

## Ecology of sessile animals on sublittoral hard substrata: The need to measure variation

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### Abstract

*This paper concerns assemblages of sessile animals occupying shaded, commonly vertical hard substrata in the shallow subtidal zone. We are interested particularly in questions about the coexistence of species and about what influences their joint dynamics. We propose a conceptual model which focuses on variation in characteristics such as birth and death rates, competitive interactions and dispersal.*

*We argue that, qualitatively, this model appears to be a satisfactory representation of the important characteristics of certain sessile assemblages. Further, we suggest that it may explain the coexistence of a large number of ecologically similar species in assemblages that appear in a sense 'stable' (but where assemblages at different sites differ in detail). There is support for this assertion from formal theoretical work on simpler versions of the model.*

*It is not sufficient merely to argue that the model seems satisfactory or plausible, so we finally consider what kind of data is needed for the further development and testing of this kind of model.*

### Introduction

Within the context of 'temperate reefs' our focus is on assemblages of animals occupying shaded, commonly vertical, hard substrata in the shallow subtidal zone. Much of our experience comes from submerged, man-made structures, but such assemblages appear also on

reefs, where there are vertical walls and overhangs.

Five to ten years ago we would have said that our focus was on questions about the coexistence of species; how can so many species coexist; why don't some exclude others; why not more, or fewer species? We now prefer to say that we are searching for a satisfactory model, or picture, of how communities function and why. Species do coexist; it no longer seems helpful to ask why they do not fail to do so, and we want to ask more broadly what influences their joint dynamics.

It would be naive to suppose that the understanding we seek will be simple (in the sense that it involves few variables) or that it can be pursued exclusively at any one scale (using scale in the broadest sense), because animals and plants exist in what Andrewartha and Birch (1984) called a 'natural population' and Levins (1970) a 'metapopulation' — see, for example, Hanski (1989). Andrewartha and Birch's idea of a natural population is one that consists of a set of local populations within which most of the interactions take place, but between which there is limited dispersal. Much research on sessile communities has been concerned with how organisms interact within the area of a local population, but not how that affects the dynamics of the metapopulation. The most realistic numerical models so far developed for subtidal sessile communities (e.g. Karlson & Jackson 1981; Karlson & Buss 1984) are essentially one-reef or one-pile models, assuming a 'bath' of larvae. We are working towards a metapopulation view in which dispersal distributions and a variety of stock-recruitment and recruit-stock relationships have to be considered, rather than set at their means.

Field ecologists have always been familiar with variability, but only recently has it been incorporated effectively into models (a term in which we include non-mathematical, generally verbal representations which we shall call conceptual models). This deficiency has had im-

portant effects. In the past there has been a tension between the knowledge and intuition of field ecologists, and the view of ecological systems fostered by predominantly deterministic models. As long as the stochastic view remained qualitative and largely verbal, this tension seemed impossible to resolve. Chesson (1986) and Chesson and Case (1986) have reviewed stochastic models that reduce the tension; later developments are reported in Chesson (1988, 1989) and Chesson and Huntly (1988, 1989); see also Chesson (1984, 1985). The models show that the sorts of things with which field ecologists are familiar — patchiness, variability and so on — are consistent with the coexistence of many species, and indeed provide additional mechanisms *promoting stable coexistence*. These mechanisms are not incompatible with the ones invented under the deterministic view. The stochastic models are still simplifications of reality, but the situation now is that the stochastic view of an ecosystem is supported by analytical mathematics, as the deterministic view has been for a long time.

Because of the theoretical work that has been done so far, our outline of that view appears as a catalogue of mechanisms for coexistence; this reflects the older questions, but we see this as a series of steps towards a quantitative understanding of the joint dynamics of many interacting species, rather than merely a set of answers to the question 'how can they coexist?' Below, we outline our conceptual model, at each step alluding to both field observations and the theory that has so far been developed. At the end, we summarize our perceived needs for field data to test the model.

The essence of our conceptual model is that it focuses on *variation*, and the main thing we will be stressing about the kind of data needed is that it is necessary to *measure variation*. Yodzis (1986) had similar aims to ours in presenting in a unified way the various dynamical mechanisms for space limited communities. Our model may be regarded as an updating of Yodzis' work as specifically applied to sessile animals on sublittoral hard substrata.

### A conceptual model

Imagine that a water body, such as the Gulf of St Vincent in South Australia, is a closed

system and consists of nothing but a few reefs and piers, separated by sandy bottoms.

Substrata for sessile animals are patchy on all scales (for review see Connell & Keough 1985), but we shall concentrate on patch sizes where it might seem meaningful to talk about 'coexistence' — not a few cm<sup>2</sup> (smaller than a colony for many of the species under consideration) nor a whole gulf (so large that it surely contains subpopulations living under very different conditions and with different dynamics). Our local populations are likely to be generally larger than the patches discussed by Connell and Keough (1985). Within them, however, the patchiness and dynamics discussed by those authors is crucially important to our concerns.

We observe that piling and reef faunas are dynamic on a small scale (the size of a 50 cm × 30 cm quadrat), but on a larger scale, taking a jetty or a reef as a spatial unit, they are 'stable' in a sense based on Chesson's (1978) idea of stochastic boundedness, and consistently different between sites through at least a few years (Kay & Butler 1983; Butler 1986; unpubl. obs), so we consider a pier or reef as a candidate for 'local population' status.

We shall assume that the piers and reefs (henceforth simply called reefs) bear local populations of sessile organisms: the Gulf contains a metapopulation of each species. The metapopulation will be assumed closed, while the local populations are affected by migration.

### Local interactions

*Mechanisms not dependent on variation*  
The local community will have traits that tend to stabilize the interaction among species competing for space and other resources. For example, there will be some microhabitat specialization. Predation may limit the growth advantage that can be achieved by competitive dominants, and sometimes may be frequency dependent, tending to stabilize relative abundances. Competition may be intransitive and there may be size refuges from competition, competitive equivalence may occur, or some species may have mutualistic interactions that alter competition (Jackson 1977, 1979a,b; Osman 1977; Buss 1979, 1980; Buss & Jackson 1979; Karlson 1980; Russ 1980, 1982; Kay &

Keough 1981; Sebens 1982; Hiscock 1983; Keough 1984a,b; Chernoff 1987; Pitcher & Butler 1987). Interaction between physical and biological processes will influence settlement of larvae, to create spatial patchiness in settlement and hence probably in recruitment (e.g. Keough 1983; Burke 1986; Hadfield 1986; G. A. Jackson 1986; O'Donnell 1986).

These processes act independently of any fluctuations over time.

*Mechanisms that depend on temporal variation* Now, to begin elaborating our conceptual model: fluctuations over time may occur in the local population. Some of these may promote local diversity, independently of inputs due to migration. If some years are especially favourable to recruitment or growth of a species, and other years to other species, then — from models of simple systems of this sort (Chesson 1986) — we can expect the interaction to be stabilized in the sense that the local community will tend to recover from extreme perturbations of the densities of any of the component species, independently of inputs from the outside.

It is important that environmentally-dependent parameters (e.g. recruitment rates or individual growth rates) of different species have somewhat asynchronous fluctuations. Thus, the correlations in these parameters between species over time must be less than 1; the lower these correlations the more strongly fluctuations promote diversity.

The mechanism requires two additional conditions:

(1) A positive covariance between environmentally dependent parameters (e.g. recruitment) and competition. Environmental fluctuations affect interactions within and between species. When a species has intense recruitment, it may mean that there is more competition for space among incipient recruits. There may be a strong intraspecific effect for a species that produces many propagules at one time, and there may also be a strong effect on individuals of other species recruiting at the same time, regardless of how strong their recruitment is at the time. Environmental fluctuations that affect recruitment will then carry over to fluctuations in competition. We refer to this as a positive co-

variance between environment (in this case reflected in recruitment) and competition.

(2) Stabilization in the presence of such fluctuations depends on subadditivity in the response of growth rates to environment and competition.

In models, subadditivity is an interaction between environment (which, in a model, may influence recruitment or mortality rates) and competition, in the way they affect the growth rate of a population. Additive has its usual meaning; the total effect of the environment and competition is the sum of their separate effects (Fig. 1a). If growth rates are *subadditive*, then, as the quality of the environment decreases, the decline of growth rate with increased competition becomes less steep (Fig. 1b). *Superadditivity* is possible; the effect of an increase in competition can be greater during a poor environmental period than during a good one (Fig. 1c).

Given a positive covariance between competition and environment, subadditivity has a buffering effect, whereas superadditivity amplifies the unfavourable effects of variations in both environment and competition, and tends to be destabilizing with respect to coexistence. From the viewpoint of a field ecologist, subadditivity represents staying power in the locality; it means that the population can grow rapidly enough when conditions are favourable to compensate even for long unfavourable periods. Several kinds of life history characteristics can lead to subadditivity, mostly by contributing to a storage effect (i.e. the effect in which a positive average population growth rate occurs because of occasional favourable periods whose effect is 'stored' in a population with overlapping generations; Chesson 1984). Long-lived adults that can retain space even when they are not able to reproduce or expand vegetatively are an important case, well known in sessile communities. In terrestrial and freshwater environments, resting stages — spores or other propagules — can lead to subadditivity, and a new-equivalent in marine sessile communities is residual pieces of sponge (Ayling 1980, 1983b) or ascidian (Millar 1971) tissue, but its prevalence and ecological importance is a topic for research. Another mechanism for subadditivity is a shift to a 'safe' resource, which may be a particular microhabitat that is never used enough to

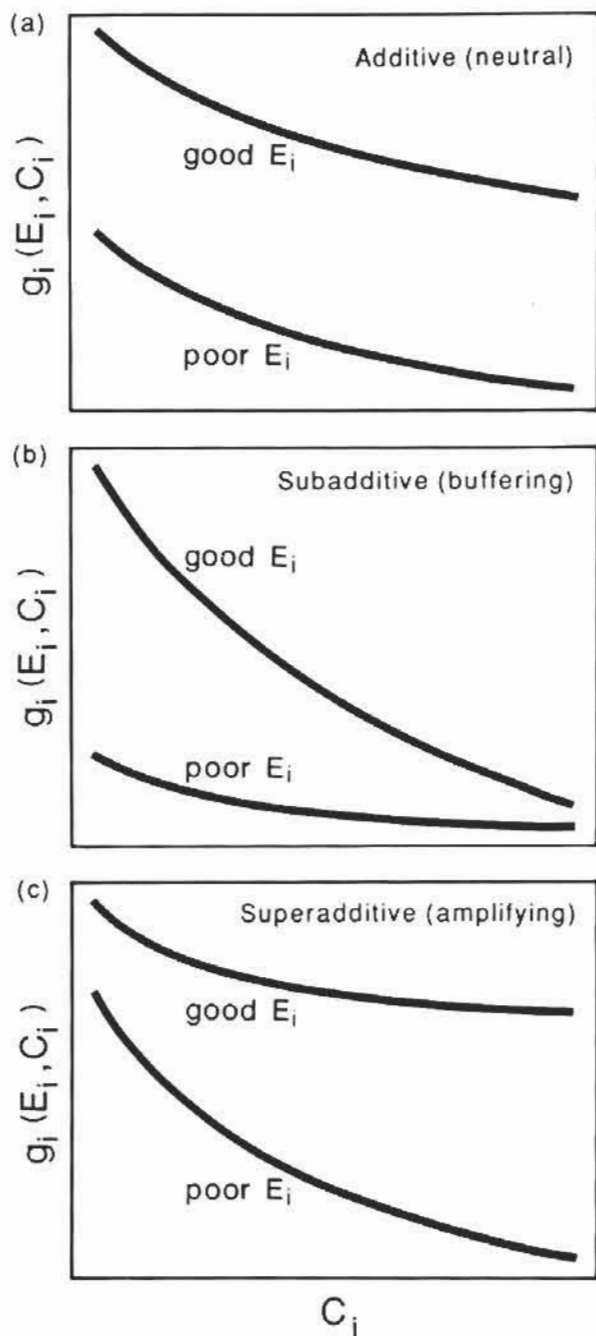


FIG. 1. The growth rate,  $g_i(E_i, C_i)$  as a function of the amount of competition  $C_i$  for two different values of an environmentally-dependent parameter,  $E_i$ . After Chesson and Huntly (1988).

cause rampant competition and may be protected from environmental fluctuations. A local example is *Pinna* shells as space for inferior competitors (Keough 1984a,b). The latter case differs from classical resource partitioning in an equilibrium context because its role is that of a source of propagules that invade the rest of the habitat when conditions there become favourable. Sessile benthic organisms, especially modular ones, can often respond strongly

when conditions are favourable (e.g. Ayling 1983a,b).

Subadditivity has two effects: it opposes competitive exclusion and it dampens population fluctuations. This stability at local population level, with many species coexisting despite competition, is one of the field observations with which we want our model to be consistent. Our conceptual model, thus, says that environmental variability — provided it involves positive covariance between environment and competition and subadditivity of their effects on growth rates — is a mechanism leading to stable coexistence of sessile species.

#### Regional mechanisms

Our model envisages movement of larvae, even within one species, over a distribution of distances. For some species (and perhaps for many), dispersal between sites may be small relative to recruitment from within the site. This supposition is reasonable and is supported by circumstantial evidence from observing the recolonization of piers, but an important topic of current research (e.g. Olson 1985; J. B. C. Jackson 1986; Young 1986; Keough & Chernoff 1987; Davis & Butler 1989; Ayre 1990; Raimondi & Keough 1990; Young 1990). Short-distance dispersal contributes to the local mechanisms above. Longer-distance, inter-reef dispersal is important in our model, however, because it facilitates coexistence mechanisms at the meta-population level.

While the local non-equilibrium mechanisms stress staying power defined in terms of subadditivity, the regional mechanisms all involve analogous staying power coming from dispersal among localities in different states.

Even those species that we know as poor dispersers (e.g. the ascidian *Podoclavella moluccensis* — Davis & Butler 1989) will colonize a new structure on a human time scale, albeit slowly (unpubl. obs. from wrecks in Gulf St Vincent and from Port Bonython in Spencer Gulf). Thus, a species excluded from a site has some probability of re-entering the community by recolonizing a vacant patch. That probability will depend on its distribution and abundance in the surrounding area. The relationship may be difficult to determine, but

we need to think not only about local interactions involved in recolonization and about the conditions conducive to re-establishment, but also about the *frequency distributions* of dispersal distances and of numbers of propagules; we might thus consider distributions of waiting times for recolonization.

*Effects of pure spatial variation* *i. Historical effects* In spite of local factors promoting coexistence, local populations may still depend on exchange of propagules with other local populations. For example, suppose that interspecific competition is stronger than intraspecific competition. Possible mechanisms in our system include chemical interference mechanisms that discriminate between, but not within species (Jackson 1977, 1979b; Buss & Jackson 1979; Dyrinda 1986), or 'shadow' effects of one suspension-feeding growth form on another (Buss 1979; Buss & Jackson 1981; Okamura 1984, 1985, 1988). Pre-emption of space, which is well-known in marine sessile communities (Dayton 1971; Sebens 1985) may have similar effects. In the classical, equilibrium mode, these mechanisms lead to a tendency toward monopoly of habitat locally by a particular species, but which species holds the monopoly may be a historical accident for a particular locality (e.g. a result of the order of colonization). This process may result in a system with multiple stable states. There have been searches for such cases in subtidal sessile communities (e.g. Sutherland 1974, 1981; Sebens 1985), though generally on very small patches and with short time-periods. Still, assume that it is possible in our model system. Levin (1974) showed that immigration in such a setting leads to a system where most species can be found in each habitat, but their relative abundances vary from one habitat to another. The greater the immigration, the more nearly equal their relative abundances in the different localities. If migration is too high, the differences among localities are eliminated, there is essentially no difference between local and metapopulations, and regional competitive exclusion ensues. However, while sufficient differences in relative abundances from locality to locality remain, this setup maintains both regional and local diversity.

*ii. Environmental differences between sites* There is another, familiar way in which spatial variation can be important. The en-

vironment of a locality (not prior history) may determine which species is competitively dominant there. In this case, migration does not eliminate the local variation because it does not affect the environment. Locally and regionally, diversity can be maintained by purely spatial environmental variation and dispersal (Goh 1980; Pacala & Roughgarden 1982; Shigesada & Roughgarden 1982; Chesson 1985; Iwasa & Roughgarden 1986; Pacala 1987).

*Effects of spatiotemporal variation* A local community may be unstable in the sense that there occurs a succession with a definite outcome, leading to a single competitive dominant. However, if localities are disturbed so that competition is reduced for a time, good colonizers that are poor competitors can have their day locally. This idea is the classical succession following a disturbance (Dayton 1971; Hastings 1980; Paine & Levin 1981; Connell & Keough 1985). At the metapopulation level, this process depends on spatiotemporal variation — the spatial pattern of conditions for population growth must change with time.

Spatiotemporal fluctuations in the environment may prevent a deterministic outcome to succession. Then we do not need colonizing ability and competitive ability to be negatively correlated across species. We rely simply on each species having times when it does relatively better than other species. In models where this is the only mechanism, each species has to have times where it is the actual dominant (in the sense that it increases relative to other species). Such spatiotemporal variation in relative competitive abilities will oppose competitive exclusion (Chesson 1985; Comins & Noble 1985).

We have referred to three kinds of environmental variation — *temporal*, *spatial* and *spatiotemporal* — all with potential for influencing the coexistence of species, in addition to those classical mechanisms that do not depend on environmental variation. It is plausible that a model combining these several mechanisms can predict the consistently different faunas at different sites *and* explain the stability of these communities and the evident facts that diversity is high and that many species maintain appreciable densities together on a reef.

As yet, there are no models containing all these possible mechanisms together, but there

are some that contain several (Chesson 1985) or permit several (Chesson 1989). Theoreticians are working towards models in which it is possible to have a variety of mechanisms included simultaneously, allowing the contribution of a particular mechanism to be assessed. Meanwhile, field workers need to collect the kinds of data that will enable these models to be evaluated. To do that, we should have in mind at least a qualitative version of the model.

### Testing

What we mean by 'testing' the model is to discover whether it provides a picture of the way the system works that is more satisfying than other kinds of view. Traditional testing, involving a well-defined prediction that is examined by experiment, can only be envisaged for more specific versions of models, which restrict the number of possible alternatives. Thus, we are developing a view of the system, rather than testing it in the traditional sense.

Models will invariably be simpler than the system being studied. Our aim is to develop a model sufficiently general to include all the mechanisms of interest. Such a model should show how its parameters can be measured using observations or experiments. Given estimates of the parameters, it should indicate the relative roles of the different mechanisms. As a test in the Popperian sense, the model, when provided with parameter values estimated from the field, might be required to predict other, independently measured data, such as relative abundances or diversity measures. But our approach is more the statisticians's one of trying to develop a model that is sufficiently general to contain all major features of the system and, within it, to estimate the relative importance of different processes.

The kind of testing we envisage is illustrated by Chesson's collaborative work with N. Huntly on terrestrial plants. They are testing the hypothesis that environmental variation is an important mechanism maintaining diversity in species of annual plants. The annual plant community theory presented in Chesson and Huntly (1988, 1989) postulates that germination fraction varies with the environment and affects subsequent competition. The presence of a seed bank creates a subadditive

interaction between environment and competition and thus promotes coexistence of species. Therefore, they are experimentally manipulating the environment, estimating germination fraction and other seed-bank parameters and assessing competition.

In its crudest form, the theory can be tested by estimating the parameters of a simple model based on the theory and assessing whether it predicts roughly the species' relative abundances that are actually observed. More sophisticated models, which require separation of inter- and intraspecific competition, can be used to assess the percentage contribution to coexistence derived from environmental variation compared with classical mechanisms that do not involve fluctuations over time. This assessment is done by partitioning a species' long-term, low-density, rate of population growth, which quantifies the ability to avoid extinction, into measurable components coming from different mechanisms.

### Data needed

The conceptual model leads us to stress two things about the collection of data: the need to measure variability and an avowed pluralism. We insist that it will not be of heuristic value to work as if one mechanism alone is the complete explanation for the community dynamics. Our view requires the estimation of the contribution of different possible mechanisms. Even without a formal model containing all of the mechanisms of interest, it is possible to make some progress.

We might begin by measuring certain variables to see whether a given mechanism seems likely to have an effect. We list such variables in Table 1, for each submodel of the conceptual model, under the headings used above.

Consider one example: in order to examine the mechanisms involving pure temporal variation discussed by Chesson and Huntly (1988, 1989), we might measure variation in recruitment and in other parameters that could covary with competition. It would also be important to measure that covariance itself. Ideally, we would like to estimate a parameter before it has been modified by competition. Therefore, we would consider eliminating density effects using regression or using relative measures, such as ratios of recruitment rates.

Next, we might proceed to estimate the rela-

TABLE 1. Parameters likely to be important in assessing each of the several mechanisms in the conceptual model

Local processes	
Mechanisms not dependent on variability	
•	Many processes that have been studied extensively in sessile communities and considered classically in competition theory, such as local resource use, habitat specificity, predator-prey dynamics, details of competitive relationships, mutualism, chemical interactions between species, and small-scale interactions with the physical environment.
Mechanisms dependent on temporal variation	
•	Estimates of recruitment rates and their fluctuations over time, divided into local recruitment and recruitment from elsewhere.
•	Covariances between competition and environmentally-dependent population parameters.
•	Mortality rates and biomass attrition rates (mortality adjusted by growth of survivors).
•	Existence and size of "refuge resources".
•	Correlation between environmentally-dependent parameters of different species.
•	An understanding of the relationships between population parameters and the environment so that suitable parameters can be identified, their variation between species predicted, and their fluctuations over time predicted.
Regional mechanisms	
Pure spatial variation	
<i>Historical effects</i>	
•	Information on the relative magnitudes of inter- and intraspecific competition.
•	Spatial variation in population densities.
•	Dispersal rates.
•	Frequency distributions of dispersal distances, to assess the scale of dispersal relative to the scale of change in environmental variables and species densities.
<i>Environmental differences between sites</i>	
•	Spatial variation in the environment that causes variation in population parameters.
•	Dispersal distances measured as under <i>Historical effects</i> .
Spatiotemporal variation	
•	An understanding of disturbance frequencies.
•	Description of successional processes.
•	The correlation, across species, between competitive and colonizing abilities.
•	Spatiotemporal variation in environmentally-dependent parameters.

tive strengths of two or more possible mechanisms. For example, in the above case, we might ask how much of the recruitment is local, so that mechanisms involving only temporal variation may be distinguished from other mechanisms that require spatial and temporal variation. It would be useful to know the extent to which a local population depends on dispersal from the outside. If recruitment from the outside were eliminated, would the population become extinct? This question might be answered experimentally by eliminating all external recruitment, if that were possible. Alternatively, it might be done by keeping account of births, deaths, immigrants and emigrants in a population. The latter method has some difficulties, however, because competition and predation (or diseases) occurring locally in space may lead to local density-dependence, and an understanding of the magnitude of such density-dependence would be necessary before it could be determined whether external recruitment is required for population maintenance. Even measuring dispersal between local populations may be very time-consuming.

The need for external recruitment, however, is obvious in at least one case, namely when it has been determined that local extinction is a frequent phenomenon. Similarly, if it has been found that local populations undergo large fluctuations, even if they do not become extinct, then the potential exists for external recruitment to aid population recovery. The magnitude of external recruitment, compared to internal recruitment, will then indicate whether external recruitment provides boosts at such times.

If a need for external recruitment is confirmed, then metapopulation-level mechanisms need attention. Investigating them involves trying to identify source and sink habitats (Pulliam 1988) and determining whether their identities as sources or sinks remain fixed over time (implicating pure spatial variation) or fluctuate with time (implicating spatiotemporal variation). If they fluctuate over time, is there a predictable succession, suggesting that species' relative colonizing and competitive abilities should be investigated, or does competitive success vary randomly, indi-

cating no need for inverse competitive and dispersal rankings?

If external recruitment is unimportant, focus can shift to mechanisms operating within individual habitats — the classical mechanisms, plus those dependent on temporal variability. Thus, we would examine species' life-histories and how they interact locally. Having identified the variables that most affect the interactions between species, we should study the variability in those quantities, for it will be this variability that most affects community processes.

On what time scale should the variability in important quantities be measured? This scale depends on the life-histories of the organisms and the detailed nature of their interactions. For example, if species differ in the timing of recruitment within a season, and density limitation can occur at different times, then it is necessary to capture the way in which different species are distributed through the season. If, on the other hand, density limitation only occurs towards the end of the season, it will be necessary to know no more than who arrived first. 'One season' may then be the time unit. With long-lived sessile organisms, a year may often be a suitable unit, but sampling will need to be more frequent within the year to capture recruitment of different species. Thus, some natural history — some understanding of detailed mechanisms — is necessary to guide the testing of these very general models.

Ideally, of course, the studies would not just be observational, but would involve manipulation of factors known to fluctuate over time. It seems possible to manipulate at least some environmentally-dependent population parameters (e.g. mortality and, in special cases, recruitment). As small-scale, nearshore physical oceanography becomes more refined, a good knowledge of the fluctuations in physical factors can be expected. We need to measure the relationship between such factors and the microenvironments in which organisms live. Studies in the laboratory of the responses of organisms to physical variables, such as water movement, will be relevant (e.g. Okamura 1984, 1985, 1988; Jamieson 1988). We envisage that it may eventually be possible to manipulate microenvironments in the field, on a small and therefore technically feasible scale, but also, by linking microenvironmental pro-

cesses to data on physical oceanography, to know the natural frequencies of the events simulated by our small-scale experiments; thus, we might predict fluctuations in population parameters that should follow from the better-known fluctuations in the variables of meteorology and physical oceanography. Spatial variation in microenvironments can be assessed relatively easily, but we have to take into account the likely interactions between spatial and temporal variation as they affect the organisms.

Table 1 suggests, for studies not designed with a quantitative submodel in mind, that certain variables are likely to be important, and might be estimated forthwith, having in mind merely a qualitative version of the whole conceptual model. Thus, it will be of general interest whether there is any correlation between adult mortality and recruitment, and between adult stock and recruitment, and to estimate the correlation between recruitment of different species. Dispersal distances (as frequency distributions, not merely averages or maxima) will be needed for determining the scale of the system and the relative importance of the several possible mechanisms.

### How much do we have?

This paper is not the place for a full review of published data and how it relates to the theoretical view outlined here, but some remarks will illustrate that: (i) some data exist; but (ii) it is important to collect data with a model in mind. Existing data can confirm the plausibility of our model, but usually cannot be used to test or develop it any further.

As an example, we shall pick on data from Butler's own group working in the South Australian Gulfs, but the same can be said of other data.

It is clear by inspection of his graphs that there is spatial, temporal and spatiotemporal variation in recruitment to small settling panels in Keough's (1983) study. Keough discussed this variation (not in these terms). Butler (1986) sought pure spatial variation in recruitment rates in order to test a hypothesis about its effect on community composition on different sized patches. In a project constrained to only one year, he had to *assume* that pure spatiotemporal variation was zero in



order to interpret the results. The follow-up study (Butler, unpubl. obs) concerns patch-size at two sites, Edithburgh (low recruitment in the 1986 paper) and Ardrossan (high). In this study, too, he implicitly assumed low spatio-temporal variation, because the experimental design gambles on the 1986 recruitment patterns being maintained. Keough (1983) was able to make some remarks about small-scale patterns of recruitment of certain animals, while Davis (1987a,b, 1988; Davis & Butler 1989) later demonstrated short-distance dispersal for one species, and there are hints of it for others (Butler, unpubl. obs). These findings on recruitment can be related loosely to work in which some estimates of growth rate were made (Kay 1980), in which qualitatively a tradeoff was recognized between competitive abilities and recruitment rates, and in which a refuge resource was identified (Kay 1980; Kay & Keough 1981; Keough 1984a). There has also been some examination of the effects of predators (Keough & Butler 1979; Kay 1980; Keough 1984b), mutualism (Chernoff 1987; Pitcher & Butler 1987) and other processes that would come under the heading of local processes in our conceptual model (Grove-Jones 1980; Davis 1987b; Jamieson 1988). These rather disparate efforts come close to giving the sort of data needed for the first (and least) of our approaches to the testing of the model, namely indicating that certain mechanisms might reasonably be expected to be important.

What we have just said about the use of the data gathered in the S.A. Gulfs is true *a fortiori* for the large amount of data that exists in the literature from other places. There is not space to review them here. They are often relevant and important, often enough to suggest that a mechanism might be operating, but no more.

## Conclusion

Our emphasis on the three kinds of variation amounts to a sophisticated version of the common plea for long-term studies. That plea has always meant implicitly that we want to know the *temporal distribution* of something in order to understand it properly. We emphasize that variation in *space* and the *interaction* between temporal and spatial variation are important also. The most important point that we make

about measuring variation is that the variances and covariances so derived tell us how the system works. They are intrinsically involved with the mechanisms of system function, determining which species may be present and what their relative abundances will be. Variances do not merely describe variation, but have a strong mechanistic role. Ecologists have long said such things; many, however, have not had an explicit theoretical reason for doing so, although they have had plenty of field experience on which to base the plea. As Darwin (1861) maintained, for an observation to be of any value, it must be for or against some idea. Likewise, we believe that data collection is best done in relation to a theory under test. There are now sufficient mathematical models to provide at least a crude theoretical basis for many of the phenomena that seem plausible in benthic communities, and we argue that data collection is best done in relation to models that represent the phenomena under test. This process means estimating parameters of a model and fitting it, to see if its predictions are consistent with information that has not been used in the fitting; and using the model to reason through qualitative tests, such as predictions about the consequences of perturbations to the system.

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