and their offspring inhabiting the same reefs (Christie et al. 2010). Thus, the local regulatory mechanisms detected and inferred here are likely to contribute to the regulation of the regional metapopulation. The fact that locally regulated populations in our study exhibited density dependence in both mortality and fecundity suggests that regulation at the scale of the regional metapopulation could possibly involve two mechanisms: (1) density-dependent mortality within local populations regulating the regional number of spawners and (2) a density-dependent regional larval supply.

In contrast to the regulated populations, one of the two unregulated local populations in our study naturally suffered extirpation, albeit temporarily. It is likely that bicolor populations at these two reefs, located far from the source of settlement-stage larvae, experiencing very low recruitment rates and showing almost no evidence of direct density dependence, were replenished by larval dispersal from other populations. These populations are thus “sinks” in the sense of requiring larval subsidies from other local populations to persist (Armsworth 2002). These reefs were also characterized by low structural complexity, and thus low availability of spatial prey refuges. The density-independent and inversely density-dependent relationships between population size and fecundity at these reefs suggest that, if all local populations were forced to sufficiently low levels due to habitat degradation, then fecundity could become inversely density dependent universally and global extinction could occur. Therefore, widespread bleaching and death of corals manifested by ocean warming, with increasing exacerbation via ocean acidification (Hoegh-Guldberg et al. 2007, Anthony et al. 2011), paints an ominous picture of the future of reef fishes with dynamics similar to those of bicolor damselfish (see also Graham et al. 2007, 2011).

Implications for marine conservation and fisheries management

Predation on new recruits was the primary mechanism underlying local density dependence and population regulation in this system, with interference competition

by territorial heterospecifics playing an important synergistic role in that both interactions were previously shown to be required to cause density-dependent mortality (Carr et al. 2002, see also Figueira et al. 2008a). Combined with prior findings in a broad variety of not only tropical species (reviews by Hixon and Webster 2002, Osenberg et al. 2002) but also temperate species, many of which are the targets of fisheries (reviews by Houde 1987, Myers and Cadigan 1993, Bailey 1994), these patterns lend credence to the conclusions of Hixon and Jones (2005) that regulating density dependence in demersal marine fishes in general often involves the effects of predation on the species of interest. Importantly, the threat of predation may exogenously cause within-species competition for prey refuges, and such competition may be more common than the simple endogenous intraspecific competition for food and other non-refuge resources assumed by single-species fisheries models. Indeed, a major manifestation of intraspecific competition for food, density-dependent growth, was the least well correlated with population regulation of all demographic parameters measured in our system, being evident in one of two regulated populations and in one of two unregulated populations. To the extent these collective findings in both temperate and tropical fishes are general, they provide a caveat to conservation biologists and fisheries managers: preservation of among-species interactions, especially predation (i.e., local biodiversity), may be necessary to conserve natural regulatory mechanisms of demersal marine species. Such holistic approaches are the essence of ecosystem-based management (Pikitch et al. 2004, Francis et al. 2007).

The next phase of understanding the dynamics and regulation of marine fish metapopulations will be the integration of the details of local demography, as documented here, with the pattern and extent of larval dispersal among local populations (Hixon 2011), which is currently being elucidated for bicolor damselfish (Christie et al. 2010, Hogan et al. 2011). Such integration will at last provide mechanistic knowledge of what drives and regulates entire metapopulations, with further insights for both fisheries management and marine conservation.

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LITERATURE CITED

- Almany, G. R. 2004. Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113.
- Almany, G. R., and M. S. Webster. 2004. Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* 85:2933–2937.
- Anthony, K. R. N., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience. *Global Change Biology* 17:1798–1808.
- Armsworth, P. R. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. *Ecology* 83:1092–1104.
- Aronson, R. B., W. F. Precht, I. G. Macintyre, and T. J. T. Murdoch. 2000. Coral bleach-out in Belize. *Nature* 405:36.
- Bailey, K. M. 1994. Predation on juvenile flatfish and recruitment variability. *Netherlands Journal of Sea Research* 32:175–189.
- Beukers, J. S., and G. P. Jones. 1997. Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59.
- Beukers, J. S., G. P. Jones, and R. M. Buckley. 1995. Use of implant microtags for studies on populations of small reef fishes. *Marine Ecology Progress Series* 125:61–66.
- Bolker, B. M. 2008. *Ecological models and data* in R. Princeton University Press, Princeton, New Jersey, USA.
- Booth, D. J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and demography. *Ecology* 76:91–106.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Cappuccino, N., and P. W. Price, editors. 1995. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, California, USA.
- Carpenter, S. R., J. J. Cole, J. R. Hodgson, J. F. Kitchell, M. L. Pace, D. Bade, K. L. Cottingham, T. E. Essington, J. N. Houser, and D. E. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. *Ecological Monographs* 71:163–186.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences USA* 99:11241–11245.
- Cerri, R. D., and D. F. Fraser. 1983. Predation and risk in foraging minnows: balancing conflicting demands. *American Naturalist* 121:552–561.
- Christie, M. R., D. W. Johnson, C. D. Stallings, and M. A. Hixon. 2010. Self-recruitment and sweepstakes reproduction amid extensive gene flow in a coral-reef fish. *Molecular Ecology* 19:1042–1057.
- Cole, K. S., and Y. Sadovy. 1995. Evaluating the use of spawning success to estimate reproductive success in a Caribbean reef fish. *Journal of Fish Biology* 47:181–191.
- Courchamp, F., T. Clutton-Brock, and B. Grenfell. 1999. Inverse density dependence and the Allee effect. *Trends in Ecology and Evolution* 14:405–410.
- Dill, L. M., and A. H. G. Fraser. 1984. Risk of predation and the feeding behavior of juvenile coho salmon (*Oncorhynchus kisutch*). *Behavioral Ecology and Sociobiology* 16:65–71.
- Doherty, P. J. 1981. Coral reef fishes: recruitment-limited assemblages? *Proceedings of the Fourth International Coral Reef Symposium* 2:465–470.
- Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. Pages 261–293 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.
- Doherty, P. J. 1998. Recruitment limitation: definitions, predictions and tests. Pages 129–131 in G. P. Jones, P. J. Doherty, B. D. Mapstone, and L. Howlett, editors. *Reef fish '95: recruitment and population dynamics of coral reef fishes*. CRC Reef Research Center, Townsville, Australia.
- Doherty, P. J. 2002. Variable replenishment and the dynamics of reef fish populations. Pages 327–355 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Doherty, P. J., and D. M. Williams. 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology: An Annual Review* 26:487–551.
- Ebert, T. A. 1980. Estimating parameters in a flexible growth equation, the Richards function. *Canadian Journal of Fisheries and Aquatic Sciences* 37:687–692.
- Emery, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida keys. *Bulletin of Marine Science* 23:649–770.
- Figueira, W. F. 2009. Connectivity or demography: defining sources and sinks in coral reef fish metapopulations. *Ecological Modelling* 220:1126–1137.
- Figueira, W. F., D. J. Booth, and M. A. Gregson. 2008a. Selective mortality of a coral reef damselfish: role of predator–competitor synergisms. *Oecologia* 156:215–226.
- Figueira, W. F., and S. J. Lyman. 2007. Context-dependent risk tolerance of the bicolor damselfish: courtship in the presence of fish and egg predators. *Animal Behavior* 74:329–336.
- Figueira, W. F., S. J. Lyman, L. B. Crowder, and G. Rilov. 2008b. Small-scale demographic variability of the bicolor damselfish, *Stegastes partitus*, in the Florida keys USA. *Environmental Biology of Fishes* 81:297–311.
- Forrester, G. E. 1990. Factors influencing the juvenile demography of a coral reef fish. *Ecology* 71:1666–1681.
- Forrester, G. E., M. A. Steele, J. F. Samhuri, B. Evans, and R. R. Vance. 2008. Spatial density dependence scales up but does not produce temporal density dependence in a reef fish. *Ecology* 89:2980–2985.
- Fox, D. R., and T. J. Ridsdill-Smith. 1996. Detecting density dependence. Pages 45–51 in R. B. Floyd, A. W. Sheppard, and P. J. D. Barro, editors. *Frontiers of population ecology*. CSIRO Publishing, Melbourne, Australia.
- Fox, G. A. 2001. Failure-time analysis: studying times to events and rates at which events occur. Pages 235–266 in S. M. Scheiner and J. Gurevich, editors. *Design and analysis of ecological experiments*. Oxford University Press, New York, New York, USA.
- Francis, R. C., M. A. Hixon, M. E. Clarke, S. A. Murawski, and S. Ralston. 2007. Ten commandments for ecosystem-based fisheries scientists. *Fisheries* 32:217–233.
- Frank, K. T., and W. C. Leggett. 1994. Fisheries ecology in the context of ecological and evolutionary theory. *Annual Review of Ecology and Systematics* 25:401–422.
- Frederick, J. L. 1997. Evaluation of fluorescent elastomer injection as a method for marking small fish. *Bulletin of Marine Science* 61:399–408.
- Graham, N. A. J., P. Chabanet, R. D. Evans, S. Jennings, Y. Letourneur, M. A. MacNeil, T. R. McClanahan, M. C. Öhman, N. V. C. Polunin, and S. K. Wilson. 2011. Extinction vulnerability of coral reef fishes. *Ecology Letters* 14:341–348.
- Graham, N. A. J., S. K. Wilson, S. Jennings, N. V. C. Polunin, J. Robinson, J. P. Bijoux, and T. M. Daw. 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish,

- fisheries, and ecosystems. *Conservation Biology* 21:1291–1300.
- Gratwicke, B., and M. R. Speight. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *Journal of Fish Biology* 66:650–667.
- Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley Interscience, Chichester, UK.
- Helser, T. E., and H. L. Lai. 2004. A Bayesian hierarchical meta-analysis of fish growth: with an example for North American largemouth bass, *Micropterus salmoides*. *Ecological Modeling* 178:399–416.
- Hixon, M. A. 2011. 60 years of coral-reef fish ecology: past, present, future. *Bulletin of Marine Science* 87:727–765.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859.
- Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.
- Hixon, M. A., and M. S. Webster. 2002. Density dependence in reef fish populations. Pages 303–325 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Hoegh-Guldberg, O., et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742.
- Hoey, A. S., and M. I. McCormick. 2006. Effects of subcutaneous fluorescent tags on the growth and survival of a newly settled coral reef fish, *Pomacentrus amboinensis* (Pomacentridae). *Proceedings of the 10th International Coral Reef Symposium* 1:420–424.
- Hogan, J. D., R. J. Thiessen, P. F. Sale, and D. D. Heath. 2012. Local retention, dispersal and fluctuating connectivity among populations of a coral reef fish. *Oecologia* 168:61–71.
- Holbrook, S. J., and R. J. Schmitt. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868.
- Holyoak, M., and J. H. Lawton. 1993. Comment arising from a paper by Wolda and Dennis: using and interpreting the results of tests for density dependence. *Oecologia* 95:592–594.
- Houde, E. D. 1987. Fish early life dynamics and recruitment variability. *American Fisheries Society Symposium Series* 2:17–29.
- Houde, E. D. 2009. Recruitment variability. Pages 91–171 in T. Jakobsen, M. J. Fogarty, B. A. Megrey, and E. Moksness, editors. *Fish reproductive biology: implications for assessment and management*. Wiley-Blackwell, West Sussex, UK.
- Hughes, T. P. 1990. Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71:12–20.
- Johnson, D. W. 2006. Predation, habitat complexity, and variation in density-dependent mortality of temperate reef fishes. *Ecology* 87:1179–1188.
- Johnson, D. W. 2008. Combined effects of condition and density on post-settlement survival and growth of a marine fish. *Oecologia* 155:43–52.
- Johnson, D. W., M. R. Christie, and J. Moye. 2010. Quantifying evolutionary potential of marine fish larvae: heritability, selection, and evolutionary constraints. *Evolution* 64:2614–2628.
- Johnson, D. W., and M. A. Hixon. 2010. Ontogenetic and spatial variation in size-selective mortality of a marine fish. *Journal of Evolutionary Biology* 23:724–737.
- Johnson, D. W., and M. A. Hixon. 2011. Sexual and lifetime selection on body size in a marine fish: the importance of life-history trade-offs. *Journal of Evolutionary Biology* 24:1653–1663.
- Jones, G. P. 1986. Food availability affects growth in a coral reef fish. *Oecologia* 70:136–139.
- Jones, G. P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on the juveniles of two coral reef fishes. *Journal of Experimental Marine Biology and Ecology* 123:115–126.
- Knapp, R. A. 1993. The influence of egg survivorship on the subsequent nest fidelity of female bicolor damselfish, *Stegastes partitus*. *Animal Behavior* 46:111–121.
- Knapp, R. A. 1995. Influence of energy reserves on the expression of a secondary sexual trait in male bicolor damselfish, *Stegastes partitus*. *Bulletin of Marine Science* 57:672–681.
- Knapp, R. A., and J. T. Kovach. 1991. Courtship as an honest indicator of male parental quality in the bicolor damselfish, *Stegastes partitus*. *Behavioral Ecology* 2:295–300.
- Knapp, R. A., P. C. Sikkil, and V. T. Vredenburg. 1995. Age of clutches in nests and the within-nest spawning-site preferences of three damselfish species (Pomacentridae). *Copeia* 1995:78–88.
- Knapp, R. A., and R. R. Warner. 1991. Male parental care and female choice in the bicolor damselfish, *Stegastes partitus*: bigger is not always better. *Animal Behavior* 41:747–756.
- Kritzer, J. P., and P. F. Sale. 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. *Fish and Fisheries* 5:131–140.
- Kritzer, J. P., and P. F. Sale, editors. 2006. *Marine metapopulations*. Elsevier Academic Press, Burlington, Massachusetts, USA.
- Malone, J. C., G. E. Forrester, and M. A. Steele. 1999. Effects of subcutaneous microtags on the growth, survival, and vulnerability to predation of small reef fishes. *Journal of Experimental Marine Biology and Ecology* 237:243–253.
- Morris, W. E., and D. F. Doak. 2002. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Myers, R. A. 2002. Recruitment: understanding density-dependence in fish populations. Pages 123–148 in P. J. B. Hart and J. D. Reynolds, editors. *Handbook of fish biology and fisheries*. 1. Fish biology. Blackwell Science, Malden, Massachusetts, USA.
- Myers, R. A., N. J. Barrowman, J. A. Hutchings, and A. A. Rosenberg. 1995. Population dynamics of exploited fish stocks at low population levels. *Science* 269:1106–1108.
- Myers, R. A., and N. G. Cadigan. 1993. Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Sciences* 50:1576–1590.
- Myrberg, A. A. 1972. Social dominance and territoriality in the bicolor damselfish, *Eupomacentrus partitus* (Poey) (Pisces: Pomacentridae). *Behaviour* 41:207–231.
- Nemeth, R. S. 1997. Spatial patterns of bicolor damselfish in Jamaica and St. Croix are determined by similar postsettlement processes. *Proceedings of the 8th International Coral Reef Symposium* 1:1017–1022.
- Nemeth, R. S. 1998. The effects of natural variation in substrate architecture on the survival of juvenile bicolor damselfish. *Environmental Biology of Fishes* 53:129–141.
- Nemeth, R. S. 2005. Linking larval history to juvenile demography in the bicolor damselfish *Stegastes partitus* (Perciformes: Pomacentridae). *Revista de Biologia Tropical* 53 (Supplement 1):155–163.
- Osenberg, C. W., C. M. S. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters* 5:715–721.

- Paris, C. B., and R. K. Cowen. 2004. Direct evidence of a biophysical retention mechanism for coral reef fish larvae. *Limnology and Oceanography* 49:1964–1979.
- Pikitch, E. K., et al. 2004. Ecosystem-based fishery management. *Science* 305:346–347.
- Pollard, E., K. H. Lakhani, and P. Rothery. 1987. The detection of density dependence from a series of annual censuses. *Ecology* 68:2046–2055.
- R Development Core Team. 2010. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.r-project.org
- Randall, J. E. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* 5:665–847.
- Rilov, G., W. F. Figueira, S. J. Lyman, and L. B. Crowder. 2007. Complex habitats may not always benefit prey: linking visual field with reef fish behavior and distribution. *Marine Ecology Progress Series* 329:225–238.
- Roberts, C. M., and R. F. G. Ormond. 1987. Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. *Marine Ecology Progress Series* 41: 1–8.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. *Ecology* 77:885–899.
- Robertson, D. R., D. G. Green, and B. C. Victor. 1988. Temporal coupling of reproduction and recruitment of larvae of a Caribbean reef fish. *Ecology* 69:370–381.
- Robertson, D. R., C. W. Petersen, and J. D. Brawn. 1990. Lunar reproductive cycles of benthic-brooding reef fishes: reflections of larval biology or adult biology? *Ecological Monographs* 60:311–329.
- Samhuri, J. F. 2009. Food supply influences offspring provisioning but not density-dependent fecundity in a marine fish. *Ecology* 90:3478–3488.
- Schmale, M. C. 1981. Sexual selection and reproductive success in males of the bicolor damselfish *Eupomacentrus partitus* (Pisces: Pomacentridae). *Animal Behavior* 29:1172–1184.
- Schmitt, R. J., and S. J. Holbrook. 2007. The scale and cause of spatial heterogeneity in strength of temporal density dependence. *Ecology* 88:1241–1249.
- Shenker, J. M., E. D. Maddox, E. Wishinski, A. Pearl, S. R. Thorrold, and N. Smith. 1993. Onshore transport of settlement-stage Nassau grouper *Epinephelus striatus* and other fishes in Exuma Sound, Bahamas. *Marine Ecology Progress Series* 98:31–43.
- Sponaugle, S., and R. K. Cowen. 1996. Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Marine and Freshwater Research* 47:433–447.
- Steele, M. A., and G. E. Forrester. 2005. Small-scale field experiments accurately scale up to predict density dependence in reef fish populations at large scales. *Proceedings of the National Academy of Sciences USA* 102:13513–13516.
- Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends in Ecology and Evolution* 14:401–405.
- Stevenson, R. A. 1972. Regulation of feeding behavior of the bicolor damselfish (*Eupomacentrus partitus* Poey) by environmental factors. Pages 278–302 in H. E. Winn and B. L. Olla, editors. *Behavior of marine animals, Volume 2, Vertebrates*. Plenum, New York, New York, USA.
- Thorrold, S. R., J. M. Shenker, E. D. Maddox, R. Mojica, and E. Wishinski. 1994a. Larval supply of shorefishes to nursery habitats around Lee Stocking Island, Bahamas. II. Lunar and oceanographic influences. *Marine Biology* 118:567–578.
- Thorrold, S. R., J. M. Shenker, R. Mojica, E. D. Maddox, and E. Wishinski. 1994b. Temporal patterns in the larval supply of summer-recruiting reef fishes to Lee Stocking Island, Bahamas. *Marine Ecology Progress Series* 112:75–86.
- Thorrold, S. R., J. M. Shenker, E. Wishinski, R. Mojica, and E. D. Maddox. 1994c. Larval supply of shore fishes to nursery habitats around Lee Stocking Island, Bahamas. I. Small scale distribution patterns. *Marine Biology* 118:555–566.
- Thresher, R. E. 1984. *Reproduction in reef fishes*. T. F. H. Publishers, Neptune City, New Jersey, USA.
- Turchin, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 in N. Cappuccino and P. W. Price, editors. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, California, USA.
- Turchin, P. 1999. Population regulation: a synthetic view. *Oikos* 84:153–159.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, New Jersey, USA.
- Warner, R. R., and S. G. Hoffman. 1980. Population density and the economics of territorial defense in a coral reef fish. *Ecology* 61:772–780.
- Webster, M. S. 2003. Temporal density dependence and population regulation in a marine fish. *Ecology* 84:623–628.
- Weisberg, S., G. Spangler, and L. Richmond. 2010. Mixed effects models for fish growth. *Canadian Journal of Fisheries and Aquatic Sciences* 67:269–277.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64:1540–1548.
- White, J. W., J. F. Samhuri, A. C. Stier, C. L. Wormald, S. L. Hamilton, and S. A. Sandin. 2010. Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale. *Ecology* 91:1949–1961.
- White, J. W., and R. R. Warner. 2007. Safety in numbers and the spatial scaling of density dependent mortality in a coral reef fish. *Ecology* 88:3044–3054.

SUPPLEMENTAL MATERIAL

Appendix A

Evaluation of Type I error rates in tests for population regulation (*Ecological Archives* M082-017-A1).

Appendix B

Coefficients associated with tests of density dependence in mortality of bicolor damselfish in each of the four study populations (*Ecological Archives* M082-017-A2).

Appendix C

Coefficients associated with tests of density dependence in growth of bicolor damselfish in each of the four study populations (*Ecological Archives* M082-017-A3).

Data Availability

Data associated with this paper have been deposited in Dryad: <http://dx.doi.org/10.5061/dryad.r6b3s>