

Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs

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ABSTRACT: Understanding the role of density dependence in the regulation of marine fish populations is particularly crucial as species face increased risk of extinction. Yet, spatial and temporal heterogeneity can easily mask density dependence. By experimentally manipulating group sizes of the yellowhead wrasse *Halichoeres garnoti* on both natural and artificial reefs, I determined that the relationship between density and mortality varied with reef spatial structure. On natural reefs, mortality rates were highly variable among reefs. However, losses also resulted from emigration to neighboring patches, and thus persistence of fish remaining on natural reefs was approximately density-dependent. On artificial reefs, mortality was density-dependent on reefs that were spatially isolated, and high and density-independent on reefs that were aggregated. Emigration was virtually zero among these reefs. Overall predator visitation rates were significantly higher to artificial than natural reefs, but a greater diversity and size range of predators were present on natural reefs. Based on observations that yellowhead wrasse formed tighter aggregations in the presence of predators (rather than seeking shelter in the reef), differences between artificial and natural reefs were likely not related to differences in reef complexity. Instead, on artificial reefs, standardizing reef spacing resulted in density-dependent versus density-independent mortality according to reef isolation. In contrast, heterogeneity in reef spacing among natural reefs likely caused variation in predation risk that in turn caused high variability in mortality rates. Small-scale spatial variation in predation may play an important role in the population dynamics of species that occur within patchy environments.

KEY WORDS: Population regulation · Density dependence · Mortality · Predation · Emigration · Habitat heterogeneity · Coral-reef fishes · *Halichoeres garnoti*

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INTRODUCTION

Understanding what drives fluctuations in marine fish populations is crucial as both exploited and unexploited species face an increased risk of extinction through global overfishing and other human activities (Roberts & Hawkins 1999, Musick et al. 2000, Pauly et al. 2002). Sources of temporal and spatial variation in abundance are particularly challenging to identify in relatively open marine populations, where the input of new individuals (i.e. the local birth rate) is unrelated to the reproductive output of resident adults (for recent exceptions, see Jones et al. 1999, Swearer et al. 1999).

Although both density-independent and density-dependent factors influence population dynamics, density dependence in at least one demographic rate is necessary for a population to persist indefinitely (Murdoch & Walde 1989, Sinclair 1989). Despite decades of intense debate, the role of density dependence in the regulation of fish populations continues to be controversial (reviews in Cushing 1995, Caley et al. 1996, Hixon 1998, Sale & Tolimieri 2000, Doherty 2002, Forrester et al. 2002, Hixon et al. 2002, Hixon & Webster 2002). Yet, successful conservation and management of marine fish populations depends on the protection of natural mechanisms of regulation. Indeed, estimates of the

strength of density dependence form the basis for much of fisheries management (Hilborn & Walters 1992).

Regulated populations may undergo tremendous fluctuations, and thus exhibit significant stochasticity in demographic rates, thereby masking the detection of density dependence (Wolda 1989). From a conservation perspective, it is dangerous to assume that density dependence is not occurring whenever it is not detected, because unknown stochastic variation or time lags could easily preclude its detection (Lande 2003). Similarly, it is risky to assume that density dependence will necessarily result in a surplus of individuals to harvest as practiced in fisheries. In addition, biased estimates of the strength of density dependence, for example those based on erroneous age-composition data, could lead to the overharvest of exploited species (Zabel & Levin 2002). The strongest evidence for density dependence, and indeed the only way to investigate its underlying mechanisms, comes from experimental manipulations (Murdoch 1970).

Coral-reef fishes are ideal systems in which to investigate density dependence, because local populations can be observed and manipulated *in situ* (Sale 1991). Studies of coral-reef fishes are relevant to understanding the population dynamics of other demersal marine fishes based on similarities between results from research conducted on reef fish and temperate species: for both, density-dependent mortality is becoming increasingly well-documented and predation is increasingly accepted as the cause of this density dependence (Hixon & Webster 2002, and references therein). Coral-reef fishes may also be the best model species for understanding how spatial and/or temporal heterogeneity affect density dependence. For example, spatial co-variance between settlement and site quality has recently been shown to mask strong density dependence in reef fishes (Wilson & Osenberg 2002, Shima & Osenberg 2003). In addition, a recent meta-analysis of density dependence in reef fishes demonstrated that the strength of density dependence did not differ between studies in which authors concluded that survival was density-dependent versus those in which they concluded it was density-independent (Osenberg et al. 2002). These findings strongly suggest the need for a better understanding of the consequences of heterogeneity for potentially density-dependent interactions.

Mortality has been shown to be density-dependent for a majority of reef fish species studied to date (review by Hixon & Webster 2002; see also Carr et al. 2002, Wilson & Osenberg 2002, Webster 2003). Predation, especially on young juveniles, has often been shown to be the proximate or ultimate source of such post-settlement mortality (e.g. Connell 1996, 1997, Hixon & Carr 1997, Connell 2000, Planes & Lecaillon

2001, Stewart & Jones 2001, Carr et al. 2002, Steele & Forrester 2002, Webster 2002). The magnitude of predation has been shown to vary with habitat complexity, within and among species, and between seasons (Carr & Hixon 1995, Beukers & Jones 1997, Steele et al. 1998, Anderson 2001, Steele & Forrester 2002). However, temporal and spatial variation in density-dependent mortality are not well documented (but see Beukers & Jones 1997, Steele & Forrester 2002).

In this study, I compared the mortality rates of yellowhead wrasse *Halichoeres garnoti* on natural and artificial reefs to examine the effects of spatial structure on the detection of density dependence. I use the term 'spatial structure' to refer to the spatial arrangement of reef habitat within a mosaic of patch reefs. I was particularly interested in mechanisms (e.g. predation) that potentially operate at the spatial scale of a collection of patch reefs (e.g. 100s of m²), yet affect demographic rates on the smaller spatial scale of an individual reef. This spatial scale of a collection of patch reefs will be referred to as a 'neighborhood' throughout the paper. I specifically addressed the following questions: (1) Are mortality rates of recently-settled wrasse density-dependent? (2) Does the relationship between mortality and density vary with spatial structure? (3) How does predation differ between the 2 systems in terms of frequency of predator visitation, predator abundance, and species composition?

MATERIALS AND METHODS

Study area and species. Experiments and observations were conducted on natural and artificial reefs in the vicinity of the Caribbean Marine Research Center (CMRC) on Lee Stocking Island, Bahamas (23° 46' N, 76° 10' W) in the summers (June to August) of 2000 and 2001. During this period, juvenile yellowhead wrasse were common on shallow reefs in this area (<15 m depth) and formed loose, nonpolarized single-species aggregations containing 3 to 30 individuals (author's pers. obs.). Like most other Caribbean labrids, settlement in this microcarnivorous species occurs when individuals bury under the sand and emerge on the reef several days later (Sponaugle & Cowen 1997). This species settles monthly, primarily around the new moon at ~11 to 12 mm standard length after being in the plankton for ~25 d (Sponaugle & Cowen 1997).

Experiment on natural reefs. In June 2000, I manipulated yellowhead wrasse densities on 12 natural patch reefs by removing recently-settled individuals (18 to 23 mm total length [TL]) to establish the same range of group sizes (6 to 18 fish per reef) on both small

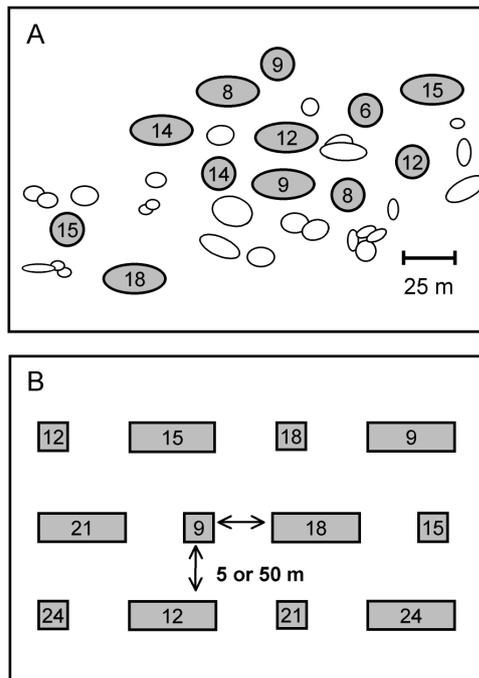


Fig. 1. Experimental design. (A) Map of natural reef site showing experimental reefs (shaded) and representative patches of intervening reef habitat (white). Numbers indicate initial group-size treatments of yellowhead wrasse (number remaining 24 h after removals). Distances between experimental reefs are drawn to scale ($\bar{x} = 28$ m). Large reefs were ~ 3 times the area of small reefs (small: 1.4 ± 0.3 [SD] m^2 , $n = 6$; large: 4.0 ± 0.9 m^2 , $n = 6$) and mean height of all reefs was similar (0.8 ± 0.1 m). (B) Design of the 2 artificial reef arrays, which differed only in terms of reef spacing (5 vs 50 m between reefs). In each array, small reefs ($0.8 \times 0.8 \times 0.6$ m, 24 concrete blocks; $n = 6$) alternated with large reefs ($2.4 \times 0.8 \times 0.6$ m, 72 concrete blocks; $n = 6$). Numbers indicate initial group size treatments of transplanted yellowhead wrasse. The spatial allocation of treatments was identical for the 2 arrays

and large reefs in a regression design. I chose reefs of 2 size categories, where the area of each large reef was approximately 3 times that of each small reef (Fig. 1A). By establishing the same treatment ranges on both reef sizes, I tested the hypothesis that mortality was a function of density measured as the number of fish per reef (i.e. independent of reef size), rather than the number of fish per unit area (see Shima 2001). I reasoned that because individuals of this species seek shelter in groups rather than in the physical structure of the reef (see 'Behavioral observations', this section), density measured per unit area would be less relevant than the number of fish per reef.

Each reef consisted of multiple heads of live scleractinian corals (*Agaricia agaricites*, *Montastrea annularis*, *Porities asteroides*, *P. porities*), gorgonians, and sponges. Reefs were interspersed within a large expanse of natural patch reefs in a matrix of seagrass (primarily

Thalassia testudinum), sponges, and small coral heads, and the average depth at this site was ~ 5 m. Relative degree of isolation did not differ substantially among replicate reefs; mean distance to nearest neighboring reef that contained conspecifics was 5 m (SD: 0.8, range: 4.0 to 6.5 m). Divers captured fish using hand-nets and the anesthetic quinaldine, and tagged all fish *in situ* with fluorescent elastomer (Beukers et al. 1995) before returning them to their original home reef. The number of fish remaining on each reef 24 h after tagging was considered to be the initial group size treatment to account for any immediate mortality due to handling effects (per capita mortality during first 24 h = 0.16 ± 0.03 [SE]). Reefs were then censused every other day for a period of 21 d. Previous studies have shown several weeks to be sufficiently long for density-dependent mortality to manifest in most reef fishes (Hixon & Webster 2002). Losses due to emigration were distinguished from those due to mortality by searches within a 20 m radius of the reef on which fish were originally tagged. All other losses were presumed to be due to predation. Results from a previous study showed that the average distance moved by recent recruits of this species at this site was 6.8 ± 0.9 m (Overholtzer-McLeod 2003). Any yellowhead wrasse that subsequently recruited to the reefs (either by settlement or immigration) were removed to maintain density treatments.

Experiments on artificial reefs. From June to July of 1999, I constructed 2 arrays of artificial reefs near CMRC in a large, shallow (~ 3 m depth) expanse of sand and sparse seagrass (primarily *Thalassia testudinum*). Each array consisted of 12 reefs, and the 2 arrays were 400 m apart and at least 250 m from the nearest island. Scattered coral heads and sponges that fringe this island were the most proximate natural reef habitat to the artificial reefs. The 2 arrays differed only in the distance between reefs within each array (5 vs 50 m), and each contained reefs of 2 different sizes. Each reef was constructed of standard concrete blocks ($20.3 \times 20.3 \times 40.6$ cm) stacked in columns (3 blocks high by 4 blocks deep) that were held together with stainless steel Band-it[®] and placed on plywood platforms. Small and large reefs consisted of 2 and 6 of these columns, respectively, such that large reefs were 3 times the size of small reefs (Fig. 1B). To supplement the shelter created by holes of the concrete blocks (two 15 cm diameter holes per block), I added a standard number of conch shells to the tops (24 per large and 8 per small reef) and to the sides (36 per side per large and 12 per side per small reef) of each reef. Reefs were naturally colonized for a period of 1 yr before the start of the following experiment, and fish assemblages on these reefs were representative of those on natural patch reefs in the surrounding area (Overholtzer-

McLeod 2003). Likewise, previous comparisons between artificial and translocated natural patch reefs in the vicinity of Lee Stocking Island have been shown to support fish assemblages that did not differ substantially (Carr & Hixon 1997).

In July 2000, I transplanted recently settled yellowhead wrasse (18 to 23 mm TL) to each of the 24 artificial reefs. I randomly assigned 1 of 6 group size treatments to each of the 6 small reefs and each of the 6 large reefs (9 to 24 fish per reef) within each array (Fig. 1B). To establish treatments, divers captured fish on natural patch reefs using handnets and the anesthetic quinaldine, tagged them with fluorescent elastomer, and released them on experimental reefs. To account for any handling mortality, the experiments did not begin until treatments remained at the target number of fish for at least 24 h. Reefs were then censused every other day for 21 d. I detected movement of individuals between reefs by using a unique tag color for all fish on each reef. Regardless of reef spacing, successful movement was negligible over the course of this experiment ($n = 2$ emigrants on 5 m array, which were excluded from mortality estimates). Therefore, all disappearances were attributed to mortality. Any yellowhead wrasse that naturally settled to the reefs during the experiment were removed to maintain the density treatments. I standardized the number of small resident groupers to 1 coney (*Cephalopholis fulva*, ~10 cm TL) per reef through removals and additions from nearby natural reefs. Repeated transplant attempts to 2 of the reefs in the 5 m array (treatment combinations: 18 fish, small reef; 9 fish, large reef) were unsuccessful (all fish disappeared within 24 to 48 h), so these reefs were subsequently dropped from the experiment.

Video observations of predators. In 2001, I used digital video cameras with automated time-lapse recording to compare the visitation rates of predators to natural and artificial reefs. For all video observations, the cameras recorded 2 seconds of video every 30 s for 8 h between approximately 09:00 and 18:30 h. I filmed each reef once ($n = 12$ natural reefs and 24 artificial reefs). On natural reefs, I filmed the same 12 patch reefs that had been used in the 2000 experiment. The number of yellowhead wrasse per reef was lower, on average, in 2001 ($\bar{x} = 7.9 \pm 2.3$ [SD]) than it was in 2000 ($\bar{x} = 11.7 \pm 3.5$). However, despite lower densities, video observations were useful to determine how predator visitation frequency, abundance, and species composition varied between natural and artificial reefs. The following 12 species were identified as diurnally active piscivores on natural reefs using the criteria of a diet of at least 20% fish by volume (Randall 1967) or direct observations of feeding on juvenile wrasse during this study: groupers (Ser-

ranidae: *Cephalopholis cruentata* [graysby], *C. fulva* [coney], *Epinephelus guttatus* [red hind], *E. striatus* [Nassau grouper], and *Mycteroperca venenosa* [yellowfin grouper]); jacks (Carangidae: *Caranx ruber* [bar jack], *C. latus* [horse-eye jack], and *C. bartholomaei* [yellow jack]); snappers (Lutjanidae: *Lutjanus apodus* [schoolmaster], *L. analis* [mutton snapper], and *Ocyurus chrysurus* [yellowtail snapper]); and a trumpetfish (Aulostomidae: *Aulostomus maculatus* [common trumpetfish]). Video observations conducted only during the day necessarily excluded observations of the activity of nocturnally active piscivores also present at this site, such as moray eels (Muraenidae). However, no moray eels or other such predators were observed on any of the 12 experimental reefs. Nonetheless, highly cryptic predators such as lizardfish (Synodontidae) and scorpionfish (Scorpaenidae) could not be observed using video, but were present at the site. Additionally, logistical constraints precluded video observations from being conducted at dusk or dawn, and thus my conclusions are restricted to the activity patterns of diurnal predators over the time period stated above.

Artificial reefs were also filmed in 2001 as part of an experiment conducted using the beaugregory damselfish *Stegastes leucostictus*. Although no yellowhead wrasse were present on the reefs during filming, the following evidence suggests that predator abundance and composition during filming were similar to that during the 2000 experiment: (1) mortality rates of both beaugregory damselfish and yellowhead wrasse were similarly affected by reef spacing over the 2 different years, (2) a differential response of transient predators to reef spacing was the most likely source of the observed variation in mortality between the 2 arrays (Overholtzer-McLeod 2003), and (3) visual observations indicated that predator abundance and composition were similar in both years. Transient piscivores visiting the artificial reefs included yellowtail snapper, bar jack, and occasionally yellow jack.

To analyze the video, I counted the number of predators of each species present within every 2 second interval. Visitation rates were calculated for each species by dividing the total number of individuals observed by the total number of intervals filmed on a reef on a particular day (e.g. for 8 h, a total of 960 two second intervals were filmed) and then multiplied the resulting per-interval rate by 30. Thus, the resultant quantity was the average per minute visitation rate for each predator species (i.e. $[\text{number of predators} \times \text{time interval}^{-1}] \times [\text{time intervals} \times 2 \text{ s}^{-1}] \times [60 \text{ s} \times \text{min}^{-1}]$). Notably, visitation rates were a measure of both the frequency of visitation and the abundance of predators present on a reef at any one time.

Behavioral observations. In August of 2001, I conducted behavioral observations of juvenile yellowhead wrasse in aggregations on natural reefs at the same study site used in the 2000 experiment to quantify my *ad hoc* observations that, in the presence of predators, these fish formed tighter aggregations rather than seeking shelter in the physical structure of the reef (as do many other reef fishes, e.g. damselfishes). I observed 10 haphazardly chosen aggregations (6 to 14 fish per group) of recently settled yellowhead wrasse for 30 min each after an initial 5 min habituation period. Resting motionless on the bottom, I recorded the behavior of the group when approached by a predator (see species list under 'Video observations of predators', this section) by recording the change in the average distance between individuals in the group (increase, decrease, or no change), as well as a detailed description of their behavioral response to the encounter. Observations of a consistent decrease in the distance between individuals in aggregations (i.e. forming a more cohesive group) rather than seeking shelter in the holes in the reef would support my assertion that any differences in mortality rates of yellowhead wrasse between natural and artificial reefs were not due to differences in habitat complexity. In addition, these observations would provide evidence supporting my prediction that loss rates for this species would be a function of group size, rather than the number of fish per unit area.

Statistical analyses. To examine the effect of the number of fish per reef on per capita mortality for each of the 3 types of reefs (natural reefs, artificial reefs separated by 50 m, artificial reefs separated by 5 m), I initially fit full multiple linear regression models that included 3 explanatory variables: number of fish per reef, an indicator variable for reef size (small or large), and number of fish per reef \times reef size interaction. In all cases, interactions and indicator variables that were not statistically significant ($p \geq 0.10$) were eliminated from the final statistical model before testing the main effect of the number of fish per reef on per capita mortality (Ramsey & Schafer 1997). A positive slope that differed from zero ($p < 0.05$) indicated density dependence.

Because there was movement of yellowhead wrasse among natural, but not artificial reefs, on the former I used linear least squares regression to examine the effect of the number of fish per reef on per capita emigration, the relationship between mortality and emigration, and the effect of the number of fish per reef on persistence rates. Per capita persistence rates ($1 - [\text{mortality} + \text{emigration}]$) were calculated for each reef by dividing the number of fish remaining at the end of the 21 d experiment by the initial number of fish on a reef.

Using video observations, I compared the visitation rates of predators to natural and artificial reefs, where visitation rates were a measure of both the frequency of visitation and the abundance of predators present on a reef at any one time. I used 1-way ANOVA to compare total and family-level visitation rates of predators among natural reefs and the 2 sets of artificial reefs. When ANOVA F -tests were significant ($p < 0.05$), I used Tukey's HSD procedure for post-hoc multiple comparisons among means. Visitation rates were transformed ($\ln [x + 1]$) to correct for heteroscedasticity prior to conducting ANOVAs. All analyses were conducted using SAS Institute statistical software (JMP Version 4.02).

RESULTS

Mortality

On natural reefs, per capita mortality rates of yellowhead wrasse were highly variable among reefs (coefficient of variation [CV]: 29%). Based on the initial full multiple regression model, there was no evidence that the effect of density on per capita mortality varied with reef size ($F_{1,11} = 1.04$, $p = 0.34$), nor was there a significant reef size \times number of fish interaction ($F_{1,11} = 2.82$, $p = 0.13$), although the power to detect this interaction was low (0.32). Although mortality appeared to increase with the number of fish per reef, particularly on small reefs, this trend was non-significant (Fig. 2A).

On artificial reefs separated by 50 m, per capita mortality rates of yellowhead wrasse were significantly density-dependent (Fig. 2B), and there was no evidence that this relationship varied with reef size ($F_{1,11} = 0.60$, $p = 0.46$). However, on artificial reefs separated by 5 m, per capita mortality rates were high ($\bar{x} = 0.67$) and density-independent, with relatively low variation among reefs (CV: 9.3%; Fig. 2C).

Emigration

On natural reefs, losses resulted not only from mortality, but also from emigration to neighboring reefs (per capita emigration over 21 d: $\bar{x} = 0.12 \pm 0.03$ [SE]). Although the rate of emigration was not related to the number of fish present on a reef (Fig. 3A), per capita emigration was significantly correlated with per capita mortality (Fig. 3B). On reefs with high mortality, emigration was low to zero, whereas on reefs with low mortality, emigration was relatively high. In contrast to the frequent movement of yellowhead wrasse among natural reefs, no movement of

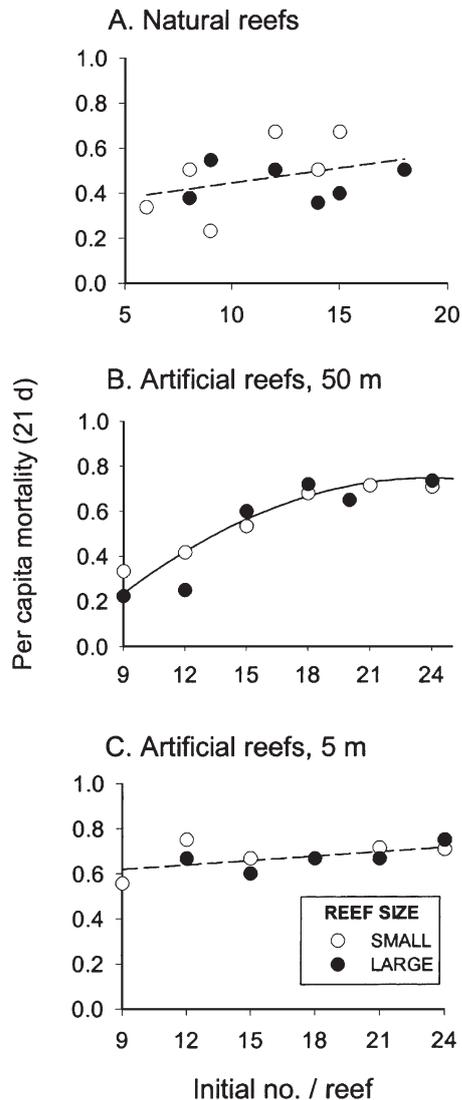


Fig. 2. Per capita mortality of yellowhead wrasse on (A) natural reefs, (B) artificial reefs separated by 50 m, and (C) artificial reefs separated by 5 m, each as a function of the initial number of fish per reef on both small and large reefs. (A) On natural reefs, the trend for density dependence was non-significant ($y = 0.013x + 0.31$, $p = 0.24$, $r^2 = 0.13$, $n = 12$). (B) On artificial reefs separated by 50 m, mortality was density-dependent, and the fit of the regression was significantly improved by the addition of a quadratic term ($y = -0.57 + 0.110x - 0.002x^2$, $p = 0.0001$, $r^2 = 0.88$, $n = 12$). (C) On artificial reefs separated by 5 m, mortality was density-independent ($y = 0.007x + 0.56$, $p = 0.09$, $r^2 = 0.32$, $n = 10$). In all cases, the relationship between mortality and density did not differ between reef sizes, so reef size is pooled for all regressions

individuals was observed between artificial reefs separated by 50 m and only 2 individuals moved between reefs separated by 5 m, indicating that emigration was not a significant demographic rate on artificial reefs.

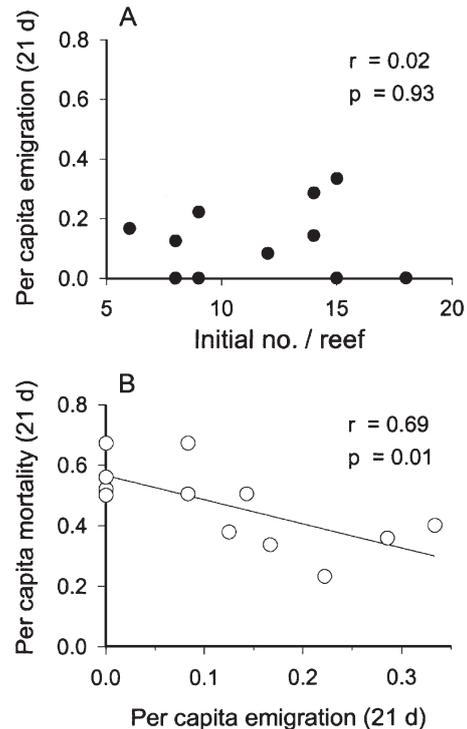


Fig. 3. Relationships between (A) per capita emigration and number of fish per reef and (B) per capita rates of emigration and mortality for yellowhead wrasse on natural reefs. (A) Emigration was not related to initial abundance. (B) Mortality varied inversely with emigration. Each point represents a reef ($n = 12$) over the 21 d of the experiment, and reef sizes were pooled for these analyses

Persistence

After accounting for losses due to both emigration and mortality, persistence of yellowhead wrasse remaining on natural reefs for 21 d decreased with density, albeit non-significantly ($r^2 = 0.27$, $p = 0.08$; Fig. 4). The poor fit of this relationship is heavily influenced by a single outlier. If this largest initial group size ($n = 18$) population on which persistence was unusually high is excluded, the fit of the regression model is much stronger ($r^2 = 0.68$, $p = 0.002$). Thus, persistence ($1 - \text{mortality} - \text{emigration}$) on natural reefs showed a trend toward density dependence. Because emigration was virtually zero on artificial reefs, persistence there was equal to survivorship (i.e. the inverse of mortality), and thus is not considered here.

Predator abundance and species composition

Total predator visitation rates to artificial reefs were significantly higher than those to natural reefs ($F_{2,33} = 27.11$, $p < 0.0001$; Tukey's HSD, $p < 0.05$ for all pair-

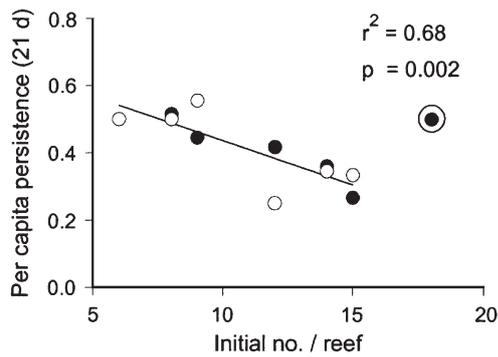


Fig. 4. Relationship between persistence (1 - mortality - emigration) and density (initial number of fish per reef) for yellowhead wrasse on natural reefs. The r^2 and p -values are for a regression model that excludes a single outlier reef (circled) with unusually high persistence. The relationship did not differ between reef sizes (small [○] vs large [●]), and therefore reef sizes are pooled for the regression ($n = 11$). (For statistics with the outlier included, see 'Results', subsection 'Persistence')

wise comparisons: artificial, 5 m > artificial, 50 m > natural reefs; Fig. 5). This pattern was influenced strongly by the high rate of yellowtail snapper visitation to artificial reefs in the 5 m array compared to snapper visitation to any other reefs ($F_{2,33} = 10.73$, $p < 0.0005$; Tukey's HSD, $p < 0.05$: artificial, 5 m > artificial, 50 m = natural reefs; Fig. 5). Jack visitation was also higher on average to artificial than to natural reefs ($F_{2,33} = 4.94$, $p = 0.01$; Tukey's HSD, $p < 0.05$: artificial, 5 m = artificial, 50 m > natural reefs; Fig. 5). All artificial reefs were inhabited by 1 small resident coney grouper, and a few Nassau groupers were resident on each array. By comparison, grouper visitation to natural reefs was low (\bar{x} per reef = 0.37 ± 0.11 [SE] present min^{-1}). However, the size range of groupers present on natural reefs greatly exceeded that on artificial reefs; for example, coney on artificial reefs (~10 cm TL) were much smaller compared to those on natural reefs (up to 25 cm TL; author's pers. obs.). There were no trumpetfish present on artificial reefs, and although the average visitation rate of trumpetfish to natural reefs from video observations was extremely low ($\bar{x} = 0.08 \pm 0.02$ present min^{-1}), this species was frequently observed actively hunting and consuming juvenile yellowhead wrasse. All predators on natural reefs were transients, i.e. they foraged over spatial scales that exceeded the area of individual reefs. The species richness of all predators observed at the natural reef site was substantially higher than those transient and/or resident (groupers) on artificial reefs (12 vs 4 species). Within families, predators visiting natural reefs were dominated by coney (60.7% of all groupers), yellowtail and schoolmaster snapper (51.1 and 44.8%, respectively, of all snappers), and bar jack (92.3% of all jacks).

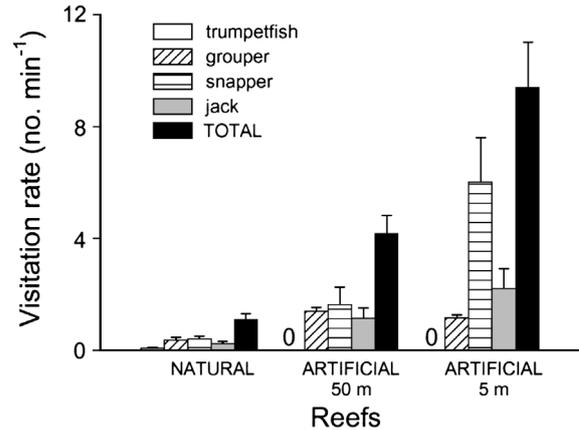


Fig. 5. Visitation rates of predators pooled by family (trumpetfish, grouper, snapper, jack) to natural reefs ($n = 12$) and artificial reefs separated by 50 m ($n = 12$) and 5 m ($n = 12$). Results (\bar{x} per reef + 1 SE) are based on remote video observations, with the exception of groupers on artificial reefs (visually censused). On natural reefs, home ranges of all reef-associated predators exceeded the boundaries of replicate reefs, i.e. there were no strictly resident predators. All artificial reefs were inhabited by 1 resident coney grouper, and each array had a few resident Nassau groupers (50 m: $n = 5$; 5 m: $n = 2$) that frequently moved among reefs within an array and are therefore included in the above calculations. Snappers and jacks were transient predators on all reefs, both natural and artificial

Responses of wrasse aggregations to predators

On natural reefs, groups of yellowhead wrasse responded to the approach of a predator (including bar jack, coney, graysby, trumpetfish, and yellowtail snapper) by decreasing the distance between individuals (inter-fish distance) within an aggregation ($n = 10$ groups) in 100% of 5 h of observation. No individuals were observed seeking shelter within any physical structure. Most often (71.4% of observations), group cohesion increased and the aggregation positioned itself such that a small coral head or gorgonian was between it and the predator. On 2 occasions, the group split in half and formed 2 more cohesive groups. During all observations, the group was observed to increase inter-fish distance after the predator left the area.

DISCUSSION

The strikingly different patterns of mortality for juvenile yellowhead wrasse on natural reefs compared to artificial reefs in this study highlight the consequences of variation in spatial structure for the demographic rates of populations in patchy environments. Among natural patch reefs, mortality rates of yellowhead wrasse were highly variable. Yet, the persistence of

individuals remaining on the reefs over the course of the experiment was approximately density-dependent because losses resulted from both mortality and emigration to neighboring patches. Although reef complexity and shelter availability were more heterogeneous among natural reefs, such differences are unlikely to explain differences in mortality patterns because yellowhead wrasse do not use the reef structure for shelter. Instead, 2 lines of evidence suggest that predation risk on natural reefs varied on a spatial scale larger than that of individual reefs (i.e. on a neighborhood scale). First, all predators foraged over spatial scales that exceeded the boundaries of replicate reefs, and therefore likely responded to relative prey availability among multiple patch reefs within a neighborhood, rather than to the number of fish present on an individual reef. Second, observed mortality and emigration rates varied inversely, suggesting that if the rate of attempted emigration was similar among regions, post-emigration survivorship (and thus the detection of successful emigrants) was lower in regions where mortality was higher. Results from the artificial reef experiments, in which reef spacing was standardized within arrays, facilitate examination of probable sources of variation in mortality rates among natural reefs.

Spatial variation in predation risk among neighborhoods

I propose that the high variation in mortality rates among natural reefs primarily resulted from spatial variation in predation. I expect such variation to be especially prevalent in coral-reef fish communities, given the diverse suite of predators that potentially consume small reef fishes (Hixon 1991). Natural reefs consisted of a mosaic of patches of variable predation risk, affected by the abundance, species composition, and age distribution of predators foraging in a particular fraction of the study site. Moreover, this risk likely varied at multiple spatial scales, depending on the home range(s) of a particular predator or suite of predators as well as the relative availability of prey present on patches within those home ranges.

To examine spatial variation at the natural reef site, I determined the signs of the residuals from the regression of per capita mortality as a function of initial wrasse density (shown in Fig. 2A) and mapped these onto the physical location of the experimental patch reefs (Fig. 6). Although the strength of the expected density dependence (i.e. exact slope of the line in Fig. 2A) is unknown, in general, reefs with positive residuals had relatively high mortality and those with negative residuals had relatively low mortality. As

shown in Fig. 6, yellowhead wrasse on reefs towards the center of this site had higher than expected mortality, while those on reefs on the periphery had lower than expected mortality rates (Fig. 6). This result supports the hypothesis that mortality rates were relatively high for wrasse on reefs in the interior of the site where a greater number of home ranges of reef-associated predators (e.g. groupers) would have overlapped compared to reefs on the periphery. Conversely, near the boundaries of this site (demarcated by either coral rubble or seagrass beds), fewer home ranges of reef-associated predators would have overlapped the reefs. Consistent with this overall pattern, the reef characterized by unusually high persistence of wrasse (potential outlier circled in Fig. 4) had a negative residual and was located near the edge of the site. It is important to note that these patterns depict relatively coarse spatial variation. Finer-scale patterns would be generated by variation in species composition and the age distribution of predators foraging in a specific region of the site that would be unrelated to edge effects.

On artificial reefs, fixed levels of reef spacing (5 vs 50 m) eliminated variance in spatial structure within arrays. In addition, the arrays were distributed over a relatively limited area. As a result, predators' use of space was discrete compared to that on natural reefs, and predators could clearly be differentiated into residents with home ranges that did not exceed the extent of individual artificial reefs (e.g. small groupers) and transients that were wide-ranging (e.g. snappers and jacks). A separate, but related study (Overholtzer-

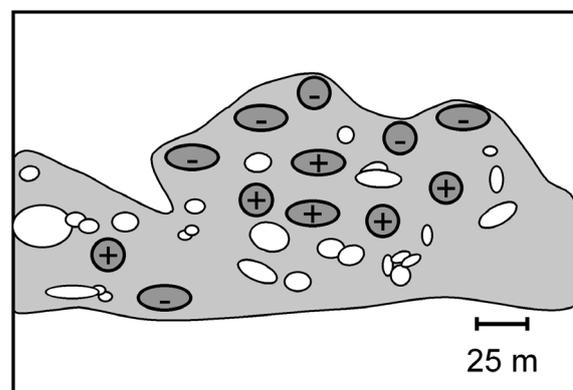


Fig. 6. Map showing spatial pattern of residuals from regression of per capita mortality of yellowhead wrasse on natural patch reefs as a function of the initial number of fish per reef (original regression shown in Fig. 2A). For each experimental reef (dark gray), positive residuals are indicated by a '+' and negative residuals are indicated with a '-'. Representative patches of intervening reef habitat are shown in white, and the spatial extent of reef habitat at this site is shown in light gray

McLeod 2003) in which mortality for another prey species (a damselfish) varied similarly with reef spacing, sheds light on potential explanations for the effects of reef spacing on the existence of density dependence and the magnitude of predation in the current study. Based on remote video data, there was no evidence that the observed density dependence (50 m array) was caused by transient predators. Consequently, resident predators were the likely source of density dependence. Given that resident predator assemblages did not differ between arrays, it is plausible to assume that they caused density-dependent mortality in their prey on all artificial reefs, independent of reef spacing. On closely spaced reefs (5 m array), visitation rates of the most common transient predator (yellowtail snapper) were significantly higher compared to reefs in the 50 m array. Thus, predation by transient predators overwhelmed the underlying density dependence and resulted in uniformly high, density-independent mortality on the 5 m array. The same mechanisms were likely operating in both the previous and current experiments given the remarkable similarity in the relationships between mortality, density, and reef spacing for both the damselfish and the wrasse (Overholtzer-McLeod 2003).

Compared to artificial reefs, a greater diversity of predators was present on natural reefs, and the variation among species' use of space was a likely source of variance in predation risk among neighborhoods. For some species (e.g. coney grouper), predators were also substantially larger than individuals of the same species present on artificial reefs. Large predatory fish have been shown to be the primary source of juvenile mortality in other reef systems (e.g. Connell 1998). In a separate experiment, I showed that even small coney (<10 cm TL) could cause substantial mortality of reef fish recruits (Overholtzer-McLeod 2003). Larger grouper could have presented an even greater predation threat to yellowhead wrasse, and thus variation in the size structure of piscivores represents a second likely source of variation in predation among natural reef patches compared to artificial reefs.

Inverse relationship between perceived emigration and mortality

The covariance of mortality and emigration rates further supports the hypothesis that variation in predation risk among neighborhoods was a source of heterogeneity in mortality rates among natural reefs. Attempts at emigration would have exposed fish to increased risk of predation during transit between patches and after arriving at a neighboring patch and attempting to immigrate. Intervening habitat, such as

sponges, gorgonians, and small coral heads, was abundant among natural reefs, but not present among artificial reefs. Such habitat likely facilitated successful emigration to neighboring natural reefs, acting as stepping-stones that provided shelter from predation while moving across otherwise inhospitable habitat. Although behavioral observations suggested that yellowhead wrasse do not use the physical structure of reefs for shelter (i.e. holes present within reef structure), I would expect the presence of intervening habitat to increase the likelihood of survivorship of transiting wrasses through the beneficial effects of providing structure to hide behind and/or camouflage to decrease conspicuousness. As shown in terrestrial systems for the movement of butterflies (Ricketts 2001), the matrix surrounding isolated patches of habitat can significantly influence the 'effective isolation' of those habitat patches. Assessment of the role of a heterogeneous matrix, such as that commonly present among coral patch reefs, in the movement of reef fishes provides a fruitful avenue for future research.

In a previous study (at the same natural reef site), the probability of emigration of yellowhead wrasse increased as reef isolation decreased (Overholtzer-McLeod 2003). I demonstrated that movement of this species was independent of the fish community present on the reef by accounting for within-species density, density of another common wrasse (bluehead wrasse *Thalassoma bifasciatum*), and total density of fishes on the reef. Thus, because I standardized isolation distance when selecting replicate natural reefs in the current study, it is reasonable to assume that the probability of emigration was approximately equal from all reefs. If this is true, why was there an inverse relationship between emigration and mortality? Perceived emigration rates are a measure of successful movement to a nearby reef, survival at that new location over the census interval, and the ability to locate emigrants. In this study, each reef was censused every 48 h, and any emigrant that died between the time it moved and the next census was recorded as a mortality. Therefore, even if the probabilities of emigration were approximately equal from all reefs, in neighborhoods where risk of mortality due to predation was higher, perceived emigration rates would be lower because post-emigration survival was lower, leading to an inverse relationship between mortality and emigration. In regions of lower risk of mortality due to predation, mortality rates of fish on the home reef were lower and the chance of post-emigration survivorship on neighboring reefs was higher, and thus emigration rates were higher. To my knowledge, the hypothesis that perceived emigration varies inversely with mortality as a result of variation in predation risk at a neighborhood scale has never been tested, at least among

fish. Future studies of population dynamics should measure multiple demographic rates and explicitly consider predation risk at multiple spatial scales.

Additionally, although emigration was clearly not a significant demographic rate for yellowhead wrasse on artificial reefs, attempted emigration may have occurred from these reefs, particularly as a response to transplanting. Indeed, this is one possible explanation for the rapid disappearance of all fish on the 2 reefs in the 5 m array where repeated transplant attempts were unsuccessful (and thus, these reefs were discarded from the experiment). Transplanted fish may have emigrated from the reefs to surrounding seagrass beds. The rapid losses observed on these reefs were relatively steep compared to the more gradual losses on all other reefs over the duration of the experiment, and thus I consider them to be unusual experimental artifacts that I controlled for by beginning each experiment (Day 0) 24 h after transplanting.

Cryptic density dependence?

On natural reefs, treatments were established via removals, rather than additions via transplanting, as on the artificial reefs. Thus, the removal of fishes itself may have precluded the detection of density dependence on natural reefs because group sizes may have been reduced to a point below which the effects of density would not be observed. However, the ranges of mortality rates observed on natural and artificial reefs overlapped considerably (see Fig. 2). Instead, the major difference between patterns observed in the 2 systems was the amount of variance associated with mortality rates on natural reefs compared to artificial reefs, rather than a difference in the absolute mortality rates as expected if populations on natural reefs were too small to observe an effect of density. Additionally, although densities were manipulated on all natural reefs, treatments could not be assigned randomly, and thus, reefs that contained fewer fish were necessarily the lower-density treatments. As a result, there may have been a correlation between habitat quality and the number of fish initially present on a reef that masked the detection of density dependence on natural reefs. Such cryptic density dependence caused by spatial variation in site quality has been shown to mask density dependence for a Pacific wrasse (Shima & Osenberg 2003) and proposed to explain discrepancies between observational and experimental results for gobies in the US Virgin Islands (Wilson & Osenberg 2002). Some potential measures of site quality (e.g. reef size and relative isolation) were controlled in the current study. Others, such as heterospecific wrasse density or rugosity, are unlikely to have had strong

effects on yellowhead wrasse survivorship (Overholtzer-McLeod 2003). However, as all sources of possible variation in habitat quality among natural reefs were not measured in the current study, some form of cryptic density dependence may explain the observed variation in mortality rates among natural reefs.

Implications for experimental design

Most studies of reef fish population dynamics have been conducted on reef isolates to ensure that losses due to mortality are not confounded with those from emigration. This method has distinct advantages. For example, in the artificial reefs used in the present study, I was able to measure all demographic rates of the focal species on all reefs in the area. In contrast, because of logistical constraints, I was able to monitor the abundances of yellowhead wrasse on only a subset of reefs in a large expanse of natural patch reefs. Consequently, the results from natural reefs are confounded by a sampling effect because I was unable to evaluate the effects of prey densities on neighboring patches. Because the impact of predation on one species may depend on the abundance of other species (e.g. Beukers & Jones 1997, Webster & Almany 2002, Overholtzer-McLeod 2003), ideally both conspecific and heterospecific prey densities would be monitored on all reefs within a study site. The results of this study suggest clear tradeoffs to consider for the design of studies examining reef fish demography. On one hand, there are problems associated with extrapolation from experiments conducted on isolated patches to more continuous reef because the use of such isolates artificially removes the effects of many processes operating at spatial scales larger than that of an individual reef. On the other hand, the use of reef isolates is extremely useful for focusing on particular processes of interest (e.g. effects of predation by resident predators on mortality) without the 'noise' of the natural system.

CONCLUSIONS

These results highlight the consequences of spatial variation in predation risk among habitat patches for density dependence of coral-reef fish populations and support Levin's (1992) hypothesis that, in general, mechanisms tend to operate at spatial scales larger than those of observed patterns. Just as the strength of density dependence has been shown to vary spatially through co-variance in habitat quality (Wilson & Osenberg 2002, Shima & Osenberg 2003), variability in predation risk among neighborhoods may affect the detectability of density dependence. Moreover, this

work adds to the emerging evidence that the spatial configuration of habitats can have important implications for both population dynamics (current study) and community composition, such as the diversity of invertebrates associated with kelp holdfasts (Goodsell & Connell 2002). Coral reefs are excellent systems in which to test the effects of spatial structure on marine populations and communities because of their inherent patchiness on multiple scales. Future research should assess the spatial scale over which predation risk varies and seek to further understand factors that affect post-settlement movement of fishes, including the potential effects of predators on emigration behavior.

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