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POPULATION GENETICS, DEMOGRAPHIC CONNECTIVITY, AND THE DESIGN OF MARINE RESERVES

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Abstract. Genetic analyses of marine population structure often find only slight geographic differentiation in species with high dispersal potential. Interpreting the significance of this slight genetic signal has been difficult because even mild genetic structure implies very limited demographic exchange between populations, but slight differentiation could also be due to sampling error. Examination of genetic isolation by distance, in which close populations are more similar than distant ones, has the potential to increase confidence in the significance of slight genetic differentiation. Simulations of one-dimensional stepping stone populations with particular larval dispersal regimes shows that isolation by distance is most obvious when comparing populations separated by 2–5 times the mean larval dispersal distance. Available data on fish and invertebrates can be calibrated with this simulation approach and suggest mean dispersal distances of 25–150 km.

Design of marine reserve systems requires an understanding of larval transport in and out of reserves, whether reserves will be self-seeding, whether they will accumulate recruits from surrounding exploited areas, and whether reserve networks can exchange recruits. Direct measurements of mean larval dispersal are needed to understand connectivity in a reserve system, but such measurements are extremely difficult. Genetic patterns of isolation by distance have the potential to add to direct measurement of larval dispersal distance and can help set the appropriate geographic scales on which marine reserve systems will function well.

Key words: *connectivity; dispersal; isolation by distance; larvae; population structure.*

INTRODUCTION

Marine reserves can be designed to augment and enhance ongoing efforts to preserve biological diversity, increase fisheries yields, and protect particularly vulnerable life stages of marine species (see Palumbi 2001 for review). The operation and effectiveness of marine reserves depends on their goals, but many reserves are envisioned to play an ecosystem role on a scale larger than the reserve boundaries (Agardy 1994). This is especially true of fisheries reserves, whose economic value depends on export of individuals into regions where fishing is allowed (DeMartini 1993). Although there is a great deal of information about the positive effects of marine reserves on the size and abundance of heavily fished species within the boundaries of a reserve (Roberts 1997, Palumbi 2001, Halpern 2003), there is much less information available on their export role.

Empirical studies of reserve export have been limited to a few cases in which (1) fish tagged within reserves have been captured outside (Attwood and Bennett 1994), (2) fisheries yields have increased outside of the reserve boundaries (McClanahan and Kaunda-Arara 1996), and (3) larvae of protected species are more abundant just outside a reserve than far outside (see Palumbi 2001 for review). Because these empirical studies have been so difficult to conduct, modeling efforts have played a strong role in developing an understanding of how marine reserves function in a regional context (see Botsford et al. 2003). Yet these models generally rely on several assumptions about the degree of demographic exchange between the reserves in a network or between reserves and the exploited habitats surrounding them (Palumbi 2001). Low dispersal between a reserve and the surrounding habitats can severely limit the ability of a reserve to enhance productivity in the overall fishery, because extra eggs, larvae, or adults are "trapped" inside the protected area. On the other extreme, infinite movement of adults from reserves to surrounding, unprotected zones severely reduces reserve effectiveness, especially when reserves are small and adults are very migratory. In such cases, individuals are protected only as long as they are inside reserve boundaries, and reserves as a management tool function only as well as traditional control of fishing effort (Hastings and Botsford 1999).

The extent to which populations in different parts of a species' range are linked by exchange of larvae, recruits, juveniles, or adults is termed connectivity. Patterns of connectivity in a network of protected areas are important in understanding the supply of adults and larvae into and out of a reserve. For example, an iso-

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lated reserve may build up a population of spawning adults of an overfished species, and several studies have documented movement of these individuals from reserves to the outside (Davis and Dodrill 1980, Attwood and Bennett 1994, McClanahan and Kaunda-Arara 1996). However, there is much less information about the fate of larvae. Will some of the larvae produced in a reserve recruit back inside the reserve boundaries? Or does recruitment into the reserve require larvae imported from elsewhere in the species' range? If coastal currents move larvae long distances from their parents, then models suggest that larvae produced in a reserve are not likely to recruit locally, but instead be transported hundreds of kilometers downstream (Roberts 1997). Emerging models suggest that for self-seeding of a species to occur, a reserve must be as large as the mean larval dispersal distance of that species (Botsford et al. 2003). If such mean larval dispersal distances are huge, then self-seeding reserves may be difficult to design.

An alternative is that a species might be able to be maintained in a non-self-seeding reserve through recruitment of larvae produced by other reserves in a coordinated system (Gaines and Gaylord 2003, Hastings and Botsford 2003). If larval connections follow average ocean currents, then marine reserve networks might be designed to serve as stepping-stones for recruits from distant populations (Roberts 1997). Whether reserves are self-seeding, require external larval input, or exist in a stepping stone array, the dynamics of larval movement is critical to reserve design and placement.

Unfortunately, there is little information about mean dispersal of most marine larvae. In general, estimates of dispersal distances are indirect (Levin et al. 1993) and are derived from inferences about oceanography (Lee et al. 1994), larval biology (Emlet et al. 1987), or the genetics of adult populations (Palumbi 2001). Very few data are available that are derived from direct observations of realized larval dispersal distances, except for larvae of very low dispersal species (Olson 1985, Stoner 1992).

Marine larvae of coastal species are commonly observed in mid-ocean plankton, showing that offshore transport of larvae is an ongoing process (Scheltema 1986) and suggesting that potential larval movement is high. Length of larval life varies greatly, but planktonic periods of about a month are common (Grantham et al. 2003). During this time, current flows of 0.1 m/s. could theoretically move a larva hundreds of kilometers downstream. Rapid spread of larvae of invading marine species corroborates the potential for long distance movement. For example, the green crab *Carcinus mineas* has spread up the west coast of the United States from an invasion originally detected in San Francisco Bay in under a decade, despite prevailing summer currents running from North to South (Geller 1994, Shanks et al. 2003).

Despite evidence of potentially long-distance larval movement in some marine species, there are increasing signs that mean larval dispersal in marine systems might be low, and that long-distance dispersal may be rare over ecological time scales (Palumbi 2001). Simulation studies of movement of larvae as passive particles have shown that larval transport may be affected strongly by local eddies and current reversals (Lee et al. 1994, Limouzy-Paris et al. 1997). Some studies show larvae travelling only km from their release point (McShane et al. 1988, Limouzy-Paris et al. 1997), although both of the cited studies focus on groups with quite short larval durations. Simulations of larval dispersal in reef habitats have shown that local retention on a natal reef is 10 times more likely than transport to downstream reef sites unless the spacing between reefs is about the same as reef diameter (Black 1993). Larval behavior may also play a critical role. Although larvae may spend weeks or months in the plankton, larval swimming, especially when it allows depth regulation, has been shown to affect retention of larvae in tidal estuaries (Tankersley et al. 1995).

These population studies thus give contradictory answers. In some, indications of long-distance dispersal are clear (e.g., Sheltema 1986), but the fate of larvae transported long distances is difficult to determine. In other studies, local retention (say, within 10–50 km) of a fraction of larvae is known to occur, but what fraction of larvae disperse long distances is completely unknown.

A different set of studies has examined the genetic structure of populations in order to try to answer questions about the average fate of larvae. Genetic surveys assay the genes of breeding adults and thus integrate over all larval mortality sources. They also tend to paint an average picture of dispersal patterns—in effect summing up the varied dispersal characteristics that might occur from year to year. These two features, a focus on larval survivors and an ability to examine long-term mean population connectivities, are critical contributions that genetic studies can make to marine population dynamics.

However, genetic surveys of marine populations also face a number of severe challenges that have limited the impact of these approaches on marine ecology, coastal management, or fisheries preservation (Waples 1998). In the following, I first review strong inferences about limited population connectivities that are emerging from genetic studies of several marine populations. Second, I show why standard studies of marine population genetics often fail to provide convincing evidence of dispersal over ecological time frames. Third, I explore a different way to analyze genetic structure that may help solve some of these difficulties and begin to provide a framework for estimating population ex-

change over ecologically relevant time frames from genetic data.

Genetic Inferences of Ecological Connectivity

There are an increasing number of studies that show quite high genetic differentiation in marine species with potentially high dispersal. These studies are surprising because a small amount of gene flow between populations is usually sufficient to prevent any strong allele frequency differences. For example, if one migrant per generation settles and enters a local breeding population, then this small amount of genetic exchange is enough to forestall the accumulation of large genetic differences (Slatkin 1987). Ten migrants per generation are enough to prevent all but minor gene-frequency differences from developing. Because such small amounts of gene flow have a strong impact on genetic differences between populations, the discovery of marked geographic structure over short spatial scales in marine species indicates extremely low levels of dispersal.

Strong genetic differentiation

The genetic break of marine invertebrates and fish along the southeast coast of the USA (reviewed in Avise 1992) provided some of the first indications that there is surprisingly little gene flow in some widespread marine species. First recognized in horseshoe crabs, similar genetic breaks have been recorded for American oysters, and several species of marine fish (Avise 1992, 1994). Horseshoe crabs have a swimming benthic "trilobite" larva with a development time of about two weeks. Yet, between southern Georgia and Cape Canaveral, Florida, there is a severe genetic break that indicates minimal demographic exchange across this distance (Saunders et al. 1986). Oysters, also with a two-week planktonic phase, show a similar pattern (Reeb and Avise 1990). Further work has identified a 20-km stretch of the Florida coastline over which a strong shift in mitochondrial and nuclear gene frequencies has been observed (Karl and Avise 1992, Hare and Avise 1998). Here, genetic breaks are seen between adjacent inshore marine lagoons currently separated by land. Strong gene frequency changes in these invertebrates and several species of fish (Avise 1992) show practically complete lack of genetic exchange between populations in the absence of obvious strong dispersal barriers. A very similar genetic break has been described along the Spanish and French Mediterranean coasts for intertidal mussels (Sanjuan et al. 1996). In both of these examples, clear genetic breaks occur only in one area, and are not apparent throughout the rest of the species' ranges.

Likewise, populations of marine invertebrates and fish separated by the Indonesian Archipelago often show strong gene frequency differences (reviewed in Palumbi 1997). For example, tiger shrimp, starfish, coconut crabs, and several species of reef fish show major genetic differences between the Indian and Pacific Oceans (McMillan and Palumbi 1995, Lavery et al. 1996, Williams and Benzie 1996, Palumbi 1997, Duda and Palumbi 1999). These studies have seldom been done on a spatial scale small enough to show the nature or geographic position of sharp genetic discontinuities (Barber et al. 2000). However, dispersal between the Pacific and Indian Oceans through the Indonesian Archipelago has clearly been low since the return of sea level to contemporary levels after the last glaciation.

Genetic breaks in tide-pool copepods (Burton and Lee 1994) and predatory snails (Marko 1998) along the western coast of North America show a complicated pattern in which different species show genetic differences along different parts of the coastline (Burton 1998). The snails have a relatively low dispersal potential, and show genetic differentiation at the species level in central California. The copepods are subject to dispersal when high tides wash individuals out of tide pools, but nevertheless show genetic differences on the scale of a few kilometers (Burton and Feldman 1982, Burton 1998).

These demonstrations of strong marine differentiation show that effective demographic mixing does not occur in these cases. It could be that dispersal is prevented by unknown oceanographic patterns, or by behavioral mechanisms that act to prevent transport of larvae between populations. Alternatively, transport may occur, but migrating individuals may not have a high chance of recruitment into new habitats. Third, recruitment may occur, but selection may prevent migrants from growing and entering the breeding population (Koehn et al. 1980). No matter what the explanation, the genetic results show the existence of a heterogeneous spatial mosaic of marine dispersal. Such mosaics indicate strong barriers to demographic exchange, and show boundaries across which marine reserve networks are not likely to function well.

Low differentiation without genetic breaks

Although the number of marine systems in which genetic breaks have been described is growing, these examples remain the exceptions among studies of marine population biology. Much more commonly, studies of marine genetics show geographic structure without distinct genetic breaks. For example, we have shown that tropical sea urchins in the genus *Echinometra* have strong genetic structure across the Indo-West and Central Pacific (Palumbi et al. 1997), but there are no severe genetic breaks and sympatric congeneric species have different patterns of geographic differentiation. Isolated archipelagoes in the Central Pacific have a low diversity of mitochondrial sequences implying that these populations have been started by relatively few long-distance migrants (Palumbi 1996). Even within the

heart of the Indo-West Pacific near Indonesia, populations can show distinct mitochondrial haplotype frequencies and island-specific mitochondrial sequences (Palumbi et al. 1997). These sea urchins have a larva with a six to eight week planktonic phase, and the scale of population genetic structure is on the order of thousands of kilometers. Yet the genetic differentiation over this scale shows that dispersal from one archipelago to another is a rare event, and that island populations must be considered self-seeding over ecological time scales.

Similarly, Benzie and Stoddart (Benzie and Stoddart 1992) showed that the crown-of-thorns starfish had significant spatial genetic structure in the Great Barrier Reef. As in the urchin example, spatial scale was seen over thousands of kilometers. Even though only a small fraction of the total genetic diversity was geographically structured, there was a distinct pattern in which more distant reefs had populations that were more genetically differentiated. In populations of the sea urchin *Strongylocentrotus purpuratus* along the west coast of North America, slight but significant population structure was observed for allozymes and mtDNA (Edmands et al. 1996). The mtDNA differences were localized to populations along the Baja coast whereas allozyme differences occurred largely at one locus and could be observed over relatively small spatial scales. Similarly, genetic data on urchins, limpets and coral-eating gastropods in western Australia suggest genetic structure over relatively short spatial scales without broad geographic differentiation (Watts et al. 1990, Johnson et al. 1993).

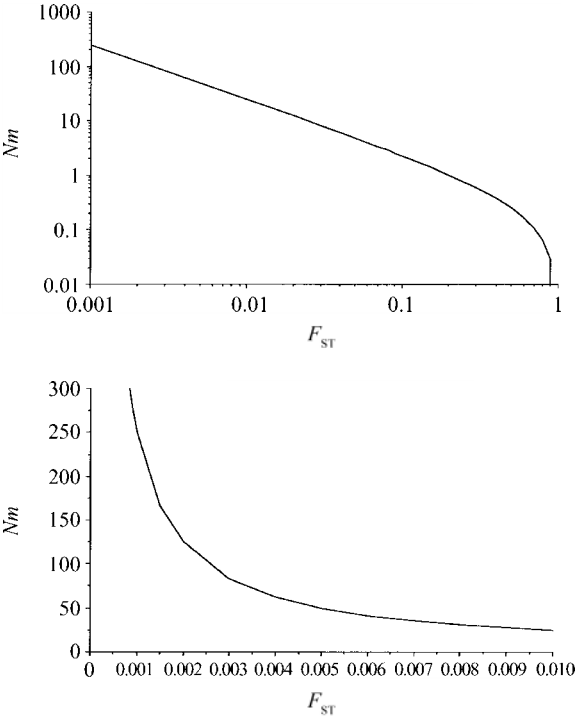

FIG. 1. Relationship between genetic differentiation (F_{ST}) and estimates of gene flow (Nm). Because of the reciprocal relationship between F_{ST} and Nm, small changes in F_{ST} can lead to large differences in Nm (top figure). This is especially true when F_{ST} is small, as is typical of many marine species with high dispersal potential (bottom figure).

Why marine genetics is hard to interpret

Understanding the ecological implications of such low but significant genetic structure is difficult because inferences about gene flow are usually made on evolutionary time scales, not the ecological time frame over which most management decisions are made. Genetic exchange is usually monitored in terms of the mean number of migrants that move between populations and enter the breeding population every generation. This value is a product of the mean population size (N) and the mean fraction of each population that are immigrants (m). Gene flow is estimated from the proportion of genetic variation that is geographically structured (F_{ST} or G_{ST}), using models of population structure that are reliable only when gene flow is relatively low. Typically, Nm is estimated from F_{ST} or G_{ST} using island model assumptions (e.g., all populations are equally linked by the same degree of migration; see Wright 1978 and Waples 1998 for full list of assumptions). Under these conditions, $4Nm = (1/F_{ST}) - 1$.

Because of the reciprocal relationship between F_{ST} and Nm, as F_{ST} becomes small, the estimate of Nm increases very quickly (Fig. 1). For example, an F_{ST} of 0.025 suggests an Nm value of 10 individuals but an F_{ST} of 0.005 suggests an Nm of 50 individuals. Because measuring very small values of F_{ST} accurately is difficult, it is often difficult to quantify Nm for high dispersal species (Waples 1998). If the error of an estimate of F_{ST} is 0.02, (as it is when sample sizes are on the order of 50 alleles per population), then it may be difficult to measure Nm to within a factor of five. Even worse, if F_{ST} is measured as 0.02 with an error of 0.02, then these data can not distinguish moderate gene flow (Nm = 12.5 individuals) from complete demographic exchange ($Nm > 10\,000$ individuals). Distinguishing Nm values of 10 000 individuals from Nm values of 100 individuals would require distinguishing an F_{ST} value of 0.000025 from 0.0025. In general the error associated with measuring F_{ST} is larger than these differences (Waples 1998), and so using this approach to measure realized larval exchange is usually impossible.

These results suggest that when genetic differences are minor, or when they consist of slight departures from random expectations of single populations (Edmands et al. 1996) or cohorts of recruits (Johnson et al. 1993), then the demographic consequences are difficult to assess. For purple sea urchins (*Strongylocentrotus purpuratus*) along the west coast of the USA, gene flow has been estimated to be high along 2500 km from Seattle to Los Angeles (Palumbi 1996, Ed-

mands et al. 1996). G_{ST} values, (an analogue of F_{ST}, and a measure of the proportion of genetic variability that is distributed geographically, see Nei 1987) are on the order of 0.01, with Nm estimated to be on the order of 20–50 individuals. Although these values are easily interpreted in a genetic and evolutionary context—the populations are not diverging—even high values of genetic exchange actually might represent a very low fraction of migrants into any one population. Only if the geography of genetic differentiation of marine species is measured very carefully and precisely can a low but significant G_{ST} be distinguished from zero. The challenges inherent in such accurate genetic determinations have slowed the use of genetic data to estimate real-time population connectivities, and have frustrated use of genetics in many conservation and fisheries contexts (Waples 1998).

Neigel (1997) provides a summary of attempts to use DNA data in a phylogenetic context to understand dispersal distances. He points out that the geography of different clades of alleles, arranged in an evolutionary framework using standard cladistic methods, can be used to estimate standard dispersal distance (Neigel et al. 1991). In this context, the variance in geographic position of a settled larva with relationship to its parents measures the width of the dispersal curve (centered on the parents in a world without advection). The approach works well for low-dispersal species, like many terrestrial animals and plants, but is subject to "range saturation" in highly vagile species where most common alleles have a range as large as the whole species. In such cases, estimates of mean dispersal are difficult with this approach (Neigel 1997).

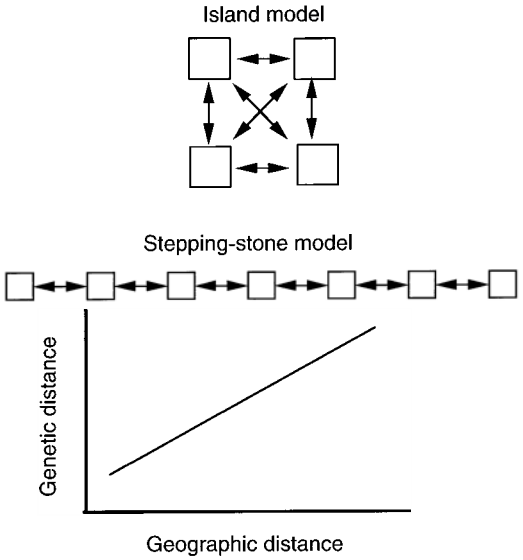

FIG. 2. Two common models of population structure. The island model assumes equal migration among populations. This is equivalent to each population contributing propagules to a larval pool and receiving a fraction of its recruits from the pool. Populations have equal geographic distance and connectivity. The stepping-stone model assumes that populations exchange propagules only with adjacent populations. Genetic differentiation can build up between distant populations even when adjacent populations remain indistinguishable due to high pairwise gene flow. In such cases, there can be a positive relationship between geographic and genetic distance.

Isolation-by-Distance Models and Marine Dispersal

There are different analytical frameworks for understanding genetic structure that may have greater power to describe marine population connectivities. Most of the application of genetic data to population questions uses Sewell Wright's island model as a way to relate the geography of gene frequency variation to levels of gene flow. In the island model (Fig. 2), all populations are linked by equal gene flow, with a proportion of migrants (m) every generation. There is no intrinsic geography to these populations—they are all equally distant from one another—and thus the island model probably does not describe most real population structures very well. The most commonly considered alternatives to the island model are stepping-stone models in which populations are assumed to be strung along a one-, two-, or three-dimensional lattice, with only adjacent populations exchanging members (Fig. 2). In such circumstances, there is a distinct geography, and populations that are closer are linked by larger amounts of genetic exchange. This seems to better reflect the organization of many coastal marine species, in which dispersal between localities is probably related to geographic distance (Hellberg 1994).

Analytical and simulation studies of stepping-stone models have shown that genetic distances between populations increase with increased geographic distance. Pairwise gene flow estimates are high for close populations, but lower for populations that are more distant (Fig. 2). The relationship between population distance and geographic distance depends on the configuration of the stepping-stone lattice, the mutation rate, and the migration rate among adjacent populations (Slatkin 1993).

Analysis of population structure as a function of the distance between samples has many advantages over estimation of a single G_{ST} for a set of populations under island model assumptions. In particular, in the stepping-stone analysis, there will be little association between G_{ST} and geographic distance if the error in estimating G_{ST} outstrips the differences among populations. Because sample sizes of individuals and loci can be standardized among comparisons, a relationship between G_{ST} and distance is much less likely to be due to sampling artifacts. This is particularly critical in marine systems where low G_{ST} values may provide biologically important information about demographic ex-

change but be similar to the noise generated by sampling error (Waples 1998; Fig. 4).

To date, stepping-stone models have been formulated only for a limited range of migration schemes, and none have been evaluated as a means to estimate high levels of gene flow. In particular, stepping stone migration is typically limited to exchange between adjacent populations only, and this is not likely to be a realistic assumption. In addition, G_{ST} and geographical distance is typically evaluated by plotting values of G_{ST} between all pairs of populations. These resulting plots have large amounts of scatter and poor statistical inference (because points are not independent). A better scheme would be to compare G_{ST} estimates for independent sets of populations chosen with different geographic spacing.

In order to understand the relationship between larval migration patterns and geographic patterns of genetic distance among populations, I have performed a series of simulations that estimate genetic structure in a variety of different dispersal schemes along a stepping stone lattice. The populations are imagined to be distributed along a coastline, and exchange larvae as a function of the distance between populations. Population structure is measured by calculating G_{ST} among 10 populations spaced equally. The spacing between sampled populations is varied, and the relationship between this spacing and measured G_{ST} is calculated. The results show that an isolation-by-distance signal is fairly robust, and occurs in populations with a wide variety of dispersal schemes and oceanographic settings. The simulations suggest that small overall genetic differentiation (e.g., G_{ST} on the order of 1% or so) can be distinguished from measurement noise by examining the relationship between G_{ST} and distance. Accurate interpretation of such slight genetic differentiation will be a powerful tool in understanding realized genetic exchange among populations and what this says about the implementation of marine reserves.

Population Modeling

Simulations are of a string of demes each with constant population size N, arrayed along a one-dimensional stepping-stone. The distance between demes is one unit. Each population is initially started with the same frequency of one allele in a single-locus, two-allele system. In every generation, genetic drift occurs through the random selection of alleles to be combined into progeny. Also, in every generation, dispersal of progeny occurs. Although a wide variety of dispersal functions might be used, these simulations use a dispersal function used in demographic models of marine reserves (Botsford et al. 2001). In this case, the probability of dispersal of a propagule from deme y to deme x is estimated as $k(x, y) = \alpha/2 \exp(-\alpha|x - y|)$, where $1/\alpha$ is the mean distance larvae disperse from their parents. For this particular larval dispersal function, ~40% of larvae travel more than the mean distance and ~15% of larvae travel longer than twice the mean dispersal distance. The populations are imagined to be arranged circularly, so that there are no edges.

In every generation, larvae are collected from surrounding demes according to the above formula and a new allele frequency is calculated that depends on the frequency of the alleles brought into the population by the dispersing larvae. This process of drift and migration is repeated for a specified number of generations, at which time 10 populations are used to calculate mean G_{ST} for this locus according to the formulae in Nei (1987). The first sample is arbitrarily chosen to be from deme 50. Results for 10 loci are averaged. Isolation by distance was tested by varying the number of demes between sampling localities (usually from 1 to 20 times mean dispersal distance), and plotting mean G_{ST} against sample spacing distance. Dispersal and population size were varied to test the influence of these factors on the pattern of isolation by distance. Because the series of populations was seeded with a constant allele frequency at the beginning of each simulation, genetic structure developed over a number of generations that was related to both population size and dispersal. In most simulations, isolation by distance is plotted for populations that have approached an equilibrium value of G_{ST}.

Simulation Results

Genetic differentiation as measured by mean G_{ST} increases with distance between sampled populations, as expected from prior modeling of simpler migration schemes (Fig. 3). These curves reflect a rapid increase in genetic differentiation of populations separated by a few multiples of mean dispersal distance. In general, at the shortest sampling scales, G_{ST} approximately triples as sample spacing increases fivefold (Fig. 3). At higher sampling distances, especially for simulations with higher dispersal, the relationship to G_{ST} tends to flatten. Other studies have shown that the relationship of G_{ST} to geographic distance depends on whether a population has reached an equilibrium between genetic drift and gene flow. In general, genetic isolation by distance builds up slowly after a range expansion, and close populations often show greater divergence than do distant ones while equilibrium is being reached (Slatkin 1993, Hellberg 1994).

The relationship between G_{ST} and distance is clearer if the geographic distance is standardized by the mean larval dispersal distance (Fig. 4). These results show that even at high larval dispersal, there is an increasing relationship between genetic differentiation and geographic distance.

The increase in G_{ST} as sample spacing is increased might be used to estimate mean larval dispersal. However, there are several other population-level factors that are predicted to affect isolation-by-distance besides dispersal, and these need to be taken into account

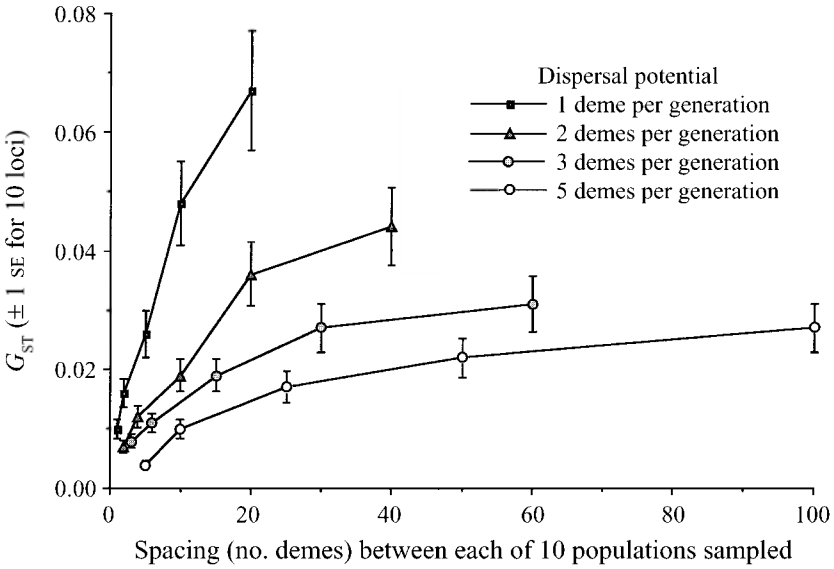

FIG. 3. Genetic isolation by distance varies with mean larval dispersal distance. In simulations of genetic structure along a linear array of populations, genetic differentiation is stronger in comparisons of more distant populations and depends on the mean larval dispersal. In these simulations $N = 100$, number of demes = 1200, and number of generations = 1000. G_{ST} was averaged among 10 independent loci.

as well. First, population divergence from starting conditions of constant gene frequencies is slower for populations with higher dispersal. In the simulations reported here, a population with $N = 100$ and with a mean dispersal of five demes required 1000 generations to equilibrate (Fig. 5), whereas populations with $N = 100$ and mean dispersal of one deme reached equilibrium after 200–300 generations.

In addition to the influence of dispersal on approach to genetic equilibrium, population size is expected to have a strong effect on overall levels of G_{ST}. Larger populations will experience smaller amounts of genetic drift and as a result, dispersal between large populations may play a more significant role in setting local gene frequencies than does drift. This effect is easily observed in simulations with mean dispersal of 1.0 deme in which population size is varied. As population size increases from 100 to 500, overall genetic differentiation declines (Fig. 6). However, the signal of isolation by distance remains clear, with the largest changes in G_{ST} occurring as sample spacing exceeds mean larval dispersal by two- to fivefold.

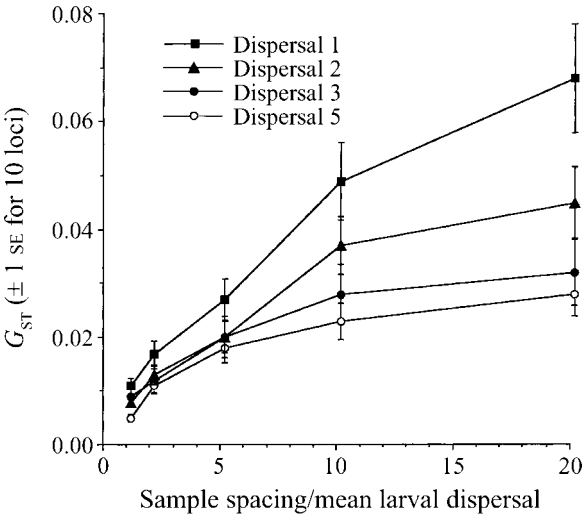

FIG. 4. Isolation by distance is similar for different larval dispersal rates if G_{ST} is plotted against relative distance (geographic distance between samples/mean larval distance).

This pattern may also be observed in simulations with high population sizes and high dispersal. For a population size of 10 000, an array of 1200 demes and a mean dispersal of 5 demes per generation, G_{ST} was substantially higher when sample spacing was 10 or 100 demes (range $1.5–3.5 \times 10^{-4}$) than when it was 5 demes (0.5×10^{-4}). However, it is extremely unlikely that any practical genetic survey will allow G_{ST} measurements this precise. Due to computational limitations, only one replicate of this weeklong simulation has been run. Further simulations may clarify the isolation by distance signal when population sizes are high.

IMPACT OF CURRENT PATTERNS

A third important aspect of potential isolation by distance in marine populations is the influence of oceanic current patterns on larval dispersal and subsequent genetic differentiation. In a preliminary investigation of this complex question, I changed the dispersal func-

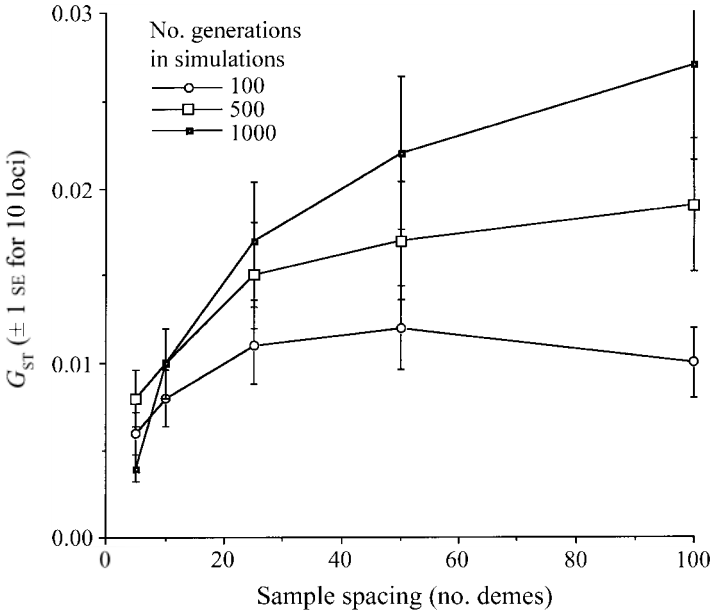

FIG. 5. Buildup of isolation by distance signal is slower for simulations with high dispersal. Plotted are relationships between G_{ST} and geographic distance for simulations with larval dispersal of five demes per generation 100, 500, and 1000 generations after the simulation was started. Starting conditions are as in Fig. 3.

tion to mimic the influence of a long-shore, unidirectional current. The diffusive spread of larvae remains the same in these simulations, but each larva is moved "downstream" a constant number of demes from where it would have been without the simulated current. Simulations were performed with a variety of current strengths. In the simulations reported here, mean advection was set to be twice mean larval diffusion (e.g., $2/\alpha$ demes per generation).

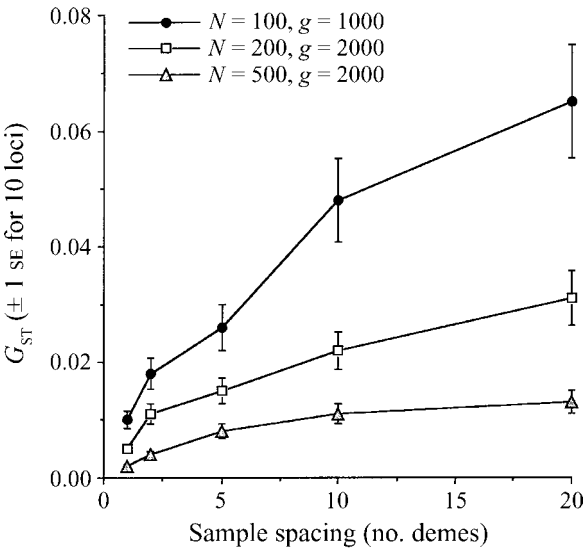

FIG. 6. Population size affects G_{ST} and patterns of isolation by distance. For larger population sizes, G_{ST} declines because genetic drift is weaker relative to dispersal. However, even for large population sizes, genetic differentiation is larger for more distant populations. Simulations were run with mean larval dispersal of 1.0 demes per generation, $N = 100$, and number of demes = 1200. The number of generations run is denoted by g.

Long-shore currents tended to decrease the signal of isolation by distance over short spatial scales but not large spatial scales (Fig. 7). In addition, the approach to equilibrium was slightly slower for simulations with larger current strengths (data not shown). Nevertheless, currents have only a mild effect on the buildup of genetic differentiation among populations in these simulations. This unexpected pattern is probably due to the carefully regulated nature of current flow in these simulations. All larvae are affected by exactly the same current regime, and essentially the entire larval settlement population is simply moved a certain number of demes from where it would have been. Because settling larvae make up the entire adult population in the next generation, the distribution of gene frequencies is very similar to what it would have been with no currents except that it is moved downstream. More realistic current flows, especially those that vary spatially and temporally will increase the spread of larvae as well as increase their distance traveled, and may have a greater affect on isolation by distance signals.

DISCUSSION

Simulation results suggest that the genetic signal of isolation by distance is fairly robust in a wide variety of populations with different characteristics. Even populations with high dispersal will show increased genetic differences with increased distance. Large populations also are predicted to show genetic isolation by distance, although in very large populations the sampling error inherent in estimating G_{ST} from a practical sample may

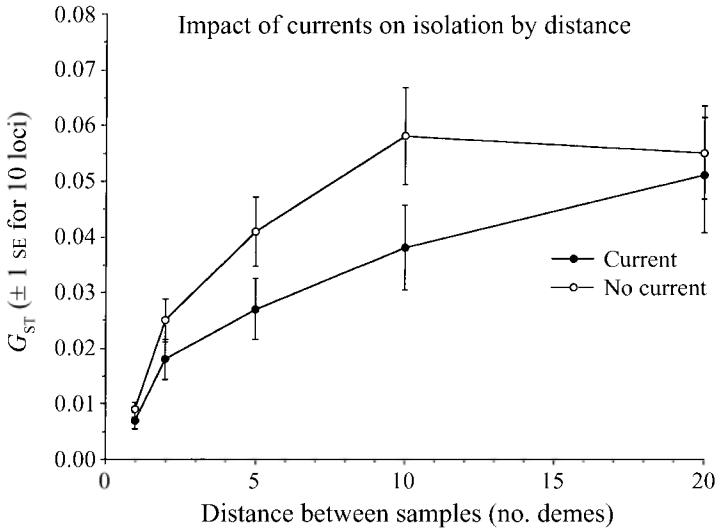

FIG. 7. Simple current patterns have little effect on the buildup of genetic differentiation. G_{ST} is plotted against the distance between sampled populations (from 1 to 20 demes) for simulations without a current and simulations in which a long-shore current is added. Mean dispersal spread was 1.0 deme per generation, and all larvae were moved two demes downstream in the simulations with a current. When such simple current patterns affect all larvae identically, the relationship between G_{ST} and distance is slightly reduced, but the genetic isolation-by-distance signal is still apparent.

be higher than the level of genetic differentiation expected (Waples 1998).

The primary value of examining population data for an isolation-by-distance signal is that comparing adjacent samples to distant ones allows standardization of sample sizes and loci. Simple calculation of the fraction of genetic variation that is distributed geographically using F_{ST} or G_{ST} statistics has been severely criticized because such statistics are highly dependent on sample size and allele frequency (Waples 1998). When F_{ST} or G_{ST} is calculated to be 1–2%, as is often the case in widespread marine species, it is difficult to be certain that this result is not largely a reflection of sampling noise. Because of this uncertainty, most marine population biologists and coastal managers have been understandably reluctant to forge strong management decisions based on the limited demographic exchange implied by small G_{ST} values.

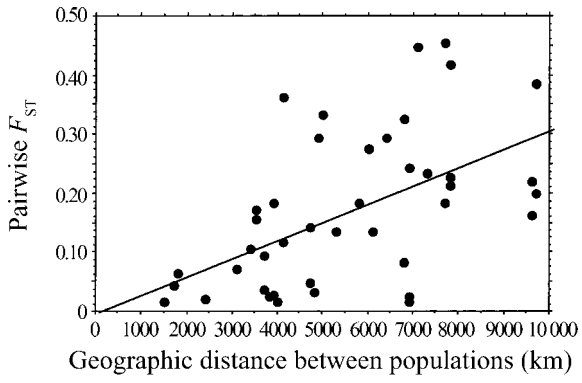

FIG. 8. Relationship between mitochondrial sequence differentiation and geographic distance for tropical Pacific sea urchins. Data points are based on comparisons of cytochrome oxidase I sequences among populations compared across the central and western Pacific (Palumbi et al. 1997). G_{ST} accumulates at the rate of 0.03 per 1000 km in this data set.

By contrast, if genetic differentiation increases with increasing geographic distance, then it is likely this pattern is due to limited larval exchange among populations. As a result, a genetic data set demonstrating marked isolation by distance could much more robustly be taken as showing that the measured amount of genetic difference was due to underlying biological features of the populations, not just sampling noise. In this case, the nonrandom distribution of the small genetic differences is more convincing than a single G_{ST} value calculated for an entire data set. Moreover, the relationship between genetic differentiation and geographic distance may reveal some of the underlying properties of larval dispersal, and show the geographic scale over which populations are ecologically linked.

For example, tropical Pacific sea urchins show a marked pattern of isolation by distance, in which F_{ST} measured with mitochondrial sequence data increases markedly with geographic distance between pairs of populations (Fig. 8). Values of F_{ST} above 0.10 occur only in populations separated by 3000 km or more, but even populations as close as 1000–2000 km show at least slight genetic differentiation. What does this pattern of geographic structure tell us about demographic exchange and the connectivity of populations across the Pacific? The slope of the line relating F_{ST} to distance shows that F_{ST} increases about 0.03 per 1000 km of distance. Although there is a huge scatter about this value, we can use the simulation approach outlined above to ask what level of larval dispersal is consistent with this degree of increase.

I ran a simulation with 1000 demes and 1000 individuals per deme in order to estimate the amount of larval dispersal consistent with a F_{ST} slope of 0.03/

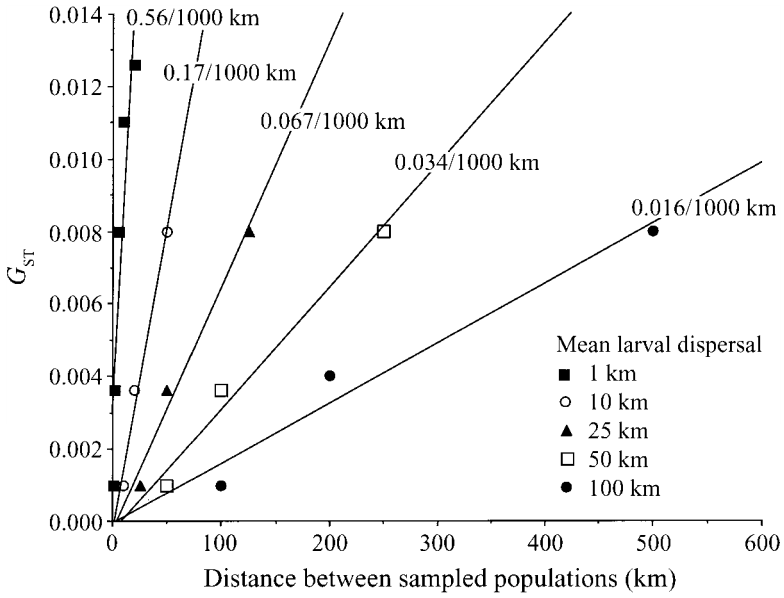

FIG. 9. Calibration of isolation by distance results from Pacific sea urchins using simulation model. For $N = 1000$, various values for mean larval dispersal were used to estimate the slope of G_{ST} with distance. The best fit to the observed slope of 0.03/1000 km is obtained when mean larval dispersal is ~50 km per generation.

1000 km. I sampled sets of populations that were from 1 to 500 km apart and let mean larval dispersal vary from 1 km to 100 km. I graphed G_{ST} calculated for 10 loci against population spacing to estimate how fast G_{ST} accumulates for different dispersal regimes. In these simulations, G_{ST} accumulates at a rate of about 0.03 per 1000 km only when mean larval dispersal approximated 50 km per generation. Although these estimates are highly dependent on the spatial array of demes that was used here, the results suggest that an increase in genetic structure of 0.03 per km, as seen in the urchin data, is consistent with limited larval movement. The values in Fig. 9 are also dependent on the population size used in the simulations. If the effective population size in a deme was higher than 1000, then estimated larval dispersal based on the urchin data would be lower than 50 km.

These levels of larval dispersal suggest that ecological connectivity is quite low in these populations except over small spatial scales. Different archipelagoes, separated by thousands of kilometers of open ocean are likely to exchange a negligible fraction of recruits. Even islands separated by hundreds of kilometers should not be considered to be part of the same population, but be managed as ecologically separate populations. If other species like reef fish and commercially important gastropods are similar, then marine protected areas should be placed within each cluster of islands.

In western Australia, the gastropod *Littorina cingulata* shows marked isolation by distance over spatial scales of up to 300 km, but not on scales from 400 to 1000 km (Johnson and Black 1998). Genetic distance (G_{ST}) was estimated from 22 allozyme loci, and increased at the rate of 0.07/1000 km among populations sampled closely together. Assuming a population size of 1000 individuals, this slope would be achieved by a mean larval dispersal distance of ~25 km for this planktonic-dispersing species (Fig. 9). Similar calculations for a variety of species that show genetic isolation by distance (Table 1) suggest mean larval dispersal distances of 25–150 km for pelagically dispersing fish and invertebrates. For one species of solitary coral with demersal larvae, isolation by distance suggests larval dispersal of only 0.5 km (Table 1).

Analysis of isolation-by-distance patterns from other marine populations can help interpret dispersal range even if the slope of the increase of genetic distance with geographic distance is unavailable. The crown-of-thorns starfish shows a marked pattern of isolation by distance across the entire Pacific (Benzie and Stoddart 1992). Within the Great Barrier Reef, F_{ST} values are ~2% for nonoutbreaking populations (Benzie and Stoddart 1992) but only ~0.7% for populations in the middle of population explosions that sweep the reef from north to south (Benzie 1992). The genetic isolation by distance and higher overall F_{ST} of nonoutbreaking populations suggests that these populations show more limited larval exchange in most years. Only during outbreaks is there significant population connectivity. Spatial autocorrelation analysis in red drum (*Sciaenops ocellatus*) and black drum (*Pogonias cromis*) from the Gulf of Mexico suggests a strong isolation-by-distance effect in these commercially important fish despite very low overall genetic differentiation among localities (Gold et al.

TABLE 1. Mean larval dispersal distances inferred by isolation by distance measurements in some marine invertebrates and fish.

Group	Species	Slope†	N‡	Mean dispersal distance (km)§	Reference
Pacific urchins	*Echinometra mathaei*	0.03/1000 km	1000	50	Palumbi et al. (1997)
Gastropod	*Littorina cingulata*	0.07/1000 km	1000	25	Johnson and Black (1998)
Common sole	*Solea vulgaris*	0.01/1000 km	1000	150	Kotoulas et al. (1995)
Tube worm	*Riftia pachyptila*	0.025/1000 km	1000	70	Vrijenhoek (1997)
Solitary coral	*Balanophyllia elegans*	0.3125/1000 km	1000	0.5	Hellberg (1994)

† Calculated from the increase of genetic distance (G_{ST} or F_{ST}) across the spatial scale of the study.
‡ Population size assumed in simulations.
§ Mean larval dispersal distance that generates the empirically observed slope in simulations of isolation by distance.

1994). A third species, red snapper (*Lutjanus campechanus*) showed no geographic pattern.

An important assumption of the simulation models is that species are distributed continuously and that larval dispersal is equal throughout the population range. In fact, populations often occupy discontinuous habitat, such as rocky outcrops interspersed by sand, or island archipelagoes separated by open ocean. Comparisons between geographically disjunct populations frequently generate much of the signal in isolation-by-distance comparisons (e.g., crown-of-thorns starfish, Benzie and Stoddart 1992). Ideally, short-range larval dispersal should be measured through genetic isolation by distance of relatively close populations (see Hellberg 1994, Johnson and Black 1998), and be compared with estimates based on genetic analyses across larger distances. In addition, it would be valuable to examine simulations in which dispersal discontinuities were built into the geographic arrangement of demes.

Not all marine species show patterns of isolation by distance. Studies of fish and invertebrates from the Mediterranean (Borsa et al. 1997) and the deep sea (Vrijenhoek 1997) show some cases of marked isolation by distance and some cases of geographic uniformity. In some cases, marked genetic differentiation in low dispersal species does not follow an isolation-by-distance pattern (Miller 1997). In other cases, high dispersal species show little or no increase in genetic distance even at high geographic scales (Williams and Benzie 1996, Vrijenhoek 1997). Interestingly, Slatkin (1993) has demonstrated that isolation by distance in a stepping-stone model can be visible in closely spaced populations, but invisible in widely spaced populations if the set of demes is far from equilibrium. Whether the instances of marine population uniformity are due in part to studies of nonequilibrium populations at too high a spatial scale (see Hellberg 1994, Johnson and Black 1998) or due to truly high larval dispersal is an important issue to resolve.

The impact of oceanic currents on genetic isolation-by-distance patterns requires more scrutiny. Simulations in which a genetic break is eroded by larval dispersal show that current patterns greatly increase the rate at which genetic differentiation disappears (S. R. Palumbi, *unpublished data*). However, an idealized current regime has only a slight effect on the buildup of isolation by distance during formation of an equilibrium between dispersal and genetic drift. In these simulations, isolation by distance develops based on the spread of sibling larvae from their source population, not the overall transport of cohorts of larvae downstream. Real currents are messier than the idealized ones employed here. If currents move larvae in one direction one year and another direction in other years, or if they serve to split larval cohorts and move different parts of a cohort to different habitats, then effective larval spread will increase and genetic differentiation should occur over larger spatial scales. These simulations serve to suggest that one of the most important impacts of oceanic conditions on genetic differentiation is due to increased variability in larval dispersal patterns that occurs in complex coastal currents.

Simulations and the examination of available data suggest that isolation-by-distance patterns in high dispersal species might be detected by geographically explicit sampling designs. The models suggest examining data from five to ten replicate populations separated by very short distances, and comparing these results with data from replicate populations separated by larger distances. Populations sampled every 10 km may be an appropriate initial scale for many species with high dispersal capacity. Populations with sampling distances of 20, 40, and 80 km could then be compared to estimate the impact of scale on genetic differentiation. Multiple loci must be examined in these populations in order for random effects of drift at independent loci to average out, and ~100 alleles per locus per population need to be examined to assure an accurate estimate of gene frequencies (S. R. Palumbi, *unpublished data*). This sampling scheme is massive, but if this approach leads to robust estimates of marine larval dispersal distances, then it will be easier than any other currently proposed method.

IMPLICATIONS FOR MARINE RESERVES

Studies of genetic structure that focus on isolation by distance models have the potential of allowing more rigorous ecological conclusions by using geographic

comparisons to look for significant genetic signals. Comparisons of close vs. distant populations can control for the noise inherent in genetic data sets, and provide added evidence that slight genetic differences are due to intrinsic biological features. For several species of fish and invertebrates with pelagic larvae, isolation-by-distance comparisons suggest mean larval dispersal distances on the order of 25–150 km: far less than that implied by the overall uniformity of marine gene frequencies, and similar to estimates from invasive species (Shanks et al. 2003). Population genetic theory shows that these estimates of mean dispersal are sensitive to assumptions about the migration model, dispersal function, and overall population size. Larger populations than those assumed here ($N = 1000$) would result in lower mean dispersal values.

In the absence of direct measurements of mean larval dispersal per generation, these genetic analyses suggest that spatial scales of connectivity may be smaller than typically assumed for many marine ecosystems, and that single-generation dispersal of a few tens of kilometers may be common. If this is so, then marine reserves designed to accommodate larval dispersal distances of species that show genetic isolation by distance could be effectively self-seeding if they were on the order of 10–20 km in size. For such species, the chance that a reserve hundreds of kilometers away will serve as an effective source population is ecologically remote. Species that do not show isolation by distance may have much longer effective dispersal distances and require alternative reserve designs.

These estimates are sensitive to oceanic conditions like long-shore currents, larval behavior patterns like off-shore/on-shore movement, and assumptions about population size and the recent history of gene flow. However, they provide a link between genetic analyses of populations and ecologically relevant connections between populations. Although there is a strong need for more direct measurement of larval dispersal for particular species, genetic analyses may provide a starting point for understanding the variation among species in mean larval dispersal distance.

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