

Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history

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We examine estimates of dispersal in a broad range of marine species through an analysis of published values, and evaluate how well these values represent global patterns through a comparison with correlates of dispersal. Our analysis indicates a historical focus in dispersal studies on low-dispersal/low-latitude species, and we hypothesize that these studies are not generally applicable and representative of global patterns. Large-scale patterns in dispersal were examined using a database of correlates of dispersal such as planktonic larval duration (PLD, 318 species) and genetic differentiation (F_{ST} , 246 species). We observed significant differences in F_{ST} ($p < 0.001$) and PLD ($p < 0.001$) between taxonomic groups (e.g. fishes, cnidarians, etc.). Within marine fishes (more than 50% of datasets), the prevalence of demersal eggs was negatively associated with PLD ($R^2 = 0.80$, $p < 0.001$) and positively associated with genetic structure ($R^2 = 0.74$, $p < 0.001$). Furthermore, dispersal within marine fishes (i.e. PLD and F_{ST}) increased with latitude, adult body size and water depth. Of these variables, multiple regression identified latitude and body size as persistent predictors across taxonomic levels. These global patterns of dispersal represent a first step towards understanding and predicting species-level and regional differences in dispersal, and will be improved as more comprehensive data become available.

Keywords: dispersal; marine; larvae; connectivity; latitude; advection

1. INTRODUCTION

Worldwide collapse of commercial marine species (e.g. Baum *et al.* 2003; Worm *et al.* 2006) and the subsequent failure of recovery efforts (Hutchings 2000) indicate large gaps in our understanding of marine ecosystem dynamics (Sale *et al.* 2005). Recent declines in species abundance have had biogeographic (Bradbury *et al.* 2008), ecological (Pauly *et al.* 2002) and evolutionary (Hutchings & Baum 2005) repercussions, all of which indicate large-scale alterations and potential destabilization of marine communities. Contemporary efforts to manage and conserve marine ecosystems suggest that an understanding of connectivity and dispersal (Botsford *et al.* 2001; Sale *et al.* 2005; Ruzzante *et al.* 2006) may be pivotal because connectivity directly influences both adaptive potential (Wright 1931) and long-term persistence (Hastings & Botsford 2006). The efficacy of current spatial management tools such as no-take marine reserves requires information on connectivity and the size and geography of the spillover cloud of exported production (Botsford *et al.* 2001; Hughes *et al.* 2005; Sale *et al.* 2005).

Nonetheless, despite substantial work relating dispersal potential and reproductive strategy in marine organisms to marine biogeography (e.g. Thorson 1950; Scheltema 1986) and life history (Levin & Bridges 1995), measures of the scales of dispersal remain elusive.

In the majority of marine organisms, the prevalence of a pelagic larval stage and high fecundities represent daunting logistical challenges for the measurement of marine connectivity and dispersal (Palumbi 2004; Levin 2006). Indeed, the prevalence of pelagic stages across taxa, widespread larval distributions, small and weakly swimming larvae and low observed genetic divergence have contributed to the widely held view over the last century that marine populations are generally characterized by broad-scale dispersal (Levin 2006). Recent decades have seen several technological advancements directed at tracking or tagging fishes (e.g. Campana & Thorrold 2001; Hellberg *et al.* 2002; Thorrold *et al.* 2006) and invertebrates (Levin 2006), substantially increasing the numbers of marine dispersal estimates, and shifting towards a paradigm that emphasizes the closed nature of marine populations (Levin 2006). Nonetheless, the number of existing estimates of marine dispersal is few, use contrasting approaches, and it is unclear whether they fully represent global patterns in dispersal and connectivity. The potential biases resulting from the current small

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sample size, contrasting methodologies, differences among taxa and geographical study area require evaluation.

The objectives of this work are threefold: (i) review measures of dispersal in the oceans, highlighting the approaches used and the spatial scales of measurement, (ii) examine the degree to which current dispersal methodologies and estimates have focused disproportionately on low-dispersal species or specific taxa and specific geographical areas, and (iii) examine correlates of dispersal among taxonomic groups from the published literature in relation to life-history traits, and geographical distribution in order to formulate global hypotheses on marine dispersal. For the purposes of this study, we define 'dispersal' as the geographical displacement of individual organisms from their natal area. Similarly, 'effective dispersal' represents the subset of dispersers that survive and successfully reproduce, often integrated over multiple generations.

2. MATERIAL AND METHODS

(a) *Review of measures of dispersal*

Methodologies used to obtain estimates of dispersal vary and have been reviewed elsewhere (e.g. Shanks *et al.* 2003; Palumbi 2004; Levin 2006). Admittedly, given the breadth of literature from which measures of dispersal may be made, this synthesis is broadly representative but not exhaustive, and instead encompasses the range of estimates to allow broad-scale comparison. We report estimates of dispersal either as dispersal distances (i.e. distance recaptured from a tagged source) or rates of homing to a point location (i.e. proportion of individuals tagged and recaptured at the same location) based on recent reviews (see Shanks *et al.* 2003) and the primary literature. To assist in comparing and contrasting approaches, dispersal estimates were organized into five categories based on the methodologies and approaches following Nathan *et al.* (2003): (i) biogeographical, (ii) Eulerian, (iii) Lagrangian, (iv) short-term genetic analysis, and (v) long-term genetic analysis. Details and sources of each estimate are contained in the electronic supplementary material.

(b) *Correlates of dispersal: genetic differentiation and planktonic duration*

We used correlates of dispersal in two forms to examine expected large-scale changes in dispersal across taxa and habitats. The duration of the planktonic egg and/or larval stage correlates with dispersal (Bradbury & Snelgrove 2001; Shanks *et al.* 2003; Siegel *et al.* 2003) and is commonly taken as a surrogate for dispersal potential (Lester & Ruttenberg 2005). Similarly, dispersal may be examined through its consequences for gene flow and population structuring (Bohonak 1999), acknowledging that these inferences integrate over multiple generations and may be influenced by vicariant events. The broad combination of these approaches allows a diverse range of species and habitats to be included in the analysis.

A database of estimates of planktonic larval duration (PLD) was drawn from previous reviews and the primary literature (e.g. Bradbury & Snelgrove 2001; Shanks *et al.* 2003; Lester & Ruttenberg 2005). Given that pelagic egg transport may also contribute to dispersal potential, data on egg type (i.e. demersal or pelagic) were also recorded. We then examined how the proportion of species with demersal eggs varied along the range of values for each dispersal

correlate (i.e. from low to high dispersal). Estimates of effective dispersal based on F_{ST} ($n=247$) were similarly compiled from the literature (1973 to present) and previous reviews (e.g. Ward *et al.* 1994; Bohonak 1999; Dewoody & Avise 2000). Inclusion was restricted to a maximum of two studies per species, and we excluded non-significant mtDNA values owing to the ambiguity associated with differentiating low structure from low locus polymorphism. The majority of estimates were based on allozyme studies (61.5%) with 14.1% mtDNA and 24.5% microsatellite studies. All mitochondrial divergence estimates were corrected for biparental inheritance and diploid gene flow; we observed no significant difference between marker types in terms of the magnitude of differentiation or the associations with life history or geography (see electronic supplementary material). To compare F_{ST} values among multiple species, it is also necessary to account for differences in the scale of geographical sampling that was done using linear regression of genetic differentiation on the maximum distance (D_m) between sampled subpopulations for each study and using the residuals in further analyses (see the electronic supplementary material for further details). We first analysed the entire dataset to explore phylogenetic-based group differences and associations between PLD and genetic structure. Given the prevalence of fish-based studies in both PLD and F_{ST} datasets, we also examined this relationship within the marine fish species for which PLD and F_{ST} data were both available ($n=30$). Similarly, following a general analysis that included all taxa, we examined associations among dispersal correlates and life history and habitat using only the database of marine fishes.

(c) *Dispersal in marine fishes: associations with latitude, body size and depth*

We determined latitudinal ranges, maximum depth of occurrence and maximum body size for each species of fish that we included in the database. To determine the latitudinal distribution for each species, we used distribution data (maximum latitude and latitudinal range) reported in the FAO Fisheries Global Information System (<http://www.fao.org>) or FishBase (www.fishbase.org) online databases. We also collated maximum body size and depth of occurrence data for each species. Species means or maxima are presented assuming that individual studies are broadly representative of patterns in that species. Frequency distributions for latitude, body size and depth of occurrence data were examined independently of dispersal, allowing us to determine whether specific geographical, taxonomic or morphological groups are disproportionately represented in correlates of dispersal.

3. RESULTS

(a) *Scales of measurement of dispersal in marine species*

Estimates of dispersal were grouped according to the methodological categories presented above and the results of the literature review are presented below (table A1 in the electronic supplementary material). The overall average dispersal estimate was 39.8 km per generation and 54% homing or recaptures when tagging and recovery were made at a single common location. However, approximately 44% of estimates were based primarily on algae, ascidians or coral species, which are all taxa that are characterized by comparatively limited dispersal. Of the

fish species studied, most fall into the categories of reef fish with demersal eggs, or rockfish species with ovoviparous development. The average latitude of published studies was between 20 and 30°. In the relatively high-dispersal species examined, approaches were generally restricted to either single-point estimates (i.e. Eulerian) or broader surveys based on long-term genetic analysis. Most of the Eulerian studies had recovery locations that were limited to a single reef, in which case the dispersal kernel was unresolved and little was revealed regarding broad-scale connectivity among habitats. By contrast, genetic studies usually encompassed large geographical areas, many of which were at moderate latitudes, and while model-based approaches such as Rousset (1997) or Palumbi (2003) allow estimation of the mean dispersal distance, they provide no information regarding the shape of the kernel. Further details are provided in the electronic supplementary material.

(b) Correlates of dispersal: genetic differentiation and PLD

Planktonic durations were examined for 392 marine species (tables A2 and A3 in the electronic supplementary material) with group sample sizes varying from less than 20 species for most invertebrate groups to 256 species for marine fishes. On average, durations were less than 50–100 days although some estimates were as much as 270 days. Similarly, F_{ST} values for 246 marine species, 83 invertebrate species (table A4 in the electronic supplementary material) and 163 fish species (table A5 in the electronic supplementary material) were primarily between 0 and 0.05, although a significant portion of values ranged as high as 0.4. No significant difference was observed among groups in the application of the various genetic markers ($p=0.422$). We observed significant differences in both genetic differentiation ($p<0.001$) and pelagic larval duration ($p<0.001$) among taxonomic groups (figure 1). Minimum PLD values were observed in macroalgae/marine plants, sponges and corals. Group maximum PLD values were observed in crustaceans, echinoderms and fish species (figure 1a). Maximum standardized F_{ST} values (indicative of limited gene dispersal) were observed in macroalgae/marine plants, sponges and polychaetes, while group minimum values included cnidarians, molluscs and fish species (figure 1b). The relationship between PLD and F_{ST} means ($p=0.15$, $R^2=0.15$; figure 1c) was not significant but suggests a decrease in genetic structure associated with increasing PLD. Within marine fishes, the relationship between F_{ST} and PLD was also not significant ($p=0.361$, $R^2=0.03$) but suggestive of a decline in PLD with F_{ST} .

(c) Marine fishes: latitude, body size and depth

Within marine fish species, significant trends in predominant egg type were observed with both F_{ST} and PLD (figure 2). The percentage of species with demersal eggs was negatively associated with PLD ($R^2=0.80$, $p<0.001$; figure 2a) and positively associated with F_{ST} ($R^2=0.74$, $p<0.001$; figure 2b). Furthermore, PLD was positively associated with all explanatory variables (i.e. latitude, size and depth; figure 3). Using a stepwise backward multiple regression, the best model included latitude and depth ($p<0.001$, $R^2=0.36$) compared with either variable (depth or latitude) independently ($p<0.001$, $R^2=0.19$

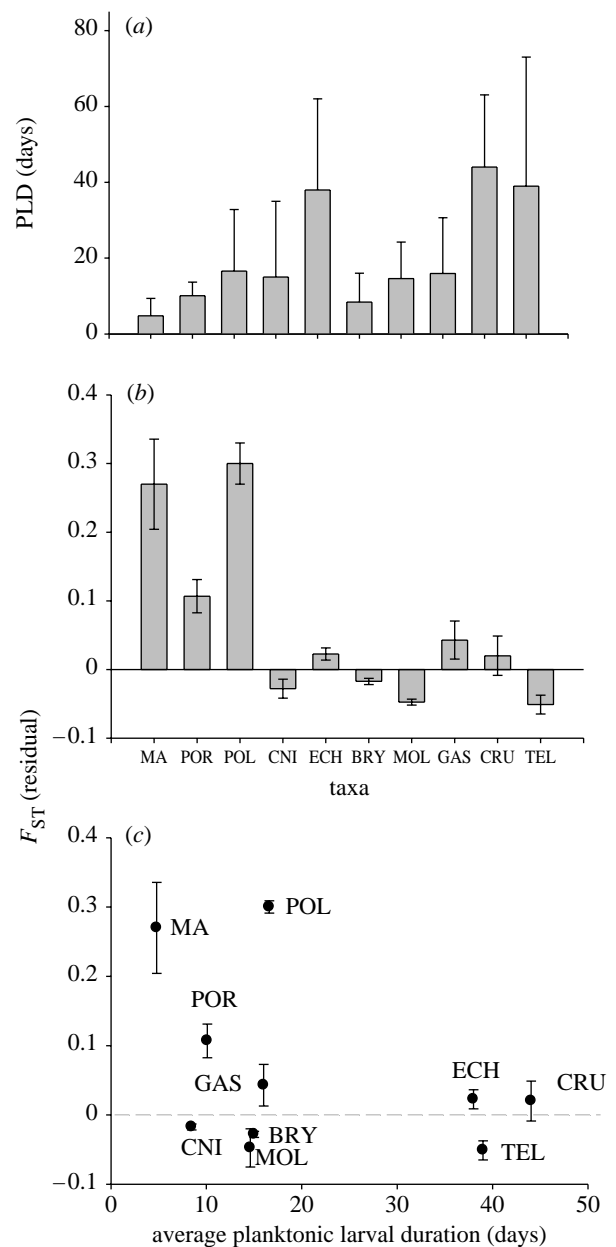


Figure 1. Taxonomic differences in (a) PLD, (b) standardized F_{ST} and (c) the relationship between planktonic period and genetic distance for marine organisms. MA, macroalgae and sea grasses; POR, porifera; ECH, echinoderms; POL, polychaetes; CNI, cnidarians; MOL, molluscs (bivalve); BRY, bryozoans; GAS, gastropods; CRU, crustaceans and TEL, teleosts.

and $p<0.001$, $R^2=0.30$, respectively; table A6 in the electronic supplementary material). Standardized F_{ST} was negatively associated with all explanatory variables (figure 4). The best fit was achieved by including latitude and size ($p<0.001$, $R^2=0.27$) compared with either size ($p<0.001$, $R^2=0.22$) or latitude ($p<0.001$, $R^2=0.17$) alone (table A6 in the electronic supplementary material). Similarly, analysis at the family level indicates that these trends are robust to concerns that overrepresentation of a few families or species might bias these relationships (figures 3 and 4; table A7 in the electronic supplementary material). Frequency distributions of dispersal correlates suggest a tendency for studies to focus on small-sized shallow tropical species with the notable exception of significant numbers of genetic studies at high latitudes

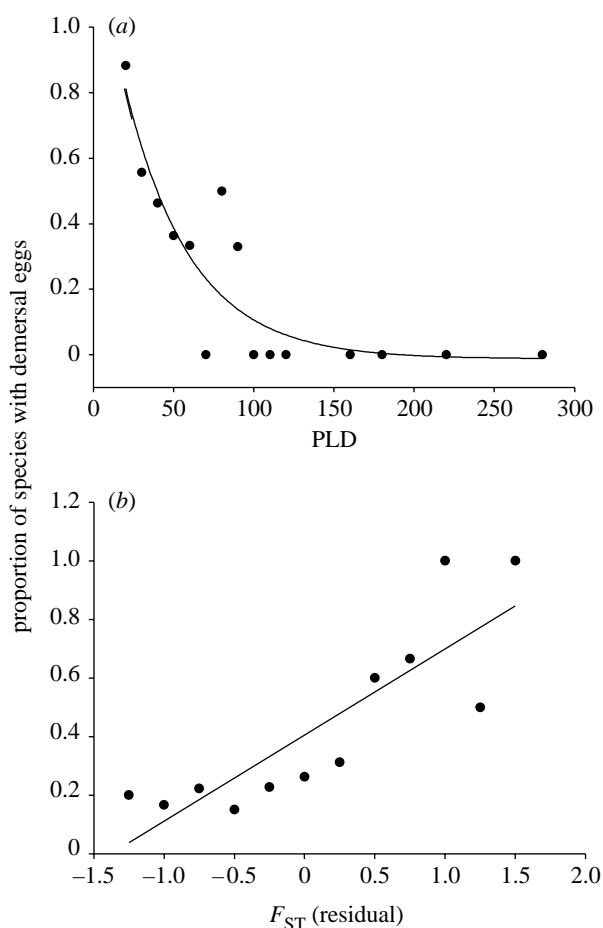


Figure 2. Association between the proportion of demersal egg species (solid circles) and (a) PLD ($R^2=0.80$; $p<0.0001$) or (b) genetic differentiation (F_{ST}) for marine fishes ($R^2=0.74$; $p<0.0001$).

(figure A1 in the electronic supplementary material). Although potential biases may exist as a result of differences in marker usage and differing levels of heterozygosity, we observed no association between the usage of marker types and latitude ($p=0.157$). Moreover, similar associations were observed within each of the three markers used (i.e. allozyme, mtDNA and microsatellites) with marker-specific slopes ranging from 0.0084 to 0.013, and all relationships were significant at $\alpha=0.05$.

4. DISCUSSION

Dispersal and connectivity in marine species are primary determinants of the evolutionary stability, spatial distribution and persistence of species and communities (Sinclair 1988; Lester & Ruttenberg 2005; Hastings & Botsford 2006). Our review suggests that current estimates of dispersal in marine species are overrepresented by studies on low-dispersal taxa in low-latitude environments, suggesting that long-distance marine dispersal is difficult to infer from them. Our use of correlates of dispersal, though admittedly less precise than actual measures, provides context and supports our assertion that current dispersal measures are not broadly applicable to other taxa or geographical regions. We build on previous work that suggests marine taxa differ in both dispersal potential and genetic differentiation (e.g. Kinlan & Gaines 2003), and we identify large-scale associations with geography and life history in marine fishes. We therefore

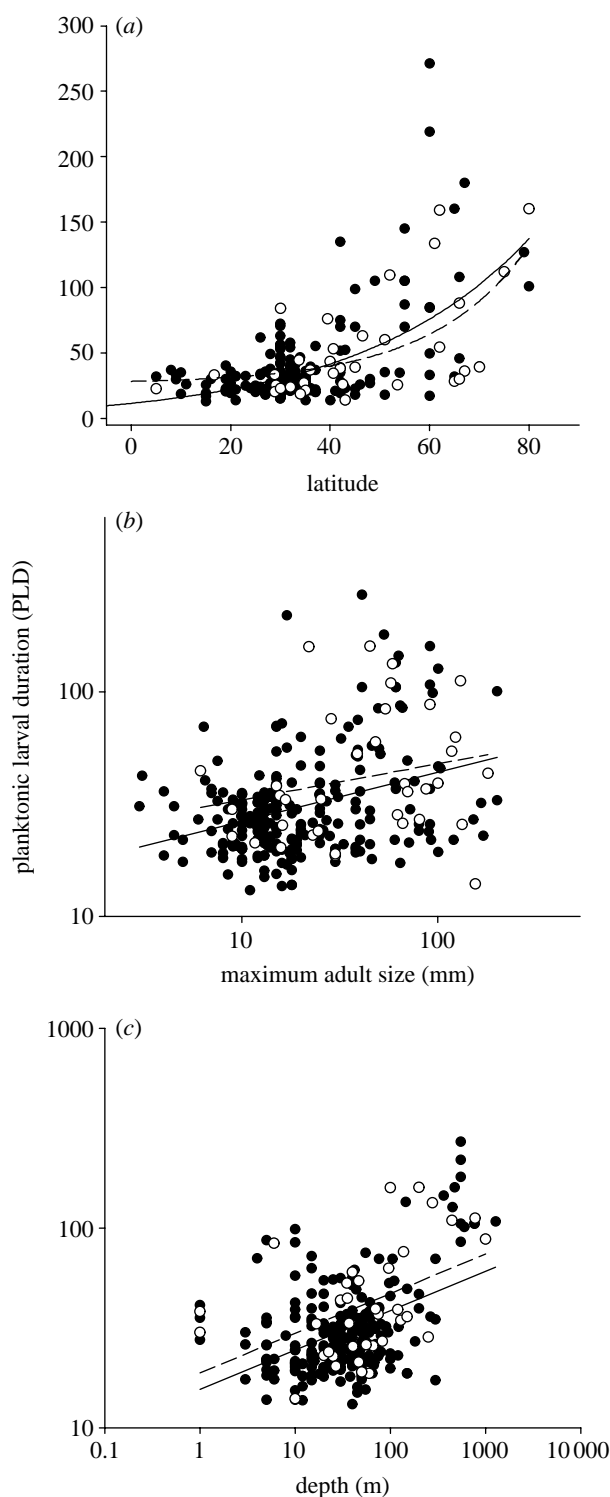


Figure 3. PLD for 254 species of marine fishes associated with species maximum values of (a) latitude, (b) size and (c) depth. Closed circles and solid lines represent individual species while open circles and dashed lines represent family averages.

suggest that extrapolation from the sparse, existing dispersal estimates to other taxa, regions and life histories is at best inaccurate and at worst may undermine conservation efforts for more broadly dispersing species such as those that dominate temperate environments.

Our review of dispersal estimates suggests large variation in the spatial scales of measurements that are probably associated with the limitations and assumptions of specific methodologies. For all methodologies, we observe a consistent tendency for studies to focus on

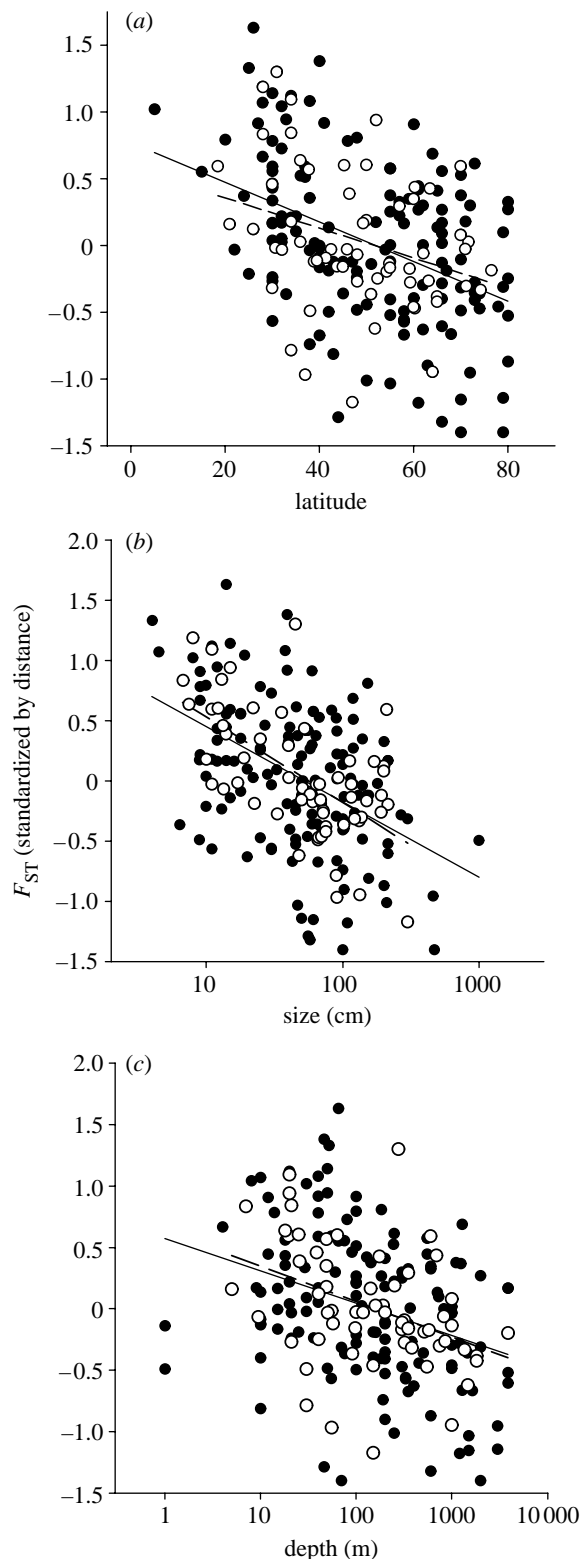


Figure 4. Standardized F_{ST} for 163 species of marine fishes associated with species maximum values of (a) latitude, (b) size and (c) depth. Closed circles and solid lines represent individual species and regression analysis, respectively, whereas open circles and dashed lines represent family averages.

species that either inhabit low latitudes and/or are characterized by low-dispersal potential. Undoubtedly, this focus on low-dispersal taxa may reflect the elevated concern in recent years for coral reef habitats as vulnerable biodiversity hot spots (Sale *et al.* 2005). Nonetheless, coincident with this increased interest in low-dispersal

taxa is a paradigm shift in marine science where scientists have recognized that marine populations are more closed than previously thought (Levin 2006). The degree to which contemporary views of marine dispersal have been influenced by the skewed subset of species for which dispersal estimates exist undoubtedly requires further evaluation. The large differences in dispersal among taxa are supported by the dispersal correlates (e.g. PLD or genetic differentiation) that indicate large heterogeneity among groups in dispersal, as indicated by previous studies (e.g. Kinlan & Gaines 2003).

Our data suggest that egg type (pelagic versus demersal) is highly correlated with dispersal in marine fish species. The significant correlation between egg type and PLD suggests that species with demersal eggs have shorter planktonic larval periods than species with pelagic eggs. The reduced PLD in species with demersal eggs compounds an already reduced dispersal potential associated with the absence of a pelagic egg stage. As predicted by reduced dispersal potential in species with demersal eggs, we observed a positive association between the prevalence of demersal eggs and genetic structure.

The trends we have shown in PLD of marine fishes indicate that longer PLDs are associated with increased latitude and greater depth distribution. The most likely mechanism for this pattern is temperature-dependent development, where development rates in marine species are directly tied to ambient water temperatures (e.g. Hoegh-Guldberg & Pearse 1995). Indeed, when latitude is converted to annual mean temperature (e.g. Reynolds *et al.* 2002), both F_{ST} ($p < 0.001$, $R^2 = 0.17$) and PLD ($p < 0.001$, $R^2 = 0.31$) display significant associations with temperature. Temperature-dependent effects on marine connectivity have been suggested at both inter- and intraspecific levels. O'Connor *et al.* (2007) hypothesize that temperature-dependent larval development may result in large-scale trends in marine connectivity and suggest that the temperature-associated increases in dispersal between the tropics and high latitudes may be as much as an order of magnitude. This pattern is consistent with the latitudinal patterns presented here for both PLD and genetic differentiation. Admittedly, longer larval duration and the presence of a pelagic egg stage may not necessarily translate into dispersal potential. Mortality may limit the survival of dispersers (Cowen *et al.* 2000) and may be an important source of variation. This explanation may also explain why we did not observe a significant association between PLD and genetic divergence in either the group-based analysis or within marine fishes, in contrast to some previous authors (e.g. Riginos & Victor 2001; Shanks *et al.* 2003).

The broad-scale trends we observed in genetic differentiation corroborate predictions based on dispersal potential (PLD) made here and elsewhere (e.g. O'Connor *et al.* 2007). The increase in genetic homogeneity associated with increased latitude supports a hypothesis of increased dispersal in temperate species and a link between PLD and genetic structure in marine species (e.g. Bohonak 1999; Palumbi 2004). Nonetheless, genetic differentiation may reflect vicariant history, equilibrium status or natural selection on the specific markers used (e.g. Bradbury & Bentzen 2007). However, empirical studies have been unable to link genetic structure or equilibrium status to time since colonization and instead

suggest that, in the majority of cases, spatial genetic pattern represents dispersal (e.g. Bohonak 1999; Crispo & Hendry 2005; Bradbury & Bentzen 2007).

Interestingly, in contrast to the analysis of pelagic larval duration, adult size explained most of the variation in the F_{ST} regression (table A6 in the electronic supplementary material). The allometry of dispersal has been documented in many terrestrial and marine species (e.g. Sutherland *et al.* 2000; Jenkins *et al.* 2007) where lifetime dispersal potential has been related to maximum body size. Jenkins *et al.* (2007) observed a clear dichotomy between passive and active dispersers where active dispersers displayed a dispersal allometry and passive dispersers did not. We observed a similar trend here in that PLD was most strongly associated with depth and latitude, yet genetic differentiation was associated with body size and latitude. We hypothesize that the associations between adult size and genetic structure support a hypothesis of large-scale non-passive dispersal in marine organisms. Alternatively, an increase in the prevalence of brooding and small adult body size over evolutionary time has been commonly observed in many invertebrate taxa (e.g. Strathmann & Strathmann 1982; Hess 1993); as fecundity increases with body size, the ability to ventilate a brood decreases (Levin & Bridges 1995). It is unclear to what degree similar physiological constraints may be acting in marine fish species and how these constraints may interact with active contributions to regulate dispersal potential, but this idea warrants further examination.

In summary, our review suggests that the current state of understanding regarding connectivity and dispersal in marine systems is insufficient and that contemporary estimates of dispersal have focused primarily on low-dispersal taxa. If broadly applied, predictions of short-distance dispersal and local recruitment could have implications for spatial management tools such as marine protected areas and inadvertently select against high-dispersal species and individuals, which disperse beyond reserve boundaries. One obvious and compelling example of this possibility are species of large high-latitude marine fishes that are characterized by high dispersal and are presently of great interest from a conservation perspective (Hutchings & Baum 2005; Laurel & Bradbury 2006; Bradbury *et al.* 2008). The broad-scale trends in dispersal observed here provide a first step towards accounting for species and life-history differences in dispersal. As depletion of marine communities and resources continue, the success of conservation efforts (e.g. Hutchings 2000) will depend in part on the connectivity of these ecosystems and a clear understanding of them.

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