

The relationship between dispersal ability and geographic range size

Sarah E. Lester,* Benjamin I. Ruttenberg, Steven D. Gaines and Brian P. Kinlan

Department of Ecology, Evolution, and Marine Biology and Marine Science Institute, University of California, Santa Barbara, CA 93106-9610, USA

*Correspondence and present address: Institute of Marine Sciences, University of California, Santa Cruz, CA 95064, USA. E-mail: slester@ucsc.edu

Abstract

There are a variety of proposed evolutionary and ecological explanations for why some species have more extensive geographical ranges than others. One of the most common explanations is variation in species' dispersal ability. However, the purported relationship between dispersal distance and range size has been subjected to few theoretical investigations, and empirical tests reach conflicting conclusions. We attempt to reconcile the equivocal results of previous studies by reviewing and synthesizing quantitative dispersal data, examining the relationship between average dispersal ability and range size for different spatial scales, regions and taxonomic groups. We use extensive data from marine taxa whose average dispersal varies by seven orders of magnitude. Our results suggest dispersal is not a general determinant of range size, but can play an important role in some circumstances. We also review the mechanistic theories proposed to explain a positive relationship between range size and dispersal and explore their underlying rationales and supporting or refuting evidence. Despite numerous studies assuming *a priori* that dispersal influences range size, this is the first comprehensive conceptual evaluation of these ideas. Overall, our results indicate that although dispersal can be an important process moderating species' distributions, increased attention should be paid to other processes responsible for range size variation.

INTRODUCTION

Why do some species have larger geographical ranges than others? This is a fundamental, yet largely unanswered, question in ecology and biogeography. Even closely related species can have dramatically different range sizes (Brown *et al.* 1996), and a variety of evolutionary and ecological explanations for range size variation have been suggested, including niche breadth or environmental tolerance, body size, population abundance, latitude, environmental variability, colonization and extinction dynamics, and dispersal ability (Stevens 1989; Brown *et al.* 1996; Gaston 1996, 2003). However, tests of many of these hypothetical causes are limited, and none has emerged as a universal driver of the extent of species' geographical distributions.

An organism's ability to disperse is one of the more commonly cited potential determinants of a species' range (Hanski *et al.* 1993; Brown *et al.* 1996; Gaston 1996, 2003). Dispersal ability is invoked as an explanation for range size

variation in both terrestrial and marine systems and for a wide range of taxa, including insects (Juliano 1983; Gutierrez & Menendez 1997; Malmqvist 2000; Brandle *et al.* 2002), plants (Oakwood *et al.* 1993; Edwards & Westoby 1996; Thompson *et al.* 1999; Clarke *et al.* 2001; Lloyd *et al.* 2003; Lowry & Lester 2006), fish (Wellington & Victor 1989; Goodwin *et al.* 2005; Lester & Ruttenberg 2005; Mora & Robertson 2005) and mollusks (Hansen 1980; Perron & Kohn 1985; Jablonski 1986; Scheltema 1989; Pfenninger 2004; Paulay & Meyer 2006).

Arguments for the effect of dispersal on range size can be constructed both from an ecological perspective, in which dispersal is viewed as a fundamental life-history attribute influencing demography and colonization, and from an evolutionary perspective, in which gene flow arising from dispersal affects rates of local adaptation, speciation and extinction. There are three main categories of mechanistic hypotheses predicting a positive dispersal ability range size relationship (explored in more detail in Part II):

- (1) Site colonization hypotheses: species with limited dispersal ability may have a difficult time colonizing or supplying individuals to more distant sites, regardless of the suitability of sites (Wellington & Victor 1989; Gutierrez & Menendez 1997; Thompson *et al.* 1999). Similarly, metapopulation dynamics (Hanski 1999) may lead to smaller ranges for limited dispersers if they have lower rates of site recolonization and thus a smaller number of equilibrium sites occupied at the range margin. Alternatively, a metapopulation 'rescue effect' (Brown & Kodric-Brown 1977; Gotelli 1991), in which immigration from productive 'source' populations maintains 'sink' populations that would otherwise go extinct, may operate at the edge of the range. If this phenomenon scales with dispersal distance, it may affect the distance that sink populations at the range edge extend the overall range size.
- (2) Speciation rate hypothesis: species with low dispersal ability may experience greater isolation and lower gene flow among populations. Decreased gene flow may increase local adaptation and the probability of speciation (Shuto 1974; Hansen 1980; Jablonski 1986; Palumbi 1992). A higher rate of speciation may also result in smaller average geographical ranges if the speciation process leads to a small starting range, because new species will not have had sufficient time to expand their ranges (Hansen 1980; Oakwood *et al.* 1993).
- (3) Selection hypothesis: range size could be the cause rather than the effect. Species with small geographical ranges might experience selection for decreased dispersal, if there is a cost, or at least no benefit, to high dispersal (Gutierrez & Menendez 1997; Thompson *et al.* 1999; Gaston 2003).

Although, these theories have been frequently mentioned in the literature, they have not been thoroughly investigated in a conceptual or theoretical manner. Studies investigating range size variation typically make only passing mention to one of these mechanisms. Furthermore, while there are numerous empirical tests, they often use different methods and have yielded conflicting answers. It is unclear, whether conflicting evidence is a result of flawed tests or whether it is because dispersal only plays a role in determining species' range sizes for specific taxa, situations, regions or habitats. To date, there has been little systematic effort to evaluate this problem.

There are three main considerations that must be taken into account when reviewing empirical studies of the relationship between dispersal ability and range size: the type of dispersal data used in the test, the spatial scale(s) at which the relationship is examined, and the taxonomic group(s) that are investigated. Categorical dispersal data have limitations that could obscure or over-emphasize a true

underlying relationship with range size. Even when quantitative dispersal data are used, dispersal may only influence species' geographical distributions at certain spatial scales or in particular habitats or environments, depending on the mechanism by which dispersal and range size are related. Lastly, dispersal may be an important driver of range size in some taxonomic groups, but not for others, and thus synthetic analyses should consider the effects of taxonomic diversity and phylogenetic history.

Here, we explore the relationship between range size and dispersal ability by synthesizing quantitative dispersal data and determining geographical range size for a broad variety of bottom-dwelling marine species, examining different taxonomic groupings, regions and spatial scales. Marine taxa are ideal study systems for this question because: (1) marine species show considerable variation in both dispersal potential and geographical distribution, (2) we were able to obtain quantitative dispersal data for a large number of marine species from a diversity of taxonomic groups, and (3) it is relatively straightforward to quantify geographical ranges for bottom-dwelling marine species because they tend to follow coastlines. We then critically review and evaluate the assumptions of the hypotheses predicting a positive relationship between dispersal ability and range size. Taken together, our empirical results and conceptual review suggest that although dispersal ability may influence species' geographical distributions under specific circumstances, in many cases a species' dispersal ability is neither expected nor observed to correlate with its geographical extent. Thus, more attention should be paid to other processes responsible for variation in range size.

PART I: EMPIRICAL SYNTHESIS

We synthesized two datasets for marine taxa (Box 1) in order to empirically evaluate the relationship between dispersal ability (defined as the actual or potential distance travelled by typical migrants) and range size. The first dataset contains estimates of average dispersal distance for 68 benthic marine species (macroalgae, invertebrates and fish) calculated from genetic isolation-by-distance slopes (Kinlan & Gaines 2003; Palumbi 2003); genetic estimates reflect long-term averages of realized dispersal distances. The second dataset uses estimates of pelagic larval duration (PLD) (PLD = the residence time of marine larvae in the plankton) as a proxy for dispersal potential (Brothers & Thresher 1985; Wellington & Victor 1989; Lester & Ruttenberg 2005). We compiled a database of larval durations for 499 demersal fish species. For both datasets, species represent many different taxonomic groups, regions and ecosystems worldwide. We compiled detailed distributional information in order to assess each species' range size using a consistent metric.

Box 1: Quantitative proxies for dispersal ability

Quantitative measures of dispersal ability are central to exploring the relationship between dispersal ability and range size. Approximating dispersal distance using categorical proxies often loses critical information, and some commonly used categories may not accurately reflect realized dispersal distances. Despite the potential value, it is difficult to directly measure dispersal distances for many taxa. Furthermore, the longer the dispersal distance, the more difficult it is to measure. As a result, what little data exist tend to be biased toward species with limited dispersal. However, there are a variety of reliable ways to obtain quantitative measures of dispersal indirectly, two of which are used in this synthesis.

Dispersal distances can be estimated using genetic techniques, which are particularly useful, because they can be applied uniformly to a broad range of taxa. One of the most common methods involves measuring the increase in genetic differentiation among populations with increasing geographical distance, a pattern called isolation-by-distance (IBD). Over time, the balance between gene flow (dispersal) and random genetic drift results in a pattern of spatial autocorrelation in the genetic structure of neutral alleles that is directly related to dispersal distance (Wright 1943). Specifically, the slope of the IBD relationship can be related to the mean effective dispersal distance, averaged over many generations, using numerical simulations of population genetic structure (Palumbi 2003). Although originally developed under a strict set of assumptions, including a Gaussian dispersal distribution, the relationship between IBD patterns and dispersal distance is actually robust to variation in the type and shape of the dispersal function (Slatkin 1993; Lee & Hastings 2006). A variety of other population and genetic processes can disrupt or obscure IBD. For example, the measured IBD slope may be time-dependent, as it can take many generations for genetic correlations to build-up. However, simulations show that the IBD slope approaches its equilibrium before overall population-wide genetic structure reaches equilibrium (Malecot 1975; Slatkin 1993, Kinlan and Gaines, unpublished data). In general, if IBD relationships are significant and the slope can be reliably estimated near the origin, this type of genetic data is a valuable source of approximate dispersal distances (Palumbi 2004; Kinlan *et al.* 2005). A fundamental limitation of this technique, however, is that although the mean dispersal distance can be estimated, there is no way to accurately capture maximum dispersal distances.

In this study, we use previously published genetic estimates of realized dispersal (Kinlan & Gaines 2003). Briefly, we simulated dispersal in a stepping-stone lattice developed by Palumbi (2003) to relate average dispersal distance to the increase in genetic differentiation with geographical distance. Simulations assumed a one-dimensional circular array of equally spaced populations, with effective population sizes ranging from 500 to 10 000 individuals. Populations exchanged migrants once per generation according to an exponential dispersal kernel. We varied the mean of the dispersal kernel and analysed the resulting equilibrium IBD slopes. A power function fit to simulation results (dispersal distance = $0.0016 (\text{IBD Slope})^{-1.0001}$, $R^2 = 0.9988$) was used to estimate average dispersal distances from these slopes. Dispersal estimates represent the average dispersal distance required to generate the observed IBD slope under model assumptions (see Kinlan & Gaines 2003 for more details).

Many marine species offer another method for indirectly estimating dispersal. Most fish and many invertebrate species have a pelagic larval phase and a sedentary or demersal adult stage. For most of these species, dispersal among populations occurs exclusively during the larval phase. This phase can be relatively long (weeks to months) and larval mortality is extremely high, making it difficult to track dispersal of individual larvae (but see Thorrold *et al.* 2006 for a promising new technique for tracking larvae). However, in fishes, it is relatively straightforward to estimate the length of the larval phase (PLD) for individuals that successfully settle from the pelagic environment (Victor 1991). For many fish species, larvae are mostly unable to detect and counteract the effects of large eddies (10–100's of km) that primarily drive horizontal dispersal, at least during much of their larval lives. Therefore, for these species the length of the larval phase is a reasonable proxy of dispersal potential (Victor 1991; Bradbury & Snelgrove 2001; Lester & Ruttenberg 2005).

Pelagic larval duration is far from a perfect measure of dispersal. There is increasing evidence that some larvae are capable of surprisingly sophisticated behaviours (Leis 2006), and both larval behaviour and complex oceanographic mechanisms can result in high levels of self-recruitment for some species with moderate to long-larval durations (e.g. Jones *et al.* 2005; Cowen *et al.* 2006). Thus, in some cases PLD may be a poor indicator of mean dispersal distance. However, compared with genetic estimates, it may provide a better index of dispersal potential, because it does not depend on larval survival post-dispersal, and of maximum dispersal distances, when used in conjunction with oceanographic models (Cowen *et al.* 2006). Numerous studies have examined the relationship between PLD and alternative quantitative estimates of realized dispersal distance and found strong correlations across a broad range of marine taxa (Riginos & Victor 2001; Shanks *et al.* 2003; Siegel *et al.* 2003). Siegel *et al.* (2003) use some of the same genetic data presented here for fish and invertebrates and document a strong empirical relationship between genetic dispersal scale and PLD ($R^2 = 0.801$, $P < 0.0001$, $n = 32$), which also agrees with theoretical predictions of dispersal distance based on oceanographic models and PLD. Thus, although PLD has important limitations that must be recognized when using it as a dispersal proxy, for many species, it is the best measure available and is an important advance over qualitative or categorical measures.

METHODS

We used genetic estimates of average dispersal distance for bottom-dwelling marine taxa from Kinlan & Gaines (2003) (see Appendix S1 in Supplementary material). Population genetic structure data taken at multiple scales was used to estimate isolation-by-distance slopes and generate quantitative estimates of mean dispersal distance (Box 1). We excluded species from the original dataset (Kinlan & Gaines 2003) for which reliable and adequately detailed geographical distributional data were not available. The resulting dataset contains eight species of macroalgae and seagrasses, 25 species of demersal fishes and 35 species of benthic invertebrates from tropical and temperate ecosystems worldwide.

For the second dataset, we synthesized data on marine fish PLDs from a comprehensive literature survey (Appendix S2). For many fish species, dispersal occurs exclusively during the larval phase, and therefore the length of this phase is an adequate measure of dispersal potential (Box 1). We included PLD data primarily from otolith ageing studies; otoliths are calcium carbonate ‘earstones’ that contain daily growth bands during the larval period (see Victor 1991 for a review). We used the mean PLD reported for a given species and averaged PLD across studies when multiple estimates were available for a given species, weighted by sample size. We eliminated species for which we could not find reliable distributional information. The resulting dataset consists of 499 fish species, from 52 families. This dataset builds on the tropical reef fish data in Lester & Ruttenberg (2005), adding temperate species and non-reef associated demersal tropical species, and includes species from all oceans and regions of the world.

For both datasets, we compiled the best available range information from field guides, published museum collections, primary literature reports and internet databases (Appendices S1 and S2) to assign range endpoint (north, south, east, west, northeast, northwest, southeast and southwest) coordinates. We calculated three measures of range size for all species: latitudinal extent, longitudinal extent and maximum linear surface distance. We determined maximum linear distance using the distance function in the mapping toolbox in MATLAB 6.1 (MathWorks, Inc., Natick, MA, USA) to calculate the rhumb-line distance between the furthest two range endpoints (following the methods of Lester & Ruttenberg 2005). For both datasets, the three range size metrics are highly collinear (Table 1), suggesting that our general results are not sensitive to the specific range metric used. Therefore, for all analyses, we report results for maximum linear distance as it is a more complete descriptor of a species’ range size. We log-transformed both measures of dispersal ability to achieve normality for all analyses and conducted all statistical tests using JMP 5.1 (SAS Institute, Cary, NC, USA).

Table 1 Correlation coefficients (r) for range size metrics

	Max linear distance	Longitudinal range	Latitudinal range
Max linear distance		0.95	0.84
Longitudinal range	0.99		0.76
Latitudinal range	0.83	0.81	

Values above the diagonal line refer to the genetics estimates dataset, while values below the diagonal are for the pelagic larval duration dataset. All correlation coefficients are highly significant ($P < 0.0001$).

RESULTS

Genetic estimates dataset

There is no significant relationship between range size, measured as maximum linear distance, and genetic estimates of average dispersal distance ($P = 0.577$, $R^2 = 0.005$, $n = 68$), even when considering taxonomic groups (sessile marine plants, demersal fish and benthic invertebrates) separately in a model with both dispersal distance and taxonomic group predicting range size (Fig. 1a; dispersal distance: $P = 0.127$). There is a significant effect of taxonomic group in this model ($P = 0.037$), independent of differences in dispersal capabilities of the different groups. The demersal fishes, benthic invertebrates and sessile marine plants in this dataset have average scales of dispersal that differ considerably [Fig. 1b; ANOVA dispersal distance: $P < 0.0001$; discussed in detail in Kinlan & Gaines (2003)], but their mean range sizes are statistically indistinguishable (ANOVA range size: $P = 0.100$).

Fish PLD dataset

There is no relationship between range size and PLD when examining the entire dataset ($P = 0.852$, $R^2 < 0.001$, $n = 499$), although this may be an inappropriately large scale. When examining the two main ocean basins, the Atlantic and Pacific, separately, there are no significant relationships (Fig. 2; Atlantic: $P = 0.462$, $R^2 = 0.005$, $n = 111$; Pacific: $P = 0.773$, $R^2 < 0.001$, $n = 388$). When considering temperate and tropical species within these two ocean basins, there is still no relationship in the Atlantic (tropical: $P = 0.770$, $R^2 = 0.002$, $n = 57$; temperate: $P = 0.157$, $R^2 = 0.039$, $n = 53$). There are significant positive relationships in the Pacific at this scale (tropical: $P = 0.0004$, $R^2 = 0.038$, $n = 328$; temperate: $P = 0.0008$, $R^2 = 0.179$, $n = 60$), although these relationships are weak and, particularly for the tropical Pacific, likely driven primarily by the large sample size.

Lester & Ruttenberg (2005) conducted detailed analyses on the relationship between PLD and range size using the

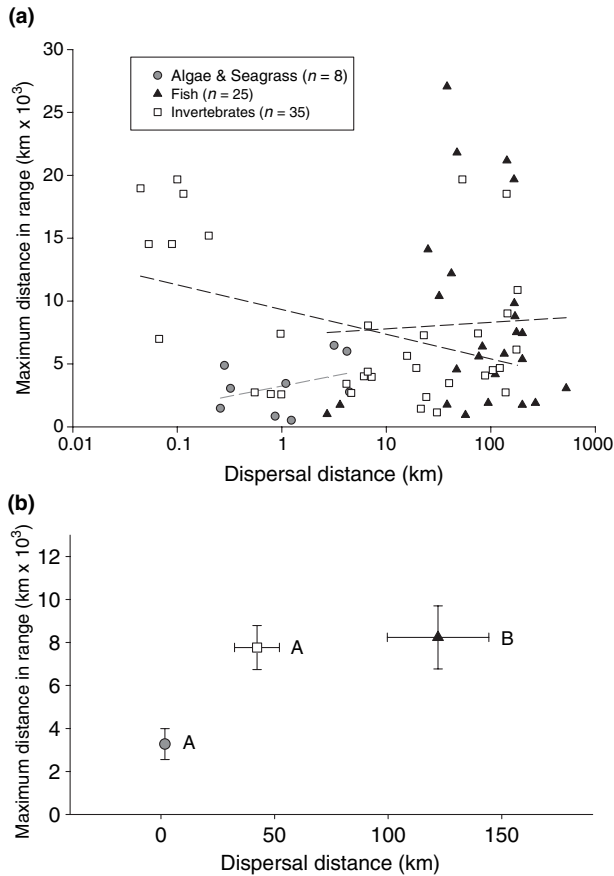


Figure 1 (a) The relationship between range size (maximum linear distance within a species' range, in km) and estimated dispersal distance (km) for the genetics dataset. The relationship within each taxonomic group is non-significant; trend lines are plotted for reference only. (b) Mean range size (km) and mean estimated dispersal distance (km) for the three taxonomic groups. Error bars indicate plus or minus one standard error. The three groups do not have statistically different average range sizes (ANOVA: $P = 0.100$), but their average scales of dispersal differ (ANOVA: $P < 0.0001$). Letters refer to the Tukey-Kramer HSD (honestly significant difference) comparison of means test, with like letters indicating no significant difference in average dispersal distance ($\alpha = 0.05$).

subset of the dataset containing tropical reef species. Thus, we focused our new analyses on the temperate species, examining these species at a variety of spatial scales. We divided the temperate species into groups based on ocean basin (Atlantic or Pacific) and region (eastern or western side of the ocean basin). Species found in the western temperate Atlantic and the western temperate Pacific show no relationship between PLD and range size, while species in the eastern temperate Atlantic and eastern temperate Pacific exhibit a significant positive relationship between PLD and range size (Fig. 3). Furthermore, the PLD-range size relationships on the eastern margins of the ocean basins

explain a considerable proportion of the variance (23 and 40% for the Atlantic and Pacific, respectively).

Fish species from the same family do not represent phylogenetically independent data points, which could affect the patterns or lack of patterns that we observe. Although a phylogenetic contrast analysis is the best way to control for phylogeny, the requisite evolutionary distances are unknown for the vast majority of the species in our dataset, and so instead we conducted analyses using the mean range size and larval duration for any family with data for three or more species. At the family level, range size is independent of larval duration in both oceans (Atlantic: $P = 0.858$, $R^2 = 0.003$, $n = 12$; Pacific: $P = 0.149$, $R^2 = 0.107$, $n = 21$). When categorizing the species in the dataset by ocean basin and region (as in Fig. 3), only two regional classifications (western tropical Pacific and eastern temperate Pacific) had sufficient families ($n \geq 9$) with data for three or more species. Parallel to findings for analyses of individual species, there is no relationship at the family level in the western tropical Pacific ($P = 0.535$, $R^2 = 0.036$, $n = 13$), but a highly significant relationship in the eastern temperate Pacific ($P = 0.011$, $R^2 = 0.623$, $n = 9$). The positive relationship in the eastern temperate Pacific strengthens at higher taxonomic levels, with larval duration explaining a larger proportion of the variation in range size for the family- vs. species-level analysis (60% vs. 40%).

Phylogeny may obscure patterns in other ways. It is possible that a positive relationship between range size and dispersal distance exists within many families, but that these significant relationships are masked by a large degree of uncorrelated inter-family variation when species from different families are considered in a single analysis. We tested the potential for within-family relationships in the two ocean basins for families represented by at least five species using a model that included PLD, family and their interaction predicting species' range sizes. Families in the Atlantic did not have significantly different range sizes ($P = 0.211$), although the interaction was significant ($P = 0.030$). In the Pacific, families did have significantly different range sizes ($P = 0.007$), although again interpretation of this result is complicated by a significant interaction term ($P = 0.005$). In both the Atlantic and the Pacific, there was no residual relationship between PLD and range size with the effect of family removed ($P = 0.169$ and 0.811 , respectively). Examining the potential for within family relationships at more regional scales (for families with $n \geq 10$), Chaetodontids, Labrids and Pomacentrids showed significant positive relationships in the tropical Pacific, as reported in Lester & Ruttenberg (2005). There is also a significant positive relationship for Labrids in the temperate eastern Atlantic ($P = 0.003$, $R^2 = 0.602$, $n = 11$). However, most families do not exhibit significant relationships at regional scales although for many, power is limited by small sample

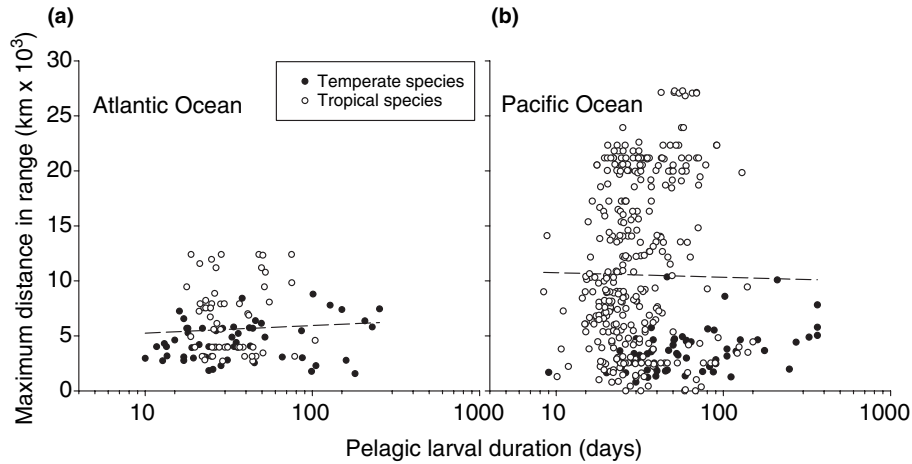


Figure 2 The relationship between range size (maximum linear distance within a species' range, in km) and dispersal distance [pelagic larval duration (PLD), in days] for the PLD dataset, analysed separately in (a) the Atlantic Ocean ($P = 0.462$, $R^2 = 0.005$, $n = 111$) and (b) the Pacific Ocean ($P = 0.773$, $R^2 < 0.001$, $n = 388$). Temperate and tropical species points are plotted as filled and open circles (●,○), respectively.

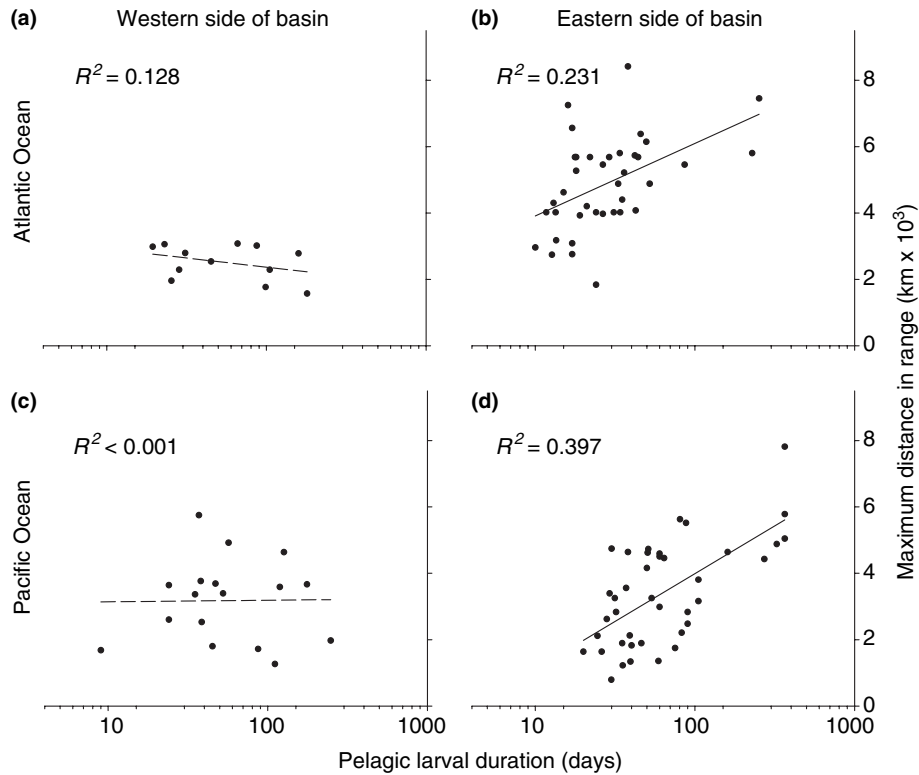


Figure 3 The relationship between range size (maximum linear distance within a species' range, in km) and dispersal distance [pelagic larval duration (PLD), in days] for temperate species in the PLD dataset, analysed separately by ocean and basin region (eastern or western side of ocean basin): (a) west temperate Atlantic ($P = 0.225$, $R^2 = 0.128$, $n = 12$), (b) east temperate Atlantic ($P = 0.002$, $R^2 = 0.231$, $n = 38$), (c) west temperate Pacific ($P = 0.960$, $R^2 < 0.001$, $n = 17$), and (d) east temperate Pacific ($P < 0.0001$, $R^2 = 0.397$, $n = 40$). Solid lines indicate significant relationships, while dotted lines indicate non-significant relationships.

sizes. Given the available data, there is limited evidence to support a general relationship between larval duration and range size within individual fish families.

DISCUSSION

Our analyses of two independent datasets reveal that, in most cases, dispersal ability is of little or no value in predicting range size, and consequently is not likely to be the principal determinant of a species' range size. However, when examining the relationship at smaller scales (e.g. within regions) and/or within certain taxonomic groups, there are specific cases in which dispersal ability and range size are positively correlated. For example, using a subset of the PLD dataset presented here, Lester & Ruttenberg (2005) demonstrate that for tropical reef fish dispersal ability is a significant driver of range size in the Indo-Pacific, which appears to be largely driven by a dichotomy between species that cross the large east Pacific Barrier and those that do not. Specifically, Indo-Pacific species whose ranges cross significant barriers to dispersal (i.e. those that extend to the Hawaiian Islands, Easter Island and/or the East Pacific) have longer PLDs than species whose ranges do not include these isolated areas. These widespread species exert considerable leverage on the positive relationship between PLD and range size among all Indo-Pacific species (Lester & Ruttenberg 2005).

In the new analyses presented here, we show that there is also a relationship between dispersal and range size for temperate fish species, but only on the eastern sides of ocean basins. Furthermore, this relationship strengthens at the family level for eastern temperate Pacific species. Unlike the case of the tropical Pacific, there is no straightforward explanation, although there are a variety of possibilities that warrant further testing as to why dispersal may influence range size on the eastern but not on the western margins of temperate oceans. These include differences in current speeds, the steepness of thermal gradients (much steeper on western than eastern margins), the range of climate seasonality, and the distribution of suitable habitat (Parmesan *et al.* 2005). When investigating a much broader range of taxa (fish, invertebrates and seaweeds) and using a measure of dispersal independent of time spent in the plankton (genetic estimates dataset), we find no strong evidence that dispersal ability is an important determinant of species' distributions, although this dataset is limited by smaller sample sizes. In summary, our analyses suggest that dispersal ability plays a relatively idiosyncratic role in setting species' geographical distributions, and is usually not a major determinant of range size. The one consistent feature that appears to drive a correlation between dispersal and range size is very large gaps in suitable habitat.

Contrary to our findings, dispersal ability is often suggested or examined as a potential key driver of species' geographical distributions (see Introduction). This is, in part, because it seems intuitive that the distances individuals can move should influence a species' ability to colonize more distant areas. Indeed, species' range sizes are constrained to be at least the size of the realized dispersal distance of individuals, but it is unclear how much of a constraint this represents. To address this question, we can examine the size of ranges relative to the average dispersal distance of individuals. We use the genetic estimates dataset to address this question by plotting average dispersal distances as a fraction of the species' range size. This analysis reveals that the average dispersal distance is $\leq 1\%$ of the maximum linear distance within the species' range for most species (Fig. 4), and 94% of the species in this dataset disperse on average $< 5\%$ of their geographical range. This implies that most individuals disperse over only a small fraction of the range that their conspecifics occupy, and highlights the fundamental mismatch in scale between demographic processes and processes at the scale of a species' range.

Nonetheless, some empirical studies have found significant relationships between dispersal and range size (e.g. Juliano 1983; Perron & Kohn 1985; Gutierrez & Menendez 1997; Duncan *et al.* 1999). However, because quantitative dispersal data are lacking for most taxa, the majority of existing studies describe dispersal ability as a categorical variable based on traits that are assumed to be correlated with dispersal potential, such as seed characteristics in plants (Oakwood *et al.* 1993; Edwards & Westoby 1996), developmental mode in marine gastropods (Hansen 1980; Scheltema 1989), and flight ability in insects (Juliano 1983;

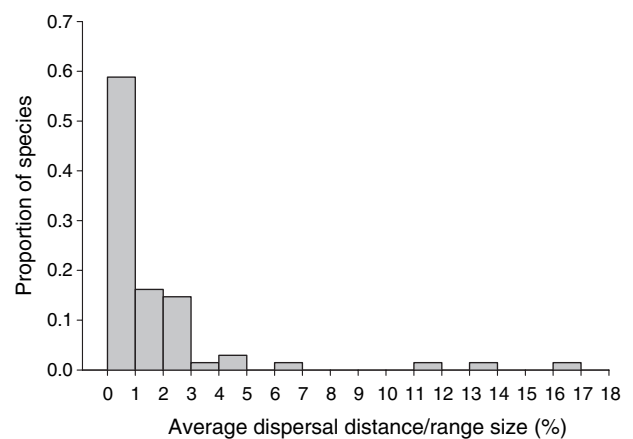


Figure 4 The proportion of species in the genetics-estimates dataset with mean estimated dispersal distances (km) that are a given fraction of their range size (maximum linear distance, in km). Most species' dispersal distances are a very small fraction of their total range size.

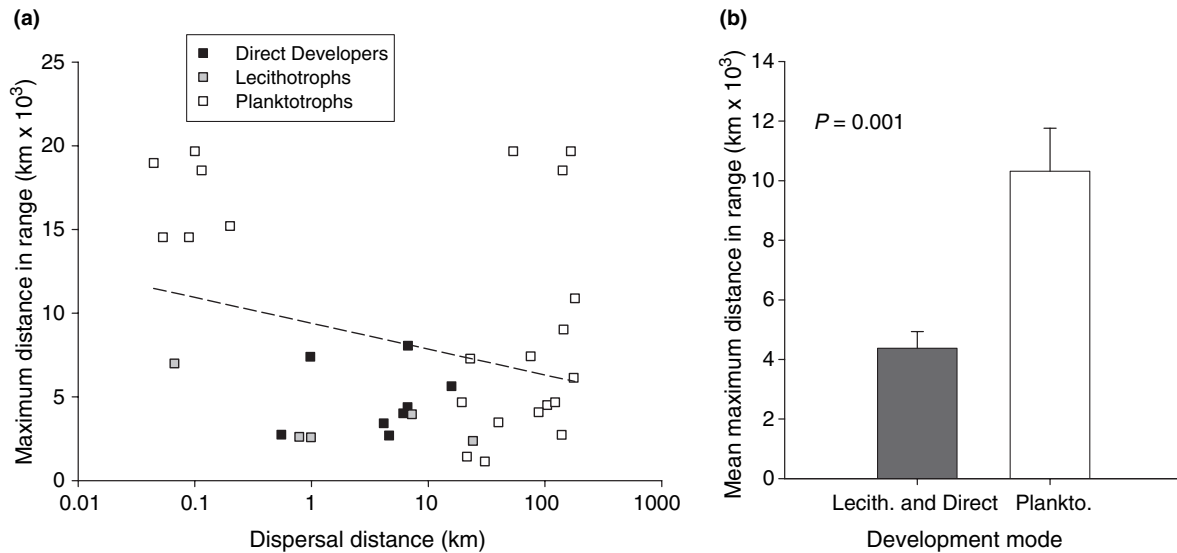


Figure 5 (a) The relationship between range size (maximum linear distance within a species' range, in km) and dispersal distance (km) for the invertebrates in the genetics dataset. There is a non-significant negative trend ($P = 0.082$, $R^2 = 0.089$, $n = 35$). (b) Mean range size (km) for lecithotrophic and directing developing species ($n = 13$) and for planktotrophic species ($n = 22$). Mean range size is significantly larger for planktotrophic species (two-tailed t -test: $P = 0.001$).

Gutierrez & Menendez 1997). These categorical descriptions can be problematic, because they may not correctly capture differences in dispersal distance. Using a categorical predictor with few classes can obscure (due to low power) or overemphasize (if the underlying relationship is nonlinear) a relationship with the dependent variable.

As a result of these potential problems, using categorical dispersal data to evaluate the relationship between dispersal ability and range size can produce misleading results. For example, consider the invertebrate data in the genetic estimates dataset. Using quantitative estimates of average realized dispersal distance, this diverse group of marine invertebrates show a non-significant and negative trend for dispersal distance predicting range size (Fig. 1a; $P = 0.082$, $R^2 = 0.089$, $n = 35$). However, if we classify these same species according to larval developmental mode (Appendix S1; Fig. 5a), the most commonly employed categorical measure of dispersal ability for marine invertebrates, we reach a very different conclusion. Range size is significantly larger for species with planktotrophic (feeding planktonic larvae) larval development compared with lecithotrophic (non-feeding planktonic larvae) and direct developing species (no planktonic phase) (Fig. 5b; two-tailed t -test: $P = 0.001$). Although the mean range size increases for species with the larval development mode presumed to result in the longest dispersal distances (planktotrophic), dispersal distance seems to play little role in generating this pattern. Within each of these groups, range size is independent of the scale of dispersal even though dispersal distances vary by orders of magnitude

across species. Given the misleading conclusions that arise from dispersal proxies in this comparison, it is not surprising that studies using comparable categorical dispersal data reach conflicting conclusions – positive relationships between dispersal ability and range size in some groups (Jablonski 1986; Scheltema 1989; Duncan *et al.* 1999), no relationship in others (Vermeij *et al.* 1990; Clarke *et al.* 2001; Goodwin *et al.* 2005).

There are other studies that have used quantitative dispersal data and the results of this empirical synthesis are generally consistent with these other analyses. Numerous studies of tropical fish families [see Table 1 in Lester & Ruttenberg (2005)] and a sea urchin study (Emlet 1995) failed to find a relationship between larval duration and range size. Although some studies examining fish larval durations do find a significant relationship with range size (Bonhomme & Planes 2000; Zapata & Herrón 2002), previous PLD studies have a strong bias towards the tropics and particular taxonomic groups, and have much smaller sample sizes [e.g. $n = 5$ for Zapata & Herrón (2002)] than the PLD dataset presented here. Our more extensive analyses argue against a general, consistent relationship between dispersal ability and range size, but do address specific cases in which dispersal may be an important driver of species' geographical distributions.

PART II: CONCEPTUAL REVIEW

Despite the fact that dispersal ability is commonly suggested to play an important role in influencing species' geographical

ranges (Hanski *et al.* 1993; Brown *et al.* 1996; Gaston 1996, 2003), the underlying rationale for such an expectation is often not explained nor critically evaluated. There are several classes of theoretical explanations for a positive relationship between range size and dispersal ability, and yet there has been no comprehensive review of these theories. Here, we review the existing mechanical hypotheses and evaluate their logic and supporting or refuting evidence. In light of our empirical results, we also investigate reasons that dispersal would not exert a strong influence on range size in the context of these hypotheses.

Site colonization hypotheses

The site colonization hypothesis assumes that poorly dispersing species may have more geographically restricted ranges simply because they fail to reach as many sites (Juliano 1983; Wellington & Victor 1989; Gutierrez & Menendez 1997; Thompson *et al.* 1999). Metapopulation theory provides an alternative formulation of the site colonization hypothesis, which is not contingent upon whether or not individuals spread to additional habitable locations (Levins 1969; Hanski *et al.* 1993). The equilibrium number of sites occupied reflects a balance between the probability of local extinction and the rate of site recolonization (Hanski 1999). If local populations at the periphery of the range occasionally go extinct, the species' geographical range will shrink until these sites are recolonized. Species with very limited dispersal may therefore occupy smaller geographical ranges because a greater fraction of habitable sites at the range margin will on average remain unoccupied. A final form of the site colonization hypothesis is a more specialized case of metapopulation theory, employing the concept of a 'rescue effect' (Edwards & Westoby 1996; Duncan *et al.* 1999). Fringe or 'sink' populations at the edge of the range that would otherwise go extinct persist because of regular immigration from more productive 'source' populations (Brown & Kodric-Brown 1977; Gotelli 1991). If a rescue effect is operating, the degree of range expansion beyond source populations (the size of the 'rescue' zone) should scale with dispersal distance; short-distance dispersers can only rescue nearby marginal populations.

The site colonization hypotheses are likely to operate when suitable habitat is patchily distributed across the landscape or when species have had relatively little time to expand their ranges following speciation or a range contraction event. For example, species that have undergone relatively recent range contractions (e.g. by glaciation) may not have had enough time to completely re-establish their ranges in all contiguous areas of suitable habitat. In this situation, we would expect to see a positive relationship between dispersal and range size, as species with greater

dispersal ability can expand their ranges more rapidly (Svenning & Skov 2004). Likewise, in situations where there are large distances between areas of suitable habitat (e.g. the 5000 km gap in tropical reef habitat from the central to the east Pacific, or the distances between oceanic islands and continental mainlands), species are unable to expand their ranges in small, incremental steps. In such instances, dispersal ability may also be a limiting factor for range size (Lester & Ruttenberg 2005).

However, the above situations are likely special cases. For many species, habitat is relatively continuous and even poorly dispersing species are able to colonize all suitable sites, even if by incrementally small steps, on the time scales over which geographical ranges are established. For these species, dispersal ability would limit the rate of species' range expansion, but not the ultimate size. Our genetic estimates dataset demonstrates that the average dispersal distance for most species is only a small fraction of their range size (Fig. 4), suggesting that the colonization advantage for species with greater dispersal potential may have little consequence over the temporal and spatial scales at which species' ranges are generated.

Colonization and subsequent expansion of the range is likely to be far more sensitive to the tails of the dispersal distribution – rare long-distance dispersal events – than to the average. Small changes in the dispersal kernel, e.g. changes in the frequency of long-distance dispersal events, can result in maximum or extreme dispersal scales that would not be predicted based on the average dispersal distance (Clark *et al.* 2001; Kinlan *et al.* 2005), and may explain why many introduced species with short average dispersal distances spread as fast as introduced species with much longer average dispersal distances (Clark *et al.* 2001). For example, a typically short disperser may experience rare long-distance dispersal events ('jump dispersal'), followed by rapid local spread via short-distance dispersal (Suarez *et al.* 2001). There is evidence for both marine and terrestrial species that rare, long-distance dispersal events may be disproportionately important in affecting species' range sizes (e.g. Johannesson 1988; Cain *et al.* 2000) and many species with short average dispersal distances may have mechanisms for episodic, long-distance dispersal (e.g. marine invertebrates rafting on drift algae, bird dispersal of seeds; Highsmith 1985; Higgins *et al.* 2003). Our empirical evidence supports this idea; the genetic estimates dataset, which captures average dispersal distances, showed no relationship between dispersal distance and range size, whereas we did find some significant relationships for the PLD dataset. The PLD dataset does a better, albeit imperfect, job at capturing the potential for rare long-distance dispersal events; in fish species that have been well studied, mean PLD is highly correlated with both the maximum and range of observed PLDs (Lester &

Ruttenberg 2005). However, the efficacy of long-distance dispersal events and their impact on range expansion and colonization is context-dependent: life-history factors, such as the stage at which dispersal occurs and the ability to survive and reproduce at low densities, and environmental factors, such as habitat structure, can severely limit or enhance the effects of extreme dispersal events on range expansion (reviewed in Kinlan & Hastings 2005).

In the context of metapopulation dynamics and the rescue effect, the lower rate of site recolonization for poorer dispersers is unlikely to have a particularly significant effect on range size. As individual dispersal distances are typically only a small fraction of a species' range size (e.g. Fig. 4), this effect should only influence the margin of the range. Even if species with more restricted dispersal have more unoccupied potential sites at the margin of the range, the effect on overall range size will be small on average. Additionally, theoretical work suggests that when edge populations act as sinks, gene flow from source populations can limit local adaptation in these sink populations, resulting in a stable range boundary without the potential for range expansion (Kirkpatrick & Barton 1997; Holt & Keitt 2000). This phenomenon would be accentuated for species with longer distance dispersal, because gene flow to edge populations would have more distant origins, further limiting local adaptation. As a result, range size could be more restricted for species with longer dispersal distances, eliminating any range size advantage from a larger 'rescue' zone.

Speciation rate hypothesis

The speciation rate hypothesis suggests that species with low-dispersal ability may experience greater isolation and lower gene flow, and thus a greater potential for local adaptation. Hence, species with limited dispersal abilities may tend to have higher rates of speciation (Shuto 1974; Hansen 1980; Jablonski 1986; Palumbi 1992). A higher rate of speciation can result in smaller distributions, since at any given point in time these species have had less evolutionary time to expand their ranges (Hansen 1980; Oakwood *et al.* 1993). Additionally, if repeated speciation occurs in a limited geographical area, further range expansion could be restricted by competition with nearby congeners.

There is some empirical evidence in support of the speciation rate hypothesis. For example, recent work with mollusks provides evidence that species with larger ranges have lower speciation rates (Jablonski & Roy 2003). Furthermore, numerous paleontological studies of marine gastropod families demonstrate that species with dispersive larvae tend to have lower speciation rates and/or longer species longevity than species with non-dispersive larvae (Hansen 1983; Jablonski 1986; Gili & Martinell 1994). Nonetheless, the speciation rate hypothesis relies on a string

of assumptions, limiting the likelihood that it could result in a consistent relationship between dispersal ability and range size.

Many of the assumptions of the speciation rate hypothesis are only likely to hold in some cases or for some taxa. For example, there are a variety of factors that can limit or enhance gene flow in species with high- or low-dispersal ability, respectively. Strong post-dispersal selection, local genetic drift, or reproductive isolation mechanisms can trump the effects of gene flow (Palumbi 1992; Hillbush 1996; Linhart & Grant 1996; Planes & Romans 2004; Garant *et al.* 2005), resulting in significant genetic differentiation and even speciation. Alternatively, dispersal and speciation may be complicated by the relative importance of the tails vs. the mean of the dispersal distribution. Demographically insignificant rates of dispersal can be sufficient to prevent evolutionary divergence (Slatkin 1985), and thus even rare long-distance dispersal events may allow species with low dispersal ability to establish and maintain large ranges without experiencing speciation.

Even in cases where low-dispersal ability results in low gene flow and presumably increased speciation, speciation rate will not necessarily mediate a positive correlation between dispersal ability and range size. The speciation rate hypothesis assumes that with higher speciation rates, species have less evolutionary time for range expansion, which results in smaller ranges. The strength of this effect depends on how many generations are required for a species to achieve its 'full' geographical extent following speciation: if expansion happens rapidly relative to the time scale of speciation events, then this model is unlikely to hold. There is some evidence from mollusk paleontological studies for a positive relationship between species durations (geological longevity of a species) and geographical range size (Hansen 1980; Koch 1980; Jablonski 1987), but other studies have failed to find a relationship in other groups (Stanley 1986; Stanley *et al.* 1988), casting further doubt on the generality of this mechanism.

Lastly, such correlations also do not distinguish cause from effect. The likelihood of speciation or extinction may depend on range size instead of the converse (Rosenzweig 1995; Chown & Gaston 2000). Jablonski (1987) presents evidence suggesting that species achieve their geographical ranges early in their histories, indicating that species durations are more likely a result of range size, rather than vice versa. It is also possible that species with large ranges may be more likely to speciate if a larger range is more likely to include a barrier to movement that isolates subpopulations (Rosenzweig 1995; Maurer & Nott 1998). Additionally, species durations are determined not only by speciation rates, but also by rates of extinction; large ranges have been linked to low extinction rates and vice versa, regardless of dispersal ability (Jablonski *et al.* 1985). In summary, upon

closer examination of the speciation rate hypothesis, we find that it offers only idiosyncratic and context-dependent predictions regarding the effect of dispersal on species' geographical distributions, consistent with the results of our empirical synthesis.

Selection hypothesis

Although the first two classes of hypotheses seek to explain how dispersal capability could drive geographical extent, the selection hypothesis posits that the causal linkage works in the opposite direction. Species with small geographical ranges might experience selection for lower dispersal if there is a cost (or at least no benefit) for high dispersal (Gutierrez & Menendez 1997; Thompson *et al.* 1999; Gaston 2003).

There are some situations in which species with small ranges might be expected to experience selection for reduced dispersal. For example, selection for limited dispersal ability may occur in extreme, highly stable or isolated environments, such as the loss of flight in high altitude and high latitude insects (e.g. Wagner & Liebherr 1992 and references therein) and in island birds (McNab 1994), where energetics favour loss of flight ability. The selection hypothesis could also operate if more geographically restricted species have a narrower range of tolerances, are more ecologically specialized, or occupy restricted, isolated or infrequently-disturbed habitats, so that the costs of broad dispersal exceed any potential benefits. Brown (1984) has suggested that ecological specialists are more geographically restricted than generalists as an explanation for the positive relationship between local abundance and geographical distribution.

However, intense selective pressure for reduced dispersal seems unlikely to be a general mechanism leading to range size-dispersal distance correlations, given that most species' average individual dispersal distances are far less extensive than their total geographical range (e.g. Fig. 4). Additionally, increased phenotypic plasticity may alleviate selection pressure for restricted dispersal in long-dispersing species by reducing the perceived effects of environmental variability; over evolutionary time this could allow short-dispersing species to develop increased dispersal without suffering prohibitive costs (Warner 1997; Parsons 1998). Lastly, the potential for a positive relationship between ecological generalism, or niche breadth, and geographical distribution has been critically challenged (Gaston & Blackburn 2000), and empirical tests provide mixed results (Burgman 1989; Thompson *et al.* 1999; Gregory & Gaston 2000; Hawkins *et al.* 2000). Thus, on closer examination, the selection hypothesis also would not be expected to result in a universal relationship between dispersal ability and range size.

CONCLUSION

Dispersal ability is frequently predicted or assumed to influence range size variation. Although this idea is intuitively appealing and seems to be supported by several mechanistic arguments, there are limited empirical tests and a variety of other factors have been proposed to explain range size variation. Most studies have been forced to use categorical dispersal data and do not investigate the relationship at multiple spatial scales, for different regions, or for a variety of broad taxonomic groups. Our synthesis of two quantitative marine datasets shows that a positive relationship between dispersal distance and geographical extent is not universal. Instead, dispersal only seems to relate to range size in special situations, and even then it is only a modest predictor. A rigorous evaluation of the theoretical mechanisms that could link dispersal and range size is consistent with the observed patterns: none of these hypotheses would be expected to result in a consistent relationship between dispersal ability and range size, and thus the equivocal results of empirical studies are largely consistent with theory. One possible reason for the inconsistent relationship between dispersal and range size is the mismatch in temporal and spatial scales of the demographic process of dispersal and of the long-term, large-scale process of range establishment.

Given that our empirical analyses are restricted to marine systems, are our conclusions unique to the oceans? There are obvious fundamental differences in these habitats, but the most significant in terms of dispersal may be habitat patchiness and the existence of an uninhabitable dispersal matrix. In marine systems, limited areas of shallow adult habitat are often surrounded by vast areas of open ocean through which larvae can disperse. In contrast, dispersal for many terrestrial organisms occurs in the adult phase, potentially requiring a more continuous matrix of adult habitat. However, many terrestrial plants (especially those with wind-dispersed seeds) may function more like marine organisms, with sedentary adults and dispersive propagules. To effectively assess the generality of our results to terrestrial systems will require a similar synthesis of terrestrial data. There is some quantitative dispersal data for terrestrial taxa, including birds and mammals (e.g. Sutherland *et al.* 2000; Bowman *et al.* 2002; Bowman 2003), plants (e.g. Willson 1993; Cain *et al.* 1998; Vander Wall 2003), and insects (e.g. Schneider 2003). The average scales of dispersal reported for these groups suggest that such an analysis would be consistent with that reported here for marine taxa. For example, direct estimates of maximum seed dispersal range from < 1 m to 22 km for a review of over 250 angiosperm species (Cain *et al.* 1998) and genetic estimates of dispersal distances for herbivorous insects ranged from 8 to

42 km (Kinlan & Gaines 2003). These relatively short dispersal distances suggest that many of the species in these datasets likely have geographical ranges considerably larger than their dispersal distance, and thus would show a similar pattern of range size relative to the average dispersal distance of individuals as documented in this study (Fig. 4).

Dispersal obviously plays an important role in biogeography: no organism could occupy an extensive geographical range without some dispersal, or colonize an area without an initial immigration event. However, the eventual size of a geographical range may often be more strongly mediated by a suite of other factors (e.g. see Gaston 2003), perhaps operating at much larger spatial and temporal scales than the average dispersal distance. Future investigations should consider some of these other factors, such as environmental tolerance, environmental variability, niche requirements, genetic processes, and large-scale changes in resources and habitat. In addition, we recommend a similar synthesis for broad groups of terrestrial organisms using quantitative dispersal data and a consistent range size metric. Examining such a synthesis in the context of the conceptual investigation presented here will further our ability to predict the specific contexts in which dispersal is likely to influence the extent of species' ranges.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Species and reference lists for the genetic estimates dataset.

Appendix S2 Species and reference lists for the pelagic larval duration (PLD) dataset.

This material is available as part of the online article from: <http://www.Blackwell-Synergy.com/doi/full/10.1111/j.1461-0248.2007.01070.x>

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