



Global biogeography of marine dispersal potential

Mariana Álvarez-Noriega^{1✉}, Scott C. Burgess², James E. Byers³, James M. Pringle⁴, John P. Wares^{3,5} and Dustin J. Marshall¹

The distance travelled by marine larvae varies by seven orders of magnitude. Dispersal shapes marine biodiversity, and must be understood if marine systems are to be well managed. Because warmer temperatures quicken larval development, larval durations might be systematically shorter in the tropics relative to those at high latitudes. Nevertheless, life history and hydrodynamics also covary with latitude—these also affect dispersal, precluding any clear expectation of how dispersal changes at a global scale. Here we combine data from the literature encompassing >750 marine organisms from seven phyla with oceanographic data on current speeds, to quantify the overall latitudinal gradient in larval dispersal distance. We find that planktonic duration increased with latitude, confirming predictions that temperature effects outweigh all others across global scales. However, while tropical species have the shortest planktonic durations, realized dispersal distances were predicted to be greatest in the tropics and at high latitudes, and lowest at mid-latitudes. At high latitudes, greater dispersal distances were driven by moderate current speed and longer planktonic durations. In the tropics, fast currents overwhelmed the effect of short planktonic durations. Our results contradict previous hypotheses based on biology or physics alone; rather, biology and physics together shape marine dispersal patterns.

Dispersal drives population dynamics, community structure, adaptation and speciation. At the local population scale, dispersal from distant patches increases phenotypic and genetic diversity and modifies density, all of which affect population growth^{1–3}. At the meta-population scale, long-distance dispersal buffers persistence against local catastrophes⁴ and enables the expansion of ranges^{5,6}. Limited dispersal isolates populations genetically, facilitating adaptation to local conditions and increasing speciation rates^{7–9}. From an applied perspective, dispersal enables the spread of invasive species and determines the size and spacing of protected areas^{10,11}. Given the ecological and evolutionary implications of dispersal, understanding patterns in dispersal is a key goal in ecology and evolution^{12–14}.

An association between dispersal and temperature is often proposed to drive well-known latitudinal patterns in biodiversity and explain why the tropics are relatively species rich. Janzen¹⁵ famously proposed that mountain passes restrict dispersal more in the tropics than they do at higher latitudes, based on temperature variation and physiology. This hypothesis has since motivated explanations of latitudinal gradients in speciation rate and species diversity in terrestrial systems^{16–18}. An analogous argument was proposed by Brown^{19,20} for marine systems—that marine islands are metaphorically ‘further apart’ in the tropics. Brown proposed that dispersal distances of ectothermic sessile or sedentary marine species are shorter in the tropics relative to the poles because the higher temperatures in the tropics hasten the time spent by their propagules developing in the water column before eventually settling to the bottom. Brown surmised that species diversity might therefore be higher in the tropical seas because islands (populations) a similar distance apart are less connected by larval dispersal relative to the poles. This intriguing hypothesis has some preliminary support^{21–23} but has not been explored comprehensively.

By affecting connectivity between populations, dispersal is a major determinant of speciation and extinction^{15,20} which, in turn,

affect diversity patterns. However, patterns of species diversity are complex and change throughout geological time (for example, refs. ^{24–26}). As such, species diversity may not necessarily mirror current dispersal patterns and, consequently, care must be taken when interpreting evidence of species richness supporting or contradicting expected dispersal patterns.

That dispersal distance should increase with latitude is based on the effect of temperature on larval development. Temperature hastens developmental rate, reducing the developmental duration of ectotherms²⁷. Larval duration declines exponentially with increasing temperature both within and among species²¹. Although long planktonic duration is only moderately correlated with estimates of dispersal, larvae that spend less time in the plankton have less potential to disperse^{28,29} so increases in temperature should decrease maximum dispersal potential²¹. Within marine systems, dispersal distances can differ by orders of magnitude among species. The variability in dispersal distances in marine systems far exceeds that in terrestrial systems³⁰.

Brown’s proposal is reasonable and compelling, but temperature is not the sole driver of the variability in dispersal distances seen in marine systems: developmental mode also affects marine invertebrate planktonic duration. Importantly, development mode covaries with temperature and so it also covaries with latitude. The covariation between development mode and latitude may counteract the effect of temperature in driving latitudinal gradients in dispersal distance. Species with feeding pelagic (planktotrophic) larvae are more common in the tropics than at high latitudes. Species with non-feeding pelagic (lecithotrophic) larvae (or no larvae (direct developers)) are more common at high latitudes than in the tropics^{31–34}. For a given latitude, since planktonic developmental period is longer for planktotrophic larvae than for lecithotrophic³⁵, developmental mode will complicate Brown’s predictions because, in addition to temperature, dispersal is dependent on the planktonic duration of planktotrophic larvae in the tropics and of lecithotrophic larvae at the poles.

¹Centre for Geometric Biology, School of Biological Sciences Monash University, Melbourne, Victoria, Australia. ²Department of Biological Science, Florida State University, Tallahassee, FL, USA. ³Odum School of Ecology, University of Georgia, Athens, GA, USA. ⁴Department of Earth Sciences and the Institute for Earth, Ocean, and Space, University of New Hampshire, Durham, NH, USA. ⁵Department of Genetics, University of Georgia, Athens, GA, USA.

✉e-mail: mariana.alvareznoriega@monash.edu

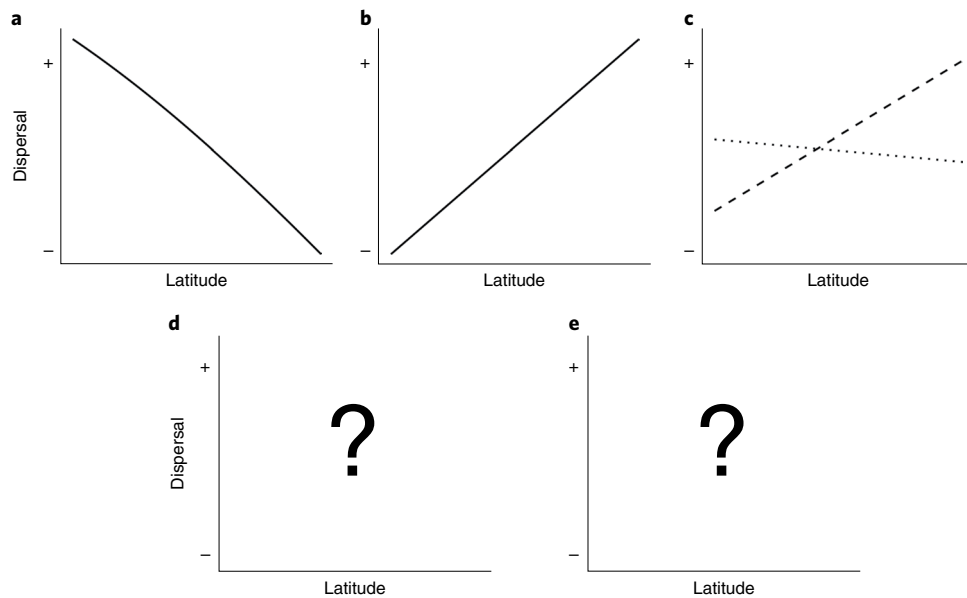


Fig. 1 | Factors affecting maximum dispersal distance across latitudes. **a–e**, Hypothetical scenarios for how maximum dispersal distance would vary across latitudes if driven solely by development (**a**), temperature (**b**), maternal investment (egg size, **c**), surface current speed (**d**) or by all factors jointly (**e**). The latitudinal gradient in maximum dispersal distance with respect to surface current speed (**d**) is unknown because hydrodynamics are place based and do not necessarily have a latitudinal pattern. The overall latitudinal gradient in maximum dispersal (**e**) is unknown because we do not know how all of the above effects combine. Solid, dotted and dashed lines show the effects for both developmental modes, for planktotrophic larvae only and for lecithotrophic larvae only, respectively.

Furthermore, developmental mode is not the only life history characteristic to vary with latitude and potentially influence dispersal distance. For marine organisms, maternal investment also increases with latitude^{33,36}. Eggs are larger at higher latitudes, and this pattern is much stronger for lecithotrophic species than for planktotrophic. Planktonic duration is positively related to egg size in lecithotrophic species because large larvae can invest more time finding a suitable surface for settlement³⁷, but it is negatively related for planktotrophic species that are usually going through obligate developmental stages during dispersal^{38–40}. For lecithotrophic species, the effect of egg size should increase planktonic durations and dispersal at higher latitudes while the latitudinal effect for planktotrophic species should be much weaker. The effects of egg size on the biogeography of dispersal potential are unclear.

Temperature and life history determine the length of time when larvae disperse, or dispersal duration. The product of this time and the current speed provided by the hydrodynamic regime determines the distance dispersed⁴¹. Different hydrodynamic regimes can uncouple dispersal duration and dispersal distance⁴². For example, if moving from a low latitude to a higher latitude increases planktonic duration by 25%, a decrease in current speeds of only 20% would be enough to counter the effect of this increase in dispersal duration on expected dispersal distance. Changes in hydrodynamics across space may therefore affect the spatial patterns in dispersal potential. For instance, the potential reduction in average planktonic duration at high latitudes caused by a lower proportion of planktotrophic larvae⁴³ would have a negative effect on dispersal that could be offset by a relatively rapid current.

The potentially countervailing effects of different drivers of dispersal potential hamper any clear expectation of how dispersal distances change at a global scale (Fig. 1). Nevertheless, some studies have given primacy to certain factors over others. In contrast to the temperature-focused hypothesis of Brown^{19,20}, Marshall et al.³³ hypothesized that there is lower connectivity at high latitudes, reasoning that the effect of developmental mode on dispersal outweighs the increase in planktonic duration within developmental

mode at high latitudes. Since then, Mercier et al.⁴⁴ found no relationship between developmental mode and larval duration because the temperature effect on duration outweighs developmental mode effects. Here, we predict that latitudinal patterns in temperature and maternal investment (within developmental mode) would combine to outweigh the effects of developmental mode such that, as Brown predicted, dispersal distances will be shorter in the tropics. However, to resolve this debate and understand global patterns in dispersal, we need to combine all the latitudinal gradients in dispersal drivers: developmental mode, temperature effects, maternal investment and hydrodynamics. We use data from the literature encompassing >750 species of sessile or sedentary marine invertebrates with planktonic larvae belonging to seven phyla, as well as oceanographic data, to quantify the independent and combined effects of drivers on the overall latitudinal gradient in larval dispersal.

Results

Maternal investment and developmental mode. Maternal investment, measured as egg size, increased with increasing latitude for lecithotrophic larvae but remained constant across latitudes for planktotrophic larvae (Extended Data Fig. 1 and Supplementary Table 1). For example, lecithotrophic egg size increased by a factor of 1.10 from the Equator to a latitude of 50° in the Southern Hemisphere, and by a factor of 1.06 in the Northern Hemisphere. In contrast, egg sizes of planktotrophic species size decreased by a factor of 0.98 in the Southern Hemisphere and 0.99 in the Northern Hemisphere across the same latitude difference. Planktotrophic larvae were more common than lecithotrophic larvae across all latitudes, but decreased in relative abundance with increasing latitude (Extended Data Fig. 2). The probability of a larva being planktotrophic decreased from 70% in the Equator to 67% at a latitude of 50°.

Planktonic duration. In lecithotrophic species, large eggs remained in the plankton for longer than did small eggs; the pattern was reversed for eggs from planktotrophic species. The effect of egg size on planktonic duration was stronger in cold temperatures than

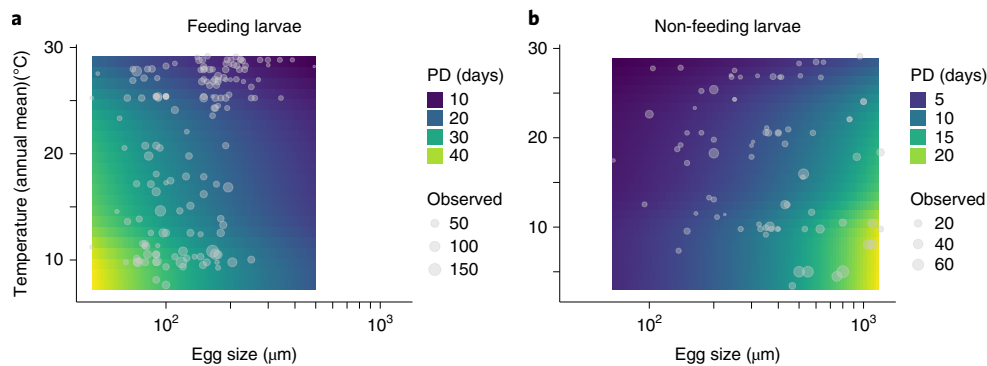


Fig. 2 | Planktonic duration across egg sizes and temperatures. **a,b**, Planktonic duration (PD) for eggs of planktotrophic (**a**) and lecithotrophic species (**b**). White circles denote data points; point size is proportional to the observed planktonic duration. Planktonic durations were predicted from a linear mixed-effects model (with developmental mode, egg size (μm , \log_{10} scale) and absolute latitude; and from interaction between (1) absolute latitude and hemisphere, (2) egg size and developmental mode and (3) absolute latitude and developmental mode). The relationship between temperature ($^{\circ}\text{C}$, annual mean) and latitude was quantified with a general additive model to obtain predictions for planktonic duration in relation to temperature. A total of 158 and 81 observations for planktonic and lecithotrophic species, respectively, is included.

in warm temperatures for both developmental modes (Fig. 2a,b). Planktonic duration was shorter in the tropics than at high latitudes for both developmental modes (Extended Data Fig. 3). For example, planktonic duration increased by a factor of 2.54 and 3.00 from the Equator to a latitude of 50° for planktotrophic species in the Northern and Southern Hemispheres, respectively; for lecithotrophic species, it increased by a factor of 3.75 and 4.43 across the same range of latitudes in Northern and Southern Hemispheres, respectively. Similarly, planktonic duration, weighted by the relative abundance of each developmental mode and adjusted for changes in egg size across latitudes, increased with increasing latitude (that is, with decreasing temperature) (Fig. 3 and Extended Data Fig. 4).

Predicted dispersal distance. Predicted dispersal distance was greatest at both the poles and tropics, and lowest at mid-latitudes (Fig. 4). The expected dispersal distance was often <100 km and, at mid-latitudes, it was about 50 km less than in the tropics and about 260 km less than that towards the southern pole (Fig. 4b). Long dispersal at high latitudes was driven by longer planktonic durations in cold water and by fast currents, particularly in the Southern Hemisphere (Extended Data Figs. 4–6); long dispersal in the tropics was solely driven by fast currents—these currents overwhelmed the relatively short planktonic durations. Differences in dispersal across western–eastern ocean boundaries were also driven by current speed, where faster currents in the western ocean boundaries increased dispersal distance relative to eastern ocean boundaries. For the locations of biological data used in this study, latitude could explain only 26% (95% confidence interval: 20.4–31.8%) of the variation in mean surface current speed predicted by the Mercator model, and 25% (95% confidence interval: 20.5–29.5%) of the variation in mean surface current speed from the drifter data. Changes in egg size and developmental mode across latitudes modified our predictions of dispersal distance by $<10\%$; changes in planktonic duration (independent of changes in egg size or in developmental mode) and in mean annual current speed altered our predictions by up to 80% and three orders of magnitude, respectively (Extended Data Fig. 7).

Discussion

In contrast to previous hypotheses^{20,21,33} and our own expectations here, the effects of temperature and life histories on global variation in dispersal distance in benthic marine invertebrates were strongly modified by oceanographic processes. Relatively fast surface current speeds in the tropics counteracted the expected effect of shorter

planktonic durations in these latitudes on reducing dispersal distance. Dispersal distances were greatest at high and low latitudes and lowest at mid-latitudes, where planktonic durations are intermediate and current speeds are relatively slow (Fig. 4). In that sense, tropical islands are not further apart; rather, temperate islands (or populations) are the most isolated by reduced dispersal. O'Connor et al.²¹ and Brown²⁰ had, reasonably, hypothesized that dispersal would be shortest in the tropics because developmental rate is faster in warm water, reducing larval duration (Fig. 1b). While the predictions about dispersal duration were upheld, hydrodynamics decoupled planktonic duration from dispersal distance (Fig. 1d). On the other hand, the predictions of Marshall et al.³³ failed to anticipate the strong effects of temperature and, in hindsight, overestimated the effects of development (Fig. 1a). Given the ecological consequences of dispersal, we would expect intermediate latitudes to have the weakest connectivity among populations. However, while the pattern of an increase in planktonic duration with increasing latitude is very clear (Extended Data Fig. 4), only about 26% of the variation in mean annual current speed predicted by the Mercator model (or 25% in the drifter data) was explained by latitude, and therefore the relationship between dispersal distance and latitude is more variable.

Our predictions contradict the suggestion by Brown and others^{20,21} that organisms in the tropics should have reduced dispersal distance; rather, we find that they should be much more connected than Brown hypothesized. Brown^{19,20} hypothesized that the effect of temperature on developmental rate should shorten dispersal distance in the tropics, promoting local adaptation and speciation and making marine islands ‘farther apart’. In general, the increase in species richness within tropical latitudes is thought to be particularly strong in marine species with pelagic larvae⁴⁵, but our predictions suggest that this pattern is not driven by dispersal. Our predictions are consistent with some recent studies showing a dip in species richness near the Equator and a peak at mid-latitudes for both fish⁴⁶ and other marine taxa^{47,48}. However, there is also evidence on speciation rates⁴⁹, geographical ranges⁵⁰ and species richness that contradicts our predictions. Perhaps most important is the fact that, if richness were driven purely by dispersal distance, we would expect similar species richness at high latitudes and in the tropics given that predicted dispersal is similar. However, this is not the case, even for taxa with bimodal distribution of species richness (for example, refs. 45,47).

We would expect that, all else being equal, organisms may present life history traits that reduce dispersal when surface currents

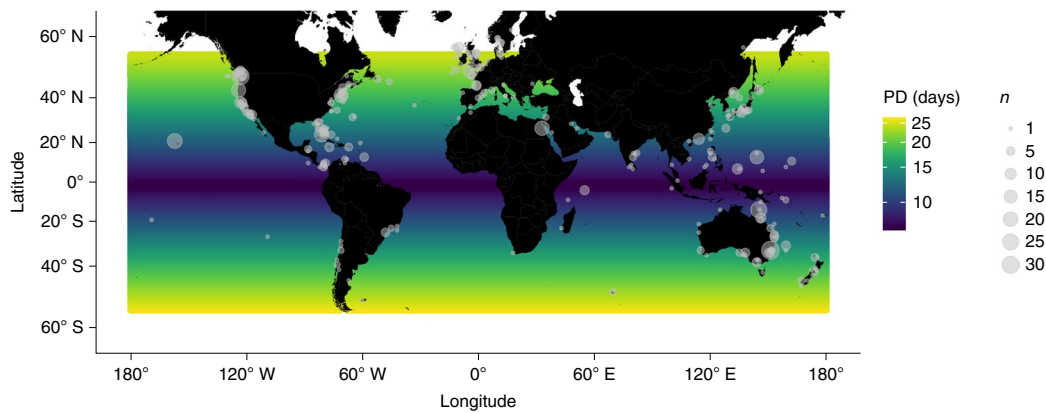


Fig. 3 | Planktonic duration across latitudes. Planktonic duration (PD) was estimated for both developmental modes and then averaged according to their predicted relative abundance across latitudes. This prediction also incorporates latitudinal changes in egg size. Grey circles show the distribution of studies from which data were obtained; circle size corresponds to the number of studies ($n=1$ –33) at each location.

are too fast, or if there is strong upwelling that transports larvae away from the coast²¹. For example, marine invertebrates without a pelagic phase (that is, direct developers not considered in this analysis) are most common at high latitudes in the Southern Hemisphere³³, where surface current speeds are faster than those at equivalent latitudes in the Northern Hemisphere, although some taxa develop directly regardless of latitude^{26,50}. A better understanding of the degree to which hydrodynamics influence life histories would be informative about the evolutionary pressures affecting dispersal. In general, the costs of larval dispersal over the scale of kilometres or more commonly seen in marine systems seem to outweigh the benefits of dispersal at that scale⁵². Planktonic durations often result in dispersal distance that exceeds that required to reduce kin competition, inbreeding and extinction risk (that is, hundreds of kilometres versus a few metres to kilometres⁵¹). Consequently, long dispersal distances should not be favoured if the probability of suitable habitat decreases with increasing distance from the natal site and they do not confer additional benefits (for example, increased fecundity⁵³).

Although we focused only on marine invertebrates, the same ideas can be extended to fish. For most fish, dispersal also occurs during early life stages⁵⁴. Fish egg size decreases with increasing temperature, resulting in the smallest mean egg sizes in the tropics and the largest at high latitudes³⁶. Since developmental time increases with increasing embryo mass for fish⁵⁵ and decreases with increasing temperature²¹, we would expect fish at high latitudes to have the longest larval durations—a pattern similar to that of marine invertebrates. Indeed, a meta-analysis of fish dispersal found an increase in planktonic duration with increasing latitude⁵⁶. Similar to our predictions for marine invertebrates, dispersal may be high near the tropics for fish larvae that are governed by currents, but probably less so for those with competent swimming abilities (for example, refs. ^{57,58}).

Given our results we hypothesize that, in general, temperate populations of marine invertebrates may have different susceptibilities to local extinctions than populations in the tropics or at higher latitudes. A local population that is dependent on external sources of larval input for replenishment (that is, a ‘sink’ population) would be more likely to persist in highly connected meta-populations⁵⁹. Assuming equivalent fecundity and mortality, when interpatch dispersal is high, extinction risk of local sink populations should decrease because immigrants ‘rescue’ populations against local decline (when decline occurs at a scale smaller than dispersal)⁴. In contrast, a local population that is dependent on local retention of larvae for population replenishment would be less likely

to persist when dispersal is high. High dispersal would favour meta-population persistence if local retention is low (replacement is <1) and larval exchange among populations compensates for the shortfall in self-persistence of each local population^{59,60}.

An early theoretical model assumed that planktonic duration should be positively correlated with egg size for lecithotrophic larvae, but for planktotrophic larvae the relationship should be negative⁴⁰. Most empirical evidence supports an increase in developmental time with increasing egg size for lecithotrophic larvae (for example, refs. ^{61,62}), but studies investigating the effect of egg size on planktonic duration for planktotrophic larvae often report contrasting patterns^{34,35}. These differences in egg size–planktonic duration relationships among planktotrophic species may be caused by differences in the relative contributions of the effects of egg size on feeding and prefeeding periods; however, low replication and assumption of the independence of phylogenetically related species may also contribute to those differences³⁵. Using data on 83 lecithotrophic species and 158 planktotrophic species, and accounting for phylogenetic relationships, our results support Vance’s⁴⁰ prescient predictions (Fig. 2a).

Overall, planktonic duration was predicted to be lowest in the tropics and highest towards the poles (Fig. 3). The direction of the gradient prevailed, despite a higher proportion of lecithotrophic larvae (with short planktonic durations) towards the poles relative to the tropics (Extended Data Fig. 2). The predicted pattern was consistent with the expected effects of temperature on developmental duration²⁷, indicating that the effect of temperature outweighed the effects of life history traits on planktonic duration (Extended Data Fig. 8). However, the scaling coefficient for the effect of temperature on larval duration among species estimated here (0.14 with 95% confidence interval 0.09–0.19 for planktotrophic larvae; 0.20 with 95% confidence interval 0.10–0.29 for lecithotrophic larvae) was much lower than that reported for within-species patterns (0.64 with 95% confidence interval 0.59–0.69) in ref. ²¹, suggesting some adaptation of species to local temperature regimes.

Dispersal is affected by additional factors that were not considered for this analysis. Importantly, we assumed that larvae disperse passively yet they can swim vertically in the water column to reach a preferred depth-dependent flow⁶³. Therefore, we expect that larval behaviour will alter the dispersal patterns predicted here. Additionally, the predicted dispersal pattern is dependent on the predicted mean surface current speed in a 1/12° grid, meaning that each mean speed corresponds to an area ranging from ~86 km² in the tropics to ~49 km² at a latitude of 55°. The level of discrepancy between the available oceanographic data and oceanographic

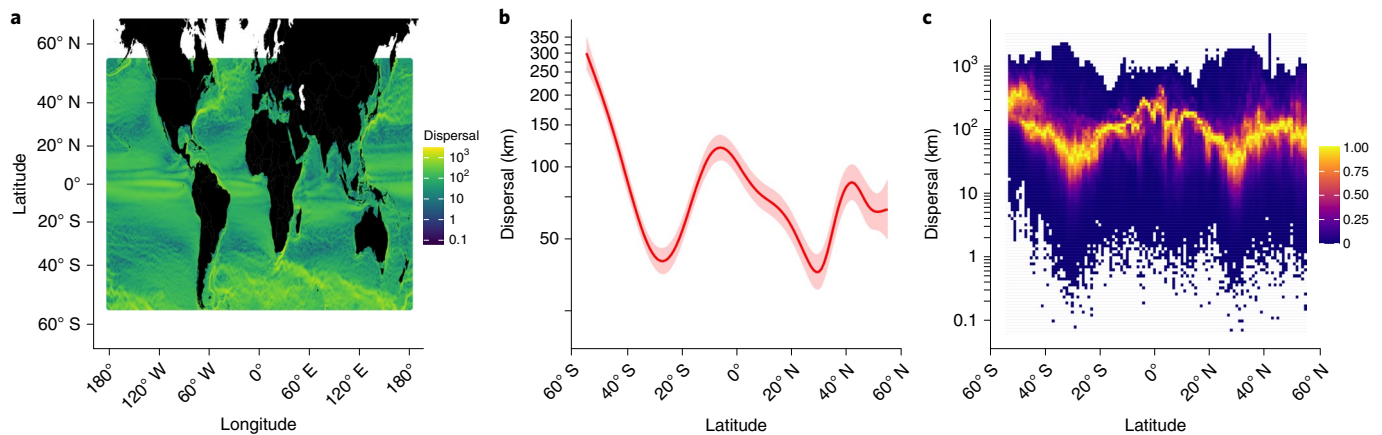


Fig. 4 | Potential dispersal distance across latitudes. **a**, Predicted dispersal distance (km, log₁₀ scale) at the surface, incorporating the probability for each developmental mode, egg size, temperature and currents. Current speed was obtained from the Mercator 1/12° modelling system. **b**, Predictions from a generalized additive model fitting dispersal distance (km) as a function of latitude. Since there was high correlation for current speed between locations within a 100-km distance, only a subset of predicted dispersal distances (from those plotted in **c**), spaced in a 500 km × 500 km grid, were used to fit the model. The red line and shaded area show the fit and 95% confidence interval, respectively. **c**, Density of predicted dispersal distances for each latitude relative to that with the highest density. Dispersal distances marked in yellow are those best predicted by the model for a specific latitude. Dispersal distances marked in blue are those that had the lowest densities of predictions relative to the most predicted dispersal distances.

processes operating at a scale relevant for larvae is not clear. However, flows that occur at smaller scales than the 1/12° grid (for example, boundary layers, water fronts, tidal currents and so on) are also important for dispersal^{64,65}. Moreover, seasonal cycles in current speed will have a strong effect on dispersal if there are systematic patterns in the timing of larval release⁴¹.

While our approach to analyse dispersal patterns at a global scale has certain limitations, empirical investigation of marine dispersal patterns is challenging (ref. ⁶⁶, although see ref. ⁶⁷ for a combination of biophysical models and empirical estimates). Because direct estimation of dispersal is unfeasible for most taxa, the majority of studies have used estimates of gene flow among populations as a proxy for dispersal. Geochemical marking can measure current dispersal but, since the geochemical signature of the source location must be known, it functions on a limited spatial scale^{68–70}. In contrast, estimation of dispersal using genetic markers allows for comparisons across any locations but represents genetic connectivity at multi-generational time scales⁶⁶. This implies that empirical evidence to test our predictions at adequate spatial and temporal scales will be difficult to obtain. However, consistent with our expectations, species of marine molluscs on the Pacific coast of North America have higher gene flow at high versus mid-latitudes²², and similar patterns occur within species for a marine copepod in North America⁷¹; both of these studies used genetic markers.

In conclusion, while the effect of temperature on planktonic duration (Fig. 1b) outweighs the effects of developmental mode (Fig. 1a) and egg size (Fig. 1c), global patterns in dispersal are mostly driven by large differences in water velocity across space (Fig. 1d). Our predictions represent potential dispersal (what is possible) rather than realized dispersal⁷², and should be interpreted as such (see Supplementary Information for further discussion). We anticipate that incorporation of other factors influencing dispersal—such as fecundity, survival or larval behaviour—may modify the dispersal patterns predicted here. Nevertheless, this study provides a first step in combining the effects of dispersal drivers to predict large-scale patterns in marine invertebrate dispersal.

Methods

Data collection. We used data on egg size and planktonic duration from the literature compiled in ref. ³³. We included only those species with a planktonic

larval period and which the authors had classified into planktotrophic (feeding) or lecithotrophic (non-feeding) larvae according to published literature. To compile the dataset, Marshall et al.³³ searched >4,000 studies; the subset we used includes a total of 766 marine invertebrate species from the following phyla: Annelida (191 species), Arthropoda (12 species), Bryozoa (3 species), Chordata (7 species), Cnidaria (18 species), Echinodermata (230 species) and Mollusca (305 species). Each species had only one observation of egg size or planktonic duration, except for 22 that had two, one that had three and two that had four (treated as spatial replicates). There were four genera for which species was not identified that had two, four, five and six replicates, respectively. We recorded the latitude and longitude at which the observations were made. The references of the studies from which we used data from, as well as the data used, are found in the Supplementary Information.

Mean annual surface current speed data. We used mean annual surface current speed as estimated by the Mercator 1/12° modelling system near the surface, from 2007 to 2017 (ref. ⁷³) (Extended Data Fig. 5). To verify that these predicted current speeds were accurate representations of reality, we compared the Mercator data to those from surface drifters released as part of the Global Drifter Project⁷⁴ (Extended Data Fig. 6). The Global Drifter Project includes data from drifters drogued to 15 m, and from drifters that lost drogues but whose trajectories were corrected with 10-m winds from the European Centre for Medium-Range Weather Forecasts at 1/4° resolution. To compare the two current speed datasets, we averaged the speed from the Mercator modelling system within a 1/4° grid. Since the agreement between both current speed datasets was high (0.83 correlation, comparing current speeds averaged at a 1/4° resolution), we used data from the Mercator model due to its higher resolution (see Supplementary Figs. 1–3 for comparison).

Although along-shore and cross-shelf current velocities have different implications for dispersal distance (that is, cross-shelf currents will probably disperse larvae away from suitable environments), we do not differentiate between them here; since along-shore flows are much stronger than cross-shelf flows^{75,76}, net displacement is assumed to capture along-shore dispersal near the coast.

Data analysis. Overview. We quantified latitudinal gradient in both developmental mode and egg size (within developmental mode) with linear mixed-effects models in a Bayesian framework using the R package ‘brms’ v.2.7.0 (ref. ⁷⁷) that uses No-U-Turn Sampler⁷⁸. Priors were obtained using the function ‘get_prior’ from ‘brms’. We calibrated the relationship between planktonic duration and latitude by including the effects of egg size and developmental mode, and the expected frequency of their effects at each latitude (from the linear mixed-effects models fitted to the data). The planktonic duration predicted for each developmental mode was weighted by the estimated proportion of species with larvae of that developmental mode across latitudes. The overall global pattern in planktonic duration (that is, the expected planktonic duration for ‘average larvae’) was then multiplied by current speed at each location to estimate dispersal potential.

To correct for non-independence in the data due to phylogenetic relatedness between species, models were phylogenetically controlled at the genus level. To do

this, we included genus as a random effect and we specified the covariance matrix of the random effects as the relatedness matrix obtained from the phylogenetic tree. We extracted the phylogenetic tree using the R package 'rotl' v.3.0.6 (ref. ⁷⁹) and estimated the length of the phylogenetic tree branches using Grafen's⁸⁰ method with the R package 'ape' v.5.2 (ref. ⁸¹). We calculated the relatedness matrix from the phylogenetic tree using the R package 'MCMCglmm' v.2.26 (ref. ⁸²). All analyses were performed in R v.3.5.2 (ref. ⁸³), and the figures were generated using the R package 'ggplot2' v.3.3.0 (ref. ⁸⁴). A second set of analyses that are not phylogenetically controlled are included in the Supplementary information for comparison; there was no qualitative difference between the two sets of analyses.

Developmental mode. Developmental mode was measured as the proportion of species with planktotrophic larval stages in the dataset. Every 10° interval in absolute latitude had at least 45 observations (792 in total). To quantify the latitudinal gradient in developmental mode, we fitted a linear model with a binomial distribution (1 for planktotrophic, 0 for lecithotrophic, with probability P_g where the subscript g indicates genus). Absolute latitude, and the interaction between absolute latitude and hemisphere, were included as fixed effects (equation (1)). Hemisphere was included because life history patterns can differ between the Northern and Southern Hemispheres³³:

$$Y_g \approx \text{Bin}(1, P_g)$$

$$\text{logit}(P_g) \approx \alpha + \beta_1 \text{absLatitude} + \beta_2 \text{absLatitude} \times \text{Hemisphere} + a_g + \epsilon \quad (1)$$

where Y_g is the dependent variable, a represents the random effects that correlated according to the phylogenetic correlation matrix Σ : $a \approx N(0, \sigma_g^2 \Sigma)$, β_1 and β_2 are coefficient estimates, and ϵ represents the residual error.

Maternal investment (egg size). Egg size was estimated as species average egg diameter (in μm) on \log_{10} scale (762 observations in total). To quantify latitudinal gradient in egg size, we fitted a linear model with developmental mode, absolute latitude, an interaction between absolute latitude and hemisphere, an interaction between absolute latitude and developmental mode and a three-way interaction between absolute latitude, hemisphere and developmental mode (that is, the change in the effect of latitudinal effect between hemispheres could differ between developmental modes) (equation (2)):

$$Y_g \approx \alpha + \beta_1 \text{absLatitude} + \beta_2 \text{mode} + \beta_3 \text{absLatitude} \times \text{Hemisphere} + \beta_4 \text{mode} \times \text{absLatitude} + \beta_5 \text{mode} \times \text{absLatitude} \times \text{Hemisphere} + a_g + \epsilon \quad (2)$$

Planktonic duration. Planktonic duration was averaged per species and measured in days (237 observations in total). To quantify the latitudinal gradient in planktonic duration, we fitted a linear model with developmental mode, egg size, absolute latitude, an interaction between absolute latitude and hemisphere, an interaction between absolute latitude and developmental mode and an interaction between egg size and developmental mode (equation (3)). We excluded the three-way interaction between developmental mode, absolute latitude and hemisphere because data on planktonic duration were available for only 16 lecithotrophic species in the Southern Hemisphere. The relationship between absolute latitude and planktonic duration is driven by the effect of temperature on planktonic duration:

$$Y_g \approx \alpha + \beta_1 \text{absLatitude} + \beta_2 \text{mode} + \beta_3 \text{eggSize} + \beta_4 \text{absLatitude} \times \text{Hemisphere} + \beta_5 \text{mode} \times \text{absLatitude} + \beta_6 \text{mode} \times \text{eggSize} + a_g + \epsilon \quad (3)$$

Global patterns in dispersal. To predict the overall latitudinal gradient in dispersal, we combined predictions for the relationships between each factor affecting dispersal distance (developmental mode, egg size and planktonic duration) and latitude. A final posterior distribution of the latitudinal gradient in planktonic duration was estimated by sampling from the individual posterior distributions of each factor. First, we randomly selected a set of parameter estimates from the posterior distributions of each fixed effect in the models predicting latitudinal changes in developmental mode, egg size and planktonic duration. Using parameter values from the model predicting developmental mode, we estimated a latitudinal gradient in the proportion of larvae being planktotrophic (Fig. 1a). Then, using parameter values from the model predicting egg size, we estimated a latitudinal gradient in egg size for each developmental mode (Fig. 1c). Using parameter values from the model predicting planktonic duration and substituting egg size values corrected for latitude (from the previous step), we estimated a latitudinal gradient in planktonic duration for each developmental mode (Fig. 1b). The two estimated relationships between planktonic duration and latitude (one for each developmental mode) were weighted by the estimated proportion of each developmental mode across latitudes, to acquire an overall estimate of latitudinal gradient in planktonic duration. Since each model parameter used had uncertainty associated with it, we repeated the process 3,000 times to estimate 3,000 overall

gradients (there were 10,000 effective samples in each posterior distribution). From those 3,000 predictions of latitudinal gradients in planktonic duration, we calculated the median and upper (97.5%) and lower (2.5%) quantiles. The expected planktonic duration at each latitude was then multiplied by the mean annual surface speed (predicted by the Mercator model) at the corresponding $1/12^\circ \times 1/12^\circ$ grid cell (Fig. 1d) to estimate dispersal distance (in km) from planktonic duration (Fig. 1e). Since net displacement was not associated with a direction, larvae that could move a distance greater than their individual grid were assumed as always maintaining the speed of their grid of origin. We expect this assumption to be reasonable in most cases, since there is high correlation (Supplementary Fig. 4) in current speed between grid cells within 100 km of distance; however, as expected, correlation decreases with increasing distance between grid cells. The Supplementary information contains a sensitivity analysis that identifies the relative importance of each factor (developmental mode, egg size, temperature and mean annual surface current) in predicting dispersal distance.

Surface current speed and latitude. To determine how deterministically latitude predicts average current speed, we fitted a generalized additive model to predict current speed (dispersal distance per unit of time) as a function of latitude using the package 'brms' v.2.7.0 (ref. ⁷⁷). Current speed was obtained from both annual means of predictions from the Mercator model and the drifter data²⁴ for locations where compiled data were available. To quantify the amount of variation in current speed explained by latitude, we used the function 'bayes_R2' from the package 'rstantools' v.1.5.1 (ref. ⁸⁵).

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

Compiled data are available as Supplementary Information.

Code availability

All code is available at Github (https://github.com/MarianaAlvarezNoriega/Marine_invertebrate_dispersal).

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Author contributions

D.J.M., S.C.B., J.E.B., J.M.P., J.P.W. and M.Á.-N. conceived the study. M.Á.-N. analysed the data and wrote the first draft, with help from D.J.M. and J.M.P. D.J.M., S.C.B., J.E.B., J.M.P., J.P.W. and M.Á.-N. contributed to subsequent drafts.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at <https://doi.org/10.1038/s41559-020-1238-y>.

Supplementary information is available for this paper at <https://doi.org/10.1038/s41559-020-1238-y>.

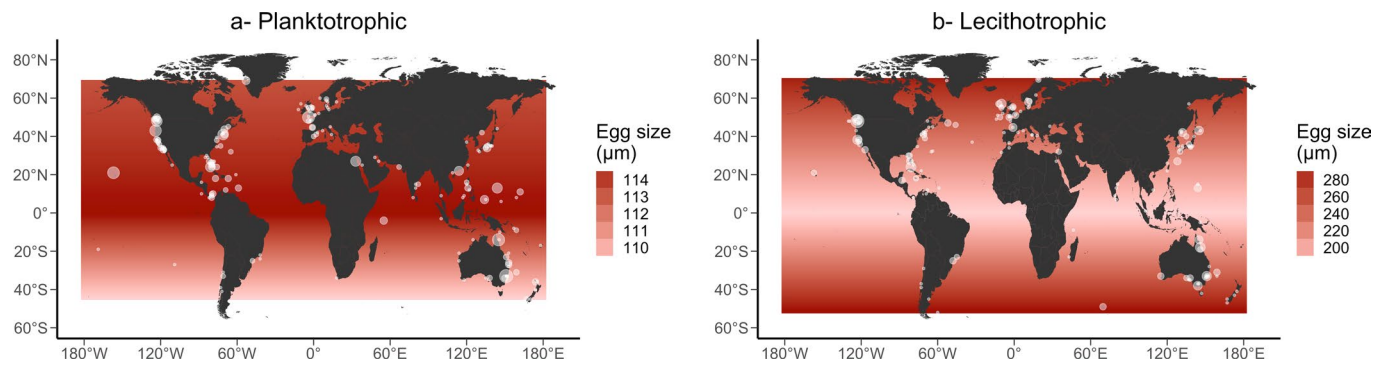
Correspondence and requests for materials should be addressed to M.Á.-N.

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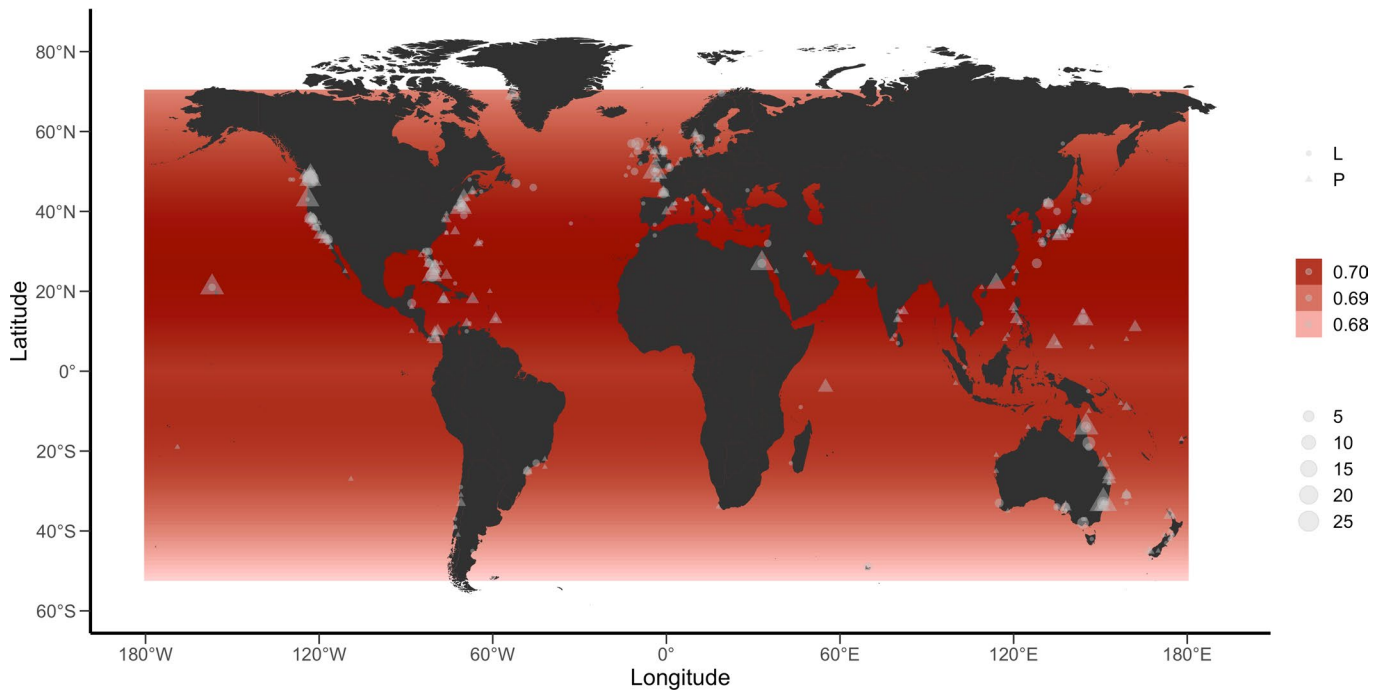
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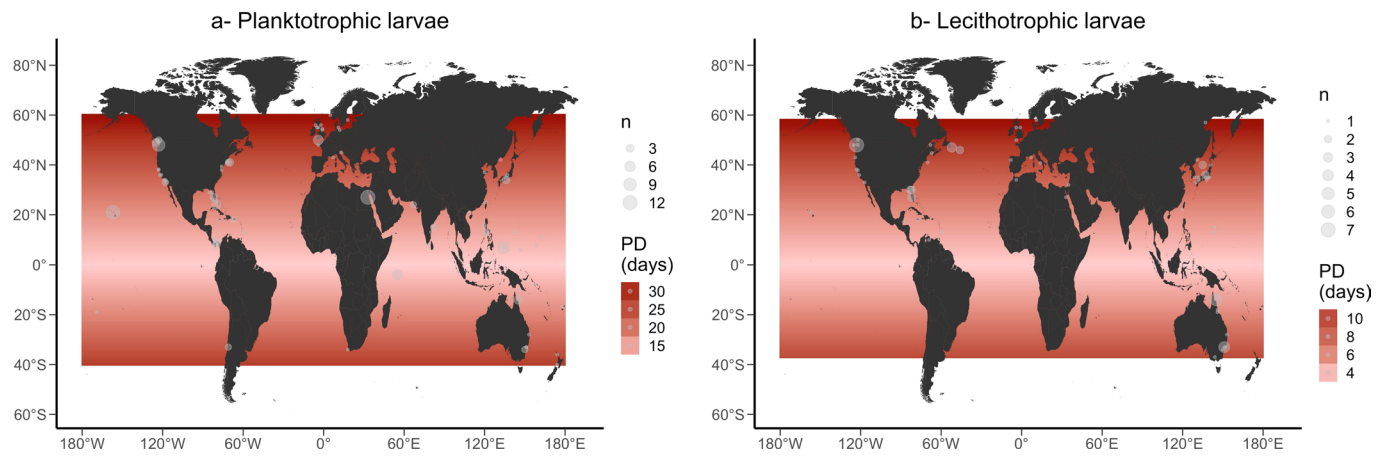
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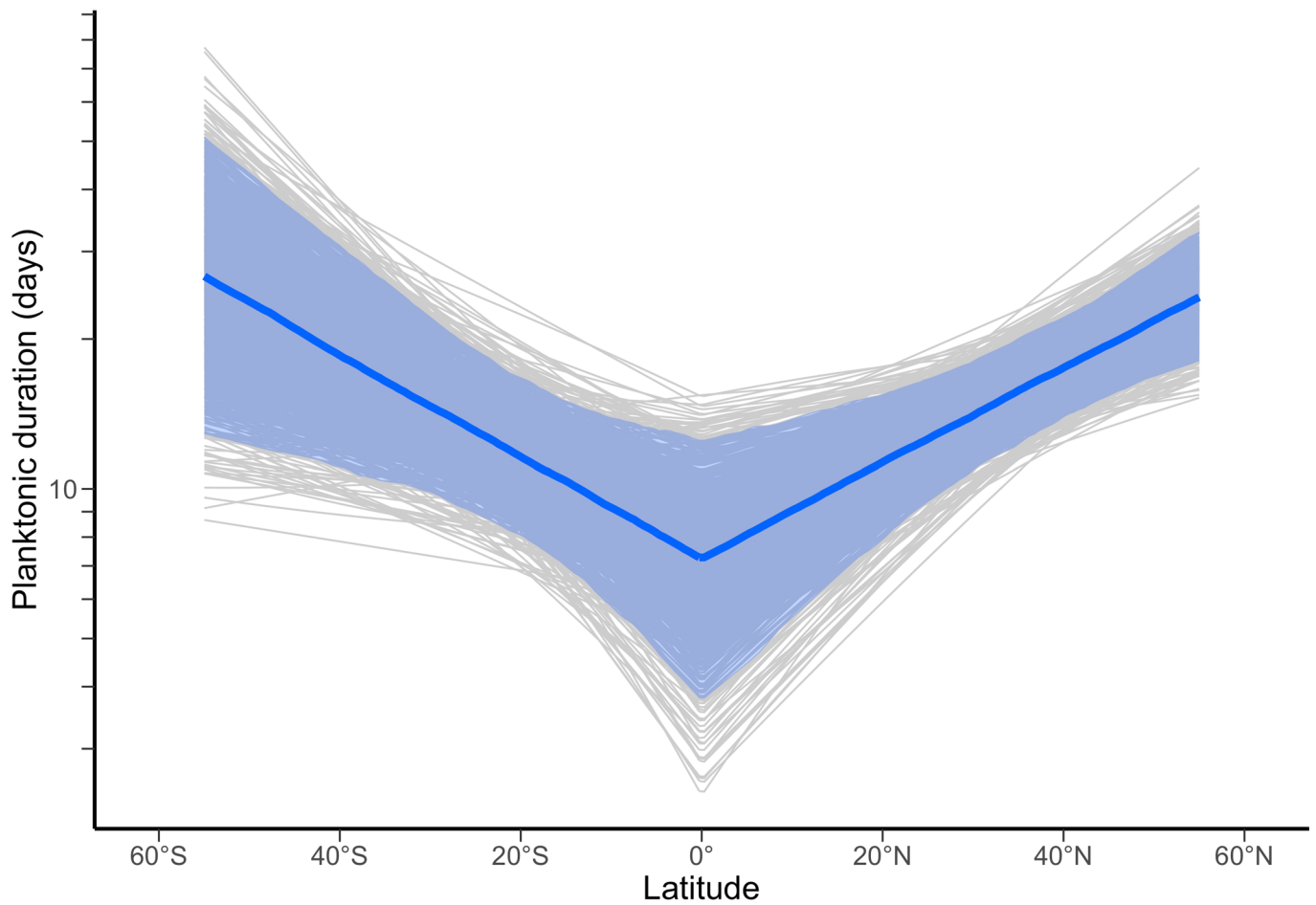
Extended Data Fig. 1 | Latitudinal gradients in egg size (predictions from the phylogenetically controlled model). Panel **a**, Egg size (μm) of planktotrophic larvae across latitudes. Panel **b**, Egg size (μm) of lecithotrophic larvae across latitudes. The gradient from dark to light red shows large to small egg sizes. Note that the scale differs between panels. White circles show the distribution of studies from which data was obtained. Larger circles indicate a higher number of studies.



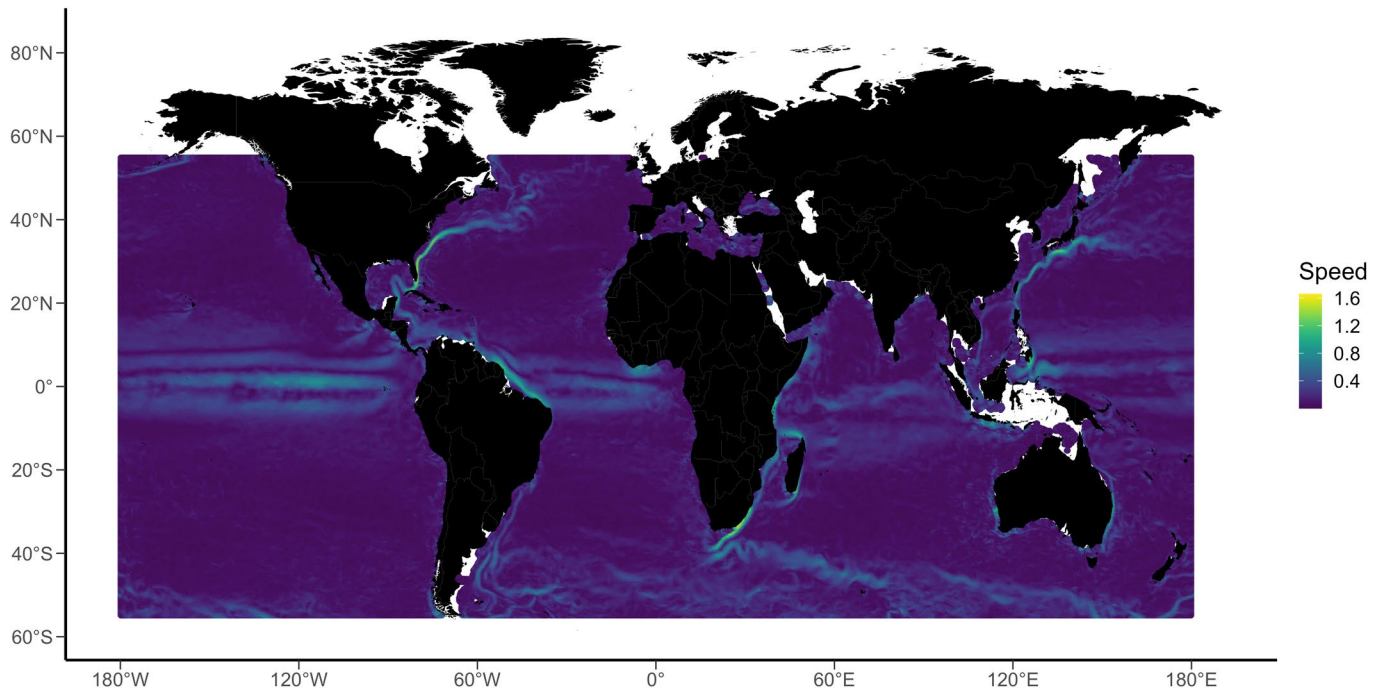
Extended Data Fig. 2 | Probability that planktonic larvae are planktotrophic vs. lecithotrophic across latitudes (predictions from the phylogenetically controlled model). The gradient from dark red to light red shows higher to lower probability that planktonic larvae are feeding. Grey circles (planktotrophic larvae) and triangles (lecithotrophic larvae) show the distribution of studies from which data was obtained. Larger shapes indicate a higher number of studies, which range from 1 to 26 for planktotrophic larvae and from 1 to 16 for lecithotrophic larvae.



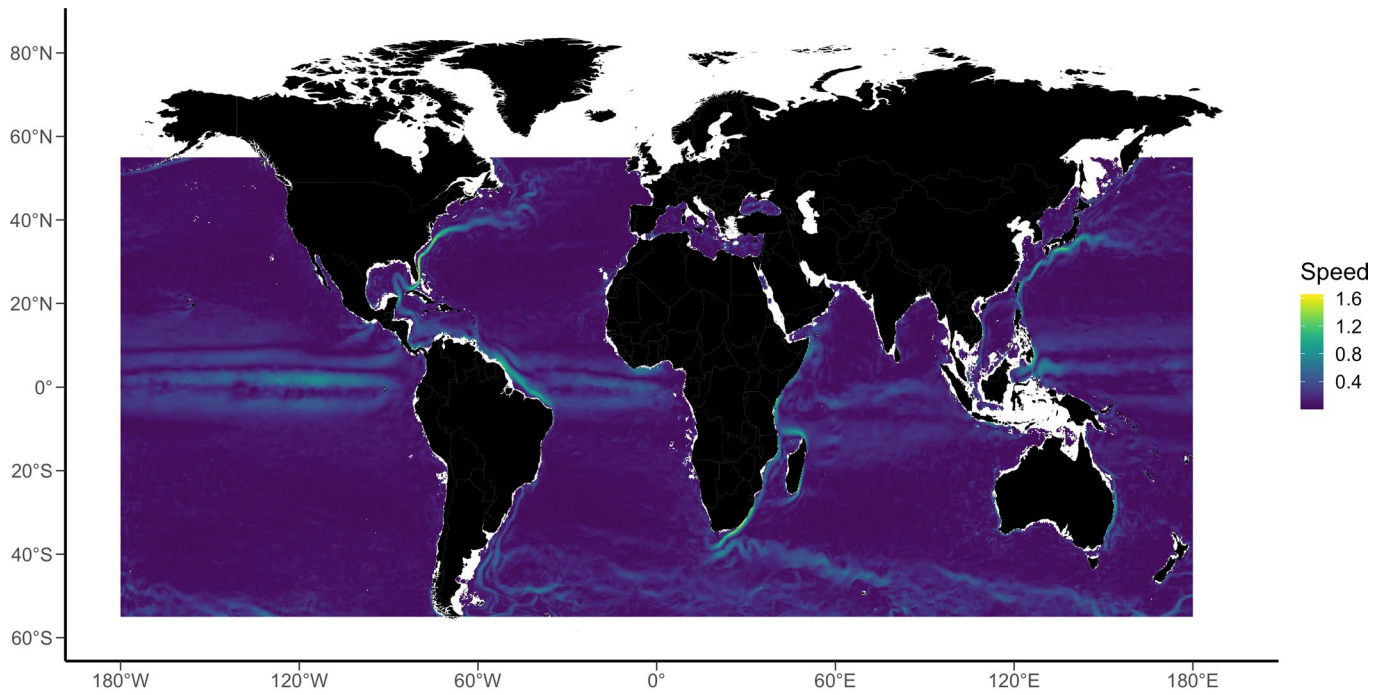
Extended Data Fig. 3 | Latitudinal gradients in planktonic duration (predictions from the phylogenetically controlled model). Panel **a**, Planktonic duration (days) of planktotrophic larvae across latitudes. Panel **b**, Planktonic duration (days) of lecithotrophic larvae across latitudes. The gradient from dark to light red shows long to short planktonic durations. Note that the scale differs between panels. White circles show the distribution of studies from which data was obtained. Larger circles indicate a higher number of studies.



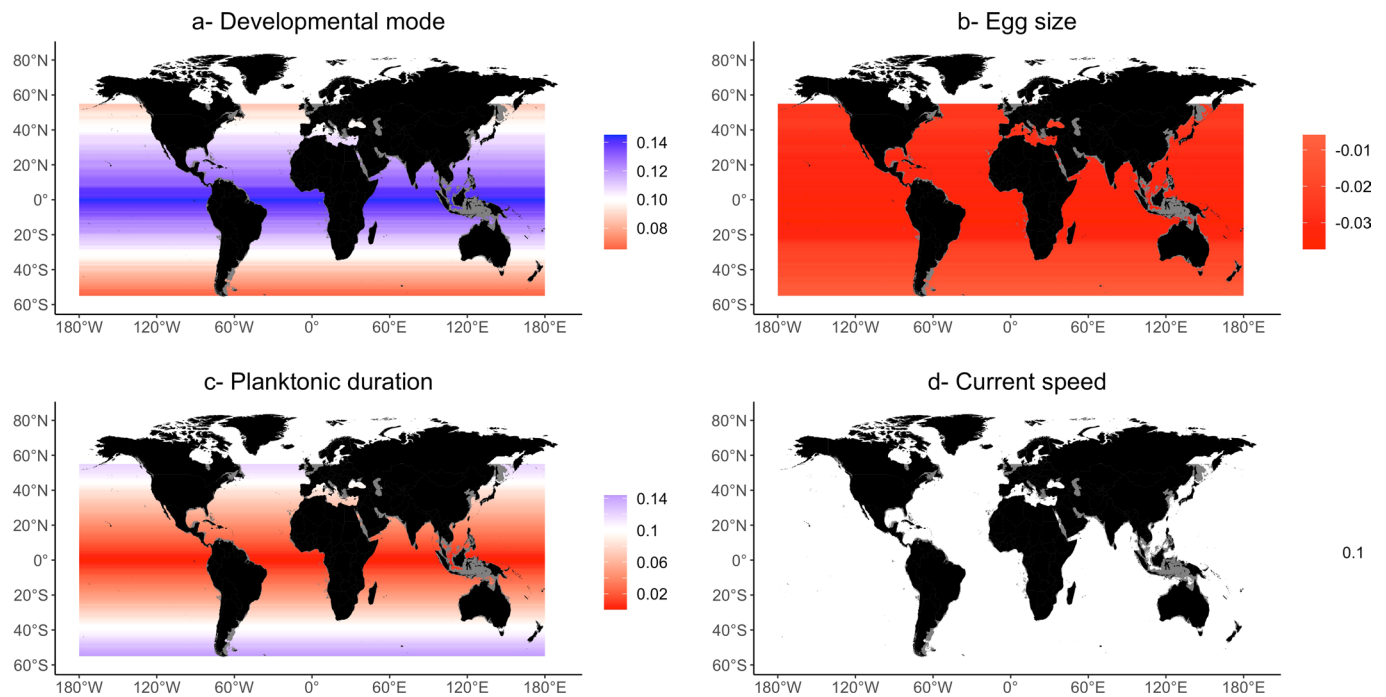
Extended Data Fig. 4 | Predicted planktonic durations (days; \log_{10} -scale) across latitudes, weighted by the predicted proportion of each developmental mode and incorporating changes in egg size (predictions from phylogenetically controlled models). The grey lines show predictions from 2000 random values from the models' posterior distributions. The blue line shows median predictions and the blue ribbon shows the 95% credible interval.



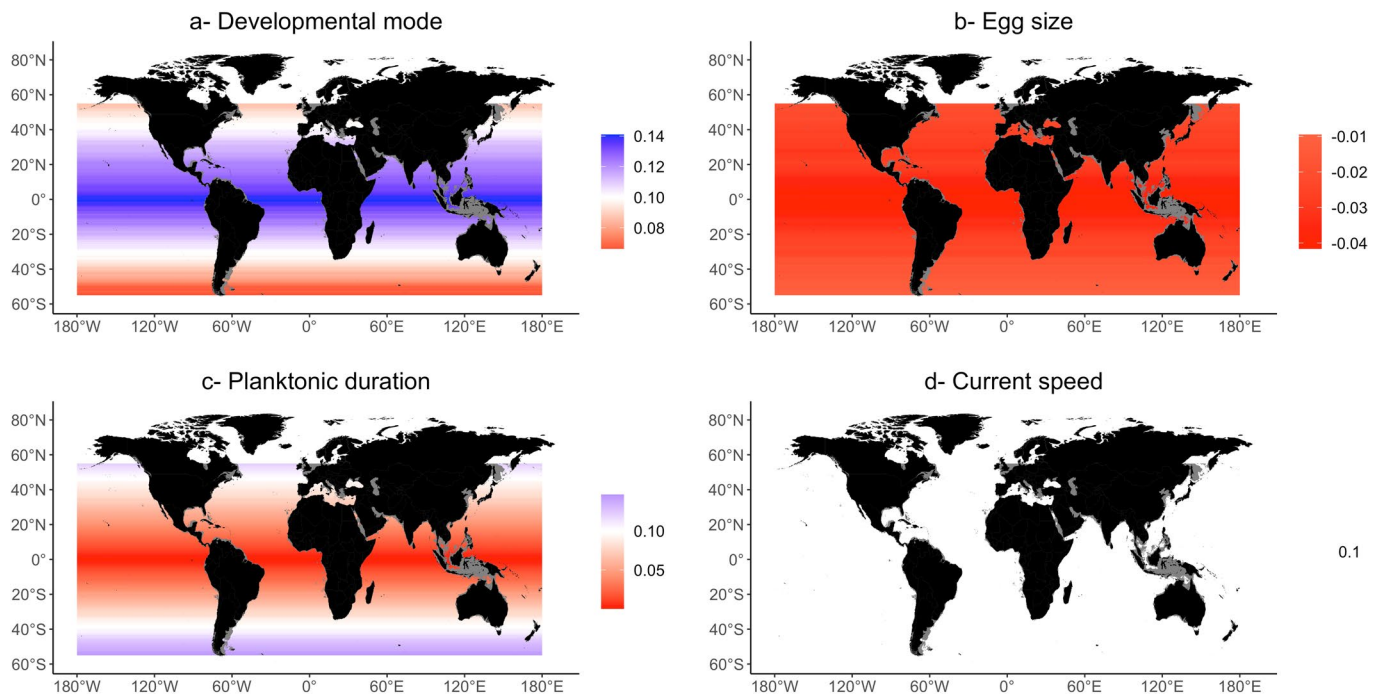
Extended Data Fig. 5 | Mean annual surface speed (ms^{-1}). Predictions obtained from the Mercator model⁷³.



Extended Data Fig. 6 | Mean annual surface speed (ms^{-1}). Data obtained from Laurindo et al.⁷⁴



Extended Data Fig. 7 | Proportional change in predicted dispersal distance with a 10% increase in the probability that a larva is planktotrophic (Panel **a**), a 10% increase in egg size (in log-scale) (Panel **b**), a 10% increase in the effect of temperature on planktonic duration (with absolute latitude as a proxy) (Panel **c**), and a 10% increase in mean annual surface speed (Panel **d**). White colour indicates areas where the proportional change in the predicted dispersal distance is equal to the proportional change in the dispersal driver of interest, blue colours show areas it is larger (that is a 10% increase in the driver of interest results in a >10% increase in predicted dispersal distance), and red colours show areas where it is smaller (that is a 10% increase in the driver of interest results in a <10% increase in predicted dispersal distance). Panel d used data from surface drifters⁷⁴.



Extended Data Fig. 8 | Ratio of the original predicted dispersal distance (with all dispersal drivers varying across latitudes) divided by the predicted dispersal distance for the case when one of the factors is kept constant across latitudes (at its mean value across latitudes 55°S to 55°N). In panel **a**, the proportion of larvae being planktotrophic is kept constant; in panel **b**, the effect of egg size is kept constant; in panel **c**, the effect of planktonic duration is kept constant; and in panel **d**, mean annual current speed is kept at its mean across space. Blue colours show locations where dispersal would be underestimated if the dispersal driver of interest was assumed to stay constant across space (ratios > 1), red colours show locations where dispersal distance would be overestimated if the dispersal driver of interest was assumed to stay constant across space (ratios < 1). White areas show locations with ratios ≈ 1 (that is where the driver of interest occurs at its mean value). Panel d used data from surface drifters⁷⁴.

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Software and code

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Data collection

No software was used.

Data analysis

Statistical analyses were performed in R (version 3.5.2). The models were fitted using the R package 'brms' (version 2.7.0). The phylogenetic tree was extracted using the R package 'rotl' (version 3.0.6), the length of the phylogenetic tree's branches were estimated with the R package 'ape' (version 5.2), and the relatedness matrix was calculated with the R package 'MCMCglmm' (version 2.26).

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For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	This study uses data from the literature encompassing more than 750 marine organisms from seven phyla, as well as oceanographic data on surface current speed, to quantify the overall latitudinal gradient in larval dispersal distance by combining predictions of developmental mode, egg size, planktonic duration, and current speed. The model predicting developmental mode (planktotrophic vs. lecithotrophic; binomial distribution) includes absolute latitude and an interaction between absolute latitude and hemisphere as fixed effects. The model predicting egg size includes absolute latitude, developmental mode, an interaction between absolute latitude and hemisphere, an interaction between developmental mode and absolute latitude, and an interaction between developmental mode, absolute latitude, and hemisphere as fixed effects. The model predicting planktonic duration included absolute latitude, developmental mode, egg size, an interaction between absolute latitude and developmental mode, an interaction between absolute latitude and hemisphere, and an interaction between developmental mode and egg size. All statistical models were phylogenetically corrected. We used mean annual surface current speed data estimated by the Mercator 1/12° modelling system near the surface from 2007 to 2017 (Lellouche, J.-M. et al. 2018).
Research sample	We use data from Marshall et al. (2012) that includes a total of 766 marine invertebrate species from the following phyla: Annelida (191 species), Arthropoda (12 species), Bryozoa (3 species), Chordata (7 species), Cnidaria (18 species), Echinodermata (230 species), and Mollusca (305 species).
Sampling strategy	Marshall et al. (2012) search more than 4000 studies to compile the data set.
Data collection	Biological data was obtained from Marshall et al. (2012), oceanographic data was obtained using EU Copernicus Marine Service Information.
Timing and spatial scale	Studies from which data were obtained dated from 1920 to 2013, and we included data ranging from 55° S to 55° N.
Data exclusions	Data above 55° N were excluded since no data below 55° S were available.
Reproducibility	No experiments were conducted.
Randomization	Not relevant for the meta-analysis.
Blinding	Not relevant for the meta-analysis.
Did the study involve field work?	<input type="checkbox"/> Yes <input checked="" type="checkbox"/> No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> Antibodies
<input checked="" type="checkbox"/>	<input type="checkbox"/> Eukaryotic cell lines
<input checked="" type="checkbox"/>	<input type="checkbox"/> Palaeontology
<input checked="" type="checkbox"/>	<input type="checkbox"/> Animals and other organisms
<input checked="" type="checkbox"/>	<input type="checkbox"/> Human research participants
<input checked="" type="checkbox"/>	<input type="checkbox"/> Clinical data

Methods

n/a	Involvement in the study
<input checked="" type="checkbox"/>	<input type="checkbox"/> ChIP-seq
<input checked="" type="checkbox"/>	<input type="checkbox"/> Flow cytometry
<input checked="" type="checkbox"/>	<input type="checkbox"/> MRI-based neuroimaging