

Ecology, 91(7), 2010, pp. 1949–1961
 © 2010 by the Ecological Society of America

Synthesizing mechanisms of density dependence in reef fishes: behavior, habitat configuration, and observational scale

J. WILSON WHITE,^{1,7} JAMEAL F. SAMHOURI,² ADRIAN C. STIER,³ CLARE L. WORMALD,⁴ SCOTT L. HAMILTON,⁵
 AND STUART A. SANDIN⁶

¹*Department of Wildlife, Fish, and Conservation Biology, University of California–Davis, Bodega Marine Laboratory, Bodega Bay, California 94923 USA*

²*NOAA Fisheries, Northwest Fisheries Science Center, 2725 Montlake Boulevard E, Seattle, Washington 98112 USA*

³*Department of Biology, University of Florida, Gainesville, Florida 32611-8525 USA*

⁴*Department of Biology, California State University–Northridge, 18111 Nordhoff Street, Northridge, California 91330-8303 USA*

⁵*Marine Science Institute, University of California, Santa Barbara, California 93106-6510 USA*

⁶*Center for Marine Biodiversity and Conservation, Scripps Institution of Oceanography, 9500 Gilman Drive, La Jolla, California 92093-0202 USA*

Abstract. Coral and rocky reef fish populations are widely used as model systems for the experimental exploration of density-dependent vital rates, but patterns of density-dependent mortality in these systems are not yet fully understood. In particular, the paradigm for strong, directly density-dependent (DDD) postsettlement mortality stands in contrast to recent evidence for inversely density-dependent (IDD) mortality. We review the processes responsible for DDD and IDD per capita mortality in reef fishes, noting that the pattern observed depends on predator and prey behavior, the spatial configuration of the reef habitat, and the spatial and temporal scales of observation. Specifically, predators tend to produce DDD prey mortality at their characteristic spatial scale of foraging, but prey mortality is IDD at smaller spatial scales due to attack-abatement effects (e.g., risk dilution). As a result, DDD mortality may be more common than IDD mortality on patch reefs, which tend to constrain predator foraging to the same scale as prey aggregation, eliminating attack-abatement effects. Additionally, adjacent groups of prey on continuous reefs may share a subset of refuges, increasing per capita refuge availability and relaxing DDD mortality relative to prey on patch reefs, where the patch edge could prevent such refuge sharing. These hypotheses lead to a synthetic framework to predict expected mortality patterns for a variety of scenarios. For nonsocial, nonaggregating species and species that aggregate in order to take advantage of spatially clumped refuges, IDD mortality is possible but likely superseded by DDD refuge competition, especially on patch reefs. By contrast, for species that aggregate socially, mortality should be IDD at the scale of individual aggregations but DDD at larger scales. The results of nearly all prior reef fish studies fit within this framework, although additional work is needed to test many of the predicted outcomes. This synthesis reconciles some apparent contradictions in the recent reef fish literature and suggests the importance of accounting for the scale-sensitive details of predator and prey behavior in any study system.

Key words: *direct density dependence; inverse density dependence; patch vs. continuous reef; reef fish; refuge-based aggregation; shoaling; social aggregation; spatial scaling.*

INTRODUCTION

Density-dependent vital rates are critical factors structuring population dynamics (Murdoch 1994). The

mechanisms underpinning density-dependent regulation are revealed best by small-scale observations and experimental manipulations (Harrison and Cappuccino 1995), and benthic marine populations provide a fertile testing ground for these efforts (Hixon 1998, Menge 2000, Hixon et al. 2002). Nonetheless, while density-dependent regulation in terrestrial systems is rather well understood (Turchin 2003), regulation in marine sys-

Manuscript received 20 February 2009; revised 26 June 2009; accepted 20 October 2009. Corresponding Editor: S. R. Thorrold.

⁷ E-mail: jwwhite@ucdavis.edu

tems is still an active and contentious area of research (Sale and Tolimieri 2000, Jenkins et al. 2008), especially for coral and rocky reef fishes with pelagic larvae (Sandin and Pacala 2005b, Anderson et al. 2007).

For most benthic fishes and invertebrates, widespread dispersal and highly variable mortality during the pelagic larval phase can decouple reproduction from subsequent recruitment at almost all spatial scales, thus eliminating regulatory feedbacks typically found in non-marine systems (Caley et al. 1996). There is a dearth of evidence for density dependence during the pelagic larval phase of any marine fish or invertebrate (e.g., Shanks and Roegner 2007), possibly due to the logistic difficulties inherent in quantifying larval mortality rates in the ocean. Most work on reef fishes, therefore, has centered on the potential for regulatory, directly density-dependent (hereafter, DDD) per capita mortality during the vulnerable postsettlement stage just after juvenile fish leave the plankton and enter the benthic environment (reviewed by Caley et al. 1996, Hixon and Webster 2002).

After early debates regarding the possibility that benthic marine populations were unregulated, Menge (2000) proposed the “recruit–adult hypothesis,” which holds that population densities are extremely sensitive to the stochastic and density-independent (DI) arrival of larval settlers so long as settlement rates are low (also see Connell 1985, Sandin and Pacala 2005a). As settlement rates increase, DDD processes become more important until, in the extreme, population density is unchanged by the arrival of additional larvae. This hypothesis has been borne out by sensitivity analysis across a range of settler densities (Schmitt et al. 1999), and a meta-analysis revealed that nondetection of DDD mortality was generally a result of using settler densities that were too low (Osenberg et al. 2002). There now appears to be consensus that (a) most benthic populations are regulated by some benthic DDD process (Hixon et al. 2002), and (b) the proximate cause is usually DDD postsettlement mortality (Roughgarden et al. 1988, Menge 2000, Hixon and Webster 2002).

What is to be made, then, of results suggesting that some reef fish species experience inversely density-dependent (IDD) postsettlement mortality (i.e., mortality rates that decline with increasing density [e.g., Sandin and Pacala 2005b, Johnson 2006a, White and Warner 2007b, Wormald 2007])? Hixon and Webster's (2002) exhaustive review of patterns of density dependence in coral reef fishes identified a few studies that reported IDD mortality (e.g., Booth 1995), but their review focused predominantly on the more common finding of strong DDD mortality. However, recent studies have provided conflicting results of both DDD and IDD mortality in the same species at different locations, or when measured at different spatial scales (*Chromis cyanea* [Sandin and Pacala 2005b, Anderson et al. 2007]; *Thalassoma bifasciatum* [Caselle 1999, White and Warner 2007b]). It is unclear in which species and

under what conditions one should expect to find IDD rather than DDD mortality. We propose a conceptual framework that explains mortality patterns based on prey and predator behavior, habitat configuration, and the scale of observation. Using this framework, we offer a synthetic interpretation of the results of prior studies of reef fishes and follow this with a prospectus for future research that is relevant for studies of population dynamics beyond reef fish systems.

PROCESSES LEADING TO DENSITY-DEPENDENT MORTALITY

We define DDD mortality as an increase in the per capita death rate corresponding to an increase in population density. Predation is usually the proximate cause of DDD mortality in reef fishes (Hixon and Jones 2005) (see Plate 1), but ultimate causes may include competition, parasitism, and disease (Holbrook and Schmitt 2002, Hixon and Jones 2005, Forrester and Finley 2006). Importantly, these mechanisms may operate during any life stage and are not mutually exclusive (Caley 1998).

Predators can generate DDD prey mortality via specific types of *aggregative responses* (Hassell and May 1974), *functional responses* (Holling 1959, Murdoch 1969), *numerical responses* (Holling 1959), and *developmental responses* (Murdoch 1971). The first two are short-term, behavioral responses and the latter two are long-term, demographic responses, though combinations of these four may operate simultaneously. All but aggregative responses can produce regulatory, temporal DDD mortality (because with aggregation, predators respond only to the relative, not absolute, density of prey in a patch [Stewart-Oaten and Murdoch 1990]).

Aggregative and functional responses are short-term, behavioral responses to prey density, and are more amenable to field study than the other mechanisms of DDD predation. For example, predator aggregation to high-density patches of prey has been reported in several studies (coral reef carangids [Hixon and Carr 1997]; the temperate serranid *Paralabrax clathratus* [Anderson 2001]; and coral reef serranids and aulostomids [Webster 2003]), though aggregation is not always observed (Sandin and Pacala 2005b, Overholzer-McLeod 2006). Alternatively, Overholzer-McLeod (2006) revealed evidence of DDD mortality of beaugregory damselfish (*Stegastes leucostictus*) through a Type III functional response, in which the predatory coney grouper (*Cephalopholis fulva*) switched from consuming damselfish when these prey were at high densities to consuming alternative prey when the damselfish were at low density. Numerical and behavioral responses are relatively long-term demographic responses, involving dynamic changes in population size or consumptive patterns, respectively, of predators. We are unaware of clear evidence of numerical or developmental responses in reef fishes, but examples have been found in other systems (Houde and Schekter 1980, Wood and Hand 1985).

Competition for limiting resources has emerged as the ultimate mechanism of DDD mortality in several species of reef fishes. Most commonly, intense competition for predator refuges (e.g., crevices in living corals or coral rubble) at high prey densities (Holbrook and Schmitt 2002, Forrester and Steele 2004, Johnson 2007) or in the presence of larger conspecifics (Schmitt and Holbrook 1999, Webster 2004, Samhuri et al. 2009a) or heterospecifics (Carr et al. 2002) causes the DDD mortality. At least two other ultimate mechanisms of DDD mortality are possible, though they may be slower to take effect. At high population densities, scramble competition for food may leave some individuals more vulnerable to predation, due either to their smaller size or weakened physiological state (Steele and Forrester 2002). Increased frequency of aggressive behaviors at high densities may produce similar effects (Booth 1995, White and Warner 2007a). In social species, such competition may lead to growth depensation, in which socially dominant individuals grow faster and have higher survival than subordinates (Jones 1987, Hixon and Jones 2005).

Parasites and diseases can also contribute to DDD mortality in reef fishes (Forrester and Finley 2006). DDD mortality will result directly from parasites or disease if the prevalence or transmission rate increases with population density, as is the case for copepod gill parasites in bridled gobies, *Coryphopterus glaucofraenum* (Finley and Forrester 2003). Alternatively, DDD mortality can arise indirectly if morbid individuals are more susceptible to predation, such as fishes that undertake riskier behaviors when parasitized by larval trematodes (Lafferty and Morris 1996).

PROCESSES LEADING TO INVERSELY DENSITY-DEPENDENT MORTALITY

IDD mortality occurs when the per capita mortality rate declines with increasing population density. Though less commonly reported than DDD mortality, several studies have detected IDD mortality in coral reef fishes, implying some benefit of aggregation in these species (Booth 1995, Sandin and Pacala 2005b, Johnson 2006a, White and Warner 2007b, Wormald 2007).

Many reef fishes occur in groups, which may produce benefits simply by virtue of group membership or via active social behaviors. In reef fishes, the degree of sociality ranges from high-density clumps of individuals that are nearby in space but interact infrequently, if at all (e.g., the goby *C. glaucofraenum* [Forrester and Finley 2006]), to *shoals* consisting of tightly grouped but nonpolarized fish (e.g., the wrasse *T. bifasciatum* [White and Warner 2007a]), to *schools*, which are shoals that exhibit regular spacing and coordinated swimming behavior (e.g., the grunt *Haemulon flavolineatum* [Hein 1996]). Some benefits of grouping accrue only to species in the latter two categories, so it can be important to distinguish group size (the number of fish within a shoal) from the areal density of individuals (Shima 2001, White

and Warner 2007b). Areal density is measured as fish per square meter. For example, a square meter of reef could contain either a shoal of four conspecifics or four noninteracting fish, each occupying its own territory. Both cases represent a density of 4 fish/m², but only in the former case will the fish be able to take advantage of active shoaling behaviors.

Per capita predation risk may be reduced passively due to attack-abatement effects. These consist of both numerical *risk dilution* (a decrease in per capita predation risk in a single predator attack) and passive *predator avoidance* (a decrease in the per capita risk of detection by predators, or the temporary swamping of predator functional responses [reviewed by Pitcher and Parrish 1993]). IDD mortality in reef fishes has been attributed to risk dilution (e.g., per capita predator attack rate declined with the size of *C. cyanea* shoals [Sandin and Pacala 2005b]), and temporary swamping at sites with low predator density (Johnson 2006b, White 2007). Notably, attack-abatement benefits apply only when handling time or satiation prevents a predator from consuming all the prey in a single shoal (Connell 2000).

In addition to the passive benefits of group living, fish living in shoals may lower their predation risk through active responses to predators. Such behaviors may include shared vigilance, in which the first individual to detect a predator shares that information with its shoalmates, reducing the average time it takes them to react to a predator (Magurran et al. 1985), and quorum responses, whereby fish in groups make faster, more accurate decisions about evading predation than solitary individuals (Ward et al. 2008). Some reef fishes also exhibit classical antipredator schooling maneuvers, such as the fountain effect in the grunt *H. flavolineatum* (Hein 1996). In addition, shoaling fishes are capable of predator deterrence behaviors such as notification and mobbing (Motta 1984), both of which have been observed in reef fishes (e.g., Sweatman 1984, Ishihara 1987).

PROCESSES LEADING TO DENSITY-INDEPENDENT MORTALITY

Most reef fish studies treat DI mortality as a null hypothesis: in the absence of evidence for any IDD or DDD processes, per capita mortality is assumed to be independent of density (described by Hixon 1998; see Schmitt et al. 1999 for an alternative framework). We favor a different conceptual model, in which DI mortality is expected when the underlying IDD or DDD process influencing prey mortality rate is obscured by either (1) low statistical power or (2) counteracting ecological interactions.

First, DI mortality may emerge when the signal of the density-dependent process is exceeded by the noise of variation in predation. For instance, when prey are sparse, variation in prey density may be low enough relative to random variability in predator movement and



PLATE 1. Spotted moray eel, *Gymnothorax meleagris* on a coral reef in Moorea, French Polynesia. Piscivores such as moray eels are usually the proximate cause of density-dependent mortality in coral reef fishes. Photo credit: A. C. Stier.

predation success that per capita mortality (via predation) is decoupled from prey density at the spatial scale of that reef. However, it is unlikely that mortality is ever strictly DI over the full range of prey densities because (a) all predator functional responses must saturate at high prey densities, leading to IDD mortality (Hassell et al. 1985), and (b) prey that compete for refuges will eventually saturate those refuges at high densities, leading to DDD mortality (Holbrook and Schmitt 2002). Thus, in the presence of predators, it is more appropriate to consider DI mortality to be akin to Type II error; rather than being a separate functional form, it represents the failure to detect the underlying DDD or IDD process due to low statistical power or testing over too narrow a range of prey/predator densities (Hixon 1998, Osenberg et al. 2002). Of course, some species may never reach densities high enough to experience DDD mortality, and the underlying DDD process may only be revealed by experiments that increase densities beyond the natural range (e.g., Jones 1988, Schmitt et al. 1999). Such populations may be *limited* by DI processes, but nonetheless ultimately *regulated* by DDD processes (Hixon et al. 2002).

A second way in which DI mortality patterns may emerge is when multiple processes with counteracting effects operate simultaneously. "Cryptic" DDD mortality may appear DI in observational studies if prey density is correlated with habitat quality (Shima and Osenberg 2003). For example, Wilson and Osenberg (2002) found that the gobies *Elacatinus evelynae* and *E. prochilos* settled preferentially to higher-quality coral heads where DDD mortality was weakest. The positive effect of habitat quality on survival offset the negative effect of density, leading to similar mortality rates across a range of prey densities. Similarly, Overholtzer-McLeod (2006) found DI mortality of the wrasse *Halichoeres garnoti* when DDD predation by a resident predator was swamped by DI visitation by transient predators. Note that in isolation, DI predator visitation should have produced IDD mortality. Recall that the null hypothesis of DI mortality assumes that the probability of a strike is distributed uniformly across individual prey, not uniformly across space. In the latter case, the realized per capita mortality of prey will be inversely related to local density (i.e., IDD mortality [Sandin and Pacala 2005b]).

THE ROLE OF SPATIAL SCALE
AND HABITAT CONFIGURATION

DDD and IDD processes are not mutually exclusive. In fact, a mixture of processes is likely to be occurring in any given species, and the process that is detected can be sensitive to the spatial scale of observation. Additionally, the type of density dependence observed in a population may be shaped by the spatial configuration of the reef itself.

Spatial scale

Most studies to date have found that DDD mortality measured at small spatial scales (approximately square meters) is also detectable when mortality and density are both measured at much larger spatial scales (e.g., >1000 m²) (Steele and Forrester 2005, Johnson 2006a, Forrester et al. 2008). By contrast, White and Warner (2007b) found that newly settled bluehead wrasse experienced IDD mortality at the scale of small groups (<1 m²), but DDD mortality at the scale of entire reefs (>1000 m²). This type of scale-dependent switch has not been reported in other reef fishes, but is known to occur among terrestrial insects (Mohd Norowi et al. 2000, Schellhorn and Andow 2005).

Whether small-scale patterns scale up could depend on the mechanism leading to prey aggregation. Many prey aggregate when exploiting limited and patchily distributed resources, such as structural refuges. In these species, mortality is likely to be related to the per capita availability of refuges (i.e., the prey-to-refuge ratio [Samhuri et al. 2009b]) across a wide range of spatial scales. This appears to be the case for rubble-dwelling gobies (Steele and Forrester 2005). The DDD relationship may deteriorate at very large spatial scales because mean-field estimates of prey density and refuge availability can obscure smaller-scale spatial covariance between those two variables (Chesson et al. 2005). Additionally, if prey distribute themselves in an approximately ideal-free manner (sensu Fretwell and Lucas 1970) with respect to refuges, or if predators distribute themselves to match the pattern of prey availability, mortality risk may be similar everywhere and appear to be DI (i.e., cryptic density dependence [Shima and Osenberg 2003, Shima et al. 2008]).

Aggregation in other species yields social risk-reduction benefits and is not associated with the acquisition of patchily distributed, limited resources. In these species, mortality may be IDD at the spatial scale of individual shoals, but DDD when measured at larger scales (e.g., White and Warner 2007b). This scale dependence may depend on the *predator foraging scale*, the spatial scale at which predators define a “patch” of prey and choose to stay in that patch or move on (Ritchie 1998). For instance, the foraging scale (tens to hundreds of meters) of certain predators (e.g., coney groupers) may exceed the spatial scale (tens to hundreds of centimeters) at which some prey (e.g., bluehead

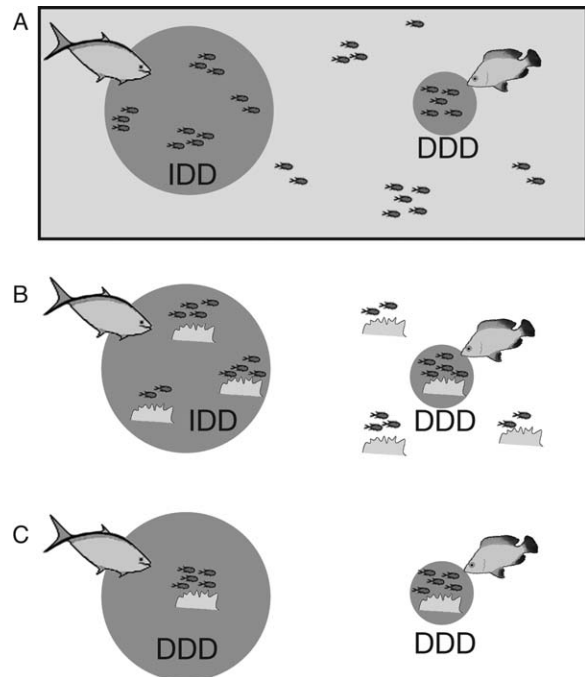


FIG. 1. Cartoon illustrating the effect of the spatial scale of predator foraging on prey mortality. Two predator species have different characteristic foraging scales; each defines a patch of prey at the spatial scale indicated by the shaded circle. The predator distributes foraging effort randomly within that patch. (A) On a continuous reef, the larger foraging scale tends to overlap multiple prey shoals, leading to IDD prey mortality at the shoal scale. The smaller foraging scale coincides with the spatial scale of prey aggregation, leading to DDD prey mortality at the shoal scale. (B) A similar pattern occurs on closely spaced patch reefs. (C) When reef spacing is wider, the foraging scale of all predators is constrained to the scale of a single prey aggregation, producing DDD mortality in all cases, given sufficient time and the appropriate type of predator functional response.

wrasse) aggregate (Fig. 1A). In such cases, variation in prey density at the scale of individual prey aggregations will not influence predator behavior, i.e., predators will forage indiscriminately among prey aggregations within a foraging patch. Consequently, prey will receive benefits of attack abatement and experience IDD mortality at the aggregation scale (Sandin and Pacala 2005b). However, at the same time and for the same set of predator and prey species, mortality measured at the larger spatial scale of predator foraging can be DDD given particular types of predator behavior (e.g., Type III functional response [White and Warner 2007b]). While few studies have considered such dynamical transitions across spatial scales in reef fishes, this phenomenon has been reported in weevils parasitized by wasps (Mohd Norowi et al. 2000), and it may be a general feature of insect consumer resource interactions (Walde and Murdoch 1988). Of course, the foraging scale of small-bodied predators (e.g., hawkfish *Paracirrhites arcatus* [Shima et al. 2008]) may be the same as

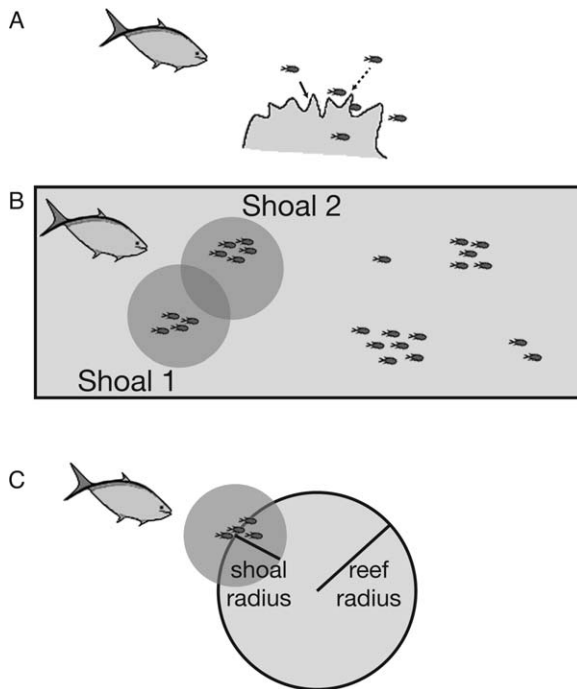


FIG. 2. Cartoon illustrating difference in predator escape behavior on isolated habitat units and contiguous reefs. (A) Prey that find a refuge (solid arrow) have a lower mortality risk than those that do not (dashed arrow). (B) Prey on a continuous reef can access refuges within a certain radius (indicated by shaded circle). If predators only attack one shoal at a time, neighboring shoals can share refuge space over time, reducing effective prey density. (C) For prey near the edge of a patch reef, no refuges are available beyond the patch edge. As the radius of the reef shrinks relative to the escape radius of the shoal, effective density increases.

or smaller than the spatial scale at which prey aggregate (Fig. 1A). Such predators will view individual prey aggregations as foraging patches, and may focus predation on high-density patches, causing DDD prey mortality.

The effects of predator foraging scale may become especially important when comparing results from continuous reefs to those from systems of small, widely spaced patch reefs. On a continuous reef, predators with larger foraging scales are less likely to view individual prey aggregations as foraging patches, and should produce IDD mortality at the scale of prey aggregations, as described in the preceding paragraph (Fig. 1A). The same pattern should hold on tightly spaced patch reef systems, in which a large spatial scale of predator foraging may still envelop multiple patch reefs and thus multiple prey aggregations (Fig. 1B). If patch reef spacing is very large, however (e.g., 50 m in Overholtzer-McLeod 2006; 200 m in Hixon and Carr 1997), and each patch reef is only large enough to support a single prey aggregation, the foraging scale of highly mobile predators may only encompass a single patch reef and thus a single prey aggregation (Fig. 1C). The

predator foraging scale then matches the prey aggregation scale, producing DDD mortality at the prey aggregation scale. For example, Overholtzer-McLeod (2006) found that mortality of a socially aggregating wrasse was DDD on an array of widely spaced reefs, but DI when reefs were closer together. On the latter set of reefs, foraging snappers established home ranges that encompassed the entire reef array, moving rapidly among the reefs and not in response to prey density, i.e., they made a foraging decision at the scale of multiple reefs rather than a single reef. The mortality caused by this behavior overwhelmed the DDD pattern produced by resident groupers (which had a Type III functional response and did not move among reefs). Overholtzer-McLeod's (2006) results suggest that there is not a clear distinction between patch and continuous reefs in this context, because any difference in the form of density-dependent mortality among habitats will depend on the relative spatial scales of movement of predators and prey. Alternatively, continuous reefs may appear patchy to some species whose preferred habitat is not continuous across the reef, such as trumpetfish (*Aulostomus maculatus*), which depend on patchily distributed gorgonians as cover for their sit-and-wait predation tactic (Sandin and Pacala 2005b).

Prey interaction with habitat configuration

A second possible effect of habitat configuration is its interaction with prey behavior. Most species that feed while hovering above the reef retreat to structural refuges when predators strike (Sandin and Pacala 2005b, White and Warner 2007a). A simple conceptual model explains how habitat configuration may influence the functional form of DDD mortality for such species. (This model is derived formally by S. A. Sandin, J. F. Samhoury, and S. L. Hamilton [*unpublished manuscript*].) In this conceptual model, we assume that the prey species occurs in shoals (e.g., *Chromis cyanea*, juvenile *Pseudanthias* sp.), each individual is identical and aware of most structural refuges within its home range, each refuge can shelter only one individual, all refuges offer equal protection, individuals do not defend particular refuges, and predators attack only one shoal at a time where multiple shoals occur in the same habitat. During a predator strike on a shoal, prey retreat to refuges. Any prey failing to find an unoccupied refuge remains exposed in the water column, where it has higher mortality risk than those in refuges (Fig. 2A). This "musical chairs" model of mortality risk was first identified in bridled gobies, *C. glaucofraenum* (Samhoury et al. 2009b), but has been discussed anecdotally for other species, including beaugregory damselfish *S. leucostictus* and surgeonfish *Acanthurus* spp. (Shulman 1984) and shoaling damselfish *C. cyanea* (Sandin and Pacala 2005b).

On a continuous reef, the escape radius of individuals in a shoal is smaller than any dimension of the habitat area, and individuals can evade predation by retreating

to a refuge in any direction. Even if multiple aggregations occur on a continuous reef and the escape radii of adjacent aggregations overlap (Fig. 2B), the probability of separate predators simultaneously striking adjacent shoals by chance alone should be small. Thus, when one shoal is attacked, its members can use refuges that might be used by the adjacent shoal were it to be attacked. Effectively, then, prey on a continuous reef could participate in temporal refuge sharing (Fig. 2B), whereby the effective number of prey per refuge is lower because adjacent groups can use the same set of refuges so long as the two groups are not attacked simultaneously. This should relax competition for refuges such that attack abatement effects may lead to IDD mortality.

In contrast, the escape radius for shoals on a patch reef may exceed the radius of the reef itself (Fig. 2C). If the area surrounding the patch reef (e.g., sand, seagrass) offers no suitable refuge from predation, prey are constrained by the total area containing refuges available for retreat during a predator strike. This area becomes severely limiting as patch reefs get small or prey densities increase. Thus, the intensity of competition for refuges should be relatively stronger on smaller patch reefs and when densities are higher, enhancing predation risk to aggregating prey and potentially causing DDD mortality.

This model predicts that per capita mortality is a bowl-shaped function of effective prey density, i.e., the prey/refuge ratio. Risk dilution causes per capita mortality to decrease with increasing effective prey density until refuges become limiting and per capita mortality begins to increase with effective prey density. (Jones 1988 reports this type of mortality function.) The reflective boundaries of patch reefs reduce the number of available refuges, increasing effective prey density and making DDD mortality more likely. In contrast, temporal refuge sharing on continuous reefs should decrease effective prey density and makes IDD mortality more likely. This hypothesis and the underlying model have not yet been tested explicitly, but they are supported by Nanami and Nishihira's (2001) finding that damselfish on continuous reefs utilized shelters in the reef surrounding their standardized habitat units and experienced lower, more weakly DDD mortality than fish in identical habitat units on patch reefs.

SYNTHESIS: SCALE, HABITAT, AND BEHAVIOR SHAPE DENSITY-DEPENDENT PROCESSES

The preceding review suggests a synthetic framework for explaining the relationships among previous empirical results and predicting the outcomes of future studies. In Fig. 3 we give the type of density dependence (DDD or IDD mortality) observed in published studies as a function of prey behavioral type, habitat configuration, predator foraging scale, and the spatial scale of observation. We also suggest conditions under which DI

or IDD mortality may be observed regardless of whether the underlying process is DDD or IDD. This framework is based on our interpretation of the existing body of reef fish literature, so where possible we have included references to studies reporting results that fall within each category in Fig. 3. In most cases it was impossible to apply a quantitative test for discrimination among prey behavioral types (Grear and Schmitz 2005), so we relied upon authors' descriptions and our own knowledge. These references are not exhaustive, as some studies are difficult to classify because of inadequate reporting of methods, a limited range of prey densities, or lack of knowledge about predators or habitat (details given in the Appendix). Although we were unable to place some studies within this table, we know of none that clearly deviate from our explanatory framework.

In describing prey behavior, we recognize three different social types among commonly studied reef fishes: nonaggregators, refuge-based aggregators, and social aggregators. Nonaggregators are nonsocial and often territorial, like many gobies. These species may occur at high densities where resources and shelter are abundant, but do not shoal. Second are refuge-based aggregators (*sensu* Safran et al. 2007), like many damselfishes, that form shoals because of the spatial patchiness of refuges (e.g., branching coral heads). Third are social aggregators (*sensu* Safran et al. 2007), like many wrasses, that form high-density aggregations independent of refuge availability, apparently yielding antipredator benefits (White and Warner 2007b). We distinguish among these behavioral types using a conceptual test like that proposed by Grear and Schmitz (2005): in a continuous habitat with an even distribution of refuges, nonaggregators and refuge-based aggregators will distribute themselves evenly in space and exploit empty refuges, while social aggregators will form shoals and leave many refuges unused. When refuges are highly clumped in space, all three social types will also exhibit clumped distributions, and both refuge-based and social aggregators will occur in shoals. Versions of this test have been implemented in the field for at least two species. The damselfish *Dascyllus flavicaudus* settled preferentially on empty coral heads rather than nearby coral heads occupied by conspecifics (Schmitt and Holbrook 2000), making it a refuge-based aggregator. By contrast, the wrasse *T. bifasciatum* settled preferentially in groups despite the availability of empty settlement habitat nearby (White and Warner 2007b), making it a social aggregator.

The delineation of social types is intended to represent the primary determinant of prey sociality in the context of density-dependent mortality, but these categories may experience similar predator-prey interactions in some situations. For example, refuge-based aggregators may enjoy risk reduction in some situations (e.g., Holbrook and Schmitt 2002: Fig. 5A), although in general they avoid predation by retreating to refuges defended in size hierarchies (Holbrook and Schmitt 2002). Conversely,

	Nonaggregators	Refuge-based aggregators	Social aggregators
Isolated habitat units	Underlying process:		
	If predator foraging scale \leq habitat unit spacing		
	DDD		
	Gobiidae (gobies) ^a	Embiotocidae (surfperch) ^b Pomacentridae (damselfish) ^b Sebastidae (rockfish) ^c	Acanthuridae (surgeonfish) ^f Labridae (wrasse) ^g Pomacentridae (damselfish) ^f
Contiguous habitat units	Underlying process:		
	DDD	If observation scale = prey aggregation and If predator foraging scale > prey aggregation scale	
		DDD	IDD
	Acanthuridae (surgeonfish) ^b Gobiidae (gobies) ^c	Pomacentridae (damselfish) ^j Grammatidae (basslets) ^k	Labridae (wrasse) ^u Pomacentridae (damselfish) ^v
	If observation scale > prey aggregation or If predator foraging scale \leq prey aggregation scale		
	DDD		
	Acanthuridae (surgeonfish) ^j Embiotocidae (surfperch) ^m Pomacentridae (damselfish) ⁿ Sebastidae (rockfish) ^o	Labridae (wrasse) ^w Pomacentridae (damselfish) ^x	
Either habitat configuration	Other potential observations:		
	If multiple opposing processes: (multiple dominant predators with different foraging scales, cryptic density dependence, etc.)		
	DI		
	Gobiidae (gobies) ^d	Pomacentridae (damselfish) ^p	Labridae (wrasse) ^y
If very low predator density or short time scale of observation:			
IDD or DI			
Gobiidae (gobies) ^e	Sebastidae (rockfish) ^q	Labridae (wrasse) ^z	
If highly abundant refuges:			
DI			
	Gobiidae (gobies) ^f	(No known examples)	

FIG. 3. Influence of prey behavior, predator foraging scale, habitat configuration, and the spatial scale of observation (or replication) on the expected functional relationship between prey density and per capita prey mortality (directly density dependent [DDD] or inversely density dependent [IDD]), as well as alternative patterns (density independent [DI] or IDD) that may be detected under certain conditions, regardless of whether the underlying form of mortality is DDD or IDD. Nonaggregators refers to prey species that may occur at high densities where resources and shelter are abundant, but which do not shoal. Resource aggregators refers to prey species that form loose shoals in response to the spatial patchiness of refuges but tend to compete for access to those refuges. Social aggregators form high-density aggregations independent of refuge availability, and reduce predation risk by shoaling. Predator foraging scale is the spatial scale at which predators define a “patch” of prey and choose to stay in that patch or move on (Ritchie 1998). If a predator’s foraging scale is relatively large, it does not recognize individual isolated habitat units or prey aggregations as patches and forages indiscriminately among them (see Fig. 1). In cases where the prediction is DDD, we have assumed that predators exhibit a Type III functional response to prey densities, and that mortality is measured over a sufficiently long time scale; observations over short time scales or with few predators will tend to exhibit saturation of the predators’ functional response. Observation scale refers to the spatial scale at which an observer measures prey density and per capita mortality. Time scale of observation refers to the time elapsed between measuring “initial” and “final” abundances to calculate mortality. Superscript lowercase letters (a–z) refer to references in the Appendix.

species considered social aggregators generally form tighter shoals when threatened (Overholtzer-McLeod 2006), although some species in this category may also utilize refuges when threatened (as described for *C. cyanea* in *The role of spatial scale and habitat configuration: Prey interaction with habitat configuration*). Overall, our intent is not to suggest that refuge-based aggregators are not social (in fact, many such species form social mating hierarchies), nor that social aggregators do not compete for resources, but rather to characterize the nature of group interactions with respect to mortality. In fact, these two categories could be treated as the opposite extremes of a continuum, although in practice we were able to satisfactorily place most species into one or the other category.

For nonaggregators and refuge-based aggregators, per capita mortality risk is generally an increasing function of the ratio of prey to refuges, so DDD mortality is likely to be observed in both patchy and continuous habitats and at all spatial scales of observation. This expectation is very clear when predators forage at the spatial scale of prey aggregations. In this case, predator foraging alone would be expected to produce DDD mortality (due to predator aggregation and/or Type III functional responses), and refuge competition would simply magnify this effect. Given sufficient competition for refuges, DDD mortality will also occur when predators forage at scales greater than the scale of prey aggregations (on continuous reefs) or of habitat spacing (on patch reefs). This appears to have been the case for two studies on continuous reefs where the scale of predator foraging exceeded the scale of prey aggregation, as DDD mortality was observed for both damselfish and basslets (Carr et al. 2002, Webster 2004). Only if predators forage at a relatively large scale and refuges are sufficiently abundant to preclude competition will DI or IDD mortality be observed.

For social aggregators, the dilution effect and active antipredator behaviors should produce IDD mortality at the observation scale of individual shoals, especially on continuous reefs where temporal resource sharing lowers effective densities. This occurs because the spatial scale of predator foraging encompasses multiple prey aggregations (Fig. 1A, B). However, if predators possess Type III functional or aggregative responses, mortality may be DDD when observed at the relatively large predator foraging scale, even if mortality is IDD when observed at the smaller scale of individual prey aggregations (White and Warner 2007b). DDD mortality could also arise when the predator foraging scale is constrained to the scale of a single prey aggregation, which may occur in some widely spaced patch reef configurations (Fig. 1C). This constraint causes predators to respond to prey at the spatial scale of individual aggregations (Fig. 1C), leading to DDD prey mortality.

For all three behavioral types, IDD (or possibly DI) mortality is possible when predator densities are very low, so that predators with saturating functional

responses are swamped for the duration of observations (Johnson 2006a, White 2007). In such cases, DDD mortality may be revealed by longer-term observations that allow time for swamped predators to resume feeding and for additional predators to aggregate (White and Warner 2007b).

The patterns proposed in Fig. 3 are intended to describe the results of pairwise predator-prey interactions. By contrast, the dynamics of most reef fish assemblages typically have multiple predator species interacting with multiple prey species, thus complicating the prediction and interpretation of density-dependent patterns. Given such trophic diversity, it is reasonable to expect patterns of mortality to fall along a continuum between the extremes of DDD and IDD, depending on predator behaviors and relative interaction strengths. For example, Hixon and Carr (1997) found that predators with different foraging styles acted synergistically to produce stronger DDD mortality in *Chromis cyanea*. There may also be more complex effects of multiple prey species on the observed pattern of density dependence. Webster and Almany (2002) showed that large schools of cardinalfish (Apogonidae) drew the attention of predators on patch reefs, leading to lower mortality of other prey species on the same reefs. In a separate study, predators focused on rare prey species in multispecies assemblages (an “oddity effect”), effectively amplifying IDD mortality in the more abundant species (Almany and Webster 2004). Additionally, emerging evidence suggests that mortality patterns in multispecies assemblages also depend on the relative timing of larval settlement of different prey species (Geange and Stier 2009). Overall, careful consideration of the potential influences of multiple factors is needed to predict patterns on natural reefs. Nonetheless, the framework proposed here provides the conceptual foundation needed to build more complex, multispecies models of prey demography.

DISCUSSION

Reef fish assemblages are widely regarded as a testing ground for both behavioral and population ecology. As such, it is important to bridge these fields in order to explain how fish behaviors may influence population-level processes like mortality. This need is becoming increasingly evident as hypotheses initially developed using refuge-competing damselfishes are tested on species with alternative behavioral strategies, such as wrasses and snappers. Similarly, efforts to scale up observations from small plots can be improved by considering the behavioral ecology of the species involved. For a nonaggregating species in homogenous habitat, small-scale interactions may scale up to entire reefs quite readily (e.g., the goby *Coryphopterus glaucofraenum* [Steele and Forrester 2005]). By contrast, species with shoaling behavior can experience dilution effects at the group scale but DDD mortality at larger scales (e.g., the wrasse *Thalassoma bifasciatum* [White

and Warner 2007b]). We urge reef ecologists to consider these behavioral factors when comparing results across species and study sites. To this end, our synthetic framework (Fig. 3) can serve as a set of predictions for future studies. We hope this framework provides a more useful set of null hypotheses for future studies that advance the field beyond the general expectation that all reef fishes experience DDD (or DI) mortality, or that there is a fundamental difference between patch and continuous reefs independent of the species involved or the quality of the reef habitat.

Our review also yielded several suggestions that may help researchers place their work in a useful context. First, when possible, it is worthwhile to conduct work on both patch reefs and continuous reefs to ensure that findings are not restricted to a single habitat type (e.g., Carr et al. 2002). Second, if shoaling is possible in the study species, it is important to be explicit about both areal density (number per square meter) and group sizes found in each habitat unit. Finally, because predators are key players in most studies of reef fish demography, it is important to determine the identity and density of likely predators, along with their typical foraging scales, and the potential consequences of predation by multiple predators with different foraging strategies.

When reporting evidence for DDD mortality, many authors note its importance for regulated population dynamics (Murdoch 1994). However, the stabilizing role of DDD mortality does not necessarily imply that species exhibiting IDD mortality have unstable population dynamics (Hassell et al. 1991). While IDD mortality is generally destabilizing, the type of IDD mortality discussed here is merely one component of the overall demography of a species and may be offset by density dependence occurring at a different spatial scale or life stage (Gascoigne and Lipcius 2004). For example, IDD postsettlement mortality may be offset by DDD adult fecundity (Samhuri 2009). Additionally, population models indicate that DDD mortality occurring at the (larger) scale of predator foraging is usually sufficient to stabilize the dynamics of a species with IDD mortality at the (smaller) scale of prey aggregations (J. W. White, unpublished manuscript).

The idea that the type of ecological process one observes depends on the scale of observation is not new (Levin 1992). Indeed, relationships between the scale of predator foraging and the spatial scale of observation have been noted in several nonreef systems. Pelagic seabirds typically have a characteristic spatial scale at which they define patches of their fish prey and at which there is a positive relationship between seabird and prey densities (e.g., Schneider and Piatt 1986, Burger et al. 2004). Several studies in other systems have explicitly considered scale-dependent transitions in the response of predators to spatial variation in prey density. For example, Cummings et al. (1997) found that wading birds did not respond to small-scale (0.25 m^2) changes in bivalve density on mudflats when overall bivalve density

at a larger scale ($2.5 \times 10^4 \text{ m}^2$) was controlled. Scale dependence may be especially relevant to many insect predator-prey interactions, where, as on reefs, the habitat itself naturally defines several distinctive spatial scales. The parasitoid wasp *Mesopolobus incultus* produced IDD mortality in the weevil *Gymnetron pascuorum* at the scale of individual seed heads, but DDD mortality at larger scales of plants and experimental plots (Mohd Norowi et al. 2000). A similar pattern was found for parasitoid-induced DDD mortality in leaf-mining flies (*Liriomyza commelinae* [Freeman and Smith 1990]). This is not to say that IDD will always be detected at the smaller of two spatial scales; Schellhorn and Andow (2005) found that coccinellid beetles responded to the density of their aphid prey more strongly at the scale of plants than at the larger scale of plots, although they did not investigate subplant scales at which the response may have been IDD. In general, the evidence from other systems matches our hypothesis for reef fishes: predators produce DDD mortality when their foraging scale coincides with the spatial scale of prey aggregation (t and Kieckhefer 2000) but IDD mortality when the spatial scale of foraging is larger than the scale of prey aggregation (Mohd Norowi 2000; also see review by Walde and Murdoch 1988).

In other cases, our hypothesis is not supported. Stiling et al. (1991) examined parasitism rates of planthoppers at two spatial scales with parasitoids of varying mobility and found no evidence for DDD mortality with any species at either scale. It is unclear why this result departs from our prediction, but as in reef studies, it is likely to be important to control for confounding factors such as cryptic density dependence when testing for DDD and IDD. Of course, it is also essential to ensure that the suite of spatial scales under consideration is broad enough to include the one actually used by the predator (Horne and Schneider 1994).

The importance of considering prey behavior when examining the demographic consequences of group size also extends beyond reef fish systems. It is commonly observed that birds, mammals, and fishes in larger groups exhibit lower per capita antipredator vigilance and spend more time foraging in risky habitats than conspecifics in smaller groups (Beauchamp 2003). Just as we have advocated distinguishing between refuge-based and social aggregators, there is a need to determine whether animals in groups undertake risky behavior because they are better able to detect predators or because they have increased resource requirements due to enhanced competition within groups (e.g., Cowlishaw 1997). Reliably distinguishing between these alternatives will be key to understanding the interplay between prey behavior, group size, and predation risk (Eggleston and Lipcius 1992, Beauchamp 2003, White and Warner 2007a). Likewise, increased attention to behavioral decision making in predators is sorely needed (Cosner et al. 1999, Lima 2002). Hopefully, consideration of the additional factors we propose in our

synthetic framework (habitat configuration, predator and prey behavior) may shed light on patterns of DDD and IDD processes in other systems as well.

Based on this synthesis of patterns of density dependence in reef fishes, we close with a prospectus. First, our framework (Fig. 3) generally agrees with published descriptions of behavior, habitats, and mortality, but no single study has examined the same species in patchy and contiguous habitats under conditions in which both (1) the foraging scale of the primary predator exceeds and does not exceed the spacing of habitat units, and (2) the scale of observation is focused both on individual prey groups and on entire reefs. Such a study, especially using a socially aggregating species, would provide a needed check on the overall validity of the framework. Second, we note that few reef fish studies have explicitly characterized the spatial scale at which predators define foraging patches, but it would be straightforward to do so and to determine whether the foraging scale interacts with the prey aggregation scale to produce IDD mortality, as we predict. Likewise, there is anecdotal evidence for temporal resource sharing occurring on continuous but not patch reefs (Nanami and Nishihira 2001), but this has not been directly tested as a factor affecting the form of density dependence. Third, some types of interactions, notably parasitism (Lafferty et al. 2008), disease (Dobson and May 1986), and sublethal predator effects (Creel and Christianson 2008), may have strong effects on prey population dynamics but are relatively unstudied in reef systems. As a result, our framework is directed primarily at density dependence caused by predation, but other interactions should not be ignored (Hixon and Jones 2005). Finally, as it becomes clearer that the nature and strength of interactions changes with habitat configuration and spatial scale, a pressing question emerges. What observation scale is the most appropriate in order to predict prey population dynamics? Providing an answer to this question will require the careful integration of population modeling and field observations.

ACKNOWLEDGMENTS

We are grateful to M. Steele, C. Osenberg, M. Hixon, M. Albins, M. Christie, D. Johnson, T. Pusack, and M. Webster for comments that greatly improved this manuscript, although any errors and oversights are our own.

LITERATURE CITED

- Almany, G. R., and M. S. Webster. 2004. Odd species out as predators reduce diversity of coral-reef fishes. *Ecology* 85: 2933–2937.
- Anderson, T. W. 2001. Predator responses, prey refuges, and density-dependent mortality of a marine fish. *Ecology* 82: 245–257.
- Anderson, T. W., M. H. Carr, and M. A. Hixon. 2007. Patterns and mechanisms of variable settlement and recruitment of a coral reef damselfish, *Chromis cyanea*. *Marine Ecology Progress Series* 350:109–116.
- Beauchamp, G. 2003. Group-size effects on vigilance: a search for mechanisms. *Behavioral Processes* 63:111–121.
- Booth, D. J. 1995. Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* 76:91–106.
- Burger, A. E., C. L. Hitchcock, and G. K. Davoren. 2004. Spatial aggregations of seabirds and their prey on the continental shelf off SW Vancouver Island. *Marine Ecology Progress Series* 283:279–292.
- Caley, M. J. 1998. Age-specific mortality rates in reef fishes: evidence and implications. *Australian Journal of Ecology* 23: 241–245.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Annual Review of Ecology and Systematics* 27:477–500.
- Carr, M. H., T. W. Anderson, and M. A. Hixon. 2002. Biodiversity, population regulation, and the stability of coral-reef fish communities. *Proceedings of the National Academy of Sciences USA* 99:11241–11245.
- Caselle, J. E. 1999. Early post-settlement mortality in a coral reef fish and its effect on local population size. *Ecological Monographs* 69:177–194.
- Chesson, P., M. Donahue, B. Melbourne, and A. Sears. 2005. Scale transition theory for understanding mechanisms in metacommunities. Pages 279–306 in M. Holyoak, M. A. Leibold, and R. D. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Connell, J. H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *Journal of Experimental Marine Biology and Ecology* 93:11–45.
- Connell, S. D. 2000. Is there safety-in-numbers for prey? *Oikos* 88:527–532.
- Cosner, C., D. L. DeAngelis, J. S. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology* 56:65–75.
- Cowlshaw, G. 1997. Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour* 53:667–686.
- Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23:194–201.
- Cummings, V. J., D. C. Schneider, and M. R. Wilkinson. 1997. Multiscale experimental analysis of aggregative responses of mobile predators to infaunal prey. *Journal of Experimental Marine Biology and Ecology* 216:211–227.
- Dobson, A. P., and R. M. May. 1986. The effects of parasites on fish populations—theoretical aspects. *International Journal for Parasitology* 17:363–370.
- Eggleston, D. B., and R. N. Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* 73:992–1011.
- Elliott, N. C., and R. W. Kieckhefer. 2000. Response by coccinellids to spatial variation in cereal aphid density. *Population Ecology* 42:81–90.
- Finley, R. J., and G. E. Forrester. 2003. Impact of ectoparasites on the demography of a small reef fish. *Marine Ecology Progress Series* 248:305–309.
- Forrester, G. E., and R. J. Finley. 2006. Parasitism and a shortage of refuges jointly mediate the strength of density dependence in a reef fish. *Ecology* 87:1110–1115.
- Forrester, G. E., and M. A. Steele. 2004. Predators, prey refuges, and the spatial scaling of density-dependent prey mortality. *Ecology* 85:1332–1342.
- Forrester, G. E., M. A. Steele, J. F. Samhuri, B. Evans, and R. R. Vance. 2008. Spatial density dependence scales up but does not produce temporal density dependence in a coral reef fish. *Ecology* 89:2980–2985.
- Freeman, B. E., and D. C. Smith. 1990. Variation of density-dependence with spatial scale in the leaf-mining fly *Liriomyza*

- commelinae* (Diptera: Agromyzidae). *Ecological Entomology* 15:265–274.
- Fretwell, S. D., and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19:16–36.
- Gascoigne, J. C., and R. N. Lipcius. 2004. Allee effects driven by predation. *Journal of Animal Ecology* 41:801–810.
- Geange, S. W., and A. C. Stier. 2009. Order of arrival affects competition in two reef fishes. *Ecology* 90:2868–2878.
- Grear, J. S., and O. J. Schmitz. 2005. Effects of grouping behavior and predators on the spatial distribution of a forest floor arthropod. *Ecology* 86:960–971.
- Harrison, S., and N. Cappuccino. 1995. Using density-manipulation experiments to study population regulation. Pages 131–148 in N. Cappuccino and P. W. Price, editors. *Population dynamics: new approach and synthesis*. Academic Press, San Diego, California, USA.
- Hassell, M. P., C. M. Lessells, and G. C. McGavin. 1985. Inverse density dependent parasitism in a patchy environment: a laboratory system. *Ecological Entomology* 10:393–402.
- Hassell, M. P., and R. M. May. 1974. Aggregation of predators and insect parasites and its effect on stability. *Journal of Animal Ecology* 43:567–594.
- Hassell, M. P., R. M. May, S. W. Pacala, and P. L. Chesson. 1991. The persistence of host-parasitoid associations in patchy environments. I. A general criterion. *American Naturalist* 138:568–583.
- Hein, R. G. 1996. Mobbing behavior in juvenile French grunts (*Haemulon flavolineatum*). *Copeia* 1996:989–991.
- Hixon, M. A. 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Australian Journal of Ecology* 23:192–201.
- Hixon, M. A., and M. H. Carr. 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946–949.
- Hixon, M. A., and G. P. Jones. 2005. Competition, predation, and density-dependent mortality in demersal marine fishes. *Ecology* 86:2847–2859.
- Hixon, M. A., S. W. Pacala, and S. A. Sandin. 2002. Population regulation: Historical context and contemporary challenges of open vs. closed systems. *Ecology* 83:1490–1508.
- Hixon, M. A., and M. S. Webster. 2002. Density dependence in marine fishes: coral-reef populations as model systems. Pages 303–325 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, San Diego, California, USA.
- Holbrook, S. J., and R. J. Schmitt. 2002. Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91:385–398.
- Horne, J. K., and D. C. Schneider. 1994. Lack of spatial coherence of predators with prey: a bioenergetic explanation for Atlantic cod feeding on capelin. *Journal of Fish Biology* 45(Supplement A):191–207.
- Houde, E. D., and R. C. Schekter. 1980. Feeding by marine fish larvae: developmental and functional responses. *Environmental Biology of Fishes* 5:315–334.
- Ishihara, M. 1987. Effect of mobbing toward predators by the damselfish *Pomacentrus coelestis* (Pisces: Pomacentridae). *Journal of Ethology* 5:43–52.
- Jenkins, S. R., J. Murua, and M. T. Burrows. 2008. Temporal changes in the strength of density-dependent mortality and growth in intertidal barnacles. *Journal of Animal Ecology* 77: 573–584.
- Johnson, D. W. 2006a. Predation, habitat complexity, and variation in density dependent mortality of temperate reef fishes. *Ecology* 87:1179–1188.
- Johnson, D. W. 2006b. Density dependence in marine fish populations revealed at small and large spatial scales. *Ecology* 87:319–325.
- Johnson, D. W. 2007. Habitat complexity modifies post-settlement mortality and recruitment dynamics of a marine fish. *Ecology* 88:1716–1725.
- Jones, G. P. 1987. Competitive interactions among adults and juveniles in a coral reef fish. *Ecology* 68:1534–1547.
- Jones, G. P. 1988. Experimental evaluation of the effects of habitat structure and competitive interactions on juveniles of two coral reef fishes. *Journal of Experimental Marine Biology* 123:115–126.
- Lafferty, K. D., et al. 2008. Parasites in food webs: the ultimate missing links. *Ecology Letters* 11:533–546.
- Lafferty, K. D., and A. K. Morris. 1996. Altered behavior of parasitized killifish increases susceptibility to predation by bird final hosts. *Ecology* 77:1390–1397.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943–1967.
- Lima, S. L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology and Evolution* 17:70–75.
- Magurran, A. E., W. J. Oulton, and T. J. Pitcher. 1985. Vigilant behaviour and shoal size in minnows. *Zeitschrift für Tierpsychologie* 67:167–178.
- Menge, B. A. 2000. Recruitment vs. postrecruitment processes as determinants of population abundance. *Ecological Monographs* 70:265–288.
- Mohd Norowi, H., J. N. Perry, W. Powell, and K. Rennolls. 2000. The effect of spatial scale on interactions between two weevils and their parasitoid. *Ecological Entomology* 25:188–196.
- Motta, P. J. 1984. Response by potential prey to coral reef predators. *Animal Behaviour* 31:1257–1259.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335–354.
- Murdoch, W. W. 1971. The developmental response of predators to changes in prey density. *Ecology* 52:132–137.
- Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271–287.
- Nanami, A., and M. Nishihira. 2001. Survival rates of juvenile coral reef fishes differ between patchy and continuous habitats. *Bulletin of Marine Science* 69:1209–1221.
- Osenberg, C. W., C. M. St. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. *Ecology Letters* 5:715–721.
- Overholtzer-McLeod, K. L. 2006. Consequences of patch reef spacing for density dependent mortality of coral-reef fishes. *Ecology* 87:1017–1026.
- Pitcher, T. J., and J. K. Parrish. 1993. Functions of shoaling behavior in teleosts. Pages 363–439 in T. J. Pitcher, editor. *Behaviour of teleost fishes*. Second edition. Chapman and Hall, London, UK.
- Ritchie, M. E. 1998. Scale-dependent foraging and patch choice in fractal environments. *Evolutionary Ecology* 12: 309–330.
- Roughgarden, J., S. D. Gaines, and H. P. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241: 1460–1466.
- Safran, R. J., V. A. J. Doerr, P. W. Sherman, E. D. Doerr, S. M. Flaxman, and D. W. Winkler. 2007. Group breeding in vertebrates: linking individual- and population-level approaches. *Evolutionary Ecology Research* 9:1163–1185.
- Sale, P. F., and N. Tolimieri. 2000. Density dependence at some time and place? *Oecologia* 124:166–171.
- Samhuri, J. F. 2009. Food supply influences offspring provisioning but not density-dependent fecundity in a marine fish. *Ecology* 90:3478–3488.

- Samhuri, J. F., M. A. Steele, and G. E. Forrester. 2009a. Intercohort competition drives density dependence and selective mortality in a marine fish. *Ecology* 90:1009–1020.
- Samhuri, J. F., R. R. Vance, G. E. Forrester, and M. A. Steele. 2009b. Density-dependent deaths caused by competition for unguarded refuges: musical chairs mortality functions. *Oecologia* 160:257–265.
- Sandin, S. A., and S. W. Pacala. 2005a. Demographic theory of coral reef fish populations with stochastic recruitment: comparing sources of population regulation. *American Naturalist* 165:107–119.
- Sandin, S. A., and S. W. Pacala. 2005b. Fish aggregation results in inversely density-dependent predation on continuous coral reefs. *Ecology* 86:1520–1530.
- Schellhorn, N. A., and D. A. Andow. 2005. Response of coccinellids to their aphid prey at different spatial scales. *Population Ecology* 47:71–76.
- Schmitt, R. J., and S. J. Holbrook. 1999. Mortality of juvenile damselfish: implications for assessing processes that determine abundance. *Ecology* 80:35–50.
- Schmitt, R. J., and S. J. Holbrook. 2000. Habitat-limited recruitment of coral reef damselfish. *Ecology* 81:3479–3494.
- Schmitt, R. J., S. J. Holbrook, and C. W. Osenberg. 1999. Quantifying the effects of multiple processes on local abundance: a cohort approach for open populations. *Ecology Letters* 2:294–303.
- Schneider, D. C., and J. F. Piatt. 1986. Scale-dependent correlation of seabirds with schooling fish in a coastal ecosystem. *Marine Ecology Progress Series* 32:237–246.
- Shanks, A. L., and G. C. Roegner. 2007. Recruitment limitation in Dungeness crab populations is driven by variation in atmospheric forcing. *Ecology* 88:1726–1737.
- Shima, J. S. 2001. Regulation of local populations of a coral reef fish via joint effects of density- and number-dependent mortality. *Oecologia* 126:58–65.
- Shima, J. S., and C. W. Osenberg. 2003. Cryptic density dependence: effects of covariation between density and site quality in reef fish. *Ecology* 84:46–52.
- Shima, J. S., C. W. Osenberg, and C. M. St. Mary. 2008. Quantifying site quality in a heterogeneous landscape: recruitment of a reef fish. *Ecology* 89:86–94.
- Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* 74:85–109.
- Steele, M. A., and G. E. Forrester. 2002. Variation in the relative importance of sublethal effects of predators and competitors on growth of a temperate reef fish. *Marine Ecology Progress Series* 237:233–245.
- Steele, M. A., and G. E. Forrester. 2005. Small-scale field experiments accurately scale up to predict density dependence in reef fish populations at large scales. *Proceedings of the National Academy of Sciences USA* 102:13513–13516.
- Stewart-Oaten, A., and W. W. Murdoch. 1990. Temporal consequences of spatial density dependence. *Journal of Animal Ecology* 59:1027–1045.
- Stiling, P., A. Throckmorton, J. Silvanima, and D. R. Strong. 1991. Does spatial scale affect the incidence of density dependence? A field test with insect parasitoids. *Ecology* 72:2143–2154.
- Sweatman, H. P. A. 1984. A field study of the predatory behavior and feeding rate of a piscivorous coral-reef fish, the lizardfish *Synodus englemani*. *Copeia* 1984:187–194.
- Turchin, P. 2003. *Complex population dynamics*. Princeton University Press, Princeton, New Jersey, USA.
- Walde, S. J., and W. W. Murdoch. 1988. Spatial density dependence in parasitoids. *Annual Reviews in Entomology* 33:441–466.
- Ward, A. J. W., D. J. T. Sumpter, I. D. Couzin, P. J. B. Hart, and J. Krause. 2008. Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences USA* 105:6948–6953.
- Webster, M. S. 2003. Temporal density dependence and population regulation in a marine fish. *Ecology* 84:623–628.
- Webster, M. S. 2004. Density dependence via intercohort competition in a coral-reef fish. *Ecology* 85:986–994.
- Webster, M. S., and G. R. Almany. 2002. Positive indirect effects in a coral reef fish community. *Ecology Letters* 5:549–557.
- White, J. W. 2007. Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality. *Ecology Letters* 10:1054–1065.
- White, J. W., and R. R. Warner. 2007a. Behavioral and energetic costs of group membership in a coral reef fish. *Oecologia* 154:423–433.
- White, J. W., and R. R. Warner. 2007b. Safety in numbers and the spatial scaling of density-dependent mortality in a coral reef fish. *Ecology* 88:3044–3054.
- Wilson, J., and C. W. Osenberg. 2002. Experimental and observational patterns of density-dependent settlement and survival in the marine fish *Gobiosoma*. *Oecologia* 130:205–215.
- Wood, C. C., and C. M. Hand. 1985. Food-searching behavior of the common merganser (*Mergus merganser*). 1. Functional responses to prey and predator density. *Canadian Journal of Zoology* 63:1260–1270.
- Wormald, C. L. 2007. Effects of density and habitat structure on growth and survival of harvested coral reef fishes. Dissertation. University of Rhode Island, Kingston, Rhode Island, USA.

APPENDIX

A summary of the literature review and list of studies referenced in Fig. 3 (*Ecological Archives* E091-133-A1).