Does fish larval dispersal differ between high and low latitudes?


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SUMMARY

Several factors lead to expectations that the scale of larval dispersal and population connectivity of marine animals differs with latitude. We examine this expectation for demersal shorefishes, including relevant mechanisms, assumptions, and evidence. We explore latitudinal differences in: 1) biological (e.g., species composition, spawning mode, pelagic larval duration (PLD)), 2) physical (e.g., water movement, habitat fragmentation), and 3) biophysical factors (primarily temperature, which could strongly affect development, swimming ability, or feeding). Latitudinal differences exist in taxonomic composition, habitat fragmentation, temperature, and larval swimming, and each could influence larval dispersal. Nevertheless, clear evidence for latitudinal differences in larval dispersal at the level of broad faunas is lacking. For example, PLD is strongly influenced by taxon, habitat, and geographic region, but no independent latitudinal trend is present in published PLD values. Any trends in larval dispersal may be obscured by a lack of appropriate information, or use of ‘off the shelf’ information that is biased with regard to the species assemblages in areas of concern. Biases may also be introduced from latitudinal differences in taxa or spawning modes, as well as limited latitudinal sampling. We suggest research to make progress on the question of latitudinal trends in larval dispersal.

Key Words: population connectivity, larval dispersal, pelagic larval duration, larval behaviour, genetic structure, habitat fragmentation
INTRODUCTION

Most bottom-associated (demersal) marine animals, including fishes, spend part of their early life as larvae in open, pelagic waters before settling into a demersal life style. Pelagic larvae are subject to dispersal, and this has profound consequences for distributions, demography, genetic connectivity, and management. Several factors lead to expectations that the scale and processes of larval dispersal and population connectivity\(^1\) of marine animals differ with latitude. These include contrasts in species composition and community structure, temperature influences on physiology and development, and differences in physical ocean processes.

Conclusions that larval dispersal, population connectivity, or a proxy thereof, differ latitudinally have been reached by influential studies, and in each case the conclusion was that dispersal takes place over wider scales in higher latitudes. Houde [1] concluded that pelagic larval duration (PLD) is inversely associated with temperature and that fish larvae in warm seas are also more likely to starve than those in cold seas. These conclusions imply more limited larval dispersal in warm waters, because shorter PLDs are conventionally considered to lead to shorter dispersal distances (but see below), and higher mortality due to starvation should reduce effective dispersal distances [2]. Based on published studies of the influence of temperature on PLD in a range of marine taxa, O'Connor et al. [3] concluded that "maximum predicted dispersal distances for larvae in colder water are much greater than those in warmer water", and "population connectivity and effective population size should, in general, be inversely related to ocean temperature". Similarly, Bradbury et al. [4], using published genetic and PLD data, concluded that dispersal

\(^{1}\) For the purposes of this paper, larval dispersal describes the two-dimensional distribution of larval settlement originating from a single source population. Connectivity describes the source-destination matrix of settlers to a series of subpopulations that comprise a metapopulation connected through larval dispersal. Both terms can be spatially explicit, and are linked: short average larval dispersal distances should lead to spatially smaller metapopulations (or connectivity networks).
distance increases with latitude: for 163 marine fish species there were significant associations between maximum latitude, body size, and genetic structure ($F_{ST}$). Although body size explained the most variation, this analysis revealed weaker genetic structure at latitudes above 40°, with the largest differences at the extremes of latitude (e.g., 20° vs. 60° latitude). Further, research using genetic parentage and otolith microchemistry techniques in warmer waters [5] has documented dispersal in larval reef fishes over much smaller scales than have been reported from temperate waters, leading to a perception that dispersal distance is correlated with latitude. Despite these perceptions, clear examples of latitudinal differences in larval dispersal or connectivity are rare.

This review is not a meta-analysis of past work investigating temperate-tropical differences in larval dispersal: such work does not exist. Instead, the intent of this review is to examine the hypothesis of latitudinal differences in larval-fish dispersal distance, the mechanisms and assumptions underlying the hypothesis, and evidence (including commonly-used proxies for larval dispersal) bearing upon it, to determine if it is supported. We also suggest research that will be useful in testing hypotheses of latitudinal differences in larval dispersal.

Why is it important to know if there are latitudinal differences in dispersal? Knowledge of the spatial scale of larval dispersal in marine species, a major contributor to both evolutionarily and ecologically significant population connectivity, is critical to understanding community processes ranging from biogeography to population demography, to management of fisheries, and to biodiversity conservation. For example, space-based management of coastal oceans, including no-take marine reserves, is being implemented widely, and such management relies
on knowing the extent and patterns of connectivity [6],[7]. We know little about the fate of the increased reproduction that typically occurs inside marine reserves. This question is critical, because it addresses both the service function of reserves (e.g., export of larvae to fished areas) and the design of reserves (e.g., conservation networks connected through larval exchange, [8],[9],[10]). At present, the suggestion that connectivity among marine populations might vary geographically remains untested, thus hampering the ability of managers to apply general criteria to local problems. There is often disagreement about whether evidence gathered from one geographic area (for example, temperate coastal waters) is applicable to other geographically distinct areas (such as coral reefs).

Our focus here is on the dispersal distance of the pelagic egg and larval stage prior to settlement in demersal marine shorefishes (i.e., teleosts, the adults of which live on or near the bottom at depths <100 m). Because these species are relatively site-attached as adults, adult movement is unlikely to contribute greatly to either genetic or demographic connectivity. Even with this limited focus, many factors influence dispersal and connectivity, and the distance travelled is the result of biophysical processes involving hydrodynamics, as well as species-specific aspects of mortality, swimming, settlement behaviour, and PLD. Although post-settlement processes modify connectivity established by movement during the pre-settlement larval phase, these are beyond the scope of the present review. Note, however, that studies estimating dispersal or connectivity from settled populations (e.g., most genetic work) include influences from both larval supply and post-settlement processes, and must be interpreted with this in mind (see Supplement). It is possible that the extent to which population connectivity is maintained by pre-settlement vs. post-settlement
processes varies latitudinally (T.J. Miller, pers. com.). Even if this is true, it is appropriate to focus on the role that larval dispersal plays, as we do here.

For clarity, we divide this review into three general classes of factors that might lead to latitudinal differences in dispersal:

1. Biological differences: latitudinal differences in species composition and associated characteristics (especially spawning mode and PLD) that could affect dispersal;

2. Physical differences: latitudinal differences in water movement and habitat fragmentation that could independently affect dispersal, regardless of the underlying species composition;

3. Biophysical differences: latitudinal differences in physical factors (principally temperature) that could strongly affect biological processes (such as development, swimming ability, and feeding), that can in turn affect dispersal.

Due to space limitations, we present details of analyses in the Supplement, and confine ourselves here to overviews of results, discussion of the implications of those results, and recommendations for future research.
1. BIOLOGICAL DIFFERENCES

(a) Taxonomy and biogeography

Taxonomic composition of demersal teleost shorefishes differs with latitude at all taxonomic levels, and different Orders or Suborders dominate at different latitudes (see Supplement for details). In tropical Hawaii, eastern Pacific, and Cuba, Anguilliformes, holocentroid Beryciformes, Tetraodontiformes, and perciform suborders Percoidei, Blennioidei, Gobiodei, Labroidei, and Acanthuroidei constitute 73-84% of the 430-700 demersal shorefish species. In contrast, in cold waters of northwestern Atlantic, northeastern Pacific and Antarctic, Gadiformes, perciform suborders Zoarcoidei and Notothenoidei, and scorpaeniform suborders Cottoidei and Hexagrammoidei and scorpaenid genus *Sebastes* constitute 73 to over 90% of the 55-198 species. To the extent that different taxa have different dispersal characteristics, apparent geographic differences in dispersal may simply reflect differences in faunal composition rather than differences in environments. To date, comprehensive information about taxon-specific dispersal differences is lacking, and given the non-independence of taxa and geographic distributions, it will be challenging to separate location-dependent physical and biological conditions from lineage-related factors.

(b) Taxonomy and pelagic larval duration

Longer dispersal distances are often assumed to arise from longer PLDs (e.g., [11], but see below for evaluation of this assumption). Aside from marine eels (mean PLD>100 days), available PLD data (see Supplement for sources and details) indicate that the Orders and Suborders dominating warm waters have shorter mean PLD values (23-52 days) than do taxa dominating cold waters (55-108 days: Supplement figure Sup1). The generality of latitudinal trends in PLD is questionable.
because these PLD values were based only on nine Orders or Suborders from warm waters and four from cold waters. There are also possible biases due to habitats sampled – tropical data come mainly from shallow reefs, whereas temperate data come from a wider range of habitats (see Supplement discussion).

(c) Spawning mode

Spawning mode (in this case, demersal eggs vs. broadcast spawning with pelagic eggs) could have a strong effect on dispersal distance ([4],[12]). The pre-hatching period of pelagic eggs potentially increases dispersal distance, particularly in colder waters, where such periods can be weeks long [13]. This period of drift is rarely included in estimates of PLD, and it does not occur in live-bearing species or most species with demersal eggs. Further, larvae of most taxa from demersal eggs begin their pelagic larval life larger and in a more developed state than those from pelagic eggs, and the earlier acquisition of swimming ability might enable these larvae to behaviourally limit dispersal [14]. Clear latitudinal differences in spawning mode exist among taxa. In warmer locations, 60 to 80% of demersal shorefish species have pelagic eggs, whereas in colder locations (i.e., >50° latitude), only 15-27% of demersal species have pelagic eggs (based on faunal lists and taxon-specific spawning modes, see Supplement, figure Sup 2, and Table Sup 1). Further, in most regions, larvae from demersal eggs have shorter PLDs than those from pelagic eggs (see Supplement and section 3(c), on PLD, also [4]). Spawning mode has a strong taxonomic component, with spawning modes being mostly consistent within a family. Exceptions exist, however, and in these, the trend is for taxa from higher latitudes to shift away from broadcast spawning (Supplement). This trend toward demersal eggs in cold waters may have implications for larval dispersal and connectivity, and
highlights the need to account for spawning-mode differences in comparisons across regions.

2. PHYSICAL DIFFERENCES

(a) Oceanography

Latitudinal gradients in seasonality, temperature, mixed layer depth (MLD), wind, and Coriolis force may potentially result in latitudinal differences in dispersal of fish larvae. The effects of physical oceanographic processes on latitudinal patterns in larval dispersal are not well discussed in the literature, and are included in few explicit, published hypotheses. Therefore, in the Supplement we develop hypotheses about how some aspects of physical oceanography might influence latitudinal patterns of larval dispersal.

Water movement itself varies with latitude, in part due to changes in Coriolis force. For example, Ekman coastal upwelling should be least important at low latitudes, perhaps leading to less upwelling-cell retention in the tropics (see Supplement). However, more energetic eddies should form at higher latitudes, and these can either advect larvae from their source, or retain them nearby, resulting in more variable larval dispersal. If the mixed layer depth (MLD) is shallow, larvae may be able to vertically migrate into slower-moving water below the MLD and thereby retard dispersal. Although MLD is more stable in the tropics, it may be shallower seasonally at higher latitudes, leading to differences in larval dispersal if the MLD interacts with vertical movement of larvae as outlined.

There are clear latitudinal differences in many variables that drive coastal circulation, but equally, there are large within-latitude regional and local differences in circulation
due to topography, coastal orientation, differences in tidal regimes, river input, and a variety of other factors [15]. Although certain latitudinal trends are expected, within-latitude spatial variation may frequently override those trends, thus obscuring them (see Supplement discussion).

(b) Habitat fragmentation

For demersal fishes with some degree of habitat association, the strength of population connections should depend not only on spatial scales of larval dispersal, but also on the scales of patchiness of benthic habitat: clearly, larvae cannot settle successfully where there is no suitable habitat, so patchiness of habitat has a direct influence on dispersal distance [16]. At coarser scales, benthic habitats for nearshore demersal species are largely determined by the spatial distribution of coastlines, found either along continental margins or around islands. Continental margins have large areas of continuous nearshore habitat whereas islands are more isolated, with the degree of isolation depending on geographic and oceanographic distances to nearby islands or continents [17]. At finer scales, particular benthic habitats are often patchily distributed. Dispersal among patches becomes less likely as distance between suitable habitat patches increases [2].

Habitat patchiness appears to affect the scale of dispersal. A review of recent literature estimating demographic connectivity (see Supplement) shows that self-recruitment (i.e., larvae settling into the same area where they were spawned) is higher along continental coastlines compared to islands (figure 1A), but this is strongly affected by the spatial scale of the study (nearly an order of magnitude larger in continuous continental coastlines compared to patchy habitats and islands, figure 1B). Controlling for spatial extent of the study, the mean scales of connectivity
differ among contexts, with species in patchy habitats dispersing about 60 to 100 km, whereas species in continuous habitats dispersed about 900 km (figure 1C).

Combined, these data suggest that larval dispersal may be more restricted in fragmented habitats.

If habitat patchiness differs between tropical and temperate systems, then landscape context could affect dispersal. In fact, islands more than 5 km apart are 2-3 times more abundant in the tropics than in higher latitudes (figure 2; see Supplement), and this is expected to lead to more fragmented populations and shorter successful dispersal distances in tropical habitats. The degree of geographical isolation of habitat patches, however, may not be a consistent predictor of the likelihood of connectivity: oceanographic barriers (rather than simple distance, [18],[19],[20]) or larval behaviour may modify the effect of habitat fragmentation ([21],[22],[23], see Supplement).

3. BIOPHYSICAL DIFFERENCES

Many variables scale with latitude including Coriolis force, seasonality, and day length, but, the most obvious and important is temperature. Many of the factors considered in this review are temperature related rather than latitude related per se, but other associated factors are also important.

(a) Temperature and larval swimming

The expectation that behaviour of larvae may influence the scale of larval dispersal is based on research in three areas. First, many studies show that vertical distribution behaviour by larvae indirectly influences dispersal [14]. Second, swimming and sensory abilities of marine fish larvae are better than previously
realized [14, 23]: larvae of many species are able to swim directionally and at high speeds in the sea [22], which implies the ability to influence dispersal outcomes. Third, larval dispersal distances can be shorter than expected from a simple combination of advection, diffusion, and PLD [5, 24],[8]. Combined with the growing perception that passive drift of larvae with currents could not account for this small scale (e.g. [25, 26]), these lines of evidence have led many to presume that behaviour by larvae may restrain dispersal.

Larval swimming is expected to be constrained by temperature due to hydrodynamic and physiological influences. For small larvae, the higher viscosity of colder water requires more swimming effort than warmer water [27], and speed is more strongly affected by viscosity than by temperature [28]. In larger larvae, effects of viscosity are reduced, but colder water should reduce metabolic rates and inhibit the motor activity required for fast swimming [27]. There is mixed support for these expectations: in the laboratory, larvae of some, but not all, species do swim faster at higher temperatures (see Supplement).

Latitudinal comparisons of swimming performance of larvae are best made with data from laboratory studies that measure "critical speed" at ambient temperatures [22, 29] because more data are available for this metric. At any size, swimming speeds differed little between tropical and warm temperate species, but speeds of cold-water species were only 25 to 50% that of warmer water species, and their ontogenetic increase in speed was slower (details in Supplement). Comparisons of larval-fish behaviour in situ, although hampered by the lack of data from cold temperate waters, give a somewhat different picture [22]. In situ, at any size, larvae of warm-temperate
species were 4–10 cm s\(^{-1}\) slower than tropical species, and the ratio of in situ speed to lab-based critical speed was larger in tropical than in warm temperate species.

The only clear latitudinal pattern in behaviour of fish larvae is that, adjusted for size, tropical and warm temperate species have similar critical speeds, and these are greater than speeds of cold temperate species. However, tropical larvae may swim faster in the sea than warm temperate species (Supplement). The limited evidence indicates that larvae in warm water environments swim faster and earlier in development, and this implies that larvae in lower latitudes should have more control over their dispersal. If behavioural abilities are used to restrict advection or to find settlement habitat from greater distances, they could decrease the spatial scale of larval dispersal, a possibility supported by dispersal modelling [30], but not tested in the ocean. If so, dispersal distances in warmer waters should be smaller.

(b) Temperature, feeding, and mortality

The perception exists that greater oligotrophy and higher temperatures in lower latitudes should result in more starvation of larvae [1],[31], which if true could influence larval dispersal by slowing growth or increasing mortality (see Supplement). Prey densities and feeding success may play a critical role in survival of pelagic larvae of marine fishes, and these factors can affect the degree to which subpopulations are connected via larval dispersal. This is because the numbers of larvae reaching any location - which affects the spatial extent of larval dispersal [15] - should be inversely related to mortality. If, however, larvae do not starve, but survive in poor condition, they may become more buoyant, and become concentrated near the surface [32]. In this case, passive larvae might be dispersed over greater distances because surface water typically moves faster than deeper water. If
feeding conditions in tropical waters are indeed poorer, one might expect increased dispersal in warmer water.

Are larvae in the tropics subject to poorer feeding conditions or greater mortality from starvation? Recent literature syntheses identified latitudinal differences feeding incidence, prey types, prey selectivity, and niche partitioning of fish larvae [33], [34]. Feeding rates are greater in the tropics Lop, and fish larvae in low and high latitudes appear similarly successful at feeding (see Supplement), contrary to expectations. However, empirical estimates of starvation mortality are very limited [35] [36], and none exist for tropical demersal species. Differences in the feeding ecologies of larval fishes between low and high latitudes are present, but little empirical evidence suggests that they result in latitudinal distinctions in dispersal or systematic geographic patterns in mortality (see Supplement).

(c) Temperature, development, and PLD

Based solely on temperature-driven variation in physiological processes, larvae of tropical species are hypothesized to have reduced potential for dispersal due to faster development times and shorter PLD than temperate species (e.g., [27],[3],[37]). To test the expectation that PLD would be shorter in low latitudes, we examined PLD data for differences among latitudes (see Supplement for details).

Surprisingly, regional differences in PLDs appear to be larger than differences between warm temperate and tropical sites (figure 3). These analyses, although attempting to control for habitat, reproductive mode, and region, are still confounded by taxonomic influences (see Supplement). Therefore, for the nearshore demersal species for which PLD data are available, the expectation that warm temperate PLDs
were longer than tropical PLDs was not fulfilled. More comprehensive coverage of taxa and high-latitude PLD data are needed to relate PLD to latitude or temperature definitively. Finally, the relationships between PLD and other proxies for dispersal (such as genetic structure or species range) are not compelling (see Supplement).

**DISCUSSION**

The widespread view that larval dispersal and the spatial scale of population connectivity of marine fish populations differ with latitude is very plausible when theoretical considerations alone are considered. Based on either limited empirical data or these same theoretical considerations, several authors have concluded that larval dispersal likely takes place over larger scales in higher latitudes. We find only partial empirical support for this view, and the existing support is based primarily on differences in spawning mode and larval-fish behaviour between tropical and warm temperate regions vs. cold temperate regions, and on habitat-fragmentation considerations.

*Biological differences:* Existing evidence indicates that species with demersal eggs have smaller scales of genetic connectivity and generally shorter PLDs than broadcast spawners, both of which are commonly assumed to be proxies for larval dispersal distance (but see above and the Supplement for a critical evaluation of the relationship between genetics, PLD, and actual dispersal distance). Most high-latitude demersal shorefish taxa are not broadcast spawners, and this should reduce the average scale of larval dispersal at high latitudes. At low to mid latitudes, most species are broadcast spawners, and this should increase the average scale of larval dispersal. This is contrary to the inferences drawn from habitat fragmentation data, some oceanographic variables, and the influence of temperature on physiology.
and behaviour. Regional differences in many factors that influence larval dispersal do exist, but the ultimate net effect of these contrasting factors on larval dispersal is far from clear: direct measures of dispersal across large geographic regions are required.

Putative latitudinal differences in spawning mode, PLD, and genetic structure have been confounded by the use of data from non-representative subsets of the resident nearshore demersal fishes, biased toward pelagic spawners at high latitudes and demersal spawners at lower latitudes. However, high-latitude demersal fish assemblages are actually dominated by demersal-spawning species whereas pelagic spawners dominate warm temperate and tropical fish assemblages. Care must be taken to ensure that questions are framed and conclusions are qualified with full regard to the mix of species for which data exist.

**Physical differences:** In contrast to the biological and biophysical variables reviewed here, physical oceanographic variables have featured in few explicit hypotheses of latitudinal differences in larval dispersal. Although we develop several physical-oceanographic-based hypotheses in the Supplement, there is little relevant information available to test them. Water movement, the strength of upwelling and the mixed layer depth are factors that differ latitudinally and are likely to affect the horizontal and vertical movements of larvae. Although factors affecting coastal circulation may vary over degrees of latitude, local and regional variation can also be large. Therefore, it will be difficult to determine how and to what extent physical factors may vary with latitude in their influence on larval dispersal.
Dispersal can also be affected by the frequency and spacing of suitable settlement targets, especially islands. Island habitat relative to continuous continental habitat changes along a latitudinal gradient, with more island habitat in the tropics. Thus it is possible that tropical fishes restricted to discontinuous habitat may have shorter dispersal distances than their temperate counterparts, although empirical evidence for this is lacking.

*Biophysical differences:* Tropical waters are warmer, and it is commonly assumed this will increase development rates: more rapid development should shorten both the pre-hatching period of pelagic eggs and PLD, and hence, it is assumed, dispersal distances. Unfortunately, the correlation between PLD and dispersal distance is weak at best in the species for which there are sufficient data for testing, and data suggesting shorter PLDs in the tropics are also subject to bias because available PLD data are not representative of the taxonomic composition or spawning modes of either tropical or temperate regions. Length of PLD is influenced not only by spawning mode, but also by adult habitat and region within the same latitudinal range, as shown here, even though our analysis is confined to nearshore demersal fishes at latitudes below 50°. Importantly, even within spawning modes, clear differences between tropical and warm temperate areas are lacking. Thus, there is no simple relationship between water temperature (or latitude) and PLD, and careful partitioning of data is required for valid latitudinal comparisons. Pelagic eggs take longer to hatch in cold water [13], and drift during this time may increase dispersal distances for broadcast spawners at high latitudes.

It is important to note that although there is ample evidence of within-species temperature-dependent responses of physiological processes related to dispersal
and survival, the actual effects in nature might be minimized through adaptation of key traits. Thus, it is unclear whether well-known physiological effects of temperature actually result in geographic variation in dispersal distance or connectivity. Certainly, the strong regional and taxonomic effects on PLD (see above and Supplement) suggest that there is wide scope for adaptation.

Larval behaviour, particularly swimming and feeding, could affect realised dispersal: both strong directed swimming and increased mortality from starvation potentially can shorten average dispersal distances. Although there is some evidence that tropical larvae swim more rapidly than temperate larvae, generalizations are difficult to make, again because of taxonomic differences and limited data from cold temperate species. Further, as with genetic and PLD data, the range of species for which larval behaviour information is available is not representative of either the taxonomic composition or spawning modes of the assemblages from different latitudes. Equally, although there are differences in the feeding ecologies of larval fishes between low and high latitudes, there is little evidence that these differences result in latitudinal distinctions in feeding rates, starvation mortality, or dispersal.

**FUTURE DIRECTIONS**

There is a clear need for more studies of larval dispersal and population connectivity across latitudinal ranges. Measuring these processes empirically remains challenging. Yet, the importance of connectivity to fisheries management, conservation, and predicting climate-driven changes to marine systems, makes a more general understanding of latitudinal and temperature effects timely and valuable.
The various oceanographic factors considered individually here will interact in the ocean, and it is difficult to predict how they will influence dispersal when combined. Biophysical modelling that incorporates many of these oceanographic factors [38] will be helpful in understanding how latitudinal changes in physical variables influence larval dispersal.

Future latitudinal comparisons will need to take into account taxonomic composition, adult habitat, and spawning mode if they are to have generality. Ideally, one would investigate a single species over large latitudinal gradients, but few species qualify. One solution is to compare species across more limited latitudinal ranges such as sub-tropical to tropical areas. In addition, there may be cases where one could control for life history and habitat difference among higher taxonomic groupings such as the Family level.

In addition, the goals for measuring connectivity must be defined clearly because these may alter the impact of any biases. For example, if the goal were fishery management or design of marine protected areas for replenishment of fished populations, a different mix of species might be appropriate to study than if the goal were biodiversity conservation or latitudinal trends in ecosystem processes. Where meta-analysis of previously published data is attempted, care must be taken to qualify interpretation and conclusions when data are biased with regard to species composition or spawning mode. Future examinations of possible latitudinal differences in larval dispersal and population connectivity will need to look beyond published data, and undertake new studies.
We must relate diet and feeding success in larvae to growth, survival, and behaviour in order to understand and model how trophic-related factors ultimately affect larval dispersal and population connectivity. Linking individual-based models of larval growth and mortality to realistic circulation models could facilitate comparisons of tropical and temperate regions [39], although many of the caveats identified here will still apply, and field-testing of model predictions is required.

Currently available estimates of PLD are largely based on few individuals from very limited locations [12]. These studies have also focused on a limited range of taxonomic groups and habitats, which makes broad latitudinal comparisons problematical. It would be valuable to broaden the taxonomic base and habitats for PLD estimates, as well as to obtain better measures of within-species variation in PLD values, especially if PLD varies with location. Most PLD estimates derive from otolith counts, and because otoliths frequently do not begin to form until some time after hatching, particularly in species with pelagic eggs, many PLD values are under-estimates of the true time in the water column. Better PLD estimates might reveal relationships with latitude-based factors that are not apparent with currently available estimates.

The very limited information available on larval behaviour of temperate species is another obstacle to general comparisons among areas. It would be useful to study larvae of the same species from different latitudes within its natural range when considering behaviour or effects of temperature on physiological processes to help determine the scope for adaptation. In addition, such information is needed on a broader range of species and habitats.
At present, most of the available genetic data for high latitudes are from the northern hemisphere (particularly the Atlantic), and are from larger, often pelagic, species that are of commercial interest. More single-species studies examining trends in dispersal and gene flow along latitudinal gradients are needed. Translating the observed genetic patterns into demographic trends remains challenging [40],[41]. Better integration of genetic, demographic, and life history studies will be needed to further disentangle the patterns observed.

Managers are most often interested in direct measures of demographic connectivity [40, 41]. Advances in otolith-based approaches and genetic-parentage approaches are being applied successfully in warmer waters, where the life histories of the fishes make these approaches particularly advantageous. They have been little applied at higher latitudes, but hold great promise.

**CONCLUSIONS**

It is important to emphasize that our conclusions apply to demersal shorefishes, and not necessarily to pelagic fishes or those from deeper waters. It is not clear that latitudinal differences in larval dispersal or associated factors exist at the level of broad faunas; certainly, they have not yet been clearly demonstrated for larvae of demersal shorefishes. This may be due to lack of appropriate data, or the use of ‘off the shelf’ data that are biased with regard to the species assemblages in the areas of concern. Biases may be introduced from both differences in taxa or spawning modes at different latitudes as well as limited latitudinal sampling, and as we move away from ideal study types, the uncertainty increases.
Many factors lead to expectations that larval dispersal should differ latitudinally, and although most suggest broader dispersal at higher latitudes, some do the opposite. Limited evidence is available to evaluate some of these expectations, especially for higher latitudes, and for a broad array of taxa. Some hypotheses of differences are not supported by the evidence that is available on demersal shorefishes. Considerations of this issue have been dominated by untested assumptions, acceptance of logical, yet unsupported assertions, and limited empirical evidence. More research on a broad array of the many factors that influence larval dispersal is required to make progress on this subject.
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JML, JEC and RRW initiated and constructed the manuscript, provided overall editorial direction, and the introduction and conclusions. JML provided sections on taxonomy, biogeography, larval behaviour, and spawning modes. IRB and RDV provided genetics sections. JKL provided feeding sections. TK and CBP provided physical oceanographic sections. MJM provided sections on eels. MIO and SMS provided sections on temperature effects. ALS provided PLD sections with additions from JML. SES and EAT provided habitat fragmentation sections. RRW provided caveats sections. All contributed to future directions section.
Figure Captions

Figure 1. Effects of the degree of habitat patchiness based on an analysis of published otolith chemistry studies on: (A) the % of self-recruitment; (B) the scale at which self-recruitment was measured; and (C) the scale over which populations were connected. Different letters above columns indicate significant pairwise differences based on post-hoc Tukey tests. Continuous refers to relatively continuous habitat on continental margins; coastal habitat patches are saltmarshes, mangroves, seagrass beds or reefs.

Figure 2. Changes in the number of: (a) all island patches and (b) non-continental island patches as a function of latitude. Each relationship was analysed by Pearson correlation. See Supplement for details of analysis.

Figure 3. Average (± 95% confidence interval) pelagic larval durations of temperate (solid squares) and tropical (open squares) reef fishes. A) Data from all geographic locations and spawning modes combined and PLDs of demersal and broadcast spawning species plotted separately. B) Data plotted by geographic region with spawning modes combined. C) Data for demersal spawning species plotted by geographic region. D) Data for broadcast spawning species plotted by geographic region. If 95% confidence intervals overlap, means are not significantly different, but if they do not overlap they are significantly different as confirmed by t-tests.

REFERENCES
Figure 1

A

$\tau = 0.755$
$p < 0.0001$

B

$\tau = 0.810$
$p < 0.0001$
Figure 3

A. All Species: Temperate vs. Tropical

- All Temperate n=110
- All Tropical n=230
- Temperate Demersal Eggs n=68
- Tropical Demersal Eggs n=126
- Temperate Broadcast n=42
- Tropical Broadcast n=104

B. All Species by Region

- Mediterranean n=67
- California Current n=43
- Central Pacific n=134
- W. Atlantic Caribbean n=43
- Eastern Pacific n=53

C. Demersal Spawning Species by Region

- Mediterranean n=38
- California Current n=30
- Central Pacific n=91
- W. Atlantic Caribbean n=18
- Eastern Pacific n=36

D. Broadcast Spawning Species by Region

- Mediterranean n=29
- California Current n=13
- Central Pacific n=43
- W. Atlantic Caribbean n=25
- Eastern Pacific n=36
1. INTRODUCTION

A large number of physical and biological variables that might affect larval dispersal vary with latitude, and many were considered in the present study. Some of these variables might theoretically have an influence, but evidence is lacking; some have been considered in previous studies to have an influence, but lack theoretical or empirical support; and for some, there is support for an influence. This supplement includes background information and analyses for each of the main factors mentioned in the text. For each category, we also provide caveats about underlying assumptions and alternative interpretations. We close with a consideration of bias introduced by differences in methodology or target species.

2. BIOLOGICAL DIFFERENCES

(a). Taxonomic composition, biogeography, PLD, and spawning modes

Taxonomic composition and biogeography: Warm waters are dominated by Anguilliformes, holocentroid Beryciformes, Tetraodontiformes, and the Perciform suborders Percoidei, Blennioidei, Gobioides, Labroidei, and Acanthuroidei. These taxa constitute 73 to 84% of the demersal, teleost shorefish species in the three tropical areas shown in Table Sup 1. In contrast, cold waters are dominated by...
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Gadiformes, Perciform suborders Zoarcoidei and Notothenoidei, and by the Scorpaeniform suborders Cottoidei and Hexagrammoidei and scorpaenid genus *Sebastes*. These taxa constitute 73 to over 90% of the demersal, teleost shorefish species in the three cold-water areas listed in Table Sup 1. Flatfishes (Pleuronectiformes) of most families are essentially warm water in distribution, but Achiropsettidae, Pleuronectidae, and to a lesser extent, Scophthalmidae have colder-water distributions. Unfortunately, there is very little information about taxon-specific dispersal differences, and given the non-independence of taxa and distributions, without this information it will be difficult to determine if any identified differences were due to adaptations to location-dependent physical and biological conditions, or due to lineage-related factors. Therefore, caution is required when attributing causes to any apparent differences in larval dispersal and connectivity between latitudes.

**PLD**: Measurement of PLD (pelagic larval duration) is typically estimated by counting daily rings in otoliths either at settlement or inside a settlement mark [1]. The PLD values used herein were from the published sources detailed below and were culled from this literature only on the basis of adult habitat, and by eliminating pelagic species. Demersal fish Orders and Suborders with primarily warm water distributions (as identified in previous section) appear to have lower mean PLD values than do taxa with primarily cold-water distributions. The PLD data in [2] and [3], which addressed 45 California Current and 727 largely tropical species, respectively, were used to determine mean values at the Ordinal and Subordinal level. These are not necessarily a representative sample of the species belonging to the Orders and Suborders identified as having either primarily warm or cold-water
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distributions above, so these data should be interpreted cautiously. The taxa and
the number of PLD estimates in each are: warm water taxa, Anguilliformes (marine
eels, i.e., not including Anguilla) 4, Holocentroidei 10, Acanthuroidei 81, Blennioidei
20, Gobiodei 36, Percoidei 87, Labroidei (Labridae) 213, Labroidei (Pomacentridae)
265, Scorpaenoidei (Scorpaena) 2, Tetraodontiformes 9; cold water taxa,
Gadiformes 9, Zoarcoidei 6, Cottoidei 13, Scorpaenoidei (Sebastes) 17. The mean
values for each taxon are shown in figure Sup 1. The mean values for each cold-
water taxon (55-108 days) are all larger than the mean values for warm water taxa
(23-52 days), with the exception of non-anguillid Anguilliformes, with mean of 118
days, more than twice that of other warm-water taxa. A challenge to interpretation of
this analysis is that the temperate-tropical comparisons are biased by habitat
differences. At least half of the temperate species in [2] were continental shelf and
slope species whereas nearly all of the tropical species in [3] were from shallow
reefs. Given that Shanks and Eckert [2] found large habitat-related differences in a
number of life history traits (including PLD), ascribing PLD differences to a latitudinal
effect without taking habitat into account is problematical.

Although these data indicate there is a taxonomic component to PLD, it is important
to note that there were more than 727 PLD values for warm-water taxa, and only 45
values for cold-water taxa, providing further reason to treat the data cautiously. The
very high PLD values for the marine eels, a largely warm-water group, are also an
indication that general statements about latitudinal differences in PLD will likely be
difficult to sustain. But here, too, the fact that only four values were available for a
group with about 800 species provides ample reason for caution, and indicates how
understudied marine eels are.
We used an ecological-based definition of PLD (i.e., the early life-history period before settlement [4]), which clearly has meaning only for demersal species with a pelagic larval stage (it may also include juveniles if they remain pelagic, e.g., many Tetraodontiform fishes and the Scorpaeniform genus Sebastes). The use of an ecological criterion avoids ambiguity introduced by morphological criteria (i.e., the early-life history period before a particular set of morphological milestones are reached, for example, formation of all fins, or scales). The latter can be relevant for both demersal and pelagic species, but we avoid it precisely because we focus on the presettlement stages of demersal fishes.

**Spawning mode**: Spawning mode, in particular the lack of a pelagic egg (i.e., demersal eggs, brooded eggs, or viviparity), has been identified as an important factor in genetic connectivity or larval dispersal in two synthetic studies that assessed a broad range of published genetic and PLD data [5],[6]. However, the study of Riginos et al. [5] was based primarily on warm-water species, with only 14 of the 148 demersal teleost species considered to have cold-water distributions. Therefore, the conclusions of [5] about the influence of spawning mode on genetic connectivity may not apply to cold-water taxa. Further, about half of the warm-water species in the Riginos et al. [5] data set spawn demersal eggs, a value considerably higher than the proportion of demersal-spawning species in warm-water faunas (figure Sup 2). Clearly, it is important to understand how spawning mode varies with latitude.
The percentage of species with pelagic eggs varies little with latitude until high
latitudes (roughly 50°N, but possibly at higher latitudes in the southern hemisphere)
are reached, after which a strong shift occurs to demersal eggs (figure Sup 2). High-
latitude fish assemblages are dominated by species with demersal eggs (Fig Sup2),
and in most cases, spawning type is consistent within families. However, several
exceptions exist, and in these, there is a trend within taxa toward demersal eggs at
higher latitudes. Some examples where taxa from higher latitudes are less likely to
be broadcast spawners include the sebastine scorpaenids, a temperate group, which
is exclusively viviparous, whereas other scorpaenid taxa, which are essentially
tropical, are broadcast spawners [7]; the temperate labrid tribe Labriini, which is
dominated by demersal-egg species, whereas all other labrids are broadcast
spawners [8]; and the important commercial taxa, Pleuronectidae and Gadus, where
some species are broadcast spawners, and other, more boreal species, spawn
demersal eggs [9].

There is also a trend for fish eggs to be larger at higher latitudes, but this seems to
apply across all latitudes only for demersal eggs. For pelagic eggs, there is little
trend between the tropics and about 50° North, but poleward of this, pelagic eggs are
larger [10]. It is not known if the same relationship applies in the southern
hemisphere. Egg size and pre-hatching period are typically correlated, so these
times should be longer for northern-hemisphere, high latitude species with pelagic
eggs. Equally, dispersal distances due to passive drift of eggs should be longer than
for species south of 50°N. In addition, independent of egg size, lower temperatures
are expected to increase the pre-hatching period, which may lead to a latitudinal
gradient in pre-hatch times and therefore dispersal distances between spawning and hatching, assuming there is no adaptation.

Another potential latitudinal factor influencing larval dispersal is the timing of spawning. Many tropical demersal species have a protracted spawning season, whereas temperate species tend to have a narrow season, presumably to coincide with appropriate biological and physical oceanographic conditions [11]. For temperate species, shifts in temperature may shift the seasonal timing of spawning. The flounder *Platichthys flesus*, for example, spawns 1-2 months earlier in years with cooler than normal temperatures [12]. In other species, spawning or occurrence of larvae is delayed by cooler temperatures [13],[14],[15]. Larvae of spring-spawning species can appear in the plankton earlier in cold years whereas larvae of summer-spawning species appear later [16]. Sheaves [17] noted a latitudinal pattern within the family Sparidae, with greater variation in spawning timing for more temperate species. Such shifts in phenology will affect potential dispersal if the oceanographic environment experienced by eggs/larvae differs from that typically experienced. Spawning that is temperature-induced could result in a mismatch of spawning timing with timing of food availability or transport mechanisms. If so, this might result in more variable dispersal distances and directions, and thus a larger scale of larval dispersal in temperate than in tropical waters (also see Feeding below). In upwelling systems like the California Current, the timing of spawning has long been recognized as a critical determinant of larval success [18], and reproductive patterns of resident fishes appear to have evolved to facilitate completion of the life cycle and minimize advective losses of larvae under ‘normal’ oceanographic conditions [2].
(b) **Diadromy**

Diadromy varies with latitude, albeit differently in its different forms, but there is only limited evidence that connectivity of diadromous species varies with latitude. Life histories of diadromous fishes are split between fresh and marine waters. We consider only species with marine larvae, which excludes anadromous taxa such as salmonids, which spend their early life history in freshwater. However, anadromy is largely confined to temperate latitudes, particularly in the northern hemisphere, with few tropical anadromous species, primarily Hilsa shads [19]. This does constitute a latitudinal difference, but an unbalanced one because there are far more anadromous fish species in the northern than southern hemisphere.

Catadromous species such as anguillid eels, two species of Australian percichthyids (warm temperate), and the tropical latids, centropomids and kuhliids migrate to estuaries or the sea to reproduce and the young enter freshwater after larval growth in the ocean. There are only a few temperate catadromous species, and other than the anguillid eels, there is no clear evidence of latitudinal differences in dispersal or connectivity. Anguillid eels, however, provide a clear example: temperate anguillid species have larger scales of larval dispersal and population connectivity than do most tropical species. All five primarily temperate anguillid species display little genetic structure across their freshwater adult ranges. Their long-lived larvae are transported by currents 1000s of km from discrete tropical, oceanic spawning areas [20],[21],[22]. *Anguilla reinhartii*, with a tropical to warm temperate adult range on the western side of the Coral and Tasman Seas, is apparently similar to the temperate species in having a discrete tropical oceanic spawning area and no apparent genetic structure [23]. *Anguilla marmorata* and *A. bicolor* are primarily
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tropical species that spawn in the Indian and Pacific Oceans and have more than one genetic lineage or spawning population [24, 25],[26],[27] within an ocean basin. The other tropical *Anguilla* species each have limited adult ranges and one or two local spawning areas [28]. They have shorter larval durations and smaller maximum larval sizes than temperate species [29], [30].

Amphidromous species such as Sicydiinae gobiids (primarily tropical), some temperate cottids, and the temperate Osmeriform families Galaxiidae and Plecoglossidae spawn in freshwater, with their larvae moving downstream to the ocean for a larval growth phase after which they return to freshwater for a juvenile growth phase [31] [32]. Amphidromous fishes are found primarily in tropical and subtropical islands, but a few extend to temperate islands such as Japan and New Zealand [33]. Most amphidromous species have long PLDs (e.g., [32],[34]) and widespread larvae compared with most marine fishes, and they have broad genetic connectivity (e.g., [35],[36],[37]). In contrast, a temperate Japanese sculpin species with a short PLD has clear population structure [38]. However, no clear latitudinal trend in larval duration, dispersal, or connectivity is evident in the species that have been studied.

3. PHYSICAL DIFFERENCES

(a) *Oceanography*

Generally, stronger winds and greater eddy propagation occur in mid to high latitudes than in the tropics [39],[40]. This can affect dispersal both directly and indirectly. Latitudinal increases in both mixed layer depth (MLD) and eddy kinetic energy (EKE) tend to increase diffusion, which influences the variation in dispersal
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distances, but an increase in MLD alone would tend to increase dispersal distance via its interaction with both diel and ontogenetic vertical migration.

Although seasonal variation in tropical MLD is generally low in any region, there are large differences in MLD among different tropical regions [41]. Temperate species that spawn when MLD decreases in spring and summer are expected to have shorter dispersal distances than those that spawn in winter, and this seasonal difference should be reinforced by the higher ML temperatures of spring and summer. This contrast may increase among-species variation in dispersal at higher latitudes.

Vertical migration behaviour of larval fish can influence dispersal differentially between tropical and temperate regions. Most fish larvae dwell within the upper 50-100 m of the water column in both tropical [42],[43],[44],[45] and temperate [46],[47] environments and are able to modify their vertical position behaviourally. Where currents vary in speed and direction with depth (e.g., [48],[49]), larval fish in the surface layer can be advected in a different direction or speed than deeper-living larvae. Therefore, vertical distribution behaviour by larvae can affect their integrated drift trajectories and geographic dispersal [50],[51],[52],[53]. Larval fish released at the same spawning ground, but that occupied different parts of the water column, become separated by hundreds of kilometers after a few months drift [54],[55],[56]. In both temperate and tropical regions, warmer temperatures and low winds during the summer cause an increase in stratification and a shallowing of the MLD. The strongest currents generally occur in the ocean's surface mixed layer and decrease with depth, particularly in the pycnocline. Stratification in the upper water column and
MLD can influence the impact of larval vertical migration on dispersal and connectivity [42],[52],[57]. In general, where MLD is large (e.g., in many temperate areas during times other than summer) dispersal distances should be relatively long, creating larger connectivity networks.

The increase in kinetic energy, and therefore eddy generation, with latitude seems directly linked to the Coriolis-dependent geostrophic motion, which increases with latitude, and with wind, which is strongest at mid to high latitudes [58]. The size of eddies decreases with latitude because the intrinsic length scale of baroclinic instabilities is directly related to latitudinal variation of Coriolis force [58], and as a result the typical size of eddies decreases from 200 km at mid latitudes to 100 km at high latitudes. The strongest variation in eddy kinetic energy (EKE) and amplitude is associated with western boundary currents [59], resulting in within-latitude regional EKE differences. Eddies in the tropics are generated at large scales by Rossby waves (very low-frequency waves in the ocean’s surface and thermocline), tropical instability waves [60], or by the interaction of currents with topography such as capes or the reef edges that can result in shedding of sub-mesoscale eddies [61],[62].

Thus, there are clear differences in eddy formation and size with latitude. Although slow-moving eddies can retain larvae near a source (e.g., [63]), fast-moving eddies can move larvae away from a source [64], so it is difficult to generalize about how latitudinal differences in eddies might influence larval dispersal.

Temperate regions are characterized by the widest seasonal temperature ranges ([41]), and frequent storms and low-pressure systems that mix the water column, and can have major impacts on the dispersal of larvae [65],[63],[66].
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249 Tropical regions have equivalent low-pressure systems, that can disperse larval fish from their source relatively quickly, but tropical cyclones are, short-term, focused storms that are much less frequent and followed by long relatively quiet periods [67].

253 Advection alone moves larvae away from the source whereas diffusion by itself increases variance in dispersal distance, but not the mean [68] (figure Sup 3). Zonal advection (i.e., along the east-west axis) in the surface layers increase with latitude, but the meridional advection (i.e., along the north-south axis) decreases [69].

257 Therefore, connectivity networks are expected to be more elongated zonally at mid- and high-latitudes and meridionally in the tropics. East-west spreading rate increases with time in the tropics but not at high latitudes [70]. Therefore, super-diffusive east-west spreading should be expected at low latitudes only for species with PLDs, like eels, but not for species with short PLDs.

262 Ekman-related coastal upwelling cells may be important for nearshore retention of larvae [63] because they allow larvae that move offshore in Ekman near-surface flow to migrate downward and be returned toward shore by deeper flow ([63],[71],[72]).

266 Coriolis force combined with long-shore wind drives Ekman coastal upwelling cells. Although Coriolis force increases with latitude, wind strength is maximal in mid latitudes, so it is expected that Ekman-cell retention would be most important at mid latitudes, and least important at low latitudes. If so, away from the tropics this phenomenon should result in a decrease in the scale of dispersal for species that utilize these cells. However, intensification of Ekman upwelling should result in greater offshore transport of shallow-living larvae. Although these arguments are
theoretically sound [73], there is little evidence that many species do utilize Ekman-cell retention in nature [72],[74].

There is currently no empirical evidence that any of these identified oceanographic factors result in latitudinal differences in larval dispersal. By identifying their potential to influence larval dispersal, we hope to stimulate research into their effects.

(b) Habitat Fragmentation

Fish larvae in warm water have good swimming abilities and can detect settlement habitat over a range of scales [75],[76],[77]), although information on larval sensory abilities in cold water is lacking. If these abilities are used to remain close to suitable benthic habitat (e.g., orientation behaviour, [78]), larvae from islands would likely remain near their origin by orientated swimming, because they are likely to receive sensory information about suitable benthic habitat only from the closest island. In contrast, a larva from coastal waters along a continental margin will receive sensory information about suitable benthic habitat as long as it minimizes offshore dispersion, even if along-shore movement is large. Hence, there is an expectation for less self-recruitment and greater population connectivity along continental margins than among islands (e.g., [79]).

The degree to which habitat patchiness influences dispersal distance in either tropical or temperate latitudes is largely untested. To explore this question, 20 recent studies of demersal fishes (Table SUP2) that used otolith geochemistry to estimate demographic connectivity were categorized based on whether the target species lived in: a) relatively continuous habitat (e.g., soft sediments in shelf waters); b)
coastal habitat patches; or c) offshore islands. For each study we then calculated:

1) the % self-recruitment observed (or stated); 2) the spatial scale over which self-
recruitment was estimated (i.e., the scale at which the population/stock was defined);
and (3) the spatial scale of observed connectivity. Whether these three metrics
differed among landscapes was tested by ANOVA.

Levels of self-recruitment in a demographic context were high (mean: 63%) and
were 30% greater in continental than island habitats ($F_{2,13} = 7.045, p = 0.009$; main
text, figure 1A). On first inspection, this appears to contradict the reasoning that
dispersal should be shorter in island areas. However, the spatial scale over which
self-recruitment was estimated differed among landscape contexts ($F_{2,15} = 9.636, p =
0.002$): self-recruitment occurred in continuous habitat at ~300 km scales whereas
for both the patchily distributed landscape contexts, self-recruitment occurred at
scales <40km (main text, figure 1B). Once we controlled for spatial extents of each
study, the mean scales of connectivity differed among contexts, with species in
patchy habitats dispersing over about 60 to 100 km, whereas species in continuous
habitats dispersed about 900 km (main text, figure 1C). Combined, these data
suggest that larval dispersal may be more restricted in fragmented habitats.

Are fragmented habitats more common in the tropics? To examine whether
landscape context plays a role in driving differences in population connectivity
between tropical and temperate species, we assembled a spatial database
consisting of the Global Self-consistent, Hierarchical, High-resolution Shoreline
(GSHHS; [80]) and a lattice of one-degree latitude boundaries between +/- 80°
latitude (Mollweide equal-area cylindrical projection). We determined the distribution of islands as a function of latitude.

To account for the observation that all suitable habitats within the sensory detection limit of larvae may not be perceived by larvae as distinct, we generalized the global shoreline data to match this scale of habitat detection. If larvae can detect habitat patches at this spatial scale, then behavioural barriers to dispersal and their impact on connectivity will be observed at scales larger than this. For this analysis we chose 5 km, which is within the range estimated for reef fishes [81, 82], although using either shorter (2.5 km) or longer (10 km) detection limits resulted in almost identical results. This generalization resulted in a grid (at 2.5 km resolution) where cell values quantify the amount of island-only habitat within the 5 km sensory radius from the centre of each cell. Island habitat cells that fell within this sensory zone were then aggregated/merged into contiguous island patches. Using the same sensory detection limit, we also reclassified island habitat patches to continental habitat if they were within the 5 km detection limit from continental shorelines. Island habitat patches were intersected with the latitude lattice to calculate the median latitude of each patch. Changes in island number with latitude were analysed by correlation. Both all-island patches (i.e., all islands regardless of distance from a continental margin) and all non-continental island patches (i.e. island patches greater than 5 km from a continental margin) declined in number with increasing latitude (main text, figure 2).

4. BIOPHYSICAL DIFFERENCES

(a) Temperature and larval behaviour
Development of swimming in larvae of demersal fishes has been recently reviewed [76, 83]. Larvae of taxa from cold-temperate waters (Cottidae, Gadidae, Pleuronectidae) had some of the slowest critical speeds [84], and consistently swam at about 5 body lengths per second (BL s\(^{-1}\)). Development of critical speed was more variable in larvae of taxa from warm-temperate waters (Moronidae, Percichthyidae, Sciaenidae, Sparidae). Larvae of these taxa were relatively slow when small (5–10 cm s\(^{-1}\)), but at sizes larger than 5 mm, sciaenids swam at 10 BL s\(^{-1}\), whereas sparids and percichthyids larger than 7–8 mm are able to swim at 15–20 BL s\(^{-1}\). Moronid larvae, in contrast, were slow (<10 BL s\(^{-1}\)) until larger than 15 mm, after which they swam at about 15 BL s\(^{-1}\). Aside from the serranids and lutjanids which were slow at smaller sizes, but eventually were among the fastest larvae, tropical taxa had larvae that were fast throughout development, with critical speeds faster than 10 cm s\(^{-1}\) and with most species swimming at 15–20 BL s\(^{-1}\) for much of their larval phase, with some reaching almost 30 BL s\(^{-1}\). Fisher [85] suggests that most coral-reef fish families have sufficient swimming capabilities to be able to influence their dispersal outcomes substantially for over 50% of their larval phase. For temperate Sebastes, in contrast, which may have PLDs of up to 6 months, the potential for using directed horizontal swimming to influence dispersal may not be developed until the pelagic juvenile stage at 20-30 mm (see below).

Although the swimming data on warm temperate species were from outside tropical latitudes, the experimental temperatures (19-27°C) overlap those of the tropical species (26-31°C). The closeness of these temperature ranges could result in the similarity in swimming performance. In contrast, a large gap exists between these and the experimental temperatures for cold temperate species (3-10°C), contributing
to the differences in swimming performance. Measures of swimming performance for larvae of species that live at temperatures within this gap are needed.

Within species, the expected pattern of increased swimming speed with increased temperatures has been observed in larvae of several temperate fish species [86],[87],[88],[84],[89, 90], but a cold temperate species of sculpin (Cottidae) had the opposite response [84], and a tropical damselfish had no temperature-induced change in swimming speed [91]. Physiological responses to temperature are typically dome-shaped, and the apparent inconsistency in the limited empirical data might be due to differences in the portion of the temperature-response curve that was under study.

It is expected not only that the development of swimming capacity is slower in cold temperate species due to protracted morphological development, but there should also be an increasing ontogenetic divergence of swimming capabilities [76]. Larvae of live-bearing Sebastes rockfishes are released at a size of 4-6 mm with incomplete fins and have critical swimming speeds of < 2 cm s\(^{-1}\) at 12\(^o\)C [92]. In contrast, tropical and warm temperate larvae at this size have more advanced fin development and \(U_{\text{crit}}\) values of 2-10 cm s\(^{-1}\) [93], but the extent to which these swimming speed differences are due to temperature or to fin development is unclear. The size-dependent rate of increase in swimming speed of cold temperate species lags behind that of tropical species, as expected. For each mm increase in size, tropical serranids (Epinephelus spp.) swam faster by 2.1-2.6 cm s\(^{-1}\) [76], whereas the increase for the temperate serranid Paralabrax clathratus and several species of Sebastes was only 1.0 cm s\(^{-1}\) [92]. Many tropical species settle at small sizes (<15
mm), and have speeds equivalent to warm temperate species at similar sizes, assuming that all fins have formed. Larvae of some species attain relatively large sizes (> 20 mm) before settlement. The tropical species are fast swimmers, with critical speeds in excess of 20 BL s$^{-1}$ by the time they settle [76, 94], but among temperate species, data are available only for species of the scorpaeniform genus *Sebastes*, which at 25-30 mm, have critical speeds of about half those of tropical species [92].

Swimming endurance of many settlement-stage tropical fish larvae is very high [95], but information on the development of endurance is limited, especially for temperate species. There was no obvious difference in swimming endurance between warm-temperate and tropical species, except that several tropical species attained greater endurance prior to settlement primarily because they settle at larger sizes [76]. There are no endurance data for larvae of cold-temperate species.

A critical aspect of behaviour-influenced dispersal is performance in relation to age (or time in the water column), not to size. The experimental data are based largely on reared larvae with growth rates that differ from those found naturally, so a simple conversion of size to age is not generally possible. However, it is generally expected that growth rates are temperature-dependent, so converting performance from a size to an age basis is expected to increase relative differences in performance between warm and cold-water species. More information is required on field-based growth rates of larvae of demersal fishes.
The identified differences in swimming performance are consistent with theoretical predictions and could arise from differences in phylogeny, sea water viscosity, temperature and associated physiological responses or to some combination. At present, none can be eliminated or shown to be relatively more important to dispersal. Although the causes for the differences are not clear, the most relevant consideration is what a larva does in conditions it typically encounters in the sea.

(b) Temperature, feeding, and mortality

Feeding can influence larval survival in several ways. Clearly, food availability must be sufficient to prevent starvation. Spatial or temporal variability in prey levels above or below a starvation threshold will translate to concurrent variability in the proportions of larvae surviving to settle, thereby influencing larval replenishment and connectivity. Suboptimal prey levels may influence larval growth rate [96],[97], ability to avoid predators [98],[99] or swimming endurance [100], [101]. Slower growth can extend the larval period, thus increasing cumulative mortality and reducing the numbers of settlers [102],[103],[104]. Similarly, slower growth extends the duration of the more passive early stages and thus the time before larvae are able to influence dispersal.

Feeding incidence (FI; the proportion of a sample of larvae with food present in the gut) is a commonly reported proxy for larval fish feeding success. Across published studies, average FIs of larvae from coastal and offshore waters were significantly higher in taxa from lower latitudes (30°S–30°N; median FI 96%) than from middle (30–45°N/S; median FI 80%) or high (>45°N/S; median FI 72%) latitudes [105]. These differences also hold when comparing within taxonomic Orders. This, along
with observed differences in gut evacuation rates, indicates feeding rates are higher
in lower latitudes, which would be expected (because of greater metabolic demands)
if levels of starvation mortality were similar among latitudinal regions.

Zooplankton prey of fish larvae differ with latitude and there are indications of greater
prey selectivity in lower latitudes [105]. Greater diversity of larval-fish prey and
apparent finer niche partitioning in lower latitudes [105] as described in the next
paragraph, could lead to species-dependent dispersal patterns if variation in
abundances of the preferred prey of different taxa does not covary, as some
evidence suggests (Llopiz and Cowen, unpublished data). If so, patterns of larval
dispersal and degrees of connectivity may be less consistent across taxa in lower
latitudes even when adult habitat, spawning behaviours, and PLDs are similar—
clearly adding to the challenges of accurately modeling the successful transport of a
particular species.

The frequency with which calanoid copepods and copepod nauplii dominate the diets
of larval fishes decreases towards the equator, while the importance of
appendicularians and several genera of cyclopoids increases. The diversity of
dominant prey types also increases towards the equator. Such prey include
cladocerans, bivalve larvae, pteropods, and ostracods, which rarely if ever compose
the majority of a taxon’s diet in high latitudes. Diets of low-latitude larvae are more
often consistent in time, space, and ontogeny, and are often unique to larvae of a
given taxon [105],[106],[107]. These factors, together with comparisons of diets to
ambient proportions of zooplankton prey types, indicate greater degrees of prey
selectivity in lower latitudes, with some evidence that highly selective larvae are
‘hard-wired’ to consume specific prey types and have a limited capacity for prey switching when preferred prey availability is low [106].

Latitudinal differences in the seasonal cycles of primary and secondary productivity may also yield trophic-related distinctions in larval dispersal and connectivity. In higher latitudes, where match-mismatch dynamics of zooplankton and fish larvae can have an important influence on larval fish growth and survival [108],[109], the timing and locations of optimal prey availability may occur over narrower spatial and temporal ranges than in lower latitudes. This could lead to greater interannual variability in growth, survival, and dispersal, and therefore connectivity at higher latitudes. In contrast, the more stable levels of productivity in the tropics, in conjunction with protracted spawning seasons, could result in more consistent among-year spatial patterns in larval dispersal.

Some studies have suggested higher instantaneous mortality rates for fish larvae in warm temperatures [110], and higher predation pressure in clear tropical waters [111]. Further, a general trend toward stronger predation in the tropics has been suggested for other taxa including marine consumers [112],[113],[114]. In contrast, expected (but not documented) longer larval durations in cold water would imply higher cumulative larval mortality [115]. Thus, physiological processes underpinning mortality rates suggest geographic variation in mortality due to temperature, but it remains unclear whether there is an overall trend that could influence connectivity.

(c) Temperature, development, and PLD
Supplement to Leis et al. Does larval dispersal in fishes differ between high and low latitudes?

Previous work showed that PLD differed among adult habitat types [2]; for example, average PLD of nearshore (<30 m adult depth) California Current fishes was much less than PLD of shelf/slope species regardless of spawning mode. Because differences in adult habitat can affect PLD, our analysis was based on tropical and warm temperate (<50° from the equator), nearshore reef fishes only, because sufficient data for higher latitudes or other habitats were not available. A notable limitation is the very restricted PLD data available from cold temperate nearshore fishes and from tropical shelf species.

Shanks and Eckert [2] compared a diversity of life history characteristics, including PLDs, of fish and benthic decapod species from the California Current and found large differences based on adult habitat. The data sorted into three groups: shelf/slope species, shallow water species (< 30 m), and shallow water species from the Southern California Bight. Shanks and Eckert suggested that differences in the life history traits were adaptations to the local hydrodynamics associated with each adult habitat. We attempted to investigate PLDs of temperate and tropical shelf/slope fishes, and although we could find adequate data for temperate species, we could not find enough data on tropical shelf/slope species to support an analysis. Similarly, data on cold temperate species were too limited for testing. Therefore, values of PLD for shallow water reef fishes from temperate and tropical locations were compiled for the Mediterranean and Eastern Atlantic [116],[117],[118],[119], the California Current [2], the Caribbean and Western Atlantic [120],[121],[122],[123],[124],[125],[126],[127],[128],[129],[130],[131],[132]), the tropical Eastern Pacific [131],[133],[134],[135], and the central Pacific [1],[136],[136],[132]. We assembled data on 110 warm temperate and 230 tropical
species from 23 publications. The publications were found by a search of Aquatic Sciences and Fisheries Abstracts back to 1980 using the terms PLD and Pelagic Larval Duration. In addition, the reference section of papers that reviewed PLD were scanned for additional publications, and Science Citation Index was searched for publications that cited the more important PLD papers. The species found in this search were included in the analysis if the data were collected in a similar fashion (e.g., shallow water/reef species, PLD from otoliths) from defined geographic settings (e.g., California Current, Caribbean, Mediterranean, etc.). The mode of reproduction (i.e., live birth, broadcast spawning, or nesting) of the species that fit within the habitat and geographic range criteria was determined from a number of sources including reference books on California Current species, Fish Base and the original publications.

PLD of warm temperate and tropical reef fishes did not differ (all areas and spawning types pooled: main text, figure 3A, for statistics see main text, figure 3 caption), but when the species were compared by reproductive mode (demersal vs. broadcast spawning), PLDs of tropical demersal and broadcast spawners were significantly shorter and longer, respectively, than warm temperate species (main text figure 3A). However, when the data were analysed by geographic location, consistent differences between PLDs in warm temperate and tropical species were not found. If PLDs are separated by region rather than reproductive mode (main text figure 3B), PLDs of warm temperate Mediterranean species are significantly shorter than temperate California Current species, even though the latitudes are similar, whereas the PLDs of tropical central Pacific species are significantly shorter than those of Caribbean and tropical Eastern Pacific species, which did not differ from each other.
Comparing warm temperate to tropical, the average PLDs for Mediterranean and central Pacific species were similar whereas average PLD for California Current species was significantly longer than in any other region, temperate or tropical. When divided by reproductive mode, the demersal-spawning species average PLD from the Mediterranean was significantly shorter than in the California Current (main text, figure 3C), but similar to the central Pacific and eastern Pacific and only slightly shorter than PLDs in the Caribbean. The broadcast-spawning-species average PLD from the Mediterranean was again significantly shorter than in the California Current and was also shorter than in the three tropical regions (main text figure 3D). The broadcast-spawning species mean PLD for the California Current was not different from the Caribbean or Eastern Pacific, but was significantly longer than the central Pacific.

The most striking differences in PLDs were not between temperate and tropical systems, but between two temperate regions: for both demersal and broadcast spawning species, Mediterranean PLDs were much shorter than in the California Current. The Mediterranean is not particularly warm, but Mediterranean PLDs were either the shortest or not significantly different from the tropical areas. Further, Caribbean and California Current pelagic-egg PLDs did not differ, showing there is not a simple relationship between PLD and temperature.

The main text points out that the geographic patterns we found in PLD are not expected based on sea-surface temperature alone. The temperature data (annual range of monthly means of sea surface temperature, viewed May 2012) supporting this statement for each region are given here. They are from
http://www.youtube.com/watch?v=4hv1a-z53Ew (Generated from NASA Giovanni v3.0.7) for the western Mediterranean (12-26°C), a temperate area, and from http://www.nodc.noaa.gov/dsdt/cwtg/oatl.html for the other regions. For temperate areas, ranges were: central California (12-16°C) and southern California (14-20°C). For tropical areas: Hawaii (22-27°C), Samoa (27-29°C), and Puerto Rico (25-28°C).

The Eastern Pacific is a huge and variable area but off Central America, sea surface temperatures range from 25-28°C [137].

We re-analyzed PLD and dispersal distance data from [138] and [139] by separating the data into temperate and tropical species. There was no obvious difference in the PLD vs. dispersal distance relationship between tropical and temperate species of invertebrates or fishes (figure Sup 4). Only 19 of the 62 comparisons of PLD with dispersal distance in [138] and [139] were from tropical species, and six of the tropical data pairs (32%) were from tunicate tadpole larvae (figure Sup 4). The overall pattern of the data is a tight cluster of points above a dispersal distance of about 20 km and PLDs of > 1 week and a broad scatter of points below about 1 km dispersal distance and with PLDs from < 1 hr to several weeks. This general pattern is displayed by both the tropical and temperate data when analysed separately: there is no obvious difference between tropical and temperate invertebrate and fish species in the PLDs vs. dispersal distance relationship. However, the small sample size of the tropical data set suggests caution in this interpretation.

An association between genetic structure and PLD is expected, but in practice the relationship is often not found [5, 6]. Although PLD is often assumed to be a strong determinant of species range, results of attempts to test this assumption have been
mixed at best. Further, recent studies have concluded that PLD is usually not a major determinant of range size [3],[140]. In contrast, a significant correlation was found between genetic differentiation and PLD in a study of 32 species (including 12 fishes) [68]. In another study, a consistent, moderate association between genetic and PLD proxies of dispersal was found in 50 marine species (21 fishes), which was significantly better at small (<650 km) spatial scales [141]. In some cases, the association between genetic structure and predicted dispersal can be improved by using modeled dispersal trajectories based on ocean currents instead of point to point straight lines [142], perhaps explaining some of the inconsistency in other studies. In contrast, two broad assessments of marine fish populations and associated proxies [6], [5], reported that egg type (demersal vs. pelagic) was a better predictor of genetic structure than was PLD, and neither found a significant association between PLD and genetic structure. It is worth noting, however, that in the analysis of PLD data here, in each region except the California Current, the average PLD of demersal-spawning species was shorter than that of broadcast spawning species by 20 to 60% (main text figure 3), consistent with [5] and [6]. This is potentially an indication that demersal-spawning species have shorter dispersal distances, albeit with all the caveats raised above.

Although Riginos et al. [5] found little effect of PLD on genetic structure, 96 of the 148 demersal study species were tropical, with only a few temperate species (mostly Sebastes), and only 2-3 species from cold water. These authors properly did not attempt to generalize their findings to temperate species. Bradbury et al. [6] did not observe a significant association between PLD and genetic divergence for 30 species of marine fishes, but their analysis included both pelagic and demersal
species. Bradbury et al. [6] also found a significant, curvilinear increase in PLD with latitude at both species and family level, and in this case, the large majority of tropical and warm temperate species were demersal, site attached reef fishes, whereas the cold water species were dominated by open shelf and pelagic species. Therefore, the higher latitude species are more likely to show an influence of adult movement on genetic structure than were the tropical species. Further, as shown herein for tropical and warm temperate species, adult habitat does influence PLD.

5. CAVEATS

Larval dispersal is very difficult to measure directly, although recent advances in otolith tagging and genetic parentage make it more feasible, if labour intensive. As a result, the use of indirect approaches and proxies to estimate larval dispersal is common. These include some population genetic approaches, estimation of PLD and dispersal modelling. For a variety of reasons touched upon here, genetic structure in marine populations may not always derive from recent patterns of larval dispersal alone. Similarly, published PLD data often do not capture the spatial and temporal variation that intensive study reveals, and the intuitively attractive hypothesis that PLD is a strong determinant of larval dispersal distance is often rejected when tested. We have not considered dispersal modelling here, but modelling larval dispersal is challenging because of the many variables that contribute to dispersal outcomes, and our often poor understanding of larval behaviour in particular. Therefore the results of proxy-based and indirect approaches should be viewed with caution.
Genetic variation among populations results from the combined influences of selectively neutral processes such as genetic drift, mutation, and gene flow as well as adaptive processes such as natural or sexual selection. The application of genetic approaches to the study of larval dispersal in temperate and tropical marine systems can illuminate trends in migration and dispersal, when differences among populations are found. Allele frequency differences among populations and individuals can provide the means for both indirect estimation of average gene flow and the direct measurement of individual dispersal events [143],[144]. Furthermore, the study of genes experiencing natural selection allows the scale of adaptation to be resolved and resulting clines can reveal trends in successful dispersal [145].

Genetic approaches can overcome some of the hurdles associated with the direct tracking of many tiny propagules and resolving the tails of dispersal kernels (i.e., determining the shape of the dispersal distance frequency distribution) As with all approaches, they are subject to their own sources of bias and misinterpretation [5] [143] [144]. For example, population genetics approaches reflect a combination of egg and larval dispersal, settlement, and post-settlement processes, as well as adult dispersal, and they may be sensitive to rare events over long or intermediate time periods as well as on processes that may no longer exist.

Genetic estimates of dispersal are most commonly based on either isolation by distance models or individual assignment, and more recently on parentage. The former are more commonly used in higher latitude studies and the latter in tropical studies because larger populations and larger spatial scales make assignment approaches challenging in colder regions. Estimates of average dispersal distance based on genetic isolation-by-distance relationships (i.e., [146] [147] [148]) suggest
local recruitment in marine species may be more prevalent than previously thought
[149], [150]. Similarly, individual assignment [151] or parentage based [152]
methods resolve single events and also often emphasize local recruitment.
However, single case studies of limited geographic scale do not allow the full
dispersal kernel to be determined and are hard to interpret in terms of the question at
hand, which is whether there are tropical-temperate trends in larval transport and
dispersal, because similar studies on higher-latitude fishes are lacking.

Undoubtedly, genetic estimates of larval dispersal in a single species along a
latitudinal gradient are best suited to address the goal of this review, yet such studies
are rare. One of the few studies to contrast genetic structure across fish species,
geographic regions and life histories [6] found significant associations between
maximum latitude, body size and genetic structure ($F_{ST}$), and weaker genetic
structure at latitudes above 40 degrees, with the largest differences observed at the
extremes of latitude (i.e., 20 vs. 60 degrees latitude). That review [6] examined
dispersal overall (not limited to larval dispersal), and was not limited to nearshore
demersal species, examining all taxa and data available. Nonetheless, genetic
structure across species of marine fish supported the hypothesis that dispersal
occurs over greater spatial scales at high than at low latitudes, consistent with
predictions based on the expected effect of temperature on development times [115],
some oceanographic variables, and conclusions of some studies of single species of
marine invertebrates [153], [154]. Although this interpretation is valid for those
species included in the meta-analysis [6], the composition of the species for which
genetic data exist is not reflective of the spawning modes of the species
assemblages that actually occur in the areas of interest. Specifically, genetic data
are available for a higher proportion of demersal-egg spawners at low latitudes and broadcast spawners at high latitudes than are found in the assemblages from those areas. This is not a criticism of such synthetic studies, but it does make it difficult to apply their conclusions to broad faunas and questions like the ones of interest here. For example, some workers have concluded that larval dispersal occurs over smaller spatial scales in demersal-spawning spawners than it does in broadcast spawners [6],[5]. If true, geographic biases in the species examined limit the utility of these approaches to single species examples until the suite of species for which data exist becomes representative. However, very few direct estimates of larval dispersal are available to test the impact of any biases due to species selection. Biases due to species selection depend on the families present at differing latitudes. For example, the families Agonidae, Ammodytidae, Anarhichadidae, Cottidae, Cyclopteridae, Pholididae, Stichaeidae and Zoarcidae constitute about half the demersal fish species in the higher latitudes of the NE Pacific and NW Atlantic (figure Sup 2), and the vast majority of the species of these families spawn demersal eggs. The available genetic data as used in [6] includes only about 5-10% of the total number of species from the listed families, and none for five of them, thus resulting in an under-representation of demersal-spawning species. The same trends were found when the data were analysed at the family level [6], but the absence of genetic data for five of these eight families limits the conclusions that can be drawn. Thus, if spawning mode is relevant to dispersal, as seems to be the case in warmer waters [5], the available genetic data are not representative of the full fauna. More study of high latitude non-commercial taxa with demersal eggs using
direct and indirect methods is needed to help evaluate potential biases and trends present.

Population genetic approaches (e.g., isolation-by-distance based methods) are also influenced by historical events such as glaciations, which may have long-lasting effects on genetic structure that are relevant for latitudinal comparisons. Species characterized by large populations recolonizing high-latitude areas following deglaciation may not have had sufficient time for differences to accumulate by genetic drift. In such cases the absence of genetic divergence tells us little regarding larval dispersal and connectivity [155] and it is difficult to discount the hypothesis that the observed low structure at high latitudes is not at least partly due to recent recolonization and large effective population sizes. Similarly, glaciations also influence genetic structure in the tropics, because some regions during the Quaternary, in particular areas between South-east Asia and Australia, were subject to high-frequency sea level fluctuations that alternatively flooded and dried many thousands of square km [156]. Direct genetic approaches based on individual assignment or parentage are not subject to these effects.

Might apparent geographic differences in dispersal arise from differing methodologies or research targets? Studies of dispersal and connectivity in the tropics tend to be on small, site-localized species ([43, 157], [158]; see sections on Habitat Fragmentation). Often, the study species are chosen for tractability (e.g., small adult size, small adult home range), and if the species is not fished, all the better: this eliminates a factor that potentially complicates population dynamics. Might this approach bias estimates of dispersal distances? These studies often
utilize techniques that involve assigning a source to individual recruits through parentage or chemical tagging, and the geographic scale tends to be small, on the order of tens of km (e.g., [79], [159], [160], [161]). Approaches such as this do not have the capacity to identify larger scales of dispersal, although a genetic study of anemonefishes that spanned hundreds of kilometres [162] suggested short dispersal distances, at approximately the same scale as geographically limited studies of similar species.

In contrast, in temperate regions many studies of population structure are conducted on large scales on exploited stocks from deeper water, often with a focus on assessing spatial scales of management [163]. If temperate fished stocks tend to be larger and more mobile than site-attached fishes on shallow coral reefs, then estimates of what constitutes a local population within the metapopulation can be very different, and this could set a different scale for connectivity estimates. However, as mentioned above, a larger spatial scale of study does not automatically result in longer estimates of dispersal. A coarse-scale genetic study of fifteen species of exploited rockfishes along the west coast of North America found little evidence of genetic structure among some species, but sharp genetic breaks among others [164]. In the more subdivided species, more detailed study could reveal fine-scale population structure and evidence of limited dispersal. Such a finding is very unlikely in the group lacking genetic structure.
**Figure Captions**

**Figure Sup 1.** Mean (±SE) pelagic larval duration for taxonomic groups of demersal shorefishes with primarily warm-water (solid bars) and cold-water (open bars) distributions. PLD data from [2] and [3]. See Supplement text for numbers of PLD estimates for each taxon.

**Figure Sup 2.** Percentages of demersal shorefish species with different spawning modes in regions of the Western Atlantic and Eastern Pacific. In each ocean, cold temperate regions have a much smaller percentage of species with pelagic eggs than do other regions. Both Argentina and Chile have a large north-south extent and their fish faunas include both warm and cold temperate components: although they have a lower percentage of species with pelagic eggs, the percentage is still about 55% as compared to 15-25% in the cold temperate regions of the northern hemisphere. Data from Hawaii in the central Pacific are very similar to the other tropical values. In the Antarctic, 16% of species spawn pelagic eggs. See Table Sup1 for details and data sources.

**Figure Sup 3.** Larval transport by Eddy kinetic energy (EKE) and eddy-driven currents: consequences of (A) strong diffusion (dotted line), (B) anisotropic advection (dotted line), (C) advection and strong diffusion (dotted line) on the mean dispersal kernel (solid line). Larval source is located at \(x = 0\).

**Figure Sup 4.** Pelagic larval duration of marine invertebrates and fishes plotted against their dispersal distance. Solid squares and open circles are data from tropical and temperate species, respectively. “T”s adjacent to values indicate data
from the dispersal of tadpole larvae of tunicates. Data are from [139] and [138], but with algal data removed.
Table Sup 1. Percentage of demersal marine teleost shorefish species with different spawning modes in selected regions. A small number of species with unknown spawning modes are omitted: these constitute at most 3% of species in any location. Species compositions from: [165] [166] [167] [168] [169] [170] [171]. Spawning modes from: [172] [169] [173].

Table Sup 2. Studies based on otolith methods to estimate demographic connectivity used in the habitat fragmentation comparison. [160], [174], [175], [176], [177], [178], [179], [180], [181], [182], [183], [184], [185], [186], [187], [188], [189], [190].
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Supplement to Leis et al. Does larval dispersal in fishes differ between high and low latitudes?


Table Sup 1. Percentage of demersal marine teleost shorefish species with different spawning modes in selected regions. A small number of species with unknown spawning modes are omitted: these constitute at most 3% of species in any location. Species compositions from: [163] [164] [165] [166] [167] [168] [169]. Spawning modes from: [170] [167] [171].

<table>
<thead>
<tr>
<th>Location (number of species)</th>
<th>Category</th>
<th>Broadcast spawner (pelagic egg)</th>
<th>Demersal spawner (demersal egg)</th>
<th>Brooder (egg held by adult)</th>
<th>Live bearer (viviparous)</th>
<th>No pelagic stage</th>
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Table Sup 2. Studies based on otolith methods to estimate demographic connectivity used in the habitat fragmentation comparison. These publications were found by searching the ISI Web of Science database using the search criteria ("otolith chemistry" or "otolith microchemistry" or "elemental fingerprints" or "environmental marker*" or "natural tag*") and (dispersal or connectivity or migration or "stock structur*"). Studies were then filtered to include only non-philopatric species where movement among populations was due to larval dispersal. [156], [172], [173], [174], [175], [176], [177], [178], [179], [180], [181], [182], [183], [184], [185], [186], [187], [188]

<table>
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<th>Species</th>
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<td>Demersal</td>
<td>Islands</td>
<td>5°S</td>
<td>60</td>
<td>0.5</td>
<td>20</td>
<td>[156]</td>
</tr>
<tr>
<td>Chaetodon vagabundus</td>
<td>Pelagic</td>
<td>Islands</td>
<td>5°S</td>
<td>60</td>
<td>0.5</td>
<td>20</td>
<td>[156]</td>
</tr>
<tr>
<td>Chaenocephalus aceratus</td>
<td>Demersal</td>
<td>Coastal</td>
<td>54-63°S</td>
<td>No estimate</td>
<td>200</td>
<td>400</td>
<td>[172]</td>
</tr>
<tr>
<td>Dissostichus eleginoides</td>
<td>Pelagic</td>
<td>Coastal</td>
<td>43-55°S</td>
<td>88</td>
<td>250</td>
<td>1200</td>
<td>[172]</td>
</tr>
<tr>
<td>Chromis viridis</td>
<td>Demersal</td>
<td>Islands</td>
<td>29°N</td>
<td>No estimate</td>
<td>No estimate</td>
<td>15</td>
<td>[173]</td>
</tr>
<tr>
<td>Rhinogobius giurinus</td>
<td>Demersal</td>
<td>Coastal Habitat Patch</td>
<td>23°N</td>
<td>94</td>
<td>0.1</td>
<td>175</td>
<td>[174]</td>
</tr>
<tr>
<td>Coris julis</td>
<td>Pelagic</td>
<td>Islands</td>
<td>37-40°N</td>
<td>85</td>
<td>20</td>
<td>600</td>
<td>[175]</td>
</tr>
<tr>
<td>Thalassoma bifasciatum</td>
<td>Pelagic</td>
<td>Islands</td>
<td>17°N</td>
<td>45</td>
<td>35</td>
<td>No estimate</td>
<td>[176]</td>
</tr>
<tr>
<td>Pomacentrus amboinensis</td>
<td>Demersal</td>
<td>Islands</td>
<td>14°S</td>
<td>35</td>
<td>7</td>
<td>No estimate</td>
<td>[177]</td>
</tr>
<tr>
<td>Species</td>
<td>Type</td>
<td>Habitat</td>
<td>Lat. Range</td>
<td>Larval Dispersal</td>
<td>Abundance</td>
<td>Ref.</td>
<td></td>
</tr>
<tr>
<td>-------------------------</td>
<td>------------</td>
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<td>-----------------</td>
<td>-----------</td>
<td>------</td>
<td></td>
</tr>
<tr>
<td><em>Amphiprion polymnus</em></td>
<td>Demersal</td>
<td>Islands</td>
<td>5°S</td>
<td>24</td>
<td>0.1</td>
<td>0.5</td>
<td>[178]</td>
</tr>
<tr>
<td><em>Pomacentrus coelestis</em></td>
<td>Demersal</td>
<td>Coastal Habitat Patch</td>
<td>23°N</td>
<td>69</td>
<td>30</td>
<td>370</td>
<td>[179]</td>
</tr>
<tr>
<td><em>Coryphaenoides rupestris</em></td>
<td>Pelagic</td>
<td>Coastal</td>
<td>50-58°N</td>
<td>71</td>
<td>300</td>
<td>2700</td>
<td>[180]</td>
</tr>
<tr>
<td><em>Sebastes melanops</em></td>
<td>Live bearer</td>
<td>Coastal Habitat Patch</td>
<td>42-46°N</td>
<td>71</td>
<td>120</td>
<td>540</td>
<td>[181]</td>
</tr>
<tr>
<td><em>Pomacentrus coelestis</em></td>
<td>Demersal</td>
<td>Islands</td>
<td>14-23°S</td>
<td>42</td>
<td>10</td>
<td>30</td>
<td>[182]</td>
</tr>
<tr>
<td><em>Coris bulbifrons</em></td>
<td>Pelagic</td>
<td>Islands</td>
<td>31°S</td>
<td>50</td>
<td>15</td>
<td>600</td>
<td>[183]</td>
</tr>
<tr>
<td><em>Sebastes atrovirens</em></td>
<td>Live bearer</td>
<td>Coastal</td>
<td>34°N</td>
<td>97.5</td>
<td>30</td>
<td>40</td>
<td>[184]</td>
</tr>
<tr>
<td><em>Merluccius merluccius</em></td>
<td>Pelagic</td>
<td>Coastal</td>
<td>36-62°N</td>
<td>No estimate</td>
<td>400</td>
<td>1000</td>
<td>[185]</td>
</tr>
<tr>
<td><em>Thalassoma bifasciatum</em></td>
<td>Pelagic</td>
<td>Islands</td>
<td>17°N</td>
<td>50</td>
<td>35</td>
<td>No estimate</td>
<td>[186]</td>
</tr>
<tr>
<td><em>Forsterygion lapillum</em></td>
<td>Demersal</td>
<td>Coastal Habitat Patch</td>
<td>41°S</td>
<td>72</td>
<td>10</td>
<td>20</td>
<td>[187]</td>
</tr>
<tr>
<td><em>Micropogonias undulatus</em></td>
<td>Pelagic</td>
<td>Coastal</td>
<td>35-36°N</td>
<td>No estimate</td>
<td>No estimate</td>
<td>330</td>
<td>[188]</td>
</tr>
</tbody>
</table>
Figure Sup 1. Mean (±SE) pelagic larval duration for taxonomic groups of demersal shorefishes with primarily warm-water (solid bars) and cold-water (open bars) distributions. PLD data from [2] and [3]. See Supplement text for numbers of PLD estimates for each taxon.
Figure Sup 2. Percentages of demersal shorefish species with different spawning modes in regions of the Western Atlantic and Eastern Pacific. In each ocean, cold temperate regions have a much smaller percentage of species with pelagic eggs than do other regions. Both Argentina and Chile have a large north-south extent and their fish faunas include both warm and cold temperate components: although they have a lower percentage of species with pelagic eggs, the percentage is still about 55% as compared to 15-25% in the cold temperate regions of the northern hemisphere. Data from Hawaii in the central Pacific are very similar to the other tropical values. In the Antarctic, 16% of species spawn pelagic eggs. See Table Sup1 for details and data sources.
Figure Sup 3. Larval transport by Eddy kinetic energy (EKE) and eddy-driven currents: consequences of (A) strong diffusion (dotted line), (B) anisotropic advection (dotted line), (C) advection and strong diffusion (dotted line) on the mean dispersal kernel (solid line). Larval source is located at x = 0.
Figure Sup 4. Pelagic larval duration of marine invertebrates and fishes plotted against their dispersal distance. Solid squares and open circles are data from tropical and temperate species, respectively. “T”s adjacent to values indicate data from the dispersal of tadpole larvae of tunicates. Data are from [139] and [138], but with algal data removed.