

PLENARY ADDRESS

Population dynamics of coral reef fishes: Let's get pluralistic!

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Understanding the processes that drive the population dynamics of coral-reef fishes is a timely endeavor from at least two perspectives. First, reef fisheries are obviously an important and often imperiled source of food for many tropical developing nations (Russ 1991), and knowledge of population dynamics is fundamental to effective management of fisheries (Rothschild 1986). Second, because they are both observable and manipulable in situ, reef fishes provide excellent model systems for studying the ecology of demersal marine fishes in general (Sale 1991). Given these perspectives, I have great expectations for this workshop because I see an opportunity to resolve some fundamental issues. These issues comprise a long-standing controversy in the literature regarding the relative importance of recruitment variation in driving local population dynamics (e.g., Doherty 1991 vs. Jones 1991). The prevailing question seems to be dichotomous: Are population dynamics of reef fishes determined before recruitment (by larval supply reaching a reef) or after recruitment (by processes following larval settlement)? The goal of this talk is to convince you that there are more appropriate questions, such as: When and where does population regulation occur? What are the relative contributions of different processes in regulating reef-fish populations? To illustrate the importance of these questions, I will: (1) review some basic theory of population dynamics and regulation as it relates to reef fishes (and most demersal and benthic marine organisms, for that matter); (2) explain why the popular 'recruitment limitation' hypothesis requires clarification; and (3) suggest that future studies of reef-fish population dynamics involve greater integration and breadth of both spatial and temporal scales, as well as more equitable focus on all the demographic rates that drive changes in population size.

Population regulation in reef fishes

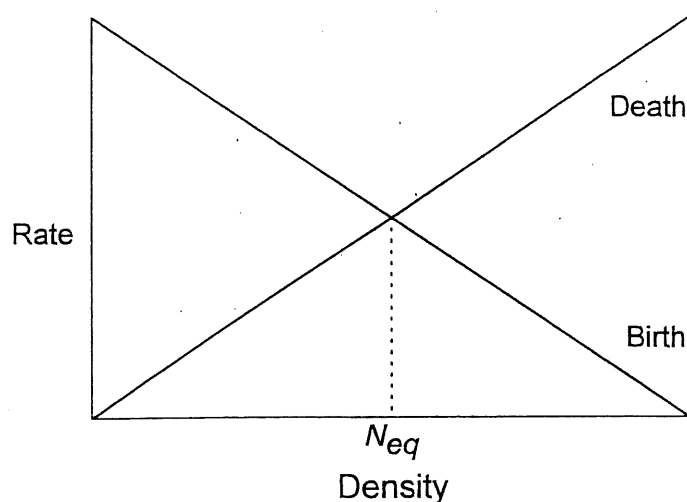
All population dynamics are driven by four demographic rates: birth, death, immigration, and emigration. By definition, all populations that persist indefinitely do so because they are regulated by (direct) density dependence, such that, as population size increases, the per capita birth and/or immigration rates decrease and/or the death and/or emigration rates increase (Hassell 1986, Murdoch 1994, Cappucino and Price 1995). Because of the patchiness of reef habitats and the bi-partite life cycle of most reef fishes (i.e., pelagic larvae followed by site-attached juveniles and adults), 'births' in locally open populations occur by larval recruitment (Sale 1991). Because

these phenomena can decouple local reproduction from subsequent recruitment, as well as introduce tremendous variation in recruitment (due to the vicissitudes of larval life), there is far too much variation in many reef fish populations to think in terms of regulation inducing a point equilibrium predicted by classic population models (Fig. 1A). On the contrary, locally open marine population dynamics are likely to be 'density-vague' (Strong 1986) in the sense that regulation produces bounded fluctuations in population size that may appear random and nonequilibrium (Fig. 1B).

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. Indeed, examining subsequent adult density as a function of initial recruit density (the recruit-adult function) can be a misleading way to test for density-dependent mortality. Although a linear recruit-adult function demonstrates density-independent mortality, whereas a flattening curvilinear function indicates density dependence, natural variation in real data can make it difficult to determine which kind of curve better fits a given data set (see, e.g., Figs. 2C and 5 of Doherty and Fowler 1994). Rather, the most direct test for density-dependent mortality is to examine directly the per capita mortality rate as a function of recruit density (Caley et al. 1996). Such evidence for early postsettlement population regulation in coral-reef fishes has appeared only recently (e.g., Tupper and Hunte 1994, Booth 1995, Forrester 1995).

Not only are simple population models inappropriate for reef fishes, but many existing metapopulation models are also largely irrelevant. Although it is true that reef fishes provide classic examples of metapopulations, in the sense of a collection of local populations connected by dispersal (Levins 1969), most terrestrial metapopulation models (reviewed by Harrison 1991 and Doak and Mills 1994) assume that: (1) local populations are semi-closed (whereas local populations of reef fishes are open); (2) all local populations are regularly subject to extinction (whereas local reef fish populations are relatively persistent); and (3) local populations are founded by infrequent dispersal events (whereas larval dispersal is the norm in reef fish). Moreover, the few explicitly marine metapopulation models (e.g., Roughgarden and Iwasa 1986) are structured mostly for sessile invertebrates by assuming, for example, potential competition for space. In any case, existing metapopulation models are mechanistically not much different from local-population models in that they incorporate some form of density dependence (Murdoch 1994), and purely density-independent model metapopulations take the same random walk to extinction as similarly modeled local populations (Chesson 1981). Thus, it seems clear that local dynamics are important for understanding population variation in reef fishes, and in any event, more explicit models of reef fish population dynamics are needed (see Gaines and Lafferty 1995).

A. Density-Dependent Point Equilibrium



B. Density-Vague "Cloud of Points" Equilibrium

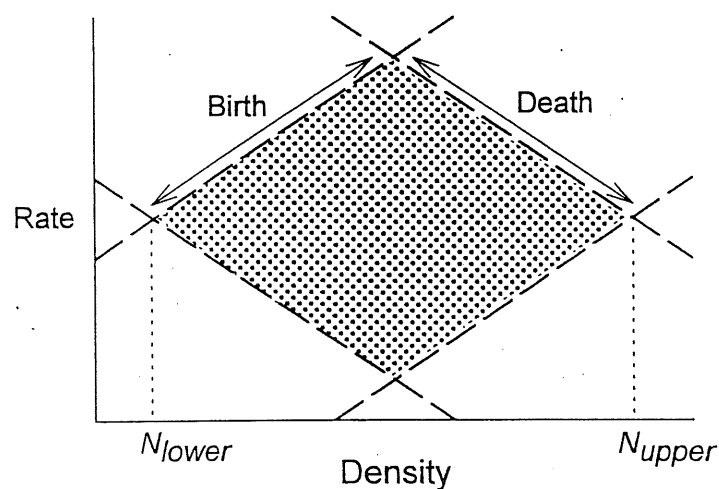


Figure 1. A. Example of a simple point equilibrium in population size (N_{eq}) caused by both the per capita birth rate and death rate being density-dependent (immigration here equals emigration). B. 'Density-vague' population dynamics, in which the position and slope of the curves for both the birth rate and the death rate vary tremendously through time, spanning the stippled space. Although vague, population regulation still exists in the sense that fluctuations in population size are bounded between N_{lower} and N_{upper} (i.e., the population neither goes extinct nor heads toward infinity). Case B is more likely to reflect population regulation in reef fishes than case A.

Why the 'recruitment limitation' hypothesis needs clarification

When formalized by Peter Doherty in 1981, the idea of recruitment limitation was truly revolutionary because the prevailing idea at the time was that reef fish populations are saturated with larvae, i.e., that only postsettlement processes drive population dynamics. Doherty (1981) proposed that larval supply is insufficient to saturate local populations, thus precluding postsettlement competition, and that variation in larval recruitment is the major process driving local population dynamics.

Since 1981, a problem has developed with this hypothesis in that the definitions of both 'recruitment' and 'limitation' have undergone vague and ambiguous changes, which have obfuscated the meaning of 'recruitment limitation'. 'Recruitment' was originally equated with larval settlement from the plankton onto reefs (Doherty 1981, Doherty and Williams 1988). Subsequently, the time of recruitment was extended to months following settlement, both explicitly (e.g., Victor's 1986 'secondary recruitment limitation'), and implicitly (e.g., Doherty and Fowler's 1994 sampling schedule). The problem is that, the closer the time of recruitment is defined operationally relative to the time of sexual maturity, the more obvious and uninteresting will be the correlation between recruit density and subsequent adult density. (This is one reason why fishery biologists have long defined recruitment as occurring when subadult or adult fish enter the harvestable stock, thus assuming a linear recruit-stock relationship. Fishery biology thus focuses on the stock-recruit relationship, which covers most of the life span of the fish [see Rothschild 1986].) 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 postsettlement mortality being density-independent. There is an important distinction here because density-dependent mortality can be caused by a variety of processes--not just competition. Thus, the original definition of 'recruitment limitation' predicted that postsettlement competition did not drive local population dynamics, whereas the latest definition predicts that no source of population regulation operates after settlement.

The bottom line is that we are now in a situation where each author will have to identify which definition of 'recruitment limitation' he or she is addressing--'recruitment limitation' has become a vague and ambiguous concept.

Suggestions for future studies

Given that understanding population dynamics requires knowledge of all four demographic rates, only a pluralistic approach can resolve the controversy on the relative importance of recruitment. It seems to me that the focus should be directed toward mechanistic answers to two questions: When and where are the four demographic rates density-dependent? What processes affect the four rates? Certainly, focusing on any one demographic rate to the exclusion of the others provides little insight.

Of course, a major problem in addressing these questions over the entire life span of a reef fish is that one would need to study both the presettlement pelagic phase and the postsettlement reef phase (Fig. 2). Challenges of understanding population dynamics during the pelagic larval phase are presently overwhelming (Leis 1991), and include the processes affecting births via spawners and their gametes (Robertson 1991), larval dispersal in and out of viable water masses (Shanks 1995), and losses due to both mortality (Houde 1987, Bailey and Houde 1989) and settlement onto the reef (Victor 1991).

Although the postsettlement 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 understanding population dynamics because small-scale studies can provide insight on the behavioral mechanisms of regulation (e.g., predation [see Hixon 1991]), whereas large-scale studies document broad patterns of population change (see Williams 1991). An example of the importance of integrating studies of different scales comes from the insect literature. Hassell et al. (1987) found that, for a population of viburnum whitefly, 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).

In summary, I encourage future studies of reef-fish population dynamics to: (1) focus on all four demographic rates, (2) examine both presettlement and postsettlement processes, and (3) integrate short-term, small-scale experimental studies with long-term, large-scale observational studies. I believe that such pluralistic approaches, although difficult to implement, will be the key for understanding what drives changes in the population sizes of marine fishes.

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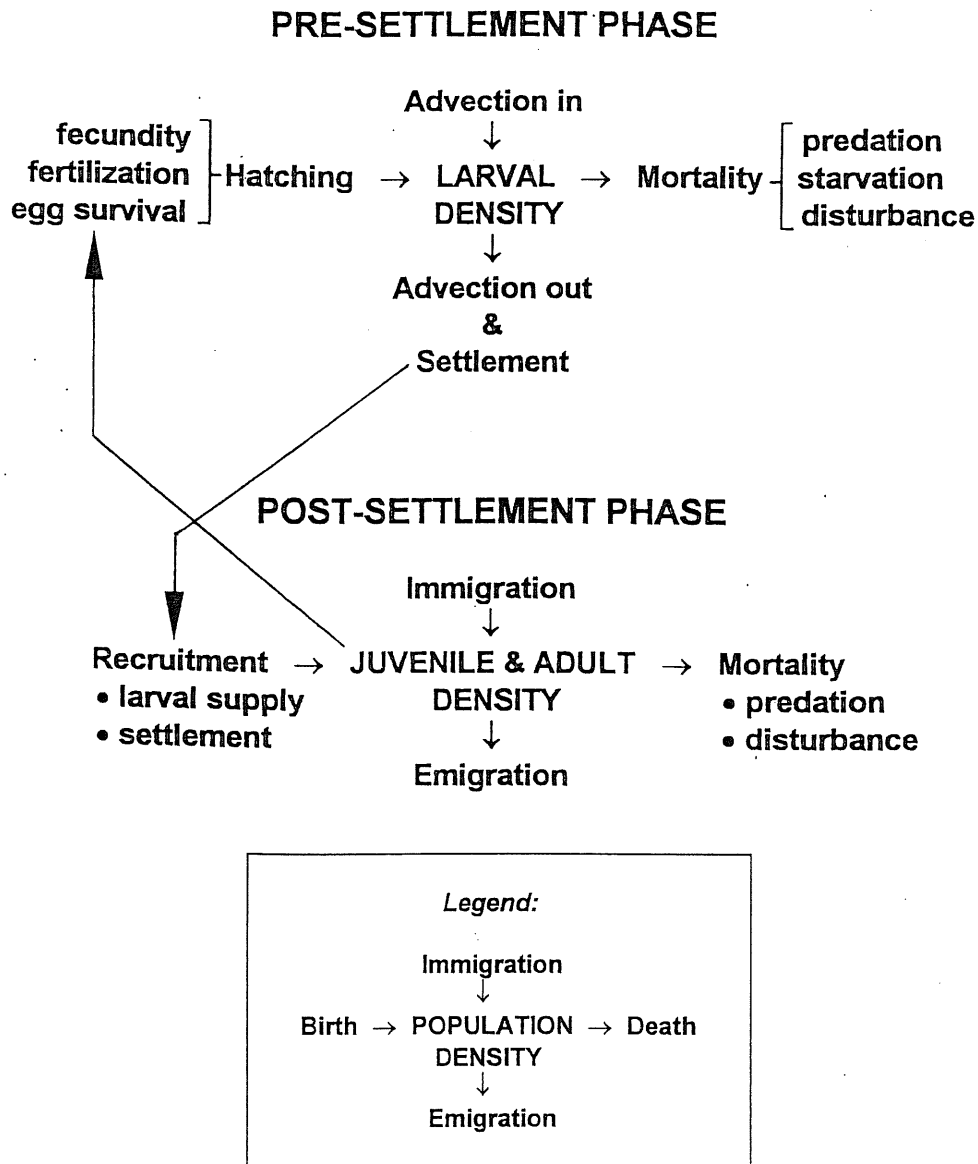


Figure 2. Two phases of the life cycle of a typical reef fish, showing that both phases are subject to processes analogous to the four general demographic rates of birth, death, immigration, and emigration. All of these (and other) processes drive population dynamics and some subset induces population regulation.

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