

# Spatial scales in the study of reef fishes: A theoretical perspective

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**Abstract** Theoretical models imply that spatial scale derives its greatest importance through interactions between density-dependent processes and spatial variation in population densities and environmental variables. Such interactions cause population dynamics on large spatial scales to differ in important ways from predictions based on measurements of population dynamics at smaller scales, a phenomenon called the scale transition. These differences can account for large-scale population stability and species coexistence. The interactions between density dependence and spatial variation that lead to the scale transition can be understood by the process of non-linear averaging, which shows how variance originating on various spatial scales contributes to large-scale population dynamics. Variance originating below the scale of density dependence contributes less to the scale transition as the spatial scale of the variation declines, while variation originating on or above the scale of density dependence contributes independently of the spatial scale of the variation.

**Key words:** density dependence, metapopulation, spatial variation, stability.

## INTRODUCTION

Various important processes taking place in reef-fish systems have recognizable spatial scales. The size of an individual's home range or the extent of its daily foraging activities are scales that may also set a scale of limitation of food resources. Variation in food density on smaller scales may not affect individuals, while changes on the same or larger scales would. The scale of predation or disease is likely to be much larger than these scales. Mobile predators, acting in a density-dependent way, must respond to prey density on a larger scale than the home range of individual prey of solitary species. Thus, the scale of food limitation may be quite different from the scale of predation.

While processes may have recognizable scales, variables, such as population density, that we use to characterize systems, can normally be defined on any scale. However, the dynamics of variables may be highly scale dependent. For example, fluctuations over time in population density will often be greater on smaller spatial scales, but more fundamental changes in the nature of population dynamics may occur with a change in scale according to modern ecological theory.

The stability of a population (Hassell 1987), the coexistence of competitors (Caswell 1978; Hastings 1980; Chesson 1985) and the stability of predator-prey interactions (Comins & Hassell 1987; Reeve 1988; Hassell *et al.* 1991; Wilson *et al.* 1993) may depend on structuring of populations in space across a variety of scales.

Variation in population densities and/or environmental variables is an essential aspect of spatial structuring. Much less appreciated is the fact that density dependence (Forrester 1995; Holbrook & Schmitt 1995) plays a critical role in the effect that scale and variation in space have on population dynamics. Although there is a tendency to regard spatial and temporal variation as eliminating or reducing the effects of density dependence (Caswell 1978; den Boer 1981; Andrewartha & Birch 1984; Doherty & Williams 1988), it is now known that such variation gains its main importance through its interaction with density dependence (Chesson 1996). Moreover, the importance of scale in ecology derives primarily from this interaction.

It is the purpose of this article to explore some simple ways of understanding the interaction between variation and density dependence in the context of reef-fish communities. Although the development below is almost entirely for the single-species case, it need not be. Indeed, much of the literature deals with interactions between species. However, the key issues can

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be understood more simply in the single-species context. The presentation here is a quantitative complement to a graphical approach used in Chesson (1996).

The analysis below considers a population structured in space. On a small spatial scale, individuals may potentially interact with one another leading to density dependence. Such density dependence could lower survival rates (Forrester 1995), reduce reproduction (Jones 1991) or inhibit recruitment into the population (Stimson 1990). Whatever the cause, the overall effect of this density dependence is to lower per capita contributions to the next generation as densities increase, except in the case of an Allee effect where the reverse situation applies. Each unit of space on the small scale is assumed to define a local population, and such local populations are connected on a larger spatial scale by dispersal of larvae. However, local populations may also be connected by migration of adults. The key question is how population dynamics on the larger spatial scale are affected by variation in population density from unit to unit on the small scale.

**CHANGES IN POPULATION DYNAMICS WITH SCALE**

There is a simple relationship between population densities on different scales: values on larger scales are averages of values on smaller scales (Chesson 1996). To understand how population dynamics change with scale, however, we must introduce some simple models. Let the population density of a species in the *i*th unit of space on a small scale at some time *t* be *N<sub>i</sub>(t)*. Population density on a larger scale including *n* units on the small scale is thus:

$$\bar{N}(t) = \frac{1}{n} \sum_{i=1}^n N_i(t) \tag{1}$$

On the smaller scale, the relationship between the density, *N<sub>i</sub>(t + 1)*, one unit of time later, and *N<sub>i</sub>(t)* can be written as some function (*F*) of density:

$$N_i(t + 1) = F(N_i(t)) \tag{2}$$

In the simplest case, *F* might represent density-independent survival and reproduction from one time to the next so that:

$$N_i(t + 1) = RN_i(t) \tag{3}$$

where *R* is the constant (and therefore density independent) finite rate of increase. In general, these relationships will not be deterministic, and at any locality there will be some deviation of *N<sub>i</sub>(t + 1)* from the predicted density, *F(N<sub>i</sub>(t))*, uncorrelated with *N<sub>i</sub>(t)*. However, such deviations do not affect the arguments here (Chesson 1981).

Larger-scale population dynamics can be obtained by averaging smaller-scale population dynamics:

$$\bar{N}(t + 1) = \frac{1}{n} \sum_{i=1}^n N_i(t + 1) = \frac{1}{n} \sum_{i=1}^n F(N_i(t)) \tag{4}$$

and in the case of density-independent survival and reproduction (equation 3), this equation reduces to:

$$\bar{N}(t + 1) = R\bar{N}(t) \tag{5}$$

Thus, the relationship describing population dynamics on the smaller scale also describes population dynamics on the larger scale. In symbols this means

$$\bar{N}(t + 1) = F(\bar{N}(t)) \tag{6}$$

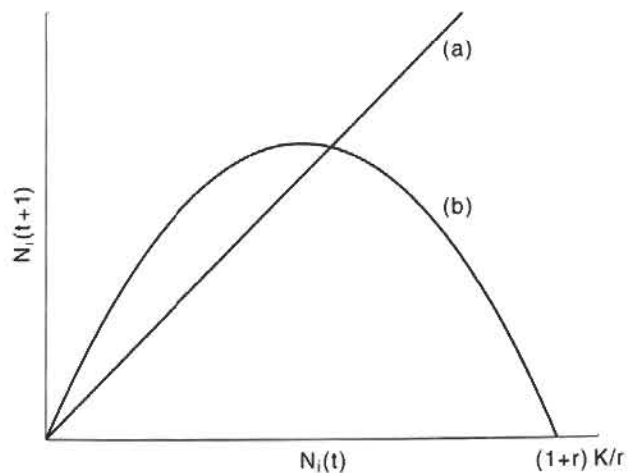
This outcome is the intuitive expectation of most people. However, it is a very special case. In general equation 6 is false, and the fact that it is false in general has profound consequences for population dynamics. Equation 6 is true only in the very special case when *F* is linear; that is, when the plot of *N<sub>i</sub>(t + 1)* against *N<sub>i</sub>(t)* is a straight line (e.g. line (a) of Fig. 1; i.e. when population dynamics are density independent).

Non-linear equations describe density-dependent dynamics. Equation 4 then involves averaging a non-linear function of *N<sub>i</sub>(t)*. Such non-linear averaging (Chesson 1996) means that the new population density, *N̄(t + 1)*, on the larger scale depends not just on the density the time before but also depends systematically on the variance, *σ<sup>2</sup>*, of the density on the smaller scale. The actual contribution of the variance is difficult to define precisely in general. However, in Appendix I, I derive a general approximation that shows that:

$$\bar{N}(t + 1) = F(\bar{N}(t)) + c\sigma^2 \tag{7}$$

where the quantity *c* may depend on population density *N̄(t)* but not *σ<sup>2</sup>*. This expression implies a change in population dynamics, passing from the small scale to the larger scale, approximately of the form:

$$N(t + 1) - F(\bar{N}(t)) = c\sigma^2 \tag{8}$$



**Fig. 1.** Relationships between small-scale population density at successive points in time; for example, successive years. (a) Density-independent dynamics, (b) logistic dynamics.

Thus, at least approximately, the prediction of the smaller-scale population dynamical equation is in error by an amount proportional to the variance on the smaller scale. I shall refer to this difference as the scale transition. The familiar logistic equation of density-dependent population growth provides an illustration, where in fact equations 7 and 8 are exact.

We can write the logistic equation in discrete time as:

$$N_i(t+1) - N_i(t) = r(1 - N_i(t)/K)N_i(t) \quad (9)$$

Rearranging to see just what  $F$  is here, we have:

$$N_i(t+1) = N_i(t) + r[1 - N_i(t)/K]N_i(t) \quad (10)$$

The right-hand side of equation 10 is  $F(N_i(t))$ , which is plotted as line (b) in Fig. 1. With this definition of  $F$ , taking the average to obtain the dynamics on the larger scale yields:

$$\bar{N}(t+1) = \bar{N}(t) + r[1 - \bar{N}(t)/K]\bar{N}(t) - (r/K)\sigma^2 \quad (11)$$

This equation is in exact agreement with equation 7; moreover, we find that the quantity  $c$  here is simply a constant,  $-(r/K)$  (Appendix I). Thus, there is a reduction in the density on the larger scale at time  $t+1$  due to variation on the smaller scale. Variance on the smaller scale has produced a stronger overall effect of competition on the larger scale. This effect can be understood intuitively by considering a simple example.

Suppose half the units on the smaller scale, which might be called 'patches', have population density  $0.5\bar{N}(t)$ , and half have density  $1.5\bar{N}(t)$ . Then three-quarters of the population are in the higher density patches. Half the patches are high density, but three-quarters of the population is in those patches. Thus, three-quarters of the population experiences competition at 1.5 times the level predicted by the average, and only one quarter experiences competition at half the level predicted by average population density. To bring the point home more strongly, consider a more extreme situation where half the patches have zero density and the other half have a density of  $2\bar{N}(t)$ . Then all of the population is in the high density patches and so all individuals in the population experience double the level of competition that one would predict from the average density alone. These examples show that variance increases the average level of competition experienced by individuals in a population over that predicted by the average density. It therefore should not be too surprising to find that smaller scale variance has an effect on the dynamics of population density on the larger scale.

Clearly the effect described here is not specific to the logistic model but applies to competition generally. It can apply also to positive density-dependent effects (Allee effects; Knowlton 1992). Such positive density-dependent effects would occur, for example, when

higher density patches provide some protection from predation if predators do not aggregate or do not persist longer in such higher density patches (Marschall *et al.* 1989). In this case, variance on the smaller scale increases the net beneficial effect of higher densities, and the quantity  $c$  is therefore positive.

To allow prediction of when these effects will occur, Appendix I gives the following general formula for  $c$ :

$$c = 0.5 F''(\bar{N}(t)) \quad (12)$$

that is, half the second derivative of  $F$  evaluated at  $\bar{N}(t)$ . The second derivative can be thought of as the deviation from a linear relationship at that point on the curve. It will be positive whenever the change in  $F(N)$ , with a change in  $N$ , increases with the value of  $N$ . It is negative in the opposite situation. The approximation (equation 8) for the scale transition will be most accurate over ranges of values where  $F''$  remains fairly constant. The formula is exact for the logistic model simply because, being a quadratic,  $F''(N)$  is the same for all  $N$ . Qualitatively, we see that the logistic given as (b) in Fig. 1 curves over in the same direction for all densities, reflecting the constant value of  $F''(N)$ .

The quantity  $F''(N)$  may change in sign with  $N$  as depicted in curves (a) and (b) of Fig. 2, which then change the nature of the scale transition. Curve (a) shows an Allee effect at low density (the accelerating portion of the curve). At higher densities, competition

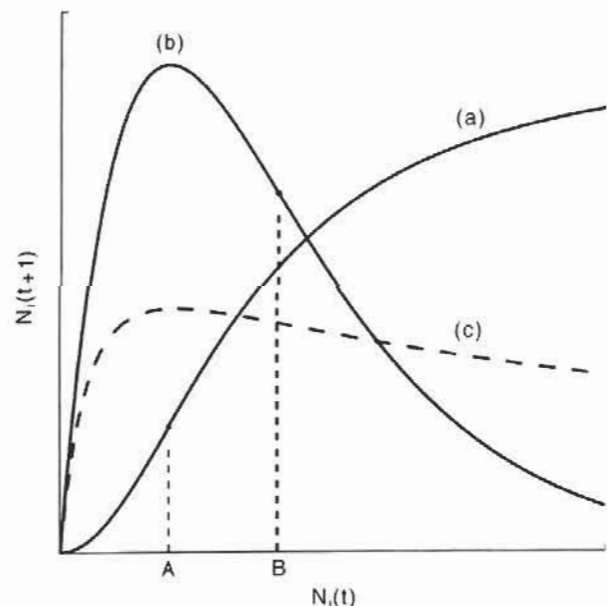


Fig. 2. Relationships between population density at successive points in time. (a) Small-scale dynamics with an Allee effect at low density and contest competition at high density. (b) Small-scale scramble competition, for example the Ricker equation (Chesson 1996). (c) Large-scale dynamics resulting from (b) and high small-scale variation in population density.

of the contest form is assumed, and thus  $N_i(t+1)$  rises to a plateau as a function of  $N_i(t)$ . In reef-fish systems, contest competition may occur, for example, if fishes are territorial and compete for space (Sale 1977). In contrast, curve (b) of Fig. 2 has a large hump, which may represent scramble competition resulting when insufficient food at higher densities leads to failure of development and death (Huston & DeAngelis 1987). Alternatively, the hump in (b) of Fig. 2 could come from strong density-dependent predation.

If curve (a) applies, the positive value of  $F''(N)$  over the range 0 to  $A$  means that smaller scale variation within this range will lead to higher population densities,  $\bar{N}$ , on the larger scale one time unit later (i.e. a positive scale transition). Beyond the point  $A$ , where competition is dominant and  $F''(N)$  is negative, smaller-scale variation leads to lower population densities on the larger scale one time unit later (a negative scale transition). These changes diminish the Allee effect on the larger scale. An Allee effect in a reef-fish system might conceivably arise from inversely density-dependent predation associated with a saturating functional response (Murdoch & Bence 1987). A population with an Allee effect would be vulnerable to extinction, but the scale transition means that such vulnerability may disappear on the larger spatial scale.

A dramatic scale transition can occur when the scramble competition curve (b), Fig. 2, applies. The quantity  $F''(N)$  is negative over the range 0 to  $B$ , and positive higher than  $B$ . Thus, there is a negative scale transition for the density range 0 to  $B$ , and a positive scale transition for local densities exceeding  $B$ . As equations 7 and 8 indicate, the scale transition depends on the magnitude of the variance on the smaller scale, but with enough variance on the smaller scale, the relationship between  $\bar{N}(t+1)$  and  $\bar{N}(t)$  is similar to the dashed curve (c) of Fig. 2 (Chesson 1996). In other words, with the change in scale, and variance on the smaller scale, scramble competition produces a result on the larger scale resembling contest competition. Population dynamics from these two sorts of competition are really quite different. The population dynamics described by curve (b) are highly unstable. Large fluctuations, and even chaotic dynamics occur (Fig. 3a). The curve (c) implies very stable population dynamics (Hassell & May 1985; Chesson 1996), as depicted in Fig. 3b. Thus, unstable dynamics on a small spatial scale coupled with variation in density from place to place on that scale may lead to stable dynamics on the larger scale.

#### DEPENDENCE OF VARIANCE ON DENSITY

For a full understanding of the scale transition, it is necessary to know how variance changes with population density and, more generally, how variance changes with

time. There are many complexities associated with migration and dispersal processes (Levin 1992; Gaines & Bertness 1993), environmental variability (Reeve 1988; Botsford *et al.* 1994), aggregation processes (Doherty 1987; Shorrocks & Rosewell 1987; Hassell *et al.* 1991) and instabilities in local population dynamics (Chesson 1981). However, spatial distributions in nature are often found to lie somewhere between a Poisson distribution and a negative binomial distribution with constant aggregation parameter (Hassell *et al.* 1991). In the Poisson case, the variance  $\sigma^2$  is simply equal to the larger scale density, while for the negative binomial distribution,  $\sigma^2 = \bar{N}(t) + [\bar{N}(t)]^2/k$ , where  $k$  is the aggregation parameter. Small values of  $k$  mean highly aggregated or patchy spatial distributions. The Poisson formula is a special case of the negative binomial with  $k$  equal to  $\infty$ .

Substituting the negative binomial variance formula in equation 11 for larger scale population dynamics yields

$$\bar{N}(t+1) = \bar{N}(t) + r'[1 - \bar{N}(t)/K']\bar{N}(t) \quad (13)$$

where  $r' = r(1 - 1/K)$ , and  $K' = (K - 1)/(1 + 1/k)$ . Thus, larger scale population dynamics remain logistic but the parameters of the equation are different. The primed values applicable on the larger scale are all less than their smaller scale counterparts, revealing slower average growth on the larger scale and a lower carrying capacity. With a Poisson distribution ( $k = \infty$ ) it should not be too surprising that the effects of variance on dynamics are quite small unless the carrying capacity is very small (just a few individuals per patch on the smaller scale). Large effects of variation require clumped distributions ( $k < \infty$ ), and the effect of such clumping is to lower the larger-scale carrying capacity.

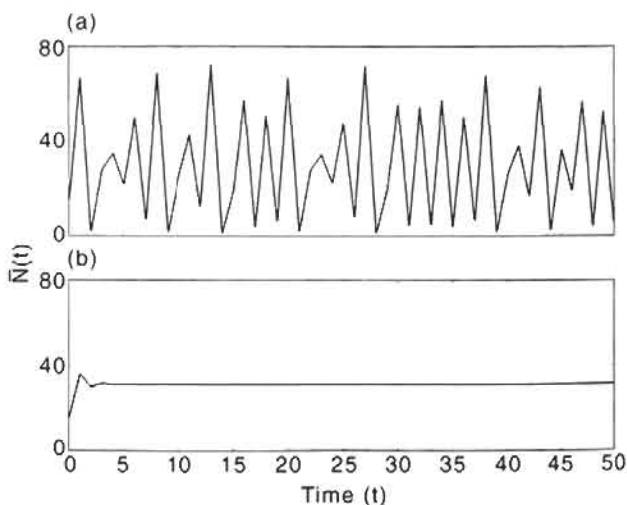


Fig. 3. (a) Simulation of large-scale dynamics with Ricker dynamics on the small scale and no spatial variation. (b) Simulation of large-scale dynamics with Ricker local dynamics and negative binomial spatial variation with  $k = 0.5$ . See Chesson (1996) for full details.

However, these results should be treated with some caution if  $r$  is large (as the logistic equation predicts negative values of  $N_i(t+1)$  for  $N_i(t) > (1+r)K/r$ ) and so should not be used whenever there is appreciable probability of local populations in this range. In fact, it is best to think of the discrete-time logistic equation as merely an approximation to models like (b) and (c) (Fig. 2) over restricted ranges of densities.

### RELATIVE SCALES OF VARIANCE AND DENSITY DEPENDENCE

The development above assumes that the smaller scale under consideration is also the scale on which density dependence occurs. However, density dependence can occur on a variety of scales. Choosing the right scales is important for understanding the interaction between spatial variation and density dependence. For example, Poisson variation only has much effect on larger scale population dynamics if smaller scale population sizes are very small. The smaller the scale of density dependence, the smaller these local population sizes will be, and the larger the effect Poisson variation will have.

Variation on smaller scales than the scale of density dependence is relevant to larger scale population dynamics only to the extent that it creates variation on the scale of density dependence. For example, the variance,  $\sigma^2$ , discussed above might be expressed as a sum (Underwood 1981):

$$\sigma^2 = \sigma_1^2 + \frac{\sigma_2^2}{n_2} + \frac{\sigma_3^2}{n_3} + \dots \quad (14)$$

where  $\sigma_1^2$  represents variation arising on the scale of density dependence, each of  $\sigma_2^2, \sigma_3^2, \dots$  represents a source of variation arising on a particular scale below the scale of density dependence, and  $n_2, n_3, \dots$  represent the total number of statistically independent units on each of these scales contributing to one unit on the scale of density dependence. As  $n_2, n_3, \dots$  is an increasing sequence, equation 14 shows that the importance of variance on small scales decreases as the scale decreases.

How does variation originating on scales higher than the scale of density dependence contribute to population dynamics on some yet larger scale? At issue is the total amount of variation between units on the scale of density dependence within a unit on the scale on which we wish to predict population dynamics. If scales 2, 3, ... are now defined as larger than the scale of density dependence (scale 1), then the total variance on the scale of density dependence is:

$$\sigma^2 = \sigma_1^2 + \sigma_2^2 + \sigma_3^2 + \dots \quad (15)$$

Thus, variation on scales higher than the scale of density dependence contributes undiminished to the modification of large-scale population dynamics.

If density dependence occurs on a small scale, but is measured on a larger scale, the results here show that the measured density-dependent relationship will not be the pure effect of density, but will already include some of the interaction between spatial variation and density dependence discussed previously (i.e. some non-linear averaging and a scale transition will already have taken place). This possibility has some important practical consequences for estimating density-dependent relationships from observational data. Choosing a scale that is too large may give a misleading impression of the nature and strength of fundamental biological interactions taking place in a system (Hassell 1987; Ray & Hastings 1996). This does not mean, however, that the observed dynamics on a larger scale are in any sense less real than those on a smaller scale. Instead, it reflects the fact that the outcome on a larger scale may have a greater number of causes, and therefore be more difficult to disentangle.

### DISCUSSION

The results here show how spatial variation in population density may interact with density-dependent processes to change the nature of population dynamics with a change in scale. This effect is called the scale transition (Chesson 1996). Spatial variation and density dependence can clearly occur on a multiplicity of scales, although for simplicity the development here assumes that density dependence arises on one scale only. The magnitude of the interaction between spatial variation and density dependence depends on their relative scales. Variation originating on scales much smaller than the scale of density dependence is unlikely to contribute substantially to variance on the scale of density dependence, and therefore is unlikely to contribute substantially to the interaction between spatial variation and density dependence.

Variation does not have important effects on scales much larger than its origin unless it interacts with density dependence (Chesson 1996). Thus, variation and density dependence should not be thought of as alternative explanations of ecological phenomena such as population persistence and species coexistence, where the nature of population dynamics on large spatial scales is critical. Indeed, explanations of such major population and community phenomena increasingly depend on the interaction between variation and density dependence. It is important to take a broad view of density dependence, however, if the full potential for its interaction with variation is to be understood. Density dependence can be indirect in its action, working through intermediaries such as resources or predators, often with a time lag (Chesson 1996). Moreover, density dependence may have its immediate effects not on numbers of individuals but on individual growth and size (Doherty & Williams 1988).

For simplicity of presentation, the discussion here has been restricted to the single-species situation with population density varying in space, while the physical environment has been assumed to be the same everywhere. However, theoretical explorations of the scale transition have more commonly examined multispecies systems where persistence of predator-prey or host-parasitoid associations, and coexistence of species, are the key outcomes of the interaction between multi-species density-dependence and spatial variation (Caswell 1978; Hastings 1980; Chesson 1981, 1985; Comins & Hassell 1987; Ives 1988; Reeve 1988; Hassell *et al.* 1991; Durrett & Levin 1994). Multi-species density dependence involves not just dependence of an individual species' per capita growth rate on its own density, but dependence of the per capita growth rate on the densities of other species too.

The role of spatial environmental variation in population dynamics has received less attention than the role of spatial variation in population densities, but there is no reason to believe that it is any less important in nature. Theoretical models implicate spatial environmental variation in species coexistence (Levin 1974; Chesson 1985; Comins & Noble 1985; Iwasa & Roughgarden 1986; Ives 1988), in essence, providing spatial niches of various sorts. For example, in a particular locality, a species may have a relative advantage over other species by having a higher competitive ability (Comins & Noble 1985) or a higher survival rate (Chesson 1985) in that locality. Alternatively, a particular species may simply have a higher rate of migration into (Chesson 1985) or aggregation at (Ives 1988) a particular locality. Such different responses to the environmental features of a locality distinguish the niches of the species. The intermediate disturbance hypothesis as explored by Hastings (1980) can also be regarded as an instance of coexistence resulting from spatial environmental variation. In Hastings' model, environmental events may be regarded as causing catastrophic mortality locally in space, which initiates succession and allows regional coexistence of species in a landscape consisting of many patches at different successional states. Spatial environmental variation also theoretically plays a role in the persistence and stability of predator-prey and host-parasitoid interactions (Reeve 1988; Hassell *et al.* 1991). Like spatial variation in population densities, interactions between environmental variation and density-dependent processes are key to the effects that spatial environmental variation has. However, this issue is far better understood in the case of temporal environmental variation (Chesson 1994).

Reef-fish systems are noted for their high variability in time and space. The results of this article encourage a view in which this variation is important through its interaction with density-dependent processes. Variation should not be seen as eliminating density dependence

but modifying it quantitatively and qualitatively when viewed on a larger scale. Population units on local scales are far from independent of one another, and so a local system cannot be understood without an understanding of inputs from larger scales. However, as population dynamics at large scales reflect the interaction between local-scale density dependence and variation from unit to unit on the local scale, the whole system cannot be understood without reference to the nature and variability of the internal structure. Perplexing problems of reef-fish systems such as population regulation and diversity maintenance may well be explained by such interactive effects of the spatial components of a system.

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## APPENDIX I

Second-order Taylor expansion of the non-linear function ( $F$ ) leads to the quadratic approximation

$$N_i(t+1) \approx F(\bar{N}(t)) + F'(\bar{N}(t))[N_i(t) - \bar{N}(t)] + 0.5 F''(\bar{N}(t))[N_i(t) - \bar{N}(t)]^2 \quad (\text{A1})$$

Summing over  $i$  and dividing by  $n$  shows that

$$\bar{N}(t+1) \approx F(\bar{N}(t)) + c\sigma^2 \quad (\text{A2})$$

where  $c = 0.5 F''(\bar{N}(t))$ . The accuracy of this approximation depends on the closeness of  $F$  to a quadratic (equation A1) across the range of variation in local density. It is more useful as an illustration of how variation interacts with non-linearities than as a precise calculation. However, equation A2 is exact for the logistic equation as the logistic equation is quadratic. Differentiating the logistic shows that  $c = -r/K$ .

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