

# Population dynamics of coral-reef fishes: Controversial concepts and hypotheses

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**Abstract** Knowledge of processes that drive the local population dynamics of coral-reef fishes is important for managing reef fisheries, and for using these species as models for understanding the ecology of demersal marine fishes in general. However, the reef-fish literature is replete with poorly defined concepts and vague hypotheses regarding the issue of population dynamics. Dichotomous arguments, such as whether or not recruitment drives population dynamics, are misdirected because they fail to incorporate several important concepts. First, changes in local population size are driven by four demographic rates (birth, death, immigration and emigration), all of which must be studied to understand population dynamics. Second, all populations that persist do so because at least one of these demographic rates operates in a density-dependent way that is both sufficiently strong and appropriately time-lagged. Therefore, identifying the source(s) of direct density dependence is critical for understanding the limits to variation in population size (i.e. population regulation). Third, regulation does not imply a simple point equilibrium in population size; density dependence in populations of reef fishes is bound to lie within a field of stochastic variation, and thus be difficult to detect. Since its formal origin in 1981, the ‘recruitment limitation’ hypothesis for explaining local population dynamics in reef fishes has undergone ambiguous changes in definition that threaten its usefulness. ‘Recruitment,’ originally defined as the appearance of newly settled fish on a reef, more recently is often measured months after settlement, thus confounding pre- and post-settlement processes. ‘Limitation,’ which originally referred to recruitment being so low as to preclude local populations from reaching densities where resources were limiting, is more recently defined as an absence of any form of density dependence after settlement. The most effective means of testing whether post-settlement mortality is in fact density-independent is to examine patterns of mortality directly, rather than indirectly by interpreting the shape of the relationship between initial recruit density and subsequent adult density within a cohort (the recruit–adult function). Understanding the population dynamics of coral-reef fishes will require a more equitable focus on all four demographic rates, be they density dependent or not, as well as greater attention to identifying sources of density dependence. Such a pluralistic focus necessitates integrated studies of both pre- and post-settlement processes conducted at multiple spatial and temporal scales. For example, recent evidence suggests that density-dependent predation on new recruits that have settled among reefs at different densities may prove to be an important source of local population regulation, especially via the aggregative response of transient piscivores.

**Key words:** competition, density dependence, emigration, immigration, mortality, population regulation, predation, recruitment.

## INTRODUCTION

Understanding the processes that drive and regulate the local population dynamics of coral-reef fishes is a timely endeavour from at least two perspectives. First, reef fisheries are an important but often imperilled source

of food for many tropical developing nations (Russ 1991; Polunin & Roberts 1996), and knowledge of the mechanisms underlying population dynamics is fundamental to effective management of fisheries (Rothschild 1986; Cushing 1995). Second, because reef fishes are both observable and manipulable *in situ*, they provide excellent model systems for studying the ecology of demersal marine fishes in general (Sale 1991).

Unfortunately, the literature on reef-fish population dynamics is replete with poorly defined concepts and vaguely worded hypotheses that inhibit progress. Indeed, my motivation for this paper stems from going weary of hearing from 'non-fish' ecologists that we reef-fish people don't seem to understand basic population dynamics. My aim is neither to pontificate (indeed, my knowledge of these concepts is basic) nor to list and chastise explicit instances of these problems (although I will provide a few examples for reference). Rather, I simply wish to help stimulate clarification of concepts and hypotheses regarding the population dynamics of reef fishes. In particular, I emphasize that the long-standing, dichotomous controversy regarding whether local population dynamics are driven before recruitment (by the supply of larvae reaching a reef that are competent to settle) or after recruitment (by processes following settlement of larvae to a reef) is misguided. In the context of data and theory from studies of population dynamics in other systems, there are at least two more appropriate issues (Hixon 1991; Jones 1991; Caley *et al.* 1996), which are the topics of this paper. First, what are the relative contributions of different processes in driving the dynamics of local populations? Second, what are the sources of density dependence that regulate these populations?

To illustrate the importance of these questions and the difficulty of answering them, I first review some basic theory of population dynamics as it relates to reef fishes (and most demersal and benthic marine organisms). I then explain why the popular 'recruitment limitation' hypothesis for explaining reef-fish population dynamics requires clarification. Next, I suggest that future studies of population dynamics involve greater integration and breadth of spatial and temporal scales, as well as a more equitable focus on the different demographic rates that drive changes in population size. I close with some speculation on the mechanisms by which post-settlement predation may be an important process inducing local density dependence in reef fishes.

## POPULATION DYNAMICS AND REGULATION IN REEF FISHES

Although the concepts reviewed in this section are well established, knowledge of these general ideas is not always evident in the reef-fish literature. Moreover, even the most basic of these concepts can be deceptively difficult to study at an operational level. Therefore, a brief overview seems relevant. For a recent comprehensive review, I suggest Cappuccino and Price (1995) and Sinclair and Pech (1996), or at a more basic level, Sinclair (1989) and Begon *et al.* (1996). In a somewhat different context, Booth and Brosnan (1995) and Caley *et al.* (1996) also review these concepts as they relate to reef fishes.

### Population structure

It is trivial to define a population as a group of individuals of the same species occupying the same habitat. However, at an operational level, it may be problematic to define the 'group,' the 'habitat,' or possibly even the 'species,' and rarely are these definitions made explicitly. In reef fishes, limited evidence suggests widespread panmixis (Shulman & Bermingham 1995), suggesting the possibility that the entire geographical range of a species may define a single, reproductively closed population. Although data are few (Doherty *et al.* 1995), it seems just as likely that reef fishes form reproductively semi-isolated 'stocks' similar to those documented in intensively studied, commercially exploited species (Cushing 1995).

All studies of reef-fish population dynamics to date have focused on local populations of juveniles and adults at the scale of individual (often small) reefs, even if studied over a large region (e.g. Doherty & Fowler 1994). These local populations, like the reefs they occupy, are patchy in distribution at virtually all spatial scales. As such, these populations are open in the sense that they are connected demographically by dispersing zygotes and larvae. Whether conclusions based on studies of local populations can be scaled-up to explain dynamics at the scale of reproductively closed populations depends on the mechanisms driving population change. Obviously, studies at multiple spatial scales conducted over periods that exceed the generation time of the study species provide the greatest insight on population dynamics.

### Demographic rates

Local population dynamics are driven by four demographic rates: birth, death, immigration and emigration. Without knowledge of all four per capita rates, the mechanisms underlying changes in population size simply cannot be elucidated. Although this assertion is true by definition, it is often overlooked in studies claiming to provide insight on the causes of population dynamics in reef fishes. Unfortunately, measuring and even defining the four demographic rates is no easy task.

In the context of larval dispersal between local populations, the definition of 'birth' in reef fishes is problematical. At the scale of stocks or closed populations, births obviously occur when eggs hatch into larvae. However, at the scale of locally open populations (again, the scale at which we normally work), 'births' occur when larvae settle from the oceanic phase to the demersal juvenile phase on a particular reef, a process that is typically called 'recruitment' (Doherty & Williams 1988). Of course, any mortality or movement that occurs between the time fish actually settle on a reef and the time they are counted can greatly affect one's estimate of recruitment (Booth 1991). This

operational problem is especially relevant when considering the concept of 'recruitment limitation' (see below).

The importance of post-settlement movements (immigration and emigration) relative to natality and mortality in driving local dynamics depends upon both the spatial structure of the population and the spatial scale of the study. In reef fishes, the less isolated the local population being studied, the more likely it is that movements between populations will affect dynamics. Given that many studies are at the scale of patch reefs separated by only a few metres of sand, the common assumption that such movements are negligible is questionable. Fortunately, recent developments in micro-tagging techniques should result in greater attention to the role of immigration and emigration (Buckley *et al.* 1994; Beukers *et al.* 1995), and will help distinguish between emigration and mortality.

Importantly, although our knowledge of recruitment patterns in reef fishes has increased tremendously during the past decade (reviews by Doherty & Williams 1988; Doherty 1991), relatively little attention has been paid to the other demographic rates.

### Regulation

By definition, all populations that persist indefinitely (i.e. neither increase without limit nor go extinct) do so because they are regulated by density-dependent processes (Hassell 1986; Murdoch 1994; Turchin 1995; Chesson 1996). That is, as population size increases, at least one of the following responses occurs in a way that bounds population fluctuations between zero and infinity: the per capita birth (i.e. recruitment) or immigration rate decreases, or the per capita death or emigration rate increases. Although direct density dependence is necessary for population regulation, it is not sufficient. For regulation to occur, density dependence through time must be sufficiently strong to counteract the disruptive effects of varying density-independent or inversely density-dependent factors, and the time lag with which density dependence operates must be short enough to prevent unstable cycling (Turchin 1995).

What defines 'sufficiently strong' density dependence? For local populations of reef fishes, this question is answered most easily by considering post-settlement mortality of single cohorts. Why mortality? Assuming emigration equals immigration, mortality is the most likely source of density dependence because recruitment (i.e. the birth rate) is known to be highly variable at all spatial and temporal scales investigated to date (Doherty & Williams 1988; Doherty 1991), and often appears to be density independent (even though, in a purely arithmetic sense, the local per capita recruitment rate may be considered density dependent as new settlers accumulate on a reef; Caley *et al.* 1996). Note

that the assumption of density-independent recruitment is not always reasonable because previously settled individuals in some highly social damselfishes may have either positive or negative effects on subsequent settlement (e.g. Sweatman 1985). Why single cohorts? This simplifying assumption allows one to illustrate relevant concepts without having to consider the cumulative effects of the dynamics and interactions of sequential cohorts on total population size (see fig. 2 in Caley *et al.* 1996).

Given these assumptions and a range of recruit densities through time or space, the mortality rate between recruitment and adulthood may be a function of both density-dependent and density-independent factors (Fig. 1a). Depending upon the strength of both kinds of factors, this mortality function is defined by its position and slope (Fig. 1b). Strong regulation occurs when density-dependent mortality results in a recruit-adult function that becomes level ('compensation') or declining ('overcompensation') across the natural range of recruit densities (Fig. 1c).

Because local populations of reef fishes are notoriously dynamic, often in ways that appear to be random, there is a tendency in the literature to assume that these populations are not regulated. It is important to realize that only the simplest heuristic models of population regulation predict a static point equilibrium. Indeed, the most explicit definition of population regulation I have found is the presence of 'a long-term stationary probability distribution of population sizes' (Dennis & Taper 1994; Turchin 1995), which is more a result than a process. Essentially, a population can undergo large stochastic fluctuations and still be sufficiently regulated that extinction does not occur. In other words, the 'equilibrium' imposed by regulation can have a strong stochastic component, so that the 'equilibrium is not a point but a cloud of points' (Wolda 1989). Therefore, tremendous temporal and spatial variance in reef-fish population sizes, or any of their demographic rates, does not mean that these populations are unregulated. With these concepts in mind, the key question shifts from 'are populations regulated?' to 'how are populations regulated?'

### Metapopulations

The fact that juvenile and adult reef fishes are distributed in locally open populations linked by larval dispersal raises the question of whether regulation of these populations can be modelled effectively as 'metapopulations.' Levins (1970) originally defined a metapopulation as a 'population of populations' that persists in a balance between stochastic local extinction and establishment of new local populations (Hanski & Gilpin 1991). Conceptually, the persistence of a metapopulation cannot be explained by regulation within local populations. However, the stability of a metapopulation does rely

on some density dependence within local populations, as well as sufficient migration between local populations and sufficient stochasticity to keep local population dynamics unsynchronized (Walde 1995).

Unfortunately, most metapopulation models were derived for terrestrial species (especially insects), and may be irrelevant for studying reef fishes. Hanski

and Kuussaari (1995) list four conditions for meta-population-level regulation. It seems that one (perhaps two) of these conditions may not be met by reef fishes: (i) within discrete habitat patches, there are local breeding populations that are usually reproductively closed, with only rare dispersal between populations (unlike reef fishes, where larval dispersal between patches is the norm); and (ii) no single local population is so large that its expected lifetime is longer than that of the remainder of the metapopulation (perhaps unlike reef fishes, where core stocks are likely to persist as long as the species itself and perhaps longer than peripheral populations). The other two conditions are met by reef fishes: (iii) the habitat patches are not too isolated to prevent recolonization; and (iv) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely. These conditions are similar to those reviewed by Harrison (1991) and Doak and Mills (1994), which also are not particularly relevant to reef fishes: (i) local populations are semi-closed (whereas local populations of reef fishes are generally considered to be widely open); (ii) all local populations are regularly subject to extinction (whereas large local reef-fish populations may be relatively persistent); and (iii) local populations are founded by infrequent dispersal events (whereas larval dispersal is the norm in reef fish).

The few explicitly marine metapopulation models (e.g. Roughgarden & Iwasa 1986) are structured mostly for sessile invertebrates by assuming, for example, potentially strong competition for space,

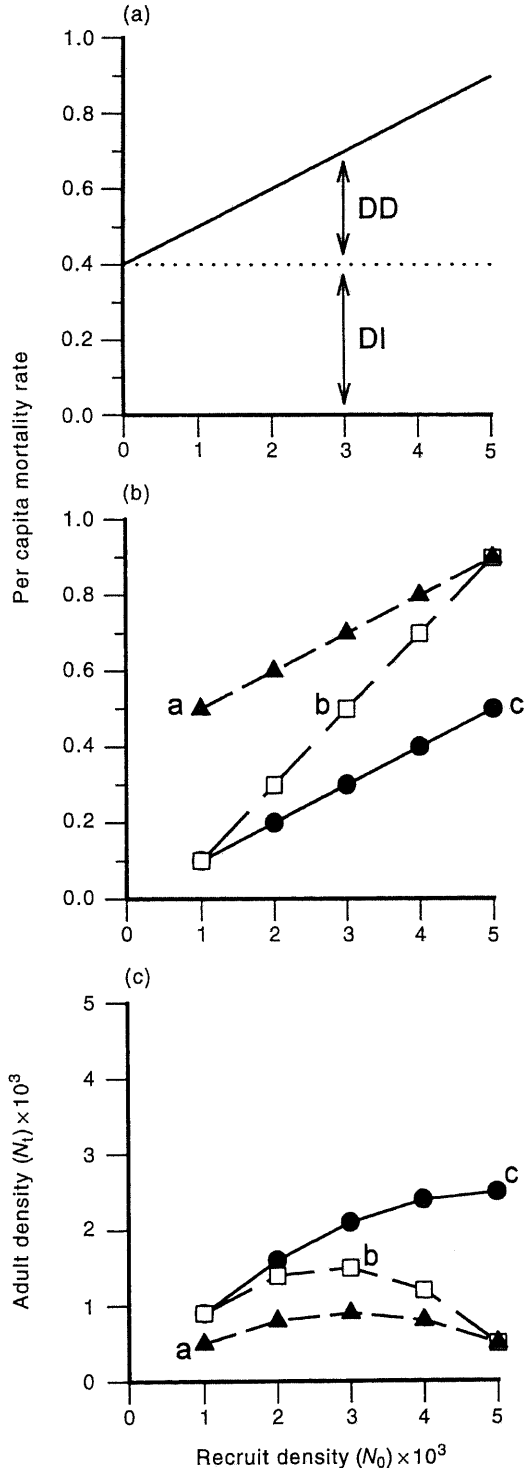


Fig. 1. (a) Linear mortality function showing that, at any given recruit density, the per capita death rate between recruitment and the time of adulthood is the sum of density-independent (*DI*) and density-dependent (*DD*) factors. Note that the position (i.e. y-intercept) of the function is determined by the level of density-independent mortality, that the slope indicates the strength of density-dependent mortality, and that the given function is linear only for simplicity (i.e. in nature, it may be curvilinear). (b). Three mortality functions that differ in position (curve *a* vs *c*) or slope (curve *b* vs *c*). (c) Subsequent recruit-adult functions calculated from the three mortality functions. Curve *a* shows strong regulation, with compensation occurring over virtually all recruit densities (i.e. adult density is nearly constant over the given range of recruit densities). Curve *b* shows 'overcompensation' at high recruit densities (i.e. adult density decreases with increasing recruit density), whereas curve *c* shows 'undercompensation' at low recruit densities (i.e. adult density increases with recruit density). Therefore, mortality that is linearly density-dependent can produce recruit-adult functions that are nearly flat or weakly unimodal (curve *a*), strongly unimodal (curve *b*), or decelerating curvilinear (curve *c*) over a given range of recruitment. In these simulations, the recruit-adult functions were calculated from the mortality functions by multiplying each initial recruit density ( $N_0$ , arbitrarily spanning 1000–5000 fish) times its per capita survival rate (i.e.  $1 - \text{mortality rate}$ ) to give subsequent adult density ( $N_t$ ).

which is not broadly evident in reef fishes (but see Chesson 1985). Moreover, most current metapopulation models are mechanistically not very different from local-population models, in that they incorporate some form of density dependence (Murdoch 1994). Indeed, model metapopulations with purely density-independent dynamics take the same random walk to extinction as similarly modelled local populations (Chesson 1981). Thus, it seems clear that local dynamics are important for understanding population variation in reef fishes; after all, it is at the local scale where individuals interact. In any event, more explicit models of reef-fish population dynamics are needed (see Gaines & Lafferty 1995).

### WHY THE 'RECRUITMENT LIMITATION' HYPOTHESIS NEEDS CLARIFICATION

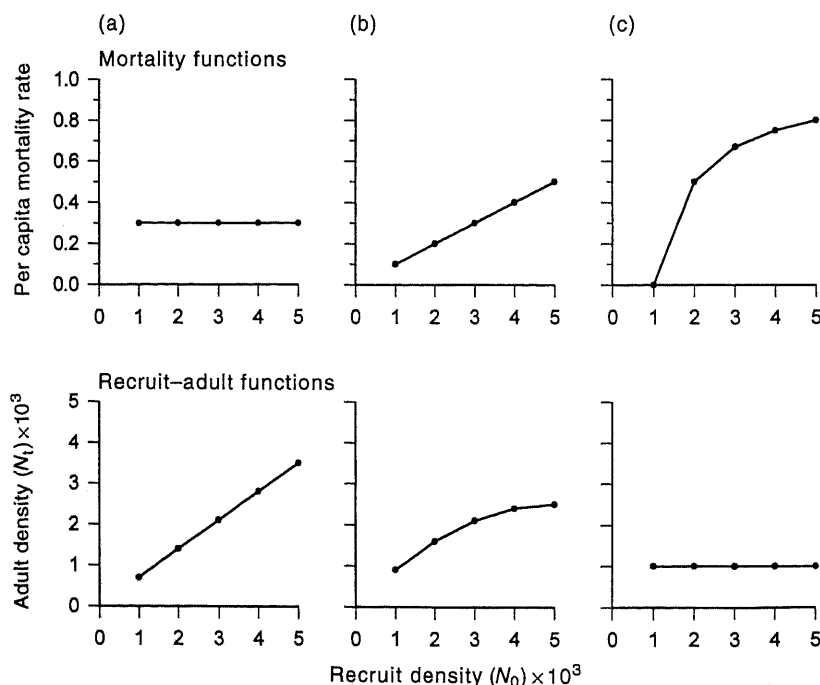
When originally formalized by Peter Doherty in 1981, the idea that recruitment limits local population size was truly revolutionary. The prevailing idea at the time was that reef-fish populations are saturated with larvae, such that only post-settlement processes (especially competition) determine population size. Doherty (1981) proposed that larval supply is insufficient to saturate local populations (thus precluding post-settlement competition), and suggested that variation in larval recruitment (then equated with settlement) is the major process driving local population dynamics.

The major predictions of the recruitment limitation

hypothesis are: (i) variation in recruitment should be reflected in subsequent variation in local population size; and (ii) post-recruitment mortality should be density-independent. Regarding the first prediction, simulations of locally open reef-fish populations by Warner and Hughes (1988) have shown that correlations between recruitment and subsequent population size are equivocal in terms of inferring the mechanisms driving population dynamics (Caley *et al.* 1996 discuss this problem in further detail).

Regarding the second prediction, examining subsequent adult density as a function of initial recruit density (the recruit-adult function) can be a misleading way to determine whether post-settlement mortality is density-independent. While it is true that a linearly increasing recruit-adult function demonstrates density-independent mortality (Fig. 2a), the alternative is not simply a flat line of zero slope (Fig. 2c), which is a special kind of strong density dependence ('exact compensation'; see Sinclair & Pech 1996). More generally, a decelerating curvilinear (or even unimodal, Fig. 1) recruit-adult function indicates density dependence (Fig. 2b). Importantly, the ascending part of a density-dependent recruit-adult function (Fig. 2b) can be quite similar in shape to a density-independent recruit-adult function (Fig. 2a). Natural variation in real data can make it extremely difficult to determine which kind of curve (curvilinear or linear) better fits a given data set (see, for example, figs 2c & 5 in Doherty & Fowler 1994). Statistically, it is easier to determine whether a mortality function has a positive slope (indicating direct

**Fig. 2.** Simple simulations (see Fig. 1 for explanation) showing the difficulty of detecting density-dependent mortality within a cohort indirectly. (a) Density independence (recruitment limitation); (b) density dependence (linear); and (c) 'exactly compensating' density dependence. There are two features shown in this figure. First, the alternative to (a) recruitment limitation or density-independent mortality is not simply (c) density-dependent mortality expressed as a flat recruit-adult function (or 'exact compensation'; *sensu* Sinclair & Pech 1996), but more generally (b) density dependence expressed as a curvilinear recruit-adult function (as in Fig. 1c). Second, the recruit-adult function has a positive slope at lower recruit densities in the case of both (a) density-independent and (b) linear density-dependent mortality. Variation in real data would tend to obscure the differences between these two recruit-adult curves, so that observing the original mortality functions would be necessary to detect density dependence. Modified after Caley *et al.* (1996).



density dependence) or a slope of zero (indicating density independence). Therefore, as illustrated by the two mortality functions in Fig. 2a,b, the most explicit test for density-dependent mortality is to examine directly the per capita mortality rate as a function of recruit density (Caley *et al.* 1996), which also requires monitoring local post-settlement immigration and emigration. Such direct evidence for early post-settlement population regulation in coral-reef fishes has emerged only recently (e.g. Tupper & Hunte 1994; Booth 1995; Forrester 1995; Hixon & Carr 1997; Sano 1997; Jones & Hixon unpubl. data).

Beyond difficulty with the predictions of the hypothesis, even the meaning of 'recruitment limitation' is unclear. Since the early 1980s, the definitions of both 'recruitment' and 'limitation' have undergone rather vague and ambiguous changes. 'Recruitment' was originally equated with larval settlement from the plankton onto reefs (Doherty 1981; Doherty & Williams 1988). Subsequently, the time of recruitment was extended to months following settlement, both explicitly (e.g. 'secondary recruitment limitation' of Victor 1986) and implicitly (e.g. the sampling schedule of Doherty & Fowler 1994). The problem is that, the closer the time of recruitment is defined operationally relative to the time of sexual maturity (i.e. reaching adulthood), the more linear will be the relationship between recruit density and subsequent adult density, thus biasing the observed recruit-adult function in favour of recruitment limitation (see previous discussion of Fig. 2). Incidentally, this is one reason why fisheries biologists have long defined recruitment as occurring when subadult or adult fish enter the harvestable stock, and thus have assumed a linear recruit-stock relationship (analogous to the recruit-adult functions illustrated in Fig. 1c). Fisheries biology therefore focuses on understanding the reciprocal stock-recruit relationship (recruitment as a function of spawning stock), which, because of the relatively late age at which fish 'recruit' to the fishery, incorporates processes typically spanning most of the life cycle of the fish (see Rothschild 1986). (Note also that traditional fisheries models consider stocks as closed populations, and therefore are not generally relevant for understanding locally open population dynamics.)

In summary, if 'recruitment limitation' predicts that larval supply to a reef is the major factor driving local population dynamics, then it is imperative that 'recruitment' be defined operationally as occurring as close to the time of larval settlement as logistically possible.

The definition of 'limitation' has also evolved. As indicated above, Doherty (1981) suggested that larval supply could limit local population sizes below levels where competition would occur. Doherty and Williams (1988) and Doherty and Fowler (1994) later expanded this definition to include the idea that limited larval supply resulted in post-settlement mortality being density

independent. Thus, the original definition of 'recruitment limitation' predicted that post-settlement competition did not drive local population dynamics, whereas the latest definition predicts that no source of population regulation operates after settlement. There is an important distinction because density-dependent mortality can be caused by a variety of processes besides competition (such as predation; see below). Given that any population that persists must be regulated by density-dependent factors, asserting that post-settlement mortality is always density independent is tantamount to declaring that population regulation occurs only during the pelagic larval phase, an assertion with little supporting data from marine fishes in general (Houde 1987; Bailey & Houde 1989; Heath 1992).

The bottom line is that we now face a situation in which each author will have to identify which definition of 'recruitment limitation' is being addressed. Recruitment limitation has become a vague hypothesis with unclear predictions, making it difficult to test rigorously. Caley *et al.* (1996) go so far as to suggest that, because the input rate (recruitment) to all populations obviously sets a limit to how large a population can become, 'recruitment limitation' is merely a truism. I propose that if the recruitment limitation hypothesis can be stated explicitly and its predictions deduced logically, then it is still worthy of serious consideration.

## SUGGESTIONS FOR FUTURE STUDIES

Given that understanding local population dynamics requires knowledge of all four demographic rates, focusing on any single rate cannot answer the question of what determines local population size in reef fishes. Clearly, a more pluralistic approach is needed. In my opinion, the focus of future studies should be directed toward mechanistic answers to two questions: (i) What processes (be they density-dependent or not) affect the four demographic rates? and (ii) What are the sources of density dependence that regulate population size?

Of course, a major problem in addressing these questions across the entire generation time of a reef fish is that one would need to study both the pre-settlement pelagic phase and the post-settlement reef phase (Fig. 3). Challenges of understanding population dynamics during the pelagic larval phase seem presently overwhelming (Leis 1991; Heath 1992), and include processes affecting 'births' via spawners and their gametes (Robertson 1991), larval dispersal in and out of hospitable water masses (Shanks 1995), and losses due to both mortality (Houde 1987; Bailey & Houde 1989) and settlement onto the reef (Victor 1991).

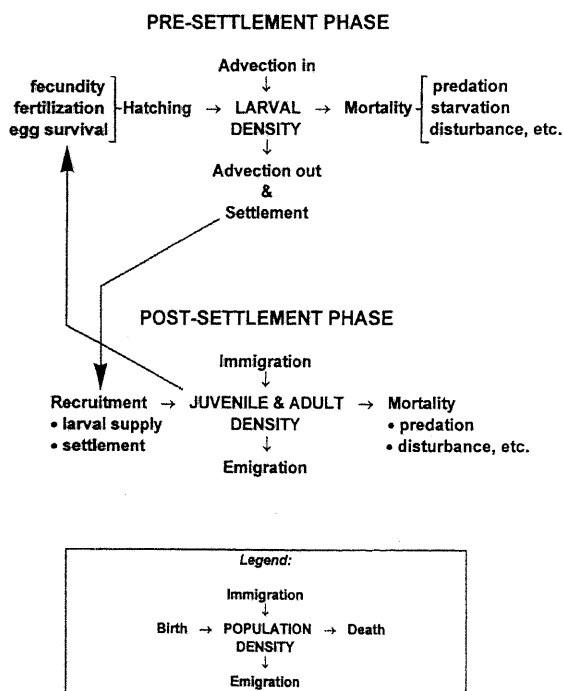
Although the post-settlement phase is amenable to experimentation, there is a need to integrate small-scale experiments with large-scale observations, so that the

issue of scale-dependence can be resolved (Doherty 1991). It seems clear that both approaches are essential to understand population dynamics because small-scale studies can provide insight on the behavioural mechanisms of regulation, whereas large-scale studies document broad patterns of population change (Williams 1991). One example of the importance of integrating studies at different scales comes from the insect literature. Hassell *et al.* (1987) found that, for a population of viburnum whitefly (*Aleurotrachelus jelinekii*), density dependence was detectable only at the small scale of individual leaves (analogous to local reefs in fishes), and not at the large scale of an entire bush (analogous to a regional cluster of reefs), because within-leaf dynamics were out of phase among leaves. As noted by Stewart-Oaten and Murdoch (1990), regulation requires that such spatial density dependence

(among patches within a generation) ultimately translates to temporal density dependence (within patches between generations).

At the scale of local reefs, there is a pressing need to incorporate detailed analyses of recruitment with studies of post-settlement mortality, immigration and emigration (Hixon 1991; Jones 1991). Knowledge of the rate at which fish move between reefs is critical to accurately assess settlement and mortality (Robertson 1988; Lewis 1997). Although the greatest source of mortality may be predation (Hixon 1991), other potentially important agents include physical disturbance (Jones 1991) and parasitism (Adlard & Lester 1994). Given that there seems to be little evidence that competition for food causes density-dependent mortality in reef fishes directly (Jones 1991), a locally important source of post-settlement population regulation (and/or density-independent limitation) may be predation (Hixon 1991; Caley 1993; Carr & Hixon 1995; Hixon & Carr 1997). Note that the effects of predation may manifest themselves indirectly as competition for prey refuges (Hixon 1991; Hixon & Beets 1993; Caley & St John 1996).

Predators may directly induce density-dependent mortality in their prey by four mechanisms (Solomon 1949; Murdoch & Oaten 1975; Taylor 1984), none of which have been explored thoroughly in reef fishes. First, the population size of predators may increase disproportionately in response to increases in prey density, and vice versa (a regulating numerical response). In reef fishes, a similar local phenomenon (but not a 'response' per se) could occur if the larvae of both predators and prey tend to co-occur in the plankton and settle together, such that more predators settle where more prey settle (see Caley 1995a,b). Otherwise, it seems unlikely that a regulating numerical response would be possible, because the vagaries of larval dispersal would preclude a positive feedback between local prey density on a reef and subsequent predator recruitment. Second, the local distribution of predators may shift in response to local prey density, thereby inducing density dependence (an aggregative response; *sensu* Hassell & May 1974). Given that piscivorous reef fishes often range more widely than their prey (presumably due to their relatively large size), this mechanism seems reasonable, especially for transient predators that regularly swim between reefs, such as schooling carangids (Holland *et al.* 1996). For example, J. P. Beets and I have observed local abundance patterns in reef fishes consistent with an aggregative response (Fig. 4), as have J. S. Beukers (pers. comm.), and G. E. Forrester (pers. comm.). Additionally, Hixon and Carr (1997) documented that schooling carangids spent more time on reefs with high prey densities than those with fewer prey. Third, predators may change their individual consumption rates in response to changes in prey density in a way that induces density dependence (a type III functional response; *sensu*

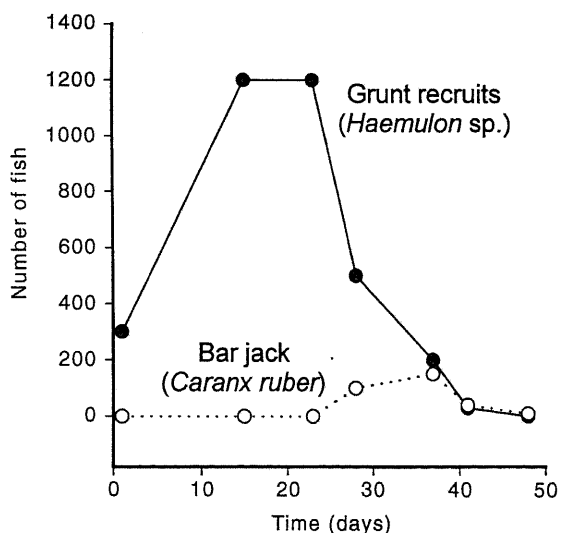


**Fig. 3.** The two phases of the life cycle of a typical broadcast-spawning reef fish, showing that both phases are subject to processes analogous to the four general demographic rates of birth, death, immigration, and emigration. Arrows between the upper and lower figure show the linkages between the life-cycle phases: the transition at settlement represents a loss from the pelagic phase and a gain to the demersal phase, and of course, demersal adults are the source of gametes for the pelagic phase. All the processes listed (among others) may drive population dynamics, and some subset induces population regulation. Note that competition (including starvation) is not included as a post-settlement mortality process because there is little evidence that competition for food is so severe in nature as to cause death directly (Jones 1991). However, interactions between competition, growth rate, refuge space, and predation are certainly possible and likely (Hixon 1991).

**Table 1.** Alternative outcomes and interpretation of a factorial experiment testing whether post-settlement mortality is density-dependent in a local reef-fish population, both in the natural presence (unmanipulated) and in the experimental absence of piscivores. Each of the four cells describes the processes that drive unmanipulated local population dynamics for each outcome, following the assumptions given in the text

		Density dependence in absence of piscivores?	
		Yes	No
Density dependence in presence of piscivores?	Yes	<b>Competition</b> (overriding all other processes) <i>or</i> <b>Predation</b> in presence and <b>Competition</b> in absence of piscivores (need more data)	<b>Predation</b> (possibly manifested as competition for prey refuges)
	No	<b>Competition</b> (probably for food)	<b>Recruitment limitation</b>

The definition of 'recruitment limitation' here is that mortality is density-independent under all circumstances.



**Fig. 4.** Local population dynamics consistent with an aggregative response by schooling predatory jacks to a settlement pulse of grunts on an artificial reef off St Thomas, US Virgin Islands during the summer of 1993 (see Hixon & Beets 1993 for reef design with 24 large holes). Over the first 23 days of the observation period, there were no jacks seen near the reef as the settlement abundance of new grunt recruits rose to over 1000 individuals. Between day 23 and 37, grunt abundance dropped precipitously as the number of jacks near the reef rose to 150 individuals, and jacks were seen eating grunts. Subsequently, the abundance of both species declined as more grunts disappeared and the jacks dispersed.

Holling 1959). Finally, predators may grow more rapidly (and survive better) where prey are more abundant, thereby enhancing a regulating functional response (a developmental response; *sensu* Murdoch 1971). At present, I know of no data on these latter mechanisms in coral-reef fishes.

In my opinion, the most effective means of distinguishing what drives local population dynamics is to test for post-settlement density-dependent mortality in both the natural presence and experimental absence of

piscivores. Such an experiment makes three assumptions, which should be tested in their own right, namely: (i) there is no inverse density dependence, (ii) post-settlement immigration and emigration are equivalent (thereby cancelling each other), and (iii) mortality sources besides predation and competition are not important. The experimental design would be orthogonal: vary the density of new settlers among reefs within the range of natural variation, and vary the presence and absence of predators at each settlement density. Table 1 shows the alternative outcomes and interpretations of such a factorial experiment. Recently, Hixon and Carr (1997) completed such experiments in the Bahamas, showing that predators alone induced local density dependence within the first month post-settlement in the damselfish *Chromis cyanea*.

In summary, I encourage future studies of reef-fish population dynamics to, first, focus on all four demographic rates, second, examine both pre-settlement and post-settlement processes, and third, integrate short-term, small-scale experimental studies with long-term, large-scale observational studies. Although difficult to implement, such pluralistic approaches are essential for understanding what drives changes in the population sizes of marine fishes.

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