CHAPTER 14

Density Dependence in Marine Fishes: Coral Reef Populations as Model Systems

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Counting fish is as easy as counting trees, except that fish are invisible and they move.

—J. G. Shepherd

I. Introduction

One of the greatest mysteries of the sea is the question of what processes drive and regulate the dynamics of marine fish populations. This issue has troubled researchers in the fields of fisheries biology and marine ecology since these disciplines originated over a century ago (Smith, 1994). Although numerous concepts and hypotheses related to this problem have been proposed, only in recent years have detailed demographic studies, and especially manipulative experiments, provided partial empirical answers. Many questions and major controversies remain. In fact, even whether density dependence is necessary (as opposed to sufficient) for long-term persistence of populations has been questioned by some reef fish ecologists (e.g., Sale and Tolimieri, 2000) (see also Chapter 16, this volume). Yet, in these days of fishery collapses on a global scale (National Research Council, 1999), and the heightened risk of extinction of marine fish species due to human activities (Roberts and Hawkins, 1999; Hawkins *et al.,* 2000), probing these questions has become more crucial than ever before. This is because the scientific basis for conservation of marine species, from conventional fisheries management to the implementation of marine protected areas (see Chapter 19, this volume), lies in understanding and conserving naturally regulating density-dependent mechanisms.

How (if at all) does the concept of demographic density dependence apply to marine fishes and why is this concept controversial? How can coral reef species serve as model systems for examining density dependence in marine fish populations, and how do data from reef populations provide understanding of underlying mechanisms? What is needed in the future to resolve the mystery of fish population dynamics and regulation in the sea? This chapter examines these questions, focusing in turn on essential concepts, empirical evidence, conceptual synthesis, and future research needs. We consider coral reef fishes in the context of all demersal (bottom-associated) marine fishes. Pelagic (open ocean) fish populations, although conceptually relevant, are beyond the scope of this review.

II. Essential Concepts

We believe that much of the controversy surrounding the notion of density dependence in demersal marine fishes, and especially coral reef fishes, is due to misunderstanding (or at least ambiguous definitions) of key concepts and relevant spatiotemporal scales. Indeed, although most population ecologists accept the existence of density dependence as necessary for any population to persist indefinitely (Cappuccino and Price, 1995), even regular practitioners require occasional clarification [e.g., the recent exchange between Murray (1999) and Turchin (1999)]. Thus, a review of basic concepts seems essential before the available data from reef fishes can be interpreted in a meaningful way (see also Chesson, 1998a; Hixon, 1998).

A. What Is Density Dependence?

By definition, all changes in population size are due to changes in vital or demographic rates (birth + immigration − death − emigration), the combination of which gives the population growth rate. Demographic density dependence is generally defined as an effect of present and/or past population sizes on the per-capita population growth rate, and thus at least one of the constituent demographic rates (Murdoch and Walde, 1989). Specifically, the overall input rate due to birth and immigration is (directly) density dependent, or "compensatory," when it varies negatively with population size, whereas the overall loss rate due to death and emigration is density dependent when it varies positively with population size (Fig. 1). These rates are inversely density dependent, or "depensatory," when they vary in the opposite directions, which can happen at low population sizes due to the Allee effect (Courchamp et al., 1999). Note that these relationships ultimately must be caused by changes in population size to comprise true density dependence (see Section II,C,2). Royama (1977, 1992) and Turchin (2001) provide detailed discussions of the concept of density dependence.

Demographic rates are density independent when they do not vary significantly as a function of population size. This is not to say that density-independent processes do not vary through time. In fact, interannual variation in density-independent mortality of marine fish larvae is considered to be the major determinant of year-class strength in marine fishes (Houde, 1987). It is important to note that both density-independent and density-dependent factors, combined, drive changes in population size—not simply one or the other—and both vary in time and space (Sinclair, 1989).

B. Why Study Density Dependence?

It is worthwhile to test for and study the mechanisms causing demographic density dependence for several related reasons. First, density dependence is the essence of population regulation, which is the long-term persistence of a population via a return tendency caused by negative feedbacks between the size of a population and its growth rate, such that fluctuations in abundance, however great and seemingly stochastic, are bounded above and below with a lower limit above zero (Royama, 1992; Cappuccino and Price, 1995; Turchin, 2001). Bounded fluctuations occur when the input rate exceeds the loss rate after the population size becomes sufficiently low, and vice versa when the population size becomes sufficiently high. By definition (some would say by tautology), this return tendency can occur only when either or both rates are density dependent (Fig. 1). More accurately, density dependence is a necessary but not sufficient condition for population regulation. Specifically, (1) density dependence must be direct and temporal (i.e., occur within each population rather than merely among populations; see Section IV,B,2), so that (2) if one demographic rate is inversely density dependent, another is sufficiently density dependent to counteract it; (3) density dependence must also be sufficiently strong to counteract any disruptive effects of density-independent or inversely density-dependent factors, but at the same time, (4) the strength and time lag of directly density-dependent responses must not be so great as to cause destabilizing population cycles (Turchin, 1995). Although how long a population must persist before it is considered regulated has not been defined explicitly, the general notion necessarily implies multiple generations.

Second, although long-term persistence of any population can by definition occur only via demographic density dependence (Haldane, 1953), past existence does not ensure future persistence. Indeed, all populations eventually go extinct, which occurs when their sources of density dependence break down.
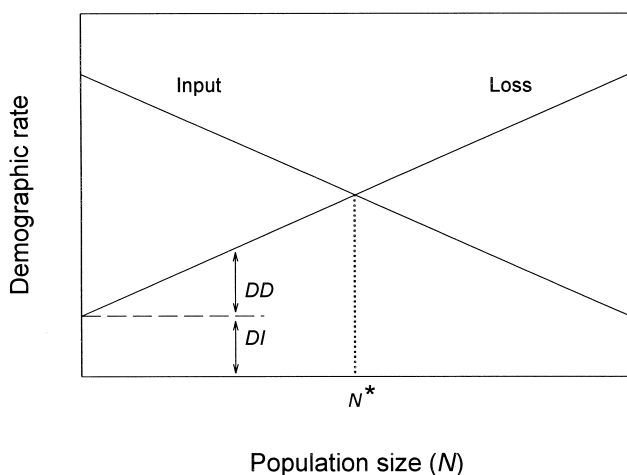

FIGURE 1 Typical textbook illustration of demographic density dependence, showing an input rate (birth, or in open local populations, settlement or recruitment) and a loss rate (typically mortality) that are both density dependent, as well as the resulting simple point equilibrium (N^*) in population size. Note that each demographic rate at each population size is actually the sum of both a density-independent component (DI, defined by the y intercept) and a density-dependent component (DD, defined by the slope), as illustrated for the mortality rate. This static picture belies the reality of reef fish populations, in which temporal variation in the position and slope of each curve will cause the equilibrium point to vary, and perhaps never be attained.

Therefore, the conservation of any population involves protection of naturally regulatory density-dependent processes (or artificial imposition of density dependence). By identifying natural density-dependent processes, we learn what aspects of a population's biotic and abiotic environment are crucial candidates for protection. Such knowledge is of fundamental importance in both fisheries management and conservation, even though we can also conserve populations with minimal data by establishing sufficiently large marine protected areas (Roberts, 1997b; Bohnsack, 1998; Johannes, 1998) (Chapter 19, this volume).

Third, tests for density dependence in demographic rates, regardless of whether density dependence actually occurs, provide means of understanding what drives population dynamics (Krebs, 1995). Ultimately, population structure is the foundation on which community-level patterns emerge. Moreover, reef fishes provide some of the few cases in which mechanisms driving population dynamics in vertebrates can be examined experimentally (Sale, 1991b). Most evidence for density dependence in animals is based on observational data, especially from studies of insects and terrestrial vertebrates (reviews by Hanski, 1990; Cappuccino and Price, 1995; Lindström *et al.,* 1999), although field experiments are slowly becoming more common (review by Harrison and Cappuccino, 1995). Particularly relevant to reef fish ecology in this context is testing the recruitment limitation hypothesis, discussed in the next section.

C. Sources of Density Dependence in Reef Fishes

Whereas basic concepts regarding density dependence are straightforward, applying them to reef fishes and other demersal marine fish populations is not. Given that a population is typically defined as a group of organisms of the same species occupying a particular area, the key issues are defining the spatial boundaries and structure of the population, the nature of the demographic rates, and the spatiotemporal scales over which they can operate in a density-dependent fashion (and be detected).

1. LOCAL POPULATIONS VS. METAPOPULATIONS

A vast majority of demersal species have a bipartite life cycle: a pelagic larval stage that is at least initially planktonic, followed by nektonic juvenile and adult stages that are closely associated with habitat patches on the sea floor (Sale, 1980). Consequently, demersal fishes may form metapopulations, at least in a simplest

Au: ok?

sense of Levins' (1969) original definition of a "population of populations" linked by dispersal. [See Harrison and Taylor (1997) and Hixon (1998), for a discussion of whether reef fish populations fit more restrictive definitions of a metapopulation.] Therefore, there are two spatial scales for population studies of demersal fishes relevant to questions regarding demographic density dependence: the local population and the entire metapopulation.

We define a local population as a group of demersal (juvenile and adult) conspecifics meeting two criteria: (1) mature members of the group (if any) spawn only with other group members, and (2) the group is sufficiently spatially isolated from other such groups that between-group movement is demographically negligible (see Section II,C,2). For coral reef fishes with extremely limited home ranges, the local population can be as small as a single coral head or patch reef (review by Sale, 1978a). For more mobile species, the range of the local population can be several orders of magnitude greater, especially in larger fishes such as groupers, which seasonally migrate to regional spawning aggregations (Domeier and Colin, 1997). In contrast, a metapopulation comprises a group of local populations linked only by larval dispersal.

Thus, the metapopulation is the entire, reproductively closed population (i.e., only rare larval dispersal events create new metapopulations). In contrast, larval dispersal and connectivity among sites create at least partially open populations at the local scale (Fig. 2). In a completely open local population, reproductive output is entirely unrelated to subsequent input. In this case, none of the larvae produced by the local population settles back to that population, and consequently, all the larvae that do settle were spawned elsewhere. Smaller local populations at the scale of patch reefs are probably completely open, whereas larger local populations at the scale of isolated oceanic islands undergo various levels of larval retention and are thus relatively closed (Jones *et al.,* 1999; Swearer *et al.,* 1999) (see also Chapters 7–9, this volume). In other words, demographic openness is largely a function of spatial scale.

Given these concepts, when one discusses whether reef fish populations are regulated, the ultimate focus is the metapopulation. It is not necessary that every local population be regulated for a metapopulation to persist, only that density dependence of the right characteristics occurs somewhere within the metapopulation (Hanski *et al.,* 1996). If one does detect substantial density dependence within local populations, then a potentially important source of regulation has been identified.
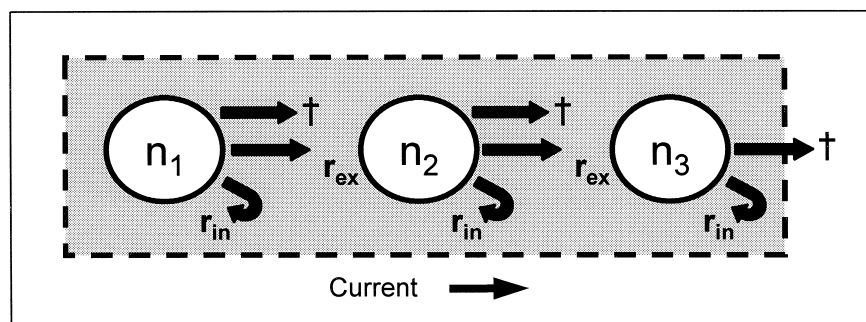
FIGURE 2   Diagram of a reef fish metapopulation (enclosed within the dashed line), illustrating possible kinds of open local populations (n_x). For each local population, dispersing larvae have three possible fates: death before settlement (†), internal retention to self-recruitment (r_{in}), or export to another local population (r_{ex}). Population n_1 depends entirely on internal retention but can export larvae, whereas population n_3 has both internal and external sources of recruitment but cannot successfully export larvae. Only population n_2 serves as both an export source and an import recipient of larvae.

2. APPROACHES FOR DETECTING DENSITY DEPENDENCE

All field studies of reef fishes reviewed here were conducted at the scale of local populations (or smaller). Because each local population is only part of a metapopulation, studies at this smaller spatial scale can provide only partial information regarding density dependence at the scale of the entire metapopulation. Thus, logistic constraints limit the spatial scale of our understanding of population dynamics in demersal marine fishes (Sale, 1998). What are the possible sources of demographic density dependence in a demersal metapopulation? There are four possibilities: (1) fecundity, (2) presettlement mortality of eggs and larvae, (3) mortality during the pelagic–demersal transition (settlement), and (4) postsettlement mortality of juveniles and adults. Given that we are presently limited almost exclusively to data from local populations, the key question is how (if at all) these possibilities can be examined with existing data.

Biological "birth" in most marine fishes occurs via spawning with external fertilization. Fecundity (egg or zygote production) is a possible source of demographic density dependence in all fishes because of two well-known relationships: (1) growth is often density dependent and (2) fecundity is a function of body size. Both these relationships have been well-documented in reef fishes, the former reviewed by Jones (1991) and the latter by Sadovy (1996). However, presently lacking and much needed are studies that integrate these patterns within a detailed demographic framework. Important contributions come from studies of the impact of maternal stress on the quality of offspring in reef fishes (McCormick, 1998b; Suthers, 1998) (see Chapter 10, this volume).

Due to larval dispersal, demographic "birth" in a local population of demersal fishes occurs by the process of settlement. Settlement is the transition from a pelagic larval stage to a demersal juvenile stage, involving an interaction between the local density of late-stage larvae competent to settle (hereafter "larval supply") and the availability of a suitable benthic environment (Kaufman *et al.,* 1992; McCormick and Makey, 1997; Booth and Wellington, 1998). Because settlement seems to occur mostly at night (reviews by Leis, 1991a; Victor, 1991; Cowen and Sponaugle, 1997), it is rarely observed directly (e.g., Holbrook and Schmitt, 1997). There is evidence that mortality at the time of settlement can be very high. Crest-net samples have shown that most nocturnally settling larvae entering the lagoon in Moorea, French Polynesia, disappear before they can be counted as new recruits the following morning (Dufour *et al.,* 1996; Doherty *et al.,* 2002). Is mortality during settlement density dependent? To our knowledge, there are no data available to answer this important question.

Because settlement is so difficult to study directly, it is typically measured indirectly as recruitment, which is the appearance of recently settled fish (review by Doherty and Williams, 1988). Thus, "recruitment" as typically used by reef fish ecologists is an estimate—subject to variation in methodology and artifacts—of the real biological phenomenon of settlement. (This definition of "recruitment" differs from that commonly used in fisheries biology, where one estimates recruitment of larger fish to a fishery. It also differs from the

general ecological definition, whereby "recruitment" is used with an explicit modifier to describe the transition between particular life history stages.) Obviously, the greater the time lag between actual settlement and measured recruitment, the greater the error in estimating settlement (due to postsettlement mortality) and the less the causal linkage between larval supply and recruitment. One of the major sources of confusion and controversy has been various authors implicitly defining recruitment based on quite different sampling frequencies, ranging from 1 day to several months (see Section III).

How relevant is measuring recruitment to the question of demographic density dependence? The answer depends on the spatial scale examined. If one wishes to understand only the dynamics of a local population, treating recruitment as a "black box" external source of settlers, then one can calculate the per-capita recruitment rate (i.e., divide the density of new recruits by the density of local residents during some time period) and examine this rate as a function of local population size. In every case we examined (see Section III,A), this procedure resulted in recruitment appearing to be density dependent, simply because each recruit represents a decreasing proportion of the total population as local population size increases (Hughes, 1984, 1990; Caley et al., 1996). Such per-capita density dependence could occur in the absence of any biotic feedbacks whatsoever if per-area settlement was constant through time and new recruits simply accumulated within an area. Although an equilibrial local population size could result, this phenomenon is not true demographic density dependence (Bence and Nisbet, 1989; Sale and Tolimieri, 2000). Rather, such apparent or "pseudo-density dependence" is simply a mathematical phenomenon and is not caused mechanistically by changes in local population size.

If one wishes to understand the role of recruitment in the dynamics of the metapopulation, then the per-capita currency is inappropriate because recruits from sources outside the local population are divided by fish within that population. From the metapopulation perspective, it is better to examine the total recruitment rate (i.e., the density of new recruits appearing during some time period). If local population size affects total recruitment, due to negative interactions between settling fishes and established residents, then chronically unsuccessful settlers are doomed to die and true density dependence is possible. In such cases, the total recruitment rate will be density dependent if it declines with increasing local population size.

Direct measures of mortality are less problematic, at least conceptually. Unfortunately, loss rates of eggs and larvae during presettlement mortality are not well documented among reef fishes (review by Boehlert, 1996), but in general are believed to be highly variable and density independent (reviews by Houde, 1987; Bailey and Houde, 1989; Heath, 1992). Note that, if density dependence indeed does not occur during the pelagic egg or larval stage, then persistence of the entire metapopulation requires that density dependence must occur during the demersal juvenile or later stage, as hypothesized by Sissenwine (1984), Houde (1987), and others. Authors asserting that their models demonstrate that a metapopulation can persist indefinitely without density dependence (e.g., den Boer and Reddingius, 1996) are mistaken because these models actually incorporate density dependence (see Chesson, 1981, 1996; Hanski, 1990; Murdoch, 1994; Walde, 1995; Hanski et al., 1996; Hanski and Gilpin, 1997, for details).

Postsettlement mortality of reef fishes is much better documented than egg and larval mortality. To test for density dependence, the mortality rate is calculated on a per-capita basis as a proportion of the population dying during some time period (alternatively, as an instantaneous rate), then examined as a function of the initial population size. Note that testing for density-dependent mortality by examining the number of adults (or larger juveniles) as a linear function of the initial number of recruits is not advisable because a significantly positive linear regression may mistakenly lead to the conclusion of density-independent mortality when the underlying pattern is actually density dependent (Caley et al., 1996; Forrester, 1998; Hixon, 1998). For such plots, data showing a decelerating curvilinear regression (which can also produce a significant linear regression of positive slope) are indicative of density-dependent mortality, not simply linear regressions of zero slope (Caley et al., 1996; Hixon, 1998). For example, the data fit by Doherty and Fowler's (1994a) density-independent linear regression is equally well fit by a density-dependent curvilinear regression (Forrester, 1998). In any case, the "initial population size" in question depends on the source of processes affecting mortality: within-cohort (a group of conspecifics that settle during the same time period), among-cohort (all conspecifics in the same local population regardless of age), or among-species (in the case of interspecific competition). The focus of this review is within-species density dependence (both within and among cohorts) because few studies have adequately examined the demographic effects of interspecific competition in reef fishes (but see Robertson, 1996). There is a clear need for more detailed studies of between-species competition. Importantly,

predation—not just competition alone—can cause density-dependent mortality (see Section IV,B).

Examining whether postsettlement mortality rates are density dependent is the fundamental test of the "recruitment limitation hypothesis." Since formalized by Doherty (1981), this popular hypothesis has undergone various changes in meaning that threaten its utility (Caley *et al.*, 1996; Hixon, 1996a, 1998; Chesson, 1998a). The latest meaning depends on the definitions of key words: recruitment limitation occurs "when the relative abundance of reef fishes among replicate units of habitat reflects the spatial distribution of their recruitment accumulated over a lifetime" (Doherty, 1998, p. 129). As worded, this pattern could occur as a result of either density-dependent or density-independent processes (Warner and Hughes, 1988; Caley *et al.*, 1996; see also Holm, 1990). Fortunately, one of the explicit predictions (stated as an "assumption") of this version of the hypothesis (even though it does not follow necessarily from the above definition) is forthright: "post-settlement mortality schedules at this scale are stable (albeit may vary with age) and density-independent" (Doherty, 1998, p. 131). Therefore, one can test the recruitment limitation hypothesis by determining whether the postsettlement death rate is density dependent. However, this "either/or" approach to the issue of what drives local population dynamics is quite restrictive. A more fruitful approach is to examine the relative roles of recruitment vs. mortality in determining local population size (see Section V,D). Moreover, a less restrictive definition of recruitment limitation—occurring when increases in recruitment cause increases in population size—can be manifested regardless of whether mortality is density dependent or density independent (and thus is irrelevant to this chapter).

Given that recruitment is better examined as a total rate, whereas postsettlement mortality is better examined as a per-capita rate, how can these rates be compared? If one wishes to understand only the dynamics of the local population, including any local "equilibrium" driven externally by incoming recruits interacting with local mortality (Bence and Nisbet, 1989), then comparing per-capita rates is useful (see Section III,C). However, if the goal is to use local rates to understand metapopulation dynamics, then comparing total rates is more appropriate.

Finally, what about emigration and immigration? Our definitions clearly separate local populations from metapopulations by eliminating postsettlement movements as demographic rates (Section II,C,1). This is not to say that emigration and immigration do not occur at smaller spatial scales. Postsettlement movement of juveniles and adults between habitat patches most certainly occurs at such scales, sometimes at substantial levels (e.g., Robertson, 1988a; Schmitt and Holbrook, 1996; Frederick, 1997; Lewis, 1997; Ault and Johnson, 1998a). However, we contend that in cases in which between-patch movement is common, the linked patches comprise only parts of a single local population (rather than multiple local populations). Studying spatial scales much less than (or even much greater than) that of the local population inhibits the ability to detect biologically meaningful density dependence (Ray and Hastings, 1996; Anneville *et al.*, 1998). At the same time, between-patch emigration and immigration can be demographically relevant. If emigration leads to death, then it is a mechanism of mortality. In addition, measuring between-patch movement is essential for defining the boundaries of local populations. Therefore, tracking movements of juveniles and adults, typically via tagging, is an important part of any meaningful demographic study. Of course, at the scale of the metapopulation, immigration and emigration have no meaning, because the entire population occurs within its boundaries by definition.

Given the above considerations, this review focuses on the two possible sources of demographic density dependence that have been reasonably well studied in reef fishes: local recruitment and natural postsettlement mortality. Note that studies of reef fishes, especially in an experimental context, comprise the most detailed data available on these demographic rates in marine fishes. Therefore, we believe that reef fishes are excellent model systems for understanding mechanisms driving and regulating population dynamics of demersal marine fishes in general (see Section V,B).

III. How Common Is Density Dependence in Reef Fishes?

We searched the literature for evidence published through 1999 regarding the presence or absence of demographic density dependence in coral reef fishes. Specifically, we compiled data sets that examined recruitment and mortality rates as a function of local population size (or density). Obviously, a reasonably broad range and number of population sizes are required to test for density dependence statistically. Therefore, we did not consider studies that examined recruitment or mortality only in the presence vs. absence of previously settled fish (i.e., two points), even though such studies provide mechanistic information on the effects of residents (e.g., Sale, 1976; Williams, 1980; Doherty, 1983a; Tolimieri, 1995; Gutierrez, 1998). Also, the design of some studies that reported density dependence did not allow determination of which demographic rates were

involved, so could not be categorized (e.g., Schmitt and Holbrook, 1999a).

Published evidence regarding demographic density dependence includes both observational studies, which provide pattern only, and experimental studies, which can additionally elucidate causation if the causative processes are appropriately manipulated. For both kinds of studies, the basic analytical design has been to examine, by regression (linear or curvilinear) or correlation, a demographic rate as a function of local population size (or density) at the beginning of the time period over which the rate was measured. We know of no long-term observational studies of reef fishes that have employed the time-series analyses so prevalent in terrestrial studies (reviewed in Cappuccino and Price, 1995), and regardless, detecting density dependence from time series of abundance alone is problematic (Shenk et al., 1998). In the case of well-designed experimental studies, initial population sizes were manipulated, with appropriate controls and replication, over a range of natural densities. To examine causation, the initial-population-density treatment was cross-factored with one or more treatments that manipulated putative causative processes (e.g., predators present or absent).

For both observational and experimental studies, the spatial scale has thus far been constrained to local populations (Section II,C,1). The appropriate temporal scale for testing for density dependence is a sufficient period for any existing density-dependent process to operate, which may be as long as a full generation when mechanisms are immediate (Harrison and Cappuccino, 1995) or longer if density dependence is delayed by time lags (Turchin, 1990). In such tests, both observational and experimental studies can employ a spatial design (i.e., compare multiple populations over the same time period) or a temporal design (i.e., compare multiple time periods within a single population). Although both designs are valid and provide insight, spatial density dependence (among populations) may not necessarily translate into the temporal density dependence (within a population) required for regulation (see Section IV,B,2). All but three studies reviewed here used spatial designs, and therefore could detect only spatial density dependence. Two of the exceptions confounded time and space during data analysis (Stimson, 1990; Caselle, 1999). Only Victor (1986b) provided a truly temporal (albeit indirect) analysis.

A. Recruitment

Table 1 summarizes studies that examined whether recruitment is density dependent. Although there have

been many publications on recruitment, few report data allowing tests for density dependence. Density dependence is not falsified simply by demonstrating high variation in recruitment in time and space, which is characteristic of virtually all reef fishes examined to date (reviews by Doherty and Williams, 1988; Doherty, 1991; Jones, 1991; Williams, 1991; Booth and Brosnan, 1995; Caley et al., 1996; see also Dixon et al., 1999).

1. OBSERVATIONAL STUDIES

We found five nonexperimental studies that explicitly examined whether recruitment was density dependent (Table 1). Seven species from four families were studied in the Pacific and western Atlantic/Caribbean. In all cases, the total recruitment rate was reported (Section II,C,2). Four different patterns were evident: (1) density dependence (Stimson, 1990; Tupper and Hunte, 1994), (2) density independence (Tupper and Hunte, 1994; Forrester, 1999), (3) inverse density dependence (Booth, 1992), and even (4) a unimodal relationship between the total recruitment rate and local population size (Schmitt and Holbrook, 1996). Note that Victor's (1983b, 1986b) extensive study of the bluehead wrasse (Thalassoma bifasciatum) in the Caribbean is also suggestive of density-independent recruitment, but the data are presented in such a way that we were unable to extract an explicit statistical analysis. On conversion to per-capita rates, recruitment appeared to be density dependent (i.e., pseudo-density dependent) in every case (Section II,C,2).

2. EXPERIMENTAL STUDIES

We found six studies that tested for density-dependent recruitment experimentally, all of which reported total recruitment rates (Table 1). These studies examined six species from four families in the Pacific and western Atlantic/Caribbean. Again, a variety of patterns emerged: (1) density dependence (Stimson, 1990; Forrester, 1995; Steele et al., 1998), (2) density independence (Forrester, 1999; Webster, 2002), and (3) inverse density dependence (Sweatman, 1985b; Booth, 1992). Note that Stimson's (1990) experiment was unreplicated. Again, conversions to per-capita rates resulted in recruitment that was pseudo-density dependent in every case (Section II,C,2).

3. INTERPRETATION AND CONCLUSIONS

Overall, given the few studies available, the wide taxonomic and geographical coverage of those studies, and the broad variety of relationships documented, we could detect no general patterns in recruitment. Such results reflect the highly variable nature of recruitment in reef fishes.

TABLE 1   Observational and Experimental Studies of the Local Total Recruitment Rate[a]

Study	Location	Total recruitment rate	Sampling frequency	Study duration	Reference
Observational studies					
Chaetodontidae	Hawaii				
Chaetodon miliaris	Oahu	DD	1 mo	>6 yr	Stimson (1990)
Pomacentridae	Caribbean				
Stegastes partitus	Barbados	DI	<2 wk	1 yr	Tupper and Hunte (1994)
	Hawaii				
Dascyllus albisella	Oahu	IDD	5 days	14 mo	Booth (1992)
	French Polynesia				
Dascyllus trimaculatus	Moorea	Unimodal	1 day	6 days	Schmitt and Holbrook (1996)
Dascyllus trimaculatus	Moorea	Unimodal	<2 mo	<2 mo	Schmitt and Holbrook (1996)
Labridae	Caribbean				
Halichoeres garnoti	Barbados	DD	<2 wk	1 yr	Tupper and Hunte (1994)
Thalassoma bifasciatum	Barbados	DI	<2 wk	1 yr	Tupper and Hunte (1994)
Gobiidae	Bahamas				
Coryphopterus glaucofraenum	Lee Stocking Island	DI	1 day	7 days	Forrester (1999)
	Caribbean				
Coryphopterus glaucofraenum	Guana Island, BVI[b]	DI	1 day	12 days	Forrester (1999)
Experimental studies					
Grammatidae	Bahamas				
Gramma loreto	Lee Stocking Island	DI	1 day	2 mo	Webster (2002)
Chaetodontidae	Hawaii				
Chaetodon miliaris	Oahu	DD	<1 mo	4 mo	Stimson (1990)
Pomacentridae	Great Barrier Reef				
Dascyllus aruanus	Lizard Island	IDD	<1 wk	2 mo	Sweatman (1985b)
Dascyllus reticulatus	Lizard Island	IDD	<1 wk	2 mo	Sweatman (1985b)
	Hawaii				
Dascyllus albisella	Oahu	IDD	1–3 days	~6 mo	Booth (1992)
Gobiidae	Caribbean				
Coryphopterus glaucofraenum	Guana Island, BVI	DD	2.5 mo	2.5 mo	Forrester (1995)
Coryphopterus glaucofraenum	Guana Island, BVI	DI	1 day	14 days	Forrester (1999)
	Bahamas				
Coryphopterus glaucofraenum	Lee Stocking Island	DD	2–4 wk	2–4 wk	Steele *et al.* (1998)

[a]These studies determined whether the local total recruitment rate was density independent (DI), density dependent (DD), inversely density dependent (IDD), or unimodal. Note that the local per-capita recruitment rate was "pseudo-density dependent" in every case (see Fig. 3). Studies with shorter sampling frequencies more accurately estimated actual patterns of settlement.
[b]BVI, British Virgin Islands.

Figure 3 illustrates four conversions from total to per-capita recruitment rates—two from observational studies and two from field experiments. Notice that this conversion shifts the rich variety of recruitment patterns to uniform apparent density dependence (i.e., a negative relationship between recruitment and local population size). These examples demonstrate how such pseudo-density dependence is a purely mathematical phenomenon rather than a biological mechanism (Section II,C,2). However, per-capita recruitment can nonetheless be used to examine equilibrial dynamics of a local population studied in isolation (see Section III,C).

B. Mortality

Compared to recruitment, far more explicit data have been published regarding postsettlement mortality

A. *Dascyllus aruanus*   B. *Dascyllus albisella*

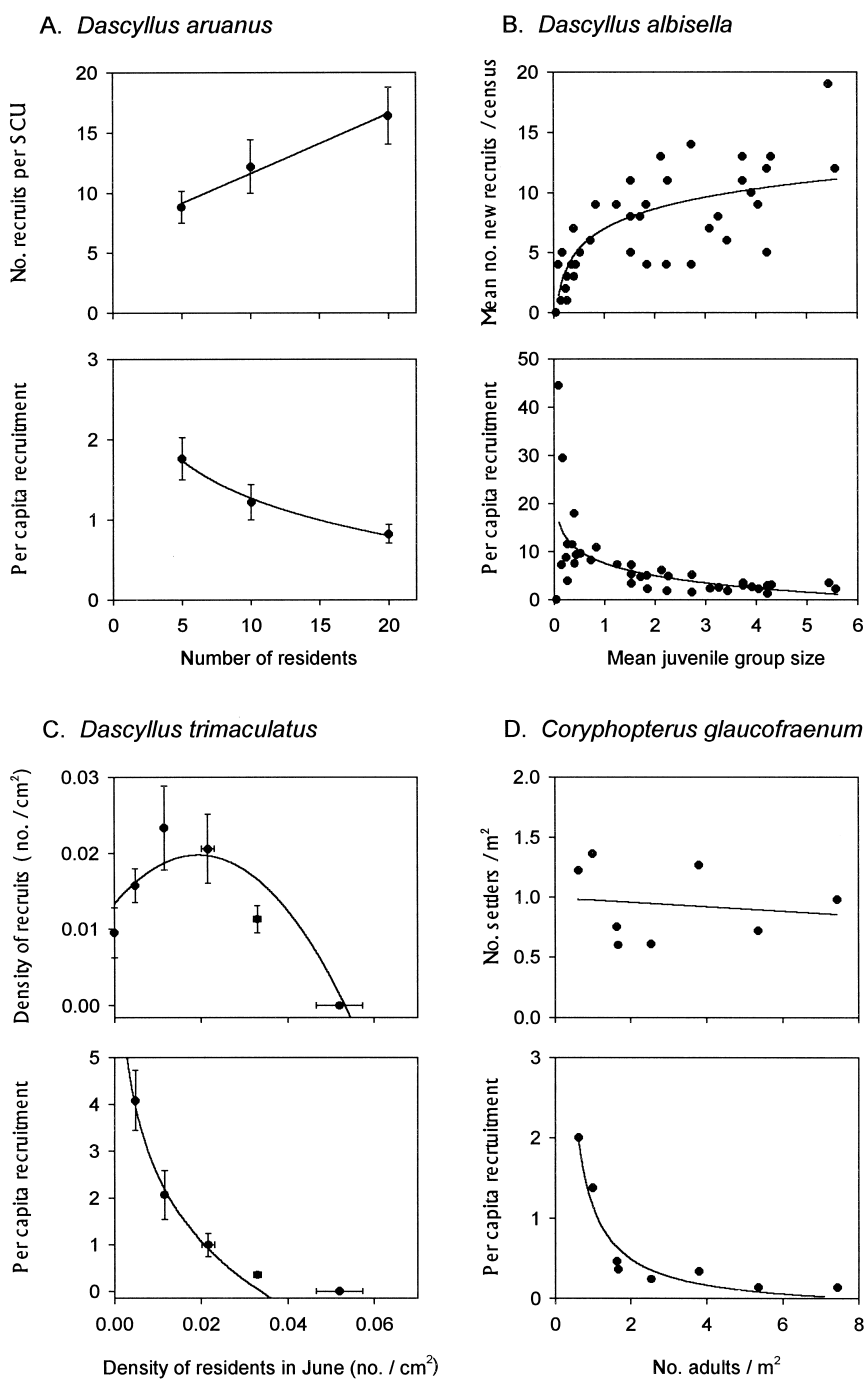C. *Dascyllus trimaculatus*   D. *Coryphopterus glaucofraenum*

FIGURE 3 Example conversions of total recruitment (upper plots) to per-capita recruitment (lower plots) from studies of (A) a damselfish in the Great Barrier Reef [experimental data from Sweatman (1985b)], (B) a damselfish in Hawaii [observational data from Booth (1992)], (C) a damselfish in French Polynesia [observational data from Schmitt and Holbrook (1996)], and (D) a goby in the British Virgin Islands [experimental data from Forrester (1999)]. Despite large variation in the shape of the total recruitment curve, per-capita recruitment appears to be density dependent (i.e., "pseudo-density dependent") in every case (A; $r^2 = 0.45$, $P = 0.006$; B, $r^2 = 0.34$, $P = 0.0001$; C, $r^2 = 0.51$, $P < 0.0001$; D, $r^2 = 0.74$, $P = 0.006$).

(Table 2). Due to difficulties of interpretation, we did not include studies in which species were pooled for analysis (e.g., Caley, 1995a; Connell, 1997a). Also inappropriate were studies (reporting density-dependent mortality) that followed members of only a single cohort through time, thus confounding density and age along a survivorship curve (e.g., Hunte and Côté, 1989). Given that type 3 (hyperbolic) postsettlement survivorship curves are common in reef fishes (reviews by Hixon, 1991; Caley, 1998), including such data would artificially inflate the reported occurrence of density dependence (Caley *et al.,* 1996).

Either from the original publication or directly from the author, we were able to extract data from most studies listed in Table 2 to calculate the instantaneous daily per-capita mortality rate as a function of local

TABLE 2   Observational and Experimental Studies of the Overall Local Per-Capita Mortality Rate[a]

Study	Location[b]	Per-capita mortality rate			Initial age of fish	Study duration	Reference[c]
		Overall	DI component (y intercept)	DD component (slope)			
Observational studies							
Serranidae	Indian Ocean						
Epinephelus merra	Reunion Island	DD	-4.2×10^{-2}	$3.9 \times 10^{-2**}$	4–5 days	7 wk	1
Pomacentridae	Bahamas						
Chromis cyanea	Lee Stocking Island 1994	DI	$2.1 \times 10^{-2**}$	5.0×10^{-3}	<1 wk	1 mo	2
Chromis cyanea	Lee Stocking Island 1995	DD	-4.2×10^{-2}	$3.3 \times 10^{-2**}$	<1 wk	1 mo	2
Chromis cyanea	Lee Stocking Island 1996	DD	8.3×10^{-3}	$1.5 \times 10^{-2*}$	<1 wk	1 mo	2
	Hawaii						
Dascyllus albisella	Oahu	IDD	—	—	1–5 days	8 mo	3
	French Polynesia						
Dascyllus aruanus	Moorea	DI/DD	$1.4 \times 10^{-2*}$	$7.6 \times 10^{-5**}$	1 day	2 wk	4
Dascyllus aruanus	Moorea	DI	$1.3 \times 10^{-2**}$	-2.1×10^{-5}	2–30 days	2 wk	4
Dascyllus falvicaudus	Moorea	DI/DD	$2.0 \times 10^{-2***}$	$1.8 \times 10^{-4***}$	1 day	2 wk	4
Dascyllus falvicaudus	Moorea	di	1.5×10^{-2}	-3.7×10^{-5}	2–30 days	2 wk	4
Dascyllus trimaculatus	Moorea	DD	—	—	1 day	2 wk	5
Dascyllus trimaculatus	Moorea	DD	1.1×10^{-2}	$4.7 \times 10^{-4***}$	1 day	2 wk	4
Dascyllus trimaculatus	Moorea	di	2.4×10^{-3}	1.0×10^{-4}	2–30 days	2 wk	4
	Great Barrier Reef						
Pomacentrus molluccensis	Lizard Island	DD	2.9×10^{-4}	$6.7 \times 10^{-3*}$	<1 mo	1 yr	6
Pomacentrus molluccensis	Southern GBR	DI	$5.7 \times 10^{-4**}$	1.4×10^{-4}	2–5 mo	9 yr	7, 8
Pomacentrus wardi	Southern GBR	di	3.1×10^{-4}	6.3×10^{-4}	2–5 mo	9 yr	8
	Caribbean						
Stegastes partitus	Barbados	DD	—	—	<2 wk	1 yr	9
Labridae	Caribbean						
Halichoeres garnoti	Barbados	DI	—	—	<2 wk	1 yr	9
Thalassoma bifasciatum	Panama	DI	—	—	1 day	3 days	10
Thalassoma bifasciatum	Panama	DI	—	—	4 days	31 days	10
Thalassoma bifasciatum	Barbados	DD	—	—	Adults	4–5 mo	11
Thalassoma bifasciatum	Barbados	DD	—	—	<2 wk	1 yr	9
Thalassoma bifasciatum	St. Croix, USVI	DD	—	—	1 mo	4–6 mo	12
	French Polynesia						
Thalassoma hardwicke	Moorea	DD	—	—	1 day	90 days	13
Acanthuridae	Caribbean						
Acanthurus bahianus SH	Panama	di	7.3×10^{-4}	2.5×10^{-3}	1 mo	8 yr	14
Acanthurus bahianus AH	Panama	DD	6.7×10^{-4}	$2.9 \times 10^{-3**}$	1 mo	8 yr	14
Acanthurus chigurgus SH	Panama	DI/DD	$1.6 \times 10^{-3*}$	$3.0 \times 10^{-3***}$	1 mo	8 yr	14
Acanthurus chigurgus AH	Panama	DI	$1.9 \times 10^{-3*}$	2.1×10^{-3}	1 mo	8 yr	14
Acanthurus coeruleus SH	Panama	di	7.6×10^{-6}	1.0×10^{-2}	1 mo	8 yr	14
Acanthurus coeruleus AH	Panama	DD	-5.7×10^{-4}	$2.0 \times 10^{-2**}$	1 mo	8 yr	14

Experimental studies

Family / Species	Location	Type	Slope	y intercept	Age	Duration	Ref
Grammatidae							
Gramma loreto	Bahamas	DD	—	—	All ages	2 mo	15
Pomacentridae	Great Barrier Reef						
Acanthochromis polyacanthus	One Tree Island	DD	—	—	<2 days	<1 mo	16
Dascyllus aruanus	One Tree Island	DD	—	—	Recent settlers	7 mo	17
Dascyllus aruanus	One Tree Island	DD	—	—	Recent settlers	1 yr	18
Dascyllus aruanus	One Tree Island	DD	—	—	3–12 days	10 mo	19
Pomacentrus ambionensis	One Tree Island	DI	—	—	Recent settlers	1 yr	20
Pomacentrus ambionensis	One Tree Island	DI	—	—	1 yr	2 yr	20
Pomacentrus ambionensis	One Tree Island	IDD	—	—	Recent settlers	1 yr	18
Pomacentrus ambionensis	Lizard Island	DI/DD	1.7×10^{-3}**	1.6×10^{-4}*	Recent settlers	17 mo	21
Pomacentrus flavicauda	One Tree Island	DI	—	—	2–5 wk	1 yr	22
Pomacentrus wardi	One Tree Island	di	2.4×10^{-3}	3.1×10^{-5}	2–5 wk	1 yr	22
	Hawaii						
Dascyllus albisella	Oahu	IDD	—	—	<1 day	35 days	3
	French Polynesia						
Dascyllus trimaculatus	Moorea	DD	-6.7×10^{-4}	9.8×10^{-5}***	≤2 days	2 wk	4
Dascyllus trimaculatus	Moorea	DI/DD	9.0×10^{-3}*	8.2×10^{-5}***	≤2 days	2 wk	4
	Bahamas						
Chromis cyanea	Lee Stocking Island	DD	8.1×10^{-3}	1.1×10^{-2}**	Recent settlers	1 mo	23
Stegastes partitus	Lee Stocking Island	DD	1.9×10^{-3}	1.6×10^{-2}*	<1 wk	54 days	24
Labridae	Bahamas						
Halichoeres garnoti	Lee Stocking Island	DD	1.2×10^{-3}	2.5×10^{-2}***	<1 wk	3 wk	25
	Caribbean						
Thalasoma bifasciatum	St. Croix, USVI	DD	—	—	1–3 days	1 day	12
Thalasoma bifasciatum	St. Croix, USVI	DI	—	—	3–6 days	1 mo	12
Gobiidae	Caribbean						
Coryphopterus glaucofraenum	Guana Island, BVI	DI/DD	8.4×10^{-3}***	1.6×10^{-3}***	Adults	2.5 mo	26
	Bahamas						
Coryphopterus glaucofraenum	Lee Stocking Island	DD	—	—	Adults	30 days	27
Coryphopterus glaucofraenum	Lee Stocking Island	DD	—	—	Adults	55–64 days	27

[a]These studies determined whether the overall local per-capita mortality rate was density independent (DI), density dependent (DD), both (DI/DD), or inversely density dependent (IDD). Determination was made by testing whether the y intercept (DI component) and positive slope (DD component) of the instantaneous daily per-capita mortality curve (see Fig. 1) were significantly different from zero by least-squares linear regression (*P, <0.05, **P, <0.0001; ***P, <0.001). Cases in which neither parameter was significant (di) indicate a low level of density-independent mortality. In cases in which the original data were unavailable, the author's published interpretation is listed without y intercept and slope values. Note that the observational study of Acanthuridae (reference 14) examined density on the basis of both a settlement habitat (SH) and adult habitat (AH), which provided different conclusions.

[b]USVI, United States Virgin Islands; BVI, British Virgin Islands.

[c]1, Letourneur et al. (1998); 2, Hixon and Carr (2002); 3, Booth (1995); 4, Schmitt and Holbrook (1999b); 5, Schmitt and Holbrook (1996); 6, Beukers and Jones (1997); 7, Doherty and Fowler (1994a); 8, Doherty and Fowler (1994b); 9, Tupper and Hunte (1994); 10, Victor (1986b); 11, Hunte von Herbing and Hunte (1991); 12, Caselle (1999); 13, Shima (1999a); 14, Robertson (1988a); 15, Webster (2002); 16, Connell (1998a); 17, Jones (1987a); 18, Jones (1988b); 19, Forrester (1990); 20, Jones (1987b); 21, Jones and Hixon (2002); 22, Doherty (1982); 23, Hixon and Carr (1997); 24, Carr et al. (2002); 25, M. A. Hixon et al. (previously unpublished); 26, Forrester (1995); 27, Forrester and Steele (2000).

population density. This conversion in turn allowed us to test via standard least-squares linear regression whether mortality had a statistically significant density-independent component (i.e., positive y intercept) and density-dependent component (i.e., positive slope), because both can determine the overall mortality rate (Fig. 1). [Data were approximately linear for all data sets except that of Schmitt and Holbrook (1999b).] In cases in which we could neither extract nor obtain the required data, we relied on the author's conclusions.

1. OBSERVATIONAL STUDIES

We found 14 studies that provided explicit nonexperimental tests for density dependence in postsettlement mortality (Table 2). These studies examined 15 species representing four families, and were conducted at various sites in the Pacific, the Caribbean/western Atlantic, and the Indian Ocean. Excluding three surgeonfishes (see next paragraph), per-capita mortality was always density dependent (with or without an additional density-independent component) in 3 species (a grouper, a damselfish, and a wrasse), sometimes density dependent and sometimes density independent in 6 species (those which were the subject of multiple studies or were examined over different time periods), exclusively density independent in 2 species (a damselfish and a wrasse), and inversely density dependent in 1 species of damselfish. Including surgeonfishes, the 12 species that showed density-dependent mortality at some time and place represented four major families of reef fishes and all three major oceans. In virtually all cases, density dependence was an early postsettlement phenomenon. The damselfish (*Pomacentrus wardi*) and the wrasse (*Halichoeres garnoti*) that showed density-independent mortality exclusively were studied in the southern Great Barrier Reef and Barbados, respectively. The single case of inverse density dependence was apparently due to antipredatory benefits of schooling in the highly social Hawaiian damselfish *Dascyllus albisella* (Booth, 1995).

Robertson's (1988a) study of Caribbean surgeonfishes defies easy categorization and shows how methodological variation can alter conclusions regarding density dependence. He forthrightly reported fish densities in terms of both "settler habitat" and "adult habitat." If one considers only settler habitat, then two surgeonfish species suffered density-independent mortality exclusively and the third species experienced a combination of density-independent and density-dependent mortality. However, if densities are calculated using adult habitat (which we believe is of ultimate demographic importance), then only one species suffered density-independent mortality and two species experienced density dependence.

In the one case in which different age classes were compared, only day-old new settlers of three species of humbug damselfish (*Dascyllus* spp.) in Moorea, French Polynesia, suffered density-dependent mortality (Schmitt and Holbrook, 1999b). Mortality of older juveniles was density independent (see also Section III,B,2), but older fishes were studied in the absence of larger juveniles and adults.

Two species were the subjects of multiple studies, allowing regional comparisons. The wrasse *Thalassoma bifasciatum* was studied off the Caribbean coast of Panama (Victor, 1986b), off Barbados (Hunte von Herbing and Hunte, 1991; Tupper and Hunte, 1994), and in the United States Virgin Islands (Caselle, 1999). Victor reported density-independent mortality, whereas the other three studies detected density dependence. The reason for this discrepancy is unknown, given that recruitment densities were similar among regions. There were differences in methods: Victor's analysis was temporal (patterns on one reef through time) and of relatively indirect and low resolution, those in Barbados were spatial (comparing multiple reefs), and Caselle's analysis combined time and space.

The other regional comparison involved studies of the damselfish *Pomacentrus moluccensis* at both the southern (Doherty and Fowler, 1994a,b) and northern (Beukers and Jones, 1997) Great Barrier Reef (GBR). The former study reported density-independent postsettlement mortality, whereas the latter detected density dependence (Fig. 4). Although both studies employed a spatial design using similar sample units (patch reefs), the methods differed in geographic coverage and temporal scale. Doherty and Fowler censused patches over an entire archipelago annually for 9 years and compared seven islands, whereas Beukers and Jones censused patches within a single location twice (1 year apart) and compared eight patches. Also, the initial age of new recruits was up to 5 months postsettlement in the former study (Doherty and Fowler, 1994a,b), but less than 2 months in the latter (J. S. Beukers, personal communication). Finally, the initial density of new recruits ranged from 3 to 40 fishes per 100 m^2 in Doherty and Fowler's (1994a,b) study, and from 25 to nearly 100 per 100 m^2 in Beukers and Jones' (1997) study.

What explains the difference in the mortality rates in the southern and northern Great Barrier Reef? There are three major possibilities. First, the different spatial resolutions of the two studies could have led to different conclusions despite no real difference, i.e., density dependence may be detectable only at the local scale of patch reefs within islands rather than at the regional scale of patch reefs pooled by island [see Hassell *et al.*
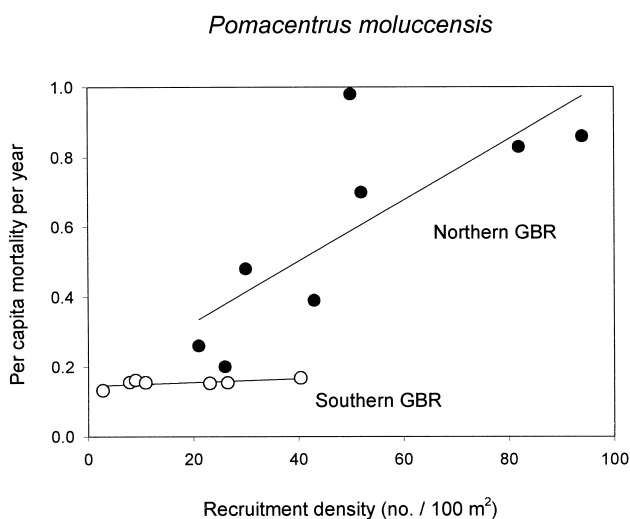
Pomacentrus moluccensis

FIGURE 4   Comparison of annual per-capita mortality of the damselfish *Pomacentrus moluccensis* between the southern Great Barrier Reef (GBR) [data from Doherty and Fowler (1994a)] and the northern GBR [data from Beukers and Jones (1997)]. Mortality rates were roughly estimated from the data of Doherty and Fowler (1994) 1 as follows: $1 - [(\text{average "annual recruitment density"} \times 9 \text{ years})/\text{"adjusted catch"}]$, which gave the overall per-capita mortality rate for a combination of 1- to 9-year-olds, so this value was divided by the average age of 5 years to estimate annual mortality.

(1987), for a similar comparison of insects on leaves vs. entire plants]. Second, density dependence may occur only at higher recruitment densities characteristic of the northern GBR (see Sweatman, 1985b; Caley, 1995b). Finally, Doherty and Fowler may have missed early postsettlement density dependence by starting their observations with older fishes. The argument that the density of older fishes in Doherty and Fowler's (1994a,b) study was highly correlated with the density of new settlers (or even larval supply), based on a study by Williams *et al.* (1994), is flawed by two serious problems in observational and analytical design of the latter study. First, multiple 40-day census intervals without removals of new recruits means that juveniles counted as settlers were up to several months old, allowing plenty of time for postsettlement mortality to obscure true patterns of settlement. Sampling settlement accurately often requires at least daily censuses to ensure that new settlers are counted before they die (Booth, 1991; personal observations). Indeed, crest net samples have shown that most nocturnally settling larvae entering the lagoon in Moorea, French Polynesia, disappear before they can be counted as new recruits (Dufour *et al.*, 1996; Doherty *et al.*, 2002). Second, the conclusion by Williams *et al.* (1994) of a tight relationship

between settler density and older recruit density was based on correlations drawn between "net total gain" of recruits and "end of season count," which as defined could be (and were in many cases) exactly the same data!

2. EXPERIMENTAL STUDIES

We found 16 experimental studies that tested explicitly whether postsettlement mortality was density dependent (Table 2). These studies examined 13 species from four families, and were conducted at various locations in the Pacific Ocean and the Caribbean/western Atlantic region. Seven species representing all four families always showed density-dependent per-capita mortality (with or without an additional density-independent component) (e.g., Fig. 5), three species (a damselfish, a wrasse, and a goby) showed density-dependent mortality at some times and density-independent mortality at other times, and two damselfishes showed density-independent mortality exclusively. The thirteenth species showed inverse density dependence, as did another damselfish in one case (see next paragraph), apparently due to antipredatory benefits of sociality.

The three species that exhibited density dependence at some times and density independence at other times experienced density-dependent mortality only as very recent recruits. This pattern suggests that local regulation due to mortality may be an early postsettlement phenomenon. One of these species, the damselfish *Pomacentrus amboinensis,* also exhibited slightly inverse density dependence at the southern Great Barrier Reef (Jones, 1988b), as well as density-independent mortality at the same site (Jones, 1987b), whereas mortality at the northern GBR showed density dependence (Jones and Hixon, 2002). The experimental designs among sites were comparable, so the difference appeared to be related to a much greater settlement rate at the northern site (Caley, 1995b), perhaps similar to the situation with *P. moluccensis* (Section III,B,1).

Both damselfish species that exhibited density-independent mortality exclusively (then named *P. flavicauda* and *P. wardi*) were studied as older juveniles at One Tree Lagoon in the southern Great Barrier Reef (Doherty, 1982). The results reviewed above suggest that this study may have missed early postsettlement density dependence by focusing on older fish. Additionally, One Tree Lagoon receives relatively low settlement compared to more equatorial locations in the northern GBR (Sweatman, 1985b; Caley, 1995b; see also Hughes *et al.,* 1999), suggesting that density dependence required higher initial densities. This hypothesis is bolstered by the fact that two
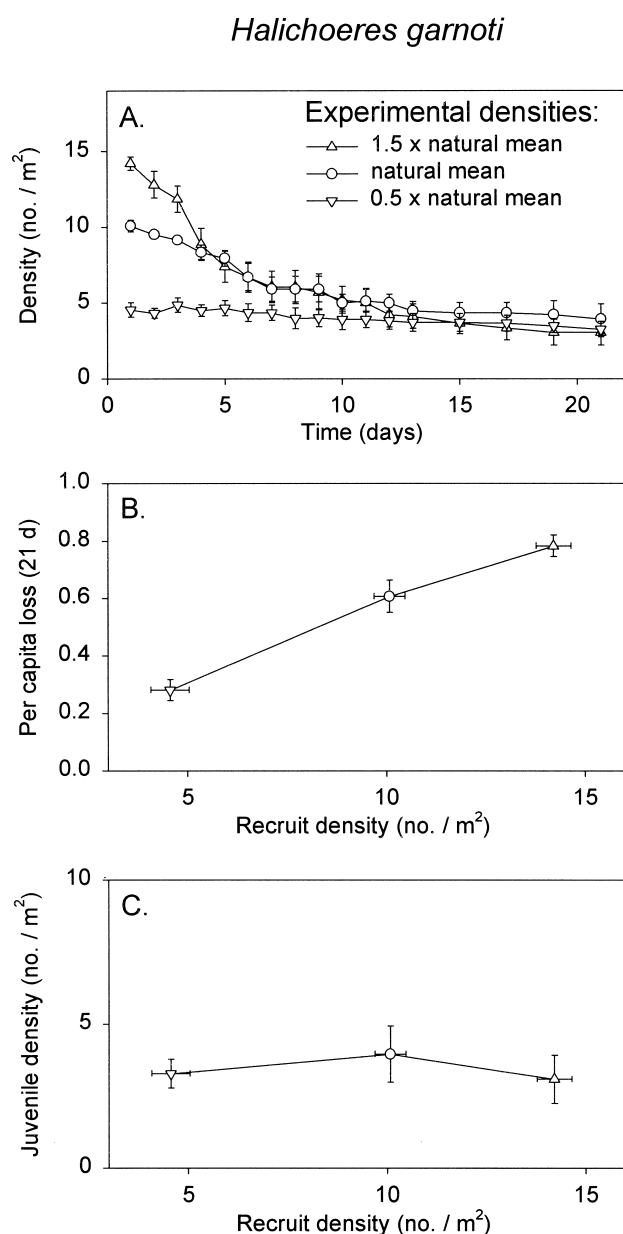
Halichoeres garnoti

FIGURE 5   Example of a field experiment demonstrating density-dependent mortality. Numbers of new settlers of the wrasse *Halichoeres garnoti* were adjusted on small patch reefs in the Bahamas to mean natural densities, 150% natural, and 50% natural (*n = 5* reefs each; results given as mean ± SEM). Results are equivalently presented as (A) raw survivorship curves, (B) per-capita loss, and (C) abundance of 21-day-old juveniles as a function of the initial abundance of new settlers. Note that the per-capita presentation shows density dependence most forthrightly. Fishes were not tagged in this study, so some loss may have been due to emigration [data from M. A. Hixon, M. H. Carr, and Kaltenberg (previously unpublished)].

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congeneric species (*P. moluccensis* and *P. amboinensis*) exhibited density-dependent mortality at Lizard Island in the northern GBR (Beukers and Jones, 1997; Jones and Hixon, 2002).

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3. META-ANALYSIS AND CONCLUSIONS

The studies summarized in Table 2 provide sufficient data for a simple meta-analysis, or analysis of analyses (Gurevitch and Hedges, 1993; Osenberg *et al.,* 1999). The goal was to determine whether density-dependent mortality was common across studies and species. We measured the strength of density dependence as the correlation (*r*) between local population density and instantaneous daily per-capita mortality rate for 24 separate data sets extracted from 14 studies of 15 species (Table 2). "Effect size" was tested as Fisher's *z*-transformation of *r* in a random-effects model using the MetaWin 2.0 software package (Rosenberg *et al.,* 2000). We ran the analysis twice, once including only the "settler habitat" data from Robertson (1988a) and once including only the "adult habitat" data. Weighted mean correlations from the two meta-analyses were 0.77 (95% CI: 0.63–0.86) and 0.79 (95% CI: 0.65–0.87), respectively. There was no evidence of publication bias or other violation of assumptions.

The high values of the mean correlations from the meta-analyses suggest that postsettlement density-dependent mortality is widespread among coral reef fishes. This conclusion is likely to be robust, given the wide range of species and sampling/experimental methods used in the 14 studies. Because we were able to extract sufficient information from only 13 of 27 studies listed in Table 2, more detailed meta-analyses will certainly be possible if and when additional studies are collated into a central archive (see Section V,D).

C. Recruitment and Mortality Combined

To our knowledge, only four published studies have simultaneously examined whether both recruitment and mortality are density dependent (Tables 1 and 2) (Booth, 1992, 1995; Tupper and Hunte, 1994; Forrester, 1995; Schmitt and Holbrook, 1996). We plot the combined results from two of these studies in Fig. 6, both as total rates and as per-capita rates. In theory, if these curves remained constant through time, then populations would stabilize at the equilibrium density where the recruitment and mortality curves intersect (see Fig. 1). However, such constancy is not apparent in reef fish populations, nor should it be expected (see Section V,C). Importantly, these
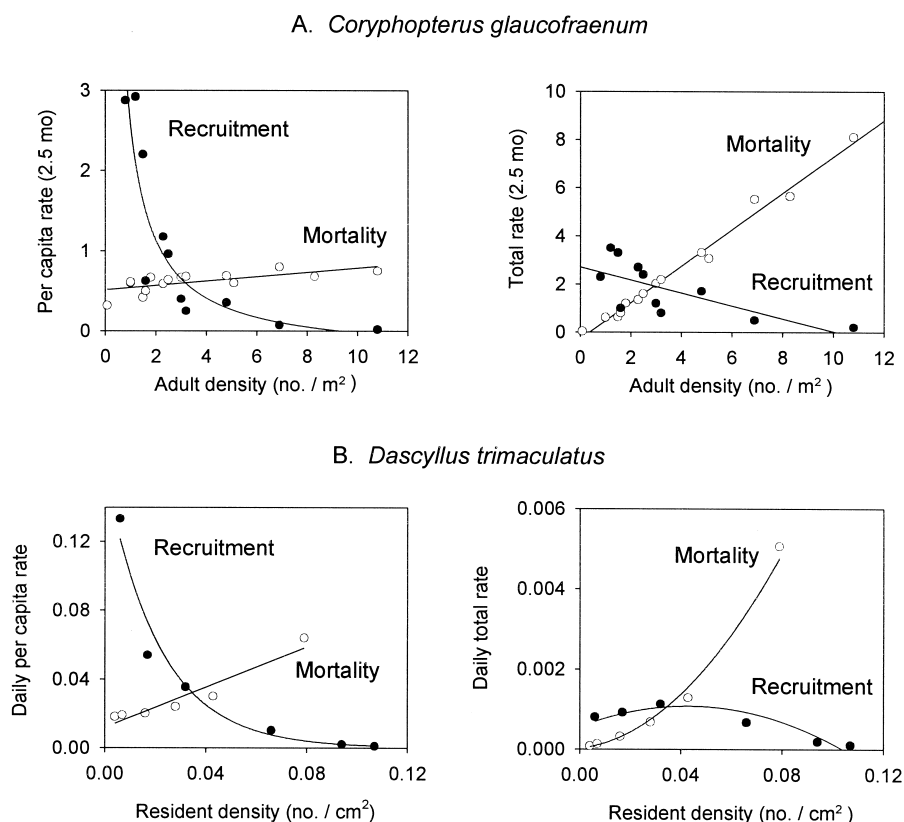
A. *Coryphopterus glaucofraenum*

B. *Dascyllus trimaculatus*

FIGURE 6 Comparisons of recruitment and mortality curves, presented equivalently as per-capita rates (left plots) and as total rates (right plots), from studies of (A) a goby in the British Virgin Islands [experimental data from Forrester (1995)] and (B) a damselfish in French Polynesia [observational data from Schmitt and Holbrook (1996)]. If these demographic curves were static and postsettlement movement was negligible, each population would come to an equilibrium at the density where the recruitment and mortality curves cross. In any case, the data suggest regulated local populations.

demographic "snapshots" are consistent with the idea that local population fluctuations are bounded due to density-dependent processes.

IV. Mechanisms Causing Density Dependence

Few studies have provided data on the processes responsible for density-dependent recruitment and mortality in coral reef fishes, so we not only review available data but also offer speculation.

A. Recruitment

The studies reviewed in Section III,A indicated that the total recruitment rate can be density dependent, density independent, inversely density dependent, or a combination of these in the form of a unimodal relationship between recruitment and local population density. Explicit data on underlying mechanisms are lacking. Density dependence in the total recruitment rate indicates that increasing densities of resident fishes inhibit subsequent establishment of new recruits, presumably due to intraspecific competition and/or cannibalism. Density independence suggests no effect of resident fishes on recruitment. Inverse density dependence indicates facilitation whereby settling fishes are attracted to conspecifics and/or enjoy enhanced survival in larger groups (Sweatman, 1985b). The unimodal pattern reported for humbug damselfishes (genus *Dascyllus*) by Schmitt and Holbrook (1996) suggests that facilitation operates at lower population densities, whereas inhibition occurs at higher densities, apparently as a function of increasing intraspecific competition. Booth

(1995) documented and modeled demographic cost–benefit trade-offs in *Dascyllus*. Survival of recruits was enhanced in larger groups, but growth was reduced.

B. Mortality

Predation is the predominant source of mortality in coral reef fishes, especially shortly after settlement [reviewed through 1990 by Hixon (1991); subsequently, see references in Table 2] (Shpigel and Fishelson, 1991; Caley, 1993, 1995a,b; Hixon and Beets, 1993; Carr and Hixon, 1995; Caley and St. John, 1996; Connell, 1996, 1997a; Beets, 1997; Craig *et al.,* 1997; Eggleston *et al.,* 1997; Nemeth, 1998). Seven of the studies listed in Table 2 provide data directly implicating predation as the source of density-dependent mortality, as well as indicating the role of habitat complexity and the synergistic effects of various groups of predators and interference competitors. These studies are interrelated conceptually, so we simply present them chronologically.

1. Empirical Evidence

Forrester (1990) determined experimentally that juveniles of the damselfish *Dascyllus aruanus* suffered density-dependent mortality (and growth) over 10 months in One Tree Lagoon, Great Barrier Reef. As part of the experiment, planktonic food was supplemented artificially, causing enhanced growth rates relative to controls. Forrester concluded that, at higher local population densities, competition for food inhibited growth, which translated to density-dependent mortality, possibly via predation. This conclusion is in accordance with what has been called the "growth-mortality hypothesis" or "stage-duration hypothesis" from fisheries biology, which predicts that increasing competition for food will increase the time required for small fishes to grow to a size relatively invulnerable to predation, thereby increasing overall mortality (Ricker and Foerster, 1948; Shepherd and Cushing, 1980; Chambers and Leggett, 1987; Houde, 1987; review by Sogard, 1997).

Beukers and Jones (1997) observed density-dependent mortality of new recruits of the damselfish *Pomacentrus moluccensis* over 1 year at Lizard Island, Great Barrier Reef (see Section III,B,1). They also observed that the mortality rate of new recruits was directly correlated with the density of piscivores, and inversely correlated with the percent cover of structurally complex corals. They determined in laboratory experiments that three common piscivores (*Pseudochromis fuscus, Cephalopholis boenak,* and *Thalassoma lunare*) were more successful at capturing these prey when they inhabited structurally simple corals (*Acropora nobilis*)

rather than complex ones (*Acropora nasuta* and *Pocillopora damicornis*). In a field experiment, they cross-factored predators (present vs. absent) and corals (simple vs. complex) with one level of initial prey density. After 2 months, reefs of high complexity with predators supported the same number of prey as reefs of low or high complexity without predators. Damselfish abundance was significantly lower on the low-complexity reefs with predators. These results implicate predation as the source of density-dependent mortality, and indicate the importance of habitat complexity in mediating predation (review by Hixon, 1991).

Hixon and Carr (1997) were the first to demonstrate unequivocally that predation causes density-dependent mortality in marine fishes. They ran a factorial experiment on new recruits of the damselfish *Chromis cyanea* at Lee Stocking Island, Bahamas, using 32 patch reefs in a regression design: eight levels of initial population size (within the natural range) × resident predators (serranid groupers, etc.) present vs. absent × transient predators (carangid jacks, etc.) present vs. absent. Predator treatments were effected using large enclosures surrounding individual reefs, which produced no substantial artifacts (see also Steele, 1996; Connell, 1997a). After 1 month, mortality of new recruits was density dependent only in the natural control treatment in which both sources of predation were present (Fig. 7A). In the absence of all predators, mortality was low and density independent. There was a trend toward density dependence in the treatments with only one source of predation, but high variance precluded statistical significance.

Behavioral observations via automated time-lapse video samples showed that these results were due to "synergistic predation" involving the combined effects of resident and transient piscivores. On reefs with no transient predators, recruits sheltered high in the water column, where they fed on zooplankton. (Resident predators did not enter the water column, presumably because they were prey of still larger piscivores, such as sharks and barracuda, as indicated by observations of such predation and tooth scars on resident predators.) Conversely, on reefs with no resident predators, *Chromis* recruits simply sheltered in the reef at the approach of schools of transient predators. In both circumstances, predation was highly variable in time and space due to the vicissitudes of prey vigilance and predator stealth. Only in the presence of both suites of predators were the prey particularly vulnerable—sandwiched between resident predators attacking from below and transient predators attacking from above. There was evidence that the mechanism of density dependence involved transient jacks (*Caranx ruber*)
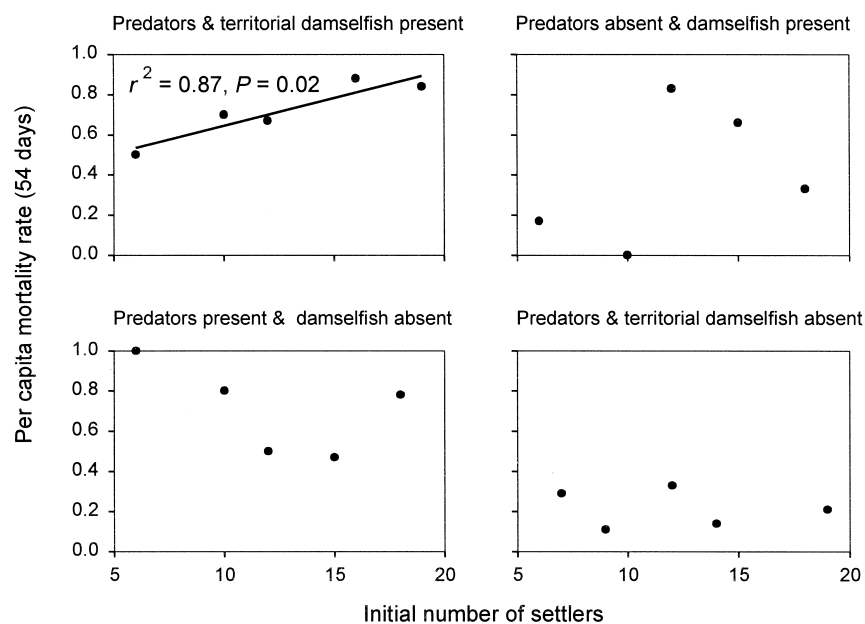
A. *Chromis cyanea*
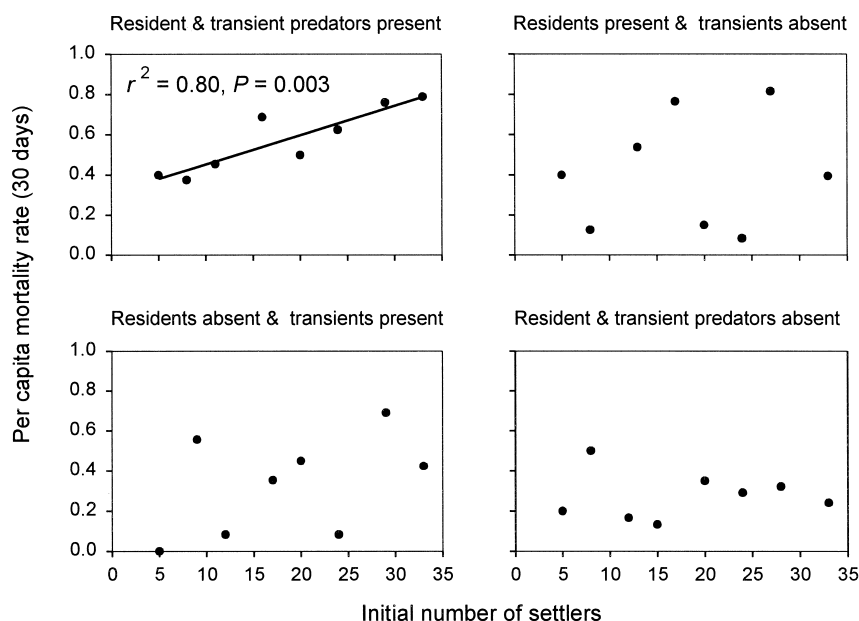
FIGURE 7 Factorial field experiments in the Bahamas illustrating that synergistic interactions cause density-dependent mortality in new settlers of damselfishes. Each point represents one patch reef. (A) For nonterritorial schooling *Chromis cyanea,* significant density dependence occurred only in the natural control treatment, where both resident and transient predators were present. Mortality was low and density independent in the complete absence of predation [data from Hixon and Carr (1997)]. (B) For individually territorial *Stegastes partitus,* significant density dependence occurred only in the natural control treatment, where both predators and larger territorial damselfishes were present. Mortality was low and density independent in the complete absence of these strong interactors [data from Carr *et al.* (2002)].

exhibiting an "aggregative response" (sensu Hassell and May, 1974), congregating at reefs with many prey and ignoring reefs with few prey. Hixon (1998) had documented a temporal aggregative response involving the same predator and prey species in St. Thomas, United States Virgin Islands (see also Hixon and Beets, 1993).

Steele *et al.* (1998), using the same experimental system in the Bahamas as Hixon and Carr (1997), found that per-capita recruitment of the goby *Coryphopterus glaucofraenum* was density dependent in the first of 2 years (the experiments running 32 and 15 days, respectively). Interestingly, this pattern appeared to occur despite predation rather than because

of it. In fact, there was a significant positive effect of resident predators on goby recruitment (and no effects of transient predators). The authors speculated that this pattern may have been an indirect effect: resident piscivores may have displaced or consumed smaller generalized predators (such as wrasses) that attacked gobies. They concluded that interference competition with adult conspecifics was the predominant mechanism causing density-dependent recruitment in this goby. In the same experiments, Forrester and Steele (2000) reported that mortality was apparently density dependent regardless of the presence or absence of predators. Besides the possibility that the cages did not exclude very small predators (such as wrasses and stomatopods), it is possible that interference competition caused gobies to emigrate from predator-exclusion cages, where they became vulnerable to predation.

Connell (1998a) also used cages to exclude larger predators from newly hatched schools of *Acanthochromis polyacanthus,* one of the few species of coral reef teleosts that do not undergo larval dispersal. Working in One Tree Lagoon in the Great Barrier Reef, he found that the difference in hatchling survival between caged and uncaged plots was the same as the difference between reef habitats where piscivores were naturally low and high, respectively. In a second experiment, per-capita mortality during the first 2 weeks posthatching was density dependent in uncaged plots but not caged plots, demonstrating that predation was the source of density dependence.

Jones and Hixon (2002) manipulated predators by removal at Lizard Island on the Great Barrier Reef. On a set of 48 patch reefs in the sandy central lagoon, they cross-factored recruitment density of the damselfish *Pomacentrus amboinensis* (three natural levels) and resident predators (present vs. absent), with eight replicates of each treatment (two-way ANOVA design). In this case, per-capita mortality after 17 months was density dependent regardless of the presence or absence of resident predators. It appeared that the highly complex coral that dominated these reefs (*Porites cylindrica*) inhibited piscivores (see also Beukers and Jones, 1997). Because density-dependent growth was evident, the ultimate cause of density-dependent mortality appeared to be exploitative competition for planktonic food, with predation on slower growing fishes being the proximate mechanism. These findings are reminiscent of the conclusions of Forrester (1990).

Finally, Carr *et al.* (2002) experimentally examined the effects of both predators (residents and transients combined) and interference competitors (territorial damselfish) on new recruits of the damselfish *Stegastes partitus* at Lee Stocking Island, Bahamas. This damselfish is loosely territorial and interacts aggressively with several congeners (Robertson, 1996). Using the same patch reefs and cages as Hixon and Carr (1997), Carr *et al.* (2002) used a regression design subjecting five natural density levels of new recruits to two cross-factored treatments: all predators present or absent × all territorial damselfishes present or absent. After 54 days, the results were similar to those of Hixon and Carr (1997) in that density-dependent mortality occurred only in the natural control treatment where all predators and territorial damselfish were present (Fig. 7B). Unlike the results of Hixon and Carr (1997), the mechanism underlying Carr *et al.'s* (2002) results appeared to be a synergistic interaction of predators and interference competitors (rather than a synergism between two kinds of predators). Again, behavioral field observations provided insight. In the absence of larger territorial damselfishes but in the presence of predators, new recruits of *S. partitus* vigilantly remained close to small shelter holes in the reef, and mortality was occasional and density independent. In the presence of larger interference competitors and the absence of predators, the larger fish territorially harassed the new recruits, but again, mortality was density independent. Only when both territorial damselfishes and predators were present was mortality density dependent, apparently because aggressive harassment by territorial fishes rendered new recruits more vulnerable to density-dependent predation (due to expulsion from shelter, increased conspicuousness, and/or decreased vigilance).

2. MECHANISTIC ISSUES

Predation has been demonstrated or implicated in most studies to date as the proximate or ultimate mechanism causing postsettlement density-dependent mortality (see also Rice *et al.,* 1997). Limited evidence suggests the importance of an aggregative response of transient predators, congregating at sites where new recruits are abundant and ignoring sites where new recruits are uncommon. Note that such spatial density dependence may not necessarily translate to the temporal density dependence required for population regulation (Stewart-Oaten and Murdoch, 1990). Predator aggregation may simply redistribute mortality among patches without changing its overall level (Harrison and Cappuccino, 1995). Of importance is the spatial range of the predator population relative to that of the prey (Hanski, 1990). The detection of density-dependent predation at scales larger than the movement patterns of transient piscivores would reflect a type 3 functional response of those predators and thus approximate temporal density dependence (Myers and Rothman, 1995). A type 3 functional response occurs if individual predators switch to alternative prey when any given prey

species is scarce (for details, see Murdoch and Oaten, 1975; Murdoch and Bence, 1987; Sinclair and Pech, 1996). In reef fishes, each piscivore would disproportionately consume new recruits of a particular species when those prey are abundant, and disproportionately ignore that prey species when it is rare. Additional, mechanistic studies of piscivory in reef fishes are sorely needed.

Few studies have adequately examined the extent to which estimates of mortality are confounded by emigration. There are two ways to separate these processes: (1) study highly reef-attached species on highly isolated reefs, or (2) tag fish and search surrounding habitats for emigrants. Of the 27 studies listed in Table 2, only 6 both examined reef-attached species and reported reef isolation distances of at least 25 m (Doherty, 1982; Hixon and Carr, 1997, 2002; Forrester and Steele, 2000; Carr *et al.,* 2002; Jones and Hixon, 2002), and only 5 used tagged fish (Jones, 1987b; Forrester, 1990, 1995; Booth, 1995; Webster, 2002). Increased effort at understanding the demographic consequences of emigration is clearly needed.

Competition can potentially be the ultimate cause of demographic density-dependent mortality. Because habitat complexity can mediate the effects of piscivory on coral reef fishes (e.g., Beukers and Jones, 1997; Jones and Hixon, 2002), predation may induce competition for structural shelter if such prey refuges are limiting (Hixon, 1991). Regarding competition for food, aggressive interference appears to be the ultimate source of density-dependent mortality in highly social species, such as planktivorous damselfishes of the genus *Dascyllus* (e.g., Forrester, 1990), and territorial species, such as more benthivorous damselfishes of the genus *Stegastes* (Carr *et al.,* 2002). Density-dependent growth (review by Jones, 1991) presumably leads to density-dependent mortality as smaller fishes are consumed by predators (Jones and Hixon, 2002). Proximally, aggressive harassment of smaller fishes by larger fishes may increase the vulnerability of small fishes to density-dependent predation (Carr *et al.,* 2002).

V. Discussion and Synthesis

A. Empirical Summary

This literature review suggests two major patterns. First, observational and experimental studies of 11 species from five families show that the total local recruitment rate varies in a broad variety of patterns as a function of local population size (Table 1; Section III,A). Tentatively, we conclude that recruitment not a consistent source of demographic density

dependence. However, in every study, conversion from total to per-capita recruitment resulted in apparent or pseudo-density dependence (Section II,C,2), which can provide a nonmechanistic kind of local population equilibrium unrelated to the regulation of the entire metapopulation (Bence and Nisbet, 1989; Hughes, 1984, 1990; Caley *et al.,* 1996) (Section III,C).

Second, data on 20 species from six families show that postsettlement mortality is often density dependent, especially shortly after settlement (Table 2; Section III,B), and caused largely by predation (Section IV,B). Overall, 17 of 20 species experienced density-dependent per-capita mortality at some time and place. In most studies that reported density-independent mortality, older juvenile fishes were studied, suggesting that regulation via mortality is an early postsettlement phenomenon.

The prevalence of density-dependent mortality has two ramifications. First, local populations may be an important source of regulation for the entire metapopulation, suggesting the importance of conserving the mechanisms causing local density dependence. Second, the more restrictive version of the recruitment limitation hypothesis, which predicts that postsettlement mortality will be density independent (Section II,C,2), has been falsified in most cases. However, evidence that some local populations are recruitment limited nonetheless exists (Section III,B). Thus, recruitment limitation remains a viable hypothesis, provided that it is defined explicitly (Caley *et al.,* 1996; Hixon, 1996a, 1998).

B. Are Reef Populations Model Systems for Marine Fishes?

Coral reef fishes support major fisheries (Russ, 1991; Polunin and Roberts, 1996) (see Chapters 16–18, this volume), are the object of conservation efforts in their own right (Roberts and Hawkins, 1999; Hawkins *et al.,* 2000), and are ideal subjects for both observational and experimental population studies (Sale, 1991b). Yet, are they relevant to understanding population dynamics in other demersal marine fishes, especially fishery species? Certainly, there are major differences between tropical reef species and temperate demersal species in terms of phylogeny, species diversity, the complexity of habitats and communities, and a variety of other parameters. Yet, we are more impressed by two major similarities.

First, despite earlier generalizations to the contrary (e.g., Shepherd and Cushing, 1990), density-dependent mortality (especially early during the postsettlement phase) is becoming increasingly well documented in temperate fishes, both in fishery species (e.g.,

Lockwood, 1981; Cook and Armstrong, 1986; van der Veer, 1986; van der Veer and Bergman, 1987; Sundby *et al.,* 1989; Fogarty *et al.,* 1991; Laevastu and Bax, 1991; Beverton and Iles, 1992; Myers and Cadigan, 1993a,b; Bailey, 1994; Rijnsdorp, 1994; Myers *et al.,* 1995a; Ralston and Howard, 1995; Bailey *et al.,* 1996; Bjørnstad *et al.,* 1999) and in nonfishery species (e.g., Jones, 1984; Carr, 1994; Tupper and Boutilier, 1995b; Sano, 1997; Steele, 1997a,b, 1998; Planes *et al.,* 1998c; Anderson, 2001; see also reviews by Jones, 1988a; Ebeling and Hixon, 1991).

Second, predation is coming under increasing scrutiny as the cause of density dependence in temperate fishes, both in fishery species (e.g., Sissenwine, 1984; van der Veer and Bergman, 1987; Fogarty *et al.,* 1991; Laevastu and Bax, 1991; Bailey, 1994) and in nonfishery species (e.g., Tupper and Boutilier, 1995b; Steele, 1997b, 1998; Anderson, 2001). These similarities suggest that concepts and hypotheses derived from mechanistic studies of coral reef fishes are worthy of consideration by temperate fisheries biologists and fishes ecologists for understanding sources of population regulation.

C. Conceptual Synthesis

What generalities, perhaps relevant to other demersal marine species, can be derived from this review regarding population dynamics and regulation of coral-reef fishes? Importantly, we are not currently in a position to evaluate what regulates entire metapopulations (see Section V,D). The substantial evidence to date focuses on local recruitment and postsettlement mortality, which do interact in a way suggesting local regulation (Section III,C), so we synthesize empirical generalities only at the local scale with a simple model.

Consider an open local population whose dynamics involve only recruitment (input) and mortality (loss). Regarding input, given that any pattern of total recruitment seems to be possible (Table 1; Section III,A), assume (to be conservative) that the total recruitment rate is generally density independent. From the discussion in Section II,C,2, we know that conversion to a per-capita rate results in apparent or pseudo-density dependence (i.e., a hyperbolic relationship between per-capita recruitment and local population size). It is also well-documented that recruitment is variable at the spatial and temporal scales thus far examined (reviews by Doherty and Williams, 1988; Doherty, 1991; Jones, 1991; Williams, 1991; Booth and Brosnan, 1995; Caley *et al.,* 1996), so temporal variation in the recruitment rate must be part of any synthesis.

Regarding loss, given that local mortality is density dependent at some time and place for the great majority

of species studied to date (Table 2; Section III,B), assume that per-capita mortality is density dependent, and for simplicity, assume a linear function. Assume further that mortality, like recruitment, is also variable through time. This assumption is based on the observation that density-dependent mortality in reef fishes appears to be caused mostly by predation (see Section IV,B), and that recruitment of predatory reef fishes is as variable as that experienced by prey species (e.g., Shenker *et al.,* 1993; see also Levin, 1998).

The above assumptions give the following per-capita model for an open local population (n):

$$\frac{1}{n}\frac{dn}{dt} = \frac{R(t)}{n} - [D(t)n + I(t)],$$

where $R(t)$ is the total density-independent recruitment rate (dividing by n makes this rate pseudo-density dependent). The quantity $D(t)n + I(t)$ describes the per-capita mortality rate, where $D(t)n$ is the density-dependent component [$D(t)$ defining the slope] and $I(t)$ is the density-independent component (y intercept; cf. Fig. 1). Both the recruitment rate and the mortality rate vary through time and thus are functions of t (Fig. 8A). Converting to total rates gives the following relation (Fig. 8B):

$$\frac{dn}{dt} = R(t) - [D(t)n + I(t)]n.$$

An equilibrial population size can be calculated from either equation, but will be of little use due to the unpredictable nature of variance in recruitment and mortality, both driven by external processes. Any theoretical equilibrium point will vary through time as the positions of the recruitment and mortality curves shift in slope and position (Fig. 8). Thus, local population size will range between some lower and upper limits, and the projected equilibrial point at which the curves cross will appear through time as a "cloud of points" (sensu Wolda, 1989). The key point is that this variation in abundance is nonetheless regulated (i.e., bounded above zero) via density-dependent mortality, but only as long as recruitment does not go to zero for the remaining life-span of the longest lived individual [cf. Chesson's (1983, 1984) "storage effect"]. (Of course, due to metapopulation structure at the global scale, a local population can go extinct and start again with a new pulse of recruitment.) Depending on time lags, the population may track but never reach the ever-changing equilibrium point, such that population fluctuations may appear stochastic, i.e., regulated populations need not be constant in size and may appear to fluctuate randomly as a stationary stochastic process (Turchin, 1990, 2001).
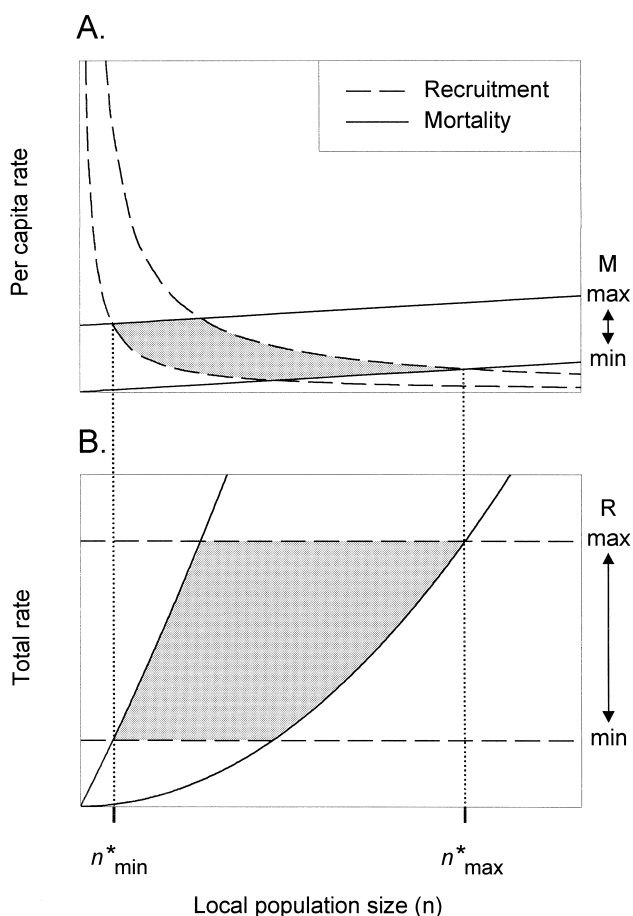
A.

B.

FIGURE 8 Synthetic model of the dynamics of an open local population based on available data (cf. Fig. 6), presented equivalently as (A) per-capita and (B) total demographic rates. Total recruitment is density independent, appearing as "pseudo-density dependent" when divided by local population size and presented as a per-capita rate. per-capita mortality is density dependent, becoming more strongly so when converted to a total rate. Both demographic rates vary between some minimum and maximum values as the positions of the curves shift through time. Consequently, the equilibrial intersection of the curves varies throughout the shaded area, and local population size varies between n^*_{min} and n^*_{max}, perhaps never reaching equilibrium. Thus, temporal variability leads to dynamics that may be substantial and appear random, even though the local population is regulated.

Note that this simple model does not include an Allee effect, whereby population growth becomes inversely density dependent at low population sizes, pushing the population toward extinction (review by Courchamp et al., 1999). The focus here is a local population sufficiently large to preclude this effect. Overall, we simply wish to stress that reef fish population dynamics cannot be explained by variation in a single process (see also Hixon, 1991, 1998; Jones, 1991; Roberts, 1996; Chesson, 1998b).

D. Future Directions

Coral reef fish ecology is a new discipline, having emerged in the 1960s but not gaining wide recognition until the 1970s. In "The Ecology of Fishes on Coral Reefs" (Sale, 1991a), several major hypotheses relevant to reef fish population dynamics were reviewed (Doherty, 1991; Hixon, 1991; Sale, 1991b; Williams, 1991), yet none of them were then corroborated by substantial data (see also Mapstone and Fowler, 1988; Sale, 1990). The new millennium is an exciting time in reef fish ecology because detailed observational and experimental studies are becoming more the norm than the exception, so definitive hypothesis testing is on the rise. With an eye on the future, we offer several suggestions for continued study of reef fish populations.

1. EXPLORE MECHANISMS UNDERLYING DEMOGRAPHIC PATTERNS

Testing for and detecting density dependence buried in a field of stochastic demographic variation is certainly a challenge in and of itself. However, for practical aspects of managing fisheries and conserving fish populations, understanding the sources and causes of population dynamics in general, and density dependence in particular, is crucial. We believe that the most useful empirical approach combines observational and experimental exploration of multiple processes at multiple spatial and temporal scales (see Hixon, 1998). Nested spatial designs, such as those reported by Hughes et al. (1999) for corals, would be especially valuable to determine the scale at which density dependence operates (see Ray and Hastings, 1996; Sale, 1998; Chesson, 1998b). Additional exploration of the density-independent component of postsettlement mortality is also needed (e.g., Shulman and Ogden, 1987; Levin, 1998), as is greater knowledge of apparently special cases of inversely density-dependent mortality (e.g., Booth, 1995). Especially welcome would be more studies examining the relative contributions of density-dependent and density-independent factors in driving population dynamics (e.g., Schmitt and Holbrook, 1999b; Schmitt et al., 1999; Shima, 1999b).

Currently, there are three major approaches to examine the relative contribution of density-dependent vs. density-independent factors. The simplest way to compare the two components of mortality is to determine the slope and y intercept of the per-capita mortality rate plotted as a function of initial population size. Assuming the slope is positive, the y-intercept divided by the overall mortality rate at any given population size is the proportion of mortality that is density independent (Fig. 1). A more sophisticated approach is to fit a Shepherd (1982) stock-recruitment curve to a

recruit-adult (or recruit-juvenile) plot and interpret the components of the descriptive equation (Schmitt *et al.,* 1999). This method has the advantage of providing the relative contribution of recruitment and both components of mortality to local population size. The disadvantage is that this approach is data intensive. The third approach is to construct detailed Leslie-matrix-type demographic models and examine the relative contribution of proportional variation in various parameters via elasticity analysis (Heppell *et al.,* 2000).

Although requiring much time and effort to implement, studies of temporal density dependence (preferably over multiple generations) are also needed. Nearly all studies to date investigated and detected only spatial density dependence, which may not necessarily translate to the temporal density dependence required for population regulation (see Section IV,B,2). Fortunately, otolith microchemistry (Thorrold and Hare, this volume), elastomer injections and microtags (Buckley *et al.,* 1994; Beukers *et al.,* 1995), and other recent advances in methodology now allow the entire lives of fishes to be tracked in unprecedented detail.

When and where possible (admittedly a major challenge), we encourage multifactorial field experiments for the strongest possible inference on causation (see Connell, 1975). Given that postsettlement density dependence is often induced by mortality caused directly or indirectly by predation (see Section IV,B), we suggest an experimental design in which a natural range of initial population sizes is monitored in the presence and absence of predators (Caley *et al.,* 1996; Hixon, 1998). Assuming that (as the data in Section III,B indicate), first, predators in fact increase prey mortality rates, and, second, mortality is not inversely density dependent, the four possible outcomes of this experimental design provide insight on the relative importance of predation and competition in causing density-dependent mortality (Fig. 9). For example, Hixon and Carr's (1997) experiment (Fig. 7A; Section IV,B,1) produced results illustrated in Fig. 9C, demonstrating that predation was the sole cause of early postsettlement density dependence in *Chromis cyanea* in the Bahamas. Carr *et al.'s* (2002) experiment gave the same results for *Stegastes partitus* in the Bahamas (Fig. 7B), but with the important difference that interference competitors were necessary for the predation effect to occur. Finally, Forrester and Steele's (2000) experiment produced results illustrated in Fig. 9D, indicating several possible sources of density dependence for *Coryphopterus glaucofraenum* in the Bahamas.

Accurate interpretation of experimental outcomes requires detailed knowledge of the study system, including the natural history and behavior of the species
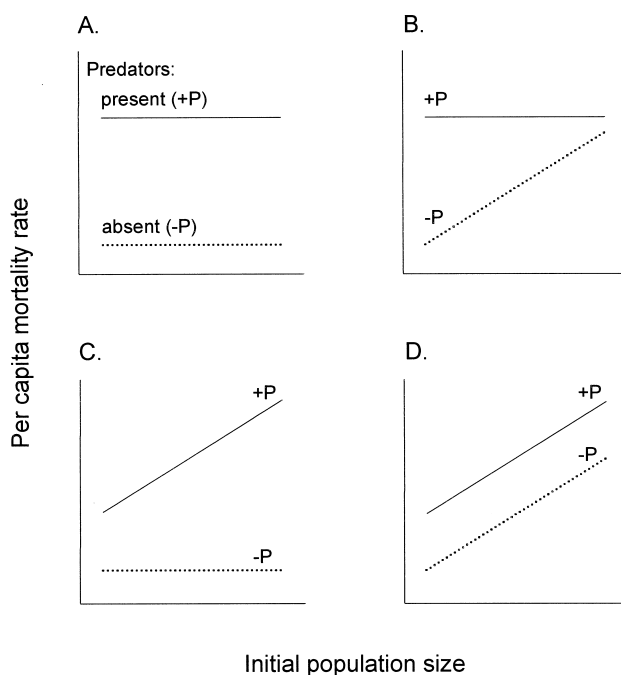

FIGURE 9 Alternative outcomes of a factorial experiment designed to test for both the presence of and the source of density-dependent mortality. (A) Mortality is density independent regardless of the presence or absence of predators that consume the study species, which indicates recruitment limitation (sensu Doherty, 1998). (B) Mortality is density independent in the presence of predators, but density dependent when predators are removed, indicating that predation normally precludes density dependence caused by competition. (C) Mortality is density dependent in the presence of predators, but density independent when predators are removed, indicating that predation alone induces density dependence. (D) Mortality is density dependent regardless of the presence or absence of predators. This fourth outcome could be due to competition causing density dependence regardless of predators, or because competition causes density dependence in the absence of predation whereas predators cause density dependence when they are present.

involved. Experiments alone cannot tell the whole story. Innovative observational methods, including ultrasonic tagging (e.g., Holland *et al.,* 1996) and automated video monitoring (e.g., Carr and Hixon, 1995; Holbrook and Schmitt, 1997), provide means of sampling fishes behavior in the absence of divers. Such approaches will help to identify the behavioral mechanisms driving and regulating population dynamics, including the roles of predation (Section IV,B), competition (both within and between species), and postsettlement movement (Section II,C,2). Carefully executed laboratory studies can also provide a useful supplement for field data (e.g., Anderson, 2001).

2. CREATE A CENTRALIZED DEMOGRAPHIC DATA BASE

Reviewing the literature for this chapter was tedious because there was extreme variation in the way demographic data were presented. Particularly difficult to interpret were indirect indices of recruitment and mortality. Recent strides in interpreting fisheries data, including meta-analyses, have been facilitated by creation of a centralized archive of stock-recruitment data by Myers *et al.* (1995b). Centrally collating and updating demographic data on reef fishes in standardized units and format would greatly facilitate exploration for general patterns.

3. DEVELOP EMPIRICALLY BASED DEMOGRAPHIC MODELS

There is an immense literature regarding population models based on field data [for entry, see Cappuccino and Price (1995)]. Such models allow one to explore the relative importance of different processes in driving and regulating population dynamics, as well as the ability to project population trends. Unfortunately, most models assume closed populations and so are not applicable to many local populations of reef fishes. However, the past decade has seen the development of practical approaches for open populations, including both size- and age-structured models (see Chapter 3, this volume, on the importance of this distinction). Earlier models of coral reef fishes were simple simulations focusing on system-specific questions (e.g., Shulman and Ogden, 1987; Booth, 1995). A spatially explicit analytical model is developed in Chapter 13 of this volume. Another approach is Leslie matrix modeling modified for open populations (e.g., Hughes, 1984, 1990). Pfister (1996) applied such a model to temperate tide pool fishes and demonstrated how one can evaluate the relative importance of recruitment vs. mortality in driving changes in local population size via sensitivity analysis. More appropriate for comparing factors measured in different currencies is elasticity analysis (Heppell *et al.,* 2000). Greater use of empirically based models, especially regarding the dynamics of metapopulations, will help to increase conceptual generalization and develop more explicit hypotheses (Gaines and Lafferty, 1995).

4. EXPAND TAXONOMIC COVERAGE AND DEMOGRAPHIC SCALE OF STUDY

Damselfishes (family Pomacentridae) are disproportionately represented in the studies listed in Tables 1 and 2. Pomacentrids are certainly superb study species, but we believe that the time has come to expand the taxonomic coverage of demographic studies, and especially to include important food fishes (see Chapter 17, this volume). Greater exploration of multispecies density dependence is needed. To truly understand population dynamics, one must examine all demographic rates and their components simultaneously. In particular, greater focus on the demographic consequences of variable growth and fecundity is needed. Ultimately, integrated studies of the entire life cycle, including the pelagic larval phase, would provide a complete picture of population dynamics (Hixon, 1998). Although theory suggests that a metapopulation can persist only if some local populations are regulated (e.g., Hanski *et al.,* 1996), the spatiotemporal pattern of density dependence required for global persistence remains unknown. Although the logistic challenges are immense, combined demographic studies of both the presettlement and postsettlement stages are needed for insight on the dynamics and regulation of metapopulations (Section II,C,1).

Studies of coral reef fishes have contributed much to basic ecology, including concepts later adopted by terrestrial ecologists, such as competitive lotteries (Sale, 1977), recruitment limitation (Doherty, 1981), the storage effect (Chesson, 1983, 1984), diffuse predation (Hixon, 1991), and synergistic interactions (Hixon and Carr, 1997). We believe that, with increased emphasis on understanding population dynamics, reef fish ecologists also have much to contribute conceptually to applied problems in fisheries management and conservation of demersal fishes worldwide.

Acknowledgments

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