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.

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

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[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, Gobioidei, 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.

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

1. Houde E.D. 1989 Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. *US Fish Bull* **87**(3), 471-495.

2.   Cowen R.K., Lwiza K.M.M., Sponaugle S., Paris C.B., Olson D.B. 2000 Connectivity of marine populations: open or closed? *Science* **287**, 857-859.

3.   O'Connor M.I., Bruno J.F., Gaines S.D., Halpern B.S., Lester S.E., Kinlan B.P., Weiss J.M. 2007 Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc Natl Acad Sci USA* **104**(4), 1266-1271.

4.   Bradbury I.R., Laurel B., Snelgrove P.V.R., Bentzen P., Campana S.E. 2008 Global patterns in marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc R Soc Lond, Ser B: Biol Sci* **275**(1644), 1803–1809. (doi:10.1098/rspb.2008.0216).

5.   Jones G.P., Almany G.R., Russ G.R., Sale P.F., Steneck R.S., van Oppen M.J.H., Willis B.L. 2009 Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. *Coral Reefs* **28**, 307-326. (doi:10.1007/s00338-009-0469-9).

6.   Botsford L.W., Micheli F., Hastings A. 2003 Principles for the design of marine reserves. *Ecol Appl* **13**, S25-S31.

7.   Roberts C.M., Granch G., Bustamante R.H., Castilla J.C., Dugan J., Halpern B.S., Lafferty K.D., Leslie H., Lubchenco J., McArdle D., et al. 2003 Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecol Appl* **12 (1) Supplement**, S215-S228.

8.   Warner R.R., Cowen R.K. 2002 Local retention of production in marine populations: evidence, mechanisms and consequences. *Bull Mar Sci* **70**(1 (supplement)), 245-249.

9.   Sale P.F., Cowen R.K., Danilowicz B.S., Jones G.P., Kritzer J.P., Lindeman K.C., Planes S., Polunin N.V.C., Russ G.R., Sadvoy Y.J., et al. 2005 Critical science gaps impede use of no-take fishery reserves. *Trends Ecol Evol* **20**, 74-80.

10.   Grorud-Colvert K., Claudet J., Carr M.H., Caselle J.E., Day J., Friedlander A., Lester S., Lison de Loma T., Tissot B., Malone D. 2011 The assessment of marine reserve networks: guidelines for ecological evaluation. In *Marine Protected Areas: effects, networks and monitoring – a multidisciplinary approach* (ed. Claudet J.), pp. 293-321. Cambridge, Cambridge University Press.

11.   Largier J.L. 2003 Considerations in estimating larval dispersal distances from oceanographic data. *Ecol Appl* **13**(1), S71-S89.

12.   Riginos C., Douglas K.E., Jin Y., Shanahan D.F., Treml E.A. 2011 Effects of geography and life history traits on genetic differentiation in benthic marine fishes. *Ecography* **34**(4), 566-575. (doi:10.1111/j.1600-0587.2010.06511.x).

13.   Pauly D., Pullin R.S.V. 1988 Hatching time in spherical, pelagic marine fish eggs in response to temperature and egg size. *Environ Biol Fishes* **21**(2), 261-271.

14.   Leis J.M. 2006 Are larvae of demersal fishes plankton or nekton? *Adv Mar Biol* **51**, 59-141.

15.   Cowen R.K., Sponaugle S. 2009 Larval dispersal and marine population connectivity. *Annual Review of Marine Science* **1**, 443-466.

16.   Pinsky M.L., Palumbi S.R., Andrefouet S., Purkis S.J. 2012 Open and closed seascapes: where does habitat patchiness create populations with high fractions of self-recruitment? *Ecol Appl* **22**(4), 1257-1267.

17.   Mora C., Treml E.A., Roberts J., Crosby K., Roy D., Tittensor D.P. 2012 High connectivity among habitats precludes the relationship between dispersal and range size in tropical reef fishes. *Ecography* **35**, 89-96.

18.   Barber P.H., Palumbi S.R., Erdmann M.V., Moosa M.K. 2000 Biogeography - A marine Wallace's line? *Nature* **406**(6797), 692-693. (doi:10.1038/35021135).

19.   Gaylord B., Gaines S.D. 2000 Temperature or transport? Range limits in marine species mediated solely by flow. *Am Nat* **155**(6), 769-789. (doi:10.1086/303357).

20.   Taylor M.S., Hellberg M.E. 2003 Genetic evidence for local retention of pelagic larvae in a Caribbean reef fish. *Science* **299**, 107-109.

21.   Kingsford M.J., Leis J.M., Shanks A., Lindeman K.C., Morgan S.G., Pineda J. 2002 Sensory environments, larval abilities and local self-recruitment. *Bull Mar Sci* **70**(1), 309-340.

22.   Leis J.M. 2010 Ontogeny of behaviour in larvae of marine demersal fishes. *Ichthyol Res* **57**, 325-342. (doi:10.1007/s10228-010-0177-z).

23.   Leis J.M., Siebeck U.E., Dixson D.L. 2011 How Nemo finds home: the neuroecology of dispersal and of population connectivity in larvae of marine fishes. *Integr Comp Biol* **51**(5), 826-843. (doi:10.1093/icb/icr004).

24.   Jones G.P., Srinivasan M., Almany G.R. 2007 Population connectivity and conservation of marine biodiversity. *Oceanography* **20**(3), 100-111.

25.   Shanks A.L., Eckert G. 2005 Life-history traits and population persistence of California Current fishes and benthic crustaceans; solution of a marine drift paradox. *Ecol Monogr* **75**, 505-524.

26.   Shanks A.L. 2009 Pelagic larval duration and dispersal distance revisited. *Biol Bull Mar Biol Lab Woods Hole* **216**, 373-385.

27.   Hunt von Herbing I. 2002 Effects of temperature on larval fish swimming performance: the importance of physics to physiology. *J Fish Biol* **61**, 865-876.

28.   Fuiman L.A., Batty R.S. 1997 What a drag it is getting cold: partitioning the physical and physiological effects of temperature on fish swimming. *J Exp Biol* **200**, 1745-1755.

29.   Leis J.M., Balma P., Ricoux R., Galzin R. 2012 Ontogeny of swimming ability in the European Sea Bass, *Dicentrarchus labrax* (L.) (Teleostei: Moronidae). *Mar Biol Res* **8**(3), 265-272. (doi:10.1080/17451000.2011.616898).

30.   Cowen R.K., Paris C.B., Sirnivasan A. 2006 Scaling of connectivity in marine populations. *Science* **311**, 522-527.

31.   Doherty P.J., Williams D.M., Sale P.F. 1985 The adaptive significance of larval dispersal in coral reef fishes. *Environ Biol Fishes* **12**(2), 81-90.

32.   Sclafani M., Taggart C.T., Thompson K.R. 1993 Condition, buoyancy and the distribution of larval fish: implications for vertical migration and retention. *J Plankton Res* **15**(4), 413-435.

33.   Llopiz J.K. 2013 Latitudinal and taxonomic patterns in the feeding dynamics of fish larvae: a literature synthesis. *J Mar Syst* **109-110**, 69-77. (doi:10.1016/j.jmarsys.2012.05.002).

34.   Peck M.A., Huebert K.B., Llopiz J.K. 2012 Intrinsic and extrinsic factors driving match-mismatch dynamics during the early life history of marine fishes. *Adv Ecol Res* **47**, 177-302. (doi:10.1016/B978-0-12-398315-2.00003-X).

35.   Gronkjaer P., Clemmesen C., St John M. 1997 Nutritional condition and vertical distribution of Baltic cod larvae. *J Fish Biol* **51**, 352-369.

36.   Tanaka Y., Satoh K., Yamada H., Takebe T., Nikaido H., Shiozawa S. 2008 Assessment of the nutritional status of field-caught larval Pacific bluefin tuna by RNA/DNA ratio based on a starvation experiment of hatchery-reared fish. *J Exp Mar Biol Ecol* **354**(1), 56-64.

37.   Munday P.L., Leis J.M., Lough J.M., Paris C.B., Kingsford M.J., Berumen M.L., Lambrechts J. 2009 Climate change and coral reef connectivity. *Coral Reefs* **28**(2), 379-395. (doi:10.1007/s00338-008-0461-9).

38.   Gallego A., North E.W., Petitgas P., Browman H.I. 2007 Advances in modelling physical-biological interactions in fish early life history. *Mar Ecol Prog Ser* **347**, 121-306

39.   Paris C.B., Cherubin L.M., Cowen R.K. 2007 Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar Ecol Prog Ser* **347**, 285-300.

40.   Lowe W.H., Allendorf F.W. 2010 What can genetics tell us about population connectivity? *Mol Ecol* **19**(15), 3038-3051. (doi:10.1111/j.1365-294X.2010.04688.x).

41.   Leis J.M., van Herwerden L., Patterson H.M. 2011 Estimating connectivity in marine fish populations: what works best? *Oceanogr Mar Biol Annu Rev* **49**, 193-234.
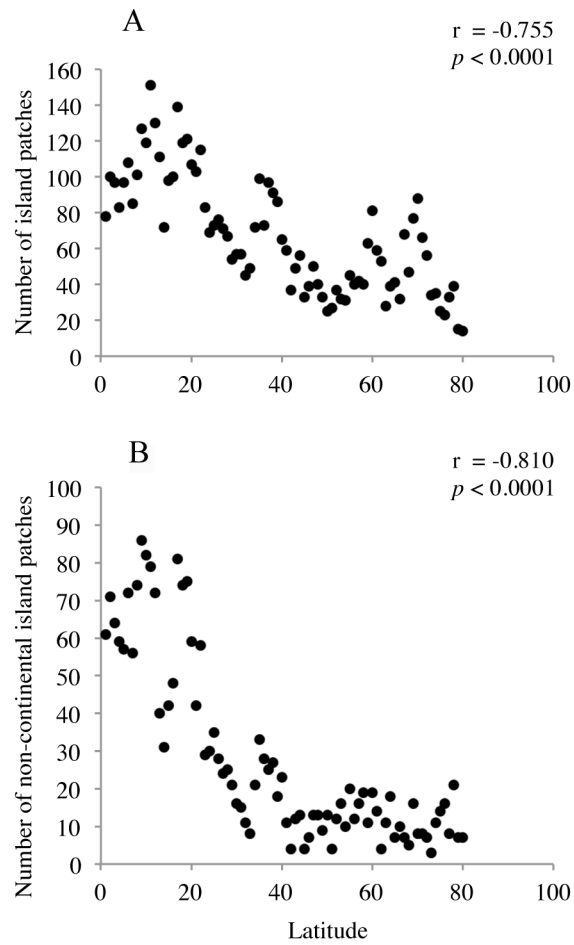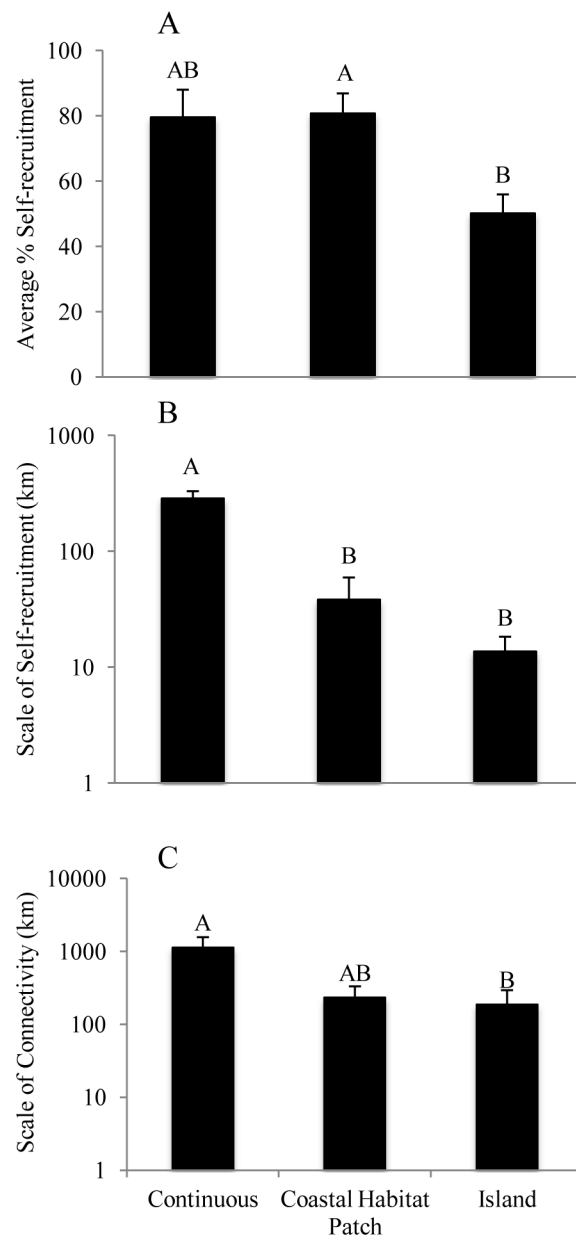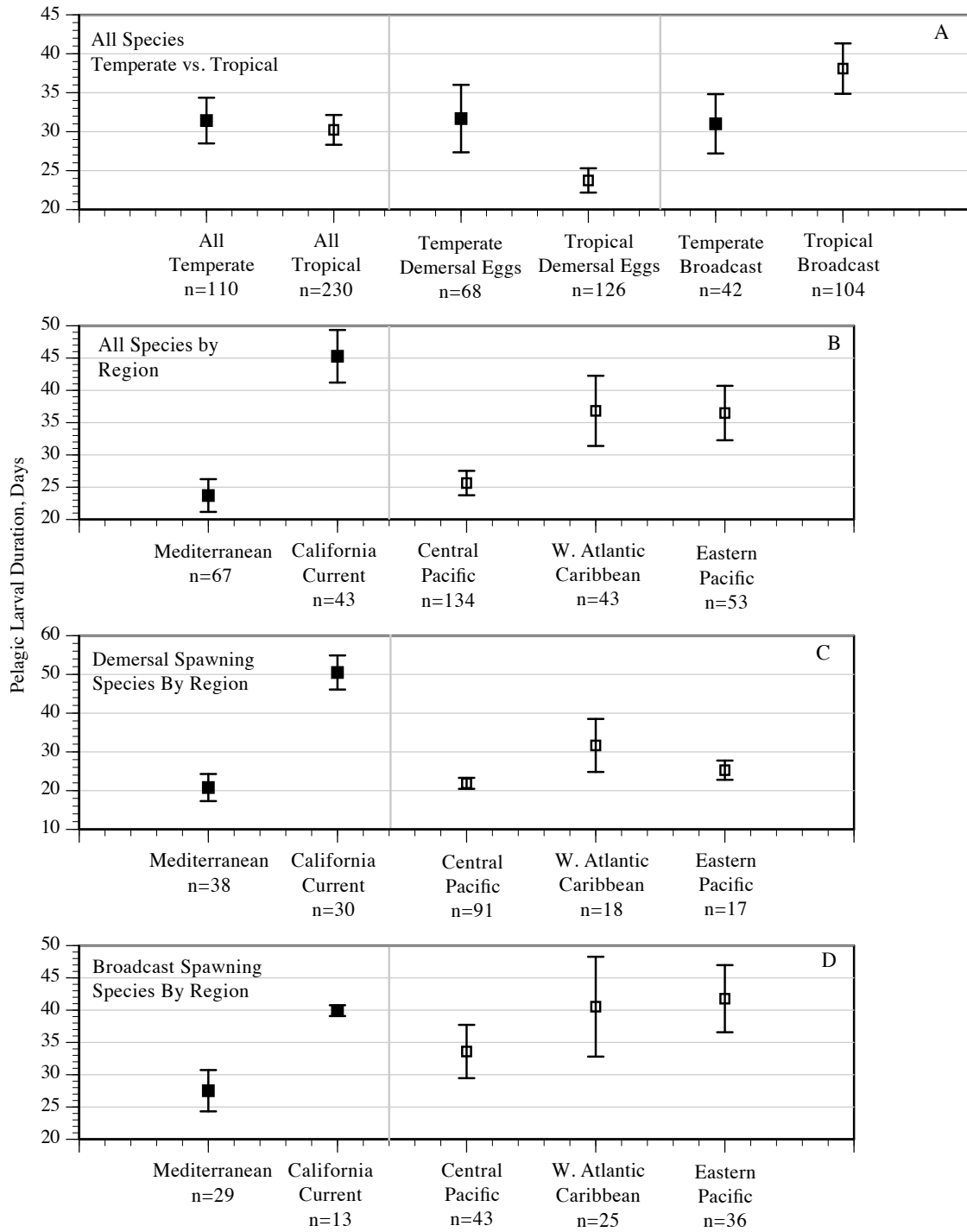
Figure 1

Figure 2

Figure 3

1 **Supplement to Leis et al. Does fish larval dispersal differ between high and**

2 **low latitudes?**

3 Jeffrey M. Leis, Jennifer E. Caselle, Ian R. Bradbury, Trond Kristiansen, Joel K.

4 Llopiz, Michael J. Miller, Mary I. O'Connor, Claire B. Paris, Alan L. Shanks, Susan M.

5 Sogard, Stephen E. Swearer, Eric A. Treml, Russell D. Vetter, Robert R. Warner

6

7

8 **1. INTRODUCTION**

9 A large number of physical and biological variables that might affect larval dispersal

10 vary with latitude, and many were considered in the present study. Some of these

11 variables might theoretically have an influence, but evidence is lacking; some have

12 been considered in previous studies to have an influence, but lack theoretical or

13 empirical support; and for some, there is support for an influence. This supplement

14 includes background information and analyses for each of the main factors

15 mentioned in the text. For each category, we also provide caveats about underlying

16 assumptions and alternative interpretations. We close with a consideration of bias

17 introduced by differences in methodology or target species.

18

19 **2. BIOLOGICAL DIFFERENCES**

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

21 *Taxonomic composition and biogeography*: Warm waters are dominated by

22 Anguilliformes, holocentroid Beryciformes, Tetraodontiformes, and the Perciform

23 suborders Percoidei, Blennioidei, Gobioidei, Labroidei, and Acanthuroidei. These

24 taxa constitute 73 to 84% of the demersal, teleost shorefish species in the three

25 tropical areas shown in Table Sup 1. In contrast, cold waters are dominated by

26 Gadiformes, Perciform suborders Zoarcoidei and Notothenoidei, and by the

27 Scorpaeniform suborders Cottoidei and Hexagrammoidei and scorpaenid genus

28 *Sebastes*. These taxa constitute 73 to over 90% of the demersal, teleost shorefish

29 species in the three cold-water areas listed in Table Sup 1. Flatfishes

30 (Pleuronectiformes) of most families are essentially warm water in distribution, but

31 Achiropsettidae, Pleuronectidae, and to a lesser extent, Scophthalmidae have

32 colder-water distributions. Unfortunately, there is very little information about taxon-

33 specific dispersal differences, and given the non-independence of taxa and

34 distributions, without this information it will be difficult to determine if any identified

35 differences were due to adaptations to location-dependent physical and biological

36 conditions, or due to lineage-related factors. Therefore, caution is required when

37 attributing causes to any apparent differences in larval dispersal and connectivity

38 between latitudes.

39

40 *PLD*: Measurement of PLD (pelagic larval duration) is typically estimated by

41 counting daily rings in otoliths either at settlement or inside a settlement mark [1].

42 The PLD values used herein were from the published sources detailed below and

43 were culled from this literature only on the basis of adult habitat, and by eliminating

44 pelagic species. Demersal fish Orders and Suborders with primarily warm water

45 distributions (as identified in previous section) appear to have lower mean PLD

46 values than do taxa with primarily cold-water distributions. The PLD data in [2] and

47 [3], which addressed 45 California Current and 727 largely tropical species,

48 respectively, were used to determine mean values at the Ordinal and Subordinal

49 level. These are not necessarily a representative sample of the species belonging to

50 the Orders and Suborders identified as having either primarily warm or cold-water

51 distributions above, so these data should be interpreted cautiously. The taxa and

52 the number of PLD estimates in each are: warm water taxa, Anguilliformes (marine

53 eels, i.e., not including *Anguilla*) 4, Holocentroidei 10, Acanthuroidei 81, Blennioidei

54 20, Gobioidei 36, Percoidei 87, Labroidei (Labridae) 213, Labroidei (Pomacentridae)

55 265, Scorpaenoidei (*Scorpaena*) 2, Tetraodontiformes 9; cold water taxa,

56 Gadiformes 9, Zoarcoidei 6, Cottoidei 13, Scorpaenoidei (*Sebastes*) 17. The mean

57 values for each taxon are shown in figure Sup 1. The mean values for each cold-

58 water taxon (55-108 days) are all larger than the mean values for warm water taxa

59 (23-52 days), with the exception of non-anguillid Anguilliformes, with mean of 118

60 days, more than twice that of other warm-water taxa. A challenge to interpretation of

61 this analysis is that the temperate-tropical comparisons are biased by habitat

62 differences. At least half of the temperate species in [2] were continental shelf and

63 slope species whereas nearly all of the tropical species in [3] were from shallow

64 reefs. Given that Shanks and Eckert [2] found large habitat-related differences in a

65 number of life history traits (including PLD), ascribing PLD differences to a latitudinal

66 effect without taking habitat into account is problematical.

67

68 Although these data indicate there is a taxonomic component to PLD, it is important

69 to note that there were more than 727 PLD values for warm-water taxa, and only 45

70 values for cold-water taxa, providing further reason to treat the data cautiously. The

71 very high PLD values for the marine eels, a largely warm-water group, are also an

72 indication that general statements about latitudinal differences in PLD will likely be

73 difficult to sustain. But here, too, the fact that only four values were available for a

74 group with about 800 species provides ample reason for caution, and indicates how

75 understudied marine eels are.

76

77   We used an ecological-based definition of PLD (i.e., the early life-history period

78   before settlement [4]), which clearly has meaning only for demersal species with a

79   pelagic larval stage (it may also include juveniles if they remain pelagic, e.g., many

80   Tetraodontiform fishes and the Scorpaeniform genus *Sebastes*). The use of an

81   ecological criterion avoids ambiguity introduced by morphological criteria (i.e., the

82   early-life history period before a particular set of morphological milestones are

83   reached, for example, formation of all fins, or scales). The latter can be relevant for

84   both demersal and pelagic species, but we avoid it precisely because we focus on

85   the presettlement stages of demersal fishes.

86

87   *Spawning mode*: Spawning mode, in particular the lack of a pelagic egg (i.e.,

88   demersal eggs, brooded eggs, or viviparity), has been identified as an important

89   factor in genetic connectivity or larval dispersal in two synthetic studies that

90   assessed a broad range of published genetic and PLD data [5],[6]. However, the

91   study of Riginos et al. [5] was based primarily on warm-water species, with only 14 of

92   the 148 demersal teleost species considered to have cold-water distributions.

93   Therefore, the conclusions of [5] about the influence of spawning mode on genetic

94   connectivity may not apply to cold-water taxa. Further, about half of the warm-water

95   species in the Riginos et al. [5] data set spawn demersal eggs, a value considerably

96   higher than the proportion of demersal-spawning species in warm-water faunas

97   (figure Sup 2). Clearly, it is important to understand how spawning mode varies with

98   latitude.

99

100   The percentage of species with pelagic eggs varies little with latitude until high

101   latitudes (roughly 50°N, but possibly at higher latitudes in the southern hemisphere)

102   are reached, after which a strong shift occurs to demersal eggs (figure Sup 2). High-

103   latitude fish assemblages are dominated by species with demersal eggs (Fig Sup2),

104   and in most cases, spawning type is consistent within families. However, several

105   exceptions exist, and in these, there is a trend within taxa toward demersal eggs at

106   higher latitudes. Some examples where taxa from higher latitudes are less likely to

107   be broadcast spawners include the sebastine scorpaenids, a temperate group, which

108   is exclusively viviparous, whereas other scorpaenid taxa, which are essentially

109   tropical, are broadcast spawners [7]; the temperate labrid tribe Labriini, which is

110   dominated by demersal-egg species, whereas all other labrids are broadcast

111   spawners [8]; and the important commercial taxa, Pleuronectidae and *Gadus*, where

112   some species are broadcast spawners, and other, more boreal species, spawn

113   demersal eggs [9].

114

115   There is also a trend for fish eggs to be larger at higher latitudes, but this seems to

116   apply across all latitudes only for demersal eggs. For pelagic eggs, there is little

117   trend between the tropics and about 50° North, but poleward of this, pelagic eggs are

118   larger [10]. It is not known if the same relationship applies in the southern

119   hemisphere. Egg size and pre-hatching period are typically correlated, so these

120   times should be longer for northern-hemisphere, high latitude species with pelagic

121   eggs. Equally, dispersal distances due to passive drift of eggs should be longer than

122   for species south of 50°N. In addition, independent of egg size, lower temperatures

123   are expected to increase the pre-hatching period, which may lead to a latitudinal

124   gradient in pre-hatch times and therefore dispersal distances between spawning and

125   hatching, assuming there is no adaptation.

126

127   Another potential latitudinal factor influencing larval dispersal is the timing of

128   spawning. Many tropical demersal species have a protracted spawning season,

129   whereas temperate species tend to have a narrow season, presumably to coincide

130   with appropriate biological and physical oceanographic conditions [11]. For

131   temperate species, shifts in temperature may shift the seasonal timing of spawning.

132   The flounder *Platichthys flesus*, for example, spawns 1-2 months earlier in years with

133   cooler than normal temperatures [12]. In other species, spawning or occurrence of

134   larvae is delayed by cooler temperatures [13],[14],[15]. Larvae of spring-spawning

135   species can appear in the plankton earlier in cold years whereas larvae of summer-

136   spawning species appear later [16]. Sheaves [17] noted a latitudinal pattern within

137   the family Sparidae, with greater variation in spawning timing for more temperate

138   species. Such shifts in phenology will affect potential dispersal if the oceanographic

139   environment experienced by eggs/larvae differs from that typically experienced.

140   Spawning that is temperature-induced could result in a mismatch of spawning timing

141   with timing of food availability or transport mechanisms. If so, this might result in

142   more variable dispersal distances and directions, and thus a larger scale of larval

143   dispersal in temperate than in tropical waters (also see Feeding below). In upwelling

144   systems like the California Current, the timing of spawning has long been recognized

145   as a critical determinant of larval success [18], and reproductive patterns of resident

146   fishes appear to have evolved to facilitate completion of the life cycle and minimize

147   advective losses of larvae under 'normal' oceanographic conditions [2].

148

149 **(b)** *Diadromy*

150 Diadromy varies with latitude, albeit differently in its different forms, but there is only

151 limited evidence that connectivity of diadromous species varies with latitude. Life

152 histories of diadromous fishes are split between fresh and marine waters. We

153 consider only species with marine larvae, which excludes anadromous taxa such as

154 salmonids, which spend their early life history in freshwater. However, anadromy is

155 largely confined to temperate latitudes, particularly in the northern hemisphere, with

156 few tropical anadromous species, primarily Hilsa shads [19]. This does constitute a

157 latitudinal difference, but an unbalanced one because there are far more

158 anadromous fish species in the northern than southern hemisphere.

159

160 Catadromous species such as anguillid eels, two species of Australian percichthyids

161 (warm temperate), and the tropical latids, centropomids and kuhliids migrate to

162 estuaries or the sea to reproduce and the young enter freshwater after larval growth

163 in the ocean. There are only a few temperate catadromous species, and other than

164 the anguillid eels, there is no clear evidence of latitudinal differences in dispersal or

165 connectivity. Anguillid eels, however, provide a clear example: temperate anguillid

166 species have larger scales of larval dispersal and population connectivity than do

167 most tropical species. All five primarily temperate anguillid species display little

168 genetic structure across their freshwater adult ranges. Their long-lived larvae are

169 transported by currents 1000s of km from discrete tropical, oceanic spawning areas

170 [20],[21],[22]. *Anguilla reinhartii*, with a tropical to warm temperate adult range on

171 the western side of the Coral and Tasman Seas, is apparently similar to the

172 temperate species in having a discrete tropical oceanic spawning area and no

173 apparent genetic structure [23]. *Anguilla marmorata* and *A. bicolor* are primarily

7

174 tropical species that spawn in the Indian and Pacific Oceans and have more than

175 one genetic lineage or spawning population [24, 25],[26],[27] within an ocean basin.

176 The other tropical *Anguilla* species each have limited adult ranges and one or two

177 local spawning areas [28]. They have shorter larval durations and smaller maximum

178 larval sizes than temperate species [29], [30].

179

180 Amphidromous species such as Sicydiinae gobiids (primarily tropical), some

181 temperate cottids, and the temperate Osmeriform families Galaxiidae and

182 Plecoglossidae spawn in freshwater, with their larvae moving downstream to the

183 ocean for a larval growth phase after which they return to freshwater for a juvenile

184 growth phase [31] [32]. Amphidromous fishes are found primarily in tropical and

185 subtropical islands, but a few extend to temperate islands such as Japan and New

186 Zealand [33]. Most amphidromous species have long PLDs (e.g., [32],[34]) and

187 widespread larvae compared with most marine fishes, and they have broad genetic

188 connectivity (e.g., [35],[36],[37]). In contrast, a temperate Japanese sculpin species

189 with a short PLD has clear population structure [38]. However, no clear latitudinal

190 trend in larval duration, dispersal, or connectivity is evident in the species that have

191 been studied.

192

193 **3. PHYSICAL DIFFERENCES**

194 **(a) *Oceanography***

195 Generally, stronger winds and greater eddy propagation occur in mid to high

196 latitudes than in the tropics [39],[40]. This can affect dispersal both directly and

197 indirectly. Latitudinal increases in both mixed layer depth (MLD) and eddy kinetic

198 energy (EKE) tend to increase diffusion, which influences the variation in dispersal

199   distances, but an increase in MLD alone would tend to increase dispersal distance

200   via its interaction with both diel and ontogenetic vertical migration.

201

202   Although seasonal variation in tropical MLD is generally low in any region, there are

203   large differences in MLD among different tropical regions [41]. Temperate species

204   that spawn when MLD decreases in spring and summer are expected to have

205   shorter dispersal distances than those that spawn in winter, and this seasonal

206   difference should be reinforced by the higher ML temperatures of spring and

207   summer. This contrast may increase among-species variation in dispersal at higher

208   latitudes.

209

210   Vertical migration behaviour of larval fish can influence dispersal differentially

211   between tropical and temperate regions. Most fish larvae dwell within the upper 50-

212   100 m of the water column in both tropical [42],[43],[44],[45] and temperate [46],[47]

213   environments and are able to modify their vertical position behaviourally. Where

214   currents vary in speed and direction with depth (e.g., [48],[49]), larval fish in the

215   surface layer can be advected in a different direction or speed than deeper-living

216   larvae. Therefore, vertical distribution behaviour by larvae can affect their integrated

217   drift trajectories and geographic dispersal [50],[51],[52],[53]. Larval fish released at

218   the same spawning ground, but that occupied different parts of the water column,

219   become separated by hundreds of kilometers after a few months drift [54],[55],[56].

220   In both temperate and tropical regions, warmer temperatures and low winds during

221   the summer cause an increase in stratification and a shallowing of the MLD. The

222   strongest currents generally occur in the ocean's surface mixed layer and decrease

223   with depth, particularly in the pycnocline. Stratification in the upper water column and

224   MLD can influence the impact of larval vertical migration on dispersal and

225   connectivity [42],[52],[57]. In general, where MLD is large (e.g., in many temperate

226   areas during times other than summer) dispersal distances should be relatively long,

227   creating larger connectivity networks.

228

229   The increase in kinetic energy, and therefore eddy generation, with latitude seems

230   directly linked to the Coriolis-dependent geostrophic motion, which increases with

231   latitude, and with wind, which is strongest at mid to high latitudes [58]. The size of

232   eddies decreases with latitude because the intrinsic length scale of baroclinic

233   instabilities is directly related to latitudinal variation of Coriolis force [58], and as a

234   result the typical size of eddies decreases from 200 km at mid latitudes to 100 km at

235   high latitudes. The strongest variation in eddy kinetic energy (EKE) and amplitude is

236   associated with western boundary currents [59], resulting in within-latitude regional

237   EKE differences. Eddies in the tropics are generated at large scales by Rossby

238   waves (very low-frequency waves in the ocean's surface and thermocline), tropical

239   instability waves [60], or by the interaction of currents with topography such as capes

240   or the reef edges that can result in shedding of sub-mesoscale eddies [61],[62].

241   Thus, there are clear differences in eddy formation and size with latitude. Although

242   slow-moving eddies can retain larvae near a source (e.g., [63]), fast-moving eddies

243   can move larvae away from a source [64], so it is difficult to generalize about how

244   latitudinal differences in eddies might influence larval dispersal.

245

246   Temperate regions are characterized by the widest seasonal temperature

247   ranges([41]), and frequent storms and low-pressure systems that mix the water

248   column, and can have major impacts on the dispersal of larvae [65],[63],[66].

249   Tropical regions have equivalent low-pressure systems, that can disperse larval fish

250   from their source relatively quickly, but tropical cyclones are, short-term, focused

251   storms that are much less frequent and followed by long relatively quiet periods [67].

252

253   Advection alone moves larvae away from the source whereas diffusion by itself

254   increases variance in dispersal distance, but not the mean [68] (figure Sup 3). Zonal

255   advection (i.e., along the east-west axis) in the surface layers increase with latitude,

256   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-

258   and high-latitudes and meridionally in the tropics. East-west spreading rate

259   increases with time in the tropics but not at high latitudes [70]. Therefore, super-

260   diffusive east-west spreading should be expected at low latitudes only for species

261   with PLDs, like eels, but not for species with short PLDs.

262

263   Ekman-related coastal upwelling cells may be important for nearshore retention of

264   larvae [63] because they allow larvae that move offshore in Ekman near-surface flow

265   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.

267   Although Coriolis force increases with latitude, wind strength is maximal in mid

268   latitudes, so it is expected that Ekman-cell retention would be most important at mid

269   latitudes, and least important at low latitudes. If so, away from the tropics this

270   phenomenon should result in a decrease in the scale of dispersal for species that

271   utilize these cells. However, intensification of Ekman upwelling should result in

272   greater offshore transport of shallow-living larvae. Although these arguments are

273   theoretically sound [73], there is little evidence that many species do utilize Ekman-

274   cell retention in nature [72],[74].

275

276   There is currently no empirical evidence that any of these identified oceanographic

277   factors result in latitudinal differences in larval dispersal. By identifying their potential

278   to influence larval dispersal, we hope to stimulate research into their effects.

279

280   **(b) *Habitat Fragmentation***

281   Fish larvae in warm water have good swimming abilities and can detect settlement

282   habitat over a range of scales [75],[76],[77]), although information on larval sensory

283   abilities in cold water is lacking. If these abilities are used to remain close to suitable

284   benthic habitat (e.g., orientation behaviour, [78]), larvae from islands would likely

285   remain near their origin by orientated swimming, because they are likely to receive

286   sensory information about suitable benthic habitat only from the closest island. In

287   contrast, a larva from coastal waters along a continental margin will receive sensory

288   information about suitable benthic habitat as long as it minimizes offshore dispersion,

289   even if along-shore movement is large. Hence, there is an expectation for less self-

290   recruitment and greater population connectivity along continental margins than

291   among islands (e.g., [79]).

292

293   The degree to which habitat patchiness influences dispersal distance in either

294   tropical or temperate latitudes is largely untested. To explore this question, 20 recent

295   studies of demersal fishes (Table SUP2) that used otolith geochemistry to estimate

296   demographic connectivity were categorized based on whether the target species

297   lived in: a) relatively continuous habitat (e.g., soft sediments in shelf waters); b)

298   coastal habitat patches; or c) offshore islands. For each study we then calculated:

299   (1) the % self-recruitment observed (or stated); (2) the spatial scale over which self-

300   recruitment was estimated (i.e., the scale at which the population/stock was defined);

301   and (3) the spatial scale of observed connectivity. Whether these three metrics

302   differed among landscapes was tested by ANOVA.

303

304   Levels of self-recruitment in a demographic context were high (mean: 63%) and

305   were 30% greater in continental than island habitats ($F_{2,13}$ = 7.045, p = 0.009; main

306   text, figure 1A). On first inspection, this appears to contradict the reasoning that

307   dispersal should be shorter in island areas. However, the spatial scale over which

308   self-recruitment was estimated differed among landscape contexts ($F_{2,15}$ = 9.636, p =

309   0.002): self-recruitment occurred in continuous habitat at ~300 km scales whereas

310   for both the patchily distributed landscape contexts, self-recruitment occurred at

311   scales <40km (main text, figure 1B). Once we controlled for spatial extents of each

312   study, the mean scales of connectivity differed among contexts, with species in

313   patchy habitats dispersing over about 60 to 100 km, whereas species in continuous

314   habitats dispersed about 900 km (main text, figure 1C). Combined, these data

315   suggest that larval dispersal may be more restricted in fragmented habitats.

316

317   Are fragmented habitats more common in the tropics? To examine whether

318   landscape context plays a role in driving differences in population connectivity

319   between tropical and temperate species, we assembled a spatial database

320   consisting of the Global Self-consistent, Hierarchical, High-resolution Shoreline

321   (GSHHS; [80]) and a lattice of one-degree latitude boundaries between +/- 80°

322   latitude (Mollweide equal-area cylindrical projection). We determined the distribution

323   of islands as a function of latitude.

324

325   To account for the observation that all suitable habitats within the sensory detection

326   limit of larvae may not be perceived by larvae as distinct, we generalized the global

327   shoreline data to match this scale of habitat detection. If larvae can detect habitat

328   patches at this spatial scale, then behavioural barriers to dispersal and their impact

329   on connectivity will be observed at scales larger than this. For this analysis we

330   chose 5 km, which is within the range estimated for reef fishes [81, 82], although

331   using either shorter (2.5 km) or longer (10 km) detection limits resulted in almost

332   identical results. This generalization resulted in a grid (at 2.5 km resolution) where

333   cell values quantify the amount of island-only habitat within the 5 km sensory radius

334   from the centre of each cell. Island habitat cells that fell within this sensory zone

335   were then aggregated/merged into contiguous island patches. Using the same

336   sensory detection limit, we also reclassified island habitat patches to continental

337   habitat if they were within the 5 km detection limit from continental shorelines. Island

338   habitat patches were intersected with the latitude lattice to calculate the median

339   latitude of each patch. Changes in island number with latitude were analysed by

340   correlation. Both all-island patches (i.e., all islands regardless of distance from a

341   continental margin) and all non-continental island patches (i.e. island patches greater

342   than 5 km from a continental margin) declined in number with increasing latitude

343   (main text, figure 2).

344

345   **4. BIOPHYSICAL DIFFERENCES**

346   **(a) *Temperature and larval behaviour***

347 Development of swimming in larvae of demersal fishes has been recently reviewed

348 [76, 83]. Larvae of taxa from cold-temperate waters (Cottidae, Gadidae,

349 Pleuronectidae) had some of the slowest critical speeds [84], and consistently swam

350 at about 5 body lengths per second (BL s^{-1}). Development of critical speed was

351 more variable in larvae of taxa from warm-temperate waters (Moronidae,

352 Percichthyidae, Sciaenidae, Sparidae). Larvae of these taxa were relatively slow

353 when small (5–10 cm s^{-1}), but at sizes larger than 5 mm, sciaenids swam at 10 BL s^{-}

354 ^{1}, whereas sparids and percichthyids larger than 7–8 mm are able to swim at 15–20

355 BL s^{-1}. Moronid larvae, in contrast, were slow (<10 BL s^{-1}) until larger than 15 mm,

356 after which they swam at about 15 BL s^{-1}. Aside from the serranids and lutjanids

357 which were slow at smaller sizes, but eventually were among the fastest larvae,

358 tropical taxa had larvae that were fast throughout development, with critical speeds

359 faster than 10 cm s^{-1} and with most species swimming at 15–20 BL s^{-1} for much of

360 their larval phase, with some reaching almost 30 BL s^{-1}. Fisher [85] suggests that

361 most coral-reef fish families have sufficient swimming capabilities to be able to

362 influence their dispersal outcomes substantially for over 50% of their larval phase.

363 For temperate *Sebastes*, in contrast, which may have PLDs of up to 6 months, the

364 potential for using directed horizontal swimming to influence dispersal may not be

365 developed until the pelagic juvenile stage at 20-30 mm (see below).

366

367 Although the swimming data on warm temperate species were from outside tropical

368 latitudes, the experimental temperatures (19-27°C) overlap those of the tropical

369 species (26-31°C). The closeness of these temperature ranges could result in the

370 similarity in swimming performance. In contrast, a large gap exists between these

371 and the experimental temperatures for cold temperate species (3-10°C), contributing

372   to the differences in swimming performance. Measures of swimming performance

373   for larvae of species that live at temperatures within this gap are needed.

374

375   Within species, the expected pattern of increased swimming speed with increased

376   temperatures has been observed in larvae of several temperate fish species

377   [86],[87],[88],[84],[89, 90], but a cold temperate species of sculpin (Cottidae) had the

378   opposite response [84], and a tropical damselfish had no temperature-induced

379   change in swimming speed [91]. Physiological responses to temperature are

380   typically dome-shaped, and the apparent inconsistency in the limited empirical data

381   might be due to differences in the portion of the temperature-response curve that

382   was under study.

383

384   It is expected not only that the development of swimming capacity is slower in cold

385   temperate species due to protracted morphological development, but there should

386   also be an increasing ontogenetic divergence of swimming capabilities [76]. Larvae

387   of live-bearing *Sebastes* rockfishes are released at a size of 4-6 mm with incomplete

388   fins and have critical swimming speeds of < 2 cm s^{-1} at 12°C [92]. In contrast,

389   tropical and warm temperate larvae at this size have more advanced fin

390   development and U_{crit} values of 2-10 cm s^{-1} [93], but the extent to which these

391   swimming speed differences are due to temperature or to fin development is unclear.

392   The size-dependent rate of increase in swimming speed of cold temperate species

393   lags behind that of tropical species, as expected. For each mm increase in size,

394   tropical serranids (*Epinephelus* spp.) swam faster by 2.1-2.6 cm s^{-1} [76], whereas the

395   increase for the temperate serranid *Paralabrax clathratus* and several species of

396   *Sebastes* was only 1.0 cm s^{-1} [92]. Many tropical species settle at small sizes (<15

397 mm), and have speeds equivalent to warm temperate species at similar sizes,

398 assuming that all fins have formed. Larvae of some species attain relatively large

399 sizes (> 20 mm) before settlement. The tropical species are fast swimmers, with

400 critical speeds in excess of 20 BL s^{-1} by the time they settle [76, 94], but among

401 temperate species, data are available only for species of the scorpaeniform genus

402 *Sebastes*, which at 25-30 mm, have critical speeds of about half those of tropical

403 species [92].

404

405 Swimming endurance of many settlement-stage tropical fish larvae is very high [95],

406 but information on the development of endurance is limited, especially for temperate

407 species. There was no obvious difference in swimming endurance between warm-

408 temperate and tropical species, except that several tropical species attained greater

409 endurance prior to settlement primarily because they settle at larger sizes [76]. There

410 are no endurance data for larvae of cold-temperate species.

411

412 A critical aspect of behaviour-influenced dispersal is performance in relation to age

413 (or time in the water column), not to size. The experimental data are based largely

414 on reared larvae with growth rates that differ from those found naturally, so a simple

415 conversion of size to age is not generally possible. However, it is generally expected

416 that growth rates are temperature-dependent, so converting performance from a size

417 to an age basis is expected to increase relative differences in performance between

418 warm and cold-water species. More information is required on field-based growth

419 rates of larvae of demersal fishes.

420

421   The identified differences in swimming performance are consistent with theoretical

422   predictions and could arise from differences in phylogeny, sea water viscosity,

423   temperature and associated physiological responses or to some combination. At

424   present, none can be eliminated or shown to be relatively more important to

425   dispersal. Although the causes for the differences are not clear, the most relevant

426   consideration is what a larva does in conditions it typically encounters in the sea.

427

428   **(b)** *Temperature, feeding, and mortality*

429   Feeding can influence larval survival in several ways. Clearly, food availability must

430   be sufficient to prevent starvation. Spatial or temporal variability in prey levels above

431   or below a starvation threshold will translate to concurrent variability in the

432   proportions of larvae surviving to settle, thereby influencing larval replenishment and

433   connectivity. Suboptimal prey levels may influence larval growth rate [96],[97], ability

434   to avoid predators [98],[99] or swimming endurance [100], [101]. Slower growth can

435   extend the larval period, thus increasing cumulative mortality and reducing the

436   numbers of settlers [102],[103],[104]. Similarly, slower growth extends the duration

437   of the more passive early stages and thus the time before larvae are able to

438   influence dispersal.

439

440   Feeding incidence (FI; the proportion of a sample of larvae with food present in the

441   gut) is a commonly reported proxy for larval fish feeding success. Across published

442   studies, average FIs of larvae from coastal and offshore waters were significantly

443   higher in taxa from lower latitudes (30°S–30°N; median FI 96%) than from middle

444   (30–45°N/S; median FI 80%) or high (>45°N/S; median FI 72%) latitudes [105].

445   These differences also hold when comparing within taxonomic Orders. This, along

446   with observed differences in gut evacuation rates, indicates feeding rates are higher

447   in lower latitudes, which would be expected (because of greater metabolic demands)

448   if levels of starvation mortality were similar among latitudinal regions.

449

450   Zooplankton prey of fish larvae differ with latitude and there are indications of greater

451   prey selectivity in lower latitudes [105]. Greater diversity of larval-fish prey and

452   apparent finer niche partitioning in lower latitudes [105] as described in the next

453   paragraph, could lead to species-dependent dispersal patterns if variation in

454   abundances of the preferred prey of different taxa does not covary, as some

455   evidence suggests (Llopiz and Cowen, unpublished data). If so, patterns of larval

456   dispersal and degrees of connectivity may be less consistent across taxa in lower

457   latitudes even when adult habitat, spawning behaviours, and PLDs are similar—

458   clearly adding to the challenges of accurately modeling the successful transport of a

459   particular species.

460

461   The frequency with which calanoid copepods and copepod nauplii dominate the diets

462   of larval fishes decreases towards the equator, while the importance of

463   appendicularians and several genera of cyclopoids increases. The diversity of

464   dominant prey types also increases towards the equator. Such prey include

465   cladocerans, bivalve larvae, pteropods, and ostracods, which rarely if ever compose

466   the majority of a taxon's diet in high latitudes. Diets of low-latitude larvae are more

467   often consistent in time, space, and ontogeny, and are often unique to larvae of a

468   given taxon [105],[106],[107]. These factors, together with comparisons of diets to

469   ambient proportions of zooplankton prey types, indicate greater degrees of prey

470   selectivity in lower latitudes, with some evidence that highly selective larvae are

471   'hard-wired' to consume specific prey types and have a limited capacity for prey

472   switching when preferred prey availability is low [106].

473

474   Latitudinal differences in the seasonal cycles of primary and secondary productivity

475   may also yield trophic-related distinctions in larval dispersal and connectivity. In

476   higher latitudes, where match-mismatch dynamics of zooplankton and fish larvae

477   can have an important influence on larval fish growth and survival [108],[109], the

478   timing and locations of optimal prey availability may occur over narrower spatial and

479   temporal ranges than in lower latitudes. This could lead to greater interannual

480   variability in growth, survival, and dispersal, and therefore connectivity at higher

481   latitudes. In contrast, the more stable levels of productivity in the tropics, in

482   conjunction with protracted spawning seasons, could result in more consistent

483   among-year spatial patterns in larval dispersal.

484

485   Some studies have suggested higher instantaneous mortality rates for fish larvae in

486   warm temperatures [110], and higher predation pressure in clear tropical waters

487   [111]. Further, a general trend toward stronger predation in the tropics has been

488   suggested for other taxa including marine consumers [112],[113],[114]. In contrast,

489   expected (but not documented) longer larval durations in cold water would imply

490   higher cumulative larval mortality [115]. Thus, physiological processes underpinning

491   mortality rates suggest geographic variation in mortality due to temperature, but it

492   remains unclear whether there is an overall trend that could influence connectivity.

493

494   **(c) *Temperature, development, and PLD***

495 Previous work showed that PLD differed among adult habitat types [2]; for example,

496 average PLD of nearshore (<30 m adult depth) California Current fishes was much

497 less than PLD of shelf/slope species regardless of spawning mode. Because

498 differences in adult habitat can affect PLD, our analysis was based on tropical and

499 warm temperate (<50° from the equator), nearshore reef fishes only, because

500 sufficient data for higher latitudes or other habitats were not available. A notable

501 limitation is the very restricted PLD data available from cold temperate nearshore

502 fishes and from tropical shelf species.

503

504 Shanks and Eckert [2] compared a diversity of life history characteristics, including

505 PLDs, of fish and benthic decapod species from the California Current and found

506 large differences based on adult habitat. The data sorted into three groups:

507 shelf/slope species, shallow water species (< 30 m), and shallow water species from

508 the Southern California Bight. Shanks and Eckert suggested that differences in the

509 life history traits were adaptations to the local hydrodynamics associated with each

510 adult habitat. We attempted to investigate PLDs of temperate and tropical

511 shelf/slope fishes, and although we could find adequate data for temperate species,

512 we could not find enough data on tropical shelf/slope species to support an analysis.

513 Similarly, data on cold temperate species were too limited for testing. Therefore,

514 values of PLD for shallow water reef fishes from temperate and tropical locations

515 were compiled for the Mediterranean and Eastern Atlantic [116],[117],[118],[119], the

516 California Current [2], the Caribbean and Western Atlantic

517 [120],[121],[122],[123],[124],[125],[126],[127],[128],[129],[130],[131],[132]), the

518 tropical Eastern Pacific [131],[133],[132],[134],[135], and the central Pacific

519 [1],[136],[136],[132]. We assembled data on 110 warm temperate and 230 tropical

520 species from 23 publications. The publications were found by a search of Aquatic

521 Sciences and Fisheries Abstracts back to 1980 using the terms PLD and Pelagic

522 Larval Duration. In addition, the reference section of papers that reviewed PLD were

523 scanned for additional publications, and Science Citation Index was searched for

524 publications that cited the more important PLD papers. The species found in this

525 search were included in the analysis if the data were collected in a similar fashion

526 (e.g., shallow water/reef species, PLD from otoliths) from defined geographic

527 settings (e.g., California Current, Caribbean, Mediterranean, etc.). The mode of

528 reproduction (i.e., live birth, broadcast spawning, or nesting) of the species that fit

529 within the habitat and geographic range criteria was determined from a number of

530 sources including reference books on California Current species, Fish Base and the

531 original publications.

532

533 PLD of warm temperate and tropical reef fishes did not differ (all areas and spawning

534 types pooled: main text, figure 3A, for statistics see main text, figure 3 caption), but

535 when the species were compared by reproductive mode (demersal vs. broadcast

536 spawning), PLDs of tropical demersal and broadcast spawners were significantly

537 shorter and longer, respectively, than warm temperate species (main text figure 3A).

538 However, when the data were analysed by geographic location, consistent

539 differences between PLDs in warm temperate and tropical species were not found.

540 If PLDs are separated by region rather than reproductive mode (main text figure 3B),

541 PLDs of warm temperate Mediterranean species are significantly shorter than

542 temperate California Current species, even though the latitudes are similar, whereas

543 the PLDs of tropical central Pacific species are significantly shorter than those of

544 Caribbean and tropical Eastern Pacific species, which did not differ from each other.

545 Comparing warm temperate to tropical, the average PLDs for Mediterranean and

546 central Pacific species were similar whereas average PLD for California Current

547 species was significantly longer than in any other region, temperate or tropical.

548 When divided by reproductive mode, the demersal-spawning species average PLD

549 from the Mediterranean was significantly shorter than in the California Current (main

550 text, figure 3C), but similar to the central Pacific and eastern Pacific and only slightly

551 shorter than PLDs in the Caribbean. The broadcast-spawning-species average PLD

552 from the Mediterranean was again significantly shorter than in the California Current

553 and was also shorter than in the three tropical regions (main text figure 3D). The

554 broadcast-spawning species mean PLD for the California Current was not different

555 from the Caribbean or Eastern Pacific, but was significantly longer than the central

556 Pacific.

557

558 The most striking differences in PLDs were not between temperate and tropical

559 systems, but between two temperate regions: for both demersal and broadcast

560 spawning species, Mediterranean PLDs were much shorter than in the California

561 Current. The Mediterranean is not particularly warm, but Mediterranean PLDs were

562 either the shortest or not significantly different from the tropical areas. Further,

563 Caribbean and California Current pelagic-egg PLDs did not differ, showing there is

564 not a simple relationship between PLD and temperature.

565

566 The main text points out that the geographic patterns we found in PLD are not

567 expected based on sea-surface temperature alone. The temperature data (annual

568 range of monthly means of sea surface temperature, viewed May 2012) supporting

569 this statement for each region are given here. They are from

570   http://www.youtube.com/watch?v=4hv1a-z53Ew (Generated from NASA Giovanni

571   v3.0.7) for the western Mediterranean (12-26°C), a temperate area, and from

572   http://www.nodc.noaa.gov/dsdt/cwtg/oatl.html for the other regions. For temperate

573   areas, ranges were: central California (12-16°C) and southern California (14-20°C).

574   For tropical areas: Hawaii (22-27°C), Samoa (27-29°C), and Puerto Rico (25-28°C).

575   The Eastern Pacific is a huge and variable area but off Central America, sea surface

576   temperatures range from 25-28°C [137].

577

578   We re-analyzed PLD and dispersal distance data from [138] and [139] by separating

579   the data into temperate and tropical species. There was no obvious difference in the

580   PLD vs. dispersal distance relationship between tropical and temperate species of

581   invertebrates or fishes (figure Sup 4). Only 19 of the 62 comparisons of PLD with

582   dispersal distance in [138] and [139] were from tropical species, and six of the

583   tropical data pairs (32%) were from tunicate tadpole larvae (figure Sup 4). The

584   overall pattern of the data is a tight cluster of points above a dispersal distance of

585   about 20 km and PLDs of > 1 week and a broad scatter of points below about 1 km

586   dispersal distance and with PLDs from < 1 hr to several weeks. This general pattern

587   is displayed by both the tropical and temperate data when analysed separately: there

588   is no obvious difference between tropical and temperate invertebrate and fish

589   species in the PLDs vs. dispersal distance relationship. However, the small sample

590   size of the tropical data set suggests caution in this interpretation.

591

592   An association between genetic structure and PLD is expected, but in practice the

593   relationship is often not found [5, 6]. Although PLD is often assumed to be a strong

594   determinant of species range, results of attempts to test this assumption have been

595   mixed at best. Further, recent studies have concluded that PLD is usually not a

596   major determinant of range size [3],[140]. In contrast, a significant correlation was

597   found between genetic differentiation and PLD in a study of 32 species (including 12

598   fishes) [68]. In another study, a consistent, moderate association between genetic

599   and PLD proxies of dispersal was found in 50 marine species (21 fishes), which was

600   significantly better at small (<650 km) spatial scales [141]. In some cases, the

601   association between genetic structure and predicted dispersal can be improved by

602   using modeled dispersal trajectories based on ocean currents instead of point to

603   point straight lines [142], perhaps explaining some of the inconsistency in other

604   studies. In contrast, two broad assessments of marine fish populations and

605   associated proxies [6], [5], reported that egg type (demersal vs. pelagic) was a better

606   predictor of genetic structure than was PLD, and neither found a significant

607   association between PLD and genetic structure. It is worth noting, however, that in

608   the analysis of PLD data here, in each region except the California Current, the

609   average PLD of demersal-spawning species was shorter than that of broadcast

610   spawning species by 20 to 60% (main text figure 3), consistent with [5] and [6]. This

611   is potentially an indication that demersal-spawning species have shorter dispersal

612   distances, albeit with all the caveats raised above.

613

614   Although Riginos et al. [5] found little effect of PLD on genetic structure, 96 of the

615   148 demersal study species were tropical, with only a few temperate species (mostly

616   *Sebastes*), and only 2-3 species from cold water. These authors properly did not

617   attempt to generalize their findings to temperate species. Bradbury et al. [6] did not

618   observe a significant association between PLD and genetic divergence for 30

619   species of marine fishes, but their analysis included both pelagic and demersal

620   species. Bradbury et al. [6] also found a significant, curvilinear increase in PLD with

621   latitude at both species and family level, and in this case, the large majority of

622   tropical and warm temperate species were demersal, site attached reef fishes,

623   whereas the cold water species were dominated by open shelf and pelagic species.

624   Therefore, the higher latitude species are more likely to show an influence of adult

625   movement on genetic structure than were the tropical species. Further, as shown

626   herein for tropical and warm temperate species, adult habitat does influence PLD.

627

628   **5. CAVEATS**

629   Larval dispersal is very difficult to measure directly, although recent advances in

630   otolith tagging and genetic parentage make it more feasible, if labour intensive. As a

631   result, the use of indirect approaches and proxies to estimate larval dispersal is

632   common. These include some population genetic approaches, estimation of PLD

633   and dispersal modelling. For a variety of reasons touched upon here, genetic

634   structure in marine populations may not always derive from recent patterns of larval

635   dispersal alone. Similarly, published PLD data often do not capture the spatial and

636   temporal variation that intensive study reveals, and the intuitively attractive

637   hypothesis that PLD is a strong determinant of larval dispersal distance is often

638   rejected when tested. We have not considered dispersal modelling here, but

639   modelling larval dispersal is challenging because of the many variables that

640   contribute to dispersal outcomes, and our often poor understanding of larval

641   behaviour in particular. Therefore the results of proxy-based and indirect

642   approaches should be viewed with caution.

643

644   Genetic variation among populations results from the combined influences of

645   selectively neutral processes such as genetic drift, mutation, and gene flow as well

646   as adaptive processes such as natural or sexual selection. The application of

647   genetic approaches to the study of larval dispersal in temperate and tropical marine

648   systems can illuminate trends in migration and dispersal, when differences among

649   populations are found. Allele frequency differences among populations and

650   individuals can provide the means for both indirect estimation of average gene flow

651   and the direct measurement of individual dispersal events [143],[144]. Furthermore,

652   the study of genes experiencing natural selection allows the scale of adaptation to be

653   resolved and resulting clines can reveal trends in successful dispersal [145].

654   Genetic approaches can overcome some of the hurdles associated with the direct

655   tracking of many tiny propagules and resolving the tails of dispersal kernels (ie,

656   determining the shape of the dispersal distance frequency distribution) As with all

657   approaches, they are subject to their own sources of bias and misinterpretation [5]

658   [143] [144]. For example, population genetics approaches reflect a combination of

659   egg and larval dispersal, settlement, and post-settlement processes, as well as adult

660   dispersal, and they may be sensitive to rare events over long or intermediate time

661   periods as well as on processes that may no longer exist.

662

663   Genetic estimates of dispersal are most commonly based on either isolation by

664   distance models or individual assignment, and more recently on parentage. The

665   former are more commonly used in higher latitude studies and the latter in tropical

666   studies because larger populations and larger spatial scales make assignment

667   approaches challenging in colder regions. Estimates of average dispersal distance

668   based on genetic isolation-by-distance relationships (i.e., [146] [147] [148]) suggest

669   local recruitment in marine species may be more prevalent than previously thought

670   [149], [150]. Similarly, individual assignment [151] or parentage based [152]

671   methods resolve single events and also often emphasize local recruitment.

672   However, single case studies of limited geographic scale do not allow the full

673   dispersal kernel to be determined and are hard to interpret in terms of the question at

674   hand, which is whether there are tropical-temperate trends in larval transport and

675   dispersal, because similar studies on higher-latitude fishes are lacking.

676

677   Undoubtedly, genetic estimates of larval dispersal in a single species along a

678   latitudinal gradient are best suited to address the goal of this review, yet such studies

679   are rare. One of the few studies to contrast genetic structure across fish species,

680   geographic regions and life histories [6] found significant associations between

681   maximum latitude, body size and genetic structure (F_{ST}), and weaker genetic

682   structure at latitudes above 40 degrees, with the largest differences observed at the

683   extremes of latitude (i.e., 20 vs. 60 degrees latitude). That review [6] examined

684   dispersal overall (not limited to larval dispersal), and was not limited to nearshore

685   demersal species, examining all taxa and data available. Nonetheless, genetic

686   structure across species of marine fish supported the hypothesis that dispersal

687   occurs over greater spatial scales at high than at low latitudes, consistent with

688   predictions based on the expected effect of temperature on development times [115],

689   some oceanographic variables, and conclusions of some studies of single species of

690   marine invertebrates [153], [154]. Although this interpretation is valid for those

691   species included in the meta-analysis [6], the composition of the species for which

692   genetic data exist is not reflective of the spawning modes of the species

693   assemblages that actually occur in the areas of interest. Specifically, genetic data

694   are available for a higher proportion of demersal-egg spawners at low latitudes and

695   broadcast spawners at high latitudes than are found in the assemblages from those

696   areas. This is not a criticism of such synthetic studies, but it does make it difficult to

697   apply their conclusions to broad faunas and questions like the ones of interest here.

698   For example, some workers have concluded that larval dispersal occurs over smaller

699   spatial scales in demersal-spawning spawners than it does in broadcast spawners

700   [6],[5]. If true, geographic biases in the species examined limit the utility of these

701   approaches to single species examples until the suite of species for which data exist

702   becomes representative. However, very few direct estimates of larval dispersal are

703   available to test the impact of any biases due to species selection.

704

705   Biases due to species selection depend on the families present at differing latitudes.

706   For example, the families Agonidae, Ammodytidae, Anarhichadidae, Cottidae,

707   Cyclopteridae, Pholididae, Stichaeidae and Zoarcidae constitute about half the

708   demersal fish species in the higher latitudes of the NE Pacific and NW Atlantic

709   (figure Sup 2), and the vast majority of the species of these families spawn demersal

710   eggs. The available genetic data as used in [6] includes only about 5-10% of the

711   total number of species from the listed families, and none for five of them, thus

712   resulting in an under-representation of demersal-spawning species. The same

713   trends were found when the data were analysed at the family level [6], but the

714   absence of genetic data for five of these eight families limits the conclusions that can

715   be drawn. Thus, if spawning mode is relevant to dispersal, as seems to be the case

716   in warmer waters [5], the available genetic data are not representative of the full

717   fauna. More study of high latitude non-commercial taxa with demersal eggs using

718   direct and indirect methods is needed to help evaluate potential biases and trends

719   present.

720

721   Population genetic approaches (e.g., isolation-by-distance based methods) are also

722   influenced by historical events such as glaciations, which may have long-lasting

723   effects on genetic structure that are relevant for latitudinal comparisons. Species

724   characterized by large populations recolonizing high-latitude areas following

725   deglaciation may not have had sufficient time for differences to accumulate by

726   genetic drift. In such cases the absence of genetic divergence tells us little regarding

727   larval dispersal and connectivity [155] and it is difficult to discount the hypothesis that

728   the observed low structure at high latitudes is not at least partly due to recent

729   recolonization and large effective population sizes. Similarly, glaciations also

730   influence genetic structure in the tropics, because some regions during the

731   Quaternary, in particular areas between South-east Asia and Australia, were subject

732   to high-frequency sea level fluctuations that alternatively flooded and dried many

733   thousands of square km [156]. Direct genetic approaches based on individual

734   assignment or parentage are not subject to these effects.

735

736   Might apparent geographic differences in dispersal arise from differing

737   methodologies or research targets? Studies of dispersal and connectivity in the

738   tropics tend to be on small, site-localized species ([43, 157], [158]; see sections on

739   Habitat Fragmentation). Often, the study species are chosen for tractability (e.g.,

740   small adult size, small adult home range), and if the species is not fished, all the

741   better: this eliminates a factor that potentially complicates population dynamics.

742   Might this approach bias estimates of dispersal distances? These studies often

743   utilize techniques that involve assigning a source to individual recruits through

744   parentage or chemical tagging, and the geographic scale tends to be small, on the

745   order of tens of km (e.g., [79], [159], [160], [161]). Approaches such as this do not

746   have the capacity to identify larger scales of dispersal, although a genetic study of

747   anemonefishes that spanned hundreds of kilometres [162] suggested short dispersal

748   distances, at approximately the same scale as geographically limited studies of

749   similar species.

750

751   In contrast, in temperate regions many studies of population structure are conducted

752   on large scales on exploited stocks from deeper water, often with a focus on

753   assessing spatial scales of management [163]. If temperate fished stocks tend to be

754   larger and more mobile than site-attached fishes on shallow coral reefs, then

755   estimates of what constitutes a local population within the metapopulation can be

756   very different, and this could set a different scale for connectivity estimates.

757   However, as mentioned above, a larger spatial scale of study does not automatically

758   result in longer estimates of dispersal. A coarse-scale genetic study of fifteen

759   species of exploited rockfishes along the west coast of North America found little

760   evidence of genetic structure among some species, but sharp genetic breaks among

761   others [164]. In the more subdivided species, more detailed study could reveal fine-

762   scale population structure and evidence of limited dispersal. Such a finding is very

763   unlikely in the group lacking genetic structure.

764

765 **Figure Captions**

766 Figure Sup 1. Mean (±SE) pelagic larval duration for taxonomic groups of demersal

767 shorefishes with primarily warm-water (solid bars) and cold-water (open bars)

768 distributions. PLD data from [2] and [3]. See Supplement text for numbers of PLD

769 estimates for each taxon.

770

771 Figure Sup 2. Percentages of demersal shorefish species with different spawning

772 modes in regions of the Western Atlantic and Eastern Pacific. In each ocean, cold

773 temperate regions have a much smaller percentage of species with pelagic eggs

774 than do other regions. Both Argentina and Chile have a large north-south extent and

775 their fish faunas include both warm and cold temperate components: although they

776 have a lower percentage of species with pelagic eggs, the percentage is still about

777 55% as compared to 15-25% in the cold temperate regions of the northern

778 hemisphere. Data from Hawaii in the central Pacific are very similar to the other

779 tropical values. In the Antarctic, 16% of species spawn pelagic eggs. See Table

780 Sup1 for details and data sources.

781

782 Figure Sup 3. Larval transport by Eddy kinetic energy (EKE) and eddy-driven

783 currents: consequences of (A) strong diffusion (dotted line), (B) anisotropic advection

784 (dotted line), (C) advection and strong diffusion (dotted line) on the mean dispersal

785 kernel (solid line). Larval source is located at x = 0.

786

787 Figure Sup 4. Pelagic larval duration of marine invertebrates and fishes plotted

788 against their dispersal distance. Solid squares and open circles are data from

789 tropical and temperate species, respectively. "T"s adjacent to values indicate data

790   from the dispersal of tadpole larvae of tunicates. Data are from [139] and [138], but

791   with algal data removed.

792

793

794 **Table Captions**

795

796 Table Sup 1. Percentage of demersal marine teleost shorefish species with different

797 spawning modes in selected regions. A small number of species with unknown

798 spawning modes are omitted: these constitute at most 3% of species in any location.

799 Species compositions from: [165] [166] [167] [168] [169] [170] [171]. Spawning

800 modes from: [172] [169] [173].

801

802 Table Sup 2. Studies based on otolith methods to estimate demographic

803 connectivity used in the habitat fragmentation comparison. [160], [174], [175], [176],

804 [177], [178], [179], [180], [181], [182], [183], [184], [185], [186], [187], [188], [189],

805 [190].

806

REFERENCES

807

808   1.   Brothers E.B., Thresher R.E. 1985 Pelagic duration, dispersal, and the distribution of Indo-
809   Pacific coral-reef fishes. In *The ecology of coral reefs (Symposium series for undersea research,*
810   *NOAA's undersea research program 3)* (ed. Reaka M.L.), pp. 53-70. Washington, DC, NOAA.
811   2.   Shanks A.L., Eckert G. 2005 Life-history traits and population persistence of California
812   Current fishes and benthic crustaceans; solution of a marine drift paradox. *Ecol Monogr* **75**, 505-524.
813   3.   Mora C., Treml E.A., Roberts J., Crosby K., Roy D., Tittensor D.P. 2012 High connectivity
814   among habitats precludes the relationship between dispersal and range size in tropical reef fishes.
815   *Ecography* **35**, 89-96.
816   4.   Paris C.B., Leis J.M., Irrison J.-O. 2009 Biological processes: Pelagic larval duration. In *Manual*
817   *of recommended practices for modelling physical-biological interactions during fish early life* (eds.
818   North E.W., Gallego A., Petitgas P.), pp. 23-24, International Council for the Exploration of the Sea
819   Cooperative Research Report.
820   5.   Riginos C., Douglas K.E., Jin Y., Shanahan D.F., Treml E.A. 2011 Effects of geography and life
821   history traits on genetic differentiation in benthic marine fishes. *Ecography* **34**(4), 566-575.
822   (doi:10.1111/j.1600-0587.2010.06511.x).
823   6.   Bradbury I.R., Laurel B., Snelgrove P.V.R., Bentzen P., Campana S.E. 2008 Global patterns in
824   marine dispersal estimates: the influence of geography, taxonomic category and life history. *Proc R*
825   *Soc Lond, Ser B: Biol Sci* **275**(1644), 1803–1809. (doi:10.1098/rspb.2008.0216).
826   7.   Moser H.G. 1996 The early stages of fishes in the California Current region. *California*
827   *Cooperative Oceanic Fisheries Investigations Atlas* **33**, 1-1505.
828   8.   Richards W.J., Leis J.M. 1984 Labroidei: development and relationships. In *Ontogeny and*
829   *Systematics of Fishes* (eds. Moser H.G., Richards W.J., Cohen D.M., Fahay M.P., Kendall A.W.,
830   Richardson S.L.), pp. 542-547. Lawrence, Kansas, American Society of Ichthyologists and
831   Herpetologists Special Publication 1.
832   9.   Marshall N.B. 1953 Egg size in arctic, antarctic and deep-sea fishes. *Evolution* **7**(4), 328-341.
833   10.   Thresher R.E. 1988 Latitidunal variation in egg sizes of tropical and sub-tropical North
834   Atlantic shore fishes. *Environ Biol Fishes* **21**(1), 17-25.
835   11.   Wright P.J., Trippel E.A. 2009 Fishery-induced demographic changes in the timing of
836   spawning: consequences for reproductive success. *Fish and Fisheries* **10**, 283-304.
837   12.   Sims D., Wearmouth V., Genner M., Southward A., Hawkins S. 2004 Low-temperature-driven
838   early spawning migration of a temperate marine fish. *J Anim Ecol* **73**, 333-341.
839   13.   Ware D.M., Tanasichuk R.W. 1989 Biological basis of maturation and spawning waves in
840   Pacific herring (*Clupea harengus pallasi*). *Can J Fish Aquat Sci* **46**, 1776-1784.
841   14.   Carscadden J., Nakashima B.S., Frank K.T. 1997 Effects of fish length and temperature on the
842   timing of peak spawning in capelin (*Mallotus villosus*). *Can J Fish Aquat Sci* **54**, 781-787.
843   15.   Sogard S.M., Able K.W., Hagan S.M. 2001 Long-term assessment of settlement and growth of
844   juvenile winter flounder (*Pseudopleuronectes americanus*) in New Jersey estuaries. *J Sea Res* **45**,
845   189-204.
846   16.   Genner M.J., Halliday N.C., Simpson S.D., Southward A.J., Hawkins S.J., Sims D.W. 2010
847   Temperature-driven phenological changes within a marine larval fish assemblage. *J Plankton Res* **32**,
848   699-708.
849   17.   Sheaves M. 2006 Is the timing of spawning in sparid fishes a response to sea temperature
850   regimes? *Coral Reefs* **25**, 655-669.
851   18.   Parrish R.H., Nelson C.S., Bakun A. 1981 Transport mechanisms and reproductive success of
852   fishes in the California current. *Biol Oceanogr* **1**, 175-203.
853   19.   McDowall R.M. 2008 Why are so many boreal freshwater fishes anadromous? Confronting
854   'conventional wisdom'. *Fish Fish* **9**, 1-6.
855   20.   Dannewitz J., Maes G.E., Johansson L., Wickström H., Volckaert F.A.M., Järvi T. 2005
856   Panmixia in the European eel: a matter of time. *Proc R Soc Lond, Ser B: Biol Sci* **272**, 1129-1137.

857 21.   Han Y.S., Hung C.L., Liao Y.F., Tzeng W.N. 2010 Population genetic structure of the Japanese
858 eel *Anguilla japonica*: evidence for panmixia in spatial and temporal scales. . *Mar Ecol Prog Ser* **401**,
859 221-232.
860 22.   Watanabe S., Miller M.J. 2012 Species, geographic distribution, habitat and conservation of
861 freshwater eels. In *Eels: Physiology, habitat and conservation* (eds. Nakashima S., Fujimoto M.).
862 Hauppauge, NY Nova Science Publishers.
863 23.   Shen K.-N., Tzeng W.-N. 2007 Population genetic structure of the year-round spawning
864 tropical eel, *Anguilla reinhardtii*, in Australia. *Zool Stud* **46**(4), 441-453.
865 24.   Minegishi Y., Aoyama J., Tsukamoto K. 2008 Multiple population structure of the giant
866 mottled eel, *Anguilla marmorata* . *Mol Ecol* **17**, 3109-3122.
867 25.   Minegishi Y., Gagnaire P.-A., Aoyama J., Bosc P., Feunterun E., Tsukamoto K., Berrebi P. 2012
868 Present and past genetic connectivity of the Indo-Pacific tropical eel, *Anguilla bicolor*. *J Biogeogr* **39**,
869 408-420.
870 26.   Gagnaire P.A., Minegishi Y., Aoyama J., Réveillac E., Robinet T., Bosc P., Tsukamoto K.,
871 Feunteun E., Berrebi P. 2009 Ocean currents drive secondary contact between *Anguilla marmorata*
872 populations in the Indian Ocean. *Mar Ecol Prog Ser* **379** 267-278.
873 27.   Gagnaire P.A., Minegishi Y., Zenbodju S., Valade P., Aoyama J., P. B. 2011 Within-population
874 structure highlighted by differential introgression across semipermeable barrier to gene flow in
875 *Anguilla marmorata*. *Evolution* **65**, 3413-3427.
876 28.   Aoyama J., Wouthuyzen S., Miller M.J., Inagaki T., Tsukamoto K. 2003 Short-distance
877 spawning migration of tropical freshwater eels. *Biological Bulletin* **204**, 104-108.
878 29.   Marui M., Arai, T., Miller, M. J., Jellyman, D. J. & Tsukamoto, K. 2001 Comparison of the early
879 life history between New Zealand temperate eels and Pacific tropical eels revealed by otolith
880 microstructure and microchemistry. . *Mar Ecol Prog Ser* **213**, 273-284.
881 30.   Kuroki M., Aoyama J., Miller M.J., Wouthuyzen S., Arai T., Tsukamoto K. 2006 Contrasting
882 patterns of growth and migration of tropical anguillid leptocephali in the western Pacific and
883 Indonesian Seas. *Mar Ecol Prog Ser* (309), 233-246.
884 31.   McDowall R.M. 1988 *Diadromy in fishes: migrations between freshwater and marine*
885 *environments*. London, Croom Helm
886 32.   Keith P. 2003 Biology and ecology of amphidromous Gobiidae of the Indo-Pacific and the
887 Caribbean regions. *J Fish Biol* **63**, 831-847.
888 33.   McDowall R.M. 2007 On amphidromy, a distinct form of diadromy in aquatic organisms. *Fish*
889 *Fish* **8**, 1-13.
890 34.   McDowall R.M., Mitchell C.P., Brothers E.B. 1994 Age at migration from the sea of juvenile
891 *Galaxias* in New Zealand (Pisces, Galaxiidae). *Bull Mar Sci* **54**, 385-402.
892 35.   Chubb A.L., Zink, R. M. & Fitzsimons, J. M. 1998 Patterns of mtDNA variation in Hawaiian
893 freshwater fishes: the phylogeographic consequences of amphidromy. *J Hered* **89**, 8-16.
894 36.   Iguchi K., Nishida M. 2000 Genetic biogeography among insular populations of the
895 amphidromous fish *Plecoglossus altivelis* assessed from mitochondrial DNA analysis. *Conserv Genet*
896 **1**, 147-156.
897 37.   Barker J.R., Lambert D.M. 1988 A genetic analysis of populations of *Galaxias maculatus* from
898 the Bay of Plenty: implications for natal river return. *N Z J Mar Freshwat Res* **22**, 321-326.
899 38.   Tsukagoshi H., Yokoyama R., Goto A. 2011 Mitochondrial DNA analysis reveals a unique
900 population structure of the amphidromous sculpin *Cottus pollux* middle-egg type (Teleostei:
901 Cottidae). *Mol Phylogen Evol* **60**, 265-270.
902 39.   Oberhuber J.M. 1988 An atlas based on the 'COADS' data set: the budgets of heat, buoyance
903 and turbulent kinetic energy at the surface of the global ocean. *Max-Planck-Institute for*
904 *Meteorology Report* **15**, 1-20.
905 40.   Chelton D.B., Schlax M.G. 1996 Global observations of oceanic Rossby waves. *Science*
906 **272**(5259), 234-238.

907 41.   Kara A.B., Rochford P.A., Hurlburt H.E. 2003 Mixed layer depth variability over the global
908 ocean. *J Geophys Res* **108**(3079). (doi:10.1029/2000JC000736).
909 42.   Cha S.S., McGowan M.F., Richards W.J. 1994 Vertical distribution of fish larvae off the Florida
910 Keys, 26 May–5 June 1989. *Bull Mar Sci* **54**, 828-842.
911 43.   Cowen R.K. 2002 Larval dispersal and retention and consequences for population
912 connectivity. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem* (ed. Sale P.F.), pp.
913 149-170. San Diego, Academic Press.
914 44.   Huebert K.B., Sponaugle S., Cowen R.K. 2010 Predicting the vertical distributions of reef fish
915 larvae in the Straits of Florida from environmental factors. *Can J Fish Aquat Sci* **67**(11), 1755-1767.
916 (doi:10.1139/F10-116).
917 45.   D'Alessandro E., Sponaugle S., Serafy J. 2010 Larval ecology of a suite of snappers (family:
918 Lutjanidae) in the Straits of Florida. *Mar Ecol Prog Ser* **410**, 159-175. (doi:10.3354/meps08632).
919 46.   Grønkjær P., Wieland K. 1997 Ontogenetic and environmental effects on vertical distribution
920 of cod larvae in the Bornholm Basin, Baltic Sea. *Mar Ecol Prog Ser* **154**, 91-105.
921 47.   Lough R.G., Potter D.C. 1993 Vertical distribution patterns and diel migrations of larval and
922 juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. *Fish
923 Bull* **91**(2), 281-303.
924 48.   Paris C.B., Cowen R.K., Lwiza K.M.M., Wang D.P., Olson D.B. 2002 Objective analysis of three-
925 dimensional circulation in the vicinity of Barbados, West Indies: Implication for larval transport. *Deep
926 Sea Res (I Oceanogr Res Pap)* **49**, 1363-1386.
927 49.   Leis J.M. 2007 Behaviour as input for modelling dispersal of fish larvae: behaviour,
928 biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. *Mar Ecol
929 Prog Ser* **347**, 185-193.
930 50.   Werner F.E., Page F.H., Lynch D.R., Loder J.W., Lough R.G., Perry R.I., Greenberg D.A., Sinclair
931 M.M. 1993 Influences of mean advection and simple behavior on the distribution of cod and
932 haddock early life stages on Georges Bank. *Fish Oceanogr* **2**(2), 43-64.
933 51.   Persson L., De Roos A.M. 2003 Adaptive habitat use in size- structured populations: linking
934 individual behavior to population processes. *Ecology* **84**, 1129-1139.
935 52.   Paris C.B., Cowen R.K. 2004 Direct evidence of a biophysical retention mechanism for coral
936 reef fish larvae. *Limnol Oceanogr* **49**, 1964-1979.
937 53.   North E.W., Schlag Z., Hood R.R., Li M., Zhong L., Gross T., Kennedy V.S. 2008 Vertical
938 swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking
939 and hydrodynamic model of Chesapeake Bay. *Mar Ecol Prog Ser* **359**, 99-115.
940 (doi:10.3354/meps07317).
941 54.   Hare J.A., Govoni J.J. 2005 Comparison of average larval fish vertical distributions among
942 species exhibiting different transport pathways on the southeast United States continental shelf. *US
943 Fish Bull* **103**(4), 728-736.
944 55.   Vikebø F., Jørgensen C., Kristiansen T., Fiksen Ø. 2007 Drift, growth and survival of larval
945 Northeast Arctic cod with simple rules of behaviour. *Mar Ecol Prog Ser* **347**, 207-219. (doi:doi:
946 10.3354/meps06979).
947 56.   Hinrichsen H.-H., Peck M.A., Schmidt J., Huwer B., Voss R. 2010 Survival probability of larval
948 sprat in response to decadal changes in diel vertical migration behavior and prey abundance in the
949 Baltic Sea. *Limnol Oceanogr* **55**(4), 1485-1498. (doi:10.4319/lo.2010.55.4.1485).
950 57.   Irisson J.-O., Paris C., Guigand C., Planes S. 2010 Vertical distribution and ontogenetic
951 'migration' in coral reef fish larvae. *Limnol Oceanogr* **55**(2), 909-919.
952 58.   Ferrari R., Wunsch C. 2009 Ocean circulation kinetic energy: reservoirs, sources, and sinks.
953 *Annu Rev Fluid Mech* **41**, 253-282. (doi:10.1146/Annurev.Fluid.40.111406.102139).
954 59.   Chelton D.B., Schlax M.G., Samelson R.M., de Szoeke R.A. 2007 Global observations of large
955 oceanic eddies. *Geophys Res Lett* **34**(L15606), 1-5. (doi:10.1029/2007gl030812).
956 60.   Jayne S.R., Marotzke J. 2002 The oceanic eddy heat transport. *J Phys Oceanogr* **32**(12), 3328-
957 3345.

958   61.   Limouzy-Paris C.B., Graber H.C., Jones D.L., Röpke A.W., Richards W.J. 1997 Translocation of
959   larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. *Bull Mar Sci* **60**(3),
960   966-983.
961   62.   Karnauskas M., Cherubin L.M., Paris C.B. 2011 Adaptive significance of the formation of
962   multi-species fish spawning aggregations near submerged capes. *Plos One* **6**(7 e22067), 1-12. (doi:
963   10.1371/journal.pone.0022067).
964   63.   Largier J.L. 2003 Considerations in estimating larval dispersal distances from oceanographic
965   data. *Ecol Appl* **13**(1), S71-S89.
966   64.   Fox H.E., Haisfield K.M., Brown M.S., Stevenson T.C., Tissot B.N., Walsh W.J., Williams I.D.
967   2012 Influences of oceanographic and meterological features on reef fish recruitment in Hawai'i.
968   *Mar Ecol Prog Ser* **463**, 259-272.
969   65.   Lasker R. 1978 The relationship between oceanographic conditions and larval anchovy food
970   in the California current: identification of factors contributing to recruitment failure. *Rapports et
971   Proces-verbaux des Reunions, Conseil International pour l'Exploration de la Mer* **173**, 212-230.
972   66.   Sinclair M.M., Illes T.D. 1989 Population regulation and specification in the oceans. *Journal
973   du Conseil international Exploration de la Mer* **45**, 165-175.
974   67.   Mumby P.J., Vitolo R., Stephenson D.B. 2011 Temporal clustering of tropical cyclones and its
975   ecosystem impacts. *Proc Natl Acad Sci, USA* **108** (43), 17626-17630 (doi:10.1073/pnas.1100436108).
976   68.   Siegel D.A., Kinlan B.P., Gaylord B., Gaines S.D. 2003 Lagrangian descriptions of marine larval
977   dispersal. *Mar Ecol Prog Ser* **260**, 83-96.
978   69.   Kamenkovich I., Cheng W., Schmidt C., Harrison D.E. 2011 Effects of eddies on an ocean
979   observing system with profiling floats: idealized simulations of the Argo array. *J Geophys Res*
980   **116**(C06003).
981   70.   Kamenkovich I., Berloff P., Pedlosky J. 2009 Anisotropic Material Transport by Eddies and
982   Eddy-Driven Currents in a Model of the North Atlantic. *J Phys Oceanogr* **39**(12), 3162-3175.
983   (doi:10.1175/2009jpo4239.1).
984   71.   Graham W.M., Largier J.L. 1997 Upwelling shadows as nearshore retention sites: the
985   example of northern Monterey Bay. *Cont Shelf Res* **17**, 509-532.
986   72.   Morgan S.G., Fisher J.L., Miller S.H., McAfee S.T., Largier J.L. 2009 Nearshore larval retention
987   in a region of strong upwelling and recruitment limitation. *Ecology* **90**, 3489-3502.
988   73.   Aiken C.M., Navarrete S.A., Pelegrí J.L. 2011 Potential changes in larval dispersal and
989   alongshore connectivity on the central Chilean coast due to an altered wind climate. *J Geophys Res*
990   **116**, G04026. (doi:10.1029/2011JG001731).
991   74.   Shanks A.L., Shearman R.K. 2009 Paradigm lost? Cross-shelf distributions of intertidal
992   invertebrate larvae are unaffected by upwelling or downwelling. *Mar Ecol Prog Ser* **385**, 189-204.
993   (doi:10.3354/meps08043).
994   75.   Kingsford M.J., Leis J.M., Shanks A., Lindeman K.C., Morgan S.G., Pineda J. 2002 Sensory
995   environments, larval abilities and local self-recruitment. *Bull Mar Sci* **70**(1), 309-340.
996   76.   Leis J.M. 2010 Ontogeny of behaviour in larvae of marine demersal fishes. *Ichthyol Res* **57**,
997   325-342. (doi:10.1007/s10228-010-0177-z).
998   77.   Leis J.M., Siebeck U.E., Dixson D.L. 2011 How Nemo finds home: the neuroecology of
999   dispersal and of population connectivity in larvae of marine fishes. *Integr Comp Biol* **51**(5), 826-843.
1000   (doi:10.1093/icb/icr004).
1001   78.   Staaterman E., Paris C.B., Helgers J. 2012 Orientation behavior in fish larvae: a missing piece
1002   to Hjort's critical period hypothesis. *J Theor Biol* **304**, 188-196. (doi:10.1016/j.jtbi.2012.03.016).
1003   79.   Swearer S.E., Shima J.S., Hellberg M.E., Thorrold S.R., Jones G.P., Robertson D.R., Morgan
1004   S.G., Selkoe K.A., Ruiz G.M., Warner R.R. 2002 Evidence of self-recruitment in demersal marine
1005   populations. *Bull Mar Sci* **70**, 251-272.
1006   80.   Wessel P., Smith W.H.F. 1996 A global, self-consistent, hierarchical, high-resolution shoreline
1007   database. *Journal of Geophysical Research-Solid Earth* **101**(B4), 8741-8743. (doi:10.1029/96jb00104).

1008   81.   Wright K.J., Higgs D.M., Cato D.H., Leis J.M. 2010 Auditory sensitivity in settlement-stage
1009   larvae of coral reef fishes. *Coral Reefs* **29**(1), 235-243. (doi:10.1007/s00338-009-0572-y).
1010   82.   Wright K.J., Higgs D.M., Leis J.M. 2011 Ontogenetic and interspecific variation in hearing
1011   ability in marine fish larvae. *Mar Ecol Prog Ser* **424**, 1-13. (doi:10.3354/meps09004).
1012   83.   Leis J.M., Balma P., Ricoux R., Galzin R. 2012 Ontogeny of swimming ability in the European
1013   Sea Bass, *Dicentrarchus labrax* (L.) (Teleostei: Moronidae). *Mar Biol Res* **8**(3), 265-272.
1014   (doi:10.1080/17451000.2011.616898).
1015   84.   Guan L., Snelgrove P.V.R., Gamperl A.K. 2008 Ontogenetic changes in the critical swimming
1016   speed of *Gadus morhua* (Atlantic cod) and *Myoxocephalus scorpius* (shorthorn sculpin) larvae and
1017   the role of temperature. *J Exp Mar Biol Ecol* **360**, 31-38.
1018   85.   Fisher R. 2005 Swimming speeds of larval coral reef fishes: impacts on self-recruitment and
1019   dispersal. *Mar Ecol Prog Ser* **285**, 223-232.
1020   86.   Batty R.S., Blaxter J.H.S., Bone Q. 1991 The effect of temperature on the swimming of a
1021   teleost (*Clupea harengus*) and an ascidian larva (*Dendrodoa grossularia*). *Comp Biochem Physiol*
1022   **100A**, 297-300.
1023   87.   Sogard S.M., Olla B.L. 2001 Growth and behavioral responses to elevated temperatures by
1024   juvenile sablefish *Anoplopoma fimbria* and the interactive role of food availability. *Mar Ecol Prog Ser*
1025   **217**, 121-134.
1026   88.   Peck M.A., Buckley L.J., Bengtson D.A. 2006 Effects of temperature and body size on the
1027   swimming speed of larval and juvenile Atlantic cod (*Gadus morhua*): implications for individual-
1028   based modelling. *Environ Biol Fishes* **75**, 419-429.
1029   89.   Koumoundouros G., Ashton C., Xenikoudakis G., Giopanou I., Georgakopoulou E., Stickland
1030   N. 2009 Ontogenetic differentiation of swimming performance in Gilthead seabream (*Sparus aurata*,
1031   Linnaeus 1758) during metamorphosis. *J Exp Mar Biol Ecol* **370**, 75-81.
1032   90.   Koumoundouros G., Ashton C., Sfakianakis D.G., Divanach P., Kentouri M., Anthwal N.,
1033   Stickland N.C. 2009 Thermally induced phenotypic plasticity of swimming performance in European
1034   sea bass *Dicentrarchus labrax* juveniles. *J Fish Biol* **74**, 1309-1322.
1035   91.   Green B.S., Fisher R. 2004 Temperature influences swimming speed, growth and larval
1036   duration in coral reef fish larvae. *J Exp Mar Biol Ecol* **299**, 115-132.
1037   92.   Kashef N.S. 2012 Ontogeny of critical swimming speed of larval and pelagic juvenile
1038   rockfishes (*Sebastes* spp.) [M.Sc. Thesis], California State University, Moss Landing Marine
1039   Laboratories.
1040   93.   Fisher R., Leis J.M. 2009 Swimming performance in larval fishes: from escaping predators to
1041   the potential for long distance migration. In *Fish locomotion: an etho-ecological approach* (eds.
1042   Domenici P., Kapoor B.G.), pp. 333-373. Enfield, New Hampshire, USA, Science Publishers.
1043   94.   Leis J.M., Fisher R. 2006 Swimming speed of settlement-stage reef-fish larvae measured in
1044   the laboratory and in the field: a comparison of critical speed and *in situ* speed. In *Proceedings of the*
1045   *10th International Coral Reef Symposium, Okinawa* (pp. 438-445, Coral Reef Society of Japan, Tokyo.
1046   95.   Stobutzki I.C., Bellwood D.R. 1997 Sustained swimming abilities of the late pelagic stages of
1047   coral reef fishes. *Mar Ecol Prog Ser* **149**, 35-41.
1048   96.   Dower J.F., Pepin P., Kim G.C. 2009 Covariation in feeding success, size-at-age and growth in
1049   larval radiated shanny (*Ulvaria subbifurcata*): insights based on individuals. *J Plankton Res* **31**(3),
1050   235-247. (doi:10.1093/Plankt/Fbn118).
1051   97.   Sponaugle S., Llopiz J.K., Havel L.N., Rankin T.L. 2009 Spatial variation in larval growth and
1052   gut fullness in a coral reef fish. *Mar Ecol Prog Ser* **383**, 239-249.
1053   98.   Neilson J.D., Perry R.I., Valerio P., Waiwood K.G. 1986 Condition of Atlantic cod *Gadus*
1054   *morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator
1055   avoidance. *Mar Ecol Prog Ser* **32**(2-3), 229-235.
1056   99.   Takasuka A., Aoki I., Mitani I. 2003 Evidence of growth-selective predation on larval Japanese
1057   anchovy *Engraulis japonicus* in Sagami Bay. *Mar Ecol Prog Ser* **252**, 223-238.

1058   100.   Fisher R., Bellwood D.R. 2001 Effects of feeding on the sustained swimming abilities of late-
1059   stage larval *Amphiprion melanopus*. *Coral Reefs* **20**, 151-154.
1060   101.   Leis J.M., Clark D.L. 2005 Feeding greatly enhances endurance swimming of settlement-stage
1061   reef-fish larvae (Pomacentridae). *Ichthyol Res* **52**, 185-188.
1062   102.   Cushing D.H. 1975 *Marine ecology and fisheries*. Cambridge, Cambridge University Press; 278
1063   p.
1064   103.   Houde E.D. 1987 Fish early life dynamics and recruitment variability. *Am Fish Soc Symp* **2**, 17-
1065   29.
1066   104.   Anderson J.T. 1988 A review of size dependent survival during pre-recruit stages of fishes in
1067   relation to recruitment. *J Northwest Atl Fish Sci* **8**, 55-66.
1068   105.   Llopiz J.K. 2012 Latitudinal and taxonomic patterns in the feeding dynamics of fish larvae: a
1069   literature synthesis. *J Mar Syst* **in press**, 9pp. (doi:10.1016/j.jmarsys.2012.05.002).
1070   106.   Llopiz J.K., Richardson D.E., Shiroza A., Smith S.L., Cowen R.K. 2010 Distinctions in the diets
1071   and distributions of larval tunas and the important role of appendicularians. *Limnol Oceanogr* **55**(3),
1072   983-996.
1073   107.   Llopiz J.K., Cowen R.K. 2009 Variability in the trophic role of coral reef fish larvae in the
1074   oceanic plankton. *Mar Ecol Prog Ser* **381**, 259-272.
1075   108.   Cushing D.H. 1990 Plankton production and year-class strength in fish populations: an
1076   update of the match/mismatch hypothesis. *Adv Mar Biol* **26**, 249-293.
1077   109.   Beaugrand G., Brander K.M., Lindley J.A., Souissi S., Reid P.C. 2003 Plankton effect on cod
1078   recruitment in the North Sea. *Nature* **426**(6967), 661-664.
1079   110.   Houde E.D. 1989 Comparative growth, mortality, and energetics of marine fish larvae:
1080   temperature and implied latitudinal effects. *US Fish Bull* **87**(3), 471-495.
1081   111.   Childress J.J. 1995 Are there physiological and biochemical adaptations of metabolism in
1082   deep-sea animals? . *Trends Ecol Evol* **10**, 30-36.
1083   112.   MacArthur R. 1972 *Geographical Ecology*. Princeton, NJ, Princeton University Press.
1084   113.   Vermeij G.J. 1978 *Biogeography and adaptation: patterns of marine life*. Cambridge, MA,
1085   Harvard University Press.
1086   114.   Menge B.A., Lubchenco J. 1981 Community organization in temperate and tropical rocky
1087   inter-tidal habitats - prey refuges in relation to consumer pressure-gradients. *Ecol Monogr* **51**(4),
1088   429-450.
1089   115.   O'Connor M.I., Bruno J.F., Gaines S.D., Halpern B.S., Lester S.E., Kinlan B.P., Weiss J.M. 2007
1090   Temperature control of larval dispersal and the implications for marine ecology, evolution, and
1091   conservation. *Proc Natl Acad Sci USA* **104**(4), 1266-1271.
1092   116.   Beldade R., Pedro T., Goncalves E.J. 2007 Pelagic larval duration of 10 temperate
1093   cryptobenthic fishes. *J Fish Biol* **71**, 376-382.
1094   117.   Fontes J., Santos R.S., Afonso P., Caselle J.E. 2011 Larval growth, size, stage duration and
1095   recruitment success of a temperate reef fish. *J Sea Res* **65**, 1-7.
1096   118.   Macpherson E., Raventos N. 2006 Relationship between pelagic larval duration and
1097   geographic distribution of Mediterranean littoral fishes. *Mar Ecol Prog Ser* **327**, 257-265.
1098   119.   Riginos C., Victor B.C. 2001 Larval spatial distributions and other early life-history
1099   characteristics predict genetic differentiation in eastern Pacific blennoid fishes. *Royal Society of
1100   London, Series B: Biological Sciences* **268**, 1931-1936.
1101   120.   Allman R.J., Grimes C.B. 2002 Temporal and spatial dynamics of spawning, settlement, and
1102   growth of gray snapper (*Lutjanus griseus*) from the west Florida shelf as determined from otolith
1103   microstructure. *Fish Bull* **100**, 391-403.
1104   121.   Bowen B.W., Bass A.L., Muss A., Carlin J., Robertson J. 2006 Phylogeography of two Atlantic
1105   squirrelfishes (Family Holocentridae): exploring links between pelagic larval durations and
1106   population connectivity. *Mar Biol* **149**, 899-913.

1107   122.   Colin P.L., Laroche W.A., Brothers E.B. 1997 Ingress and settlement in the Nassau grouper,
1108   *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. *Bull Mar Sci* **60**,
1109   656-667.
1110   123.   Powell A.B., Tucker J.W. 1992 Egg and larval development of laboratory-reared Nassau
1111   Grouper, *Epinephelus striatus* (Pisces, Serranidae). *Bull Mar Sci* **50**(1), 171-185.
1112   124.   Robertson J. 1988 Extreme variation in settlement of the Caribbean triggerfish *Balises vetula*
1113   in Panama. *Copeia* **3**, 698-703.
1114   125.   Searcy S.P., Sponaugle S. 2000 Variable larval growth in a coral reef fish. *Mar Ecol Prog Ser*
1115   **206**, 213-226.
1116   126.   Shulzitski K., McCartney M.A., Burton M. 2009 Population connectivity among Dry Tortugas,
1117   Florida and Caribbean populations of mutton snapper (*Lutjanus analis*), inferred from mulitple
1118   microscatellite loci. *Fish Bull* **107**, 501-509.
1119   127.   Sponaugle S., Cowen R.K. 1994 Larval durations and recruitment patterns of two Caribbean
1120   gobies (Gobiidae): contrasting early life histories in demersal spawners. *Mar Biol* **120**, 133-143.
1121   128.   Taylor M.S., Hellberg M.E. 2003 Genetic evidence for local retention of pelagic larvae in a
1122   Caribbean reef fish. *Science* **299**, 107-109.
1123   129.   Tyler J.C., Johnson G.D., Brothers E.B., Tyler D.M., Smith C.L. 1993 Comparative early life
1124   histories of western Atlantic squirrelfishes (Holocentridae): age and settlement of Rhynchichthys,
1125   meeki, and juvenile stages. *Bull Mar Sci* **53**, 1126-1150.
1126   130.   Victor B. 2007 *Coryphopterus kuna*, a new goby (Perciformes: Gobiidae: Gobiinae) from the
1127   Western Caribbean, with the identification of the late larval stage and an estimate of the pelagic
1128   larval duration. *Zootaxa* **1526**, 51-61.
1129   131.   Victor B.C. 1986 Duration of the planktonic larval stage of one hundred species of Pacific and
1130   Atlantic wrasses (family Labridae). *Mar Biol* **90**, 317-326.
1131   132.   Wellington G.M., Victor B.C. 1989 Planktonic larval duration of one hundred species of
1132   Pacific and Atlantic damselfishes (Pomacentridae). *Mar Biol* **101**, 557-567.
1133   133.   Victor B.C., Wellington G.M. 2000 Endemism and the pelagic larval duration of reef fishes in
1134   the eastern Pacific Ocean. *Mar Ecol Prog Ser* **205**, 241-248.
1135   134.   Wellington G.M., Victor B.C. 1992 Regional differences in duration of the planktonic larval
1136   stage of reef fishes in the eastern Pacific Ocean. *Mar Biol* **113**, 491-498.
1137   135.   Zapata F.A., Herron P.A. 2002 Pelagic larval duration and geographic distribution of tropical
1138   eastern Pacific snappers (Pisces: Lutjanidae). *Mar Ecol Prog Ser* **230**, 295-300.
1139   136.   Thresher R.E., Colin P.L., Bell L.J. 1989 Planktonic duration, distribution and population
1140   structure of western and central Pacific damselfishes (Pomacentridae). *Copeia* **1989**, 420-434.
1141   137.   Sverdrup H.U., Johnson M.W., Fleming R.H. 1942 *The oceans: their physics, chemistry and
1142   general biology*. Englewood Cliffs, N.J., Prentice-Hall, Inc.
1143   138.   Shanks A.L. 2009 Pelagic larval duration and dispersal distance revisited. *Biol Bull Mar Biol
1144   Lab Woods Hole* **216**, 373-385.
1145   139.   Shanks A.L., Grantham B.A., Carr M.H. 2003 Propagule dispersal distance and the size and
1146   spacing of marine reserves. *Ecol Appl* **13**, S159-s169.
1147   140.   Lester S.E., Ruttenberg B.I., Gaines S.D., Kinlan B.P. 2007 The relationship between dispersal
1148   ability and geographic range size. *Ecol Lett* **10**(8), 745-758. (doi:10.1111/j.1461-0248.2007.01070.x).
1149   141.   Selkoe K.A., Toonen R.J. 2011 Marine connectivity: a new look at pelagic larval duration and
1150   genetic metrics of dispersal. *Mar Ecol Prog Ser* **436**, 291-305. (doi:10.3354/meps09238).
1151   142.   White C., Selkoe K.A., Watson J., Siegel D.A., Zacherl D.C., Toonen R.J. 2010 Ocean currents
1152   help explain population genetic structure. *Proc R Soc Lond, Ser B: Biol Sci* **277**, 1685-1694.
1153   (doi:10.1098/rspb.2009.2214).
1154   143.   Lowe W.H., Allendorf F.W. 2010 What can genetics tell us about population connectivity?
1155   *Mol Ecol* **19**(15), 3038-3051. (doi:10.1111/j.1365-294X.2010.04688.x).
1156   144.   Leis J.M., van Herwerden L., Patterson H.M. 2011 Estimating connectivity in marine fish
1157   populations: what works best? *Oceanogr Mar Biol Annu Rev* **49**, 193-234.

1158   145.   Sotka E.E., Palumbi S.R. 2006 The use of genetic clines to estimate dispersal distances of
1159   marine larvae *Ecology* **87**, 1094-1103.
1160   146.   Buonaccorsi V.P., Kimbrell C., Lynn E., R. Vetter R. 2005 Limited realized dispersal and
1161   introgressive hybridization influence genetic structure and conservation strategies for brown
1162   rockfish, *Sebastes auriculatus*. *Conserv Genet* **6**, 697–713.
1163   147.   Gunderson D.R., Vetter R.D. 2006 Temperate Rocky Reef Fishes. In *Marine Metapopulations*
1164   (eds. Kritzer J.P., Sale P.F.), pp. 69-117. Amsterdam, Elsevier Academic Press.
1165   148.   Bradbury I.R., Bentzen P. 2007 Non-linear genetic isolation by distance: implications for
1166   dispersal estimation in anadromous and marine populations. *Mar Ecol Prog Ser* **340**, 245-257.
1167   149.   Kinlan B.P., Gaines S.D. 2003 Propagule dispersal in marine and terrestrial environments: a
1168   community perspective. *Ecology* **84**(8), 2007-2020.
1169   150.   Palumbi S.R. 2003 Population genetics, demographic connectivity, and the design of marine
1170   reserves. *Ecol Appl* **13**((1) Supplement), S146–S158.
1171   151.   Manel S., Gaggiotti O., Waples R.S. 2005 Assignment methods: matching biological questions
1172   with appropriate techniques. *Trends Ecol Evol* **20**(3), 136-142.
1173   152.   Blouin M.S. 2003 DNA-based methods for pedigree reconstruction and kinship analysis in
1174   natural populations. *Trends Ecol Evol* **18**, 503-511.
1175   153.   Kelly R.P., Eernisse D.J. 2007 Southern hospitality: a latitudinal gradient in gene flow in the
1176   marine environment. *Evolution* **61**(3), 700–707
1177   154.   David G.K., Marshall D.J., Riginos C. 2010 Latitudinal variability in spatial genetic structure in
1178   the invasive ascidian, *Styela plicata*. *Mar Biol* **157**(9), 1955-1965.
1179   155.   Hauser L., Carvalho G.R. 2008 Paradigm shifts in marine fisheries genetics: ugly hypotheses
1180   slain by beautiful facts. *Fish Fish* **9**(4), 333-362. (doi:10.1111/j.1467-2979.2008.00299.x).
1181   156.   Potts D.C. 1983 Evolutionary disequilibrium among Indo-Pacific corals. *Bull Mar Sci* **33**(3),
1182   619-632.
1183   157.   Polunin N.C.V., Roberts C.M., Pauly D. 1996 Developments in tropical reef fisheries science
1184   and management. In *Reef Fisheries* (eds. Polunin N.C.V., Roberts C.M.), pp. 361-377. London,
1185   Chapman & Hall.
1186   158.   Cowen R.K., Sponaugle S. 1997 Relationships between early life history traits and
1187   recruitment among coral reef fishes. In *Early Life History and Recruitment in Fish Populations* (eds.
1188   Chambers R.C., Trippel E.A.), pp. 423–449. London, Chapman & Hall.
1189   159.   Thorrold S.R., Jones G.P., Hellberg M.E., Burton R.S., Swearer S.E., Neigel J.E., Morgan S.G.,
1190   Warner R.R. 2002 Quantifying larval retention and connectivity in marine populations with artificial
1191   and natural markers. *Bull Mar Sci* **70**(1, supplement), 291-308.
1192   160.   Almany G.R., Berumen M.L., Thorrold S.R., Planes S., Jones G.P. 2007 Local replenishment of
1193   coral reef fish populations in a marine reserve. *Science* **316**, 742-744.
1194   161.   Planes S., Jones G.P., Thorrold S.R. 2009 Larval dispersal connects fish populations in a
1195   network of marine protected areas. *Proc Natl Acad Sci USA* **106**(14), 5693-5697.
1196   (doi:10.1073/pnas.0808007106).
1197   162.   Pinsky M.L., Montes H.R., Jr., Palumbi S.R. 2010 Using isolation by distance and effective
1198   density to estimate dispersal scales in anemonefish. *Evolution* **64**(9), 2688-2700.
1199   (doi:10.1111/j.1558-5646.2010.01003.x).
1200   163.   Carr M., Syms, C. 2006 Recruitment. In *The Ecology of Marine Fishes: California and Adjacent*
1201   *Waters* (ed. L.G. Allen D.J.P., and M. H. Horn), pp. 411-427. Berkeley, University of California Press.
1202   164.   Sivasundar A., Palumbi S.R. 2010 Life history, ecology and the biogeography of strong
1203   genetic breaks among 15 species of Pacific rockfish, *Sebastes*. *Mar Biol* **157**(7), 1433-1452.
1204   (doi:10.1007/s00227-010-1419-3).
1205   165.   Hart J.L. 1973 Pacific fishes of Canada. *Fish Res Bd Can Bull* **180**, 1-740.
1206   166.   Dahlberg M.D. 1975 *Guide to the coastal fishes of Georgia and nearby states*. Athens,
1207   Georgia, University of Georgia Press; 186 p.

1208 167.   Collette B.B., Klein-Macphee. 2002 *Bigelow and Schroeder's Fishes of the Gulf of Maine*
1209 *(Third Edition)*. Washington, D.C., Smithsonian Books; 882 p.
1210 168.   Robertson D.R., Allen G.R. 2008 *Shorefishes of the tropical Eastern Pacific online information*
1211 *system*. www.stri.org/sftep
1212 169.   Matarese A., Blood D., Bahl K., Konieczna M. 2011 *Ichthyoplankton Information System*.
1213 http://access.afsc.noaa.gov/ichthyo/index.cfm.
1214
1215 170.   Polack D. 2012 *Fishwise Universal Fish Catalogue*. http://www.fishwise.co.za/.
1216
1217 171.   GuelphUniversity. 2012 *Biodiversity of [Canadian] Fishes*.
1218 http://www.aquatic.uoguelph.ca/fish/biodiversity/atlparent.htm.
1219
1220 172.   Leis J.M. 1991 The pelagic phase of coral reef fishes:larval biology of coral reef fishes. In *The*
1221 *ecology of fishes on coral reefs* (ed. Sale P.F.), pp. 183-230. San Diego, Academic Press.
1222 173.   Kendall A.W. 2011 Identification of eggs and larvae of marine fishes. (p. 379. Tokyo, Tokai
1223 University Press.
1224 174.   Ashford J., La Mesa M., Fach B.A., Jones C., Everson I. 2010 Testing early life connectivity
1225 using otolith chemistry and particle-tracking simulations. *Can J Fish Aquat Sci* **67**(8), 1303-1315.
1226 (doi:10.1139/f10-065).
1227 175.   Ben-Tzvi O., Kiflawi M., Gaines S.D., Al-Zibdah M., Sheehy M.S., Paradis G.L., Abelson A. 2008
1228 Tracking recruitment pathways of *Chromis viridis* in the Gulf of Aqaba using otolith chemistry. *Mar*
1229 *Eco Prog Ser* **359**, 229-238. (doi:10.3354/meps07343).
1230 176.   Chang M.Y., Tzeng W.N., Wang C.H., You C.F. 2008 Differences in otolith elemental
1231 composition of the larval *Rhinogobius giurinus* (Perciformes, Gobiidae) among estuaries of Taiwan:
1232 Implications for larval dispersal and connectance among metapopulation. *Zool Stud* **47**(6), 676-684.
1233 177.   Fontes J., Caselle J.E., Sheehy M.S., Santos R.S., Warner R.R. 2009 Natal signatures of juvenile
1234 *Coris julis* in the Azores: investigating connectivity scenarios in an oceanic archipelago. *Mar Eco Prog*
1235 *Ser* **387**, 51-59. (doi:10.3354/meps08116).
1236 178.   Hamilton S.L., Regetz J., Warner R.R. 2008 Postsettlement survival linked to larval life in a
1237 marine fish. *Proc Natl Acad Sci, USA* **105**(5), 1561-1566. (doi:10.1073/pnas.0707676105).
1238 179.   Jones G.P., Milicich M.J., Emslie M.J., Lunow C. 1999 Self-recruitment in a coral reef fish
1239 population. *Nature* **402**(6763), 802-804. (doi:10.1038/45538).
1240 180.   Jones G.P., Planes S., Thorrold S.R. 2005 Coral reef fish larvae settle close to home. *Curr Biol*
1241 **15**, 1314-1318.
1242 181.   Liu S.Y.V., Wang C.H., Shiao J.C., Dai C.F. 2010 Population connectivity of neon damsel,
1243 *Pomacentrus coelestis*, inferred from otolith microchemistry and mtDNA. *Mar Freshwat Res* **61**(12),
1244 1416-1424. (doi:10.1071/mf10079).
1245 182.   Longmore C., Trueman C.N., Neat F., O'Gorman E.J., Milton J.A., Mariani S. 2011 Otolith
1246 geochemistry indicates life-long spatial population structuring in a deep-sea fish, *Coryphaenoides*
1247 *rupestris*. *Mar Eco Prog Ser* **435**, 209-224. (doi:10.3354/meps09197).
1248 183.   Miller J.A., Shanks A.L. 2004 Evidence for limited larval dispersal in black rockfish (*Sebastes*
1249 *melanops*): implications for population structure and marine-reserve design. *Can J Fish Aquat Sci*
1250 **61**(9), 1723-1735. (doi:10.1139/f04-111).
1251 184.   Patterson H.M., Kingsford M.J., McCulloch M.T. 2005 Resolution of the early life history of a
1252 reef fish using otolith chemistry. *Coral Reefs* **24**, 222-229.
1253 185.   Patterson H.M., Swearer S.E. 2007 Long-distance dispersal and local retention of larvae as
1254 mechanisms of recruitment in an island population of a coral reef fish. *Austral Ecol* **32**(2), 122-130.
1255 (doi:10.1111/j.1442-9993.2006.01669.x).
1256 186.   Standish J.D., Sheehy M., Warner R.R. 2008 Use of otolith natal elemental signatures as
1257 natural tags to evaluate connectivity among open-coast fish populations. *Mar Eco Prog Ser* **356**, 259-
1258 268. (doi:10.3354/meps07244).

1259   187.   Swan S.C., Geffen A.J., Morales-Nin B., Gordon J.D.M., Shimmield T., Sawyer T., Massuti E.
1260   2006 Otolith chemistry: an aid to stock separation of *Helicolenus dactylopterus* (bluemouth) and
1261   *Merluccius merluccius* (European hake) in the Northeast Atlantic and Mediterranean. *ICES J Mar Sci*
1262   **63**(3), 504-513. (doi:10.1016/j.icesjms.2005.08.012).
1263   188.   Swearer S.E., Caselle J.E., Lea D.W., Warner R.R. 1999 Larval retention and recruitment in an
1264   island population of a coral-reef fish. *Nature* **402**, 799-802.
1265   189.   Swearer S.E., Shima J.S. 2010 Regional variation in larval retention and dispersal drives
1266   recruitment patterns in a temperate reef fish. *Mar Eco Prog Ser* **417**, 229-236.
1267   (doi:10.3354/meps08801).
1268   190.   Thorrold S.R., Jones C.M., Campana S.E. 1997 Response of otolith microchemistry to
1269   environmental variations experienced by larval and juvenile Atlantic croaker (*Micropogonias
1270   undulatus*). *Limnol Oceanogr* **42**(1), 102-111.
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1272

1273 Table Sup 1. Percentage of demersal marine teleost shorefish species with different
1274 spawning modes in selected regions. A small number of species with unknown spawning
1275 modes are omitted: these constitute at most 3% of species in any location. Species
1276 compositions from: [163] [164] [165] [166] [167] [168] [169]. Spawning modes from: [170]
1277 [167] [171].
1278

Location (number of species)	Category	Broadcast spawner (pelagic egg)	Demersal spawner (demersal egg)	Brooder (egg held by adult)	Live bearer (viviparous)	No pelagic stage
Atlantic Ocean						
Canada Atlantic (91)	cold temperate	27.5	64.8	1.1	3.3	0
Mid Atlantic Bight (Northern Florida to Cape Hatteras) (227)	warm temperate	77.1	15.9	4.0	0.00	2.2
Cuba (535)	tropical	64.9	24.5	6.4	2.2	0.9
Argentina (124)	temperate	55.7	34.7	4.0	0.8	4.0
Pacific Ocean						
NE Pacific (Oregon Border to Bering Strait) (198)	cold temperate/ boreal	15.2	65.7	0.5	14.1	4.6
Californian (Cabo San Lucas to Point Conception) (306)	warm temperate	68.6	25.2	2.6	1.3	2.3
Equatorial E. Pacific (696)	tropical	60.9	30.9	2.4	1.3	4.5
Chile (115)	temperate	55.7	32.2	3.5	5.2	1.7
Hawaii (429)	tropical	75.5	20.3	3.7	0.2	0
Southern Ocean						
Antarctic (55)	polar	16.4	83.7	0	0	0

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1280   Table Sup 2. Studies based on otolith methods to estimate demographic connectivity used in the habitat fragmentation comparison. These
1281   publications were found by searching the ISI Web of Science database using the search criteria ("otolith chemistry" or "otolith microchemistry"
1282   or "elemental fingerprints" or "environmental marker*" or "natural tag*") and (dispersal or connectivity or migration or "stock structur*"). Studies
1283   were then filtered to include only non-philopatric species where movement among populations was due to larval dispersal. [156], [172], [173],
1284   [174], [175], [176], [177], [178], [179], [180], [181], [182], [183], [184], [185], [186], [187], [188]
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Species	Egg Type	Habitat Type	Latitude	Mean % Self-recruitment	Scale of Self-recruitment (km)	Minimum Scale of Connectivity (km)	Reference
Amphiprion percula	Demersal	Islands	5°S	60	0.5	20	[156]
Chaetodon vagabundus	Pelagic	Islands	5°S	60	0.5	20	[156]
Chaenocephalus aceratus	Demersal	Coastal	54-63°S	No estimate	200	400	[172]
Dissostichus eleginoides	Pelagic	Coastal	43-55°S	88	250	1200	[172]
Chromis viridis	Demersal	Islands	29°N	No estimate	No estimate	15	[173]
Rhinogobius giurinus	Demersal	Coastal Habitat Patch	23°N	94	0.1	175	[174]
Coris julis	Pelagic	Islands	37-40°N	85	20	600	[175]
Thalassoma bifasciatum	Pelagic	Islands	17°N	45	35	No estimate	[176]
Pomacentrus amboinensis	Demersal	Islands	14°S	35	7	No estimate	[177]

Species	Type	Habitat	Latitude				Ref
Amphiprion polymnus	Demersal	Islands	5°S	24	0.1	0.5	[178]
Pomacentrus coelestis	Demersal	Coastal Habitat Patch	23°N	69	30	370	[179]
Coryphaenoides rupestris	Pelagic	Coastal	50-58°N	71	300	2700	[180]
Sebastes melanops	Live bearer	Coastal Habitat Patch	42-46°N	71	120	540	[181]
Pomacentrus coelestis	Demersal	Islands	14-23°S	42	10	30	[182]
Coris bulbifrons	Pelagic	Islands	31°S	50	15	600	[183]
Sebastes atrovirens	Live bearer	Islands and Coastal Habitat Patch	34°N	97.5	30	40	[184]
Merluccius merluccius	Pelagic	Coastal	36-62°N	No estimate	400	1000	[185]
Thalassoma bifasciatum	Pelagic	Islands	17°N	50	35	No estimate	[186]
Forsterygion lapillum	Demersal	Coastal Habitat Patch	41°S	72	10	20	[187]
Micropogonias undulatus	Pelagic	Coastal	35-36°N	No estimate	No estimate	330	[188]

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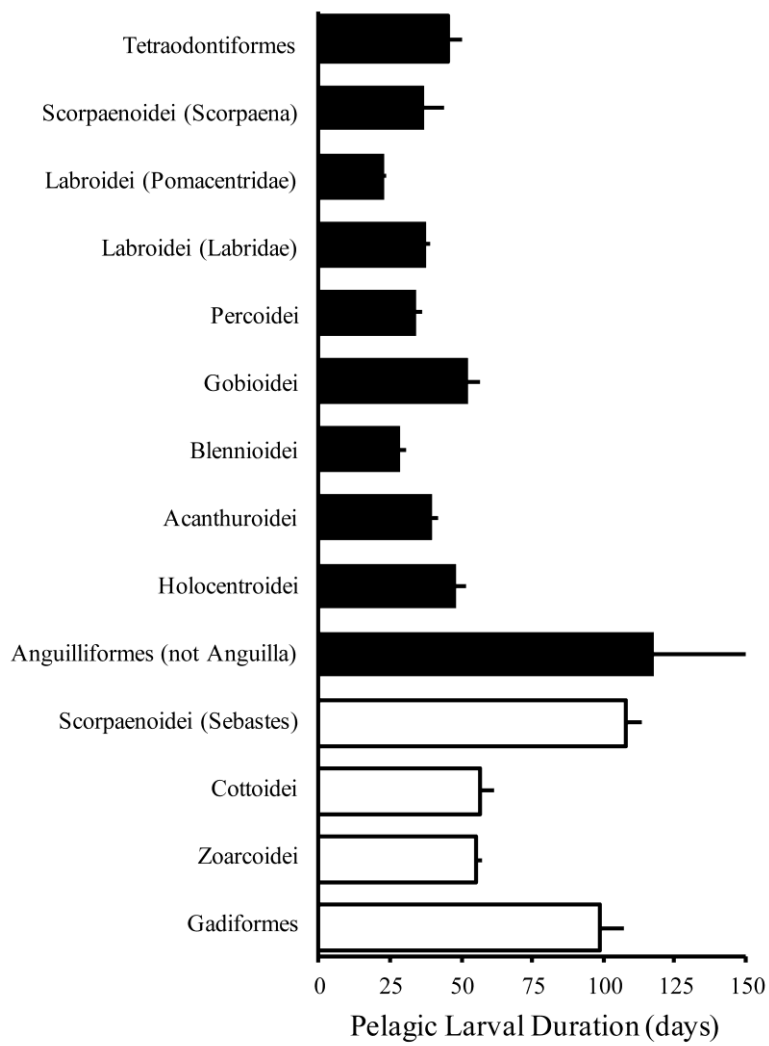
Figure Sup 1. Mean (±SE) pelagic larval duration for taxonomic groups of demersal shorefishes with primarily warm-water (solid bars) and cold-water (open bars) distributions. PLD data from [2] and [3]. See Supplement text for numbers of PLD estimates for each taxon.
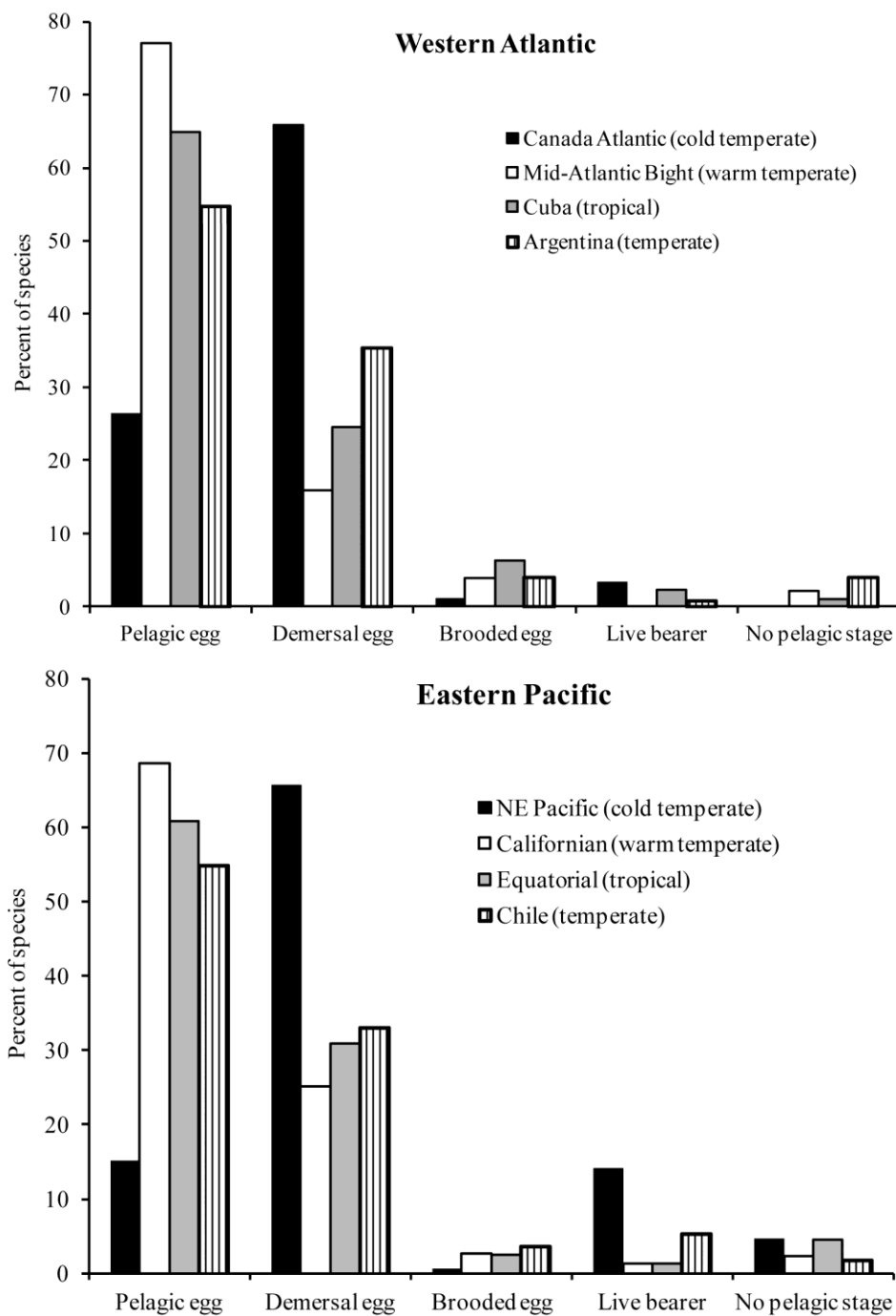
Figure Sup 2. Percentages of demersal shorefish species with different spawning modes in regions of the Western Atlantic and Eastern Pacific. In each ocean, cold temperate regions have a much smaller percentage of species with pelagic eggs than do other regions. Both Argentina and Chile have a large 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.
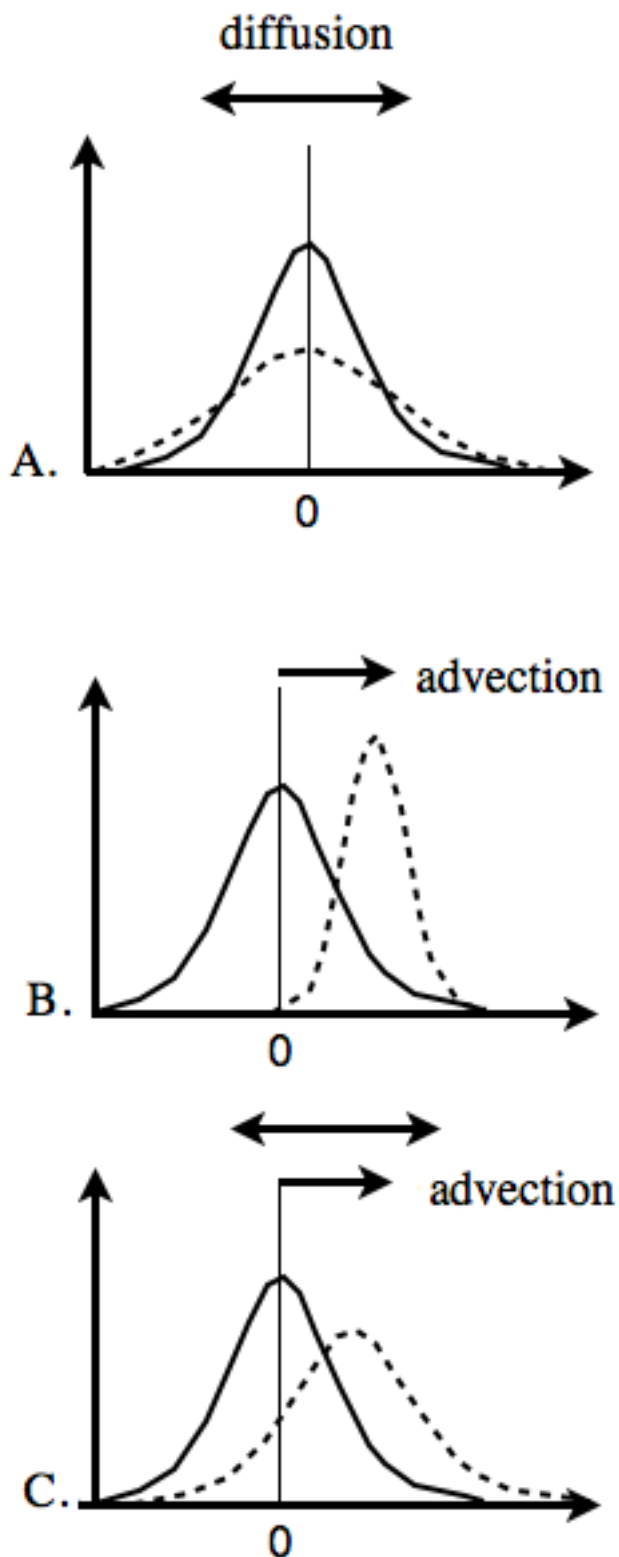
Figure Sup 3. Larval transport by Eddy kinetic energy (EKE) and eddy-driven currents: consequences of (A) strong diffusion (dotted line), (B) anisotropic advection (dotted line), (C) advection and strong diffusion (dotted line) on the mean dispersal kernel (solid line). Larval source is located at x = 0.
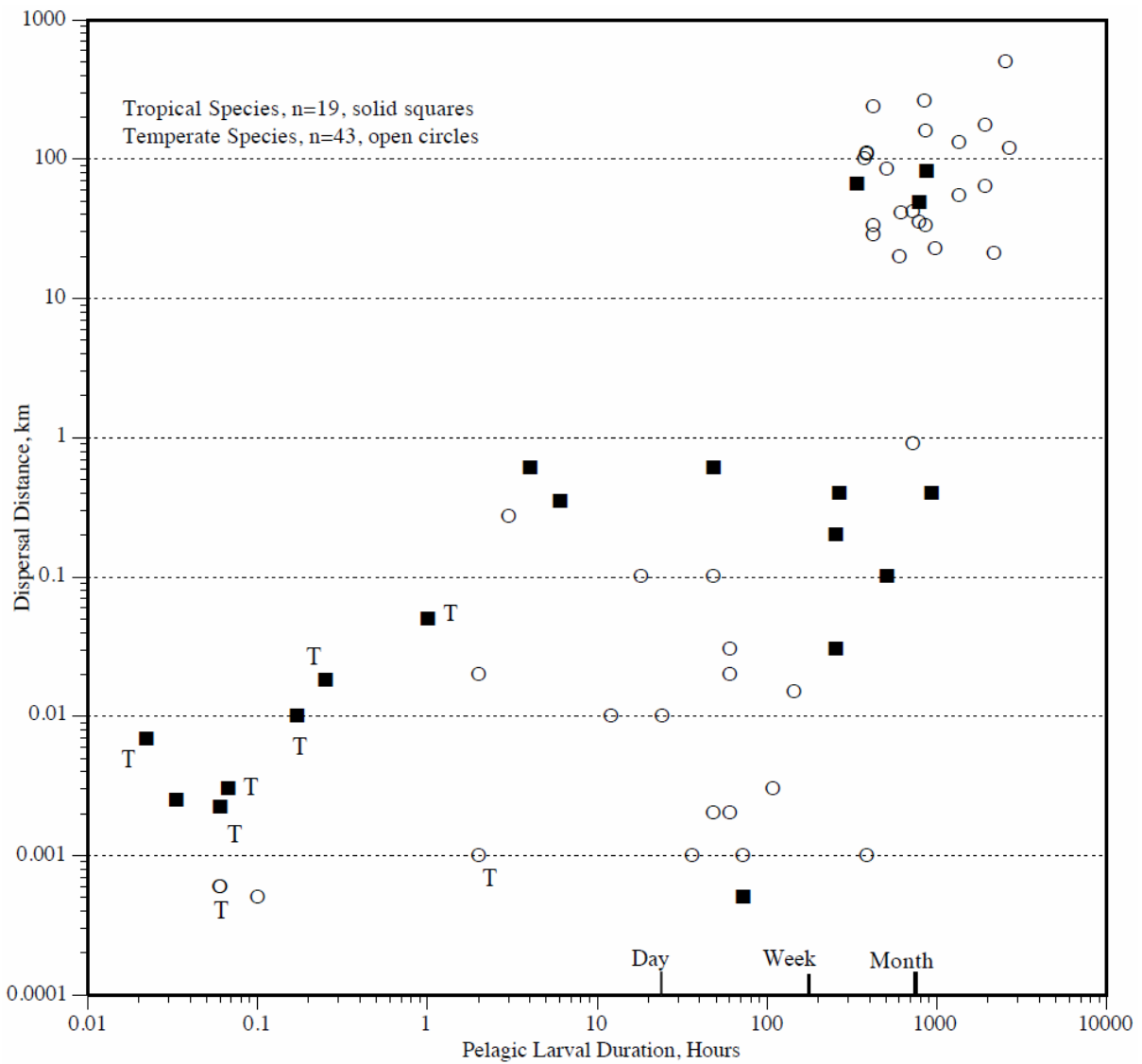
Figure Sup 4. Pelagic larval duration of marine invertebrates and fishes plotted against their dispersal distance. Solid squares and open circles are data from tropical and temperate species, respectively. "T"s adjacent to values indicate data from the dispersal of tadpole larvae of tunicates. Data are from [139] and [138], but with algal data removed.