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Appropriate spatial scales for reef-fish studies: a theoretical perspective

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Processes and variables

Processes such as dispersal, nondispersive movement (within the home range), foraging activities, agonistic interactions and supply of resources may have particular spatial scales that can be recognised.

Variables such as population density, biomass, community composition, and species diversity are not attached to a particular scale but in principle have values on any scale. Variables are normally the way in which we seek to describe or characterise a system. And we normally seek to understand variables in terms of processes.

Properties of variables with changes in spatial scale

Larger scale values of variables are mostly numerical averages of their values on smaller scales (Chesson 1996). This is true for the variables population density and biomass, but not necessarily for species diversity, depending on the diversity measure used. However, even in the case of species diversity, the measure is generally based on vectors of species densities which do have the property that large-scale values are simple averages of smaller scale values. This fact means that characterising a variable with changes in scale is relatively simple in principle, as discussed below. Understanding is behaviour, however, is not necessarily so simple.

Describing what happens with changes in scale

For definiteness, take for example community composition, which we measure as the abundances of the list of potential species that may be found in the total region in question. A small area on a reef, for example tens of square metres, is likely to have composition that varies substantially over time and substantially in space as one examines other areas of reef of the same size. Such variation does not rule out characterising composition, but it must be done statistically. A statistical description of how composition varies in time and space becomes the characterisation of composition at the particular scale. Statistical description is simplest when composition can be assumed stationary in time and space (i.e. has constant statistical properties as reference points in time and space are moved), but on large scales such stationarity can never be the case. Instead, one needs a model of habitat variation that invariably has to be taken as given from measured physical attributes of the environment. Given such a model, larger scales can be characterised easily.

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Explaining the behaviour of a variable in terms of processes occurring at different scales

Density-dependence on a small scale is modified by heterogeneity to produce a different and often milder result on the larger scale: Consider first an example of the dynamics of population density. Assume that juveniles settle out of the plankton independently of the local population density, but that density limitation occurs on a local scale, say on a small patch of reef (e.g. Forrester 1995). (Such spatially local density limitation could occur if the species are territorial and compete for space, with failure to secure space leading to death rather than the ability to move elsewhere without a mortality cost. Alternatively, spatially local density limitation may come from something like limited local food production, e.g. for algal grazers with limited foraging range and limited mobility.) In such cases, there is some nonlinear function relating local density at some time after settling to local density at settling. Nonlinearity is the critical issue here and it follows from density dependence. If there were no variation in space, this nonlinear function would describe the dynamics of population density on all larger scales. However, variation in space means that it describes the dynamics just on this scale and just for a time interval that excludes the settling process (the settling process is a dynamical feature that depends on what is happening elsewhere in space too).

The reason that the local nonlinear function does not describe dynamics on a larger scale is *nonlinear averaging* (Chesson 1996). The result is a different nonlinear function for dynamics on larger scales which can be calculated on from the small-scale nonlinear function and a description of spatial variation (Hassell 1987, Chesson 1996). This function describing population dynamics on the larger scale frequently describes milder density dependence than that on the smaller scale. For example, the small-scale nonlinear function may suggest that population dynamics are chaotic, while the large-scale function implies that dynamics are in fact quite stable with just a very weak relationship between population density at one time and the density at the time before.

Nonlinear averaging means that any small-scale density-dependent interactions either within or between species are modified on the larger scale by small or intermediate scale heterogeneities: Most biological interactions within and between species lead to a density-dependent relationship between densities at one time and densities at another time. (These are not always densities of the same thing, for example, as in the single-species example above, the density at the earlier time is the density of the settling larvae, the density measured at a later time may be the density of recruits to the adult population derived from this cohort of larvae.) Density dependence, as remarked above, means that the relationship is nonlinear. Just as in the discussion of the dynamics of a single species, local density dependence and local variation will modify community dynamics on the larger scale. New issues in the multispecies context concern how the relationships between species are affected by nonlinear averaging. Within a guild of competing species (e.g. Holbrook and Schmitt 1995), will local interactions, coupled with variation lead to different relationships on the larger scale

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than the local relationships suggest? For example, will species that show strong interspecific competition in small-scale experiments have strong effects on each other on the larger scale? There is a possibility that interactions will not a change with a change in scale. The evidence to date, coming mostly from studies of temporal variation, with which spatial variation has parallels (Comins and Noble 1985, Chesson 1985), suggests that species must vary differently in space, or have different nonlinear responses to resource variation if there are to be fundamental changes in the relationships between species as one moves from the smaller to the larger scale (Chesson 1994). Of course species differ to some degree in many respects and so this may seem like a requirement likely to be satisfied (see e.g. Williams 1983). The point is however, that the changes in the relationships between species as the scale is changed depend quantitatively on the differences between species in their responses to space, or to spatially varying resources. Moreover, variation in space must lead to changes in the local intensity of competition ('covariance between environment and competition' Chesson 1994).

These issues can also be considered for predator-prey relationships. The question there is often, will variation and local interactions have the effect of stabilising what is often seen as an unstable interaction? The answer in general seems to be yes (Hastings 1977, Hassell and May 1985, Reeve 1988, Wilson et al 1993), but a study of host-parasitoid interactions has revealed some particular features involved (Hassell et al 1991). There, stability comes as a moderation of relationship between parasitoid density and host mortality on the larger scale due to small-scale variation in the risk of parasitism (Chesson and Rosenzweig 1991). Variation not involving the risk of parasitism, or only weakly related to it, would seem to have no effect or just a weak effect on stabilising the relationship.

In both the single-species and multispecies settings, the effects described depend on local variation either in densities of organisms or other factors affecting density-dependent dynamics. If such local variation in density is very small, then the difference between the local density relationship and the global one is very small. However, there are substantial effects from the major variation that we might expect in nature.

These findings belie the common assumption that density-dependent and equilibrium phenomena should be regarded as applying in different systems than density-independent phenomena and fluctuations. A study of scale implies that ecological systems can only be understood by studying the interactions between density dependence and fluctuations. Fluctuations may have density-dependent or density-independent origins, and an equilibrium on a large scale may be an outcome of lack of equilibrium on a small scale (Chesson and Huntly 1993).

Heterogeneity on a scale smaller than the scale of density limitation does not modify density-dependent relationships with changes in scale: If density limitation occurs on the scale of the whole system (e.g. if limitation occurs in a well mixed plankton, or if the food

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comes from a well mixed plankton in the case of food limitation), then local variation is irrelevant. Attempts to determine a local density relation will probably fail in any case--such a relation could perhaps be produced by artificial tank experiments where plankters are confined.

In the intermediate situation where the scale of local density limitation is less than the scale of the whole system, but larger than the scale of local variation, then local variation is still relevant to the change in density dependence with scale, but to determine how the density relation will change with scale, variation must be measured on the same scale as the scale of density dependence.

Observations or experiments on a larger scale than the scale of density dependence

In the single species context, the moderating of density dependence by nonlinear averaging can create the appearance on the larger scale of no density dependence with a density-independent rate of increase fluctuating close to zero. Indeed, a model fit to large-scale observations could give this impression but leave the observer with the puzzling observation of a growth rate fluctuating about zero for no apparent reason Hassell (1987). It is not, however, that there is truly no density dependence on this scale, just that the relationship is weaker (Hassell 1987).

In the multispecies context, observations on a larger scale may suggest that species function more or less independently of each other in spite of rather intense interactions that may be occurring on the lower scale. Whether or not the difference is this great, it is a common finding that relations between variables like species densities become weaker on higher spatial scales. For example, predator-prey relations can lose the tendency for predator-prey cycles as the spatial scale is enlarged (Hassell 1978). Moreover, competing species may not appear to influence each other's densities on the large scale: evidence from competition models indicates that the influence of interspecific density dependence is lessoned by small-scale variation (Comins and Noble 1985, Chesson 1985, Ives 1988, Durrett and Levin 1994). The study of Durrett and Levin (1994) emphasises that such effects are even possible from demographic stochasticity operating on a very small spatial scale if the scale of density dependence is very local.

Observations made on the large scale suggesting little density dependence or weak species interactions may be reasonable descriptions of dynamics at that scale, but do not explain some of the details, for example, why the growth rates are adjusted to near zero, even though density dependence is undetectable. And they may give the false impression that species do not interact. Perhaps most significantly, they lead to inaccurate predictions about the future as the temporal scale is enlarged. For instance, in the single-species context, to conclude that the population is truly density-independent is to assume also that its density will drift in the long run, so that some time in the future average population densities may be quite different from what they are now, or that augmenting the population by artificial increase in density may

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successfully increase the abundance of the species. In the multispecies context, one might conclude that removal of a predator or competitor would have little effect, when in fact in the long run dramatic changes in the system might ensue.

Observations or experiments on a scale smaller than the scale of density dependence

Experiments manipulating densities on a scale smaller than the scale of density dependence are likely to fail, as the manipulation is likely to be weaker than intended or ineffectual. Observational studies where such a mismatch occurs will generally involve much error in the independent variable (the density examined), weakening correlations and biasing any relationship that is present.

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