

PROPAGULE DISPERSAL IN MARINE AND TERRESTRIAL ENVIRONMENTS: A COMMUNITY PERSPECTIVE

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Abstract. Studies in terrestrial systems suggest that long-distance propagule dispersal is important for landscape pattern and dynamics, but largely inconsequential for local demography. By contrast, in marine systems, dispersal at regional scales may drive local dynamics, because many species may have large mean dispersal distances. To assess variation in marine dispersal scales, we estimated mean dispersal distances from genetic isolation-by-distance slopes. Estimates ranged widely, from a few meters to hundreds of kilometers. Dispersal differed among taxonomic groups (macroalgae, invertebrates, and fish) and among species in different functional groups (e.g., producers and herbivores). Differences in dispersal scale have important implications for marine community dynamics, reserve design, responses to large-scale perturbations, and evolution of interacting species.

To place genetic estimates of marine dispersal in context, we compared them to other measures of dispersal in the ocean and to estimates of dispersal on land. Maximum scales of dispersal by sedentary marine species exceeded maximum estimates of terrestrial plant dispersal by at least one to two orders of magnitude. Direct and genetic estimates of terrestrial plant dispersal were comparable to estimates of marine plant dispersal. Rates of marine macroalgal range expansion, however, far exceeded spread rates of terrestrial plants. Terrestrial plant spread rates were more similar to those of short-dispersing marine organisms that lack secondary dispersal by drifting adults. Genetic estimates of dispersal by different functional groups suggest that herbivores typically disperse much farther than their plant resources both on land and in the sea, although the timing, frequency, and consequences of dispersal may differ in the two systems. Terrestrial herbivores have more flexible dispersal behavior than marine organisms that disperse each generation by planktonic transport of larvae.

Our results validate some long-standing views about the greater dispersal potential of species in the ocean, but also highlight the extreme heterogeneity in dispersal scale among marine species. As a result, development of a community perspective on marine connectivity will require consideration of multiple dispersal mechanisms and scales.

Key words: *benthic invertebrates; connectivity; demersal fish; dispersal scale; functional groups; genetic structure; invasion; isolation-by-distance; long-distance dispersal; macroalgae; marine reserve design; marine-terrestrial comparisons.*

INTRODUCTION

Dispersal determines the scale at which species interact with their environment, respond to perturbations, and evolve. The scale and pattern of dispersal can have important consequences for population dynamics (Roughgarden et al. 1988, Hanski 1999), species interactions (Gaines and Lafferty 1995, McCauley et al. 1996), spatial and temporal patterns of distribution (Sousa 1984, Tilman and Kareiva 1997, Reed et al. 2000), population genetics (Loveless and Hamrick 1984, Grosberg and Cunningham 2001), macroevolution (Valentine 1986, Palumbi 1994), and biogeography (Scheltema 1988, Brown and Lomolino 1998, Gaylord and Gaines 2000). Dispersal is particularly important

for organisms with sessile or sedentary adults, including terrestrial plants, marine algae, and many invertebrates and fish. Sessile organisms can escape unfavorable conditions only through the dispersal of propagules, which is restricted to a limited phase of the life cycle.

Local-scale studies of propagule dispersal have been successful at describing the local dynamics of terrestrial plant populations (e.g., Pacala et al. 1996). However, there is growing evidence that the local pattern of dispersal is inadequate for describing regional and landscape processes (reviewed in Cain et al. 2000), including community responses to climate change (e.g., Cain et al. 1998), habitat fragmentation, and large-scale disturbances. The bulk of seeds may travel only a short distance, but the long tails of a dispersal distribution may be the most important determinant of colonization dynamics, migration rate, and genetic connectivity (Clark et al. 1999, Cain et al. 2000).

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In contrast to the terrestrial case, local-scale demographic models often fail to describe marine population dynamics (Roughgarden et al. 1988, Gaines and Lafferty 1995, Carr et al. 2003). Recruitment is frequently decoupled from local population size, suggesting that nonlocal recruitment plays a substantial role in dynamics. Long mean dispersal distances may control the demographics of established marine populations, in addition to the dynamics of colonization, range expansion, and genetic exchange (e.g., Gaylord and Gaines 2000). Despite the likely importance of long-distance dispersal in the ocean, marine ecologists have found it difficult to characterize dispersal patterns for any but the shortest dispersing taxa. For most marine organisms the shape and scale of the entire dispersal curve—not just the tail region—is poorly characterized.

Many lines of evidence have been used to infer dispersal scale in the ocean, but few provide quantitative information on the scale over which propagules successfully disperse and establish. Here, we use evidence from direct observations of propagules, rates of spread of invasive species, and genetic differentiation among populations to characterize patterns of realized dispersal. Direct and invasion estimates of dispersal have been reported elsewhere (Shanks et al. 2003), but the large volume of marine population genetic data has not been systematically used to estimate quantitative scales of dispersal. When population genetic structure is studied at multiple scales, demographic rates of dispersal may be estimated from the attenuation of gene flow with distance (Wright 1943, Palumbi 2003). Such estimates require assumptions about the distribution of effective dispersal in space (dispersal kernel), the effective size of populations, and the manner in which populations exchange migrants (model of gene flow) (Wright 1978).

To assess the range of variation in dispersal within marine communities, we quantify scales of dispersal for a broad range of benthic marine taxa, including macroalgae, invertebrates, and fish. Representatives of these groups co-occur in virtually all marine communities, but few studies have explored the implications of intertaxonomic differences in dispersal scale for community dynamics (McLaughlin and Roughgarden 1992, Gaines and Lafferty 1995). We also compare estimates of dispersal in the ocean to estimates of dispersal for terrestrial plants and herbivorous terrestrial insects. Plants, like the marine taxa we studied, have a sessile life history. Phytophagous insects differ in that dispersal is mediated by adult behavior, but their inclusion allows us to contrast dispersal of herbivore and producer guilds on land and in the sea. In these comparisons, we explicitly ask: (1) Are mean dispersal distances greater in marine systems? (2) Do patterns of dispersal vary across taxonomic and functional groups within communities? and (3) Do results from different measures of dispersal, which vary in sensitivity to different mechanisms and components of dis-

persal (e.g., secondary dispersal by adults, long-distance dispersal events), differ across systems and taxonomic groups? Results have important implications for development of a community approach to spatial problems in marine ecology, and for understanding differences in dynamics of marine and terrestrial communities.

METHODS

Genetic dispersal estimates for marine organisms

We used simulations of dispersal in a modified stepping-stone lattice developed by Palumbi (2003) to relate mean dispersal distance to the increase in genetic differentiation with geographic distance (isolation-by-distance, IBD). IBD slope was defined as the increase in F_{ST} (a measure of the proportion of total variance in allele frequencies partitioned among subpopulations; see Wright [1978]) or an equivalent measure of population differentiation per unit distance. Simulations assume a one-dimensional circular array of 1000 equally spaced demes, each with effective population size $N_e = 1000$. All pairs of demes exchange migrants once per generation as a function of pairwise distance (assuming demes are spaced 1-km apart). For a species with mean dispersal distance $1/\alpha$, the probability k of migration between any two demes x and y is given by, $k(x,y) = (\alpha/2)\exp(-\alpha|x-y|)$, a double-exponential dispersal kernel previously used in models of marine population connectivity (Botsford et al. 2001). Spatial patterns of allele frequencies are robust to the choice of other commonly used kernels with different kurtoses (C. Lee and A. Hastings, *personal communication*). Palumbi (2003) reported the equilibrium IBD slope expected for various average dispersal distances under this model. We used a power function fit to simulation results (dispersal distance = $0.0016(\text{IBD slope})^{-1.0001}$, $R^2 = 0.9988$) to estimate mean dispersal distances from IBD slopes. Dispersal estimates represent the equivalent mean dispersal distance required to generate the observed IBD slope under model assumptions.

Data on the increase in F_{ST} with spatial scale were obtained from the literature (see *Methods: Literature survey*). IBD slopes were calculated from ordinary least squares (OLS) regressions of F_{ST} vs. distance. Two approaches were employed to estimate F_{ST} at different scales. The first used pairwise estimates of F_{ST} for all subpopulations in a study. Pairwise F statistics were obtained in several ways. When OLS regressions of pairwise F_{ST} vs. distance were reported by authors, we used regression slopes directly. When studies assessed IBD by regressions of $\log(M)$ vs. $\log(\text{distance})$ (where $M = (1/F_{ST} - 1)/4$; Slatkin 1985) or $F_{ST}/(1 - F_{ST})$ vs. distance (Rousset 1997), regression equations were used to generate values of M and $F_{ST}/(1 - F_{ST})$ which were converted to F_{ST} and used to estimate an equivalent F_{ST} vs. distance slope. Otherwise, pairwise F_{ST} values were obtained directly from tables and graphs

in each study. The second method used hierarchical F statistics reported for increasing spatial scales. Since F statistics depend on the scale at which subpopulations are defined, hierarchical values of F_{ST} were used only if they employed the same definition of subpopulations. Dispersal distances calculated by pairwise and hierarchical methods did not differ significantly (t test, $t = 1.142$, $df = 61$, $P = 0.26$). Geographic distances were obtained directly from references, measured from published site maps, or measured from an atlas based on reported locations of study sites. When distances were measured, we used the shortest over-water distance between subpopulations. For the pairwise F_{ST} method, distances were recorded for each pair of populations in a study. For the hierarchical F_{ST} method, the geographic scale of each F statistic was equal to the largest pairwise geographic distance among subpopulations.

The majority of our estimates were derived from allozyme studies of population structure (69 of 95, 73%). However, we also included studies employing other molecular markers to estimate population structure, including RAPD (seven), microsatellite (four), mtDNA sequencing (13), AFLP (one), and SSCP (one) methods. To compare F statistics derived from mitochondrial and plastid (SSCP) studies to those based on nuclear markers, we assumed an equal sex ratio and equal migration of sexes. Estimates of mitochondrial gene flow based on Wright's (1978) island model for a haploid locus, $(Nm)_{mt} = 0.5[(1/F_{ST,mt}) - 1]$, were doubled to account for biparental inheritance of nuclear markers and F_{ST} was recalculated assuming an island model with diploid gene flow, $F_{ST, diploid, biparental} = [1/(4(2[Nm]_{mt}) + 1)]$. Dispersal distances estimated by non-allozyme methods did not differ significantly from allozyme estimates (t test, $t = 0.125$, $df = 93$, $P = 0.90$).

Literature survey

Estimates of IBD slopes were compiled from a literature survey. A variety of factors, including mating system, population dynamics, historical factors, dispersal barriers, and cryptic speciation can influence the increase in population genetic structure with distance. To minimize the influence of these confounding factors and of violations of model assumptions, we established criteria for study selection. We limited our search to species with sedentary adults in which propagules (larvae, spores, etc.) are the primary agent of dispersal. Pelagic species and species with high rates of adult migration were excluded. We excluded organisms for which there was evidence of substantial asexual reproduction. Exceptions were made for studies that used population genetic data to demonstrate the dominance of outcrossed sexual reproduction, or corrected for the presence of clonal genotypes in calculations of F statistics. Organisms in which drifting adults or reproductive fragments may play a secondary role in dis-

persal (e.g., macroalgae, encrusting invertebrates) were not excluded by this criterion. To be included, studies must have surveyed at least three populations and assessed genetic differentiation at multiple scales. Allozyme studies were included only if they surveyed multiple loci. We examined studies for evidence of contemporary or historical dispersal barriers between subpopulations, differential selection on non-neutral markers, and nonequilibrium conditions (i.e., recent range expansion, frequent extinction and recolonization, historical isolation). In some cases, it was possible to exclude populations or regions which were clearly influenced by dispersal barriers, differential selection, or nonequilibrium conditions, and IBD slopes were calculated from remaining data. Otherwise, studies with obvious confounding factors were excluded. Studies were included only if they detected a significant increase in F_{ST} or equivalent with spatial scale. Studies that detected significant genetic structure but no geographic pattern were excluded. This reduced the likelihood of including populations for which dispersal was not a primary factor determining differentiation. Potential biases in the distribution of dispersal estimates introduced by these selection criteria are discussed in *Results: Distribution of genetic dispersal estimates*. Of 228 studies surveyed, 55 met the specified criteria (9 of 26 macroalgal studies, 28 of 144 invertebrate studies, 16 of 51 fish studies, and two of seven angiosperm studies). From these studies, we calculated 63 independent estimates of IBD slopes for 60 marine species (nine macroalgae, 34 invertebrates, 15 fish, and two angiosperms). Independent estimates for the same species were averaged to obtain a single dispersal scale used in all analyses.

Extending estimates of IBD slope to single-scale studies

For a well-mixed, sexual, outcrossing population $F_{ST} \approx 0$ at geographic scales below the mean dispersal distance (Wright 1978, Palumbi 2003). When a study finds significant genetic structure at only one spatial scale, but otherwise satisfies all of the criteria outlined above, a reasonable estimate of IBD slope might be obtained by assuming $F_{ST} = 0$ at distance = 0. To evaluate the validity of this assumption, we recalculated all IBD slopes from previously collected multiscale data using only two points: F_{ST} at the maximum geographic scale and $F_{ST} = 0$ at distance = 0. When mean dispersal distances derived from these single-scale IBD slopes were plotted against dispersal estimates based on the actual IBD slope, points were distributed along the line of equality. Residuals were evenly distributed on either side of the 1:1 line, with no apparent systematic bias. 88% of single-scale estimates fell within $\pm 0.2 \log(\text{distance})$ (where distance is measured in kilometers) of the corresponding estimate based on multiscale isolation-by-distance data, 96% of estimates fell within $\pm 0.4 \log(\text{distance})$, and all ob-

served points were $<0.5 \log(\text{distance})$ from the actual value. Given our focus on comparisons over much wider ranges of dispersal scales (one to five orders of magnitude), we consider this amount of error an acceptable tradeoff for a large potential gain in sample size. We collected 14 studies containing 32 single-scale F_{ST} estimates for 30 species that met assumptions of sexual, outcrossed reproduction. Studies met all criteria defined above for inclusion in our literature survey, including detection of significant geographic structure (e.g., via cluster analysis of genetic distance among sites), but did not estimate F_{ST} at multiple scales. We used single-scale F_{ST} estimates to approximate IBD slopes and dispersal distances for these species (4 macroalgae, 14 invertebrates, 10 fish, and 2 angiosperms). This raised the total number of independent dispersal estimates in our data set to 95, for 90 distinct species (Appendices A and B).

Sensitivity analysis

In the absence of confounding factors, equilibrium IBD slopes are determined by four basic demographic parameters: effective population size (N_e), pattern of gene flow (e.g., one-dimensional vs. two-dimensional stepping stone arrangements), functional form of the dispersal kernel (i.e., distribution of dispersal about the mean), and mean dispersal distance. We make assumptions about the first three parameters in order to derive estimates of the fourth. Model assumptions are difficult to evaluate directly, because little is known about effective population sizes, large-scale patterns of connectivity, and dispersal kernels in marine populations. Demographic factors may vary across species and geographic locales, and may be systematically different for short vs. long dispersers. Demographic parameters of marine organisms clearly fluctuate in space and time, with poorly characterized effects on population genetic structure. These issues highlight the need for improved models of demographic and genetic connectivity that take explicit account of unique features of the marine environment. In particular, models are needed to incorporate different dispersal kernels, demographic patterns, and spatiotemporal dynamics into expectations of genetic structure.

Given the uncertainty in underlying demographic factors, it is important to assess the likely impacts of deviations from model assumptions. Simulation studies suggest that equilibrium IBD slopes are relatively robust to variation in effective population size for $N_e > \sim 500$ (Palumbi 2003), a criterion likely to be satisfied for most marine populations (but see Hedgecock 1994). Two-dimensional stepping-stone gene flow (e.g., in an island or patch reef system) leads to smaller IBD slopes than the linear case (Slatkin and Barton 1989), but the expected change in slope would inflate genetic dispersal estimates by much less than an order of magnitude. Simulation studies have shown that spatial patterns of allele frequencies are robust to the form of

dispersal kernel tails (C. Lee and A. Hastings, *personal communication*), though the relationship between dispersal kernels and genetic patterns needs further quantitative study. Our dispersal estimates assume that populations are in drift-migration equilibrium, which is difficult to test, but simulations by Slatkin (1993) suggest that IBD slopes approach their equilibrium value much more rapidly than the overall level of genetic differentiation.

Clearly, estimates of dispersal derived from IBD slopes are subject to substantial uncertainty introduced by sampling error and deviations from model assumptions. However, the above results suggest that variation in effective population size, gene flow model, and details of the dispersal kernel are likely to generate far less than an order of magnitude scatter around true mean dispersal estimates. In contrast, variation in the average scale of dispersal itself can result in dispersal estimates ranging over many orders of magnitude (Palumbi 2003). We focus on these scales of comparison in our analysis.

Direct observational and experimental dispersal estimates

Direct estimates of dispersal were obtained from a recent review (Shanks et al. 2003) and our own literature survey. We found two primary types of direct dispersal estimates. In the first, movements and behavior of propagules were observed in the field, from release until settlement or recruitment (e.g., Stoner 1992). In the second, settlement or recruitment of propagules was measured at increasing distances from the propagule source (e.g., Anderson and North 1966). We found direct dispersal estimates for 27 species (14 macroalgae, 11 invertebrates, one fish, and one seagrass; Appendices A and B). When multiple estimates were available for a given species, we used only the maximum estimate. The rationale behind this choice was that direct estimates of propagule dispersal often underestimate dispersal scale, but seldom overestimate it (Cain et al. 1998, Nathan and Muller-Landau 2000).

Estimates of dispersal from rates of invasion and colonization

Estimates of invasion rate were obtained from a recent review (Shanks et al. 2003) and our own literature survey. Invasion rate was defined as the mean rate of linear expansion of an advancing colonization front in kilometers per year (Shigesada and Kawasaki 1997). This was estimated from field surveys of the increase in distribution of invasive species with time. Where mean invasion rate differed across regions, directions of spread, or time periods within a study, we recorded the maximum mean rate. When available, invasion rates for independent introductions of the same species were averaged to obtain a single invasion rate estimate used in all analyses. Only presumed natural (i.e., non-anthropogenic) spread from single-point introductions

was considered. We found invasion estimates of dispersal for 18 species (seven macroalgae, nine invertebrates, one fish, and one seagrass; Appendices A and B).

Compilation of terrestrial dispersal data

We compiled direct, genetic, and invasion estimates of dispersal for terrestrial plants following the conventions described in *Methods: Literature survey* for marine data (Appendix C). Direct estimates of seed dispersal for 261 terrestrial angiosperms were obtained from a recent review including woody and herbaceous species (Cain et al. 1998). A focused survey of the recent literature on genetic structure of plants yielded 18 estimates of IBD slopes, which were used as described in *Methods: Genetic dispersal estimates for marine organisms* to calculate mean dispersal distances. Estimates spanned 12 families and included both woody (11) and herbaceous plants (7). Invasion estimates were based on two types of studies. The first method followed paleo-distributions of pollen to measure the rate at which holocene tree populations colonized new habitat (Davis 1981, $n = 19$ trees). The second method inferred spread of plants from an initial source on the basis of contemporary field surveys of distribution (Matlack 1994, $n = 47$ woodland herbs; Fastie 1995, $n = 1$ tree; Rouget et al. 2001, $n = 3$ trees). All invasion rates were recorded in kilometers per year. When not reported in original studies, invasion distances were measured from scaled site maps or an atlas as described in *Methods: Estimates of dispersal from rates of invasion and colonization*. Since trees and herbaceous plants can have very different dispersal scales (Cain et al. 1998), we grouped invasion rates for trees (23) and woodland herbs (47) and reported these separately.

IBD slopes for phytophagous insects were obtained from Peterson and Denno (1998). Nonsignificant regression slopes were excluded. IBD estimates covered 6 orders, 14 families, and 19 species of insects. The original study classified dispersal potential for each species as sedentary (<1 km), moderately mobile (1–20 km) or highly mobile (>20 km). Our estimates included four sedentary species, seven moderately mobile species, three highly mobile species, and five species for which direct assessments of dispersal were not available.

Functional group classifications

Trophic modes and organism–substrate relationships often dictate species interactions (e.g., predation, competition for space). To compare dispersal scales among potentially interacting guilds of species, we classified each organism in the genetic database by mode of resource acquisition and relationship to the substrate. Categories of trophic mode included producers, macroherbivores (herbivores feeding on macroalgae), and filter feeders (organisms obtaining food from the plank-

ton). Categories of organism–substrate relationship were sessile (directly attached to the substrate surface) and nonsessile (demersal, epibenthic, and infaunal).

Statistical analyses

To assess the effect of study scale on genetic dispersal estimates, we plotted dispersal estimates against the maximum geographic distance at which genetic differentiation was analyzed. The range of observed dispersal estimates varied with study scale. Dispersal distance estimates were a mean of 2.1 orders of magnitude smaller than the study scale (least-squares regression, $\log(\text{dispersal distance}) = 2.11 + 1.12(\log[\text{study scale}])$, $P < 0.001$; slope not significantly different from 1, $t = 1.28$, $df = 62$, $P = 0.10$), but ranged ~1.8 orders of magnitude above and 0.7 orders of magnitude below this mean. Thus the maximum dispersal scale a study could estimate was ~0.3 orders of magnitude smaller than the study scale, and the minimum was ~2.8 orders of magnitude below the study scale.

We used Monte Carlo simulations to test the null hypothesis that the observed distribution of log-transformed dispersal distances did not differ from a uniform distribution when constrained by the observed study scales. We constructed null distributions of 90 log-dispersal estimates drawn at random from uniform[$\text{scale}_i - 0.3$, $\text{scale}_i + 2.8$] distributions, where scale_i denotes the i th maximum study scale in the data set. To assess the significance of nonuniformity in the distribution of marine dispersal scales (Fig. 1, top), we compared the maximum histogram bin height in the observed distribution to maximum bin heights calculated from 10 000 simulated distributions. A Monte Carlo P value was calculated as the proportion of realizations in which the simulated maximum bin height was greater than or equal to the observed maximum bin height. All statistical tests were carried out using JMP 4.0 (SAS Institute, Cary, North Carolina, USA). Simulations were carried out using Matlab 6.0 Release 12 (Mathworks, Natick, Massachusetts, USA).

RESULTS

Distribution of genetic dispersal estimates

Dispersal scales estimated from isolation-by-distance slopes for 90 benthic marine organisms ranged over approximately five orders of magnitude, from several meters to several hundred kilometers (Fig. 1, top). The data set covered 28 major taxonomic groups (three divisions of macroalgae, eight invertebrate phyla, 15 families of fish, and two groups of marine angiosperms; Appendix A). Dispersal estimates derived from single-scale studies of genetic structure were distributed similarly to estimates derived from multiscale studies, indicating that the use of single-scale data did not substantially bias results (Fig. 2).

Certain life history traits make inclusion of an organism in the genetic data set less likely, leading to

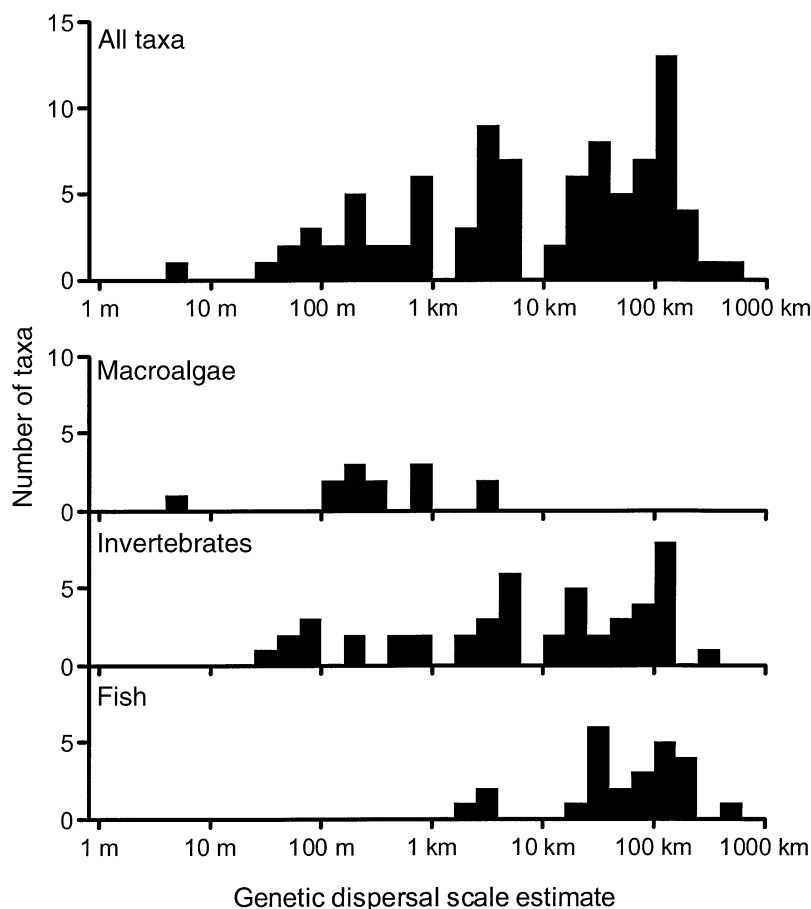


FIG. 1. Distribution of mean dispersal distance estimates for marine benthic organisms, based on a literature compilation of genetic isolation-by-distance slopes. Top panel: all taxa ($n = 90$). Bottom panel: sessile macroalgae ($n = 13$), sessile and sedentary invertebrates ($n = 48$), and demersal fish ($n = 25$). Bin size = $0.2 \log(\text{distance})$, distance measured in kilometers.

probable biases in the distribution of genetic dispersal estimates. These traits include predominance of asexual reproduction, repeated range expansion and contraction, extremely short dispersal, and extremely long dispersal (Grosberg and Cunningham 2001). As a consequence, the distribution of genetic dispersal estimates cannot be taken as representative of all benthic marine organisms. In particular, the upper and lower bounds of the true distribution probably extend further, and certain types of organisms (e.g., ephemeral algae, anemones, ascidians) are poorly represented. Our estimate of the range of marine dispersal scales is therefore conservative, and our analysis of patterns within the distribution applies only to taxa that are well represented in the data set (Appendix A).

Because certain taxa and geographic scales have been studied more intensively than others, the height of different peaks in the distribution of dispersal scales cannot be directly compared. However, several distinct modes are apparent in the distribution, suggesting that certain dispersal scales are more prevalent than others among the taxa we studied. Monte Carlo simulations indicate that the observed data are significantly more

clustered than expected either by chance or the non-uniform distribution of study scales ($P = 0.040$ based on 10 000 simulated distributions). The apparent clustering of dispersal scales could be due to the disproportionate influence of one or a few well-studied taxonomic groups whose member species have similar dispersal. However, each local peak on the histogram includes examples from at least two of the three major taxonomic groups (macroalgae, invertebrates, and fish), and the most frequent dispersal scales tend to coincide across groups (Fig. 1, bottom). The data set includes a broad range of phylogenetic groups (Appendix A). Although some groups are better represented (e.g., gastropod mollusks, $n = 12$), species within these groups often differ widely in dispersal ability (e.g., gastropods, dispersal estimates range 0.5–139 km). This suggests that the multimodal appearance of the dispersal scale distribution is due, at least in part, to clusters of common dispersal scales among the species we studied.

Taxonomic patterns

Macroalgae, invertebrates, and fish exhibited different patterns of dispersal scale (Fig. 1, bottom). Algal

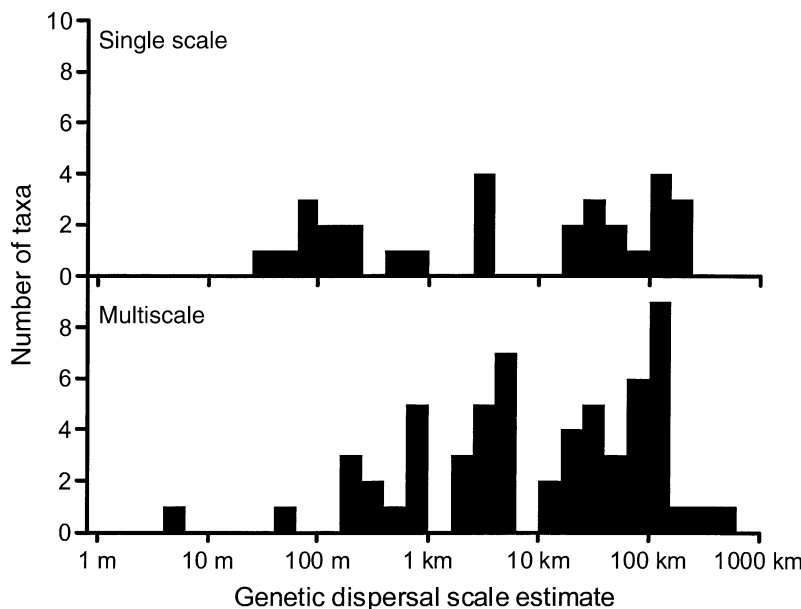


FIG. 2. Genetic estimates of dispersal distance based on single-scale (top) and multiscale (bottom) estimates of isolation-by-distance slopes. See *Methods* for details. Bin size = $0.2 \log(\text{distance})$, distance measured in kilometers.

dispersal estimates ranged from a few meters to <5 km (2.7 orders of magnitude). Estimates of dispersal for fish ranged from a few kilometers to several hundred kilometers (2.3 orders of magnitude). Invertebrate taxa spanned the widest range of dispersal scales, from tens of meters to hundreds of kilometers (four orders of magnitude). Though limited, marine angiosperm data suggest dispersal scales similar to longer-dispersing macroalgae (mean ± 1 SE = 3.65 ± 0.90 km, $n = 3$ seagrasses, 1 mangrove).

Dispersal of interacting species

The distribution of genetic dispersal estimates differed markedly among marine producers (macroalgae), their predators (macroherbivores), and their competitors for space on hard substrates (sessile filter feeders) (Fig. 3, top, center). Dispersal scales of the shortest dispersing herbivores were comparable to estimates for the longest-dispersing macroalgae in the data set (~ 1 –6 km). Other herbivores dispersed one to two orders of magnitude further than the longest dispersing macroalgae (~ 25 –270 km). Dispersal estimates for sessile filter feeders ranged over the same small scales as macroalgae, but extended one to two orders of magnitude beyond the maximum macroalgal estimate. Differences in dispersal scale among sessile filter feeders followed taxonomic lines: the shortest dispersing filter feeders were corals (0.044–0.785 km), followed by sponges (1–4 km), and long-dispersing barnacles, bivalves, and anemones (20–500 km). There was no clear taxonomic pattern for short vs. long dispersing herbivores. Instead, dispersal scales differed widely even among congeneric herbivores (e.g., *Littorina* spp., dispersal estimates = 1, 7, 23, 139 km).

On land, genetic estimates of dispersal suggest that phytophagous insects also move over larger scales than their plant resources (Fig. 3, bottom). Direct estimates of angiosperm seed dispersal ranged from 0.00003 to 22 km, while genetic estimates for herbivorous insects ranged from 8 to 42 km. Direct estimates were used instead of genetic estimates for plants because the two distributions share the same upper bound, and the direct dispersal data set is far more extensive (direct [$n = 261$] vs. genetic [$n = 18$]). Genetic estimates may not, however, reflect typical within-generation dispersal for insect populations. Direct dispersal estimates for at least four of the insect species in our data set indicate that typical within-generation adult dispersal is <1 km, much less than genetic dispersal estimates suggest (Peterson and Denno 1998). Typical mark-recapture dispersal estimates for phytophagous insects range from tens of meters to a few kilometers (Wahlberg 2002). However, invasion rates measured for several phytophagous insects range even higher than genetic estimates (10–170 km, Grosholz 1996). Many phytophagous insects are known to exhibit episodic migration in response to changing local conditions (reviewed in Loxdale and Lushai 1999). Even within a generation some individuals may leave the local population and travel long distances (Loxdale and Lushai 1999). Genetic and invasion estimates of dispersal are more likely to record these episodic and long-distance events (Slatkin 1987, Cain et al. 2000).

Direct and invasion estimates of dispersal

Compared to genetic estimates, direct estimates of dispersal were skewed toward smaller scales for both macroalgae and invertebrates (Fig. 4, top, center). Min-

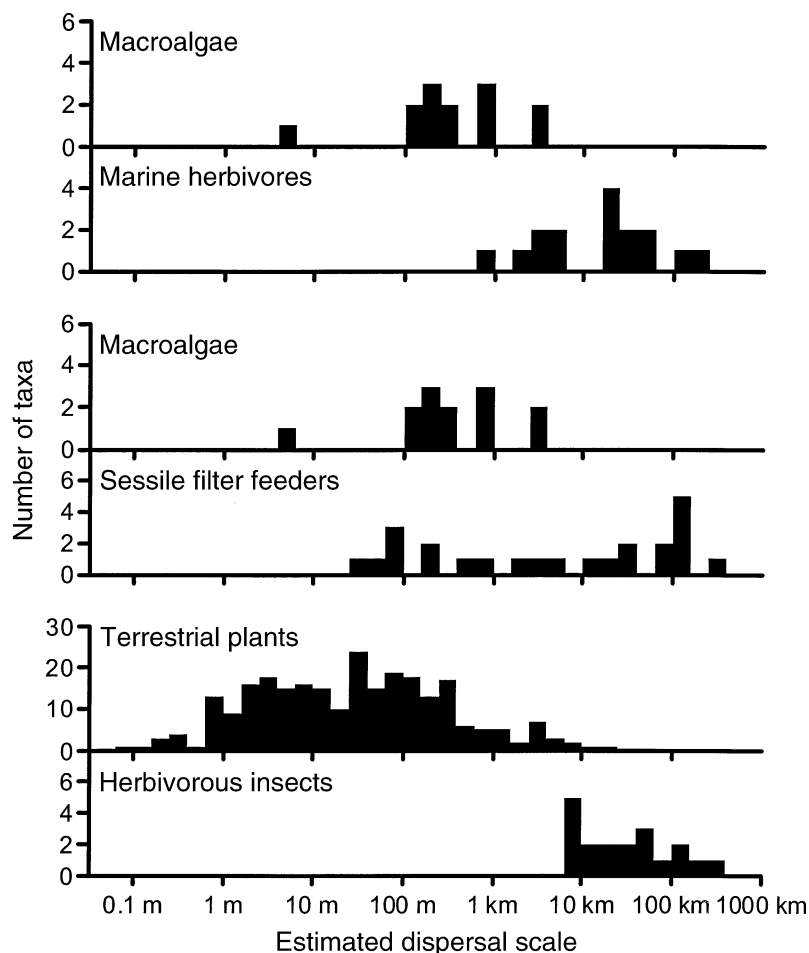


FIG. 3. Dispersal scales of interacting functional groups. Top panel: sessile macroalgae ($n = 13$) vs. herbivorous invertebrates and fishes ($n = 16$). Center panel: sessile macroalgae ($n = 13$) vs. sessile filter feeders ($n = 24$). Bottom panel: terrestrial plants (direct estimates, $n = 261$) vs. phytophagous insects (genetic estimates, $n = 18$). With the exception of terrestrial plants, all dispersal scales are derived from genetic isolation-by-distance slopes. Direct dispersal estimates are shown for plants because the range of this data set includes the range of genetic and invasion estimates and thus represents the full spread of plant dispersal scales in our data. Bin size = $0.2 \log(\text{distance})$, distance measured in kilometers.

imum direct dispersal estimates were one to two orders of magnitude smaller than minimum genetic dispersal estimates for both taxonomic groups (algae, a factor of eight smaller; invertebrates, a factor of 80 smaller). In contrast, invasion estimates of dispersal for macroalgae and invertebrates were skewed toward larger scales (Fig. 4, top, center). Invasion rates of invertebrates were comparable to the largest genetic dispersal scales, but did not exceed the maximum genetic estimate. Macroalgal invasion rates, on the other hand, exceeded the maximum genetic estimate of algal dispersal by up to 1.2 orders of magnitude. Macroalgal invasion rates were also more variable (values differed by a factor of 160) than invertebrate invasion rates (values differed by a factor of 16).

For fish, our data set was limited to one direct and one invasion estimate of larval dispersal. These estimates were consistent with the pattern established for invertebrates above; the direct estimate (1 km) was

comparable to the lowest genetic dispersal scale, whereas the invasion estimate (130 km) was comparable to the high end of the genetic dispersal distribution.

Maximum estimates of terrestrial plant dispersal from direct, genetic, and invasion data were ~ 1.5 orders of magnitude smaller than maximum dispersal estimates for sessile and sedentary marine species (Fig. 4). However, genetic and direct dispersal estimates were similar for terrestrial plants and marine macroalgae (Fig. 4, top, bottom); marine invertebrates and fish accounted for the larger marine dispersal scales (Fig. 4, center). Genetic and direct estimates of terrestrial plant dispersal shared a similar upper bound, though the minimum genetic estimate was two orders of magnitude larger than the minimum direct estimate. Invasion rates of trees were skewed high relative to most direct estimates of terrestrial plant dispersal, but the successional spread of woodland herbs was much slow-

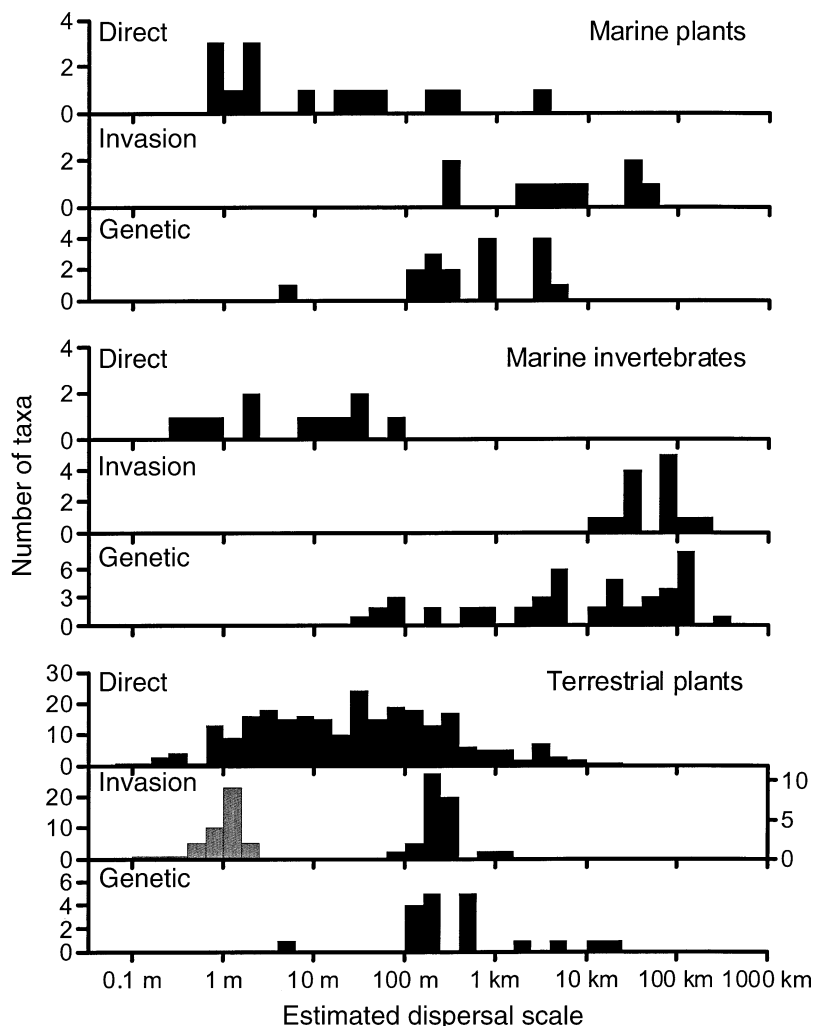


FIG. 4. Comparison of direct, invasion, and genetic estimates of dispersal scale. Top panel: benthic marine macroalgae and marine angiosperms ($n = 14$ direct, 9 invasion, 17 genetic estimates). Center panel: benthic marine invertebrates ($n = 11$ direct, 13 invasion, 48 genetic estimates). Bottom panel: terrestrial angiosperms ($n = 261$ direct, 71 invasion, 18 genetic estimates). Separate invasion estimates are shown for trees (black bars, $n = 23$) and woodland herbs (shaded bars, $n = 47$). Terrestrial direct dispersal estimates are taken from Cain et al. (1998). Sources of terrestrial invasion and genetic estimates are listed in Appendix C. Bin size = $0.2 \log(\text{distance})$, distance measured in kilometers.

er (Fig. 4, bottom). In contrast with algal invasion rates, spread rates of terrestrial plants did not exceed the upper bound of direct or genetic dispersal estimates (Fig. 4, top, bottom).

DISCUSSION

Accounting for the pattern of genetic dispersal estimates

Dispersal scales of marine organisms estimated from genetic isolation-by-distance (IBD) slopes vary over five orders of magnitude, appear to cluster around several modes, and exhibit distinct patterns within taxonomic and functional groups. Though some of the variation in genetic dispersal estimates may be attributed to variation in the appropriateness of model assumptions (see *Methods*), a parsimonious explanation for

broad differences in genetic dispersal estimates (one to five orders of magnitude) is extensive variation in dispersal scale itself.

Genetic dispersal estimates may or may not directly reflect patterns of propagule dispersal, because these estimates reflect only dispersal of propagules that successfully establish and reproduce (i.e., effective dispersal) (Levin 1981, Slatkin 1987). Thus, one possible explanation for the clustered distribution of dispersal scales we observed is a non-uniform distribution of scales at which propagule establishment is possible. This might be driven by different characteristic scales of the distribution of marine habitats or climates, or differential survivorship of propagules moving different distances.

Alternatively, effective dispersal patterns may reflect actual differences in propagule dispersal distances.

Very large discrepancies in genetic dispersal estimates (e.g., 10 vs. 100 km) are likely to be due, at least in part, to differential movement of propagules. Differences in propagule movement could result from variation in physical transport processes, mode of propagule development, propagule morphology and behavior, and secondary mechanisms of dispersal (e.g., drifting adults, floating reproductive fragments). Systematic variation in these physical and biological factors offers another explanation for the clustered distribution of dispersal scales. Preliminary results (B. Kinlan, *unpublished data*) indicate that genetic dispersal estimates are concordant with common proxies of dispersal ability (planktonic larval duration, developmental mode, and adult drift potential). Organisms lacking planktonic larval stages and secondary mechanisms of dispersal have genetic dispersal estimates $\ll 1$ km. Dispersal estimates for taxa that lack planktonic larvae but have secondary dispersal mechanisms such as rafting adults and drifting reproductive fragments range up to ~ 10 km. Invertebrates with nonfeeding larvae have smaller genetic dispersal estimates (mean ≈ 30 km) than invertebrates with feeding larvae (mean ≈ 100 km). Planktonic larval duration explains $>50\%$ of the variation in genetic dispersal estimates for fish and invertebrates that are in the plankton for >2 d. These findings suggest that much of the variation in genetic dispersal estimates can be explained in terms of life history characteristics. Genetic estimates of dispersal may lend quantitative power to common qualitative proxies for dispersal ability of marine species.

Variation among taxonomic and functional groups

Dispersal scales of marine benthic taxa not only vary over several orders of magnitude but differ among major taxonomic and functional components of communities. Macroalgal dispersal scales are more restricted than those of fish, and dispersal of invertebrate taxa ranges widely. As a consequence, herbivores and competitors of macroalgae may disperse from one to five orders of magnitude further than the algae they interact with. Many aspects of local and regional community dynamics may be influenced by the wide-ranging, non-random distribution of dispersal scales across taxonomic and functional groups.

Differences in dispersal scale can translate directly to differences in spatial and temporal patterns of distribution and abundance (Levin 1992, Reed et al. 2000). Abundances of long-dispersers may vary more than short-dispersers in space and time due to fluctuations in supply (Gaines and Lafferty 1995), but short dispersers are more sensitive to fluctuations in local environmental conditions. A comprehensive review of >500 marine abundance time series suggested that species with planktonic larval stages exhibit less temporal variation than species lacking larval stages (Eckert 1999). Studies of spatial pattern in long vs. short dispersers have suggested that long-distance dispersal re-

sults in more homogenous recovery following large disturbances (Reed et al. 2000) and larger geographic patch scales (kilometers vs. meters, Johnson et al. 2001). Theoretical studies suggest different scales of temporal and spatial heterogeneity can be important to dynamics of interacting species (e.g., McLaughlin and Roughgarden 1992, de Roos et al. 1998).

Wide dispersal can decouple propagule supply from local conditions altering local interactions and coevolutionary dynamics (e.g., Hay 1988, Gaines and Lafferty 1995, de Roos et al. 1998, Parsons 1998). The scale and efficiency of local adaptation to environmental gradients varies with dispersal ability (Warner 1997, Kirkpatrick and Barton 1997). Longer dispersal scales may partially account for the prevalence of generalism among large marine herbivores (e.g., Hay 1988) and increased phenotypic plasticity in organisms with extended planktonic development (e.g., Parsons 1998).

The extreme heterogeneity of marine dispersal scales implies that no local event or single management strategy can be expected to affect all species in a community evenly. Community responses to climate change, large-scale perturbations, management regimes, and point impacts may be strongly influenced by the nonrandom distribution of dispersal scales across taxonomic and functional groups. Following climate change or large-scale perturbation, expansion of a community into uncolonized habitat is likely to be a complex process depending on the mean dispersal scale of different community components, the relative importance of long-distance dispersal events for different taxa, and community assembly rules (e.g., Belyea and Lancaster 1999). The requirement for initial colonization by relatively short-dispersing habitat-forming species (e.g., kelps, corals) may be especially critical. In established communities, mean dispersal scales determine the degree of demographic connectivity among regions, which in turn dictates the scale at which local impacts (e.g., point-source pollution, local exploitation) and management strategies (e.g., marine reserve implementation) propagate through surrounding communities. Future models of marine community connectivity should take explicit account of the non-random distribution of dispersal scales among community components.

Inferences from multiple measures of dispersal

Direct and invasion estimates may differ from genetic estimates due to (1) systematic differences in taxonomic focus of the methods or (2) intrinsic differences in the way each method measures dispersal scale. There was clear taxonomic bias in the coverage of direct vs. invasion methods. Direct estimates of dispersal for marine invertebrates focused on bryozoans, corals, and ascidians whereas invertebrate invasion estimates dealt chiefly with bivalves, gastropods, and crustaceans (Appendix A). Direct estimates of dispersal are smaller, in

TABLE 1. Comparison of direct, invasion, and genetic dispersal estimates for similar species.

Taxa†	Dispersal scale (km)‡		
	Direct	Invasion	Genetic
Macroalgae and seagrasses			
<i>Alaria esculenta</i> (D) vs. <i>Alaria marginata</i> (G)	0.010	nd	4.2
<i>Caulerpa taxifolia</i>	nd	0.500	0.249
<i>Gracilaria gracilis</i>	0.0025	nd	4.0
Kelps (D, 5) vs. <i>Undaria pinnatifida</i> (I)	0.151 ± 0.094§	0.5	nd
<i>Sargassum muticum</i>	0.03	43	nd
<i>Sargassum polyceratum</i>	0.001	nd	0.323
<i>Silvetia compressa</i> , spores	0.001	nd	0.259
<i>Silvetia compressa</i> , drifting fragments	0.150		
<i>Zostera japonica</i> (I) vs. <i>Zostera marina</i> (D, G)	0.200	6.0	5.3
Invertebrates with short planktonic periods			
<i>Balanophyllia elegans</i>	0.0005	nd	0.785
<i>Botrylloides</i> sp. (D) vs. <i>Botrylloides leachi</i> (I)	0.0006	16	nd
<i>Pocillopora damicornis</i>	0.04	nd	0.008
Invertebrates with long planktonic periods			
<i>Littorina littorea</i>	nd	42	23
Bivalves (G, 7) vs. Bivalves (I, 4)	nd	144 ± 31§	171 ± 59§

† For grouped comparisons, letters in parentheses indicate the source of each estimate (D = direct, I = invasion, G = genetic); numbers indicate size of groups.

‡ Based on direct, invasion, and/or genetic methods; nd, no data.

§ Mean ± 1 SE.

|| Estimated from field observations and laboratory culture studies (short, <1 wk; long, >2 wk).

part, because direct dispersal studies tend to focus on organisms with shorter planktonic development periods. However, in addition to taxonomic biases, there appear to be intrinsic differences in the way direct, invasion, and genetic methods measure dispersal scale. Although there were no clear differences in major taxonomic groups of macroalgae covered by the three methods (Appendix A), direct estimates of algal dispersal tended to be smaller than genetic estimates (Fig. 4; median direct estimate = 0.0065 km, median genetic estimate = 0.323 km). In a few cases, we were able to compare direct, invasion, and genetic estimates for the same or similar species (Table 1). These comparisons demonstrate that direct estimates of dispersal for short-dispersing organisms such as corals and macroalgae can be substantially smaller than genetic and invasion estimates, by up to approximately three orders of magnitude. However, results also indicate that this pattern is not universal; some direct estimates are quite comparable to genetic estimates (e.g., *Undaria pinnatifida*, *Pocillopora damicornis*, floating reproductive fragments of *Silvetia compressa* in Table 1).

A likely explanation for discrepancies between direct, genetic, and invasion estimates is the failure of direct estimates to account for secondary (i.e., adult-mediated), episodic, and long-distance dispersal events. Genetic estimates reflect these events because they are a long-term average of effective dispersal from all sources (Slatkin 1987). Invasion estimates are similarly inflated because they are sensitive to the tails of dispersal distributions, i.e., the longest distances propagules can successfully travel and establish (Cain et al.

2000, Nathan and Muller-Landau 2000). Since the role of long-distance dispersal mechanisms may vary from one organism to another, genetic and invasion estimates will often, but not always, be higher than direct estimates. The relationship between these three measures of dispersal may contain important information about underlying dispersal processes.

For example, patterns of direct, invasion, and genetic dispersal estimates were more divergent for marine species than for terrestrial plants. Though this is partly due to major differences in taxonomic coverage of the three methods, but it may also indicate a greater role of long-distance dispersal processes ("fat-tailed" dispersal kernels) in marine systems. Because of differences in the density of the fluid medium (water vs. air), drifting and rafting adults, floating reproductive material, and resuspended juveniles are far more common in marine environments. These processes, combined with episodic events such as high-energy storms, shifts in current patterns, and reproductive synchrony, can greatly extend dispersal scales of organisms with limited dispersal of primary propagules (e.g., Highsmith 1985, Worcester 1994, Reed et al. 1997, Hobday 2000). Comparison of invasion rates of marine and terrestrial plants provides strong evidence for fatter-tailed dispersal kernels in the marine environment. Macroalgal invasion rates greatly exceed genetic estimates of mean dispersal distance, whereas terrestrial plant invasion rates are within the bounds of dispersal distances measured by direct and genetic methods. However, the relative importance of long-distance dispersal events may vary across taxonomic groups in the marine environ-

ment. Maximum macroalgal invasion rates are similar to invasion rates of invertebrates with much longer larval durations (e.g., barnacles, bivalves; Table 1 and Appendix B). Though long-distance dispersal events may be relatively uncommon in benthic macroalgae (leading to low direct and genetic estimates), the life histories of many algae allow a few propagules landing at distant sites to generate large populations rapidly by local, short-distance dispersal. In contrast, many organisms with very long mean dispersal distances lack life history features that allow rapid colonization by a few individuals (e.g., barnacles, bivalves, fish). Small "frontier" populations of these organisms are unlikely to grow rapidly from local recruitment. Invasion rates of these long-dispersing marine organisms are likely to be more similar to the mean propagule dispersal distance, a prediction supported by the similar upper bounds of invertebrate invasion and genetic estimates (Table 1, Fig. 3). These results agree with previous theoretical studies (e.g., Lewis 1997) which suggest that long-distance dispersal mechanisms and the capacity for rapid local population increase from low initial densities can cause invasion rates of short-dispersing taxa to approach those of much longer (mean) dispersers.

Compared to direct and invasion estimates for marine organisms, genetic estimates of dispersal are relatively free from taxonomic bias; they are not limited to high-profile invasive species or very short dispersers. However, a disadvantage of genetic estimates is the lack of detailed models describing exactly how multiple dispersal mechanisms (e.g., propagules vs. drifting adults) and episodic fluctuations of dispersal scale (e.g., large storms, current reversals) are "averaged" over generations. The resulting average may not be arithmetic, and genetic structure may be disproportionately influenced by relatively rare, episodic events (Slatkin 1987). Moreover, the assumption of a particular dispersal pattern in the process of deriving genetic estimates means that estimates reflect only the equivalent mean dispersal distance under that dispersal kernel and spatial arrangement of populations. Genetic estimates may be most useful in a comparative context, especially when combined with other direct and indirect measures of dispersal. Comparison of multiple measures of dispersal can be a powerful tool for assessing the relative importance of different dispersal mechanisms (e.g., propagule vs. secondary dispersal) and patterns (e.g., mean vs. long-distance dispersal).

Marine-terrestrial comparisons

Although terrestrial plants share a sedentary life history with benthic marine taxa, many marine organisms disperse at larger scales (Carr et al. 2003). This may be attributed either to differences between terrestrial and marine environments or to biological differences between plant and animal taxa. Genetic and direct dispersal estimates for terrestrial plants are similar to those

of marine macroalgae, but smaller than dispersal scales of many benthic invertebrates and most demersal fish. Many marine animal taxa have complex life cycles that require growth and development in the water column and may impart a greater range of potential dispersal behaviors than possessed by seeds or spores. Alternatively, a greater range of mechanisms that facilitate long-distance dispersal may be available in the marine environment simply because of its fluid dynamics.

Herbivorous terrestrial insects appear to disperse further, over genetic time scales, than their plant resources. This intriguing pattern is similar to that observed for marine herbivores in comparison to macroalgae. However, genetic measurements of insect dispersal are discordant with typical field estimates of dispersal in natural populations. Insect dispersal is mediated by adult behavior, and may vary greatly among populations and generations due to fluctuations in local adult density, resource levels, or environmental conditions (Slatkin 1987, Loxdale and Lushai 1999). Flexible, adult-mediated dispersal may have very different community-level consequences from the more obligate differences in movement scale generated by passive dispersal of marine propagules.

A community perspective on marine dispersal

Previous studies of marine dispersal have focused on the population level and have been limited in taxonomic scope. A community perspective, incorporating interactions among species with potentially different dispersal scales (Gaines and Lafferty 1995), is needed to broaden our understanding of marine community dynamics, genetics, and evolution. To develop this perspective, we need better estimates of connectivity that take into account multiple mechanisms (i.e., propagules vs. drifting adults) and multiple components of dispersal (i.e., average vs. episodic events). Sources of this information may include improved estimates of realized dispersal from genetic and chemical tagging methods (e.g., Swearer et al. 1999) and process-based models of larval transport (e.g., Siegal et al. *in press*). Incorporating a realistic pattern of dispersal scales and mechanisms into regional-scale models of marine communities is essential to developing a more predictive understanding of the large-scale, long-term dynamics of marine ecosystems.

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APPENDIX A

A table showing the taxonomic distribution of marine dispersal distance estimates is available in ESA's Electronic Data Archive: *Ecological Archives* E084-045-A1.

APPENDIX B

Estimates of dispersal scale for marine taxa are available in ESA's Electronic Data Archive: *Ecological Archives* E084-045-A2.

APPENDIX C

Estimates of dispersal scale for terrestrial taxa are available in ESA's Electronic Data Archive: *Ecological Archives* E084-045-A3.