

# *Simulating Large-Scale Population Dynamics Using Small-Scale Data*

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## I. Introduction

### A. A Brief Overview—What Is the Focus of This Chapter?

Population ecology has been one of the main foci of research on reef fishes since the early 1980s. This research has generated considerable controversy over which processes are primarily responsible for driving population dynamics, and over the nature and strength of population regulation (for reviews, see Doherty, 1991; Jones, 1991; Booth and Brosnan, 1995; Caley *et al.*, 1996; Hixon, 1998). In this chapter we address questions about population ecology that have been at the center of the controversy: (1) What influence do density-dependent interactions among reef fishes have on fluctuations in their abundance? (2) Are the sort of density-dependent interactions observed among reef fishes likely to result in population regulation? (3) Will density-dependent interactions at small scales appreciably influence population dynamics at larger scales, i.e., does small-scale density dependence scale up? These questions are, we feel, important ones in ecology generally. In addressing them, our aim is to illustrate how some insights and approaches from other systems might

help us better understand the population dynamics of reef fishes, and also to point out a few ways that the study of reef fishes can contribute to ecology in general.

The main lesson we apply from other systems is that density-dependent interactions often occur at particular scales both in space and time. Understanding the influence of density-dependent interactions, and even detecting them in the first place, depends critically on being able to identify the scale at which they occur and then being able to extrapolate their effects to other scales. We think reef fishes have a lot to offer to the study of population dynamics, in part, because they are one of the few groups of vertebrates that can be readily experimented with in the field. Field manipulations are viewed as the best way to detect density-dependent interactions, identify the stage in the life cycle at which they occur, and isolate their biological causes. Reef fishes have now been the subjects of a reasonably large collection of such experiments (reviewed in Chapter 14, this volume), and the results of these experiments may provide valuable insights into the ecology of other species that are more difficult to study, or occupy less accessible habitats. This chapter is motivated by the fact that virtually all experimental studies on reef fishes (as well as related observational studies) were done on habitat patches smaller than a coffee table and lasted for just a small segment of the fishes' generation time. There are compelling reasons to desire an understanding of population dynamics at much larger spatial scales and over multiple generations in time, and therefore the central focus of

this chapter is to determine whether the results of this small-scale work on reef fishes might be expected to scale up.

## B. Density Dependence and Population Regulation

A substantive understanding of population dynamics requires that we determine the causes of both fluctuations in and regulation of abundance. By regulation we mean the long-term persistence of a population within upper and lower bounds (Murdoch and Walde, 1989). Density dependence, when one or more per-capita demographic rates are related to current or past population density, is a necessary, but not sufficient, condition for regulation. Regulation occurs when density dependence has a direct effect (population growth is negatively related to density) that is strong enough to put bounds on temporal fluctuations in abundance, but not so strong or delayed in its effect as to have a destabilizing effect on abundance (Murdoch, 1994; Cappuccino and Price, 1995). Density *independence* means, of course, that demographic rates do not vary as a function of population density and the population's abundance is on an unregulated "random walk" over time (e.g., den Boer, 1968). Variation in demographic rates that is unrelated to density can, obviously, have major effects on population dynamics, but can never regulate populations. Questions about fluctuations in abundance and the regulation of population size are clearly interrelated, but the interrelation need not be a close one. For example, density-dependent interactions may have a trivial influence on dynamical patterns in abundance but still keep the population within bounds (e.g., Davidson and Andrewartha, 1948; Smith, 1961), and, conversely, intense density dependence may have an overwhelming effect on dynamics without stabilizing the population (e.g., Nicholson and Bailey, 1935).

One lesson reef fish ecologists can draw from other systems is that we have very limited ability to test directly whether reef fish populations are regulated. It is generally agreed that the best way to identify regulation is to use a time series of census data and test directly for boundedness in the observed fluctuations of abundance (Turchin, 1995). The accuracy of these tests increases dramatically with the length of the time series, and we simply do not have the sort of census data spanning multiple generations that are needed to perform these tests reliably (e.g., Hassell *et al.*, 1989; Holyoak, 1993; Wolda and Dennis, 1993). We do, in contrast, know a reasonable amount about the occurrence and nature of density dependence in reef fishes (see Chapter 14, this volume). Another lesson we should learn from the

general ecological literature is that the mere existence of density dependence in some form does not tell us much about its effect on population dynamics. Our chapter is a modest attempt to improve our understanding of the role that density-dependent interactions play in population dynamics of reef fishes.

## C. The Spatial Structure of Reef Fish Populations

In order to predict the outcome of density-dependent interactions, we need to recognize that there can be different sorts of density dependence that vary in the spatial and temporal scales over which they operate. We therefore begin by describing the spatial structure of reef fish populations. Reef habitats are patchy at a number of scales, but for the purposes of this chapter we will simplify things and assume that reef fish populations are organized at three basic spatial scales:

1. *A local population occupying a single patch of reef habitat.* The fishes occupying a single patch are defined as a local population. We focus on this scale first, because patch occupants interact with one another on a regular basis, and so this is the spatial scale at which fishes actually experience "density." The movement of juvenile and adult fishes among patches is often possible, but does not occur routinely. Because reef fish larvae are in the pelagic environment for weeks to months, it is likely that local populations are completely demographically open—i.e., larval input to a patch is unrelated to the reproductive output of the resident adults. The sort of habitat we have in mind here is a patch reef that is typically a few to tens of meters in extent, and is usually physically separated from other patches by inhospitable habitat (usually sand or seagrass). Such patch reefs have been the setting for virtually all field experiments on reef fishes, and they support reasonably large local populations of many smaller species that have home ranges of a few square meters or less. We note, though, that a group of regularly interacting conspecifics in any sort of habitat could be viewed as a local population.

2. *A mesopopulation occupying a large array of patch reefs.* We introduce this term to describe a collection of local populations occupying an array of neighboring habitat patches. The key feature of a mesopopulation is that, as a whole, it is sufficiently isolated from other reefs that the successful migration of juveniles and adults into, or out of, the mesopopulation does not occur. The replenishment of mesopopulations thus occurs only by the settlement of planktonic larvae, and losses

occur only through mortality (because any emigrants die). We assume that mesopopulations are demographically open to some degree, because at least some of the larvae arriving to replenish it are spawned elsewhere. For our purposes, it does not matter what fraction of larvae arrive from elsewhere. To give a realistic example, the fish occupying the reefs associated with a single island might constitute a mesopopulation, and so an actual mesopopulation might commonly be a few to tens of kilometers in extent.

3. *A metapopulation: a collection of mesopopulations.* A metapopulation is large enough so that all larvae arriving at the constituent reefs originated from within the metapopulation. In other words, a metapopulation is a demographically closed collection of mesopopulations.

### D. Density Dependence at Multiple Scales

In general terms, there can be both spatial and temporal density dependence, and both of these can operate at different scales of space and time. Spatial density dependence occurs between populations and so, for reef fish populations structured in the simplified manner we have specified, spatial density dependence might occur among a set of local populations, or among a set of mesopopulations. In either case, if locations supporting greater population densities suffer higher loss rates and/or lower gain rates, then those demographic rates are spatially density dependent. Temporal density dependence refers, instead, to a single population whose loss and/or gain rates vary as a function of density such that the loss rate increases and/or the gain rate declines when population density increases (Stewart-Oaten and Murdoch, 1990). For reef fishes, temporal density dependence might occur at the scale of a single local population, a single mesopopulation, or a single metapopulation. To make matters more confusing, both spatial and temporal density dependence may occur at specific stages in the life history and therefore operate within a generation, or conversely might occur among generations (e.g., Hassell, 1986). To give a hypothetical example, larval and juvenile mortality might be negatively related to density, whereas adult mortality might be positively related to density, and the two might cancel each other out so that mortality over the entire life-span was density independent! Making these distinctions and outlining this complex set of possibilities underscore the importance of specifying carefully the spatial and temporal domain over which answers to questions about the causes of population dynamics will apply.

This hierarchical spatial structure of reef fish populations also highlights the fact that the four basic demographic rates that influence population size—birth, death, immigration, and emigration—will vary in their importance among spatial scales. For local populations, the immigration and emigration of postsettlement fishes will affect local abundance. Losses will also occur via mortality of residents, but the birth rate has no influence on future population size within the patch. Instead, the settlement of planktonic larvae effectively substitutes for the birth rate, because it results in the arrival of offspring. Biologically, though, it is more analogous to immigration, because the reproductive activity of patch residents does not influence the rate at which larvae are added to the population. At the mesopopulation scale, successful postsettlement migration does not occur, and so abundance is the balance of input by larval settlement and losses by mortality of settled individuals. The input rate via settlement may, or may not, be affected by the reproductive output of the resident females, depending on (1) the fraction of larvae spawned by mesopopulation residents that return to settle into the population and (2) the relationship between spawning output from the mesopopulation and the subsequent mortality of those larvae. Finally, at the metapopulation scale, population size is affected only by births and deaths within the population.

### E. What We Know about Density Dependence in Reef Fishes

Having outlined different forms of density dependence, the spatial and temporal scales over which they operate, and which demographic rates are likely to be involved at these scales, we must point out that we have data on reef fishes for only a small subset of the possible forms and scales. First, as we have noted above, most empirical work, and all experimental work, has been done on local populations—typically using patches of reef a few or tens of meters in extent. Of course, this bias toward small plot sizes is a general one in ecology (Kareiva and Andersen, 1986). Second, most of these local populations have occupied habitat patches that were physically isolated from other reefs by inhospitable habitat (usually sand). Generally, the distance among patches was small (less than 20 m), but was in some cases hundreds of meters (e.g., Hixon and Carr, 1997). The choice of widely spaced habitat patches was usually made with the deliberate aim of minimizing two of the demographic rates that may affect local populations, immigration and emigration by settled fishes. There were good reasons for this: migration among replicate patches makes it difficult

to maintain experimental treatments, and also makes it difficult to measure accurately other demographic responses (mortality and recruitment). A third, and related, bias is toward within-generation studies that focus on a limited part of the life cycle—usually the first few weeks or months after larval settlement. The paucity of among-generation studies is caused by logistical constraints that limit the duration of experimental manipulations to weeks or months, whereas many reef fishes can live for several years. Several good summaries of older literature support these generalizations (Jones, 1991; Booth and Brosnan, 1995; Caley *et al.*, 1996), as does the more recent literature (e.g., Hixon and Carr, 1997; Tolimieri, 1998b; Caselle, 1999; Schmitt and Holbrook, 1996, 1999a,b), including our own work (e.g., Forrester 1990, 1991, 1995, 1999; Steele, 1996, 1997a,b, 1998; Steele *et al.*, 1998; Forrester and Steele, 2000). In summary, then, virtually all of the tests for density dependence that we know of focus on spatial density dependence within generations, and use local populations as replicates. A few tests for spatial density dependence have used mesopopulations as replicates (e.g., Doherty and Fowler, 1994a), and a few studies have tested for temporal density dependence by tracking local populations over time (e.g., Victor, 1986b). In general, though, spatial and temporal density dependencies at both the mesopopulation and metapopulation scales remain largely unexplored.

Focusing most of our attention on local-scale, short-term studies has had some benefits and some drawbacks. Working at small scales does facilitate experimental manipulations of density, which is considered to be the best means of testing for density dependence in demographic rates (Nicholson, 1957; Murdoch, 1970; Sinclair, 1989; Harrison and Cappuccino, 1995). Experiments of this sort have revealed variable relationships between the mortality of juvenile and adult fishes and local density, but density dependence at both stages can be intense. Some experiments have gone a step further, and identified the biological interactions that cause density dependence (Forrester, 1990; Hixon and Carr, 1997; Forrester and Steele, 2000). In a few species, mortality inflicted by predators has been found to increase with prey density (Hixon and Carr, 1997; Forrester and Steele, 2000), but other agents of mortality can also be density dependent (Forrester and Steele, 2000, and unpublished). Detailed experimental evidence defining the intensity and biological cause of density-dependent interactions is not available, nor easily obtainable, for many taxa (Harrison and Cappuccino, 1995), and so it is important for us to make the best use of this understanding that we have gained by studying reef fishes.

Working at small scales has also facilitated tests of density dependence based on examining relationships between the rate of larval settlement or recruitment and the abundance of fishes remaining at the site some time later (e.g., Doherty and Fowler, 1994a; Levin, 1996; Robertson, 1988a, 1992; Caselle, 1999; Schmitt and Holbrook, 1999a,b; Shima, 1999b). Because accurately measuring larval settlement in reef fishes is very labor intensive, increases in the spatial scale of such studies have always come at a cost in terms of accuracy and precision of settlement estimates (e.g., Doherty and Fowler, 1994a; Caselle 1999). Some local-scale studies have thus been able to correlate settlement with the abundance of older fishes to test for density-dependent mortality starting at, or just after, settlement (e.g., Schmitt and Holbrook, 1999a,b), whereas studies using mesopopulations as replicates have not been able to encompass mortality acting early in reef-associated life (e.g., Doherty and Fowler, 1994a). At both local and mesopopulation scales, relationships between settlement/recruitment and the abundance of older life stages are sometimes apparently linear, implying density-independent mortality in the intervening period (e.g., Doherty and Fowler, 1994a). In other cases, there is evidence that they may be curvilinear, indicating density-dependent mortality (e.g., Caselle, 1999; Schmitt and Holbrook, 1999a,b). A synthesis of these results is difficult, however, precisely because they were done at different spatial scales and focus on different portions of the life cycle.

## F. Some Reasons for Wanting to Extrapolate to Larger Scale Population Dynamics

In this chapter we will take this body of information on short-term, local-scale relationships between density and demographic rates and attempt to predict the consequences for longer term mesopopulation dynamics. Knowing the extent to which local-scale, within-generation findings can be extrapolated would be desirable for several reasons. First, and very simply, much of the field research on reef fishes has dealt with local “populations” comprising just a handful of fishes, and so are hardly large enough to constitute actual populations (colleagues working on other taxa sometimes laugh at us when we refer to them as populations). A more important practical reason for wanting to extrapolate to the mesopopulation spatial scale is that, for many reef fishes, a mesopopulation occupies a spatial region that might be subject to a local

fishery, or be designated as a marine reserve. Extrapolating to multigenerational time scales would be helpful because plans for managing fisheries and conserving natural habitats are usually implemented over years rather than weeks or months (e.g., Done, 1998; Done and Reichelt, 1998). We would, therefore, be able to provide better advice to fisheries scientists and conservation biologists if we knew whether our findings might apply over appropriately large domains of space and time.

Along these lines, we also hope that our work might provide a means of forging more explicit links with research done on commercially exploited species in temperate waters (e.g., Beverton and Holt, 1957; Rothschild, 1986; Cushing, 1995; Quinn and Deriso, 1999). This extensive body of research is mostly descriptive in nature, and has been conducted at large spatial and temporal scales. In some cases these temperate populations are believed to form distinct stocks, and so are demographically equivalent to reef fish metapopulations, but in other cases the populations studied are probably demographically open to some degree, and so are directly comparable to reef fish mesopopulations. The type of detailed experimental fieldwork that we can do on reef fishes is often impossible in many other habitats where fishes are commonly harvested. These two bodies of work are therefore complementary in nature, and we would benefit tremendously from increasing the degree of overlap and exchange between them.

### G. Can Small-Scale Results Be Expected to Extrapolate?

Researchers studying reef fishes have been skeptical that the results of small-scale studies will scale up (e.g., Doherty and Williams, 1988; Doherty, 1991; Doherty and Fowler, 1994a; Caley *et al.*, 1996; Caselle, 1999). A common view, well summarized by Caley and co-workers (1996), is that density-dependent interactions detected by experiments on small isolated habitat patches may be less important at large scales because "density-dependent emigration can ameliorate competition and competition may occur only at a limited number of sites." The potential for this is supported by tagging studies indicating that even small reef fishes can redistribute themselves, and their ability to do so improves in areas of continuous reef habitat, or where patches are closely spaced (e.g., Frederick, 1997). Density-dependent interactions experienced by fishes restricted to isolated reefs might, therefore, not occur if those fishes have the opportunity to disperse from high-density patches to more favorable locations.

Models of predator-prey and host-parasitoid interactions in patchy habitats generally find that making patches more homogeneous has a destabilizing effect (e.g., Hassell *et al.*, 1991), but the opposite has also been found (e.g., Kareiva, 1987; Murdoch and Oaten, 1989). There is, as a result, no clear basis from which to predict the consequences of studying reef fishes mainly on isolated patches of reef. We, therefore, address the issue of whether varying the rate of migration among patches affects the outcome of local-scale density dependence.

Another important insight from the wider literature is that density-dependent interactions may be explicit to certain spatial and temporal scales, and not detectable at other scales. This has been particularly well studied in insects that are patchily distributed in space and subject to predation by parasitoids. In this system, aggregation by parasitoids to dense prey patches can be an important mechanism of density-dependent predation. The appropriate spatial scale to detect this response depends on exactly how prey are distributed in space and on the searching abilities of the parasitoids (e.g., Heads and Lawton, 1983; Freeman and Smith, 1990; Rothman and Darling, 1990; Hopper *et al.* 1991; Stiling *et al.* 1991; Ray and Hastings, 1996). Similarly, the spatially density-dependent prey mortality that results is sometimes experienced only by certain life stages of the prey population. Theoretical analyses show that this spatial density dependence within generations does not always lead to temporal density dependence over multiple generations (e.g., Hassell, 1986; Murdoch and Oaten, 1989; Stewart-Oaten and Murdoch, 1990). These theoretical analyses of insect-parasitoid interactions are not directly applicable to reef fish populations, but the general message is clear—we can not assume that relationships between density and demographic rates will remain constant when we change our scale of observation. We must, therefore, develop models for reef fishes to reconcile the varying results of tests for density dependence performed at different scales.

The last and perhaps most important reason why we wrote this chapter is that detecting density dependence says very little about its *quantitative* effect on population dynamics. It has long been recognized that, although field experiments provide a rigorous means of identifying interactions, they cannot identify the role those interactions play in controlling population size (e.g., Weinberg *et al.*, 1986). This argument applies equally to interactions that are dependent on or independent of population density. It is obvious that all of the demographic rates affecting abundance will have some influence on population dynamics, and the

same is true of the environmental factors that control those demographic rates. There are now some excellent methods to evaluate the relative influence of processes occurring at different life history stages on overall population dynamics (e.g., Nisbet *et al.*, 1996; Pfister, 1996; Schmitt *et al.*, 1999). These approaches can be used with data collected at any spatial scale, but are not designed to extrapolate among different spatial scales.

Models focusing explicitly on extrapolating population dynamics across spatial scales indicate that extrapolating from small-scale results to larger spatial domains is greatly complicated by density dependence operating at the small scale (e.g., Chesson, 1996, 1998a; Anneville *et al.*, 1998; Pascual and Levin, 1999). For example, Chesson (1996, 1998a) analyzed the dynamics of a set of populations (each equivalent to a mesopopulation by our definition) that, as a group, formed a single, closed metapopulation. These analyses show that density-dependent interactions within mesopopulations can have dramatically altered consequences when viewed across the entire metapopulation (Chesson, 1996, 1998a). Chesson argued that these "scale transitions" in population dynamics result from the interaction of density dependence with small-scale heterogeneity in density. Our work tackles similar questions, but we focus instead on a set of local populations that are connected to form a single mesopopulation. We made this different choice of scales for reasons already outlined: (1) virtually all empirical data on reef fish concern local populations and (2) extrapolating to the mesopopulation scale will be helpful because marine reserves and fisheries are often managed at this scale. A third important reason was that we wanted to make quantitative predictions about population dynamics that would be empirically testable. The logistics of testing predictions about the dynamics of mesopopulations are more manageable than testing similar predictions about metapopulation dynamics!

## II. Questions

We used computer simulations to examine local populations of fishes, each of which occupies a small patch of habitat (a patch reef) isolated from similar neighboring patches by expanses of inhospitable space (sand). The model simulates a large collection of neighboring local populations that, as a whole, form a mesopopulation. We are thus able to address questions about the relationships between the demography and population dynamics of a mesopopulation and its component local populations.

We employed systematic variation of selected parameter values to address four questions.

- Question 1:** How does local-scale density dependence in different demographic rates affect the meso-scale relationship between larval supply and abundance?
- Question 2:** How does local-scale density dependence in different demographic rates affect temporal fluctuations in mesopopulation abundance?
- Question 3:** Are relationships between density and demographic rates the same for the mesopopulation and its component local populations?
- Question 4:** How does the amount of adult migration between local populations influence the answers to Questions 1–3?

The qualitative features of our model fish species closely resemble attributes of the bridled goby *Coryphopterus glaucofraenum*, a fish we have studied extensively and so can provide reasonable estimates of the model parameters (e.g., Forrester 1995, 1999; Steele *et al.*, 1998; Forrester and Steele, 2000). The reason for developing a detailed, empirically parameterized, simulation model is that the questions we address do not have qualitative "either/or" answers. Instead they have *quantitative* answers based on the relative effect of different processes and interactions. The model makes detailed quantitative predictions about the answers to these questions for *C. glaucofraenum*, which can be tested in the field. It is important to stress here that the answers to these questions are likely to vary among species and circumstances. With appropriate parameterization, our model can be widely applied to any reef fish that has dispersing planktonic larvae and an adult stage that occupies patchy reefs surrounded by uninhabitable habitat. It is thus a tool that can be used to address general questions about when, and why, we would expect the processes driving population dynamics to differ.

## III. Model Formulation

### A. Basic Structure

The habitat that contains our hypothetical mesopopulation consists of small, discrete reefs, suitable for fish occupancy, that are surrounded by inhospitable habitat. These reefs lie at the 625 nodes of a  $25 \times 25$  square array that is well isolated from any reefs outside the array. Each reef supports a population of adult

fishes. In most simulations, adult fishes were allowed the possibility of moving from each reef to the nearest neighboring reefs. Because the location of each reef influences the dynamics of its population explicitly, this model is "spatially explicit" in the sense of Hanski (1996).

The population abundance of adult fishes on each reef is measured as an integer. Each population obeys a difference equation of the form

$$\begin{aligned} \text{adult abundance}(t+1) = & \text{adult abundance}(t) \\ & + \text{larval recruits}(t) + \text{adult immigrants}(t) \quad (1) \\ & - \text{adult deaths}(t) - \text{adult emigrants}(t), \end{aligned}$$

with time  $t$  measured in weeks and a step size of 1 week. At each time step, the effect of each of the four demographic processes of larval recruitment, adult immigration, adult death, and adult emigration is described by an integer-valued random variable. Accordingly, our mesopopulation model consists of a system of simultaneous, stochastic, difference equations. These equations concern an idealized fish species whose adults are all functionally identical; that is, the model makes no attempt to distinguish between adults of different ages or sizes. To begin each simulation, we set the initial abundance of each reef's population equal to the estimated long-term average abundance. Analytical calculation of this estimate will be described below.

Our interest centers on the behavior over the long term of a collection of local populations surrounded by neighboring populations on all sides, a condition probably typical of mesopopulations in nature. To examine typical mesopopulation behavior, we ran each simulation for 12 years (624 time steps). As an attempt to eliminate effects of the initial condition, we discarded all population data for the first 2 years (104 time steps) and examined mesopopulation behavior only over the following 10 years (520 time steps). We performed all calculations for all populations in the full  $25 \times 25$  reef array. However, to eliminate boundary effects, in calculating mesopopulation properties we discarded all population data from the outer 2 rows. Thus, our examination focused on the dynamics over what we view as a typical 10-year period of what we consider a typical  $21 \times 21 = 441$ -reef mesopopulation situated in the interior of a larger array. All calculations employed Mathematica 4.0 software (Wolfram Research Inc.).

Demographic parameters fall into two classes. The first contains parameters associated with "normal" population densities usually encountered in nature and for which we can supply reasonable empirical estimates for bridled gobies from published sources (Forrester, 1995, 1999; Steele *et al.*, 1998; Forrester and Steele,

2000) or from our unpublished data. The next subsection concerns these parameters. The second class includes parameters that describe how demographic rates depend on population density. Field data required for estimating these parameters are sparse at best for any fish species. The subsection after next describes a simple, intuitively interpretable, and yet versatile formulation of density dependence in the demographic rates of reef fishes, as applied to the bridled goby.

## B. "Normal" Demographic Rates

Field population data for well-studied reef fish species can supply reasonable estimates, or at least inspired guesses, of demographic rates that usually apply when fish abundance lies within "normal" limits. Our estimates and guesses concern bridled gobies that occupy hypothetical 2- to 8-m<sup>2</sup> patch reefs like the experimental reefs we have studied in the Bahamas and Caribbean (Forrester 1995, 1999; Steele *et al.*, 1998; Forrester and Steele, 2000; G. E. Forrester and M. A. Steele, unpublished data).

### 1. LARVAL RECRUITMENT

We envision larval recruitment onto a reef as proceeding in two steps, arrival of larvae into the immediate vicinity of the reef followed by recruitment of these larvae to the adult population there. Larval arrival is not a function of adult density, so the mesopopulation is effectively demographically open. We set the expected fraction of arriving larvae that successfully recruit at 0.2416, meaning that the fraction 0.7584 die while attempting to recruit. In combination with other parameter values given below, this expected recruitment success gives rise (as described below) to an estimated long-term average population abundance of 10 individuals, a figure consistent with our field observations.

Larval arrival on each reef is influenced by multiple processes that are both ecologically complex and poorly understood. Accordingly, we formulated the model's hypothetical larval arrival pattern to mimic the well-documented qualitative features of reef fish species in general (e.g., Doherty and Williams; 1988; Doherty, 1991), and our field monitoring of bridled gobies over 3 years (M. A. Steele and G. E. Forrester, unpublished). Figure 1 displays a typical random sample produced by our algorithm of 10 years of larval arrivals to the mesopopulation. This sample displays four important qualitative features. (1) Each year there occurs a larval arrival season during which most larvae arrive onto adult habitats. These larval arrival seasons have variable length, and they are separated by off-seasons

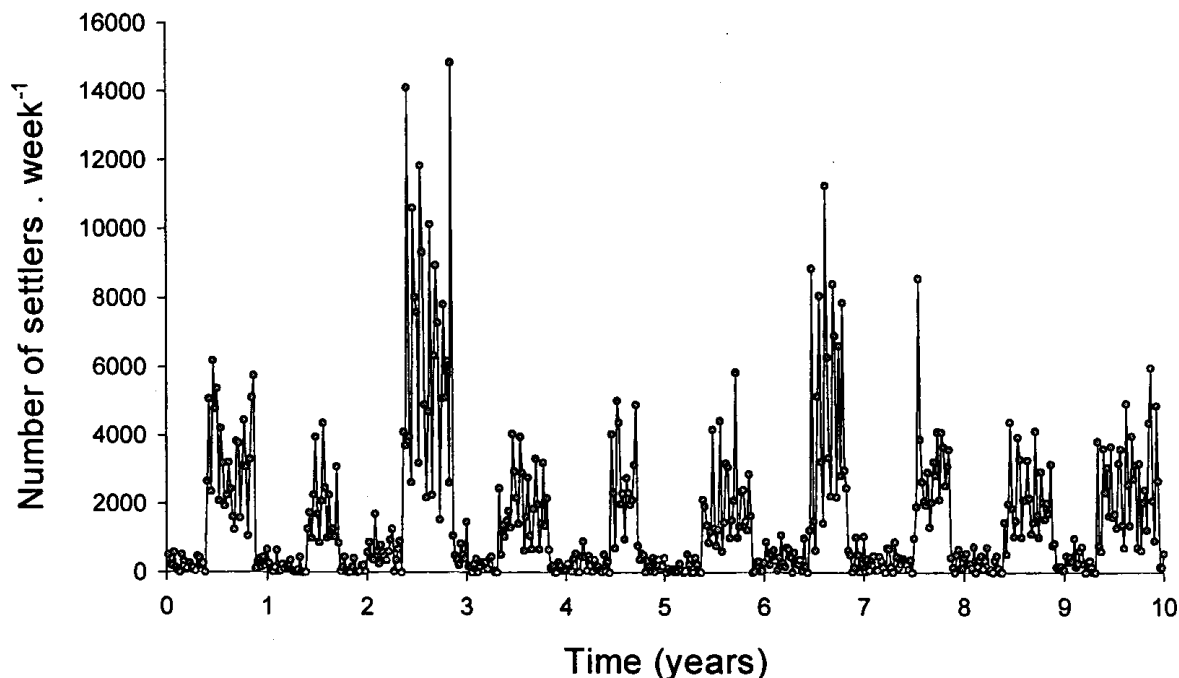


FIGURE 1 An example of the pattern of larval settlement generated by the simulation model. Note that this simulated pattern of settlement closely mirrors many empirically measured patterns (see, e.g., Doherty and Williams, 1988). Displayed is the total number of settlers to the mesopopulation each week during one 10-year run of the model. The simulation shown was selected haphazardly from those generated for this chapter.

during which only a few larvae arrive from time to time. (2) Wide and irregular variation occurs from year to year in the annual total of larval arrivals onto a reef. (3) Considerable variation in weekly larval arrival occurs through the larval arrival season but with an overall trend of fewer arrivals near its beginning and end than during its long middle period. (4) Average larval arrival rate during the 2 weeks surrounding the time of new moon exceeds the average during the 2 weeks surrounding the time of full moon. Details of the larval arrival algorithm's structure appear in the following paragraphs. Statistical distributions and parameter values were selected to produce the qualitative pattern displayed in Fig 1.

Variable length and timing of each year's larval arrival season is achieved by making the season's beginning and ending dates random variables. Specifically, the beginning week of each year is a random variate, rounded to the nearest integer, selected from a normal distribution with mean 18 (= first week in May) and standard deviation 4. The ending week is another independent random variate, rounded to the nearest integer, selected from a normal distribution with mean 44 (= last week in October) and standard deviation 4. "Pathological" years are avoided by requiring that both initial and final weeks lie between week 1 and week 52

and that the ending week not precede the beginning week.

The number of larvae that actually arrive on a reef during each week is a complicated random quantity whose overall pattern through time incorporates variation on three time scales—annual, seasonal, and lunar. Specifically, this number of larval arrivals is a gamma-distributed random variable with expectation

$$A \times S \times L,$$

where  $A$ ,  $S$ , and  $L$  describe the annual, seasonal, and lunar effects. The annual contribution  $A$  is a random variate selected each year from a gamma distribution with parameters  $\alpha_A = 5$  and  $\beta_A = 2$ . The seasonal contribution  $S$  is deterministic. It increases from  $S = 0$  in the larval arrival season's first week to  $S = 1$  at its midpoint, and then it decreases again to  $S = 0$  in the larval arrival season's final week. This curve has a broad hump. Specifically, its shape is given by the tenth root of the positive portion of a sine wave that passes through these three points, and the value of  $S$  during each week of the season is just the height of this curve at that time. During the off-season, this variable is assigned the constant value  $S = 0.1$ . Consequently, the seasonal contribution to larval arrivals during the off-season is one-tenth as great as during the larval arrival



season's peak. The lunar contribution  $L$  is a random variate selected each week from a gamma distribution. This gamma distribution has parameters  $\alpha_N = 5$  and  $\beta_N = 0.2$  during the 2 weeks of each month that surround the new moon, and it has parameters  $\alpha_F = 5$  and  $\beta_F = 0.1$  during the 2 weeks of each month that surround the full moon. With these parameters, the expected value of  $L$  during the two weeks surrounding the new moon is twice its expected value during the 2 weeks surrounding the full moon. Each week's values of  $A$ ,  $S$ , and  $L$  apply to all reefs in the array. The actual number of larvae that arrive on each reef during any given week is specified by an independent random variate selected from a common gamma distribution with parameters  $\alpha = 5$  and  $\beta = A \times S \times L/\alpha$ .

## 2. MORTALITY

Field observations of tagged gobies in the Bahamas and Virgin Islands have revealed that on average the fraction of adults that fail to survive from one week to the next is about  $1/11 = 0.0909$ , which implies an average adult life length of about 10 weeks. In the model, each week the fate of each goby, anywhere in the reef array, was decided randomly and independently of the fates of all other gobies. When local density on each reef did not influence deaths there, each goby experienced probability  $1/11$  of dying each week.

## 3. ADULT EMIGRATION, MOVEMENT, AND IMMIGRATION

To study effects on mesopopulation behavior of adult movement between reefs, we examined three hypothetical movement rates: zero, low, and high. The fraction of adults each week that emigrate from any reef and successfully immigrate to another is 0% in the zero-movement case, 2% in the low-movement case, and 10% in the high-movement case. The low-movement case employs the measured movement rate of marked gobies from patch reefs in the Virgin Islands (G. E. Forrester, unpublished). Because we do not know in detail what fate befell any individuals that disappeared from the reef array there, we were forced to base calculated numerical values for some model parameters on two educated guesses. The first guess is that when adults can move between reefs, half of all adult deaths are experienced by reef residents and the other half by reef emigrants. The second guess is that 90% of the deaths experienced by emigrants occur during movement across inhospitable habitat between reefs, and the remaining 10% during attempted immigration into another reef's population.

Back-calculations of primary model parameters from these guesses, which apply when population

densities influence neither emigration nor immigration, give rise to different sets of parameter values for the three adult movement rates. In the zero-movement case, all adult deaths necessarily occur to reef residents, and emigration occurs with probability zero. In this case, reef residents experience death with probability  $1/11$  each week as explained above. In the low-movement case, each week reef residents experience death with probability  $1/22 = 0.04545$ , each individual emigrates with probability  $0.06465$ , each emigrant dies over inhospitable habitat with probability  $0.6216$ , and each individual that arrives alive on a reef dies while attempting to immigrate there with probability  $0.1825$ . In the high-movement case, resident death occurs with probability  $1/22$  each week, emigration with probability  $0.1415$ , death over inhospitable habitat with probability  $0.2637$ , and death while attempting to immigrate with probability  $0.3980$ .

In one time step, emigrants from any reef may move only to the four immediately adjacent reefs. Each emigrant's movement is random, independent of each other emigrant's movement, and equally likely to occur in each of the four cardinal directions. All emigrants from edge reefs that move away from the reef array die, but these fatal movements constitute only 4% of all possible adult movements in the reef array.

## 4. AVERAGE POPULATION ABUNDANCE

Choosing the probability of larval death during attempted recruitment, namely, the figure  $0.7584$  mentioned above, requires knowing the long-term average population abundance on individual reefs. This average must be determined ahead of time by some method independent of the main computer runs. Calculating its exact value by analytical means seems unlikely and perhaps even impossible, and so we employed an approximation.

The approximation takes place in two steps. The first step is estimating the average number of larval arrivals on a single reef over a full year. Our estimate involved summing the expected weekly larval arrivals over the 52 weeks of a year for which larval arrival season has the expected beginning and ending dates. This analytical estimate is  $195.7$  larvae per reef. To check this figure against numerical results, we used the model to generate larval arrivals on a single reef over a 1000-year period. The resulting annual average was  $197.01$ , with a standard error of  $3.05$ , in excellent agreement with the analytical estimate. Our field observations make this figure seem plausible.

The second step is estimating the long-term average population abundance. Our procedure consisted of calculating expected population abundance directly from

the original difference equation [Eq. (1), Section III,A] with zero adult movement and with every week's larval arrivals replaced by the weekly average of the expected 195.7 larval arrivals per year. This procedure produced an algebraic expression for expected population abundance in terms of the probability of larval death during attempted recruitment into an adult population. Our field observations suggest that average population abundance on individual reefs is about 10 individuals. Inserting this figure into this algebraic equation gave rise to the calculated recruitment failure probability of 0.7584 mentioned earlier.

To check whether our computer model produces a long-term average population abundance near to the assumed value of 10 individuals, we did not perform any 1000-year computer runs. Instead, we performed many separate calculations of 10-year averages under different kinds and degrees of density dependence and adult movement as described in the next section. These 10-year averages fell close to the assumed value, and deviations were symmetrically arranged about this figure.

### C. Density Dependence

Dynamical behavior of the mesopopulation arises from larval arrivals, adult movements and deaths over inhospitable habitat, and four demographic processes that take place at the level of populations on individual reefs. These reef-associated demographic processes are (1) deaths of newly arrived individuals in the week between their arrival as larvae and recruitment to the adult population 1 week later, (2) deaths of reef residents, (3) emigration from reefs, and (4) deaths of emigrants while they attempt to immigrate into a reef's population. Because of their association with individual reefs, it is possible for population density on individual reefs to influence the rates at which these four processes occur. Experiments indicate that the first three of these processes are density dependent in bridled gobies (Forrester, 1995, 1999; Steele *et al.*, 1998; Forrester and Steele, 2000; unpublished data), but in no case are the data precise enough to establish the mathematical form of density dependence. For the purpose of our exploration, we imposed density dependence on these processes of the simplest and most easily interpreted mathematical form. Though this mathematical form lacks rigorous empirical foundation, it produces an excellent fit to our field measurements of mortality rates (G. E. Forrester and M. A. Steele, unpublished data) and also arises from a mechanistic (albeit simplified) description of how spatial refuges might influence death rates (R. R. Vance, unpublished data).

This simplest possible relation between a demographic rate and population density is a straight line whose slope measures the strength of density dependence. Examining effects of varying the strength of density dependence with all other factors held constant requires that each demographic rate function retain its "normal" value whenever population size lies at its long-term mean. That is, lines of all slopes must pass through the same fixed point that specifies normal demographic rates at the long-term mean population abundance.

Explicit algebraic expression of the demographic functions clarifies this point. Let  $x$  represent population abundance on any particular reef, and let  $x^*$  denote its long-term average. Let  $f(x)$  represent the magnitude of a demographic rate when the population has abundance  $x$ . Let  $f^*$  denote this magnitude when the population lies at its long-term average abundance; this definition implies that  $f^*$  satisfies  $f^* = f(x^*)$ . The general function  $f$  can represent any one of the four reef-associated demographic rate functions, namely, the probability during one time step of (1) recruit mortality, (2) adult mortality while residing on a reef, (3) adult emigration from a reef, or (4) adult death during attempted immigration into a reef's population.

The linear character of this function  $f(x)$  can be expressed algebraically in two equivalent ways that emphasize different features. The first is

$$\frac{f(x) - f^*}{f^*} = m \left( \frac{x - x^*}{x^*} \right). \quad (2)$$

The left-hand side of this expression is the fractional deviation of the demographic rate from its long-term average value, and the parenthetical quantity on the right-hand side is the fractional deviation of population abundance from its long-term average value. The equation asserts simply that these two quantities are directly proportional to each other. The proportionality constant  $m$  cannot be negative because, by assumption, all four of the reef-associated demographic rates either increase with population abundance or remain constant at all abundances. The lower limit of  $m$  is 0 when the demographic rate does not depend on density. Its upper limit is 1 because any higher value would force  $f(x)$  to become a negative quantity for small values of  $x$ , a nonsensical situation because  $f(x)$  represents a probability. Figure 2a displays a graph of Eq. (2).

Algebraic rearrangement of Eq. (2) produces an explicit expression for  $f(x)$ ,

$$f(x) = (1 - m)f^* + \left( \frac{mf^*}{x^*} \right)x, \quad (3)$$

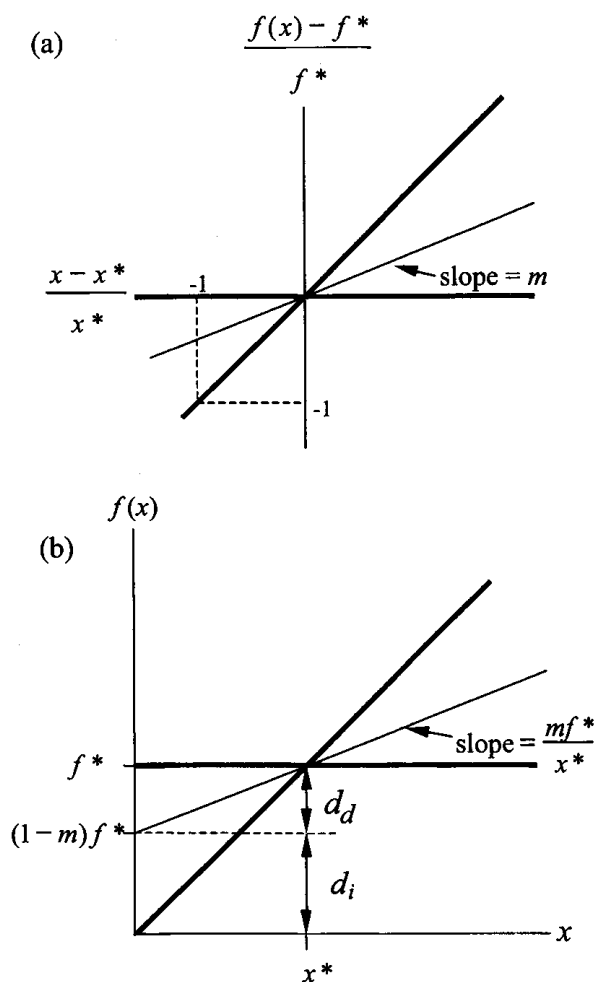


FIGURE 2 Density dependence in the generic demographic rate function  $f$ . (a) Equation (2) describes a straight line that lies somewhere between the two heavy lines and passes through the origin. In our model, we varied the strength of density dependence by varying  $m$  from 0 (no density dependence) to 1 (complete density dependence). (b) Equation (3) describes a straight line that lies somewhere between the two heavy lines and passes through the point  $(x^*, f^*)$ . In a population with abundance  $x^*$ , the demographic rate  $f^*$  can be thought of as consisting of a density-independent component of magnitude  $d_i$  and a density-dependent component of magnitude  $d_d$ .

which is graphed in Fig. 2b. The graph of Eq. (3) provides a simple biological interpretation of the proportionality constant. The demographic rate  $f^*$  experienced by a population at its long-term mean size  $x^*$  can be expressed as the sum of two quantities, a portion  $d_i$  that arises from purely density-independent processes, and a second portion  $d_d$  due to density-dependent mechanisms. It follows that the fraction of demographic events that arise from density-dependent

processes satisfies

$$\begin{aligned} \frac{d_d}{d_i + d_d} &= \frac{f^* - f^*(1 - m)}{f^*} \\ &= 1 - (1 - m) \\ &= m. \end{aligned} \quad (4)$$

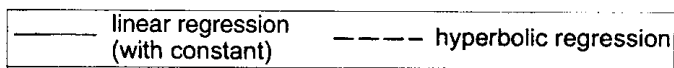
Thus, the proportionality constant  $m$ , the slope of the line in Fig. 2a, is just the fraction of demographic events in a population of abundance  $x^*$  due to density-dependent processes. This constant ranges from 0 when no demographic events result from density-dependent processes to 1 when all demographic events result from density-dependent processes.

Equation (3) has the undesirable property that whenever  $m$  is positive,  $f(x)$  exceeds 1 for large enough values of  $x$ , a nonsensical feature for a quantity meant to represent a probability. Populations in our simulations reached such high abundances very rarely, but to prevent unrealistic behavior even at these few times, our model actually employs a slightly modified definition of  $f$  that lacks this undesirable property, namely,

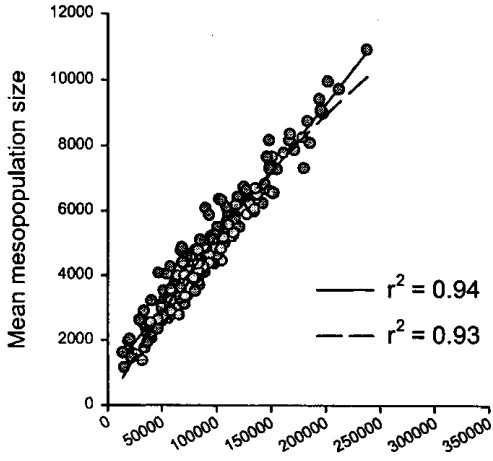
$$f(x) = \min \left\{ 1, (1 - m)f^* + \left[ \frac{mf^*}{x^*} \right] (x) \right\}.$$

Our collection of simulations examined mesopopulation consequences of density dependence in all four reef-associated demographic processes, both individually and in certain combinations. Explorations of mesopopulation variability under fixed conditions employed replicated runs with the same parameter values. For maximum contrast between sets of runs, density dependence in each demographic rate was either absent ( $m = 0$ ) or complete ( $m = 1$ ) throughout each set. Examinations of how mesopopulation behavior changes with alterations in the strength of density dependence employed sets of runs with graded values of  $m$ , but otherwise identical parameter values. For clarity, we describe in this chapter only a small subset of our rather large collection of numerical results that best illustrates the main features of the full collection.

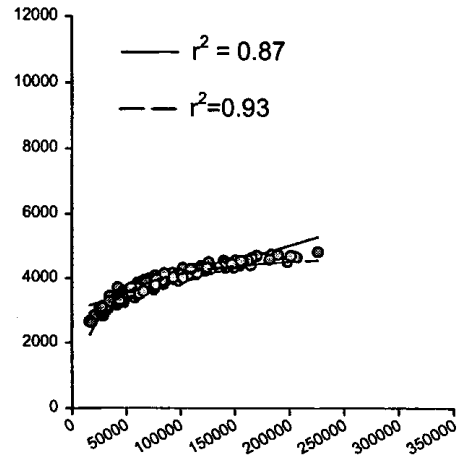
It will not have escaped the reader's attention that our method necessarily rests on the tacit assumption that density dependence and adult movement do not influence average population abundance. Actually, our simulations suggest that this assumption is probably false. However, most correlations (not shown) between numerically calculated 10-year average population abundance and strength of density dependence under any adult movement regime proved to be quite weak and nonsignificant statistically. We interpret these findings as indicating that these correlations probably do not influence the model's main qualitative features to be discussed in the remainder of this chapter.



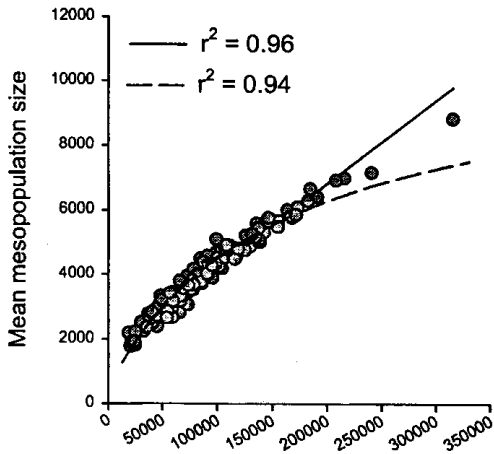
**(a) No density dependence**



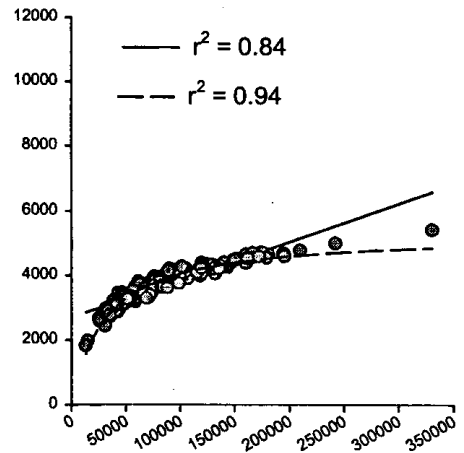
**(b) All demographic rates density-dependent**



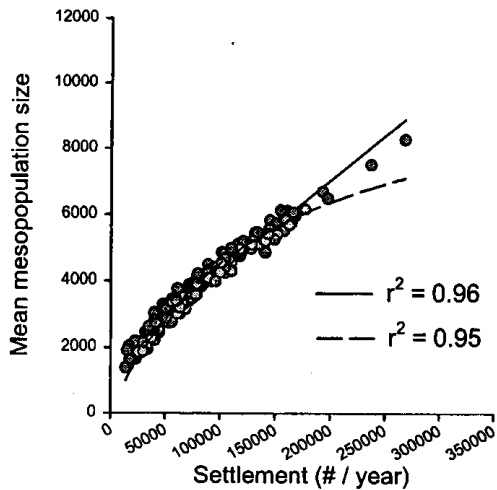
**(c) Adult mortality density-dependent**



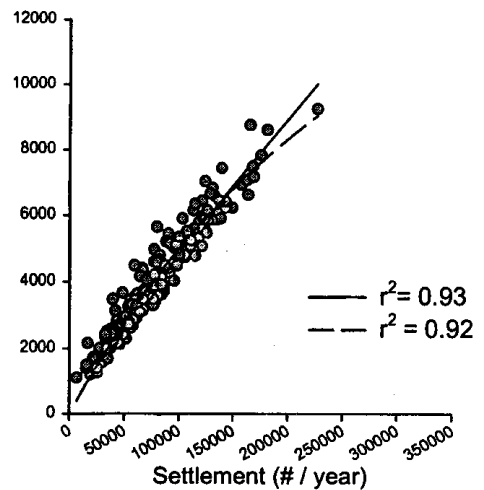
**(d) Recruit mortality density-dependent**



**(e) Adult emigration density-dependent**



**(f) Immigrant mortality density-dependent**



## IV. Results from Model Simulations

### A. Question 1: How Does Local-Scale Density Dependence in Different Demographic Rates Affect the Meso-Scale Relationship between Larval Supply and Abundance?

To address this question, the mean mesopopulation abundance in a given year was compared to the total settlement in that year. To evaluate the nature of the relationships between settlement and mesopopulation abundance, we fitted simple linear and nonlinear functions to the data. Our intent was to get a rough idea of how well each type of relationship fit the data, and not to provide a mechanistic description of the relationship. The nonlinear relationship we fitted to the data is the simple hyperbolic function

$$y = ax/(b + x)$$

also used to model enzyme kinetics (Real, 1977) and the type II functional response (Holling, 1959). This model fit the empirical results as well as either of two other simple nonlinear models we tried, and it can be algebraically rearranged to match the Beverton–Holt stock-recruitment function (Beverton and Holt, 1957).

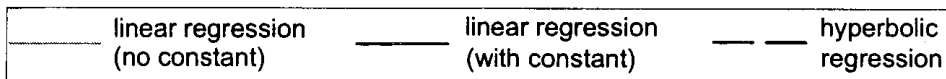
For linear functions, we employed standard Model I regressions either with or without a constant. Regression without a constant is biologically appropriate because zero settlement certainly produces zero population abundance (Cushing, 1996), but it does not yield  $r^2$  values that are comparable to those of the nonlinear functions we used. Regression with a constant yields  $r^2$  values that are more directly comparable to the  $r^2$  of the nonlinear model (Myers, 1986), and always fit the data better than a straight line forced through the origin. This was true even when there was no density dependence in any demographic rates. As expected under these circumstances, mesopopulation abundance appeared to be directly proportional to the settlement rate (Fig. 3). Linear relationships with and without a constant fit the data very well, and there was no

improvement in  $r^2$  shown by fitting a nonlinear function (Fig. 3a). However, the conclusion that the true relationship is actually nonlinear seems inescapable, because the best fitting straight line has a significantly positive intercept whereas the true relationship must pass through the origin. We suspect that the nonlinearity lies near the origin and has no biological significance in this case. Most likely, it arises from some combination of rounding continuous random variables to integers and lack of independence of successive years' mesopopulation averages in each run. The effects of either of these features should cause the greatest deviation from linearity at very low average settlement intensities. Understanding this issue will require further study.

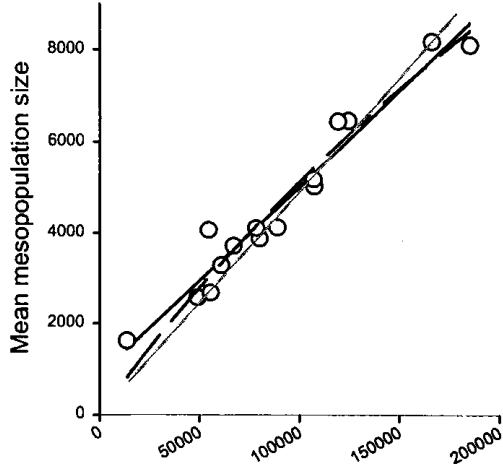
In contrast, when all demographic rates were density dependent, the relationship between settlement and abundance was obviously and strongly nonlinear. Increased settlement appeared to result in progressively smaller increases in abundance as the settlement rate reached higher levels, and abundance appeared to approach an asymptote at very high settlement rates. In this case, the nonlinear regression was clearly a better fit to the data than was the linear model (Fig. 3b), and linear regression with a constant has a large positive intercept. In this case, the large positive intercept of the linear regression arises because our data sample only a small portion, located far from the origin, of an underlying function whose true shape is nonlinear.

Our results also indicate that the extent to which density dependence affects the relationship between settlement and abundance depends strongly on which demographic rates were density dependent. When the survival of immigrants was density dependent, the influence was negligible and mesopopulation size appeared to be directly proportional to the rate of larval settlement and the hyperbolic regression did not fit better than either linear regression model (Fig. 3f). When the mortality or migration of adult gobies was density dependent there was a definite but modest influence on mesopopulation size (Fig. 3c and e). These relationships were slightly nonlinear, so that any given increase in settlement resulted in a smaller increase in mesopopulation size than would be the case with no

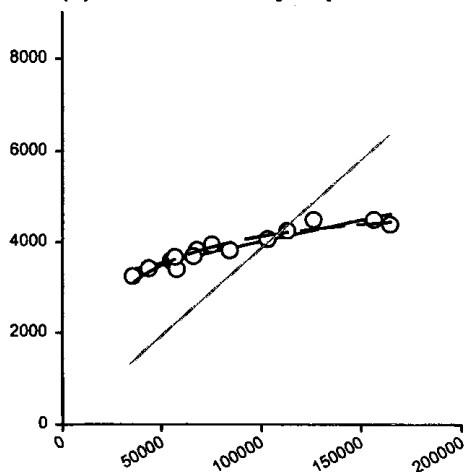
**FIGURE 3** Plots of mean mesopopulation size in a given year versus the total settlement that year. The six plots show cases in which (a) there is no density dependence or (b) all demographic rates are density dependent, and in which (c) just adult mortality, (d) just recruit mortality, (e) just adult emigration, or (f) just the mortality of adults immigrating to new reefs is density-dependent. Note that effect of density dependence (i.e., the curvature of the relationship) in cases c–f hinges on which rate is density dependent. Moreover, the effect of density dependence just in recruit mortality (d) is nearly equivalent to density dependence in all demographic rates (b). All six plots show cases in which migration among reefs occurs at normal rates. We have plotted data for each of the 10 years simulated in each of the 20 simulation runs for a given parameter set, yielding 200 points (years) per plot. Linear regression (with constant) and hyperbolic regression lines are fitted to the data.



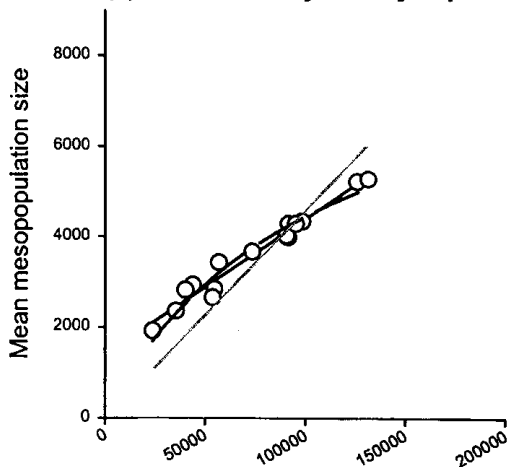
**(a) No density dependence**



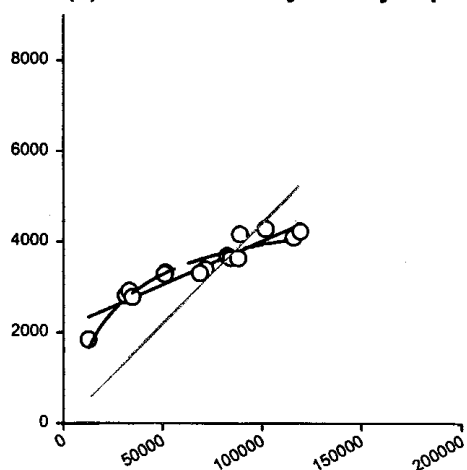
**(b) All rates density-dependent**



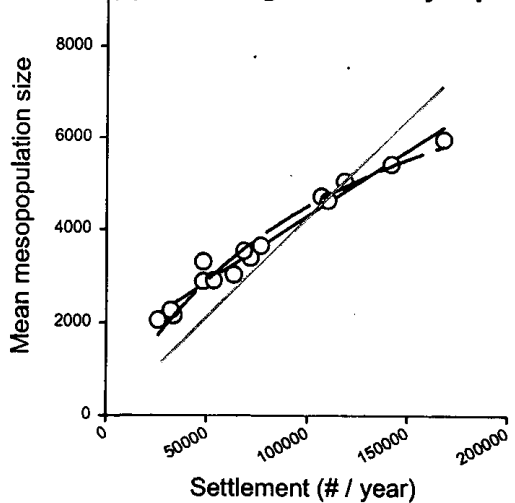
**(c) Adult mortality density-dependent**



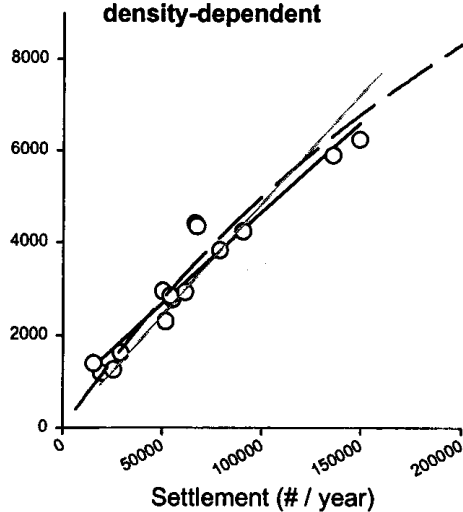
**(d) Recruit mortality density-dependent**



**(e) Adult emigration density-dependent**



**(f) Immigrant mortality density-dependent**



density dependence. In contrast, density dependence in recruit mortality strongly moderated abundance at the mesopopulation scale, and the effect was almost as great as that seen when all demographic rates are density dependent (Fig. 3d).

Using years as replicates yielded 200 data points with which to define the settlement–abundance relationship. The only published empirical study presenting such data was based on 7 data points, despite the fact that the study involved an extraordinary and impressive amount of effort on the part of the investigators (Doherty and Fowler, 1994a). We therefore also wanted to examine settlement–abundance relationships using smaller, more realistic, sample sizes. To do this, we randomly picked data for 1 year from 15 of the simulation runs for a given parameter set, so that we now had 15 data points per plot instead of 200 (Fig. 4). When we used smaller sample sizes, nonlinearity in the settlement–abundance relationship was less obvious (Fig. 4). Only when recruit mortality alone or when all demographic rates were density dependent was it still clear visually (Fig. 4, b and d). When density dependence affected only the mortality and movements of adults, curvilinearity was visually obvious with 200 data points (Fig. 3, c and e). With 15 data points, however, the departure from a straight line was minimal even when the linear regression was forced through the origin, and we believe would be difficult to demonstrate statistically (Fig. 4, c and e). In summary then, local-scale density dependence does cause curvilinearity in large-scale relationships between settlement and abundance, with the degree of curvature depending on which demographic rates are density dependent. The curvilinearity may, though, be sometimes hard to detect with the small sample sizes feasible in empirical studies.

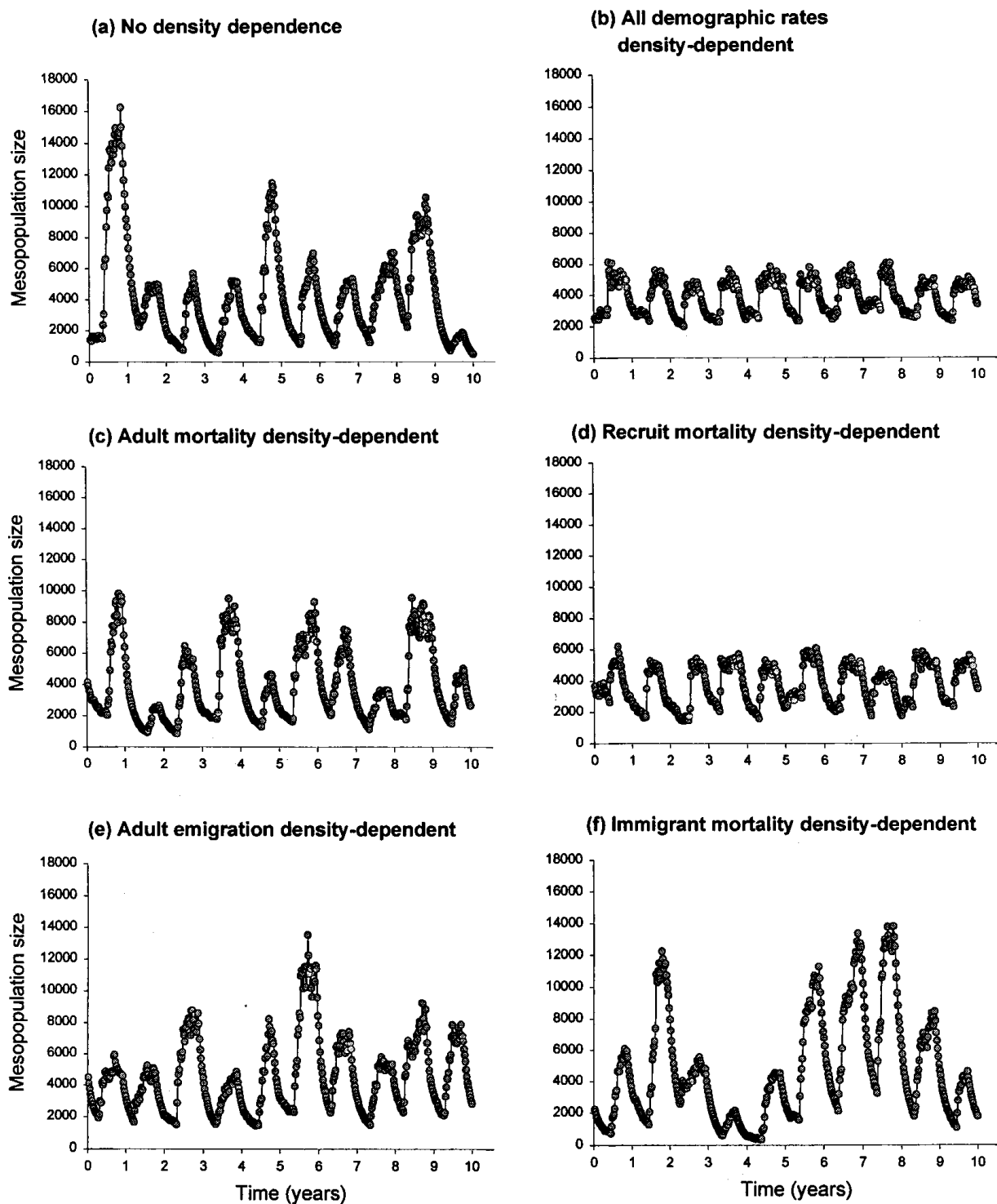
## B. Question 2: How Does Local-Scale Density Dependence in Different Demographic Rates Affect Temporal Fluctuations in Mesopopulation Abundance?

We addressed this question informally by inspecting plots showing how mesopopulation abundance fluctuates over time in the presence and absence of

density dependence (Fig. 5). We conducted a more rigorous test of the stabilizing influences of density dependence by systematically varying the strength of density dependence in demographic rates. To accomplish this, simulations were run with density dependence in demographic rates set to 20 different levels, ranging from absent to complete ( $m$  was varied from 0 to 1 in increments of 0.05). One simulation was run at each level of density dependence and, as usual, each simulation yielded 10 years of data on goby abundance. Mesopopulation variability for a given strength of density dependence was measured as the coefficient of variation (CV) around the mean annual abundance (averaged across the 10 years of the simulation).

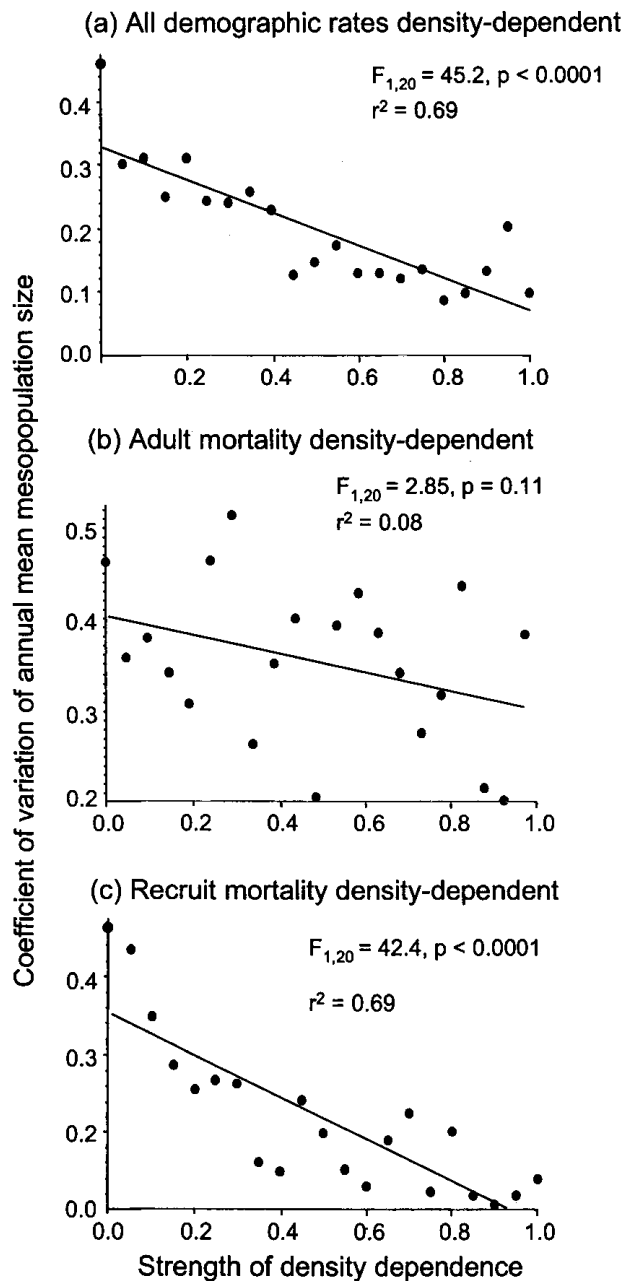
Inspection of fluctuations in abundance simulated with and without density dependence shows that goby abundance oscillated on an annual cycle under all conditions simulated because of the seasonality in larval settlement (Fig. 1) and the short life-span of the species. In the absence of density dependence, the amplitude of the oscillations was quite variable from year to year (Fig. 5a). Temporal fluctuations in mesopopulation abundance were, though, damped to varying degrees by spatial density dependence at the population level. Relationships between the strength of density dependence and mesopopulation variability were always negative (Fig. 6). The relationship was strong, and statistically significant, when all demographic rates were density-dependent (Fig. 6a) and the stabilizing effect was visually obvious in this case (Fig. 5b). When density dependence occurred in only one demographic rate, its influence depended on which rate was density dependent. Population-level spatial density dependence in recruit mortality had a visually obvious stabilizing effect on mesopopulation abundance (Fig. 5d). The stabilizing effect on mesopopulation dynamics was highly significant (Fig. 6c), and nearly as strong as when density dependence occurred in all demographic rates (compare Fig. 5, b and d and Fig. 6, a and c). A less visually obvious (Fig. 5f) but statistically significant stabilizing effect was apparent when only the survival of immigrants was related to population density (linear regression of CV on strength of density dependence;  $F_{1,20} = 10.6$ ,  $p = 0.004$ ,  $r^2 = 0.33$ ). In contrast, when density-dependent mortality was experienced only by resident adults, the effect on mesopopulation dynamics

**FIGURE 4** Plots of mean mesopopulation size in a given year versus the total settlement that year, as in Fig. 3, except that only 15 points selected randomly from the corresponding graph in Fig. 3 are shown in each case. Fifteen points is an optimistic estimate of the sample size possible in field studies that measure the relationship between mesopopulation size and settlement. Note in some cases in which the actual relationship is clearly curvilinear (see Fig. 3, c and e), with a sample size of 15, it is difficult to distinguish the curvilinear fit of those points from a linear fit (c and e). Linear regression (with and without a constant) and hyperbolic regression lines are fitted to the data.



**FIGURE 5** Plots of mesopopulation size over time for individual simulation runs under six different conditions. Plots differ in whether spatial density dependence at the local population level was (a) absent, (b) present in all demographic rates, (c) present in adult mortality only, (d) present in recruit mortality only, (e) present in adult emigration only, or (f) present in the mortality of immigrating adults. Note that the fluctuations in abundance were strongly dampened when recruit mortality (d) or all demographic rates were density dependent (b), and dampened to a lesser degree when other rates were related to density (c, e, and f). Each simulation run displayed was selected at random from the 20 runs generated using each parameter set. All populations experienced normal migration rates.





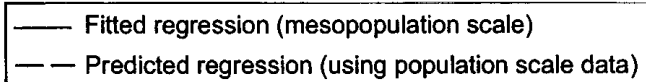
**FIGURE 6** Relationships between temporal variability in mesopopulation size (coefficient of variation around the mean of annual abundance) and the strength of spatial density dependence at the local population level. Each point represents the result from a single simulation run. All populations experienced normal migration rates. They differed in whether spatial density dependence at the population level was (a) present in all demographic rates, (b) present only in adult mortality, or (c) present only in recruit mortality. In all three cases, variability in population size declined as the strength of density dependence increased; however, this decline was statistically significant only in a and c.

appeared to be slight (Fig. 5c) and, in fact, density-dependent adult mortality did not have a statistically significant dampening effect on fluctuations in abundance (Fig. 6b). Similarly, there was also no significant effect on mesopopulation dynamics of altering the degree of density dependence in adult emigration (Fig. 5e; linear regression of CV on strength of density dependence;  $F_{1,20} = 2.41$ ,  $p = 0.14$ ,  $r^2 = 0.07$ ). In general, local-scale density dependence causes damping of temporal fluctuations in mesopopulation size, the strength depending on which rates were density dependent.

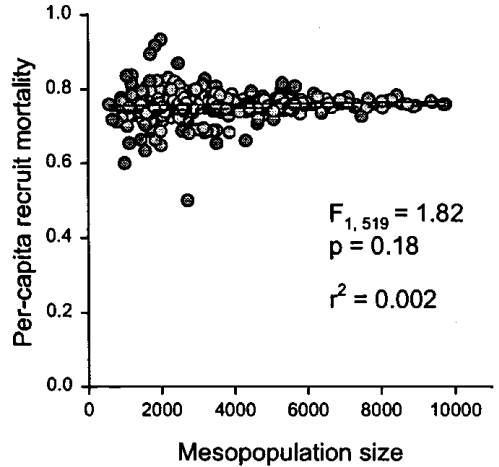
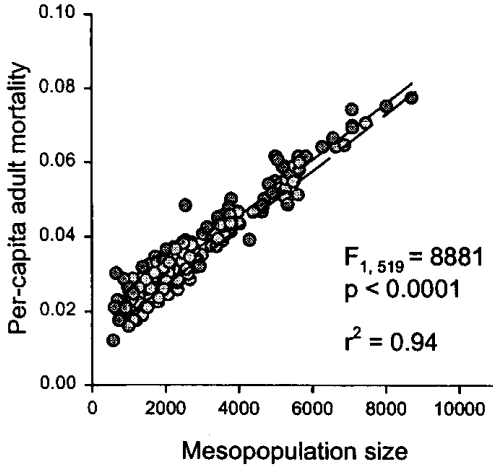
### C. Question 3: Are Relationships between Density and Demographic Rates the Same for the Mesopopulation and Its Component Local Populations?

The demographic characteristics of the entire mesopopulation matched closely the characteristics of populations on individual reefs. This result is well illustrated by a simulation in which density dependence occurred only in adult mortality and all other demographic rates remained density independent (Fig. 7a). When density-dependent mortality occurred at the population level, it appeared also at the mesopopulation level. Per-capita mortality of adults throughout the mesopopulation increased significantly when their abundance over the entire reef array increased (Fig. 7a). The form of the function appears linear. In addition, this functional relationship between per-capita mortality rate and abundance at the mesopopulation level very closely resembles the population-level per-capita mortality rate function scaled up to the mesopopulation level (Fig. 7a). For any demographic rate in this model, this scaling up is accomplished simply by creating a new mesopopulation demographic function  $F(X)$  by replacing  $x$  on the right-hand side of Eq. (3) with  $X/441$ , where  $X$  represents mesopopulation abundance and 441 is the number of censused reefs in the array. This extrapolation from the population to the mesopopulation level tacitly assumes that population abundances on individual reefs are always equal. Except at time 0, this condition is never satisfied, of course, and the slight difference between the fitted regression line and the scaled-up population function certainly arises from between-reef variation in population abundance.

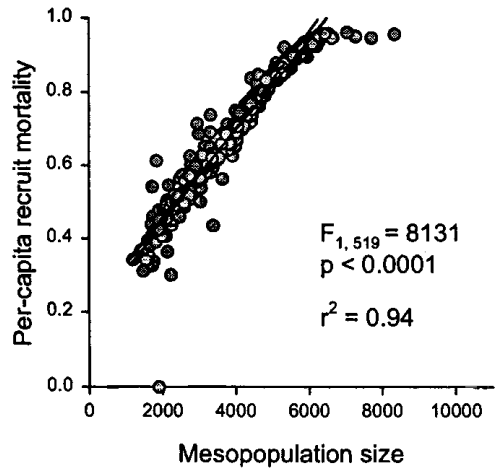
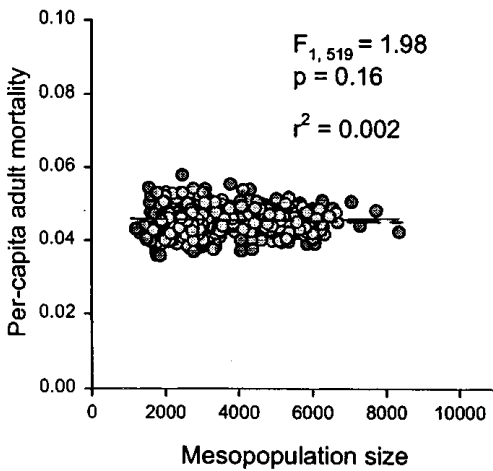
When population-level density dependence occurred only in the adult mortality rate, all other mesopopulation-level demographic rates proved independent of mesopopulation density. For example, recruit mortality observed over the entire mesopopulation was density independent, as it was on individual



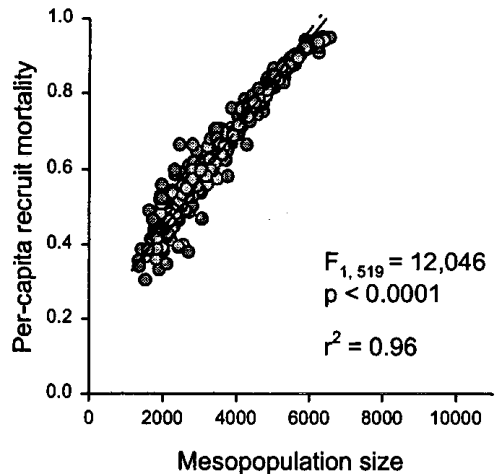
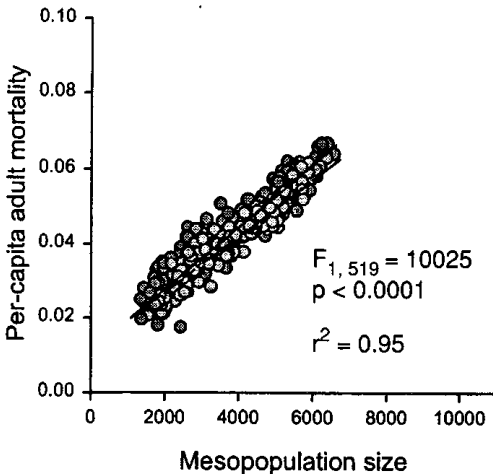
(a) Density dependence only in adult mortality ( $m = 0.75$ )



(b) Density dependence only in recruit mortality ( $m = 0.75$ )



(c) Density-dependence in adult and recruit mortality ( $m = 0.75$ )



reefs (Fig. 7a). Again, the statistically fitted mesopopulation function closely matched the scaled-up population function. The same was true for emigration and emigrant survival (data not shown).

Similar patterns arose in simulations involving density dependence in other demographic rates. By way of illustration, we consider a simulation in which only the mortality of recruits was density dependent (Fig. 7b). When the loss during recruitment was higher on high-density patches of reef, per-capita recruit mortality across the mesopopulation was also positively related to abundance across the entire reef array. The large-scale relationship between per-capita recruit mortality and density again closely resembled the scaled-up population-level function. In this case, deviations from linearity arose at very high mesopopulation densities, at which the recruitment mortality probability in most individual populations reached its maximum value of 1, as specified by Eq. (4). As before, other demographic rates that were independent of density at the population level remained so at the mesopopulation level, and observed rates closely matched scaled-up population-level rates (Fig. 7b).

The close match between demographic rate functions at small and large scales was preserved when more than one population-level demographic rate depended on abundance. For example, the simulation involving population-level density dependence in mortality of both adults and recruits displayed similar density dependence at the mesopopulation level (Fig. 7c). This pattern prevailed with density dependence in all possible combinations of demographic rates. In all cases, observed mesopopulation per-capita rate functions closely resembled scaled-up versions of the corresponding population-level functions. The most conspicuous deviations from linearity again occurred at mesopopulation densities sufficiently high to cause complete mortality in many individual populations. Simply put, demographic functions developed using data on small habitat patches always "scaled up" accurately to populations at larger spatial scales.

TABLE 1 Linear Regression Statistics<sup>a</sup>

Migration rate	Regression equation	$r^2$	P
Zero	$y = 0.040x + 658$	0.95	<0.0001
Normal	$y = 0.042x + 877$	0.94	<0.0001
High	$y = 0.033x + 311$	0.98	<0.0001

<sup>a</sup>These regression statistics describe relationships between mean mesopopulation size in a given year ( $y$ ) versus the total settlement that year ( $x$ ) when all demographic rates are density independent ( $n = 200$ ). Results are shown for three different rates of migration among individual reefs.

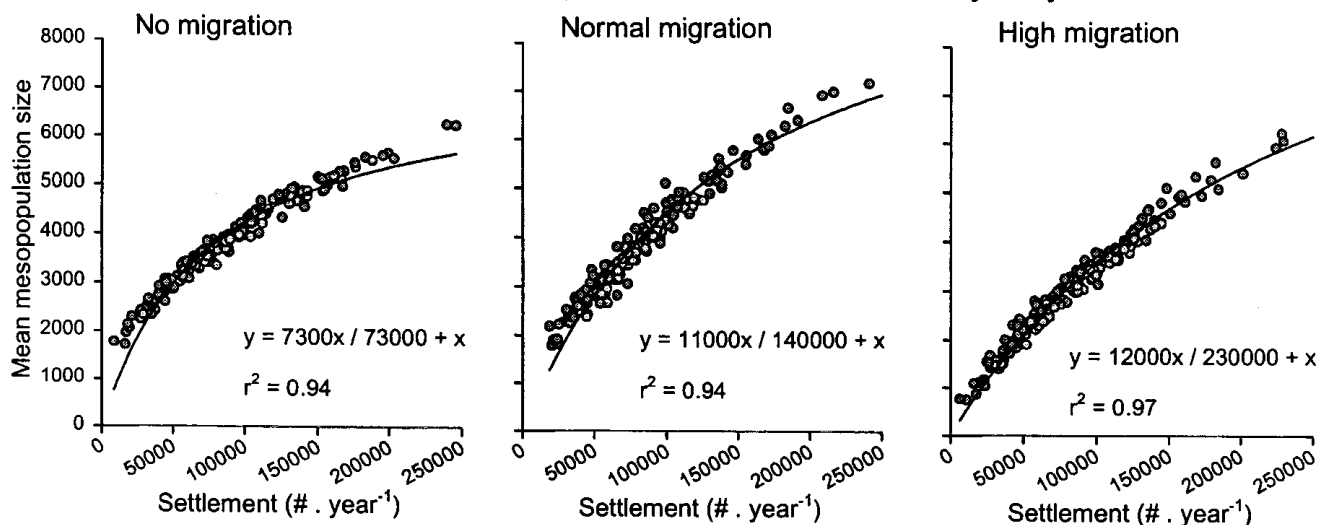
#### D. Question 4: How Does the Amount of Adult Migration between Local Populations Influence the Answers to Questions 1–3?

Not surprisingly, varying the rate of movement among reefs had little influence on the large-scale relationship between settlement and abundance in the absence of small-scale density dependence, (Table 1). At each of the three levels of migration we simulated, the relationship was very well described by a straight line and the regression equations best fitting the data are quite similar (Table 1).

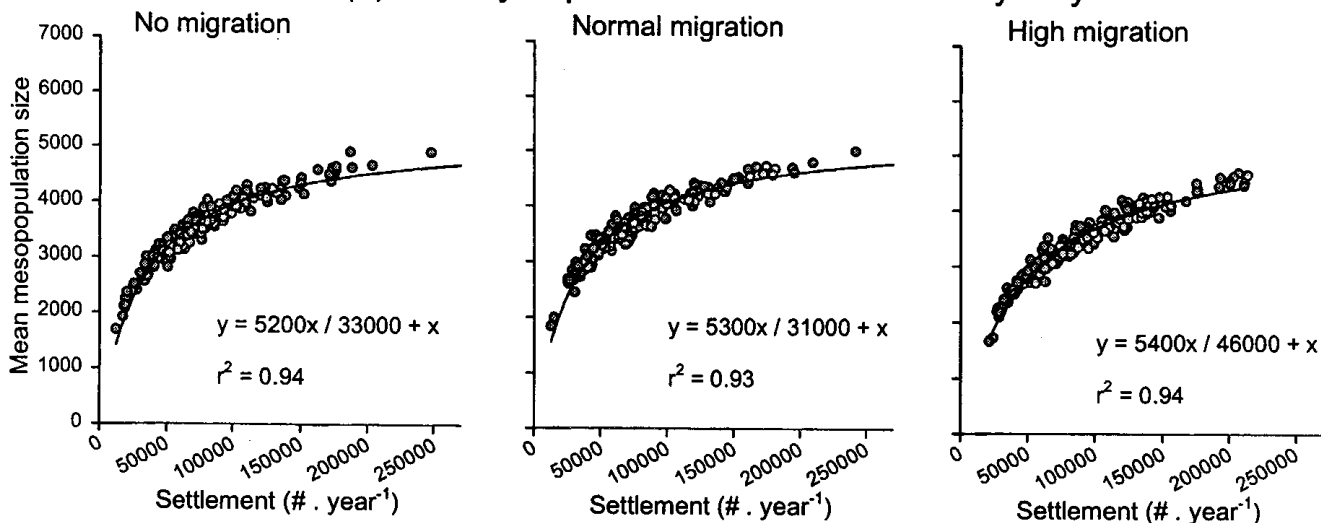
When fishes on individual reefs experienced density-dependent mortality, an increase in migration among patches of reef always reduced the degree of curvature in the large-scale relationship between settlement and abundance, and increased the level at which the mesopopulation abundance appeared to level off at high settlement rates. The quantitative influence of migration depended on whether it was recruits or adults that suffered density-dependent mortality. To illustrate this point, we consider simulations for which small-scale spatial density dependence was occurring in either adult mortality only, or in recruit mortality only (Fig. 8). In both cases, the large-scale relationship between settlement and abundance is more curvilinear and the asymptotic mesopopulation size is lower when gobies remain on the reef to which they settle as larvae,

**FIGURE 7** Relationships between demographic rates and abundance at the mesopopulation level. Per-capita demographic rates were calculated for each week during simulation runs, 10 years in duration each (yielding 520 points per graph). Gobies migrated at normal rates during all simulations, and the strength of density dependence ( $m$ ) was always 0.75. Displayed are simulations run when density dependence occurred (a) only in adult mortality, (b) only in recruit mortality, and (c) in both demographic rates. Relationships between demographic rates and abundance at the mesopopulation level are defined by linear regression (solid lines), with regression statistics shown on each plot. Also shown is the mesopopulation-level relationship predicted from the underlying function at the population level (dashed line). Note that the observed relationships differ little, if at all, from the predicted relationships; in other words, density dependence at the local scale "scaled up" almost perfectly to the mesopopulation scale.

## (a) Density dependence in adult mortality only



## (b) Density dependence in recruit mortality only



**FIGURE 8** Plots of mean mesopopulation size in a given year versus the total settlement that year. The plots show cases in which there is density dependence (a) just in adult mortality or (b) just in recruit mortality. In both cases, plots are displayed for cases in which migration among reefs did not occur, occurred at normal rates measured for bridled gobies, or occurred at five times the normal rate. Note that variation in the rate of migration had no effect on the qualitative relationship between mesopopulation size and settlement rate, but it did quantitatively affect the relationships between these variables, particularly when only adult mortality was density dependent (a). Data are plotted for each of the 10 years simulated in each of the 20 simulation runs for a given parameter set, yielding 200 points (years) per graph. Hyperbolic regression lines are fitted to the data.

compared to situations when they are able subsequently to migrate among reefs. This effect of increased migration is visually obvious when density dependence was restricted to adult mortality, and is apparent from the changes in the parameters of the hyperbolic regression fitted to the settlement–abundance relationships

(Fig. 8a). Increased migration among patches of reef had a much less obvious effect when density-dependent mortality occurred during recruitment. In this case, the degree of curvature in the relationship between settlement and mesopopulation size, and the abundance at which mesopopulation size appears to “level off” at

high settlement rates, did not vary appreciably with the migration rate (Fig. 8b). As a result, the regression equations best fitting the relationships between settlement and abundance were similar at each of the migration rates simulated (Fig. 8b).

When movement among individual reefs was density dependent, either because emigration was related to density or because the survival of immigrants declined at high densities, increasing the overall rate of movement exaggerated the large-scale consequences of density dependence (Fig. 9). Specifically, an increase in migration among patches of reef from "normal" to "high" levels increased the curvature in the large-scale relationship between settlement and abundance, and lowered the level at which the mesopopulation abundance appeared to asymptote at high settlement rates (Fig. 9).

We evaluated the effect of migration on mesopopulation stability using simulations in which we varied both the strength of density dependence in demographic rates and the rate at which adult fishes moved among reefs. Simulations were run when density dependence occurred only in adult mortality, or only in recruit mortality. Twenty simulations were run with density dependence in the specified demographic rate varying progressively from absent to complete. One simulation was run at each level of density dependence and each simulation yielded 10 years of data on goby abundance. Mesopopulation variability for a given strength of density dependence was measured as the coefficient of variation around mean annual abundance (averaged across the 10 years of the simulation). To test the influence of migration, we ran a set of 20 simulations at each level of migration among reefs (zero, normal, and high).

The overall rate of adult migration did not markedly affect temporal mesopopulation variability, regardless of which demographic rates were density dependent. For example, when adult gobies experienced density-dependent mortality on reefs, there was a stabilizing effect on fluctuations in abundance at the mesopopulation level. This was true whether migration was simulated at the "normal" levels estimated from our empirical data, was set to zero, or was simulated at higher rate than normal (Fig. 10a). We compared the relationship between mesopopulation variability and the strength of density dependence among the different migration regimes using analysis of covariance (ANCOVA). This analysis confirmed a significant negative relationship between mesopopulation variability and the strength of density-dependent mortality (indicated by a significant effect of "density dependence" in the ANCOVA, Table 2). There was, however, no detectable influence of the movement rate on the slope or

elevation of the relationship (indicated by a nonsignificant "migration" term, and a nonsignificant "interaction" term in the ANCOVA, Table 2). A similar pattern emerged from simulations in which small-scale density dependence was restricted only to recruit mortality. The stabilizing influence on mesopopulation dynamics appeared slightly stronger and more consistent under these circumstances (Fig. 10b). There was still, however, no significant effect of changing the rate of migration on mesopopulation dynamics (Table 2). Overall, then, changes in the rate at which fishes redistributed themselves among local populations had quantitative effects on mesopopulation dynamics that were sometimes very subtle and other times quite pronounced. There were, however, no qualitative changes in mesopopulation dynamics.

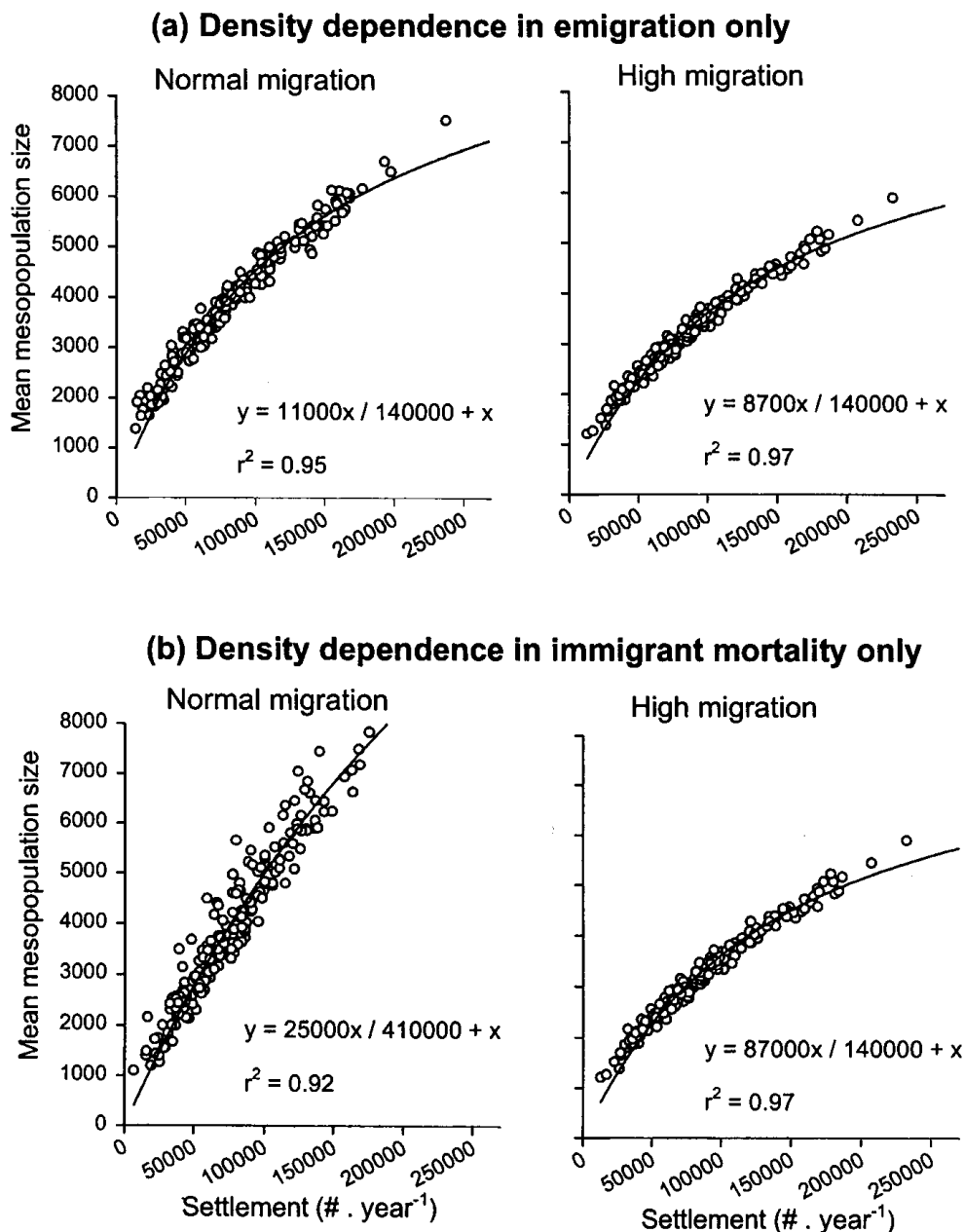
## V. Discussion

### A. Local-Scale Density Dependence Does Affect Population Dynamics at Large Scales

Overall, our model predicts that density-dependent interactions occurring among groups of fishes occupying small patches of reef, a few meters across, are not irrelevant when we expand our field of vision to areas that are kilometers in extent. As a result of local-scale density dependence, mesopopulation abundance ought to show a nonlinear relationship with settlement so that mesopopulation size will begin to level off when settlement rates are very high. Correspondingly, the mesopopulation should fluctuate within bounds that are sufficient to prevent abundance from precisely tracking variation in settlement. Our results are thus in accord with other models for open populations that incorporate variable recruitment and density dependence, but do not address multiple spatial scales (Warner and Hughes, 1988; Holm, 1990; Pfister, 1996).

### B. The Effects of Density Dependence Vary Depending on Which Demographic Rates Are Related to Density

Interestingly, the model indicated that the quantitative influences of local density dependence on mesopopulation abundance were strongly conditional on which demographic rates were functions of density. These differences arose from the specifics of bridled goby demography that we used to parameterize the model. For example, density dependence in recruit mortality



**FIGURE 9** Plots of mean mesopopulation size in a given year versus the total settlement that year. The plots show cases in which there is density dependence (a) just in adult emigration or (b) just in the mortality of adults immigrating to new patch reefs. In both cases, plots are displayed for cases in which migration among reefs occurred at normal rates measured for bridled gobies, or occurred at five times the normal rate. For both cases (emigration and immigrant survival), increasing the rate of migration strengthened the effect of density dependence (i.e., lowered the asymptotic density of the mesopopulation). Data are plotted for each of the 10 years simulated in each of the 20 simulation runs for a given parameter set, yielding 200 points (years) per graph. Hyperbolic regression lines are fitted to the data.

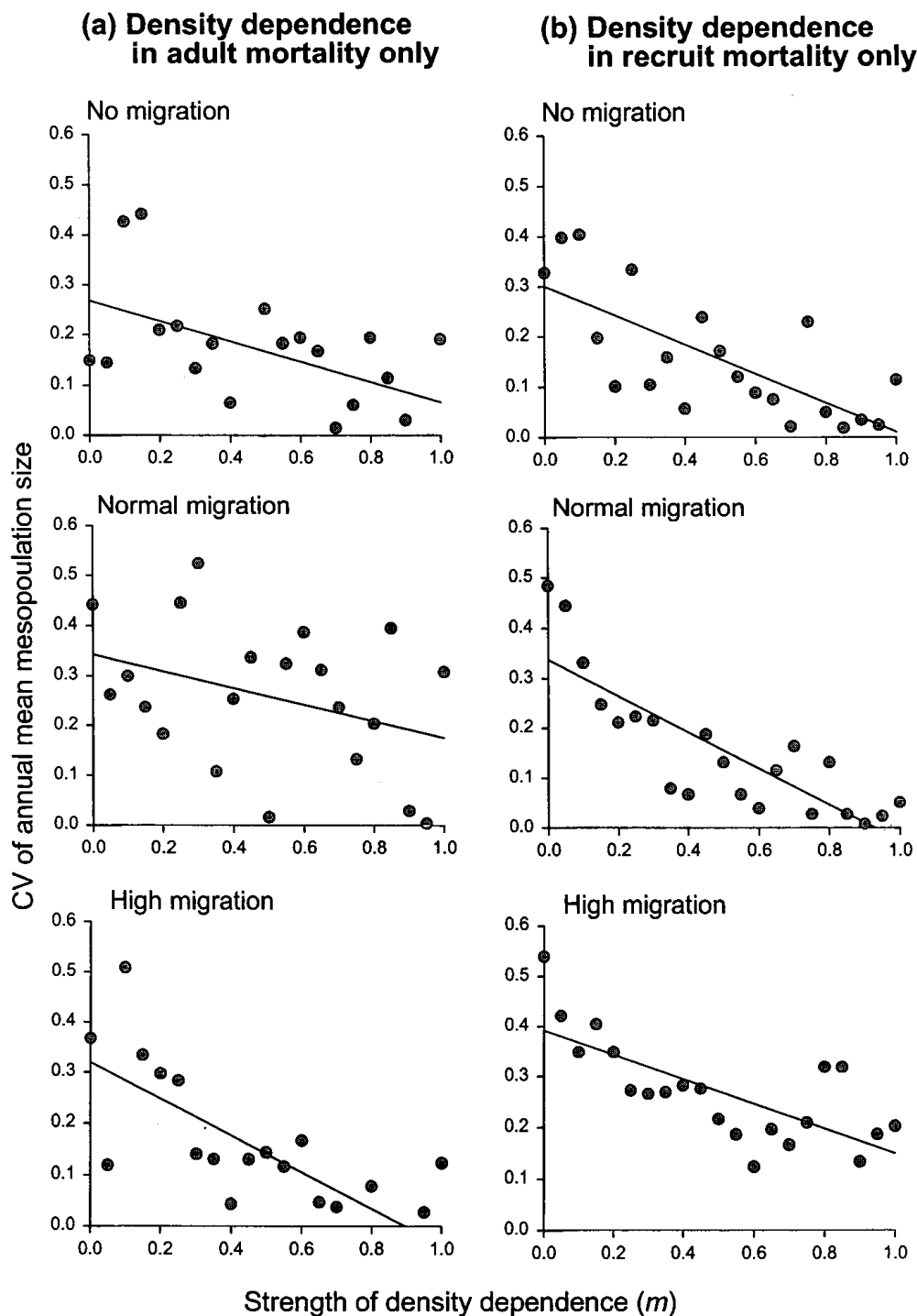


FIGURE 10 Relationships between temporal variability in mesopopulation size (coefficient of variation around the mean of annual abundance) and the strength of spatial density dependence at the population level ( $m$ ). Each point represents the result from a single simulation run. Populations differed in whether spatial density dependence at the population level was (a) present in adult mortality only or (b) present in recruit mortality only. In each case, plots are displayed for simulations during which gobies migrated among reefs at three different rates: zero, normal, and high (five times normal). Variation in the rate of migration did not alter the moderating influence of density dependence on fluctuations in mesopopulation size (i.e., slopes of the relationships did not differ among the three levels of migration; see Table 2).

**TABLE 2** Analyses of Covariance Testing the Effect of Migration Rate on the Relationship between Mesopopulation Variability and the Strength of Density Dependence<sup>a</sup>

Source	Sum-of-squares	df	Mean square	F ratio	P
<b>Density dependence only in adult mortality</b>					
Migration	0.017	2	0.008	0.64	0.529
Density dependence	0.336	1	0.336	25.72	0.000
Interaction	0.039	2	0.019	1.49	0.234
Error	0.732	56	0.013	—	—
<b>Density dependence only in recruit mortality</b>					
Migration	0.024	2	0.012	1.96	0.150
Density dependence	0.510	1	0.510	84.74	0.000
Interaction	0.014	2	0.007	1.17	0.319
Error	0.343	57	0.006	—	—

<sup>a</sup>Temporal variability in mesopopulation size was measured as the CV around the annual mean of mesopopulation size measured during a 10-year simulation. The strength of density dependence was varied systematically from absent ( $m = 0$ ) to complete ( $m = 1$ ). Migration of gobies among reefs was set to one of three levels: zero, normal, or high.

exerted a greater influence on mesopopulation properties than did density dependence in adult mortality, simply because the death rate of gobies is higher early in life. Similarly, density dependence in migration (when migration occurred at normal rates) exerted a relatively minor influence because adult gobies do not redistribute themselves among patches very frequently. More interestingly, density dependence in all four demographic rates together exerted a stronger moderating influence on mesopopulation abundance than did density dependence in any one rate alone. However, the combined effect was far less than additive because the number of individuals that experienced each demographic process had already been moved closer to the long-term average population abundance by density dependence in earlier demographic events. These findings are enlightening for those of us who have conducted density manipulations and measured responses over limited periods in the life cycle. They highlight the value of models in assessing the relative "importance" of such interactions for population dynamics.

### C. Local Density Dependence Should Lead to Population Regulation

Most of the other open-population models for marine species are tailored to organisms for whom space is clearly limited (such as barnacles on the rocky shore or kelp plants on hard substrata), and therefore incorporate density dependence in a form that may not be applicable to most reef fishes (Hughes, 1984; Roughgarden

*et al.*, 1985; Bence and Nisbet, 1989; Nisbet and Bence, 1989; Possingham *et al.*, 1994; Johnson, 2000). In these space-limited marine communities, adults inhibit settlement by occupying space necessary for settlement and this has a strong influence on population dynamics. Settlers arriving at one point in time inhibit settlement at some point in the future once they grow to become adults. The time lag between settlement and the inhibition of later settlement can introduce cyclic fluctuations in abundance into what is otherwise a stable population (Bence and Nisbet, 1989) [but see also Possingham *et al.* (1994), for an alternative explanation]. The same sort of time-lagged inhibitory interactions at the time of settlement have not been documented in reef fishes, and space limitation is unlikely to operate in the same fashion in reef fishes. We do know, however, that adult reef fishes can have other types of inhibitory effect on juveniles (e.g., Sale, 1976; Jones, 1987a,b; Tupper and Boutilier, 1995b). It would be informative to explore the consequences of these interactions through the inclusion of more stage structure in future models.

Apart from the specific form of density dependence caused by space limitation, other agents of density-dependent mortality tend to stabilize abundance in previous models of open marine populations (Gaines and Lafferty, 1995), and density-dependent mortality consistently had the same effect on the mesopopulation in our simulations. The important implication is that local density dependence in reef fishes is of the sort that ought to regulate abundance and so may contribute to the global, long-term persistence of reef fish populations.



Of course, because our simulated mesopopulation is demographically open, it shared another feature with previous models for open marine populations—that the absolute settlement rate was independent of local population density. This pattern of simulated settlement was based on our field observations of bridled gobies and on published data on other reef fishes and so is realistic. Density independence in the absolute rate of settlement also stabilizes populations because it causes per-capita rates of settlement to be density dependent (Hughes, 1984; Roughgarden *et al.*, 1985; Bence and Nisbet, 1989), but knowing this does not help us understand population regulation unless we know what controls the settlement rate (Chesson, 1996). In other words, it means we need to identify the regulatory interactions that occur at scales larger than the mesopopulation and that put bounds on the settlement rate.

#### **D. Migration among Local Populations Does Not Obscure the Effects of Local-Scale Density Dependence**

Encouragingly, the model results predict that changes in the overall rate at which adult fishes move among reefs should not cause qualitative changes in mesopopulation dynamics. For example, allowing fishes to redistribute themselves among patches did not negate the influence of local density-dependent interactions, as some workers have speculated, though the influences of density-dependent recruit mortality and adult mortality were reduced somewhat when migration rates were highest. Local interactions detected by experiments should not, therefore, be dismissed *carte blanche* as irrelevant to population dynamics at large scales. The potential influences of local movement are, in reality, more complex than to simply to homogenize patches, because the propensity to move and the ability to relocate successfully may be functions of population density. Density dependence in the rate at which fishes leave reefs, and in their chance of successfully relocating to a new reef, both had a measurable effect on mesopopulation abundance. Not surprisingly, the strength of these regulatory effects increased when movement became more frequent.

#### **E. Local Density Dependence Scales Up Accurately**

The close similarity of mesopopulation-level demographic rates in our simulations to scaled-up population-level demographic rate functions is perhaps

somewhat surprising in light of Chesson's (1996, 1998a) perceptive observations about spatial averaging of nonlinear population growth rates. Chesson points out that between-population variation can potentially cause growth of an assemblage of interconnected local populations to differ qualitatively from growth of a single isolated population. Biologically, this difference arises from the fact that the average individual selected from a collection of local populations experiences a higher local density than occurs in the average local population. Mathematically, it arises because, with nonlinear functions, the operations of arithmetic averaging and function evaluation do not commute; that is, the average of a function is not in general equal to the function of the average.

Although Chesson states his observations in terms of complete population growth functions, his argument applies also to their components, namely, the rates at which various demographic processes occur. Calculations similar to his (not shown) establish that the true mesopopulation-level per-capita demographic rates in our model are actually not linear functions of mesopopulation density, even when the corresponding population-level demographic rate functions are. Rather, deviations from linearity occur, and their magnitudes increase, with the variance in local population abundance. However, our numerical results, which employ parameters we consider realistic for the bridled goby, show that deviations from linearity appear so slight as to be visually indistinguishable in appropriate graphs (e.g., Fig. 7). The sole exception to this pattern arises at very rarely achieved mesopopulation abundances that are high enough to kill most individuals present in most local populations. Except at such high densities, enlarging the perspective in our bridled goby model from the population level to the mesopopulation level preserves not just the qualitative forms of the per-capita demographic rate functions, but also their actual numerical values. That is, numerically calculated mesopopulation demographic rates fall very close to the population demographic rate functions scaled up to the mesopopulation level.

How faithfully scaling up population properties reproduces corresponding properties at the mesopopulation level (and the metapopulation level) in other fish species (and other organisms in general) is a topic that richly deserves further study. Chesson's (1996, 1998a) calculations suggest that accuracy of scaled-up demographic functions will deteriorate as local populations become more variable. Whether this subtle mathematical principle will exert a measurable effect when accompanied by other powerful natural processes that operate at larger spatial scales (such as nonrandom

movement of large ocean water masses) remains to be learned.

## **F. Does the Form of Density Dependence in Reef Fishes Match That in Our Model?**

How closely our model results resemble the properties of real mesopopulations depends entirely on whether our modeling assumptions are realistic. A key question is whether the functions relating demographic rates to population density are a good fit to relationships derived from field data. We have found that the relationship between the finite rate of mortality in bridled gobies and their population density closely approximates the function we chose for the model (G. E. Forrester, R. R. Vance, and M. A. Steele, unpublished). Migration in bridled gobies can also be density dependent (G. E. Forrester, unpublished), but the data are insufficient to define the form of the relationship. We need to better define these relationships for bridled gobies and test how well they describe these same relationships in other species. Density manipulations with this purpose in mind should treat population density as a continuous variable (e. g., Forrester, 1995; Steele, 1997b; Schmitt and Holbrook, 1999a) rather than as a categorical variable with just a few levels (e.g., Jones, 1987a,b; Forrester, 1990).

## **G. Do Our Findings Apply to Reef Fishes in General?**

Although our efforts in this chapter were focused on simulating bridled goby populations, the model could easily be parameterized with demographic data from other species. In this way, it would be possible to make comparisons among species and ask questions about the generality of our findings. For example, how might changing factors such as the longevity of the species, or the seasonality of recruitment, influence mesopopulation dynamics? The substantial body of published research on damselfishes could easily be used for this purpose, and would provide a useful contrast to our results. Another possibility would be to utilize demographic data on larger species that are the subject of commercial and artisanal fisheries (e.g., Matheson and Huntsman, 1984; Polovina and Ralston, 1987, and references therein; Acosta and Appeldoorn, 1992; Bullock and Murphy, 1994; Kara and Derbal, 1995; Chakraborty and Vidyasagar, 1996; Rocha-Olivares, 1998). We desperately need information on the population ecology of many such species in order to more effectively manage their exploitation

and conserve their populations (Russ, 1991). These species are, however, much harder to study in the field compared to the smaller species that we know the most about, and are usually studied using methods borrowed from temperate fisheries biology (e.g., Polovina and Ralston, 1987, and references therein). Along with other colleagues (e.g., Doherty and Fowler, 1994a; Hixon and Carr, 1997), we have sometimes argued that small reef fishes are good "model systems" that provide insights into the ecology of larger exploited reef fishes, and of demersal fishes in general (usually we have made this argument when trying to secure funding for our work on small species!). Frankly, we have seen no evidence that either supports or refutes this contention. If, however, gobies and damselfishes are good models for understanding groupers and snappers, then our model ought to predict qualitatively similar population dynamics when parameterized with demographic rates appropriate for both small and large species.

## **H. How Should We Best Test for Density Dependence at Large Scales?**

Testing for density dependence at large spatial scales, and assessing its effects on dynamics, would obviously be a lot of work, and so one of our major goals was to gain some insight into how we can best perform such a test in the field. Testing for the regulation of mesopopulation abundance by examining the relationship between settlement (not recruitment) and adult abundance is feasible, though logistically demanding (M. A. Steele and G. E. Forrester, unpublished data). In our simulations, the nonlinearity in this relationship caused by local density dependence was not always visually obvious with a realistically small sample size (15 points), and the relationship would be hard to differentiate statistically from a straight line. The two key messages to field ecologists are, therefore; that (1) exploring the relationship between adult abundance and settlement may be an insensitive, and ineffective, way to test for the regulation of mesopopulations, and that (2) apparently linear relationships between juvenile and adult abundance (e.g., Doherty and Fowler, 1994a) do not rule out density dependence.

To be more optimistic, our model suggests that relationships between population size and demographic rates scale up very well. Significant relationships between mortality and density at the local scale have been detected with as few as eight replicates (e.g., Forrester, 1995), so collecting mortality data at large scales and relating death rates to population size may perhaps be

a more effective way to test for density dependence in real mesopopulations. The discovery of annual growth rings in some reef fishes (e.g., Fowler and Doherty, 1992) is significant in this context, because it means that constructing an age-specific mortality schedule for a mesopopulation is feasible. It then would be possible to use the conventional life-table approach (e.g., Varley *et al.*, 1973) to test for regulation of a real mesopopulation. Ironically, one of the criticisms of this method in other systems is that it can detect temporal density dependence among generations, but often fails to detect exactly the sort of spatially localized, density-dependent interactions occurring within specific life history stages that we know to be quite common among reef fishes (Hassell, 1986, 1987). What has been a drawback in some systems is thus a boon to those of us reef fish ecologists eager to understand the long-term dynamical behavior of populations.

Of course, we really need to collect long-term census data on reef fishes to assess adequately whether our model simulations capture the essential features of population dynamics. For many species this will take a concerted and patient effort because they have lives that are not much shorter than our own. We make this point

because of the rapid expansion of monitoring programs on coral reefs in most parts of the world. So far, most of the programs are being designed to collect qualitative or semiquantitative community-level data. We think there is a case for including quantitative censuses in these programs, perhaps of just a few well-chosen species, and that the information gained might improve our children's ability to manage and conserve populations of reef fishes.

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