

AN ABSTRACT OF THE DISSERTATION OF

Karen L. Overholtzer-McLeod for the degree of Doctor of Philosophy in Zoology presented on June 9, 2003.

Title: Population Dynamics of Coral-Reef Fishes: Spatial Variation in Emigration, Mortality, and Predation.

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Abstract approved: \_\_\_\_\_

Mark A. Hixon

Understanding the dynamics of open marine populations is difficult. Ecological processes may vary with the spatial structure of the habitat, and this variation may subsequently affect demographic rates. In a series of observational and experimental studies in the Bahamas, I examined the roles of emigration, mortality, and predation in the local population dynamics of juvenile coral-reef fishes. First, I documented mortality and emigration rates in populations of bluehead and yellowhead wrasse. Assuming that all losses were due solely to mortality would have significantly underestimated survivorship for both species on patch reefs, and for yellowheads on continuous reefs. Mortality differed between species, but emigration did not differ between species or reef types. Mortality of blueheads was density-dependent with respect to both conspecific density and total wrasse density on continuous reefs. In contrast, mortality of yellowheads varied inversely with the density of blueheads on patch reefs. Emigration rates varied

inversely with distance to the nearest reef inhabited by conspecifics. In subsequent experiments, I manipulated densities of yellowhead wrasse and beaugregory damselfish, and determined that the relationship between density and mortality varied with reef spatial structure. On natural reefs, mortality rates of the wrasse were highly variable among reefs. On artificial reefs, mortality rates of both species were density-dependent on spatially isolated reefs, yet high and density-independent on aggregated reefs. Heterogeneity in the spatial structure of natural reefs likely caused variation in predation risk that resulted in high variability in mortality rates compared to artificial reefs. A final experiment demonstrated that a single resident predator caused substantial mortality of the damselfish, regardless of reef spacing. Patterns suggested that resident predators caused density-dependent mortality in their prey through a type 3 functional response on all reefs, but on aggregated reefs this density dependence was overwhelmed by high, density-independent mortality caused by transient predators. These results (1) suggest post-settlement movement should be better documented in reef-fish experiments, (2) demonstrate that the role of early post-settlement processes, such as predation, can be modified by the spatial structure of the habitat, and (3) have ramifications for the implementation of marine reserves.

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Population Dynamics of Coral-Reef Fishes: Spatial Variation in  
Emigration, Mortality, and Predation

by

Karen L. Overholtzer-McLeod

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Karen L. Overholtzer-McLeod, Author

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**POPULATION DYNAMICS OF CORAL-REEF FISHES:  
SPATIAL VARIATION IN EMIGRATION,  
MORTALITY, AND PREDATION**

**CHAPTER 1: GENERAL INTRODUCTION**

All ecological systems exhibit patchiness on a broad range of spatial and temporal scales. Patterns of abundance can be determined by processes that occur on spatial scales from centimeters to 100's of kilometers, especially for open marine populations (Menge and Olson 1990). Even local-scale processes, such as competition and predation, can act across a range of smaller spatial scales, particularly within patchy landscapes such as coral reefs. Fishes on coral reefs have served as model organisms for investigations of fundamental behavioral, population, and community-level ecological questions, and thus have contributed tremendously to advances in the field of ecology (Sale 1991a). My research has focused on understanding how mortality and emigration rates of local populations of coral-reef fishes are affected by density, predation, and reef isolation, as well as the consequences of variation in predation risk at spatial scales of 10's to 100's of meters for local populations of prey.

Population dynamics are influenced by both density-independent and density-dependent factors. However, density dependence in at least one

demographic rate is necessary for a population to persist indefinitely (Murdoch and Walde 1989, Sinclair 1989). After decades of intense debate, the degree to which density dependence allows populations to persist continues to be controversial (e.g., Sale and Tolimieri 2000), although a majority of researchers agree that most populations are regulated (reviews in Hixon et al. 2002, Hixon and Webster 2002). Successful conservation and management of marine fish populations depends on the protection of natural mechanisms of regulation. Thus, determining the role of density dependence in the regulation of marine fish populations is especially crucial as species face increased risk of extinction both globally and locally (Roberts and Hawkins 1999, Musick et al. 2000, Pauly et al. 2002).

Understanding the determinants of population dynamics is especially challenging for open marine populations in which the local birth rate depends on the settlement of new individuals likely spawned elsewhere. Because local populations can be observed and manipulated *in situ*, coral-reef fishes are excellent systems in which to investigate population dynamics (Sale 1991b). For the last half century, debate has raged among reef fish ecologists about whether adult abundances are determined by variation in the input of larvae vs. post-settlement modification of that input (reviews in Hixon 1998, Sale and Tolimieri 2000, Doherty 2002, Forrester et al. 2002, Hixon et al. 2002, Hixon and Webster 2002). More recently, the focus has shifted towards the relative importance of pre- vs. post-settlement factors at different times and places (e.g., Caley et al. 1996, Steele 1997b, Schmitt and Holbrook 1999, Schmitt et al. 1999, Shima 1999).



One post-settlement factor that has been relatively ignored as a potential modifier of spatial patterns established at settlement is movement of recent recruits among patches (but see Schmitt and Holbrook 1996, Frederick 1997). Historically, studies of reef fish populations have focused on strongly site-attached species, such as territorial or highly-social damselfish, leading to the generalization that coral-reef fish rarely move after settlement (Sale 1991a). In addition, to avoid confounding mortality with emigration, most studies have been conducted on patch reefs separated from others by some distance of inhospitable habitat such as sand. Distances between reefs have ranged from just a few meters (e.g., Sale et al. 1984, Doherty 1987, Nemeth 1998, Caselle 1999, Shima 2001) to intermediate distances of 25 to 50 m (e.g., Doherty 1982, Hixon and Beets 1993, Webster 2002) to as high as 200 m (e.g., Carr and Hixon 1995, Hixon and Carr 1997). The tendency to perform studies on relatively isolated reefs may bias demographic studies of reef fish in two ways: (1) at low levels of isolation, mortality and emigration may be confounded such that survivorship estimates are underestimated (Frederick 1997) and (2) at high levels of isolation, mortality may be experimentally inflated because isolation may hinder the ability to successfully disperse to more favorable habitats (Robertson 1988).

I have focused on the roles of emigration, mortality, and predation for the population dynamics of juvenile coral-reef fishes. All observations and experiments were conducted on reefs in the Exuma Cays of the Bahamas. Using both natural and artificial reefs, I demonstrated that (1) post-settlement movement

of reef fish between patches was demographically relevant and affected by the degree of reef isolation, (2) spatial variation in predation at scales larger than that of an individual patch reef masked density dependence, and (3) the spatial distribution of reef habitat affected the magnitude of total predation and the existence of density dependence.

In Chapter 2, I examined loss rates (emigration and mortality) from populations of yellowhead wrasse and bluehead wrasse on both patch and continuous reefs. Assuming that all losses were due solely to mortality would have significantly underestimated survivorship for juveniles of both species on patch reefs and for yellowhead wrasse on continuous reefs. Overall, interspecific differences were greater than those between reef types. Mortality rates were significantly lower for a cleaning species (bluehead wrasse) than a non-cleaner (yellowhead wrasse). Within-species density dependence in mortality was observed for bluehead wrasse on continuous reefs. Yellowhead wrasse mortality varied inversely with the density of bluehead wrasse on patch reefs, demonstrating the potentially important effects of between-species density on populations. Emigration rates for both species were not related to density, but instead varied inversely with isolation distance (distance to the nearest neighboring reef inhabited by conspecifics). These results suggested that previous studies of reef fish may have confounded losses due to emigration with those truly due to mortality, and therefore underestimated survivorship.

In Chapter 3, I used two experiments to compare the mortality rates of juvenile yellowhead wrasse on natural and artificial reefs and examine the effects of spatial structure on the detection of density dependence. Among populations on natural reefs, mortality and emigration rates were highly variable, but inversely related to one another. 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 all artificial reefs. Video observations showed that overall predator visitation rates were significantly higher to artificial reefs than to natural reefs, but a greater diversity and size range of predators were present on natural reefs. Variation in mortality rates among natural reefs most likely resulted from variation in predation risk among neighborhoods containing numerous patch reefs (i.e., scales of 100's of m<sup>2</sup>).

In Chapter 4, I examined the effects of reef spacing on predator-prey interactions among coral-reef fishes using artificial reefs. Mortality rates of juveniles of two ecologically dissimilar species (beaugregory damselfish and yellowhead wrasse) were similarly affected by reef spacing in two different years. For both species, mortality was density-dependent on reef patches that were spatially isolated (separated by 50 m), and density-independent on reef patches that were aggregated (separated by 5 m). A subsequent experiment using only the damselfish as prey demonstrated that substantial mortality could be caused by a single common resident predator (the coney, a small grouper), regardless of reef spacing. Based on video observations, I found no evidence that transient predators

(jacks and snappers) were the source of the observed density dependence. These results suggested that resident predators were the source of density dependence on all reefs, but on aggregated reefs, this density dependence was overwhelmed by high, density-independent mortality caused by transient predators (primarily yellowtail snapper). These experiments showed that reef spacing influences whether and how density-dependent predation occurs.

The shared theme among these studies is that the spatial structure of the habitat can modify the role of early post-settlement processes, such as predation, for population dynamics. Such spatial variation in predation subsequently affects mortality and emigration rates, and can influence our ability to detect density dependence. In addition, these studies highlight potential dangers associated with studying site-attached species on reef isolates for understanding the population dynamics of a broader suite of species on more continuous reefs. In a broader context, these studies have ramifications for the implementation of marine reserves and suggest that habitat fragmentation caused by human disturbance and other forms of habitat loss may disrupt natural mechanisms of population regulation.

## CHAPTER 2: RELATIVE ROLES OF EMIGRATION AND MORTALITY IN LOCAL POPULATION DYNAMICS OF CORAL-REEF FISHES

### ABSTRACT

Understanding population dynamics within open marine populations is inherently complex, and this complexity has led to decades of debate regarding the relative importance of pre- vs. post-settlement processes in structuring these populations. Movement between habitat patches may be an important modifier of spatial patterns established at settlement, yet local immigration and emigration have been ignored relative to other demographic rates. I examined loss rates (mortality plus emigration) from tagged populations of juvenile wrasses (yellowhead wrasse *Halichoeres garnoti* and bluehead wrasse *Thalassoma bifasciatum*) in the Bahamas. Assuming that all losses were due solely to mortality would have significantly underestimated survivorship for both species on patch reefs, and for yellowhead wrasse on continuous reefs. Per capita mortality rates were higher for yellowhead than bluehead wrasse on both patch and continuous reefs, but per capita emigration rates did not differ between species or reef types. There was no evidence for density-dependent mortality in yellowhead wrasse on either reef type or for bluehead wrasse on patch reefs. However, bluehead wrasse mortality was significantly density-dependent with respect to both conspecific density and total

wrasse density on continuous reefs. Regarding the effects of between-species density, per capita mortality of yellowhead wrasse was inversely related to bluehead wrasse density, or was negatively density-dependent. Emigration rates were not a function of density for all comparisons both within and between-species, but instead varied inversely with distance to the nearest reef inhabited by conspecifics. Because many studies of reef fishes have been conducted on patch reefs separated by only a few meters of sand, these results suggest that such studies potentially confounded losses due to emigration with those truly due to mortality. Post-settlement movement should be better documented in small-scale reef-fish experiments and needs further experimental exploration in its own right.

## INTRODUCTION

Understanding population dynamics is especially challenging for open marine populations in which the local birth rate depends on the settlement of new individuals likely spawned elsewhere. For decades, debate raged among reef fish ecologists about whether adult abundances are determined by variation in the input of larvae or post-settlement modification of that input (recent reviews in Hixon 1998, Sale and Tolimieri 2000, Doherty 2002, Forrester et al. 2002, Hixon et al. 2002, Hixon and Webster 2002), although more recently, the focus has shifted towards the relative importance of these two extremes (e.g., Caley et al. 1996,

Steele 1997b, Schmitt and Holbrook 1999, Schmitt et al. 1999, Shima 1999).

Numerous processes have been shown to modify settlement patterns, including competition (Forrester 1990, 1995, Robertson 1996, Schmitt and Holbrook 1999), ontogenetic habitat shifts (Lirman 1994, Eggleston 1995), and most notably, predation (Carr and Hixon 1995, Connell 1996, 1997, 2000, Hixon and Carr 1997, Carr et al. 2002, Steele and Forrester 2002, Webster 2002, 2003). However, our knowledge of the extent to which post-settlement movement modifies spatial patterns established at settlement is minimal (but see Hixon and Beets 1993, Schmitt and Holbrook 1996, Frederick 1997).

Historically, studies of reef fish populations have focused on strongly site-attached species such as damselfishes, leading to the generalization that coral-reef fish rarely move after settlement (Sale 1991a). In addition, to avoid confounding mortality with emigration, most studies have been conducted on patch reefs separated from others by some distance of inhospitable habitat such as sand. Distances between reefs have ranged from just a few meters (e.g., Sale et al. 1984, Doherty 1987, Nemeth 1998, Caselle 1999, Shima 2001) to intermediate distances of 25 to 50 m (e.g., Doherty 1982, Hixon and Beets 1993, Webster 2002) to as high as 200 m (e.g., Carr and Hixon 1995, Hixon and Carr 1997). The tendency to perform studies on relatively isolated reefs may be biasing demographic studies of reef fish in two ways: (1) at low levels of isolation, mortality and emigration may be confounded such that survivorship estimates are underestimated (Frederick 1997) and (2) at high levels of isolation, mortality may be experimentally inflated

because isolation may hinder the ability to successfully disperse to more favorable habitats (Robertson 1988).

There is emerging evidence that post-settlement movement of fish among reefs can affect local population size (Robertson 1988, Lewis 1997, Ault and Johnson 1998). However, previous studies merely inferred movement based on repeated censuses of untagged fishes with long periods of time between observations, ranging from monthly or bimonthly (Lewis 1997, Ault and Johnson 1998) to annual intervals (Robertson 1988). A study in Hawaii by Frederick (1997) was the first attempt to examine post-settlement movement of individually tagged new recruits within an experimental context. An important limitation of this study was that it was conducted on very small artificial reefs (composed of 2 concrete blocks each). Clearly, there are gaps in our knowledge about the frequency and determinants of post-settlement movement of fishes among natural reefs.

The best-documented demographic rate, mortality, has been shown to be density-dependent for a majority of reef fish species studied to date (reviews by Hixon and Webster 2002, Osenberg et al. 2002, see also Carr et al. 2002, Wilson and 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, 2000, Hixon and Carr 1997, Planes and Lecaillon 2001, Stewart and Jones 2001, Carr et al. 2002, Steele and Forrester 2002, Webster 2002, 2003). Although relatively unexplored for reef fishes, predation could influence emigration in several ways. First, the tendency to



emigrate may be either increased or decreased by the presence of a predator, as shown in stream systems (review by Sih and Wooster 1994). If the presence of a predator increases the likelihood of movement, and more predators are attracted to reefs with more prey (e.g., through an aggregative response, see Hixon and Carr 1997), emigration could be positively density-dependent. If predators decrease emigration rates (e.g., by increasing sheltering behavior), then there could be negative density dependence. Finally, attempted emigration could expose fish to increased risk of predation during movement or while immigrating to a neighboring patch. Thus, both the propensity to move and the ability to relocate successfully may be functions of population density (Forrester et al. 2002).

The goal of this study was to compare losses due to mortality with those due to emigration for two wrasses (yellowhead wrasse *Halichoeres garnoti* and bluehead wrasse *Thalassoma bifasciatum*) on two reef types (patch reef vs. continuous reef) in the Bahamas. I specifically asked four questions: (1) To what degree are survivorship estimates biased by assuming that all losses are due to mortality? (2) Do mortality and emigration rates vary between species and reef types? (3) What are the effects of density (both within and between-species) on mortality and emigration rates? (4) What factor(s) best explain variation in emigration rates among reefs?

## MATERIALS AND METHODS

### Study area and species

This study was conducted on natural reefs in the vicinity of the Caribbean Marine Research Center (CMRC) on Lee Stocking Island, Bahamas (23°46' N, 76°10'W) from June to September of 1998. Yellowhead and bluehead wrasse are common on shallow reefs in this area and are ubiquitous throughout the western Atlantic (Bohlke and Chaplin 1993). Juveniles of both wrasses form loose, nonpolarized single-species aggregations that contain between 3 and 30 individuals (K. Overholtzer-McLeod, *personal observation*). Like most other Caribbean labrids, settlement in these microcarnivorous species occurs when individuals bury under the sand and emerge on the reef several days later (Victor 1982, Sponaugle and Cowen 1997). Both species settle monthly, primarily around the new moon, at ~ 10 to 12 mm standard length (SL) after a planktonic larval duration of ~ 25 days (yellowhead wrasse) or ~ 45 days (bluehead wrasse) (Caselle 1997, Sponaugle and Cowen 1997).

## Sampling design

I monitored rates of emigration and mortality in tagged aggregations of these two wrasse species at two sites ( $n = 10$  aggregations of each species per site). At both sites, reefs were composed of live and dead hard corals, gorgonians, and sponges. Reefs at the patch reef site occupied expanses of sand and seagrass, and the average depth at this site was  $\sim 5$  m. In contrast, at the continuous reef site, live hard coral patches were embedded in a matrix of dead limestone pavement and rubble at an average depth of  $\sim 10$  m. Relative degree of isolation, measured as the distance to the nearest neighboring reef with conspecifics, differed among reefs (range: 2 to 12 m), and was considered as a potential variable to explain variance in the likelihood of emigration among reefs.

I marked recently-settled fish (18 to 26 mm TL) *in situ* with injections of colored elastomer (see Beukers et al. 1995) so that all individuals within a group had identical tags. Group sizes ranged from 3 to 29 individuals per group, and adjacent aggregations were tagged with different colors of elastomer and separated by at least 30 m. At the patch reef site, 7 of the 10 replicates for the two species were paired (i.e., yellowhead and bluehead wrasse aggregations were located on the same reefs), and at the continuous reef site, all samples were paired. This design allowed me to examine the effect of both conspecific and total density on loss rates. Measured as the area of an oval, average reef size of patch reef site replicates was  $2.8 \pm 1.2 \text{ m}^2$  (SE) while that at the continuous reef site was  $4.5 \pm 1.1 \text{ m}^2$ . I

censused all aggregations every other day to monitor mortality, emigration, and the addition of any new individuals (immigrants and recruits) over 30 days. I distinguished losses due to mortality from losses due to emigration by complete searches for tagged individuals within a 15 m radius of the home reef on which the fish were originally tagged.

At the completion of the experiment, I conducted a complete community census of resident fishes on all reefs (both patch and continuous) to evaluate how much variation in rates of emigration from reefs was explained by total fish density. Families recorded in these censuses included: Cirrhitidae (hawkfishes), Grammatidae (basslets), Holocentridae (squirrelfishes), Labridae (wrasses), Pomacanthidae (angelfishes), Pomacentridae (damsel-fishes), Scaridae (parrotfishes), and Serranidae (grouper). For several families (e.g., grouper and parrotfish), only small juveniles whose home ranges did not exceed the size of one of the replicate reefs were included in these counts. Highly cryptic species (e.g., blennies and gobies) and more vagile species (e.g., butterflyfishes and surgeonfishes) were not censused.

### Statistical analyses

To examine patterns of emigration, I used two-way ANOVA to test whether the distance moved differed between species (yellowhead vs. bluehead wrasse) or

reef type (patch reef vs. continuous reef). I evaluated the effect of ignoring emigration on survivorship estimates using paired, one-tailed t-tests to compare the average survivorship for each group ( $n = 10$  per species per site) at the end of the experiment (day 30) with the average estimated survivorship if I had ignored emigration. In other words, I tested whether “actual survivorship” ( $1 - \text{mortality}$ ) was lower than “apparent survivorship” ( $1 - [\text{mortality} + \text{emigration}]$ ). I used separate two-way ANOVAs to determine whether average loss rates (mortality or emigration) varied between species and/or sites.

Because most of the yellowhead and bluehead wrasse aggregations co-occurred on the same reefs (patch reefs:  $n = 7$  pairs, continuous reefs:  $n = 10$  pairs), I evaluated both the effects of within and between-species initial density on mortality and emigration. Analyses were conducted separately for the two demographic rates. I used linear regression to examine the effect of conspecific density, heterospecific density, and the two species combined (total density) on both per capita mortality and emigration of each species. For yellowhead wrasse on patch reefs, 2 of the 3 unpaired reefs had zero bluehead wrasse. These reefs were included in the tests for heterospecific density effects, and thus,  $n = 9$  for yellowhead wrasse on patch reefs for these tests. Additionally, I tested for total density effects on overall mortality and emigration rates for both species combined, i.e., ignoring species identity. Different density metrics were used for the two species. For yellowhead wrasse, I used number of fish per reef as the density measure based on the following observations: (1) juveniles of this species do not

seek refuge in the reef itself (see Chapter 3) and (2) mortality rates of this species vary with group size, but not reef size (see Chapter 4). For bluehead wrasse, I used number of fish per unit area – the typical density metric. Juveniles of this species seek shelter in holes within the reef itself (K. Overholtzer-McLeod, *personal observation*), and thus the appropriate density metric for this species should account for reef area.

Finally, I explored potential factors affecting the probability of movement on a per reef basis. I used a stepwise forward multiple regression analysis, with per capita total emigration (yellowhead + bluehead wrasse) as the response variable. The initial full model included the following explanatory variables: site (patch reef vs. continuous reef), isolation distance, reef size, density of yellowhead + bluehead wrasse, and total fish density. Isolation distance was *ln* transformed to meet parametric assumptions. Based on this analysis, I fit a final reduced regression model. All analyses were conducted using SAS Institute statistical software (JMP version 4.02).

## RESULTS

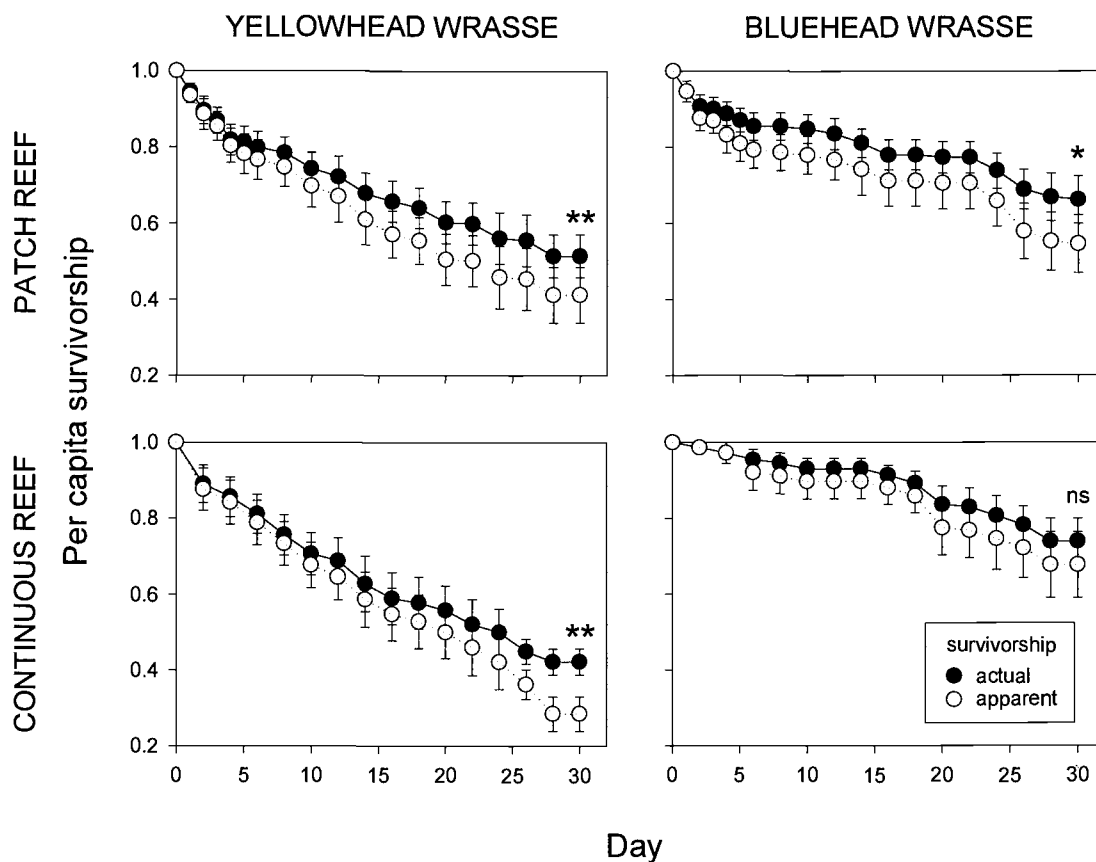
Losses of tagged individuals of both species occurred through both mortality and successful emigration to adjacent aggregations of conspecifics. The average distance moved was  $7.0 \text{ m} \pm 0.6$  (grand mean  $\pm$  SE) and did not differ

between patch reef vs. continuous reef or between species (2-way ANOVA, site:  $F_{2,42} = 1.56$ ,  $p = 0.22$ , species:  $F_{2,42} = 2.07$ ,  $p = 0.16$ ). However, for bluehead wrasse, emigration was observed from only 2 of 10 aggregations at the continuous reef site (compared to half of the reefs at the patch reef site for this species).

Assuming that all losses were due to mortality alone would have significantly underestimated survivorship after 30 days for both species on patch reefs and for yellowhead wrasse on continuous reefs (Fig. 2.1; paired, one-tailed  $t$ -tests: yellowhead, patch,  $t_9 = 3.711$ ,  $p = 0.002$ ; bluehead, patch,  $t_9 = 2.210$ ,  $p = 0.03$ ; yellowhead, continuous,  $t_9 = 2.919$ ,  $p = 0.009$ ; bluehead, continuous,  $t_9 = 1.494$ ,  $p = 0.08$ ). In other words, actual survivorship ( $1 - \text{mortality}$ ) was higher than apparent survivorship ( $1 - [\text{mortality} + \text{emigration}]$ ) if I had not accounted for emigrants surviving on nearby reefs.

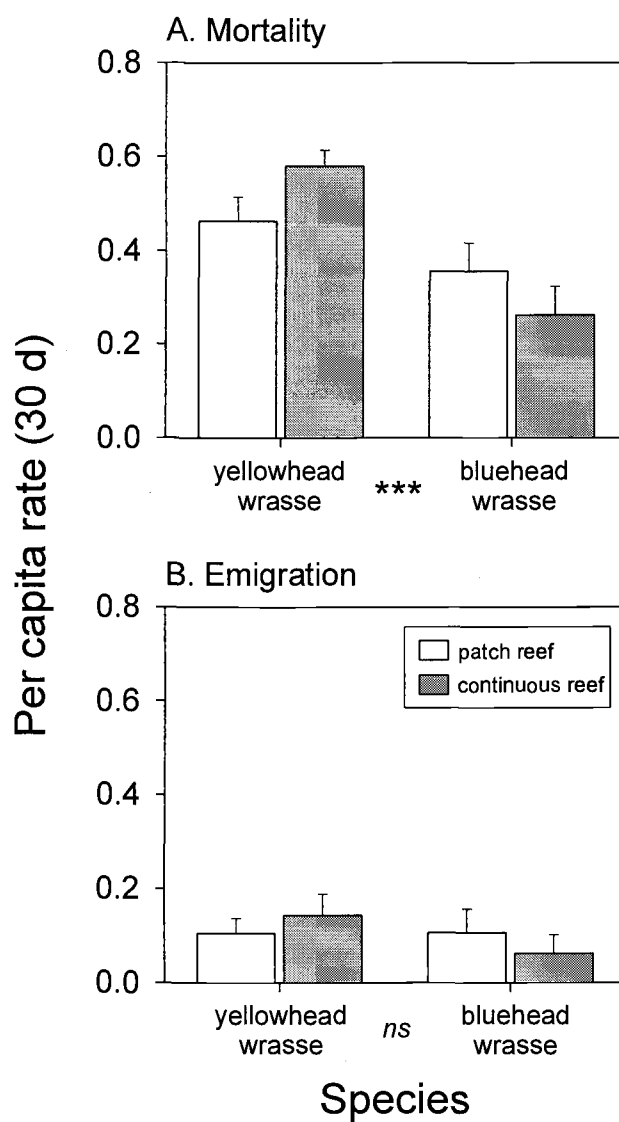
Per capita mortality rates were higher for yellowhead wrasse than for bluehead wrasse (Fig. 2.2A; 2-way ANOVA:  $F_{1,36} = 14.59$ ,  $p = 0.0005$ ). However, within species, mortality rates did not differ between reefs of different types ( $F_{1,36} = 0.05$ ,  $p = 0.83$ ), nor was there a species  $\times$  reef type interaction ( $F_{1,36} = 3.63$ ,  $p = 0.07$ ). In contrast, per capita emigration rates did not differ between species or reef types (Fig. 2.2B; 2-way ANOVA, species:  $F_{1,36} = 0.79$ ,  $p = 0.38$ ; site:  $F_{1,36} = 0.07$ ,  $p = 0.80$ ; species  $\times$  site:  $F_{1,36} = 0.93$ ,  $p = 0.34$ ).

Regarding density effects within-species, there was no evidence for density-dependent mortality for yellowhead wrasse on either reef type or for bluehead wrasse on patch reefs. However, mortality was positively density-dependent for



**Figure 2.1: Per capita survivorship ( $\bar{x} \pm 1$  SE) for yellowhead and bluehead wrasse on patch reef vs. continuous reef (n = 10 populations per species per site). “Actual” survivorship values are the true survivorship for each species at each site (i.e., 1 – mortality). “Apparent” survivorship values are based on total loss and assume that emigration rates were zero (i.e., 1 – [mortality + emigration]). The difference between the two curves is equal to emigration. Mean survivorship values at the end of the study (day 30) were compared with paired, one-tailed t-tests. (\* =  $p < 0.05$ , \*\* =  $p < 0.01$ ).**

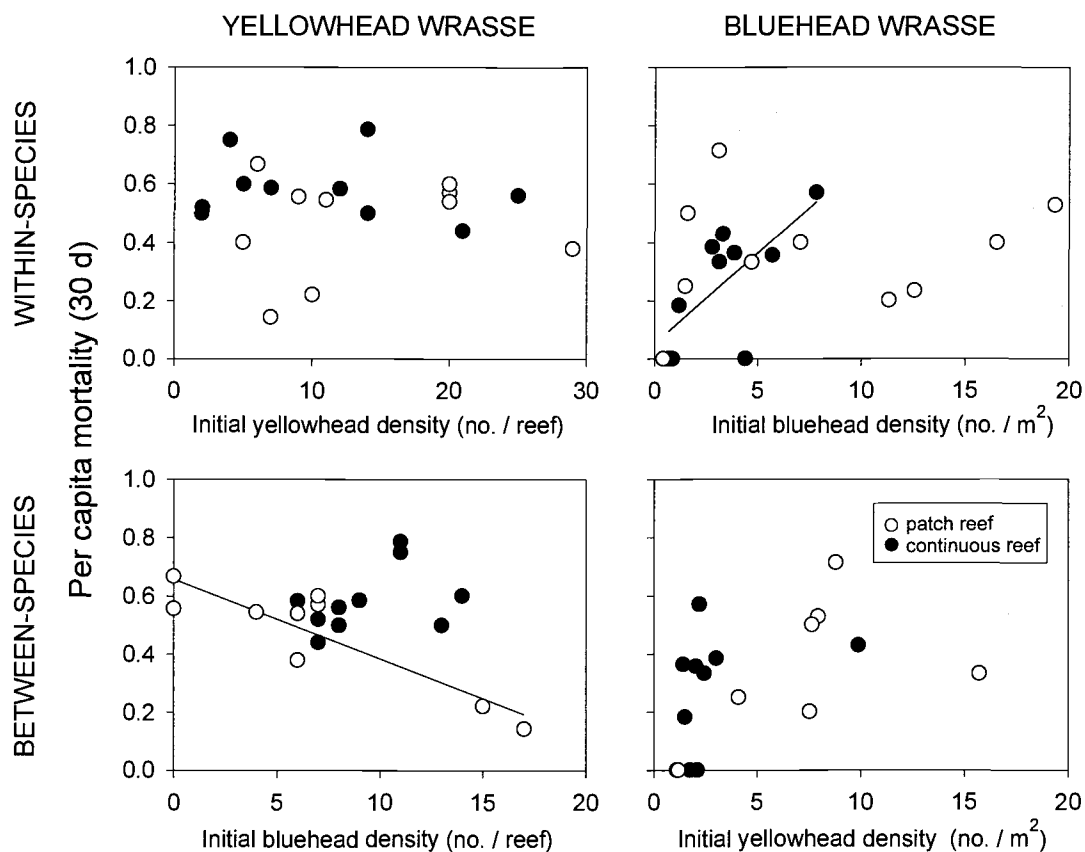




**Figure 2.2: Per capita rates ( $\bar{x} + 1 \text{ SE}$ ) of (A) mortality and (B) emigration for yellowhead and bluehead wrasse on patch reef vs. continuous reef over the 30 day study ( $n = 10$  populations per species per site). Per capita mortality rates of yellowhead wrasse were higher than those of bluehead wrasse on both types of reef (2-way ANOVA:  $p < 0.001$ ), but mortality did not differ between reef types ( $p > 0.80$ ). Per capita emigration did not vary between species or reef types (2-way ANOVA:  $p > 0.30$  for all comparisons).**

bluehead wrasse on continuous reefs (Fig. 2.3; Table 2.1). Regarding density effects between-species, there was no evidence for density-dependent mortality for bluehead wrasse on either reef type or for yellowhead wrasse on continuous reefs. However, yellowhead wrasse mortality decreased as the density of bluehead wrasse increased. In other words, mortality was negatively density-dependent (Fig. 2.3; Table 2.1). Evaluating combined within and between-species effects (yellowhead + bluehead wrasse), overall mortality of the two species combined and that of yellowhead wrasse was density-independent on both reef types. However, bluehead mortality on continuous reefs was significantly positively density-dependent with respect to the combined wrasse density (Table 2.1).

Per capita emigration rates were not a function of density for all within and between-species comparisons on both patch and continuous reefs ( $p > 0.15$  for all tests). Although emigration did not vary with density of conspecifics, heterospecifics, or all resident fish present on the reef, the overall per capita emigration rate (yellowhead + bluehead) decreased with increasing isolation distance, measured as the distance to the nearest neighboring reef with conspecifics (Fig. 2.4). There was no evidence that this effect of isolation distance on emigration rate varied between patch and continuous reefs ( $F_{1,19} = 0.012$ ,  $p = 0.91$ ).

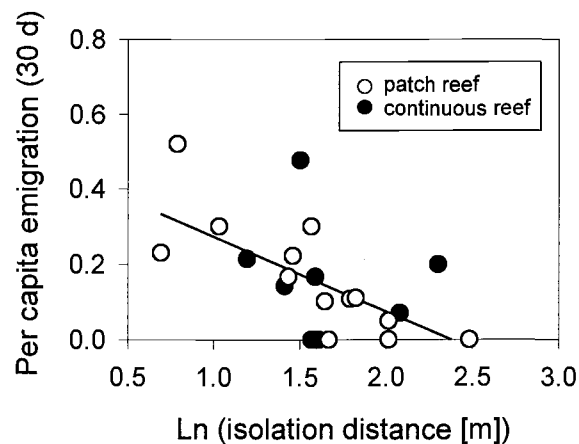


**Figure 2.3: Effects of within vs. between-species density on per capita mortality rates of yellowhead and bluehead wrasse on patch vs. continuous reef.** Regarding within-species effects, mortality was density-independent for yellowhead wrasse on both types of reef and for bluehead wrasse on patch reefs. However, on continuous reefs, bluehead wrasse mortality was positively density-dependent ( $p = 0.03$ ). For between-species effects, mortality was density-independent for bluehead wrasse on all reefs and for yellowhead wrasse on continuous reef. However, on patch reefs, yellowhead wrasse mortality was negatively density-dependent ( $p = 0.002$ ; see Table 1 for regression statistics). Each circle represents a per capita rate for a single aggregation ( $n = 10$  per species per site) over 30 days. Note that the x-axis metric for initial density differs for the two species (see Methods: Statistical analyses).

**Table 2.1: Evaluation of effects of within vs. between-species density on per capita mortality rates of yellowhead and bluehead wrasse, using linear regression.** Total density numbers include both wrasse species. Significant regressions are in bold.

Species	Patch reef		Continuous reef	
	$r^2$	p	$r^2$	p
Density effect				
<b>Yellowhead + bluehead wrasse</b>				
Initial total density (no. / reef)	0.05	0.44	0.06	0.50
Initial total density (no. / m <sup>2</sup> )	0.18	0.14	0.02	0.71
<b>Yellowhead wrasse</b>				
Initial yellowhead density (no. / reef) <sup>†</sup>	0.03	0.63	0.02	0.68
Initial bluehead density (no. / reef) <sup>†</sup>	<b>0.78</b>	<b>0.002</b>	0.15	0.26
Initial total density (no. / reef)	0.15	0.28	0.00	0.92
<b>Bluehead wrasse</b>				
Initial bluehead density (no. / m <sup>2</sup> ) <sup>†</sup>	0.03	0.65	<b>0.47</b>	<b>0.03</b>
Initial yellowhead density (no. / m <sup>2</sup> ) <sup>†</sup>	0.22	0.29	0.14	0.28
Initial total density (no. / m <sup>2</sup> )	0.09	0.40	<b>0.55</b>	<b>0.01</b>

<sup>†</sup> See Figure 2.3 for plotted data.



**Figure 2.4: Per capita emigration of yellowhead and bluehead wrasse (combined) as a function of isolation distance (distance to nearest neighbor with conspecifics) on patch and continuous reefs.** Emigration rate varied inversely with isolation distance, or distance to nearest neighboring reef with conspecifics ( $r^2 = 0.34$ ,  $p = 0.005$ ). This relationship did not differ between patch ( $n = 13$ ) and continuous reefs ( $n = 10$ ), so sites were pooled for regression.

## DISCUSSION

Contrary to the prevailing view that post-settlement movement of coral-reef fishes in general is negligible, this study demonstrates demographically relevant emigration of juvenile wrasses over small spatial scales. Although mortality was, on average, about 4 times greater than emigration, assuming that all losses were due solely to mortality would have significantly underestimated survivorship for both wrasse species on patch reefs and for yellowhead wrasse on continuous reefs.

Because the vast majority of previous studies of reef fish have focused on site-attached species on relatively isolated reefs, these findings suggest two sources of potential bias for wrasses and ecologically similar species: underestimation of survivorship and experimentally-induced barriers to movement between patches.

#### Interspecific variation in mortality

Overall, differences in mortality between wrasse species were greater than those between patch and continuous reefs. Mortality rates for bluehead wrasse were consistently lower than those for yellowhead wrasse. Unlike yellowhead wrasse, juvenile bluehead wrasse are well-documented cleaners of predatory fishes (Losey 1974), and this behavior appears to reduce their susceptibility to predation. Consistent with this interpretation, Carr and Hixon (1995) observed lower mortality rates for bluehead wrasse compared to either rainbow wrasse (*Halichoeres pictus*) or blue chromis (*Chromis cyanea*) at a nearby site in the Bahamas. The similar mortality rates observed for wrasses between patch and continuous reefs in this study concur with previous work with a damselfish (*Stegastes planifrons*) in St. Croix (Levin et al. 2000) and another damselfish (*S. partitus*) in the Bahamas (Carr et al. 2002), but contradict patterns of higher mortality for a third damselfish (*Acanthochromis polyacanthus*) on continuous reef compared to patch reefs in Australia (Connell 1996, 1998). The latter study suggested that higher mortality on

continuous reef was related to higher predator density at that site compared to patch reefs. In fact, predator density may be more likely to influence mortality than habitat type (Stewart and Jones 2001). Although I did not collect data on predator densities in the current study, qualitative observations suggest that predator densities did not differ substantially between the patch and continuous reef sites.

Effects of within-species density on mortality were evident only for bluehead wrasse on continuous reefs. Similarly, in Barbados, Tupper and Hunte (1994) found density-dependent mortality for bluehead wrasse, but not for yellowhead wrasse. Caselle (1999) also observed density-dependent mortality for bluehead wrasse in St. Croix, although only for very recent recruits (1-3 days old). Other studies have shown early post-settlement mortality patterns to vary among species, even when they are taxonomically and ecologically similar (e.g., Steele and Forrester 2002, review by Hixon and Webster 2002). For both species, mortality rates were extremely variable among reefs (coefficient of variation [CV]: bluehead wrasse = 65%; yellowhead wrasse = 29%). In a related study (conducted at the same patch reef site), spatial variation in predation risk at a spatial scale larger than that of individual reefs (i.e., at the neighborhood scale) was a source of heterogeneity that masked density dependence (see Chapter 3). Such variation in predation likely contributed to the high variation in mortality rates observed in the current study. Likewise, Wilson and Osenberg (2002) proposed that another factor – habitat quality – co-varied with goby density in their field observations as compared to their experimental study. Density dependence was detected in their

experiment, but not in their observations, suggesting a similar masking effect.

Effects of between-species density on mortality were observed for yellowhead wrasse on patch reefs: yellowhead wrasse mortality varied inversely with the density of bluehead wrasse. This pattern suggests that, with an increase in bluehead wrasse density, predators may have focused their attention on bluehead wrasse and ignored yellowhead wrasse. In other words, predators were likely switching between these two prey types. Switching behavior occurs when predators disproportionately feed on a prey species when it is relatively abundant, but feed on alternate prey items when the first species is relatively rare (see Murdoch 1969, Murdoch et al. 1975). Ideally, to examine switching behavior, one would set up paired treatments that inversely vary the relative proportion of the two prey types. Given the fact that densities of the two wrasse species were not manipulated in the current study, there was low power to detect between-species effects. This fact may explain why between-species effects were seen for only one of the four possible species  $\times$  site combinations. Several past studies suggest that the impact of predation on one species may depend on the abundance of other species (e.g., Beukers and Jones 1997, Stewart and Jones 2001, Webster and Almany 2002, see also Chapter 4). There is clearly a need to further examine between-species density effects on reef fish populations, preferably using experimental manipulations.



### Isolation distance determines likelihood of emigration

For the two species combined, the average distance moved was approximately 7 m, and emigration rates, on average, did not differ between species or sites. However, for bluehead wrasse, emigration was observed from very few reefs at the continuous reef site compared to patch reefs. Extremely low emigration rates for bluehead wrasse may be related to increased costs or decreased benefits of movement among continuous reefs compared to patch reefs. A likely cost is that of increased risk of predation while in transit between patches. Because the overall percent cover of live, hard coral was low (< 20%) at the continuous reef site, the amount of intervening habitat (e.g., sponges, gorgonians, and small coral heads) among replicate reef patches was higher at the patch reef than the continuous reef site (see Appendix A). Such habitat likely facilitated successful emigration to neighboring natural coral heads, acting as stepping-stones that provided shelter from predation while moving across otherwise inhospitable habitat. Alternatively, there may have been decreased benefits to emigration for bluehead wrasse on continuous reefs. In fact, survivorship for this species at the continuous reef site was quite high ( $\bar{x} = 0.74$ ) relative to yellowheads at this site or either species on patch reefs, and thus, there may have been no impetus for this species to emigrate.

There was no evidence for an effect of density on emigration rates no matter how density was measured (within-species, between-species, or both). In contrast, small-scale movement of a planktivorous damselfish (*Dascyllus trimaculatus*)

among anemones in Moorea was density-dependent (Schmitt and Holbrook 1996). The authors suggested that this density dependence was a response to intraspecific competition with other residents, and that by moving to a lower density patch, damselfish could enhance their growth rates. This assertion is consistent with the predictions of habitat selection models, such as the Ideal Free Distribution (IFD) (Fretwell and Lucas 1969), which state that animals will move from areas of high density to areas of lower density with respect to resource availability. The wrasses used in this study may have been less likely to experience intraspecific competition. A recent study of six Caribbean labrids, including bluehead and yellowhead wrasse, found extremely low rates ( $< 0.3\%$  of observations) of either inter- or intraspecific competition (Martha and Jones 2002). In addition, a major limitation of IFD models with respect to reef fish is that they ignore differences in predation among habitats, presumably because these models were developed using adult bird communities where predation is rare (Houston and McNamara 1997). Given the importance of predation for coral-reef fishes (reviews by Hixon 1991, Hixon and Webster 2002), both the propensity to move and the ability to relocate successfully may be related to predation, and the effect of predation on emigration is likely related to density.

For both species on both reef types, the probability of successful emigration varied inversely with the distance to the nearest neighboring reef inhabited by conspecifics. In other words, isolation from other groups of conspecifics was shown to be the most important factor affecting the propensity to move. This

finding has important ramifications for the methods typically employed to study reef fish population dynamics. First, experiments conducted on artificial or transplanted patch reefs that are highly isolated (i.e., separated by 50 to 100's of m) may artificially restrict movement between patches. Because habitats differ in their growth potential and mortality risk due to predation, this situation could lead to an experimental decrease in growth or increase in mortality compared to natural conditions because fish are not able to successfully relocate to higher quality habitat. Second, in order to evaluate demographic rates for local populations, one must determine the boundaries of those populations. The use of reef isolates could artificially bound the populations of many reef fish species, with the exception of highly site-attached species, which are either highly social (Booth 1995, Webster 2003) or territorial (Robertson 1996, Carr et al. 2002).

## Conclusions

A majority of demographic studies of reef fish have been conducted on patch reefs separated by only a few meters of sand, and often on untagged fish. The results of this study suggest that such research has potentially confounded losses due to emigration with those due to true mortality. On the other hand, studies conducted on highly isolated artificial or transplanted reefs may have experimentally inflated mortality because fish are unable to relocate to more

favorable habitats. However, this is not to say that reef isolates are not a useful tool for addressing particular questions. Rather, this is a cautionary note about extrapolating from studies of site-attached species inhabiting isolated patch reefs to more vagile species in less-isolated natural mosaics of patch reefs or continuous reef. The level of post-settlement movement should be documented in small-scale reef-fish experiments and the impact of predation on post-settlement movement should be further explored experimentally. Regardless of the influence of predation on fish movements, a better understanding of factors affecting density-dependent emigration in marine fishes is critically important to their efficient management through marine reserves.

**CHAPTER 3: SPATIAL VARIANCE AMONG NEIGHBORHOODS MASKS  
DENSITY DEPENDENCE OF CORAL-REEF FISH POPULATIONS  
ON NATURAL VS. ARTIFICIAL REEFS**

**ABSTRACT**

Understanding the role of density dependence in the regulation of marine fish populations is especially crucial as species face increased risk of extinction. Yet, spatial and temporal heterogeneity can easily mask density dependence. By experimentally manipulating group sizes of a coral-reef fish (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, although persistence was approximately density-dependent because losses also resulted from emigration to neighboring patches. On artificial reefs, mortality was density-dependent on reefs that were spatially isolated (separated by 50 m), and high and density-independent on reefs that were aggregated (separated by 5 m). 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 vs. 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. These findings highlight the difficulties of detecting density dependence in natural systems and the complex population dynamics of species that occur within patchworks of varying predation risk.

## 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 and 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 local birth rate depends on the settlement of new individuals that were likely spawned elsewhere. 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 and 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 and Tolimieri 2000, Doherty 2002, Forrester et al. 2002, Hixon et al. 2002, Hixon and 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 and Walters 1992).

Regulated populations may undergo tremendous fluctuations, and thus exhibit significant stochasticity in demographic rates, thereby masking 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). 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 and 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 1991b). 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 and 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 and Osenberg 2002, Shima and 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 and Webster 2002, see also Carr et al. 2002, Wilson and 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, 2000, Hixon and Carr 1997, Planes and Lecaillon 2001, Stewart and Jones 2001, Carr et al. 2002, Steele and Forrester 2002, Webster 2002). The magnitude of predation has been shown to vary with habitat complexity, within and among species, and between seasons (Carr and Hixon 1995, Beukers and Jones 1997, Steele et al. 1998, Anderson 2001, Steele and Forrester 2002). However, temporal and spatial variation in density-



dependent mortality are not well documented (but see Beukers and Jones 1997, Steele and 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., 100's of m<sup>2</sup>), yet affect demographic rates on the smaller spatial scale of an individual reef. This spatial scale 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? I addressed this question by comparing the results of experiments conducted on natural reefs (high variance in reef spacing) vs. artificial reefs where reef spacing was standardized. (3) How does predation differ between the two 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 (K. Overholtzer-McLeod, *personal observations*). 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 and Cowen 1997). This species settles monthly, primarily around the new moon at ~ 11-12 mm standard length after being in the plankton for ~ 25 days (Sponaugle and Cowen 1997).

### Experiment on natural reefs

In June of 2000, I manipulated yellowhead wrasse densities on 12 natural patch reefs by removing recently settled individuals (18 to 23 mm TL) to establish the same range of group sizes (6 to 18 fish per reef) on both small and large reefs in

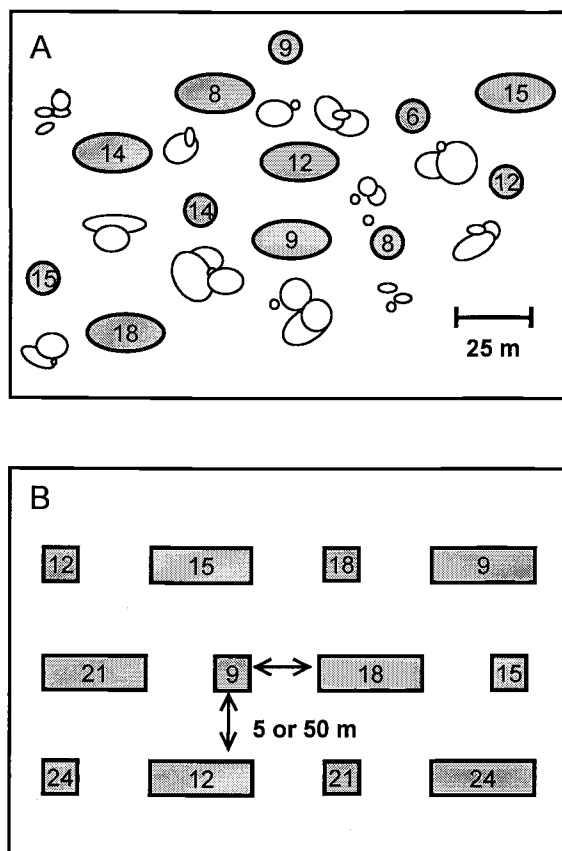
a regression design. I chose reefs of two size categories, where the area of each large reef was approximately 3 times that of each small reef (Fig. 3.1A). By establishing the same treatment ranges on both reef sizes, I tested the hypothesis that mortality was a function of density measured as the number 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), density per unit area was not relevant.

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 among replicate reefs; mean distance to nearest neighboring reef that contained conspecifics was 5 m. Divers captured fish using handnets and the anesthetic quinaldine and tagged all fish *in situ* with fluorescent elastomer (Beukers et al. 1995) before returning them to their 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 =  $0.16 \pm 0.03$ [SE]). Reefs were then censused every other day for a period of 21 days. Previous studies have shown several weeks to be sufficiently long for density-dependent mortality to manifest in most reef fishes

(Hixon and 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  $6.8 \pm 0.9$  m (see Chapter 2). 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 two arrays of artificial reefs near CMRC in a large, shallow ( $\sim 3$  m depth) expanse of sand and sparse seagrass (primarily *Thalassia testudinum*). Each array consisted of 12 reefs, and the two 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 two arrays differed only in the distance between reefs within each array (5 vs. 50 m), and each contained reefs of two different sizes. Each reef was constructed of standard concrete blocks (20.3 cm  $\times$  20.3 cm  $\times$  40.6 cm) stacked in columns (3 blocks high by 4 blocks deep) that were held together with stainless steel Band-it<sup>®</sup> and placed on plywood platforms. Small and large reefs consisted of 2 and 6 of these columns, respectively, such that large reefs were



**Figure 3.1: 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  $\sim 3$  times the area of small reefs (small:  $1.4 \pm 0.3$  [SD]  $\text{m}^2$ ,  $n = 6$ ; large:  $4.0 \pm 0.9$   $\text{m}^2$ ,  $n = 6$ ) and mean height of all reefs was similar ( $0.8 \pm 0.1$  m). (B) Design of the two artificial reef arrays, which differed only in terms of reef spacing (5 vs. 50 m between reefs). In each array, small reefs ( $0.8$  m x  $0.8$  m x  $0.6$  m, 24 concrete blocks;  $n = 6$ ) alternated with large reefs ( $2.4$  m x  $0.8$  m x  $0.6$  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 two arrays.

three times the size of small reefs (Fig. 3.1B). 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 2 sides (36 per side per large and 12 per side per small reef) of each reef. Reefs were naturally colonized for a period of one year 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 (see Appendix B).

In July of 2000, I transplanted recently settled yellowhead wrasse (18-23 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. 3.1B). 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 days. 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 one coney (*Cephalopholis*

*fulva*, ~10 cm TL) per reef through removals and additions from nearby natural reefs. Repeated transplant attempts to two of the reefs in the 5 m array (treatment combinations: 18 fish, small reef; 9 fish, large reef) were unsuccessful (all fish disappeared within 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 seconds for 8 hours between approximately 0930 and 1730 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 the predator visitation frequency, abundance, and species composition varied in general 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 (Serranidae:

*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.

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 experiment: (1) mortality rates of both beaugregory damselfish and yellowhead wrasse were similarly affected by reef spacing over the two 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 two arrays (see Chapter 4) 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 s 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 hours, 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., [number of predators/time interval]  $\times$  [time intervals/2 s]  $\times$  [60 s/min]).

### 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) 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 and 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 natural reefs 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-day experiment by the initial number of fish on a reef.

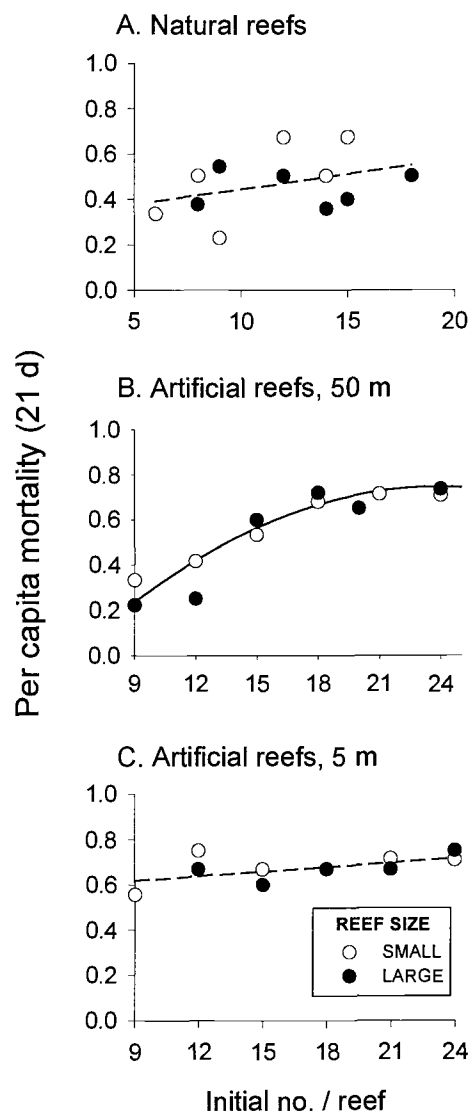
Using video observations, I compared the visitation rates of predators to natural and artificial reefs, where visitation rates were a measure of both the frequency of visitation and the abundance of predators present on a reef at any one time. I used one-way ANOVA to compare total and family-level visitation rates of predators among natural reefs and the two 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 did reef size interact with number of fish ( $F_{1,11} = 2.82$ ,  $p = 0.13$ ), 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, the trend for density dependence among populations was non-significant (Fig. 3.2A).

On artificial reefs separated by 50 m, per capita mortality rates of yellowhead wrasse were significantly density-dependent (Fig. 3.2B), 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. 3.2C).



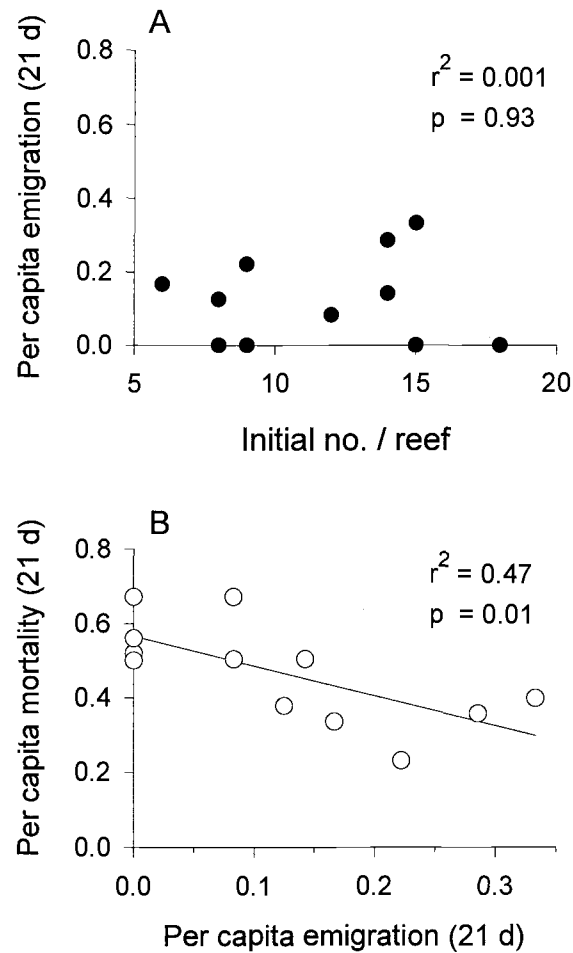
**Figure 3.2: Per capita mortality of yellowhead wrasse on (A) natural reefs, (B) artificial reefs separated by 50 m, and (C) artificial reefs separated by 5 m, each as a function of the initial number of fish per reef on both small and large reefs. (A) On natural reefs, the trend for density dependence 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.**

## 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. 3.3A), per capita emigration explained a significant amount of the variation in per capita mortality (Fig. 3.3B). 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 individuals was observed between artificial reefs separated by 50 m and only two individuals moved between reefs separated by 5 m, indicating that emigration was not a significant demographic rate on artificial reefs.

## Persistence

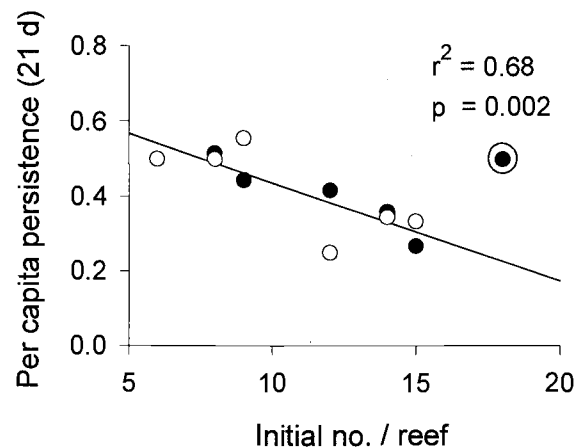
After accounting for losses due to both emigration and mortality, persistence of yellowhead wrasse remaining on natural reefs for 21 days decreased with density, albeit non-significantly ( $r^2 = 0.27$ ,  $p = 0.08$ ; Fig. 3.4). The poor fit of this relationship is heavily influenced by a single outlier. 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 ( $r^2 = 0.68$ ,  $p = 0.002$ ).



**Figure 3.3: 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 days of the experiment.

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.



**Figure 3.4: 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 an unusually high persistence. The relationship did not differ between reef sizes (small [○] vs. large [●]), and therefore reef sizes are pooled for the regression ( $n = 12$ ). (For statistics with the outlier included, see RESULTS: Persistence.)

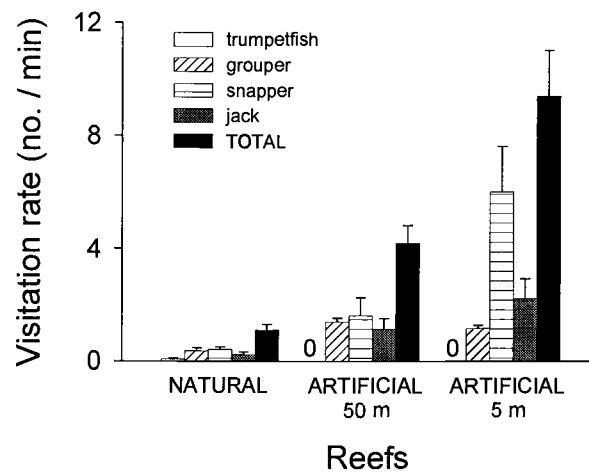
#### Predator abundance and diversity

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 pairwise comparisons: artificial, 5 m > artificial, 50 m > natural reefs; Fig. 3.5).

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. 3.5). 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. 3.5). All artificial reefs were inhabited by one 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 =  $0.37 \pm 0.11$ [SE] present min<sup>-1</sup>). 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). There were no trumpetfish present on artificial reefs, and although the average visitation rates of trumpetfish to natural reefs from video observations were extremely low ( $\bar{x} = 0.08 \pm 0.02$  present min<sup>-1</sup>), this species was frequently observed actively hunting and consuming juvenile yellowhead wrasse. All predators at the natural reef 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 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).



**Figure 3.5: 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 one 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 two occasions, the group split in half and formed two 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, two 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 was primarily the result of 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.

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 of the bottom. As a result, predators' use of space was discrete compared to that on natural reefs and predators could clearly be differentiated into residents (grouper) and transients (snappers and jacks). Although the diversity of predators present was much lower than that on natural reefs, visitation rates of species that were present was significantly higher. In particular, visitation rates of the most common species of transient predator (yellowtail snapper) were significantly higher to reefs in the 5 m array than to those in the 50 m array. Density-dependent mortality (probably via switching among prey types) was likely caused by resident predators on all reefs in both arrays; however, on closely spaced reefs, intense predation by transient predators overwhelmed this underlying density dependence and resulted in uniformly high, density-independent mortality (for details, see Chapter 4).

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 (see Chapter 4). 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 exposed fish to increased risk of predation both during transit between patches or 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.

In a previous study (at the same site), the probability of emigration of yellowhead wrasse varied inversely with reef isolation (see Chapter 2). Because I standardized isolation distance of 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 did emigration vary inversely with 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. However, it provides an impetus for future studies of population dynamics to measure multiple demographic rates and explicitly consider predation risk at multiple spatial scales.

## 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 and Jones 1997, Webster and Almany 2002, see also Chapter 2), 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 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 and Osenberg 2002, Shima and Osenberg 2003), variability in predation risk among neighborhoods can affect the detectability of density dependence. This study demonstrates the efficacy of using artificial reefs, in concert with comparable work on natural reefs, for isolating the effects of spatial structure on population dynamics. Future research should assess the spatial scale over which predation risk varies and seek to further understand factors that affect post-settlement movement, including the potential effect of predators on emigration behavior.

#### **CHAPTER 4: VARIATION IN DENSITY-DEPENDENT MORTALITY OF CORAL-REEF FISHES: SCALE-DEPENDENT PREDATOR-PREY INTERACTIONS**

##### **ABSTRACT**

The spatial distribution of habitat patches can profoundly affect ecological interactions at the scales of individuals, populations, and communities. I examined the effect of reef spacing on predator-prey interactions among coral-reef fishes in the Bahamas. Using manipulative field experiments, I determined that reef spacing influences whether and how density-dependent predation occurs. Mortality rates of recently settled juveniles of two ecologically dissimilar coral-reef fishes (beaugregory damselfish and yellowhead wrasse) were similarly affected by reef spacing in two different years; for both species, mortality was density-dependent on reef patches that were spatially isolated (separated by 50 m), and density-independent on reef patches that were aggregated (separated by 5 m). A subsequent experiment using only the beaugregory damselfish as prey demonstrated that substantial mortality of this species was caused by a single common resident predator (the coney, a small grouper), regardless of reef spacing. Transient predators (jacks and snappers) showed no evidence of having either an aggregative response or a type 3 functional response, and therefore were not the source of density dependence during these month-long (within-generation)

experiments. However, snappers had significantly higher visitation rates to aggregated reefs than to isolated reefs, regardless of prey density, and here mortality rates approached 100% for both prey species. These patterns suggest that resident predators caused density-dependent mortality in their prey through a type 3 functional response on all reefs, but on aggregated reefs, this density dependence was overwhelmed by high, density-independent mortality caused by transient predators. Thus, the spatial distribution of reef habitat affects the magnitude of total predation and consequently the existence of density-dependent mortality. A possible ramification is that the increasing fragmentation of coral reef habitats may lead to the breakdown of natural regulatory mechanisms within reef-fish populations.

## INTRODUCTION

The spatial subdivision of patches of habitat within a landscape profoundly affects a broad spectrum of ecological interactions. For example, the frequency of aphid outbreaks (Kareiva 1987), the abundance and distribution of birds (Pulliam et al. 1992), functional responses of lizard predators (Pitt and Ritchie 2002), and coexistence among competing fly species (Hanski 1987) have all been shown to vary with the spatial structure of the environment. If spatial structure partly determines the outcome of predator-prey interactions, then population dynamics,

and perhaps population regulation, may be intimately linked to habitat patchiness.

The inherent patchiness of coral reefs at multiple scales makes them ideal systems for examining the effects of the spatial arrangement of habitat patches on species interactions. Here, I focus on the responses of resident and transient predators to reef patchiness and the subsequent effects of patchiness on prey mortality. Given, first, the diverse suite of predators that potentially consume small reef fishes (Hixon 1991), and second, the relative immobility of reef fish prey relative to generally more vagile predators (Demartini 1998), the existence and/or intensity of predation will likely vary with the spatial distribution of prey and the movements of predators, as evident in other systems (e.g., Ryoo 1996, Pitt and Ritchie 2002).

For a population to persist indefinitely, it must be regulated in such a way that it fluctuates between upper and lower bounds above zero (Murdoch 1994, Turchin 1995). A population so regulated is characterized by demographic density dependence, an inverse relationship between the population growth rate and density (reviewed by Hixon et al. 2002). The nature and strength of population regulation in reef fishes has been strongly debated (reviews in Caley et al. 1996, Hixon 1998, Sale and Tolimieri 2000, Doherty 2002, Forrester et al. 2002, Hixon et al. 2002, Hixon and Webster 2002). However, numerous recent studies have detected density-dependent mortality within both temperate (e.g., Tupper and Boutilier 1995, Steele 1997a, Anderson 2001) and tropical reef fish populations (review by Hixon and Webster 2002, see also Carr et al. 2002, Wilson and Osenberg 2002,

Webster 2003). In addition, a recent meta-analysis suggests that density-dependent mortality is widespread among coral-reef fishes (Hixon and Webster 2002).

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, 2000, Hixon and Carr 1997, Planes and Lecaillon 2001, Stewart and Jones 2001, Steele and Forrester 2002, Webster 2002).

Despite the extensive evidence for density-dependent mortality and the fact that predators are the most likely source of that mortality, the behavioral mechanisms underlying density dependence have only recently been elucidated (Beukers and Jones 1997, Hixon and Carr 1997, Forrester and Steele 2000, Anderson 2001, Carr et al. 2002, Webster 2003). For prey mortality within a collection of patches to be density-dependent over short (within-generation) time scales, predators must have a type 3 functional response and/or individual predators must exhibit an aggregative response (Murdoch and Oaten 1975). A type 3 functional response occurs when the per capita consumption rate of predators is a sigmoid function of prey density. The accelerating portion of this function induces density dependence (Murdoch and Oaten 1975). Unfortunately, functional response data are particularly difficult to obtain for fish either in the field or under semi-natural conditions (e.g., Anderson 2001). The aggregative response is the redistribution of predators to higher density prey patches, whereby either the time spent per predator or the number of predators present per unit time increases in areas of higher prey density (Hassell and May 1974). There is limited evidence for

this phenomenon for both temperate (Anderson 2001) and tropical reef fishes (Hixon and Carr 1997, Hixon 1998).

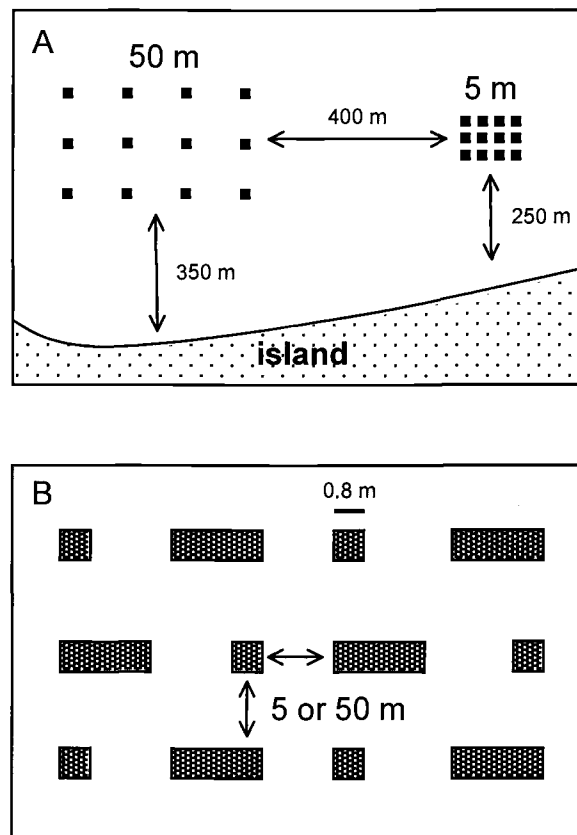
The goals of this study were to examine how the mortality of juvenile coral-reef fishes in the Bahamas varied with density and to determine the effect of reef spacing on the presence and strength of short-term demographic density dependence. I addressed the following questions: (1) What is the effect of density on the mortality rates of yellowhead wrasse (*Halichoeres garnoti*) and beaugregory damselfish (*Stegastes leucostictus*)? (2) How do mortality rates of the two species differ between reefs that are relatively isolated (50 m apart) versus those that are aggregated (5 m apart)? (3) What are the potential mechanisms underlying different mortality rates? Specifically, is mortality most likely caused by resident or transient predators and which components of predation are density-dependent?

## METHODS

### Study system and study species

In 1999, I constructed two arrays of artificial reefs in a large, shallow (~ 3 m depth) expanse of sand and sparse seagrass (primarily *Thalassia testudinum*) near the Caribbean Marine Research Center on Lee Stocking Island, Bahamas (23°46' N, 76°10' W). Each array consisted of 12 reefs, and the two arrays were at

least 250 m from each other and the nearest island (Fig. 4.1A). Scattered coral heads and sponges that fringe this island provided the closest natural habitat for reef fishes. The two arrays differed only in the distance between reefs within the array (5 vs. 50 m), and each contained reefs of two different sizes. Each reef was



**Figure 4.1: Spatial arrangement of experimental arrays of artificial reefs.** (A) Design of reef spacing treatments (5 vs. 50 m between reefs) indicating distances between arrays and distance from the closest island to each array. (B) Close-up view of one array showing reef size treatments. In each array, small reefs (0.8 m x 0.8 m x 0.6 m, 24 concrete blocks) alternated with large reefs (2.4 m x 0.8 m x 0.6 m, 72 concrete blocks), and the two arrays differed only in terms of reef spacing ( $n = 12$  reefs per array).

constructed of standard concrete blocks (20.3 cm × 20.3 cm × 40.6 cm) stacked in columns (3 blocks high by 4 blocks deep) that were held together with stainless steel straps (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 three times the size of small reefs (Fig. 4.1B). To supplement the shelter created by the holes of the concrete blocks (two 15 cm diameter holes per row), I added to each reef a standard number of conch (*Strombus gigas*) shells to the tops (24 per large and 8 per small reef) and 2 sides (36 per side per large and 12 per side per small reef).

Reefs were naturally colonized by fish, invertebrates, and algae for a period of one year before the start of any experiments, and fish assemblages on these reefs were representative of those on natural patch reefs in the surrounding area (see Appendix B). Resident predators on these reefs included groupers (*Cephalopholis cruentata* [graysby], *C. fulva* [coney], *Epinephelus guttatus* [red hind], *E. striatus* [Nassau grouper], and *Rypticus subbifrenatus* [spotted soapfish]). I selected two common and ecologically dissimilar prey species that colonized the reefs to examine experimentally the effect of reef spacing on patterns of mortality: the yellowhead wrasse (*Halichoeres garnoti*) and the beaugregory damselfish (*Stegastes leucostictus*). Juveniles of the micro-carnivorous yellowhead wrasse form loose, nonpolarized schools that become more cohesive in the presence of predators or when exposed to aggression from interference competitors (see



Chapter 2). In contrast, beaugregory damselfish are benthic omnivores that defend individual territories.

### Prey density manipulations

In two separate experiments, I manipulated the density of either yellowhead wrasse or beaugregory damselfish on each of the 24 artificial reefs (Table 4.1). The goal was to establish a range of prey densities (within the range naturally occurring in this region) to determine whether mortality rates varied with density, reef size, and reef spacing. Within each experiment, density treatments were randomly assigned to reefs within an array and the spatial allocation of treatments was identical for the two arrays. To establish treatments, I collected recently settled fish from natural patch reefs using handnets and the anesthetic quinaldine, tagged them with fluorescent elastomer (see Beukers et al. 1995), and released them on the experimental reefs. The experiments did not begin until treatments remained at the target number of fish for at least 24 hours to account for any handling mortality. Reefs were then censused every other day for the duration of the experiments (yellowhead wrasse: 21 d, beaugregory damselfish: 30 d). Previous studies have shown several weeks to be sufficiently long for density-dependent mortality to manifest (Hixon and Webster 2002). I detected any movement of individuals between reefs by using a unique tag color for all fish on each reef. Regardless of

**Table 4.1: Experimental design of two manipulations of prey density.**

Factor	Experiment 1	Experiment 2
Prey species	Yellowhead wrasse	Beaugregory damselfish
Size range (TL, mm)	18 - 23	17 - 22
No. transplanted to small reefs	9, 12, 15, 18, 21, or 24	4, 6, 8, 10, 12, or 14
No. transplanted to large reefs	9, 12, 15, 18, 21, or 24	8, 12, 16, 20, 24, or 28
Manipulation of conspecifics	none present	adults standardized to 6/m <sup>2</sup>
Duration of experiment	21 d	30 d
Date experiment began	June 2000	June 2001

reef spacing, movement among reefs was negligible over the course of both experiments (yellowhead wrasse:  $n = 2$  emigrants seen per array, not included in mortality estimates; beaugregory damselfish:  $n = 0$  emigrants seen). Therefore, reefs were treated as independent replicates and all disappearances were attributed to mortality. Any yellowhead wrasse or beaugregory damselfish that naturally settled to the reefs during the experiments were removed to maintain the density treatments. In both experiments, I standardized the number of small resident groupers to one coney (*Cephalopholis fulva*, ~ 10 cm TL) per reef through removals and additions from nearby natural reefs.

### Experiment 1: Yellowhead wrasse as prey

By transplanting the same number of fish to both small and large reefs (Table 1), I tested whether loss rates were a function of density measured per unit area (i.e., dependent on reef size) or a function of density measured as the number of individuals per reef (i.e., independent of reef size). For a schooling species such as yellowhead wrasse, I predicted that loss rates would be a more significant function of the number of individuals per reef, rather than per unit area, because individuals seek shelter in groups rather than in the structure of the reef itself (see Chapter 2). Repeated transplant attempts to two of the reefs in the 5 m array (treatment combinations: 18 fish, small reef; 9 fish, large reef) were unsuccessful (all fish disappeared within 48 h), so these reefs were dropped from the experiment.

### Experiment 2: Beaugregory damselfish as prey

I randomly assigned density treatments to each of the 6 small and 6 large reefs within each array to achieve a natural range of densities on the basis of area (4.0 to 21.2 fish/m<sup>2</sup>). In contrast to the yellowhead wrasse experiment, I used an overlapping range of density treatments on small and large reefs. I predicted that loss rates for the damselfish would be a more significant function of the number of individuals per unit area, rather than the number of individuals per reef because (1)

they are not a schooling species and (2) they compete for shelter within the structure of the reef itself, rather than seeking cover within a group of conspecifics (K. Overholtzer-McLeod, *personal observation*). I added or removed adult beaugregory damselfish to establish equal adult densities ( $6/m^2$ ) on all 24 reefs, and thus standardize the level of intraspecific competition from adults on all reefs. Because recently settled beaugregory damselfish occasionally inhabited natural depressions in the sand, I also searched for potential emigrants within a 20 m perimeter of all reefs. Emigration at this scale, regardless of reef spacing, was zero over the course of the experiment. Repeated transplant attempts to one of the reefs in the 50 m array (treatment combination: 8 fish, small reef) were unsuccessful (all fish disappeared within 48 h), so this reef was dropped from the experiment.

#### Video observations of transient predators

During Experiment 2, I used a digital video camera with automated time-lapse recording to measure the visitation rates and proportion of time spent feeding for transient predators (primarily yellowtail snapper, *Ocyurus chrysurus*, and bar jack, *Caranx ruber*). I recorded 2 seconds of video every 30 seconds for 8 hours between approximately 0930-1730 h and filmed each of the 24 artificial reefs twice over the course of the experiment, resulting in a total of 64 min of film for each reef. I analyzed the video by counting the number of transient predators of each

species present within every 2 s 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 hours, a total of 960 two-second intervals were filmed). I then multiplied the resulting per-interval rate by 30 (i.e., [number of predators/time interval]  $\times$  [time intervals/2 s]  $\times$  [60 s/min]) to obtain an average per minute visitation rate for each predator species. In addition to visitation rates, I also estimated the proportion of time that predators were feeding while present at a reef. Predators that were  $\leq 1$  body length away from the reef and oriented towards the probable locations of beaugregory prey (i.e., conch shells on the tops or sides of the reefs) were scored as feeding, based on field observations of such postures immediately preceding predatory attacks. Predators that simply passed by the reef or were oriented toward the larger holes of the reefs were scored as present (i.e., counted for visitation rates as described above), but not feeding. The proportion of time feeding was calculated for each species by dividing the total number of feeding events over 8 h by the total number of individuals observed.

### Experiment 3: Effects of a resident predator on damselfish mortality

In August of 2001, I set up an additional experiment to isolate the effects of the most common species of resident predator (coney grouper, *C. fulva*) on the

mortality of recently settled beaugregory damselfish by establishing  $2 \times 2$  factorial treatments (+ or - coney and 5 or 50 m reef spacing). I transplanted high, constant densities of juvenile beaugregory damselfish ( $n = 14$  fish; 17 to 22 mm TL) to each of 3 replicate small reefs in each of the 4 treatments after removing any damselfish remaining from Experiment 2. I also standardized the number of damselfish on the surrounding large reefs to 6 individuals per reef (the lowest number remaining on any of the reefs). By creating a constant density of beaugregory damselfish on neighboring large reefs, I ensured that the background densities of prey to which transient predators could be responding were constant throughout the arrays. All fish were tagged with fluorescent elastomer using a unique tag color and location (side of the body) for each reef. Coney used in this experiment ranged from 8.1-9.0 cm TL, sizes that frequently attack and consume juvenile beaugregory (K. Overholtzer-McLeod, *personal observation*). All 12 reefs were censused every day for the 14-day duration of the experiment, and surrounding large reefs were searched for potential emigrants. Successful movement of individuals between reefs (both beaugregory damselfish and coney), regardless of reef spacing, was zero over the course of the experiment, and thus reefs were treated as independent replicates, with all disappearances attributed to mortality.

## Statistical analyses

For Experiments 1 and 2, I used multiple linear regression (MLR) to evaluate the relative amount of variance in per capita mortality explained by two different measures of density: number of fish per reef vs. number of fish per unit area. For yellowhead wrasse, the explanatory variables in the model included number of fish per reef, number of fish per  $m^2$ , and an interaction between these two variables. For beaugregory damselfish, an interaction term could not be included in the model because there was no replication of treatment combinations (i.e., the same number of fish were not transplanted to small and large reefs as was the case in yellowhead wrasse experiment). Based on these analyses, I then fit multiple linear regression models to determine how mortality varied with the initial density of fish present on each reef for both the 5 and 50 m arrays, using the appropriate metric for density for each prey species. Per capita mortality rates were calculated for each reef by dividing the number of fish remaining at the end of the experiment (yellowhead wrasse: 21 d, beaugregory damselfish: 30 d) by the initial number of fish on a reef. A positive slope that differed from zero ( $p < 0.05$ ) indicated density dependence.

On reefs in which there was evidence for density dependence (i.e., 50 m array), I analyzed data from automated time-lapse video observations to determine whether visitation rates and/or the proportion of time spent feeding by transient predators varied with the ambient density of prey. I used linear regression to

determine the relationship between visitation rates of the two most common transient predators (yellowtail snapper and bar jack) and the density of beaugregory damselfish prey. If transient predators exhibited an aggregative response, visitation rates should have increased with prey density. In this study, 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 also determined whether the proportion of time spent feeding by transient predators varied with prey density, using linear regression, and evaluated the shape of the functional response by visual inspection. If the time predators spent feeding increased exponentially over some range of prey density, this would provide evidence for the density-dependent portion of a type 3 functional response (Murdoch and Oaten 1975). For both explanatory variables (visitation rates and proportion of time feeding), analyses were conducted separately for the two transient predator species. The two sampling days over which each reef was filmed were pooled, rather than averaged, because prey density on each reef changed between filming periods, there was no correlation between time 1 and time 2 ( $r^2 < 0.10$  for all comparisons), and the analysis of separate or pooled data produced similar results.

Additionally, I used video observations to investigate whether the overall visitation rates of the two transient predator species varied between the two reef spacing treatments. I initially used a nested ANOVA (model terms: reef spacing (5 vs. 50 m), sampling day [reef spacing], predator species (yellowtail snapper vs. bar



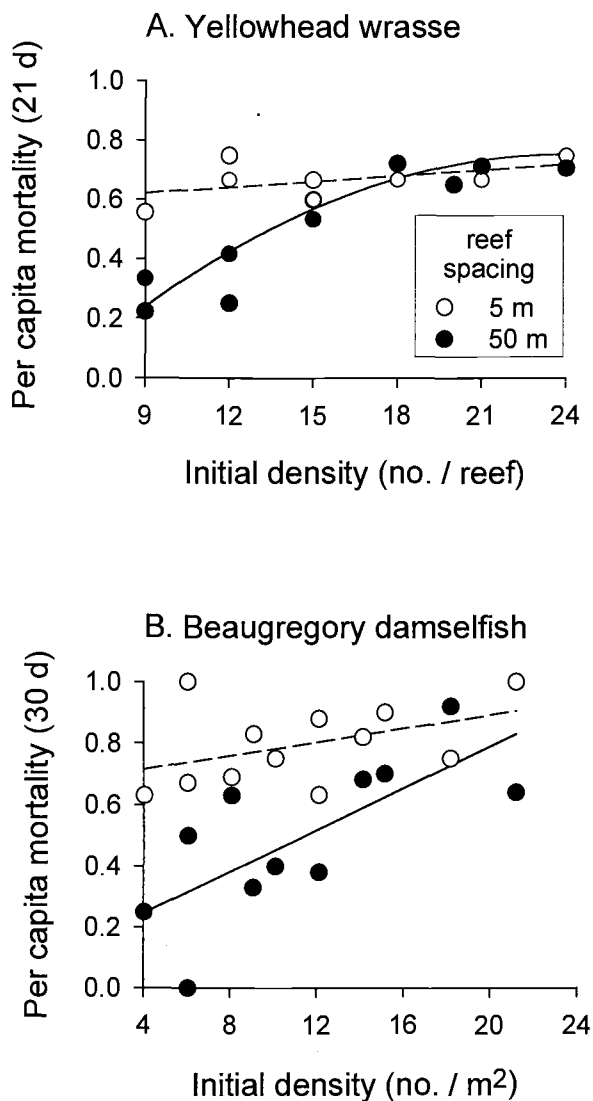
jack), reef spacing  $\times$  predator species interaction). The effect of sampling day was nested within the reef spacing treatment because the two arrays were not videotaped at the same time for the two different sampling periods; however, this factor was not significant ( $F_{2, 86} = 1.14$ ,  $P = 0.33$ ), and was subsequently dropped in favor of the reduced model. Visitation rates were transformed ( $\ln [x + 1]$ ) to correct for heteroscedasticity prior to conducting ANOVAS. ANOVA results were back-transformed to estimate effect sizes.

In Experiment 3, I tested the effects of the presence or absence of a single species of resident predator (coney) on the per capita mortality of beaugregory damselfish using two-way ANOVA (model terms: reef spacing, coney presence [+ or -], reef spacing  $\times$  coney interaction). All analyses were conducted using the JMP statistical package, version 4.02 (JMP 2000).

## RESULTS

### Prey mortality

For both prey species, the relationship between density and mortality clearly differed with reef spacing (Fig. 4.2). On reefs separated by 50 m, per capita mortality rates of yellowhead wrasse (Experiment 1) were density-dependent (Fig. 4.2A). As predicted, mortality scaled with density measured as the number of fish



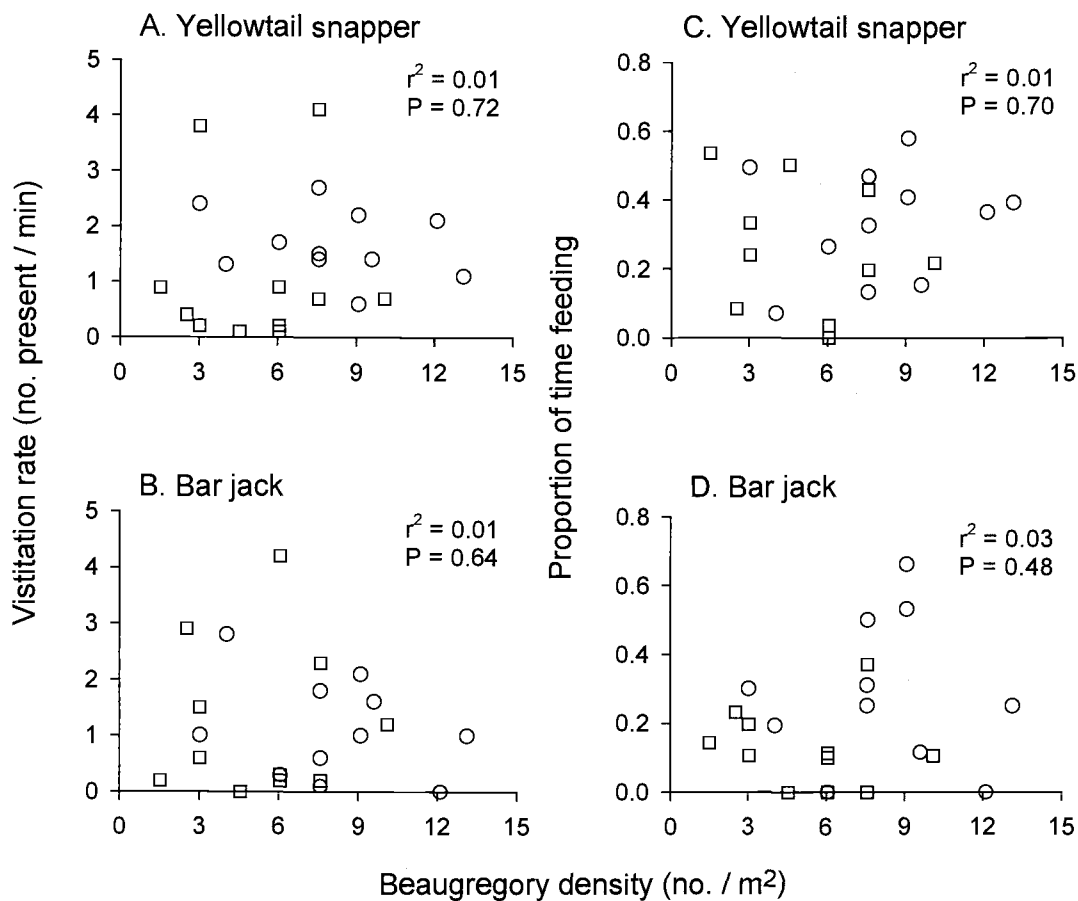
**Figure 4.2: Per capita mortality of (A) yellowhead wrasse and (B) beaugregory damselfish as a function of initial density for two reef spacing treatments (5 vs. 50 m).** (A) For the wrasse, at 5 m reef spacing, mortality was density-independent ( $y = 0.007x + 0.56$ ,  $P = 0.09$ ,  $r^2 = 0.32$ ,  $n = 10$ ); at 50 m reef spacing, mortality was density-dependent, and the fit of the regression was significantly improved by the addition of a quadratic term ( $y = -0.57 + 0.110x - 0.002x^2$ ,  $P = 0.0001$ ,  $r^2 = 0.88$ ,  $n = 12$ ). (B) For the damselfish, at 5 m reef spacing, mortality was density-independent ( $y = 0.006x + 0.67$ ,  $P = 0.16$ ,  $r^2 = 0.19$ ,  $n = 12$ ); at 50 m reef spacing, mortality was density-dependent ( $y = 0.11 + 0.017x$ ,  $P = 0.002$ ,  $r^2 = 0.52$ ,  $n = 11$ ).

per reef, rather than the number of fish per unit area or some combination of these two factors (MLR TYPE III tests, no. per reef:  $F_{1,8} = 20.47$ ,  $p = 0.002$ ; no. per  $m^2$ :  $F_{1,8} = 1.97$ ,  $p = 0.20$ ; no. per reef  $\times$  no. per  $m^2$ :  $F_{1,8} = 3.36$ ,  $p = 0.10$ ). Results of this analysis are reported only for the 50 m array because the proportion of variance in mortality explained by different density metrics cannot be clarified using a constant relationship between mortality and density. On reefs separated by 5 m, per capita mortality rates were high and density-independent (Fig. 4.2A).

In striking similarity to the results for yellowhead wrasse, beaugregory damselfish (Experiment 2) also showed density-dependent per capita mortality on reefs separated by 50 m, and high and density-independent mortality on reefs separated by 5 m (Fig. 4.2B). As expected, and in contrast to the wrasse, mortality scaled with the number of fish per unit area rather than the number of fish per reef for this species (MLR TYPE III tests, no. per reef:  $F_{1,8} = 0.07$ ,  $p = 0.79$ ; no. per  $m^2$ :  $F_{1,8} = 8.37$ ,  $p = 0.02$ ).

#### Effects of transient predators

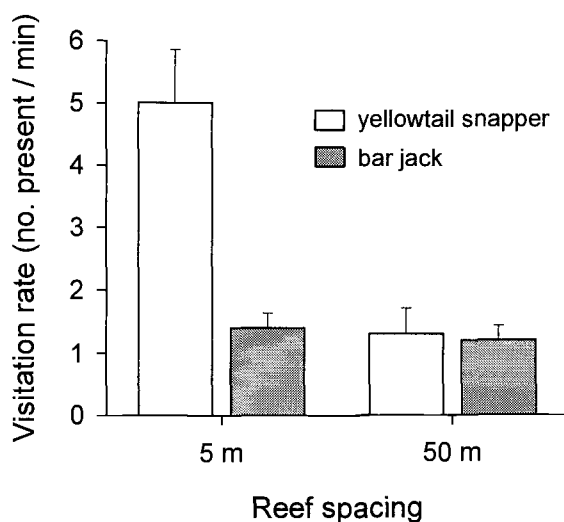
On both arrays of reefs, visitation rates and the proportion of time spent feeding were highly variable among reefs for both yellowtail snapper and bar jack. For reefs separated by 50 m, neither visitation rates nor the proportion of time feeding by either species varied with the density of beaugregory damselfish over



**Figure 4.3: Relationships between visitation rates (A, B) and proportion of time feeding (C, D) for two transient predators (yellowtail snapper and bar jack) and the density of beaugregory damselfish on reefs within the 50 m reef array.** There is no indication that transient predators exhibited either an aggregative response (A, B) or a type 3 functional response (C, D). Each symbol represents one sampling day on one reef: day 1 filmed (circles), day 2 filmed (squares). Statistical results from linear regressions of each factor (two days pooled) are given.

either or both sampling periods (Fig. 4.3). Thus, there was no evidence for an aggregative response (visitation rates did not vary with prey density) or any evidence for the accelerating (density-dependent) portion of a type 3 functional response (feeding rates did not increase with prey density) for either of the two most common transient predators on the reefs on which there was evidence for density-dependent mortality.

Although visitation rates of transient predators were not affected by prey density, they varied significantly with both reef spacing and species of predator (Fig. 4.4). However, the presence of a significant reef spacing  $\times$  predator species interaction ( $F_{1,88} = 12.5$ ,  $P = 0.0007$ ) precluded interpretation of simple main effects. For yellowtail snapper, visitation rates were 3.3 times higher to reefs in the 5 m array relative to those in the 50 m array (linear contrast,  $P < 0.0001$ ). However, visitation by bar jacks was not similarly affected by reef spacing (linear contrast,  $P = 0.80$ ). Within the 5 m array, visitation rates of yellowtail snapper were 4.5 times higher than those of bar jacks (linear contrast,  $P < 0.0001$ ). Because there was a high degree of correlation ( $r = 0.84$ ) between visitation rates and total number of feeding events observed, higher visitation rates to the 5 m array necessarily translated to higher feeding rates on that array.

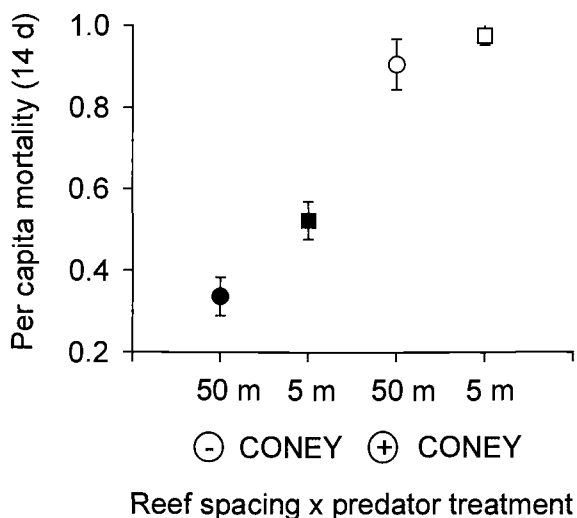


**Figure 4.4: Effects of reef spacing (5 vs. 50 m) on visitation rates of two transient predator species (yellowtail snapper and bar jack).** Data are means of pooled visitation rates for the two sampling days on which each reef was filmed + 1 SE (5 m: n = 12 reefs; 50 m : n = 11 reefs). Pooled data are shown for clarity because there was no effect of sampling day (reef spacing).

#### Effects of a resident predator

Mortality rates of beaugregory (Experiment 3) were affected by both the presence of a common resident predator (coney grouper) and reef spacing treatment (Fig. 4.5). Although there was no significant interaction between coney treatment and reef spacing, the power to detect an interaction was low (< 20%). When coney were present, per capita mortality was extremely high on both arrays (5 m:  $0.98 \pm 0.02$  [SE]; 50 m:  $0.90 \pm 0.05$ ) and 2.2 times higher, on average, than in the absence

of coney. However, when coney were absent, mortality was significantly higher on the 5 m array ( $0.52 \pm 0.04$ ) than on the 50 m array ( $0.33 \pm 0.04$ ; linear contrast,  $P < 0.0001$ ). In other words, the relative proportion of mortality caused by coney was higher when reefs were separated by 50 m than by 5 m.



**Figure 4.5: Per capita mortality of beaugregory damselfish (mean  $\pm$  1 SE;  $n = 3$  reefs per treatment) as a function of reef spacing (5 vs. 50 m) and predator treatment (coney absent (-) or present (+)).** Mortality was affected by both reef spacing (2-way ANOVA,  $F_{1,8} = 7.56$ ,  $P = 0.025$ ) and the presence of coney ( $F_{1,8} = 115.56$ ,  $P < 0.0001$ ), but there was no interaction between these treatments ( $F_{1,8} = 1.56$ ,  $P = 0.25$ ).

## DISCUSSION

The results of this study are consistent with those from terrestrial systems indicating that the spatial distribution of habitat patches can strongly affect predator-prey interactions (e.g., Pitt and Ritchie 2002). Reef spacing had a

substantial effect on the presence of density-dependent predation on two behaviorally and ecologically dissimilar coral-reef fishes. Mortality rates of recruits of a schooling wrasse and territorial damselfish were strongly density-dependent on reefs that were relatively far apart, but high and density-independent on reefs that were closely spaced. A common resident piscivore (coney grouper) had substantial effects on prey mortality, but the effects of resident predators alone did not differ with reef spacing. Therefore, the observed difference in mortality rates with reef spacing must have been the result of differential susceptibility of prey to transient predators on the two arrays. Previous work with reef fishes has shown the magnitude of predation to vary with habitat complexity, within and among species, and between seasons (e.g., Carr and Hixon 1995, Beukers and Jones 1997, Steele et al. 1998, Steele and Forrester 2002). Yet, this is the first study to show an effect of the spatial distribution of reef habitat on the magnitude of predation and the existence of density dependence.

#### Mechanisms causing density dependence

What is the likely mechanism by which mortality was density-dependent at one level of habitat spacing, but not at the other? Over short time scales, density dependence caused by predators necessarily involves an aggregative response and/or a type 3 functional response (Murdoch and Oaten 1975). Because mortality



was density-dependent on reefs separated by 50 m for both prey species, either resident predators and/or transient predators must have exhibited one or both responses on these reefs. Based on video data, neither of the two most abundant transient predators in this system (bar jacks and yellowtail snappers) exhibited an aggregative response (increase in predator visitation rate with prey density) or a type 3 functional response (exponential increase in predator foraging rate with prey density). This result implicates resident predators as the likely source of density dependence. In addition, a field experiment demonstrated that one common resident predator species (coney grouper) had a substantial effect on beaugregory mortality. As defined in this study, resident predators did not move between reefs, and thus could not have exhibited an aggregative response among reefs. Thus, by process of elimination, resident predators must have caused density-dependent mortality in wrasse and damselfish recruits through a type 3 functional response.

I hypothesize that this functional response was the result of switching behavior by resident predators (see Murdoch 1969, Murdoch et al. 1975). This hypothesis is plausible given the abundance of naturally-occurring alternate prey available during the experiments (e.g., gobies *Coryphopterus glaucofraenum* and *Gnatholepis thompsoni* [both experiments] and beaugregory damselfish [Experiment 1 only]) and the fact that groupers and other resident piscivores on coral reefs are generalist predators (Randall 1967, Clavijo et al. 1980). Under this scenario, predators disproportionately fed on the target prey species when it was relatively abundant, but fed on alternate prey items when the target species was

relatively rare. As a result, the mortality rate of the target prey increased with density. Switching behavior is likely to have occurred on all reefs, independent of reef spacing, because resident predator assemblages did not differ between the two reef arrays. Recent work on coral reef fishes in Australia by Webster and Almany (2002) also suggested that resident piscivores switched among prey types.

#### Predator responses to the spatial distribution of prey

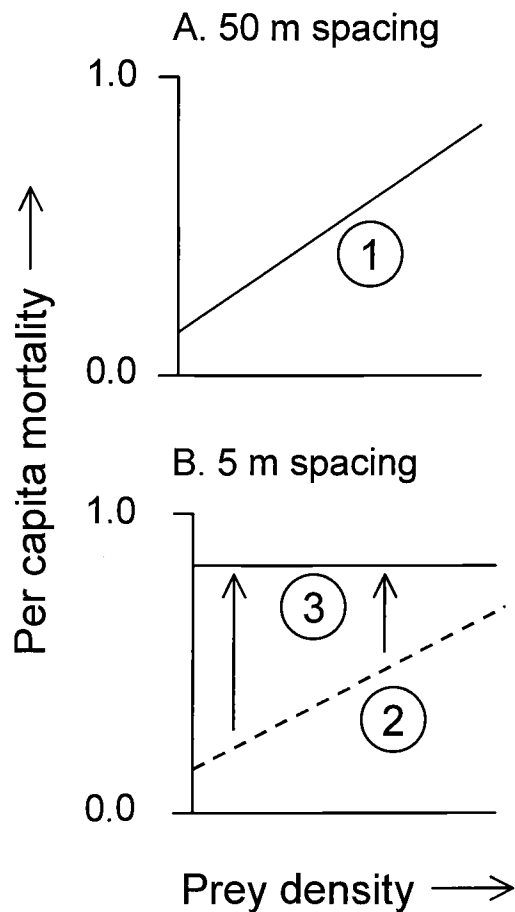
Whereas the effect of resident predators likely explains the density dependence observed on the 50 m array of reefs, the behavior of residents cannot explain why mortality was high and density-independent on the 5 m array. The effect of reef spacing on mortality is likely a result of the differential response of transient predators to the two arrays. Visitation rates of the most common transient predator species (yellowtail snapper) were significantly higher to reefs in the 5 m array than to reefs in the 50 m array. Recent tank experiments with yellowtail snapper have shown them to be voracious predators on coral-reef fish recruits, including wrasses (K. Grorud, *unpublished data*). The density of prey present within the entire 5 m array would have always exceeded that present on any single reef within the 50 m array, thereby potentially attracting more transient predators. Higher consumption rates of relatively clumped prey are widespread in other vertebrate predators and are predicted by theory (e.g., Hassell and May 1974, Real

1979, Kareiva 1990, Pitt and Ritchie 2002).

In addition to experiencing increased predation from transient predators, prey on reefs within the 5 m array exhibited density-independent mortality rates, suggesting that transient predators fed indiscriminately among prey patches within that array. Both jacks and snappers moved frequently among reefs at this smaller spatial scale (K. Overholtzer-McLeod, *personal observation*), and as a result, likely responded to prey density at the scale of the entire array of reefs rather than to the number of prey present on any single reef. Previous experimental work has shown that, for both lizards (Pitt and Ritchie 2002) and mites (Ryoo 1996), less transit time between patches leads to reduced selectivity and therefore less time spent in any particular patch.

#### Implications for population regulation of reef fishes

The effects of different types of predators on prey populations may combine in complex ways. In this study, resident predators apparently caused density-dependent mortality in wrasse and damselfish recruits on reefs separated by either 5 m or 50 m (Fig. 4.6). However, on reefs separated by only 5 m, intense predation by transient predators overwhelmed the effect of resident predators and resulted in uniformly high, density-independent mortality (Fig. 4.6). Thus, density-dependent mortality was evident only on reefs that were 50 m apart, where the effects of



**Figure 4.6: Hypothesized mechanisms by which habitat spacing affects per capita mortality rates due to predation.** (A) For reefs separated by 50 m (1) resident predators exhibit a type 3 functional response that results in density-dependent mortality of prey. (B) For reefs separated by 5 m, (2) resident predators also exhibited a type 3 functional response that would result in density-dependent mortality of prey, but (3) high visitation rates of transient predators at the scale of the entire array of reefs swamp the effects of resident predators, resulting in high, density-independent per capita mortality of prey.

transient predators were lower. In contrast, Hixon and Carr (1997) found that recruit mortality of another damselfish was density-dependent only when the

effects of resident predators were combined with a strong aggregative response by transient predators on highly isolated reefs (200 m reef spacing). Hixon and Carr's (1997) work focused on a planktivorous damselfish (*Chromis cyanea*) that feeds in the water column above reefs, whereas the present study focused on two species that forage from the benthos: an omnivorous damselfish and a carnivorous wrasse. The discrepancy between this study and Hixon and Carr's (1997) suggests that the combined effects of these two suites of predators will vary with both the spatial distribution and behavior of their prey.

Recent modeling simulations conducted by Forrester et al. (2002) predict that density-dependent interactions occurring among fishes on small patch reefs, such as those used in the current study, are relevant to larger scales. Using data from gobies, they demonstrated that strong spatial density dependence in recruit mortality significantly dampened fluctuations at the mesopopulation scale, where a mesopopulation is defined as a collection of local populations occupying an array of neighboring habitat patches. If the mechanism of density-dependent mortality in coral-reef fishes is a type 3 functional response by resident predators, as suggested by the present study, then the predictions of the above model of temporal density dependence at large scales should be born out in nature. If predators focus their attention on a particular prey species during periods of high settlement, then the spatial density-dependent mortality observed in this study will result in the temporal density dependence necessary for population regulation.

Overall, these findings highlight how spatial scale influences the interactions between predators and their prey. The population dynamics of relatively immobile prey occur at the small scale of individual reefs, but more mobile predators can respond to prey availability at the larger spatial scale of groups of reefs. On reefs that were only 5 m apart, this larger scale response of transient predators overwhelmed the density-dependent effect of resident predators, and thus the existence of density dependence depended upon the spatial distribution of patches in the landscape. In a broader context, these results suggest that habitat fragmentation caused by human disturbance and other forms of habitat loss may lead to the breakdown of natural mechanisms of population regulation.

## CHAPTER 5: GENERAL CONCLUSIONS

Synthesizing this dissertation reveals how the effects of early post-settlement processes (such as predation) and emergent demographic rates (such as mortality and emigration) can vary spatially, especially in the complex spatial structure of coral-reef habitats. Such spatial variation affected the detectability or even the presence of density dependence.

### Major findings

The principal conclusions stemming from my research on juvenile coral-reef fishes are: (1) post-settlement movement over small spatial scales was demographically relevant, (2) emigration rates varied inversely with the distance to the nearest neighboring reef inhabited by conspecifics, (3) the effects of both within- and between-species density on mortality varied between wrasse species (yellowhead and bluehead wrasse) and reef types (patch vs. continuous), (4) on natural reefs, spatial variation in predation risk at a spatial scale larger than an individual patch reef (i.e., among neighborhoods) masked density-dependent mortality, (5) the spatial distribution of habitat patches strongly affected predator-prey interactions and the existence of density-dependent mortality for two

ecologically-dissimilar prey species (yellowhead wrasse and beaugregory damselfish), (6) the effects of resident and transient piscivores were non-additive, and (7) resident predators were the most likely source of the observed density-dependent mortality.

In the study reported in Chapter 2, assuming that all losses were due solely to mortality would have significantly underestimated survivorship of juvenile bluehead and yellowhead wrasse on patch reefs and yellowhead wrasse on continuous reefs. Thus, post-settlement emigration was demographically relevant to understanding local population dynamics. Overall, interspecific differences were greater than those between reef types. Mortality rates were significantly lower for a facultative cleaner species (bluehead wrasse) than a non-cleaner (yellowhead wrasse). In general, mortality was highly variable among reefs, and patterns with density may have been masked by spatial variation in predation (see Chapter 3). Within-species density dependence in mortality was observed only for bluehead wrasse on continuous reefs. Yellowhead wrasse mortality varied inversely with the density of bluehead wrasse on patch reefs, demonstrating the potentially important effects of between-species density on population dynamics. Emigration rates for both species were not related to density, but instead varied inversely with isolation distance (distance to the nearest neighboring reef inhabited by conspecifics). These results suggest that previous studies of reef fish may have confounded losses due to emigration with those due to true mortality, and therefore underestimated survivorship.



In the experiments reported in Chapter 3, I contrasted demographic rates of yellowhead wrasse on natural and artificial reefs. Among populations on natural reefs, mortality and emigration rates were highly variable, but inversely related to one another. I hypothesized that post-emigration survivorship (and thus the detection of successful emigrants) was lower in regions where mortality was higher, and vice versa. On artificial reefs, mortality was density-dependent on reefs that were spatially isolated, yet high and density-independent on reefs that were aggregated. Emigration was virtually zero among all artificial reefs, presumably because of the absence of intervening habitat. Video observations showed that overall predator visitation rates were significantly higher to artificial reefs than to natural reefs, but a greater diversity and larger individual predators were present on natural reefs. In addition, all predators foraged over spatial scales that exceeded the boundaries of individual natural reefs. Based on these patterns, I proposed that variation in mortality rates among natural reefs was the result of variation in predation risk among neighborhoods containing numerous patch reefs (i.e., scales of 100's of  $m^2$ ).

In the experiments reported in Chapter 4, I showed that the mortality rates of juvenile beaugregory damselfish were similarly affected by reef spacing as shown in Chapter 3 for juvenile yellowhead wrasse. In other words, for both species, mortality was density-dependent on reef patches that were spatially isolated (separated by 50 m), and density-independent on reef patches that were aggregated (separated by 5 m). A subsequent experiment using the damselfish as

prey demonstrated that substantial mortality could be caused by a single common resident predator (a small grouper), regardless of reef spacing. Based on video observations, I found no evidence that transient predators exhibited either a type 3 functional response or an aggregative response. Therefore, transient predators were likely not the source of the observed density dependence. I proposed that resident predators were the source of density dependence on all reefs, but on aggregated reefs, this density dependence was overwhelmed by high, density-independent mortality caused by transient predators (mainly yellowtail snapper). These experiments showed that reef spacing influences whether and how density-dependent predation occurs and provide evidence for the likely mechanism.

All of these studies suggest cautions for the design of experiments of demographic studies of coral-reef fishes. Experiments conducted on artificial or transplanted patch reefs that are highly isolated may have artificially restricted between-patch movement, and thus experimentally decreased growth or increased mortality. Such studies have also likely altered natural predator-prey encounters, given my results showing the effects of reef spacing on predation. Other studies, carried out on patches only a few meters apart may have confounded losses due to mortality with those due to emigration. This problem can be solved by explicitly documenting movement of tagged individuals and searching for emigrants.

## Ramifications for marine reserves

The lack of density dependence in emigration rates in these studies is counter to the predictions of the Ideal Free Distribution (Fretwell and Lucas 1969). The IFD model, later applied to fish populations by MacCall (1990) as the Basin Model, predicts that fish should move from areas of high density to areas of low density with respect to resource availability. This logic has been used to predict that fish will “spillover” from crowded marine reserves, thereby replenishing nearby fisheries (for a recent review, see Russ 2002). Given the current crisis in the oceans, and the gradual shift towards adopting ecosystem-based management, marine reserves represent a key spatial management tool (Hixon et al. 2001, Pauly et al. 2002). I contend that we need to better understand factors affecting movement of fishes in general, and effects of density and predation in particular. Fortunately, recent technological advances have spawned an increase in studies of dispersal and/or movement of reef fishes at various life history stages across multiple spatial scales. Examples include otolith microchemistry (e.g., Swearer et al. 1999), tagging otoliths with tetracycline (e.g., Jones et al. 1999), and ultrasonic telemetry techniques (e.g., Zeller 1997, Zeller and Russ 1998).

## Ecological neighborhoods and future investigations

I was particularly interested in mechanisms (e.g., predation) that potentially operated at the spatial scale of a collection of patch reefs (e.g., 100's of m<sup>2</sup>), yet affected demographic rates on the smaller spatial scale of an individual reef. I referred to this larger spatial scale as a “neighborhood”. Neighborhood is a fitting analogy for coral reefs as they are 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 a site. Increased attention should be paid to mechanisms potentially operating at spatial scales larger than the scales over which demographic rates are observed. Although this scaling phenomenon may be recognized by theoreticians (e.g., Levin 1992), it is not necessarily often considered in an experimental context by reef fish ecologists (but see Hixon and Carr 1997, Webster 2003).

Many unanswered questions remain to be explored. Results in Chapters 2 and 4 suggested that predators “switched” among prey types (*sensu* Murdoch 1969). Several previous studies of reef fishes have suggested that the impact of predation on one species may depend on the abundance of other species (e.g., Beukers and Jones 1997, Stewart and Jones 2001, Webster and Almany 2002), and the effects of between-species density on predation and population dynamics are promising avenues for future research. However, addressing these issues necessarily involves logistically intensive monitoring of both conspecific and

heterospecific prey densities, ideally on all reefs within a site to avoid sampling effects (see Chapter 2). My findings in Chapter 2 suggested that the degree of isolation from conspecifics was an important determinant of movement among habitat patches. However, when isolation distance among reefs was standardized in a subsequent study (Chapter 3) emigration was still variable among reefs, independent of density. I proposed that perceived emigration varied inversely with mortality as a result of variation in predation risk on a neighborhood spatial scale. This hypothesis remains to be tested. Additional potential factors influencing the propensity to move among reefs merit further study, as does explicit consideration of predation risk at multiple spatial scales. Finally, further research is needed to evaluate the combined effects of multiple predators on different prey types (e.g., planktivores vs. benthivores) to address the differences between this study and previous work (e.g., Hixon and Carr 1997).

The combined results of these studies emphasize the effects of variation in spatial structure of the habitat on various post-settlement processes (predation, emigration, and mortality). Increasing fragmentation of reefs through human disturbance and other forms of habitat loss may cause populations to become increasingly patchy (i.e., more widely-spaced). My findings suggest that such increased clumping could lead to (1) decreased abilities of fish to successfully redistribute themselves among patches, (2) increased susceptibility to predation by transient piscivores, and (3) over longer time scales, the breakdown of regulatory

mechanisms. In order to effectively manage and conserve our remaining marine fish populations, we must protect natural mechanisms of population regulation.

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APPENDICES

**APPENDIX A: INTERVENING HABITAT SURROUNDING REPLICATE  
REEFS AT A PATCH VS. A CONTINUOUS REEF SITE NEAR  
LEE STOCKING ISLAND, BAHAMAS**

A. Patch reef site

Reef ID	Search radius from original reef*								
	5 m			10 m			15 m		
	SMALL	MEDIUM	LARGE	SMALL	MEDIUM	LARGE	SMALL	MEDIUM	LARGE
A1	7	2	0	11	6	2	8	5	1
A7	2	2	0	7	2	4	5	4	4
A11	4	0	1	7	0	1	6	5	2
B2	5	0	0	12	1	0	14	5	1
B4	2	1	0	6	4	1	4	8	6
B5	7	2	1	5	4	4	3	12	7
B6	3	0	0	4	3	0	6	1	0
B7	2	2	2	10	2	5	9	3	4
B8	2	3	1	5	5	1	6	5	6
B9	4	1	1	6	5	3	6	8	4
B10	4	1	2	7	5	3	7	4	1
B11	4	1	0	5	2	1	7	2	1

B. Continuous reef site

Reef ID	Search radius from original reef*								
	5 m			10 m			15 m		
	SMALL	MEDIUM	LARGE	SMALL	MEDIUM	LARGE	SMALL	MEDIUM	LARGE
C1	3	2	0	5	5	2	3	3	5
C2	1	1	0	3	1	1	5	2	0
C3	4	2	0	5	2	3	5	5	2
C5	0	0	0	1	2	0	4	3	0
C6	0	0	0	1	0	0	1	0	0
C7	0	0	0	0	0	0	0	1	0
C8	0	0	0	0	0	0	0	1	0
C9	0	0	0	0	0	0	0	1	0
C10	4	1	0	6	1	3	6	0	0

\* All substrata counted within a 5, 10, and 15 m radius of the home reef on which fish were originally tagged. Patches contained both live and dead corals, sponges, and gorgonians.

\*\* Size categories for substrata delineated as follows: small (< 1 m in any dimension), medium (1 - 2 m in longest dimension), and large (> 2 m in longest dimension).

**APPENDIX B: COMPARISON OF FISH COMMUNITIES ON NATURAL VS. ARTIFICIAL PATCH REEFS  
NEAR LEE STOCKING ISLAND, BAHAMAS IN 2000**

Family Species	A. Natural patch reefs											B. Artificial patch reefs (50 m spacing)											
	B10	B15	B1	B4	B9	B2	B20	B12	B6	B13	B14	C3	B3	B2	C2	C1	B1	A2	A3	A1	A4	B4	C4
Acanthuridae																							
<i>Acanthurus bahianus</i>			2					1					1									1	
Chaetodontidae																							
<i>Chaetodon capistratus</i>												1					1	1					
Holocentridae																							
<i>Holocentrus ascensis</i>	1		1	2	1			1	1			1	3		2	3	1	2	1		1	3	
Labridae																							
<i>Halichoeres bivittatus</i>			5			5		1			1	9	2	10	2	4	2	2	8	6	10	4	5
<i>Halichoeres garnoti</i>	6	6	16	13	8	9	14	8	15	13													
<i>Halichoeres maculipinna</i>			1					4			1							1					
<i>Halichoeres pictus</i>			1					5															
<i>Thalassoma bifasciatum</i>	2	4	10	5	1	19	1	13	2	7	5	1				3	4					1	1
Pomacanthidae																							
<i>Holacanthus ciliaris</i>																		1	1			1	
<i>Pomacanthus arcuatus</i>												1	1		1	1	1				1	1	1
Pomacentridae																							
<i>Chromis cyanea</i>	8	5	8	5		9		2	24	2													
<i>Microspathodon chrysurus</i>		1		1																			
<i>Stegastes leucostictus</i>												5	6	2	8	3		11	6	4	9	3	9
<i>Stegastes partitus</i>			4					2			6	1									1		
<i>Stegastes planifrons</i>							1		3														
<i>Stegastes variabilis</i>			1	3							1		1						1		1		2
Scaridae (juvenile only)																							
<i>Scarus croicensis</i>		1	4			5					2		4	2		2	2	3		1	2		
<i>Sparisoma aurofrenatum</i>			1					2				1	3	2	1	4	3		1	1		1	4
<i>Sparisoma viride</i>					1	2	1					1	3		1	2	3		1	1	1	1	1
Serranidae																							
<i>Cephalopholis cruentata</i>			1		1														1			1	
<i>Serranus tigrinus</i>			1		1					1				1		1			1			1	
Tetraodontidae																							
<i>Canthigaster rostrata</i>	1		1	1		1	1						1										2

Note: community census counts exclude highly cryptic species (e.g., families Gobiidae, Clinidae) and highly vagile species (e.g., Carangidae, Haemulidae, Lutjanidae, Mullidae, larger Serranidae). All censuses conducted in August of 2000.

**APPENDIX B: COMPARISON OF FISH COMMUNITIES ON NATURAL VS. ARTIFICIAL PATCH REEFS  
NEAR LEE STOCKING ISLAND, BAHAMAS IN 2000 (CONTINUED)**

Family Species	C. Artificial patch reefs (5 m spacing)												
	C4	B4	A4	A3	C3	B3	B2	C2	C1	B1	A1	A2	
Acanthuridae													
<i>Acanthurus bahianus</i>													
Chaetodontidae													
<i>Chaetodon capistratus</i>													
Holocentridae													
<i>Holocentrus ascensis</i>			2	1		1	1	2	2	1	1		
Labridae													
<i>Halichoeres bivittatus</i>	4	2	9	2	2	3	1	3		5	2	5	
<i>Halichoeres garnoti</i>													
<i>Halichoeres maculipinna</i>	1												
<i>Halichoeres pictus</i>													
<i>Thalassoma bifasciatum</i>	2			1		3				2	1		
Pomacanthidae													
<i>Holacanthus ciliaris</i>													1
<i>Pomacanthus arcuatus</i>	1												
Pomacentridae													
<i>Chromis cyanea</i>													
<i>Microspathodon chrysurus</i>													
<i>Stegastes leucostictus</i>	9	3	10	3	3	7	2	12	4	9	3	10	
<i>Stegastes partitus</i>													
<i>Stegastes planifrons</i>													
<i>Stegastes variabilis</i>			1			1		1					1
Scaridae (juvenile only)													
<i>Scarus croicensis</i>	1		4			2		3		4	1	4	
<i>Sparisoma aurofrenatum</i>					1								
<i>Sparisoma viride</i>	1	1	2			2			1	2	1	2	
Serranidae													
<i>Cephalopholis cruentata</i>													
<i>Serranus tigrinus</i>						1							
Tetraodontidae													
<i>Canthigaster rostrata</i>		1				1		2		1			