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Propagule dispersal and the scales of marine community process

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ABSTRACT

Benthic marine organisms are characterized by a bipartite life history in which populations of sedentary adults are connected by oceanic transport of planktonic propagules. In contrast with the terrestrial case, where 'long distance dispersal' (LDD) has traditionally been viewed as a process involving rare events, this creates the possibility for large numbers of offspring to travel far relative to the spatial scale of adult populations. As a result, the concept of LDD must be examined carefully when applied in a marine context. Any measure of LDD requires reference to an explicit 'local' scale, often defined in terms of adult population demography, habitat patchiness, or the average dispersal distance. Terms such as 'open' and 'closed' are relative, and should be used with caution, especially when compared across different taxa and systems. We use recently synthesized data on marine propagule dispersal potential and the spread of marine invasive species to draw inferences about average and maximum effective dispersal distances for marine taxa. Foremost, our results indicate that dispersal occurs at a wide range of scales in marine communities. The nonrandom distribution of these scales among community members has implications for marine community dynamics, and for the implementation of marine conservation efforts. Second, in agreement with theoretical results, our data illustrate that average and extreme dispersal scales do not necessarily covary. This further confounds simple classifications of 'short' and 'long' dispersers, because different ecological processes (e.g. range expansion vs. population replenishment) depend on different aspects of the dispersal pattern (e.g. extremes vs. average). Our findings argue for a more rigorous quantitative view of scale in the study of marine dispersal processes, where relative terms such as 'short' and 'long', 'open' and 'closed', 'retained' and 'exported' are defined only in conjunction with explicit definitions of the scale and process of interest. This shift in perspective represents an important step towards unifying theoretical and empirical studies of dispersal processes in marine and terrestrial systems.

Keywords

Biological invasions, dispersal kernel, invasive spread, larval retention, long-distance dispersal, marine conservation, pelagic larval duration, spatial ecology.

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INTRODUCTION

Life histories and fluid characteristics in the ocean create the possibility for extremely long-distance dispersal (Thorson, 1950; Scheltema, 1988; Roberts, 1997; Shanks *et al.*, 2003). At the same time, larval behaviours, life history strategies, and persistent oceanographic features may limit dispersal, thus enhancing local retention of propagules (Olson, 1985; Shanks, 1995; Bellwood *et al.*, 1998; Wing *et al.*, 1998; Jones *et al.*, 1999; Cowen *et al.*, 2000; Armsworth *et al.*, 2001; Swearer *et al.*, 2002). Although marine propagule dispersal is difficult to quantify directly, recent reviews provide evidence of both extremes and many intermediate scenarios (Bradbury & Snelgrove, 2001; Mora & Sale, 2002; Kinlan & Gaines, 2003; Shanks *et al.*, 2003).

The wide range of possible dispersal distances and the scarcity of quantitative dispersal data for marine taxa have led to a debate over the degree to which marine larvae produced in a local population are likely to return to that population (self-recruitment, or retention) or emigrate to another population (export). Evidence of decoupling of local population processes from local production argues that marine systems are open and broadly connected over larger spatial scales than terrestrial systems (Roughgarden *et al.*, 1988; Underwood & Fairweather, 1989; Gaines & Bertness, 1992; Caley *et al.*, 1996; Carr *et al.*, 2003). Yet, a growing body of research has highlighted evidence of restricted dispersal, questioning the paradigm that marine populations are demographically open at scales of tens to thousands of kilometres (e.g. Jones *et al.*, 1999; Swearer *et al.*, 1999; Sotka *et al.*, 2004; reviewed in Swearer *et al.*, 2002).

Recent syntheses argue against broad generalization of the relative open or 'closedness' of marine populations, confirming that marine dispersal scales are not uniformly polarized towards long or short distances, but instead are distributed over a wide continuum of scales (Bradbury & Snelgrove, 2001; Mora & Sale, 2002; Kinlan & Gaines, 2003; Shanks *et al.*, 2003). Evidence from hydrodynamic models and genetic structure data indicates that the average scale of dispersal can vary widely even within a given species, at different locations in space and time (e.g. Cowen *et al.*, 2003; Sotka *et al.*, 2004). Theoretical and empirical studies emphasise that the appropriate dispersal scale to consider depends on the process of interest, such as colonization vs. population replenishment (Cain *et al.*, 2000; Kinlan & Gaines, 2003; Lessios *et al.*, 2003; Trakhtenbrot *et al.*, 2005). Finally, the degree to which a population is 'open' or 'closed' depends on the scale at which population dynamics are being studied, but this is often not acknowledged or quantified. Thus, some of the supposed variation in 'openness' of marine populations may be a function of how the local scale has been defined.

Similarly, the concept of long-distance dispersal (LDD) must be rigorously defined for its importance in the marine environment to be evaluated. There are at least two senses in which the term LDD has been applied (Cain *et al.*, 2000; Higgins *et al.*, 2003). LDD may be defined relative to some ecologically relevant scale, such as the distance over which adults interact and reproduce, the size of discrete habitat patches, or the length scale of synchrony in adult growth, fecundity, and mortality. We refer to this here as the local population scale. Alternatively LDD may be defined relative to the mean or median dispersal distance (i.e. as individuals that travel much further than the bulk of propagules). In this paper, we will refer to these as Case I and Case II, respectively. They have also been referred to as scale-dependent (Case I), and shape-dependent (Case II), where the latter case emphasizes the so-called 'tails' (extremes) of the dispersal kernel (Higgins *et al.*, 2003). In both cases, there are practical problems with definition of the reference scale. In Case I, the local population scale is often not known precisely, and is seldom made explicit in empirical studies. In Case II, an estimate of the dispersal distribution must be available, and the portion of the dispersal kernel that comprises extreme events must be specified, defining LDD using quantiles (e.g. 99th percentile) or extreme value distributions based upon the dispersal kernel (Clark *et al.*, 2003; Higgins *et al.*, 2003).

For terrestrial plants, which have been the focus of recent interest in LDD, the two possible reference scales are of a similar order of magnitude. Terrestrial plants generally have small neighbourhoods of adult interaction and reproduction (meters to kilometres), and their average propagule dispersal scales are also quite small (Pacala *et al.*, 1996; Kinlan & Gaines, 2003). For this reason, the distinction between Case I and Case II LDD has not been emphasized (but see Higgins *et al.*, 2003 and references therein). In fact, the issue of LDD in plant populations was long-overlooked because the propagules that travel beyond small local neighbourhoods do not have a major influence on the demography of established distant populations, because they are so few. The recent surge of interest in LDD in plant communities has been driven by the realization that LDD can play a crucial role in colonization, spread,

diversity, landscape pattern, genetic structure and evolution (Cain *et al.*, 2000; Levin *et al.*, 2003).

The marine environment presents a different scenario. If the first definition of long-distance dispersal is applied (Case I), then the question of how prevalent LDD is in the sea reduces to whether populations are open or closed, relative to some local population scale. In this case, many marine populations have the potential for very high levels of LDD, because LDD is defined merely as long-distance travel relative to the adult population scale (open demography). By this definition, LDD is crucial to the demography of established marine populations in addition to its known importance for colonization, landscape pattern, and evolution (Roughgarden *et al.*, 1988; Caley *et al.*, 1996). On the other hand, if the second definition is taken (Case II), then the importance of LDD may vary greatly among marine species based on the fraction of successful propagules that travel much further than the average. In this case, long distance dispersal is irrelevant to the question of open vs. closed demography, as species anywhere along the spectrum between open and closed could exhibit high or low rates of LDD. Here, the role of marine LDD may be analogous to its impact in terrestrial environments (i.e. it may be crucial in landscape and evolutionary processes but not for demography). Under this definition, it is not immediately clear whether LDD is more or less prevalent in the marine environment, as it depends not on the absolute dispersal distance but on the 'fatness' of marine dispersal tails, which is difficult to measure.

To understand the distinction between these two definitions, consider a sedentary marine fish whose adults move and mate in a neighbourhood of about 1 km in diameter, yet whose larvae disperse an average of 250 km. Under the Case I definition of LDD, a larva travelling 50 km would be categorized as an extremely long-distance disperser (50 km > 1 km). Under the Case II definition, that same larva would be seen as a relatively short disperser (50 km < 250 km).

In this study, we synthesize data on average dispersal distances, planktonic larval durations (PLD), and spread rates with theory to examine the range of average and long-distance dispersal scales in benthic marine organisms. We use these data to explore the possible roles of LDD in marine systems, and to highlight important areas for future research. Our goal is not to provide a comprehensive review of marine dispersal, nor to discuss all the processes that may enhance or limit long-distance dispersal in the sea. Instead, we outline a basic framework for studying marine dispersal scales in a comparative, multispecies context, employing comparisons of empirical data with simple null models of transport based on a minimum set of physical and biological variables (Siegel *et al.*, 2003). In doing so, we explicitly ignore two potentially important sets of processes: (1) specific behavioural and oceanographic features that may limit or enhance dispersal (reviewed in Sponaugle *et al.*, 2002), and (2) anthropogenic long-distance transport (reviewed in Carlton & Geller, 1993). We briefly consider secondary dispersal in the ocean (i.e. rafting and drifting of adults), but do not review the large body of evidence for this process in detail. We hope others will build on the framework presented here.

Our results underscore the heterogeneity in scales of marine dispersal processes, and the pitfalls of categorical classification of

organisms as 'local' or 'long-distance' dispersers without explicit reference to the scale and process of interest. We argue for a more quantitative and less categorical approach to marine dispersal studies that recognizes the inter- and intraspecific variation in dispersal, and takes account of the scale of study or management when considering questions such as larval retention, export, and long-distance dispersal.

METHODS

Dispersal estimates

To evaluate Case I and Case II long-distance dispersal, we require estimates of both average dispersal and the dispersal kernel. As empirical quantification of dispersal kernels in the marine environment is logistically difficult, we rely on a combination of empirical data and models to develop approximations of marine dispersal kernels.

We use two types of data to estimate average dispersal distances for sedentary marine species. Kinlan & Gaines (2003) compiled information on genetic isolation-by-distance (Wright, 1943) in a diverse array of benthic marine taxa ($n = 90$), and use these data to derive estimates of average dispersal distance based on genetic simulations, under certain assumptions about population size, shape of the dispersal kernel, and spatial arrangement of populations (Palumbi, 2003). This data set includes fish, invertebrates, and macroalgae with a variety of life histories, and represents the most comprehensive available database of empirical marine dispersal estimates. Subsequent work has shown that, for the subset of these species where planktonic larval duration (PLD) data were available, average dispersal distances calculated from genetic structure are in good first-order agreement with predicted dispersal distances based on oceanographic models (Siegel *et al.*, 2003).

Genetic estimates of dispersal, however, entail considerable uncertainty and represent averages over many generations and a large spatial extent (Kinlan & Gaines, 2003; Palumbi, 2003). Moreover, they are available only for a small subset of benthic marine species. Because most marine larvae are small and weak relative to prevailing ocean currents, the length of the planktonic period is often used as a proxy for dispersal ability (Shanks *et al.*, 2003). A variety of biological and oceanographic features can prevent a propagule from reaching its full passive dispersal potential (Sponaugle *et al.*, 2002; Swearer *et al.*, 2002), but recent syntheses support a general agreement between PLD and dispersal distance (Shanks *et al.*, 2003; Siegel *et al.*, 2003). The greatest deviations from the passive dispersal model probably involve large, post-flexion fish larvae, and larvae with extensive vertical migration behaviour (Leis, 2002). Siegel *et al.* (2003) simulated dispersal of passive larvae with a range of PLD's in an idealized near shore region, parameterized with surface velocity statistics typical of coastal currents. This model differs importantly from traditional advection-diffusion models, as it accounts for serial correlation in larval trajectories induced by large turbulent eddies (10–100 s of km), which violate the assumptions of simple diffusion. Eddies are modelled by enforcing serial correlation of larval movements governed by a Lagrangian decorrelation time scale τ_L

that increases logarithmically from 0.5 days in the extreme near shore to 3 days offshore (consistent with coastal oceanography, Davis, 1985). Siegel *et al.* (2003) found that, for organisms with PLD's greater than several days, the dispersal kernel was well-approximated by a Gaussian curve parameterized in terms of the mean and variance of alongshore current velocity and the mean larval duration. As noted above, mean dispersal distances predicted by the Gaussian model were in accord with genetic estimates of average dispersal distance. These results are consistent with data from coastal ocean surface drifters (e.g. Poulain & Niiler, 1989; Winant *et al.*, 1999) and more complex hydrodynamic models of coastal larval dispersal (e.g. Dight *et al.*, 1990; D.A. Siegel, pers. comm.).

We therefore combine empirical estimates of PLD with the simulation results of Siegel *et al.* (2003) to derive additional dispersal estimates. PLDs are widely available for marine fish, because they can be measured by counting daily rings laid down in calcium carbonate earbones (otoliths). We compiled PLD estimates from the literature for 390 benthic and demersal marine fish based on previously described methods (Lester & Ruttenberg, in press; S.E. Lester, unpublished data). We used the mean PLD, T_m , to determine the parameters of the Gaussian dispersal kernel in terms of U , the mean alongshore velocity (advection), and σ_u , the alongshore velocity variance (diffusion), from the empirical equations (Siegel *et al.*, 2003):

$$x_d = 0.994 \times T_m U \quad (\text{Eqn. 1})$$

$$\sigma_d = 2.238 \times \sigma_u T_m^{1/2} \quad (\text{Eqn. 2})$$

$$D_d = 0.695 \times T_m U + 0.234 \times T_m \sigma_u \quad (\text{Eqn. 3})$$

In these equations, x_d represents drift (Gaussian mean), τ_d the spread (Gaussian variance), and D_d the average dispersal distance, a function of drift and spread. Assumed values of U and τ_u are noted where this model is applied (*Results and Discussion*), and are based on typical velocity statistics obtained from moored current meters, surface drifters, and HF-RADAR measurements of surface currents in coastal margins (e.g. Davis, 1985). This avoids the problematic issue of estimating eddy diffusivities for parameterization of subgrid-scale turbulence used in other Lagrangian models (e.g. Cowen *et al.*, 2000). We note that time- and space-averaged estimates of current velocity often have much lower mean values (and higher standard deviations) than the short-term current observations that are often used to parameterize advection-diffusion models. Outputs of this Lagrangian null model should only be viewed as estimates of *potential* dispersal, in the absence of species- and location-specific behavioural and oceanographic factors that may limit or enhance dispersal, particularly in large and strong-swimming larvae with well-developed sensory capabilities (reviewed in Leis, 2002; Mora & Sale, 2002; Sponaugle *et al.*, 2002; Swearer *et al.*, 2002). Our goal was to develop a common framework to compare dispersal among different species groups in marine communities, to illustrate the patterns and consequences of among-species variation in dispersal ability, and to identify likely deviations from the null-model.

To examine differences in dispersal ability across marine species groups, we classified each species in the genetic data set according to higher taxonomy (algae, invertebrate, or fish), and each fish in the PLD data set according to trophic group (herbivorous/omnivorous or carnivorous) and level of exploitation (commercially exploited or not commercially exploited), based on information from FishBase (Froese & Pauly, 2004). Species listed as of minor, average, or high commercial importance were considered commercially exploited. Species listed as noncommercial, of potential commercial interest only, gamefish only, or aquarium trade only were considered noncommercially exploited. Species whose main diet items included algae were considered herbivorous/omnivorous; all others were considered carnivorous.

Estimating larval retention

Case I long-distance dispersal is evaluated by calculating the fraction of propagules produced at a given scale that land within their natal region. Here, the scale corresponds to some ecologically relevant reference scale (e.g. the scale of local adult interaction, the scale of study, or the scale of management).

To examine the effect of scale on the percentage of larvae produced in a region that settle in the same region (larval retention, or self-recruitment), we considered a hypothetical population of sedentary adult organisms distributed homogeneously along an infinite linear coastline. If progeny disperse according to a Gaussian function, the fraction of larvae p_r retained in a region of interest of length L with lower boundary at coordinate $y = 0$ is given by

$$p_r = \frac{1}{\sqrt{2\pi\sigma_d^2}} \int_0^L \int_0^L e^{-(y-x_d)^2/2\sigma_d^2} dy dx_d \quad (\text{Eqn. 4})$$

where x_d and σ_d are parameters of the dispersal kernel (Eqns. 1–2). This approach assumes uniform larval production and a stationary dispersal kernel across the region.

We compared species across taxonomic, trophic, and other groups by plotting the average retention fraction p_r vs. scale L , using either standard deviation or interquartile range of the ensemble to show within-group variation.

Spread rates

Theoretical and empirical work has demonstrated that spread rates of organisms into uncolonized, suitable habitat are strongly influenced by the maximum distance of effective dispersal (that is, dispersal by individuals that subsequently establish and reproduce) (Lewis & Kareiva, 1993; Clark, 1998; Higgins & Richardson, 1999; Cain *et al.*, 2000). Therefore, comparison of spread rates with indices of average dispersal distance may yield insight into the importance of Case II LDD in the marine environment (i.e. the influence of dispersal events at scales \gg average dispersal). Recognizing that a variety of other factors can influence spread rates of invading organisms (Levin *et al.*, 2003), we take a macroecological approach here, using data from a wide variety of species in different environments to assess overall patterns.

Estimates of spread rates for benthic marine organisms were obtained from recent reviews, using the methods described therein (Kinlan & Gaines, 2003; Shanks *et al.*, 2003; B.P. Kinlan & A. Hastings, in press). Invasion rate was defined as the average rate of linear expansion of an advancing colonization front in kilometres per year (Shigesada & Kawasaki, 1997). This was estimated from field surveys of the increase in distribution of invasive species with time. We limited our search to studies of invasive species expanding by natural dispersal in the absence of factors which might slow spread (e.g. dispersal barriers, competitive displacement of native species, differences in habitat quality, or environmental gradients), and used only the subset of species where we could also estimate the average length of the planktonic period as a proxy for average dispersal distance. We found estimates of spread rate fitting these criteria for 31 species (15 macroalgae, 14 invertebrates, and two fish). Sources and numerical estimates are given in Kinlan & Gaines (2003) and B.P. Kinlan & A. Hastings (in press), and omitted here for brevity.

Gaussian extreme value analysis

To facilitate comparison of spread rates to average dispersal distances, we incorporated expectations about the maximum propagule dispersal distance expected during a given amount of time under a particular dispersal kernel. Cases where spread rates are much less than the expected maximum and closer to the average suggest a reduced importance of extreme dispersal events (dispersal tails). On the other hand, cases where spread rates are much greater than the average and similar to or greater than the expected maximum value suggest an important role of Case II LDD events.

Using well-developed theory on the statistics of extreme values, the expected maximum value in a given time period, or equivalently the expected return interval for a dispersal event of a given magnitude, can be derived for any dispersal distribution (Gaines & Denny, 1993). Here, we illustrate the approach using the Gaussian distribution, for which the expected maximum value can be computed via the exact analytical form

$$\bar{Z}_{\max}(k) = E\{Z_{\max}(k)\} = \int_0^{+\infty} z \cdot \frac{d}{dz} \left[\int_0^z |e^{-(y-x_d)^2/2\sigma_d^2}| dy \right]^k dz \quad (\text{Eqn. 5})$$

where x_d , σ_d , and y are as in Eqn. 4, z is the absolute distance dispersed, $Z_{\max}(k)$ denotes the maximum observed dispersal distance in an interval of length k , and $\bar{Z}_{\max}(k)$ is the expected value of the maximum in repeated observation intervals of length k (Gaines & Denny, 1993).

The critical parameter here is k , the number of times the dispersal kernel is sampled in the observation interval. The appropriate observation interval for comparison with annual rates of spread is one year. How many independent larval releases from a given location can be expected to occur during this time interval? Recall that coastal ocean flows are characterized by temporal autocorrelation on the scale of days. Typical values of the decorrelation time scale for the coastal ocean range from $\tau_L \sim 0.5$ –7 days (Davis, 1985). Taking $\tau_L =$ three days, a population that

releases larvae continuously for 365 days independently samples the flow field only ~ 120 times. If decorrelation scales are extremely short (0.5 days) and release occurs continuously, there may be as many as ~ 720 independent releases. If an organism reproduces seasonally or sporadically, as is common, there may be many fewer independent draws from the long-term dispersal distribution (on the order of 10–50). These first-order calculations allow us to estimate a range of likely maximum annual dispersal distances given only a PLD estimate. The PLD estimate is used to derive a Gaussian dispersal kernel according to Eqns. 1–2, and the expected maximum dispersal distance is calculated using Eqn. 5.

RESULTS AND DISCUSSION

Case I: The role of nonlocal dispersal

Figure 1 illustrates the variation in estimates of 'local' dispersal, or larval retention that is possible with different definitions of the reference scale. Here, a Gaussian dispersal kernel based on a hypothetical organism with a mean PLD of 30 days dispersing passively by surface currents (Siegel *et al.*, 2003) is used to predict the number of larvae produced in linear sections of an island coastline of variable size (10, 50, and 200 km) that will settle in those same sections of coast. Adults are assumed to be distributed homogeneously along the coast; where the curve shown is an example for larvae dispersing from a single site marked as A. The fraction of retained propagules varies substantially, from 2–33%, depending on the chosen scale. This simple Lagrangian model excludes potentially important oceanographic and behavioural processes that may limit or enhance dispersal, and alter the shape of the dispersal kernel (Sponaugle *et al.*, 2002). However,

for many species, PLD has been shown to be a reasonable first-order predictor of realized dispersal distance (Siegel *et al.*, 2003).

Because marine larvae are almost impossible to track directly, the relatively few studies of larval retention have relied on natural or artificial chemical tags or genetic markers to estimate the proportion of larvae produced in a region that return to that region (e.g. Levin, 1990; Jones *et al.*, 1999; Swearer *et al.*, 1999; Sotka *et al.*, 2004; reviewed in Swearer *et al.*, 2002). The spatial resolution of these markers is often inadequate, and consequently, most of these studies are only able to estimate the proportion of retained larvae in regions measuring tens to several hundred km. Often, such studies have found a substantial fraction of self-replenishment — a seemingly surprising result in light of the perception that marine populations are demographically open at very large scales. However, as Fig. 1 illustrates, substantial self-seeding is not unexpected at the mesoscale (approx. 10–100 km), even for larvae with planktonic durations of a month or more that experience both advection and diffusion during that period. For example, using a chemical tag-recapture approach, Jones *et al.* (1999) estimate that 15–60% of damselfish larvae spawned in an island region ~ 50 km in circumference returned to that region after their 18 to 21-day PLD. The wide range of their estimate arises from considerable uncertainty about population demographic parameters including larval production and larval mortality. Applying the passive dispersal model of Siegel *et al.* (2003), the expected retention fraction ranges from five to 20% under a range of possible surface currents ($U = 0\text{--}15$ cm/s, $\sigma_u = 0\text{--}40$ cm/s). Although the high end of the Jones *et al.* (1999) estimate suggests the action of biophysical processes that enhance retention, the low end could be explained on the basis of passive dispersal alone.

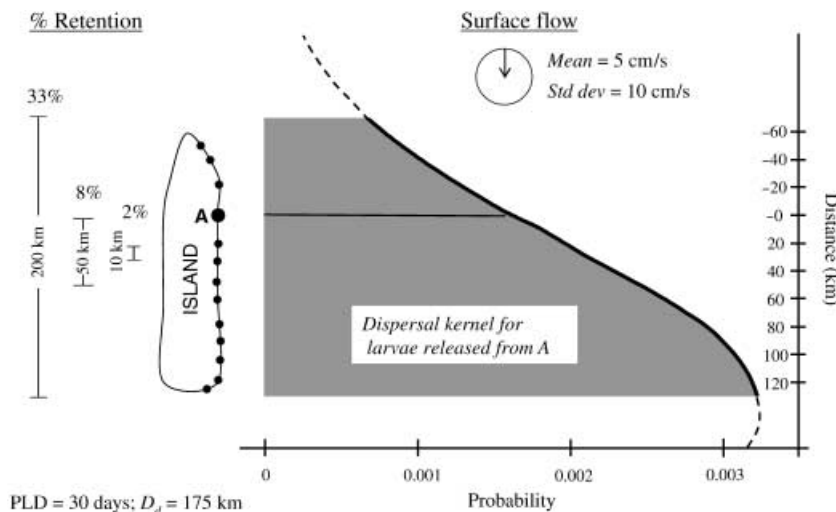


Figure 1 An idealized island coastline. An example of a *single* Gaussian dispersal kernel is shown, describing dispersal of a hypothetical passively dispersing organism with average planktonic period of 30 days from point A to other points along the linear island coast. Dots represent discrete populations. Shaded area of kernel denotes the fraction of larvae produced at site A that settle on the east shore of the island after 30 days. The Gaussian kernel is based on model fits to Lagrangian simulation results of Siegel *et al.* (2003), parameterized with surface velocities typical of the coastal ocean ($U = 5$ cm/s, $\sigma_u = 10$ cm/s), leading to an average dispersal distance, D_0 , of 175 km. The scale bars and percentages at left indicate the fraction of larvae produced in the indicated area that are expected to settle in that same area (i.e. the integral described in Eqn. 4 in the text). The result is a null model of larval retention as a function of spatial scale, in the absence of behavioural or oceanographic features that limit or enhance dispersal.

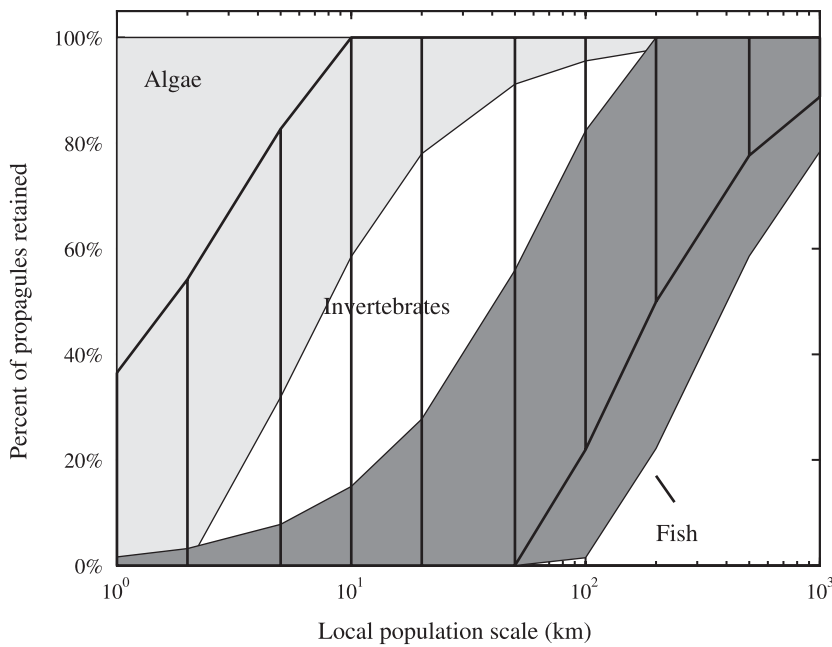


Figure 2 The percentage of propagules that are 'locally' retained depends on the size of the area that is considered local, and differs systematically among marine taxa. Variation (interquartile range) in simulated propagule retention is shown for three marine taxonomic groups (algae, $n = 13$; invertebrates, $n = 48$; fish, $n = 25$). Larval retention was calculated using genetic estimates of average dispersal (D_a , Kinlan & Gaines, 2003) to parameterize Gaussian dispersal kernels (Eqns. 1–3), which were then integrated according to Eqn. 4. See Siegel *et al.* (2003) for details of the oceanographic simulation model used to relate D_a to kernel parameters.

High levels of self-replenishment at the spatial resolution of chemical or genetic markers (which, at best, are able to localize the origin of recruits to certain clades, islands, bays, estuaries, or water masses) do not imply self-seeding on the much smaller scales of ecological experimentation. Historically, the majority of marine ecological experiments and observations have been conducted at scales of several to hundreds of meters (Levin, 1992), while many management efforts are focused on scales ranging from hundreds of meters to several km (Halpern, 2003). Figure 1 demonstrates the pitfalls of generalizing results on larval retention without explicit reference to the scale of study.

Efforts to categorize marine populations as open or closed at a specific scale may often be less relevant than the continuous functional relationship between scale and self-recruitment, such as the example shown in Fig. 2. Here, genetic estimates of average dispersal distance for a variety of benthic marine algae, invertebrates, and fish (Kinlan & Gaines, 2003) are combined with models of dispersal kernel shape and variance (Siegel *et al.*, 2003) to predict the fraction of locally retained larvae in a given region. This simple example is limited by its assumption of passive dispersal, and the possibility of systematic biases in the genetic data set (the longest and shortest dispersing species are less likely to be included), but it serves to illustrate the differences in retention among species in marine communities. As previous studies have noted, algae tend to exhibit quite restricted dispersal, fish tend to disperse widely, and invertebrates have extremely variable dispersal patterns (Kinlan & Gaines, 2003; Shanks *et al.*, 2003).

Figure 2 indicates that, at any particular scale, the degree to which marine populations are 'open' depends greatly on the species and, more generally, on the taxonomic group of interest. This has interesting implications for both marine community dynamics and spatial marine management initiatives (e.g. no-take marine reserves). From an ecological perspective, depending on the focal scale, species differ greatly in the extent to which

local recruitment depends on local larval production. This in turn can influence the outcome of biotic interactions and responses to environmental variability (Levin, 1992). The imposition of any external force with a characteristic scale, be it disturbance, habitat patchiness, or biotic interactions (e.g. with a habitat-former or predator) may have different effects on different community components because of among-species differences in the scale of demographic processes (Rougharden, 1977; McLaughlin & Rougharden, 1992; Hastings, 1993; Reed *et al.*, 2000).

From a management perspective, such large variance in the scale of demographic processes among taxa presents challenges for management of marine communities (Walters, 2000; Carr *et al.*, 2003). Management efforts with a single characteristic scale can force compromises in the level of protection or enhancement of individual stocks within diverse multispecies assemblages. For example, to create no-take marine reserves with the goal of enhancing yield of a single fishery, reserve size (or the size and spacing of a reserve network) can be selected to optimize overall yield. However, if one wants to maximize yield of a multispecies assemblage whose stocks vary in dispersal ability, no single reserve can maximize benefits for all species (Walters, 2000). In extreme cases, a single large reserve managed for sustainable harvest of long-dispersing fish may have no benefit at all for algal or short-dispersing invertebrate fisheries (e.g. kelp, abalone). Recent modelling efforts point towards a solution that can eliminate this compromise: networks of smaller reserves, even of uniform size and spacing, under a wide range of circumstances can optimize benefits across all stocks, in some cases leading to greater fisheries yields than those under traditional effort-based management (Neubert, 2003; B. Gaylord, S.D. Gaines, D.A. Siegel, and M.H. Carr, *in review*). Reserve networks can also help protect species where dispersal rates are too high for a single reserve to be practical (Trakhtenbrot *et al.*, 2005).

The management issues raised by the high variance in marine dispersal scales are further explored in Fig. 3. Here, fish species of

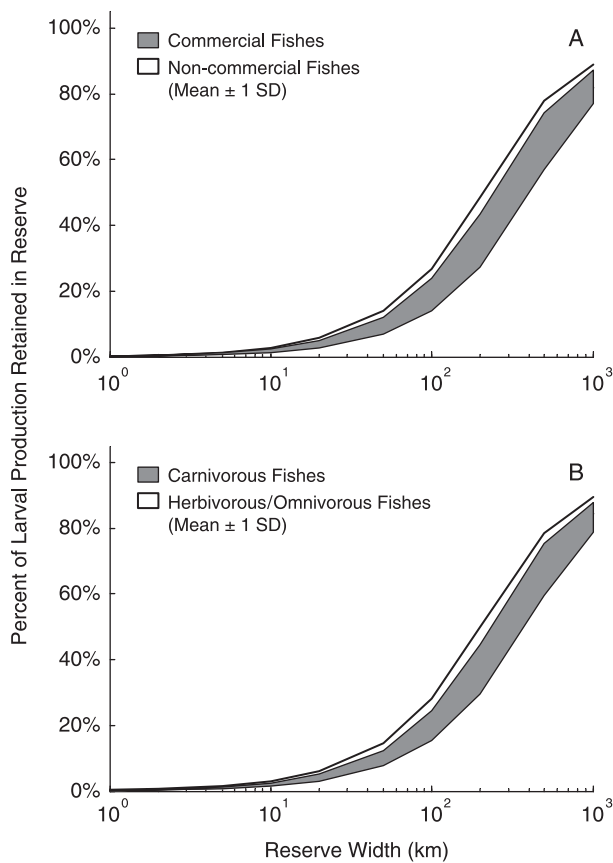


Figure 3 Retention vs. reserve size curves based on mean planktonic larval duration, T_m , for (A) commercially fished ($n = 104$) vs. noncommercial ($n = 280$) fish species, and (B) herbivorous/omnivorous ($n = 146$) vs. carnivorous fishes ($n = 230$). Larval retention was calculated using estimates of mean T_m to parameterize Gaussian dispersal kernels (Eqns. 1–3), which were then integrated according to Eqn. 4. See Siegel *et al.* (2003) for details of the oceanographic simulation model used to relate T_m to kernel parameters. Values of T_m were compiled from a literature survey (Methods).

different trophic and commercial exploitation levels are shown to differ significantly in PLD (t -test; commercial vs. noncommercial, mean ± 1 SE = 47.8 ± 2.2 vs. 31.1 ± 1.3 days, $P < 0.0001$; carnivorous vs. noncarnivorous, mean ± 1 SE = 41.7 ± 1.4 vs. 24.8 ± 1.7 days, $P < 0.0001$), hence, in their dispersal potential and predicted fraction of self-seeding under the assumption of passive dispersal. Note that the retention curves of fish predicted from PLD (Fig. 3) are comparable to those predicted from genetic data (Fig. 2), but the larger sample size allows us to explore differences among functional groups of fishes. Carnivorous and commercially exploited species tend to have longer scales of potential dispersal and lower larval retention at any given scale. Single reserves of any particular size will thus, on average, tend to protect a greater fraction of the production of species at lower trophic levels and with lower levels of exploitation, possibly leading to shifts in the trophic dynamics and structure of communities in reserve areas (Walters, 2000; Micheli *et al.* 2004). Reserve

networks, by reducing the variance in protection among species, may buffer against such cascading effects on community structure. However, more complex and subtle changes are possible and further study of community changes following implementation of reserve networks is essential (Carr *et al.*, 2003; Micheli *et al.* 2004).

Case II: The role of extreme dispersal

If LDD is defined as dispersal much farther than the average, rather than dispersal beyond the local population, a very different picture of the importance of LDD in marine organisms emerges. Species with broad larval dispersal and restricted local population scales (e.g. barnacles, which are sessile, occupy discrete rocky intertidal habitats, and are limited in their choice of mates to a few cm) will have high levels of 'nonlocal' dispersal equivalent to LDD under the Case I definition. However, their limited adult movement and scale of reproduction can render the extremes of the dispersal distribution unimportant, making Case II LDD less likely. Allee effects can effectively eliminate the influence of extreme dispersal events in sexually reproducing species (Lewis & Kareiva, 1993; Kinlan & Hastings, *in press*), decoupling the importance of 'nonlocal' (Case I) and 'extreme' dispersal events (Case II).

As a first step toward examining the relative influence of extreme dispersal events across marine taxa, we compare estimates of annual spread rates into uncolonized habitat for a variety of species with (1) predicted average dispersal distance (i.e. the distance travelled by the bulk of propagules), and (2) predicted maximum annual dispersal distance. Both average and maximum dispersal predictions are derived from the Gaussian kernel approximations (see Methods). We view these as expectations under a null model excluding effects of behaviour, physical retention features, anthropogenic dispersal, and processes that might extend the tails of dispersal kernels. Deviations from these null expectations suggest the operation of one or more of these alternative processes.

Results of this comparison suggest that the importance of extreme dispersal events for spread of marine populations is mixed (Fig. 4). The majority of invasive invertebrates and fish, which tend to have large average dispersal distances, have annual spread rates that are similar to or less than their predicted average dispersal distance. Only a third (6 of 16) have spread rates close to expected maximum dispersal distances. In striking contrast, a majority of macroalgae (9 of 15) have annual spread rates that exceed Gaussian-based estimates of average and maximum dispersal distances by up to several orders of magnitude. Although the planktonic duration of the primary propagules of these algae is not known precisely, a large body of evidence on macroalgal dispersal suggests that most macroalgal propagules have planktonic periods of less than a day and dispersal distances on the order of tens to hundreds of meters (reviewed in Santelices, 1990).

Rapid spread rates for macroalgae and other taxa with very short planktonic durations could be explained by deviations from the simple Gaussian dispersal kernel assumption. First, physical models of passive transport by ocean currents predict

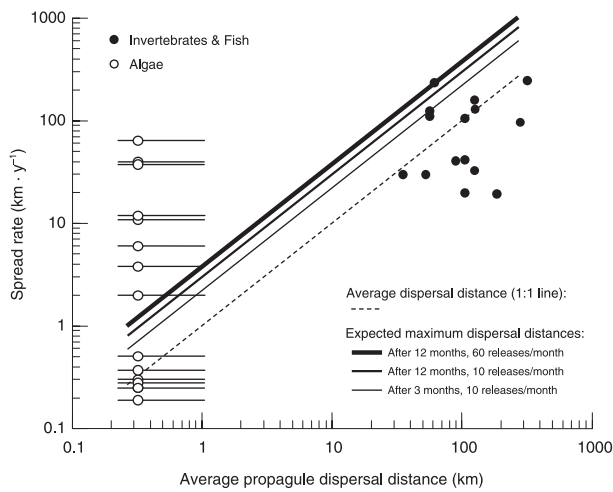


Figure 4 Empirical estimates of average annual spread rate for invasive species of benthic marine algae (open circles, $n = 15$), invertebrates (solid circles, $n = 14$) and fish (solid circles, $n = 2$). Spread rates are compared with predictions of average (dotted line) and maximum (solid lines) dispersal distances based on Gaussian dispersal kernels. Planktonic periods for algal propagules are not known exactly, but are generally $\ll 1$ day. Therefore, all algae have been placed at a dispersal distance corresponding to a PLD of 0.1 day. To give a sense of the uncertainty in this estimate, horizontal error bars show the interquartile range of algal dispersal distance estimates from Kinlan & Gaines (2003). Average and maximum dispersal distances were predicted using a Gaussian dispersal kernel based on literature estimates of mean planktonic period. Average dispersal distances were calculated using Eqn. 3. Expected maximum dispersal distances were calculated using Eqn. 5, with the specified values of k (number of releases), which are based on the temporal autocorrelation of coastal surface currents.

more leptokurtic dispersal kernels for short PLD organisms (e.g. Fig. 4 in Siegel *et al.*, 2003). This occurs because of the limited degrees of freedom with which the flow field is sampled; when propagules spend only a short time in the plankton, they are more sensitive to strong, short-duration turbulent transport events. A similar phenomenon is crucial to LDD in the atmosphere (Nathan *et al.*, 2005). However, other factors are likely to contribute to fatter tails in short-PLD marine taxa. Many marine organisms with short primary dispersal abilities can effectively disperse over long distances by drift and reestablishment of reproductive adults or adults capable of vegetative reproduction (Highsmith, 1985; Martel & Chia, 1991; Williams & Di Fiori, 1996; Hobday, 2000; Shanks *et al.*, 2003; Kinlan & Hastings, in press). Because of algal buoyancy, high fecundity, and frequent ability for asexual reproduction, the 'tails' of algal dispersal are likely to be substantially extended. The same is true of other taxa capable of drifting, or of rafting on algal mats. Similar comparisons of invasion rates to average dispersal distances for terrestrial plants suggest that the role of such 'fat-tailed' dispersal kernels may be greater in the marine environment than on land (Kinlan & Gaines, 2003; Kinlan & Hastings, in press).

Although spread rates of many taxa were consistent with a Gaussian dispersal model, this does not mean that Case II LDD is

unimportant in these taxa. Successful LDD events may be too rare in these taxa to influence spread rates over time scales of a few generations, but could still be extremely important for genetic connectivity, speciation, and long-distance colonization. Two strong lines of evidence for the importance of LDD events in marine taxa are the rich suites of endemic species on isolated oceanic islands separated by great distances from their 'parent' taxa (Robertson, 2001), and the wide distribution of shared alleles in populations separated by barriers of thousands of kilometers of unsuitable habitat (Lessios *et al.*, 2003).

These results demonstrate that simple flow models, though they may adequately model the bulk of propagule dispersal, often fail to predict rates of spread and other processes sensitive to extreme dispersal events, such as genetic structure, evolution, biogeography, and patterns of diversity. To address such questions in both marine and terrestrial systems will require models that incorporate secondary modes of dispersal and allow for non-Gaussian dispersal kernels (Clark, 1998; Higgins & Richardson, 1999; Cain *et al.*, 2000).

CONCLUSIONS

As these data illustrate, the prevalence and importance of long-distance dispersal in the marine environment depends both on the definition of LDD and on the choice of the 'local' scale used to identify LDD events. If LDD is defined as dispersal beyond the local population scale (Case I), then any study of LDD in the marine environment is equivalent to asking whether the population is demographically open or closed at the focal scale. The wide variation in scales of larval retention estimated here argues that the best answer to the oft-debated question 'How open are marine populations?' is, 'It depends.' (Mora & Sale, 2002).

Nevertheless, because adults of many marine organisms are extremely sedentary relative to their larvae, the long-standing view that marine populations are more open than their terrestrial counterparts will often hold, especially when the scale of adult movement is used to define the local population scale. However, exceptions to this pattern are common, and a focus on strictly open population dynamics, or categorical contrasts between open and closed populations is better replaced by an understanding of the functional form of the shift from open to closed demography with increases in geographical scale.

Similarly, the relatively long absolute dispersal distances observed for many species in the marine environment do not necessarily translate into a greater role for extreme dispersal events (Case II) over ecological time scales. In fact, organisms in which most propagules disperse short distances seem to exhibit a disproportionately high rate of extreme dispersal events, as evidenced by colonization of distant sites and rates of spread far higher than expected on the basis of primary dispersal distances.

A much better understanding of the role of dispersal in marine population dynamics can be gained from quantitative study of the continuum of dispersal and movement scales that exist in the marine environment. Two avenues of research are important to advance this agenda. First, we need a continued synthesis of theoretical and empirical approaches to estimate the realized dispersal distance of marine propagules, integrating information

from chemical tags, novel genetic approaches, improved hydrodynamic models, and detailed descriptions of larval behaviour. Second, it is critical to develop a quantitative description of spatial scales of mortality, growth, and reproduction across species' biogeographical ranges — processes which collectively define the scales of local population dynamics — so that larval dispersal distances may be viewed in the context of these 'local' process scales. Overall, studies of marine dispersal will be advanced by a less dichotomous perspective that acknowledges and quantifies the wide range of scales at which marine population processes can act.

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