

## Scale of Dispersal in Varying Environments and its Implications for Life Histories of Marine Invertebrates

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**Summary.** We present several models concerning the short term consequences of spreading offspring in varying environments. Our goal is to determine what patterns of spatial and temporal variation yield an advantage to increasing scale of dispersal. Of necessity, the models are somewhat artificial but we feel they are a reasonable approximation of and hence generalizable to natural systems. With these models we examine consequences of dispersal arising from environmental variation: increased environmental variance, different degrees of spatial and temporal correlation, some arbitrary spatial patterns of favorability and finally some patterns derived from long-term, large-scale weather data collected along a contiguous stretch of coastline from southern Oregon to northern Washington (USA). We examine the costs and benefits of increasing scale of dispersal in both density dependent and density independent models.

Several conclusions may be drawn from the results of these models. In the absence of any spatial or temporal order to favorability (where favorability is directly proportional to either fitness or carrying capacity) increasing scale of spread produces a higher rate of population increase. At larger scales, though, an asymptote of maximum relative advantage is approached, so each added increment of spread has a smaller contribution to fitness. This asymptote is higher and the approach to it relatively slower with increasing environmental variance. For a given environmental variance, increasing spatial correlation results in a slower approach to the same asymptote. In density independent models, increasing temporal correlation of fitness selects against increased dispersal if expected differences between sites are sufficiently great relative to variation within sites; but in this instance, density dependence yields a somewhat different result: dispersers have a refuge at sites of low carrying capacity or sites lacking non-dispersers. Finally, optimum intermediate scales of dispersal can occur where differences in expected fitness increase with increasing distance from the parental site, such as in a gradient, but where the environmental variation at a given site is fairly large relative to differences in expected fitness between adjacent sites.

The foregoing results are extended for the following predictions. When greater longevity in a resistant phase of the life cycle reduces temporal variation in survival and fecundity, increased generation time should decrease the *benefits* of spreading offspring in an environment that would otherwise favor spread

and could either increase or decrease the *costs* of spreading offspring in an environment selecting against spread. We speculate that if large scale patterns of varying survival and fecundity are similar to the variation in the physical environment which we examined with weather data, there should be little or no short term advantage to large scale spread of offspring (on the order of 50 kilometers or more) because expected differences increase and seldom if ever decrease with increasing distance between sites.

This suggests that feeding larvae of benthic invertebrates with their concomitant long planktonic period, receive little if any advantage from increased scale of dispersal, and consequently that the advantages to planktotrophy over lecithotrophy must lie in other life history aspects, such as the ability to produce a greater number of smaller eggs.

### Introduction

In spite of the potential importance of dispersal for many species, little is known of the consequences of increasing scale of dispersal in a spatially and temporally varying environment. Using computer simulation, we examine both the *costs* and *benefits* of increasing spread of sibling offspring under various environmental regimes, where costs or benefits of dispersal refer respectively to decreases or increases in population size when compared to non-dispersers in the same environment. Though the models are relevant to many dispersing organisms, the simplifications of the models and objectives of the study arise primarily from an interest in benthic marine invertebrates with pelagic larval stages. Planktonic larvae can be released in a single batch or over a longer period. They can be feeding or non-feeding. They can bunch at one depth or spread throughout the water column. All of these differences in reproduction, development, and behavior can affect the spread of larval offspring during the pelagic period (Strathmann 1974). At the extremes, some invertebrates may spread a portion of their offspring across an ocean while others' offspring never leave the bottom [See Scheltema (1977) and Spight (1976) for these extreme examples among the gastropods]. Understanding the consequences of these different life histories requires an understanding of the consequences of dispersal on different spatial scales. Previous models of larval dispersal (Crisp 1974, 1976; Strathmann 1974) have not adequately considered effects of different scales of spread in varying environments.

Throughout this paper scale of dispersal refers to spread of siblings relative to each other. The mean distance offspring travel

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from their parents also increases with scale of dispersal in our models but it is spread of siblings which is our primary concern.

The magnitude of spatial and temporal variation in aspects of the environment which are important to organisms is poorly known, but even the available data have not been interpreted in terms of selection for scale of dispersal. The purpose of our models is to investigate the effects environmental pattern may have on selection for scale of spread of offspring and thereby aid interpretation of the data available. We are particularly interested in patterns of temporal and spatial variation in environmental favorability which offer a substantial advantage to spread of offspring over very large regions (circa 50 km or more) as compared to more moderate scales of dispersal. A spread of about 50 km is the usual result of development with a feeding larva as opposed to the smaller spread experienced by a non-feeding but swimming larva in the life cycles of benthic invertebrates, an estimate supported both by diffusion studies (Okubo 1971) and rates of expansion of species' ranges (Crisp 1958; Gerdes 1977; Quayle 1964). Environmental favorability, as we use the term in this paper, may be interpreted as local environmental attributes influencing either: 1) per individual reproductive output of arriving propagules (a component of fitness) or 2) the final number of reproducing adults (carrying capacity) at a given site.

Cohen (1967) provides a two site model of the optimal fraction of offspring dispersing between sites with density independent variation in survival and reproduction. He finds that independent variation in survival and reproduction at the two sites selects for spreading offspring between sites, whereas consistent differences in expected survival and reproduction between the two sites selects against the dispersal of offspring. When there is independent variation among sites, spreading offspring over sites damps temporal variation in rate of increase and thereby nondispersers have a relatively lower rate of increase. Gadgil (1971) obtained similar results simulating an environment with varying carrying capacities. Balkau and Feldman (1973) have also found for a haploid, two-island model that reduced migration is favored in the absence of temporal variation when fitnesses are different and constant at the two islands. Further, Van Valen (1971) has shown that the risk of random extinction of local island populations necessarily favors dispersal, since ultimately all populations of non-dispersers will go extinct. Reddingius and den Boer (1970) have also examined stabilization of numbers as a result of dispersal. Though dealing with spatial and temporal patterns of favorability, none of the above papers considers the effect of spreading offspring on different spatial scales. In Roff's (1974) model a larger scale of dispersal resulted in a longer time to extinction, but Roff examines only three scales of dispersal and only one type of environmental variation.

Our model addresses scales of dispersal, and spatial and temporal variation in environmental favorability. We examine scales of dispersal using several simulation models whose results are presented along with verbal supporting arguments. We also discuss the probable effects of increased generation time on the advantages or costs of dispersal. In addition, we present an example using these dispersal models with environmental data. Finally we discuss our results in relation to larval dispersal of benthic marine invertebrates.

We do not assume that dispersal is advantageous. It may be merely the result of different patterns of development which have evolved for other reasons, as in Vance's (1973) model, for example. Observed scales of dispersal are thus not necessarily set by selection for optimal scale of dispersal *per se*, but may be strongly influenced by other factors not related to dispersal advantage.

## The Models

We have endeavored to keep the models simple and defer the justification of the assumptions and the restrictions on their application until the discussion.

All the models consist essentially of two sections: a section which generates a two-dimensional matrix of favorability values and a dispersing section. Since we only consider dispersal in one dimension, a situation more accurately reflecting conditions experienced by coastal benthic invertebrates, the two dimensions of our matrix correspond to space and time respectively. This matrix, which we refer to as the favorability matrix, consists of elements  $R_{ij}$  where each element represents the reproductive output per individual arriving at time  $i$  at site  $j$ . Sites correspond to homogeneous areas of undefined absolute size and for simplicity we consider the time interval to be years, though this is also arbitrary. Most of our models exclude carrying capacities or density dependent mortality. To check for artifacts introduced by the lack of density dependence, we examined alternate models in which each element in the favorability matrix represents a carrying capacity  $K_{ij}$  equal to  $R_{ij}$  of the density independent models. In the density dependent models, reproduction is sufficient to saturate every site each time interval, and several types of organisms compete equally except for their different scales of spreading offspring. In all models, the costs or benefits of spreading offspring are expressed as rates of change in population size relative to rates of change with no dispersal for organisms which are identical except that they spread offspring on different scales. Scale of dispersal is defined as the number of sites reached by offspring dispersing from a single site.

Generations are non-overlapping, and only periods of 100 generations or less are considered. A per generation change in population size is calculated for the whole population summed over all sites. (The per generation change for an organism with a given scale of dispersal is divided by the per generation change for an organism with no dispersal to obtain the relative rate of change per generation. Thus values of relative rates of increase greater than one indicate an advantage, and those less than one, a cost to dispersal.) The per generation change is the  $n$ th root of the change over the entire period where  $n$  is the number of generations. Organisms with different scales of dispersal do not interbreed. This is equivalent to either an asexual model or interspecific competition. The scale of dispersal is constant for a given type of organism, and dispersal is always associated with reproduction. Equal numbers of offspring are dispersed to each site within the range of dispersal from the parental site (Fig. 1). An increase in dispersal is not associated with cues indicating that the parental site is deteriorating, and settlement is as likely at sites which will prove favorable as it is at sites which will be unfavorable. At any given site, all parents produce the same number of settling offspring regardless of scale of dispersal. Differential extinctions of populations and local extinctions at sites are not permitted, though their possible consequences are discussed. Edge effects are eliminated differently depending on the model, so that dispersal does not extend past habitable areas.

Three patterns of dispersal are employed, each represented by a separate model (see Fig. 1 for schematic representations of these models). In the *cell pattern* (Fig. 1 bottom), all sites in the spatial array are occupied in the first generation by the same number of adults and all produce offspring. Offspring within a group of sites (a cell) disperse evenly over all the sites in that group each generation but never disperse into neighboring groups of sites. Sites are grouped into cells of increasing size to increase the effective scale of dispersal (e.g. 1,2,4,8,...256 sites per cell in Fig. 2 to 6). The advantages of this model are: (1) that all sites are encountered with each scale of dispersal (i.e. the entire favorability matrix will be sampled over the time period considered), (2) dispersers do not fall off the edge of the array of sites, (3) it permits very large scales of spread, and (4) finite arrays of environmental data may be easily incorporated. Although the spread of offspring is quite unlike that observed in nature, the grouping of sites into progressively larger cells should qualitatively mimic the spatial averaging that would occur as the offspring derived from a single parent are spread more widely.

To check for possible artifacts introduced by the cell pattern, we

consider two additional dispersal patterns where the spread of offspring is centered on the parental site. In one of these, losses off the end of the array of sites are eliminated by reflecting dispersing offspring from both ends of the site array (*reflecting pattern*, Fig. 1 middle). Since all sites produce offspring starting in the first generation, this is computationally equivalent to joining the array of sites to its mirror image, forming a circular array. (Circular models have been used in a number of theoretical population genetics models, see Felsenstein 1976 for a review.) The reflecting model introduces little error when the scale of dispersal is small relative to the number of sites, and it has the advantages of the cell model but the disadvantage that with increasing scale of spread, more and more sites may be sampled twice by offspring dispersing from a single site as they reflect about the boundaries of the spatial array. In this model, the maximum scale of spread examined was approximately one-half the length of the spatial array.

In the second of these centered dispersal patterns, the first dispersers start from a single site at the center of the spatial array, and the favorability matrix is large enough that none ever reaches an edge over the time period examined. Although this *single source pattern* (Fig. 1 top) eliminates edge effects and more accurately represents patterns of dispersal observed in nature, larger and consequently different areas of the favorability matrix are encountered with each increased scale of dispersal, introducing additional variation in rates of change, and increasing our sampling error substantially. In addition, space and time limitations on computers do not permit very large scales of spread with this model and it is not readily adapted to environmental data or density dependent models.

Environmental variation, in the form of favorability matrices, is obtained in three ways. In the first, values in the favorability matrix are made to conform to a lognormal distribution whose variance, spatial correlation and temporal correlation are specified (cell and single source models only, see Table 1). The computational formula used to generate favorability values for an underlying normal distribution, kindly supplied by J. Felsenstein, is:

$$\omega_{ij} = \rho\omega_{i,j-1} + \tau\omega_{i-1,j} - \rho\tau\omega_{i-1,j-1} + \eta$$

where  $\eta$  corresponds to the background environmental variance or noise  $\eta \sim N\{\mu, \sigma^2(1-\rho^2)(1-\tau^2)\}$ ,  $\rho$  to the spatial and  $\tau$  to the temporal correlation.  $\mu$ , or the expected mean of the normally distributed favorability values is arbitrarily set and kept at a value such that the expected mean of the lognormal will be one, though its actual value is irrelevant since we are interested only in advantages to spreading *relative to no dispersal* and not in absolute rates of increase.  $\sigma^2$ , the variance, is computed such that the expected variance of the lognormal will achieve the specified value. The values of the favorability matrix ( $\omega_{ij}$ ) are then exponentiated to yield a lognormal distribution ( $R_{ij}$ ). When spatial correlation was increased, the spatial variance was held constant; but when temporal correlation was increased, the temporal variance was allowed to decrease (a decision justified in results, section 4). Actual temporal and spatial correlations in the matrices are somewhat smaller than the values of  $\rho$  and  $\tau$  introduced in the computational formula. The specified values of  $\rho$  and  $\tau$  were 0.0, 0.5, 0.9, and 0.99; the actual values in the matrices are given in the figure captions.

In the second pattern of environmental variation, differences in favorability are uniformly distributed. In some cases the distribution of favorabilities is uniform in both space and time; in some cases a temporally uniform distribution of favorabilities is superimposed on a linear spatial gradient of expected favorabilities from the expected best to the worst sites; and in some cases spatial variation has a uniform distribution among sites with no variation over time.

In the third pattern of environmental variation, favorability at sites is based on minimum daily air temperatures from the Oregon and Washington coasts from 1948 to 1972 obtained from the U.S. National Climatic Center.

## Results

When there is independent temporal variation in favorability among sites, in the absence of any predictable spatial order, organisms spreading their offspring will average this variation

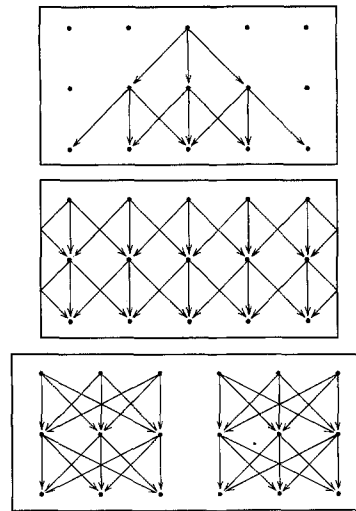


Fig. 1. Patterns of dispersal used in the models: *top*, spread from a single source; *middle*, reflecting pattern; *bottom*, cell pattern. Horizontal axis = space, vertical axis = time

Table 1. Combination of environmental pattern, dispersal pattern, and density dependence or independence used in the models

Patterns of Environmental Variation	Dispersal patterns			
	Cell patterns		Single source	Reflecting
	density independent	density dependent	density independent	density independent
<i>Lognormal</i> (variance and spatial and temporal correlation altered)	+	+	+	
<i>Uniform</i> (variance altered)	+			+
<i>Uniform variation temporal correlation of one</i>				+
<i>Uniform variation superimposed on a gradient</i>				+
<i>Weather</i> (severity of freezing along a coast)	+	+		+

among sites. Hence, these organisms will experience less temporal variation than organisms retaining their offspring at the parental site. Because dispersers experience decreased temporal variation, even though the *arithmetic* mean of the favorabilities at all sites is the same, the product of multiplication over generations is greater for the dispersers. The relative rate of increase of dispersers and non-dispersers is determined by the *geometric* mean of fitness over generations, not the arithmetic mean (see Cohen 1967; Strathmann 1974). On the other hand, when there are consistent differences in survival and reproduction of organisms at different sites, dispersers will export more offspring from favorable to unfavorable sites than are received in the reverse direction, and will therefore decline relative to non-dispersing

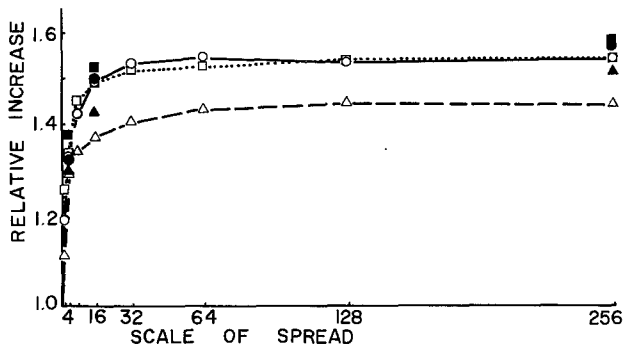


Fig. 2. Diminishing returns with increased scale of dispersal: rates of increase per generation are given relative to increase with no dispersal (cell pattern of dispersal and a lognormal distribution of favorability,  $\mu=1.0$ ,  $\sigma^2=3.0$ ,  $\rho=0.0$ ,  $\tau=0.0$ ). The three types of symbols are for three replicate runs with both the density independent model (*open symbols* connected by lines) and density dependent model (*solid symbols*)

organisms. (This would not be the case when favorability of sites is negatively related to presence of adult organisms; however, if one considers scales large relative to patchiness of adults, this negative correlation is not expected.) These results from Cohen's (1967) discussion of two sites suggest a number of questions regarding dispersal over many sites. To simplify presentation, we will discuss the manipulations of spatial and temporal correlation ( $\rho$  and  $\tau$ ) or magnitude of variation ( $\sigma^2$ ) separately. The salient aspects of the three principal models and the manipulation of the various factors are indicated in Fig. 1 and Table 1.

### (1) Environments with no Spatial or Temporal Order

When there are no differences in expected favorabilities among sites (environment is uniform), each added increment to the scale of dispersal produces a *higher* rate of increase. As scale of dispersal is increased further the relative advantage of dispersal approaches an asymptote such that each added increment of dispersal has a progressively smaller contribution to fitness. This occurs because each additional increment in the dispersal scale contributes proportionately less to the damping of temporal variation. It is as if a parent samples the environment with its offspring to obtain an estimate of mean conditions; as its estimate approaches the true value there is less benefit from further sampling. All the models lacking temporal correlation yield this result, including the cell model with density dependence. The results from the cell pattern are plotted in Fig. 2. If mortality associated with the dispersal phase were to increase with scale of dispersal, as is likely in nature, an intermediate scale of dispersal would result instead of an asymptotic increase.

### (2) Environments with no Spatial or Temporal Order, but Increased Variance

With no differences in expected favorabilities among sites, increasing the variance of the favorability values, relative to the mean, increases the advantage gained with each added increment to the scale of dispersal, but the approach to this higher asymptote of maximum possible advantage is slower. In other words, as variance increases, the sampling for a given scale of spread

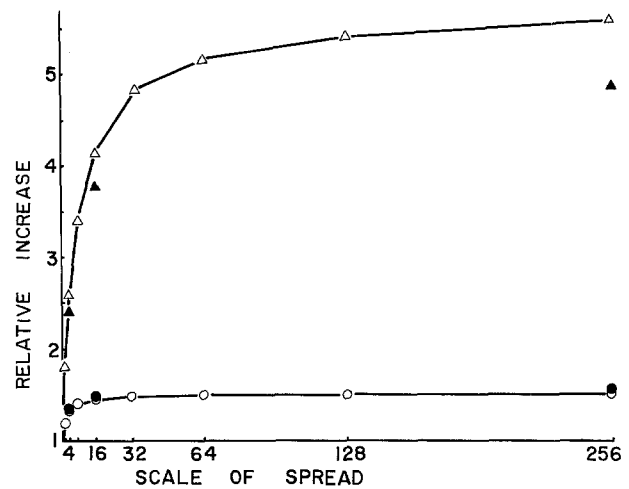


Fig. 3. Effect of higher variance in favorability on relative rates of increase per generation of organisms dispersing on different scales (cell pattern of dispersal and a lognormal distribution of favorability,  $\mu=1.0$ ,  $\rho=0.0$ ,  $\tau=0.0$ ). The variance ( $\sigma^2$ ) is 3.0 (*circles*) or 81.0 (*triangles*). Each symbol is the mean of three replicate runs with the density independent model (*open symbols* connected by lines) or density dependent model (*solid symbols*)

becomes less reliable and the advantage of large relative to small scale of dispersal becomes somewhat greater. This result is obtained both with and without density dependence in the cell model (Fig. 3), and for the other two models as well.

It is apparent from Fig. 3 that regardless of the magnitude of the variance, the greatest change in relative rate of population increase occurs between no dispersal and small scale dispersal, hence considerable advantage is gained simply by dispersing to closely adjacent sites. Since in nature mortality is likely to increase with time in the plankton, why do so many invertebrates produce larvae whose planktonic life is several weeks? Is it some benefit other than dispersal? Many invertebrates disperse offspring over tens or hundreds of kilometers. Are there patterns of variation which would favor dispersal on this scale? Our results indicate that to be advantageous in the short run, large scale dispersal requires either a cost free method of enhancing dispersal, or patterns of spatial and temporal variation which provide a more substantial advantage for dispersal on a large scale when compared to the advantage achieved by dispersing over only a few sites. (Please note that again we are comparing large versus small scale dispersal, and not dispersal versus no dispersal.) With independent variation among sites as the sole source of variation, a very high ratio of variance to the mean is needed to provide such an advantage.

Since these models do not specify absolute size of sites, one could argue that large scale dispersal would be favored when there are large homogeneous sites with abrupt borders which vary independently in time. We doubt this is common in nature. However, it seems likely that adjacent sites are more similar to each other than to more distant sites at any given time. One might expect such a pattern to require larger scales of dispersal to achieve the same damping of temporal variation and consequently the same relative advantage. We consider this pattern of variation in the next section.

### (3) Environments with Increased Spatial Correlation

With no consistent differences in expected favorabilities among sites (i.e. no temporal correlation), greater spatial correlation

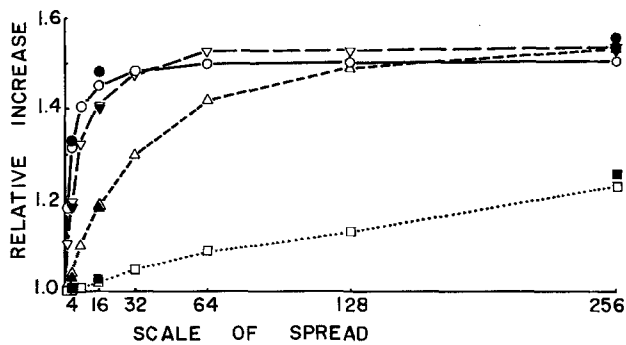


Fig. 4. Effect of increased spatial correlation on relative rates of increase per generation of organisms dispersing on different scales (cell pattern of dispersal and a lognormal distribution of favorability,  $\mu = 1.0$ ,  $\sigma^2 = 3.0$ ,  $\tau = 0.0$ ). The actual spatial correlations ( $\rho$ ) in the model are about zero (circles and solid line), 0.35 (triangles apex down and long dashes), 0.80 (triangles apex up and short dashes), and 0.96 (squares and dotted line). Each symbol is the mean of three replicate runs with density dependence (open symbols connected by lines) or density independence (solid symbols)

of favorability between adjacent sites within a given generation results in a slower approach to the asymptote of maximum dispersal advantage with increased scale of dispersal. In other words, with increasing spatial correlation, the offspring must be spread progressively farther to adequately sample the spatial ups and downs in favorability. This result is obtained with both density dependence and density independence in the cell model (Fig. 4). (In this example, neither the (a) absolute rate of increase with no dispersal, (b) temporal correlation, nor (c) variance within sites over time change much as spatial correlation is increased. The mean of variances among sites for each generation is held constant. The variance in favorability among sites, though, does differ more among years in matrices with greater spatial correlation.) When examining the single source model, variation from one trial to the next was so great and the scales of spread so restricted that the approach to approximately the same asymptote was not clear, although the same trends were apparent. Thus in the absence of long lasting expected differences among sites (low temporal correlation) increased spatial correlation not only provides a greater advantage for dispersal on a large compared to a small scale, but it also requires a larger scale of dispersal to achieve the same advantage relative to non-dispersing organisms.

Up to this point, under conditions with no temporal correlation, both the density independent and the density dependent models have given very similar results (Fig. 2, 3 and 4). The reason for the dispersers' *advantage* has been the same in all cases: dispersal damps temporal fluctuations in success of offspring entering the population each generation, increasing their product over time. However, in the next section we will examine a pattern of favorabilities that results in a *cost* to dispersal – a cost whose magnitude is sensitive to the presence of density dependent limits on population size.

#### (4) Environments with Temporal Correlation: Introducing Persistent Differences in Favorability Among Sites

If differences in expected fitness among sites are sufficiently great relative to independent temporal variation of fitness within

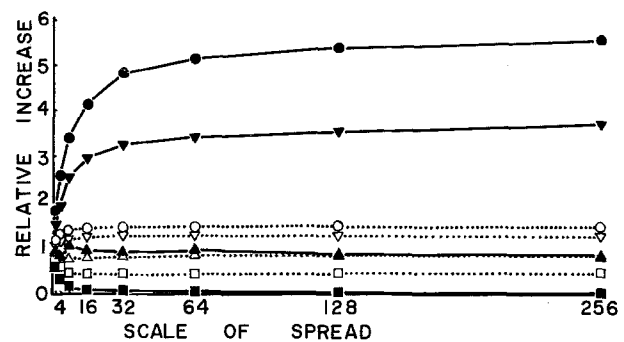


Fig. 5. Effect of increased temporal correlation (and its concomitant decrease in temporal variance) on relative rates of increase per generation of organisms dispersing on different scales (density independent model with cell pattern of dispersal and lognormal distribution of favorability,  $\mu = 1.0$ ,  $\rho = 0.0$ ). Each symbol is the mean of three replicate runs with  $\sigma^2 = 3.0$  (open symbols, dotted lines) or  $\sigma^2 = 81.0$  (solid symbols, solid lines). Temporal correlation is increased (and temporal variance thus decreased) by setting  $\tau$  at 0.0 (circles), 0.5 (triangles apex down), 0.9 (triangles apex up), or 0.99 (squares). Actual temporal correlations are about zero, 0.34, 0.78, and 0.93 for  $\sigma^2 = 3$ , and about zero, 0.19, 0.63, and 0.90 for  $\sigma^2 = 81.0$ . Note that a value of relative increase greater than 1 represents an advantage and values less than 1 a cost to dispersal

sites, dispersers will decrease relative to non-dispersers. This occurs because with larger scales of spread there is a greater net export of offspring from persistently favorable to persistently unfavorable sites. In such environments, then, there is a relative *cost* to dispersal when compared to no dispersal. This result is obtained with density independence in the cell model (Fig. 5) and in the single source model. In both of these models, favorabilities are lognormally distributed and expected differences among sites are introduced by increasing temporal correlation and allowing temporal variance to decrease over the interval examined. We also obtain the same result with the reflecting model where expected differences among sites are established by either 1) superimposing a temporally uniform distribution of favorabilities on a linear spatial gradient of expected favorability, or 2) excluding temporal variation ( $\tau = 1.0$ ) with a spatially uniform distribution of favorabilities.

In the cell and single source models, where lognormally distributed favorabilities have been generated to achieve specified degrees of temporal correlation, a necessary consequence of increased correlation in finite arrays is a decrease in the variance. The shorter the array, the greater the decrease in the variance for a given level of correlation.

Because there is no direct correspondence of sites in our models to actual distances in nature, we have adjusted the variance in space such that it remains the same regardless of the degree of spatial correlation. However, units of time are less arbitrary; a generation is a unit of time defined by the organisms, and natural selection clearly may act over a limited number of generations. One of the effects, then, of increasing temporal correlation in nature will be to decrease the range of favorabilities experienced over a given number of generations. Consequently, when we introduce temporal correlation, no attempt is made to hold the temporal variance constant. Hence by dealing with finite arrays, we are really only considering short term advantages or costs to dispersal (on the order of 100 generations), whereas other factors such as local population extinctions (Van

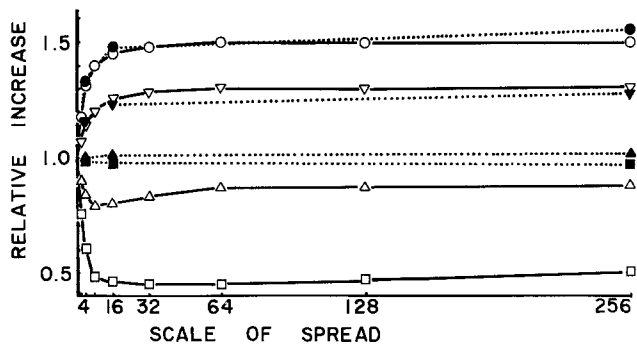


Fig. 6. Costs of dispersal with density independence (open symbols and solid lines) contrasted with costs with density dependence (solid symbols and dotted lines). Each point is the mean of three runs with cell pattern of dispersal and with lognormal distribution of favorability,  $\mu=1.0$ ,  $\sigma^2=3.0$ ,  $\rho=0.0$ . Symbols and line types as in Fig. 5. Note that a value of relative increase greater than 1 represents an advantage and values less than 1 a cost to dispersal

Valen 1971) may become important on a longer evolutionary time scale.

As mentioned above, decreased temporal variance (due to increased correlation) results in a relative *cost* to dispersal when compared to no dispersal. Where there is density independence and no spatial correlation of favorabilities (in the cell and single source models), this cost will approach an asymptote (Fig. 5), both because the probability of encountering sites worse than those already encountered decreases with increasing scale of spread and because smaller and smaller proportions of a given brood are encountering each site with increased spread. A similar result is obtained with the reflected pattern of dispersal and a linear gradient in expected favorabilities between best and worst sites. Dispersal beyond the end of a species' range is a special case of an environment with high spatial and temporal correlation of site favorability, where the cost would continue to increase with increased spread of offspring.

Density dependence complicates the effect of high temporal correlation with its attendant low temporal variance. In the cell dispersal pattern with lognormally distributed carrying capacities, greater temporal correlation decreases the advantage to dispersal as before, but much greater temporal correlations are required to impose costs on dispersal (Fig. 6). The reasons for this effect of density dependence are suggested by a simpler three site model with constant carrying capacities and complete versus no dispersal. Two possible refuges for dispersers are obvious in this model: 1) the site of lowest carrying capacity, and 2) any site initially (and thus always) lacking non-dispersers. When all sites have some non-dispersers at the outset, dispersers decline relative to non-dispersers until their abundance at each site is less than or equal to their abundance at the site of lowest carrying capacity. The equilibrium depends on initial numbers of dispersers and non-dispersers at each site. In a constant environment in which dispersers encounter sites of zero carrying capacity and non-dispersers occur at all habitable sites, dispersers in competition with otherwise identical non-dispersers decline to zero.

In the density dependent models with many sites (Fig. 6) dispersers and non-dispersers start equally at all sites, so sites of low carrying capacity rather than sites lacking non-dispersers are the refuge for dispersers. One cause of the apparently low cost of dispersal appears to lie in the large number of generations

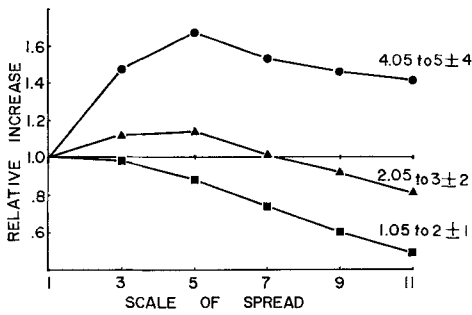
examined (100). For example, with a lowest carrying capacity of 0.01 and a mean carrying capacity of 1.0, the lowest that dispersers could fall relative to non-dispersers is 0.01, but the 10th root of 0.01 is 0.631 and the 100th root is 0.955. Since the dispersers cannot fall below an equilibrium level in the density dependent model, the *cost* as measured by relative rate of increase per generation must decline when computed for progressively greater numbers of generations. Also, the decline of dispersers relative to non-dispersers is limited during those periods when carrying capacities of sites are consistently ranked, so that occasional reversals of conditions may provide an increase of dispersers relative to non-dispersers when increase is calculated over the entire period.

The decline of dispersers to an equilibrium level in the presence of low temporal variation and high temporal correlation in the density dependent model suggests two rather distinct components to the cost of dispersal under these conditions: (1) the final equilibrium population levels of dispersers, and (2) the rate at which dispersers decline relative to organisms with less dispersal. At equilibrium, in an environment with spatial variation but no independent temporal variation ( $\tau=1.0$ ), dispersers will neither increase nor decrease relative to organisms with less dispersal. The equilibrium level, however, depends not only on the particular pattern of spatial variation but also on the starting population size, and the preceding population may have been the product of a previous equilibrium. Thus if intervals of relative temporal constancy are followed by rapid shifts to a different spatial pattern (punctuated equilibria in an environmental sense), selection on the scale of spread will depend on both the frequency of environmental change and the relative numbers of organisms with different scales of spread at each preceding equilibrium. If shifts are very infrequent, short term costs or benefits resulting from differing scale of spread will be weak, and other features of long dispersal periods will be more important (for example, time for planktonic larval feeding versus probability of a larva being eaten before metamorphosis).

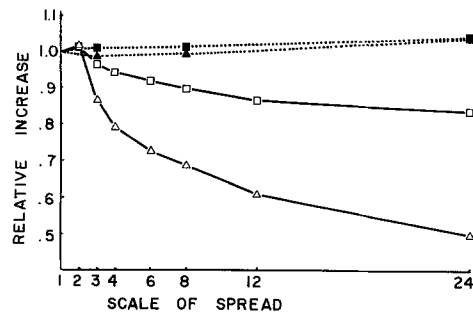
#### (5) Environments Resulting in Optimum Intermediate Scales of Spread

When differences in expected favorability increase with increasing distance between sites, independent variation among sites can result in an optimum intermediate scale of dispersal. If distant sites differ consistently in favorability but nearby sites vary independently with only small differences in expected favorability, then small scale spread produces a higher rate of increase than no dispersal, but large scale spread produces a lower rate of increase. This was observed in the reflected dispersal models with uniformly distributed favorabilities at each site superimposed on a linear gradient of expected favorabilities between best and worst sites (Fig. 7). This also occurred, although to a smaller extent, with a cell model supplied with weather data as described below (Fig. 8).

M. Turrelli (personal communication) has suggested some consequences of dispersing on a gradient of environmental favorability of infinite extent, and these may have some relevance to finite environments. The advantage or cost of dispersal centered about the parental site depends on the curvature of the gradient in favorability. If the gradient is concave upward, dispersal is favored relative to non-dispersal. If the gradient is convex upward, non-dispersal is favored relative to dispersal. We did not explore the effect of the shape of gradients between best and worst sites in a finite environment.



**Fig. 7.** Intermediate optimum scale of dispersal resulting from variation superimposed on a gradient of expected favorability between expected best and worst sites (density independent model with reflecting pattern of dispersal). Numbers next to curves give the endpoints of the gradient in expected favorabilities over 20 sites, plus or minus the maximum possible deviation of values drawn from a uniform distribution centered on the expected favorability at each site



**Fig. 8.** Model of relative increase with dispersal on different scales based on severity of freezing at coastal weather stations of Oregon and Washington (cell pattern of dispersal). The density independent model gives an intermediate optimum at spread over two sites and a cost to greater dispersal (*open symbols and solid lines*). The density dependent model reduces or eliminates the cost to dispersal (*solid symbols, dotted lines*). Two runs for different threshold values for counting a severe freeze give similar results (4 days below  $-9^{\circ}\text{C}$ , *triangles*; 4 days below  $-9^{\circ}\text{C}$ , *squares*)

**Table 2.** Number of four day sequences with minimum temperature below  $-4^{\circ}\text{C}$  at weather stations on the Oregon and Washington coasts. (Brookings, 1055; Port Orford, 6784; Cape Blanco, 1360; Brandon Fish Hatchery, 0471; North Bend, 6073; Reedsport, 7082; Newport, 6032; Otis, 6366; Cloverdale, 1682; Seaside, 7641; Willapa Harbor, 9291; Grayland, 3320; Hoquiam, 3807; Point Grenville, 6584; Clearwater, 1496; Quillayute, 6858; Port Angeles, 6624; Sequim, 7538; Port Townsend, 6678; Coupville, 1783; Anacortes, 0176; Olga, 6096; Bellingham, 0574; Blaine, 0729)

Winter (Years)	Station codes																							
	6784		0471		7082		6366		7641		3320		6584		6858		7538		1783		6096		0729	
	1055	1360	6073	6032	1682	9291	3807	1496	6624	6678	0176	0574												
48/49	1	1	1	1	1	2	2	2	3	5	4	4	2	5	2	4	8	3	9	6	7	16	18	
49/50	1	1	1	1	1	3	4	3	6	13	11	11	4	13	4	11	16	9	16	15	16	16	18	
50/51	1	1	1	1	1	1	1	1	2	3	3	3	2	3	1	3	3	2	7	3	3	9	10	
51/52	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	9	
52/53	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	3	1	1	4	8	
53/54	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	4	1	5	1	4	6	9	
54/55	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	3	
55/56	1	1	1	1	1	2	3	2	4	6	4	5	4	6	3	4	8	4	8	7	7	12	13	
56/57	1	1	1	1	1	3	3	2	4	5	4	4	3	4	3	4	9	4	10	6	7	18	20	
57/58	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
58/59	1	1	1	1	1	1	1	1	1	2	1	11	1	1	1	1	2	1	2	2	2	3	4	
59/60	1	1	1	1	1	1	1	1	1	2	1	1	1	1	2	1	3	1	3	2	3	4	4	
60/61	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	2	
61/62	1	1	1	1	1	2	2	1	3	3	3	3	3	3	2	3	4	3	4	3	3	6	6	
62/63	1	1	1	1	1	1	1	1	1	2	1	2	1	2	1	2	3	1	4	2	2	8	10	
63/64	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	3	
64/65	1	1	1	1	1	1	1	1	1	2	1	1	1	2	1	1	2	1	3	2	2	4	4	
65/66	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	1	2	2	
67/68	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	1	3	1	2	4	4		
68/69	1	1	1	1	1	2	4	1	5	12	5	12	4	12	2	7	13	5	14	12	13	17	17	
69/70	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	2	
70/71	1	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	3	1	5	2	2	5	12	
71/72	1	1	1	1	1	2	3	1	3	5	4	4	3	4	2	4	9	3	11	5	7	11	13	
72/73	1	3	1	3	3	4	5	6	4	8	10	8	9	7	10	5	8	10	8	11	10	10	12	16

(6) Increasing Longevity of Organisms in the Resistant Phase of a Life Cycle

When greater longevity in a resistant phase of the life cycle reduces temporal variation in survival and fecundity, increased generation time can decrease the relative advantage of spreading offspring in an environment otherwise favoring spread. However, it could either increase or decrease costs of spreading offspring in an environment selecting against spread. This prediction follows from the results above. Spreading reproduction (or germina-

tion or growth) over a longer time has some of the bet hedging effects of spreading offspring in space (Cohen 1964; Murphy 1968; Stearns 1976). Since spreading offspring in space and spreading risk in time both serve to damp variation in fitness over time, an interaction between these two life history traits is likely. For example, increased longevity in the adult phase of life and repeated reproduction could decrease the variation in reproductive output per dispersing offspring. A decrease in the variance in favorability relative to the mean lowers the asymptote of maximum relative advantage from spreading off-

spring (Fig. 3) and thus results in less advantage to large scale dispersal. In an environment with expected differences in favorability among sites and selection against spread of offspring, the effect of increased adult longevity and repeated reproduction depends on the pattern of temporal variation. When the expected differences among sites are the result of a few very good or very bad years at certain sites (as in Table 2), increased longevity could *decrease the costs* of dispersal, because it would decrease the spatial variation in survival and reproduction (favorability). When departures from expected favorability occur randomly at all sites and sites differ in expected favorability, increased longevity could *increase the costs* of spreading offspring. In this case, a decrease in temporal variation in survival and reproduction per arriving propagule would result in a more similar ranking of sites from year to year as regards favorability for arriving propagules. We did not attempt models with overlapping generations to confirm these predictions but did confirm them in a crude way by averaging favorability over increasing periods of time and using the reflected pattern of dispersal with the uniform distribution of favorabilities (alone or superimposed on a gradient) and the cell pattern of dispersal with the weather data of Table 1. These arguments on effects of longevity can be reversed as well. A change in scale of dispersal could change selection on generation time and iteroparity.

#### (7) Patterns of Variability in Nature

If patterns of varying survival and fecundity are similar to variation in the physical environment, we would expect there to be little or no short term advantage to large scale spread of offspring (> 50 km). This is a highly speculative prediction, but it receives some support from the common observation that differences among monthly or yearly mean values for a physical variable often become greater and seldom become less as distance between sites of measurement increases. This is clearly true as one samples a line from the arctic to the tropics. It is less certain whether differences between mean values usually increase appreciably within distances of 50 to 100 kilometers, and we may be biased from living near a long estuary and a north-south coastline.

The premise that favorability is proportional to some combination of physical variables is also open to doubt, though favorability is affected by extremes of these variables (see references below). Data on survival and reproduction for large areas over many years are seldom obtained. However, some commonly measured quantities such as temperature, wind velocity, salinity, or rainfall are often correlated with survival or reproduction and these data are available for many regions and for long periods. We are aware of the difficulties in using such quantities but feel that they provide an approximation of a *pattern* of relative variation in favorability which is useful both in forming hypotheses and in demonstrating pitfalls inherent in this approach. We have selected severe freezing as an example.

Freezing affects survival of many species of intertidal invertebrates. Bowman and Lewis (1977) observed poor recruitment of limpets in England when freezing weather followed a set. Caullery (1929) and Orton and Lewis (1931) found mortality in *Thais lapillus* from low temperatures. R.T. Paine (personal communication) has observed high mortality of snails in the genus *Thais* when temperatures fall to about  $-5^{\circ}$  to  $-10^{\circ}$  C for several days. Dayton (1971) and Paine (personal communication) both noted an increase in the barnacle *Balanus glandula* following a severe freeze which may have resulted in the decline of *Thais* and other predators. In the following model freezing is considered beneficial, as would be the case for *B. glandula*.

Minimum daily temperatures for coastal weather stations from 1948 to 1972 were obtained from the National Climatic Center. In order to avoid fitnesses of zero, the index of favorability at all sites for all years was initialized at 1. Another one was added to the index for each 4 consecutive days of minimum temperatures below a threshold of  $-4^{\circ}$  or  $-9^{\circ}$  C. These indices of severity of freezing corresponding to favorability values are presented in Table 2. For indices based on 4 days below  $-4^{\circ}$  C, variance among sites is 7.8, among years 8.5; spatial correlation is 0.70 and temporal correlation 0.32. The variances are smaller and correlations higher for indices based on 4 days below  $-9^{\circ}$  C, but the patterns are similar for both different numbers of consecutive days and for different threshold values, so the results are not sensitive to the particular values chosen. The favorability matrix forms the basis of calculations just as in the above models.

If fitness is assumed to be proportional to these indices of freezing, then there is a strong gradient in favorability and a large cost to dispersal with density independence and the reflecting pattern of dispersal. In this model dispersal is always over an odd number of sites. There is a cost to dispersal in this model with data from the open coast only (Brookings, Oregon to Clearwater, Washington), for inland waters only (Shelton to Blaine, Washington), and for a series from southern Oregon through the Straits of Juan de Fuca and then north to the Canadian border (Brookings, Oregon, to Blaine, Washington). The cost to dispersal is less severe for the open coast, where the gradient in conditions is weakest, and more severe for the two series which include inland waters, where the gradient in conditions is strong. The mean distance between weather stations is about 45 km on the open coast and about 20 km in the inland waters. Thus in the density independent model there is a cost of dispersal with spreads of 40 km (3 sites) or more. (In another version of this model the gradient in favorability was eliminated by dividing the index of favorability for each site and year by the geometric mean for all years at that site. Under these conditions, for non-dispersing organisms all sites are equally favorable for the time interval considered, and the advantage of dispersal depends on the *relative* ups and downs scaled for each site rather than *absolute* severity of freezing. The northern sites, which have the most severe freezing, then also have the greatest temporal variation in favorability. With the gradient removed, the cost to dispersal is removed and the advantage from spreading offspring approaches an asymptote of maximum advantage. Thus it is the gradient in expected severity of freezing at coastal stations which imposes the cost on dispersal in this model.)

Density dependent and density independent models were compared with the cell pattern of dispersal and the Brookings to Blaine series of stations (Table 2, Fig. 8). In the density independent model there is an advantage to dispersal over 2 sites and a cost which increases with greater spread of offspring. The optimum intermediate scale of dispersal results from independent variation combined with a gradient in expected favorabilities, as described in section (5) above. With density dependence the cost at higher scales of dispersal disappears for the reasons discussed in section (4) above.

These models indicate no substantial advantage to spreading offspring beyond about 40 km on the open coast or 20 km in Puget Sound and inland waters. A more closely spaced array of stations might have given an optimal scale of dispersal or plateau of maximum advantage at a much smaller scale of spread. Density dependence removes the cost of dispersal, but does not provide a substantial advantage. These negative conclusions must be qualified, however, because only a single environmental variable has been considered. Severe freezing may have



different effects in different regions because of interaction with other factors. Dayton (1971) thought that freezing which kills snails of *Thais* spp. is more favorable to barnacles in inland waters and speculated on regional differences in the abundance and foraging of predator species and hence the effects of freezing.

## Discussion

The models suggest, at best, diminishing returns from added increments of spreading offspring. When there are no differences in expected favorability among sites (e.g.  $\tau=0.0$ ), independent variation in favorability selects for spread of offspring. A higher ratio of variance in favorability to the mean (e.g. high  $\sigma^2$ ) or a higher spatial correlation (high  $\rho$ ) increases the advantage of large scale spread relative to smaller scales of spread. Put another way, either a high variance relative to the mean or a high spatial correlation slows the approach to the asymptote of maximum advantage. Consequently, incremental increases in the scale of spread continue to yield an increased advantage over a broader range of spreads. Persistent increased differences in expected favorability among sites (e.g., increasing temporal correlation) either decrease the advantages of spread or increase its costs. Similar results are obtained for both density independent and density dependent models.

The models used here were kept simple to aid interpretation of the results and are not intended as a realistic description of the population dynamics of any organism. The assumptions are nevertheless not an unreasonable approximation of some major features of passive larval dispersal in marine benthic invertebrates. The results can thus be extended to the real world of benthic invertebrates and their larvae if certain limitations to their applicability are recognized. We will first mention similarities to invertebrates and implications for larval dispersal. We then discuss exceptions to the assumptions of the models and restrictions on application.

In many species of benthic invertebrates most of the dispersal (a) occurs in the pelagic larval period, (b) is an obligate feature of reproduction, and (c) varies greatly in scale among species. Extensive dispersal often occurs *before* larvae are competent to select a substratum and settle. Hence many suitable settling sites, sites with potentially high expected favorabilities, may be passed up during early development and not contribute an advantage to increased spread. Also, although larvae of benthic invertebrates select favorable microhabitats, the cues which affect settling do not accurately predict all the variation in expected survival and reproductive output per settling larva. The increased risk of death associated with increased pelagic period may be balanced by increased advantages from growth when larvae feed in the plankton. Since the advantage to producing smaller and more numerous eggs may balance or exceed costs in mortality during dispersal (Thorson 1946; Vance 1973), the increased dispersal associated with feeding larvae may simply be a fortuitous byproduct of a developmental pattern favored for other reasons. It is therefore reasonable to consider both the costs and advantages associated with environmental pattern separately from other hazards or advantages of dispersal.

Our models are most applicable to differences in spread of offspring associated with feeding versus non-feeding larval development. (They are also restricted to short term consequences of spreading offspring over time periods of 100 generations or less). Feeding larvae often have a longer pelagic period than non-feeding larvae. Presumably sibling feeding larvae spread from each other more widely than do sibling non-feeding larvae (Strathmann 1974). Studies of passive diffusion from a point

source (Okubo 1971) suggest spread in the range of ten to one hundred kilometers associated with pelagic periods on the order of a week to a month. Expansion of species ranges provide similar estimates (Crisp 1958; Gerdes 1977; Quayle 1964). Consider two types of invertebrates: one with feeding larvae which spread over 100 km and one with non-feeding larvae which spread over 10 km. Would patterns of variation in the benthic phase favor the type with the larger spread? We are unaware of data on survival and reproduction on the appropriate temporal and spatial scales but feel that differences in mean conditions for periods of several years are likely to become greater as one moves from adjacent 10 kilometer stretches of coastline to adjacent 100 km stretches of coastline. If this is correct, then our density independent models predict that the larger scale of spread will provide a relatively lower rate of increase, other things being equal, and optimal spread of offspring could usually be obtained with non-feeding larvae. Our density dependent models provide reduced costs or in some instances a slight advantage to large scale dispersers under these conditions, but the relative advantage of large scale dispersal is small for the variances and correlations examined. It would follow that development with feeding larvae is maintained by selection in the short term because of advantages other than the spreading of offspring. More extensive data on patterns of environmental variation, survival, and reproduction are needed to test the assumptions in this argument.

Patterns of closed and open areas in fisheries management schemes are often on the same scale as spread of larval offspring. When species with different scales of dispersal are affected, the size of permanently closed areas and rotated areas will affect the relative increase or decline of species.

The interactions among adult longevity, dispersal, and environmental pattern (see above) are potentially important but are not given much attention in general life history theories or in theories proposed for marine invertebrates. (See Stearns (1976) and Menge (1975) for reviews.) Ignoring the interacting effects of longevity and dispersal could lead to errors of interpretation when hypotheses are tested by comparisons among species.

Some restrictions on application of our models follow:

(1) We assess the costs and benefits of spreading offspring in terms of relative, not absolute, rates of increase. Hence, the models are relevant to coexisting genotypes within species that influence scale of spread, or to coexisting species with different scales of spread. If there is no heritable variation in spread of offspring within a species and no similar coexisting species differing in scale of spread, the models are irrelevant to costs and advantages of dispersal.

(2) Only short periods of 100 years or less are considered. Some long term consequences of dispersal which affect speciation and differential extinction of species have been ignored (Hansen 1978; Scheltema 1977).

(3) In some species adult dispersal is comparable to larval dispersal, or dispersal is not an obligate part of reproduction. In such species dispersal could be cued to deterioration of the local environment, and other advantages to dispersers become important. Our models are least applicable to the no dispersal versus some dispersal case.

(4) Complications arising from interbreeding are ignored.

(5) Complications arising from unsaturated sites (when carrying capacity varies) are ignored (Gadgil 1971), and density dependent mortality may provide complications beyond those already considered here.

(6) Only a few dispersal patterns are considered. An even spread of offspring over all sites reached is unlikely in nature. Actual patterns of spread of sibling larvae are unknown, so

we adopted the simplest pattern of spread in our models. We doubt that decay in numbers with distance from parental site would qualitatively affect our conclusions. Some patterns of dispersal which may occur in nature could produce quite different results, however. The center of distribution of a dispersing cloud of sibling larvae can move relative to the parental site. Variation in currents, as from winds, could produce large year to year changes in such movement. This variation in center of larval distribution could produce large temporal variations in survival and reproduction of larvae originating from each parental site in a benthic environment even though the benthic habitat varied spatially but not temporally. Our models suggest that such an environment would not select for a larval dispersal phase when no planktonic larval stage existed, but once a planktonic larval stage is established in a life cycle, selection could maintain spread of siblings in such situations.

(7) Mortality during the dispersal phase of the life cycle is not included in the models. If mortality increases with length of time in the plankton, optimal intermediate scales of spread will occur instead of an approach to an asymptote of maximum relative rate of increase. Varying mortality in the dispersing phase could produce less obvious complications. If a longer dispersal phase is associated with greater variation in numbers settling, then the relationship between adult longevity and scale of spread can be altered. Also, varying conditions for larvae in the plankton could select for or against spread of sibling larvae in much the same manner as varying conditions in the benthic phase of life. However, measuring spatial and temporal variation in favorability during the planktonic phase of life is likely to be much more difficult than measuring such differences for the benthic phase of life.

(8) Differential extinction of populations and local extinctions at sites are not included here. These events are rare for many populations of invertebrates if a site is defined as a large area, such as one kilometer of shoreline. However, if local extinctions are permitted with any frequency, there will always be an advantage to dispersing since only dispersers can both recolonize vacant sites and avoid eventual large scale extinction.

(9) Edge effects have also been eliminated or minimized in the models. Dispersal beyond the edge of a species' range may impose a high cost on dispersal. The closest approach to this situation in our models is the case of high spatial and low temporal variance in favorability, such that dispersers are constantly being exported from good sites.

Two larval traits greatly reduce the costs of larval dispersal and may provide the major advantages of a pelagic larval stage. One is growth in the plankton; the other selection of a favorable site for benthic life. Most of the larval growth occurs before larvae are capable of settling. Our models ignore habitat selection, and this is an appropriate assumption for dispersal during the earlier part of larval development. The habitat selection could aggregate settling larvae at fewer sites, however, narrowing the spread of larvae and eliminating consistently unfavorable sites.

Relative rates of increase are measured for the total population in our models. If one calculates a rate of increase separately for each site (a geometric mean) and then takes the arithmetic mean of these increases for the average rate of increase, quite different results are obtained. Expected differences in favorability do not appear to select against dispersers when relative rate of increase is calculated by the latter method because poor sites are given the same weight as favorable sites. Dispersers increase relative to non-dispersers at consistently poor sites and non-dispersers increase relative to dispersers at consistently favorable sites. If one were examining a change in gene frequencies over

time, it would be important to estimate total numbers at each site and not just frequencies at each site.

Most of the results of these models seem intuitively obvious in retrospect, but they were not all obvious to us at the beginning of this study, and they have received little or no attention in the literature on dispersal of invertebrate populations. We feel that the use of such highly simplified simulation models is justified because they give simple results, can accommodate many sorts of data on patterns of environmental variation, and may encourage the development of analytical solutions to these problems.

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