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Projecting marine developmental diversity and connectivity in future oceans

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Global change will alter the distribution of organisms around the planet. While many studies have explored how different species, groups and traits might be re-arranged, few have explored how dispersal is likely to change under future conditions. Dispersal drives ecological and evolutionary dynamics of populations, determining resilience, persistence and spread. In marine systems, dispersal shows clear biogeographical patterns and is extremely dependent on temperature, so simple projections can be made regarding how dispersal potentials are likely to change owing to global warming under future thermal regimes. We use two proxies for dispersal—developmental mode and developmental duration. Species with a larval phase are more dispersive than those that lack a larval phase, and species that spend longer developing in the plankton are more dispersive than those that spend less time in the plankton. Here, we explore how the distribution of different development modes is likely to change based on current distributions. Next, we estimate how the temperature-dependence of development itself depends on the temperature in which the species lives, and use this estimate to project how developmental durations are likely to change in the future. We find that species with feeding larvae are likely to become more prevalent, extending their distribution poleward at the expense of species with aplanktonic development. We predict that developmental durations are likely to decrease, particularly in high latitudes where durations may decline by more than 90%. Overall, we anticipate significant changes to dispersal in marine environments, with species in the polar seas experiencing the greatest change.

This article is part of the theme issue 'Integrative research perspectives on marine conservation'.

1. Introduction

Global temperature increases are changing the distribution of species everywhere [1]. On land and in the oceans, species are moving poleward, and the ranges of high latitude species are contracting. For most species, it is unclear whether they will keep pace with an environmental change from both an ecological (demographic) and evolutionary perspective [2]. A range of approaches have been used to understand and predict how different species will cope with a global environmental change. For example, thermal safety margins can predict how robust populations are likely to be to future change [3]. Mapping climate velocities can identify which regions will be subject to the most rapid change relative to current conditions [4], and species distribution models can predict future ranges given current thermal niches [5]. One factor that has received relatively less attention with regard to global change is dispersal and the traits that affect dispersal.

Dispersal can determine the capacity of species to withstand and adapt to change, as well as change their range [6,7]. Dispersal determines the degree to which populations are connected, the resilience of meta-populations and how populations expand or contract as a conditional change [8,9]. Anything that affects dispersal will therefore shape how species are affected by a global change. Unfortunately, for the vast majority of marine organisms, dispersal

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itself is likely to be modified strongly and systematically because global temperature increases. This temperature effect on marine dispersal has at least two implications: it complicates predictions about how organisms will respond to global change, but at the same time, it simplifies the identification of which groups are likely to be especially vulnerable to change. We will explore both these issues here with the broad goal of understanding how larval life histories and dispersal are likely to change under future climates in marine organisms.

For marine organisms, particularly those that are sedentary or sessile as adults, dispersal occurs primarily via the larval phase [10]. Most marine organisms reproduce by producing tiny larvae that spend minutes to months in the water column and while they can swim, they are usually dispersed by currents [11]. Larvae can therefore be transported across entire ocean basins and distant populations can be connected demographically by larval transport. Dispersal of larvae is particularly important in marine organisms, mediating speciation rates, persistence and the rate at which species expand their range [12,13]. If marine larval dispersal is altered by temperature, predicting these dynamics under future change becomes even more challenging.

Dispersal potential is notoriously variable in marine organisms, ranging from millimetres to thousands of kilometres [10,14], but the development mode (whether species have a larval phase, and whether they feed as larvae) is one of its few reliable predictors [15]. While the relationship is noisy, the duration of the larval period is positively correlated with dispersal and connectivity [15]. Species lacking a pelagic larval phase (which we will call 'aplanktonic developers' *sensu* [16]) disperse less than species that spend days to weeks in the plankton as larvae. Within those species that have a pelagic larval phase, around half have larvae that feed, while the other half do not [16]. At any given latitude, those species with feeding larvae (known as planktotrophs) tend to have longer larval periods than those species with non-feeding larvae [11]. Importantly, the different developmental modes (and hence dispersal potentials) are not distributed randomly across the globe, rather they covary strongly with latitude and temperature [17].

Developmental mode has long been recognized to vary systematically with latitude [18]. Thorson [19–21] noted that tropical marine invertebrates tended to have feeding larvae, while polar species lack a larval phase. These patterns were debated through the last century [16,22], but today it is clear that the general trend is for lower latitudes to have a higher prevalence of species with small eggs and larval feeding stages. In higher latitudes, species tend to have much larger eggs and either a non-feeding larval stage or lack a larval stage altogether [16]. Obviously, these latitudinal gradients in the developmental mode covary strongly with temperature [16]. The mechanisms driving the covariance between the developmental mode and the temperature are unclear however. It could be that temperature mediates selection on developmental mode indirectly through selection on offspring size via oxygen tolerance [23]. Alternatively, the developmental mode specifically could be the target of selection. Regardless, the phenomenological association between developmental mode and temperature is so strong, and so taxonomically widespread [16], we would argue that it is sufficiently reliable to use for projections under future climates.

Current patterns in marine invertebrate life histories provide useful indications as to how increasing temperatures might alter the distribution of developmental modes in the near future. The approach is analogous to classic species distribution models [5], but the 'developmental mode' is being used in place of 'species'. For example, we might expect that species with aplanktonic development would be 'losers' under future climate conditions and species with feeding larvae will become more prevalent at higher latitudes. Here, we explore how future temperature increases will alter the global distribution of developmental modes, based on their current distributions. We show a net decrease in relative developmental diversity across all latitudes, with species that display aplanktonic development in Antarctic waters being the most vulnerable.

Because temperature affects the distribution of developmental modes and developmental modes affect dispersal, the future of marine connectivity may seem straightforward to anticipate. However, such predictions are complicated by the fact that temperature affects another key driver of dispersal in marine systems—development duration [24].

The larval developmental rate depends strongly on temperature [13,25]. The relationship between temperature and developmental duration is exponential (at least within benign temperature ranges)—a small increase in temperature can reduce developmental durations significantly [26]. Temperature effects are relatively consistent across species, but there are indications that the temperature-dependence of development is itself temperature-dependent [13]. For example, Rombough [27] notes that temperature dependencies of fish development are greatest in cold-water species, and the few examples of temperature-dependence in polar marine invertebrates also similarly seem to be particularly high [28]. Thus, accurate predictions about how developmental durations will change in the future across latitudes should probably incorporate any systematic patterns in temperature dependencies. Formal comparisons of how the temperature-dependence of development itself changes with temperature are rare however [29].

We explore the links between temperature and predicted dispersal durations in two stages. We first examine how temperature and developmental mode covary currently, and how the relative prevalences of those modes are therefore likely to change under global warming. We then estimate how the temperature dependency of development rate changes across temperature for a range of marine organisms in a phylogenetically controlled analysis. We then use this empirically derived estimate of temperature-dependence to estimate how developmental durations will shift under future temperature regimes. In other words, we project how dispersal durations will change based on temperature-specific temperature dependencies. Together, our estimates here provide a first step towards understanding how marine invertebrate life histories will be redistributed with rising temperatures and the impacts of rising temperatures on marine connectivity in the future.

2. Material and methods

(a) Current versus future distributions of developmental modes

We extracted the distribution of different development modes from the database compiled for [16]—a biogeographical compilation of over 1500 marine invertebrates from five phyla. In that paper, we fit logistic regressions between the temperature and the developmental mode, first for planktonic versus aplanktonic developing species and then for feeding versus non-feeding species among those with planktonic development (for details on how environmental data and life-history data were sourced, see [16]). It is important to note that a variety of other environmental factors (e.g. environmental predictability) affect the distribution of developmental modes in marine invertebrates [17]. However, because spatially explicit predictions regarding the future environmental predictabilities are lacking, we refrained from incorporating these effects, but future studies should include them when they become available.

In the earlier work, we found evidence for an interaction between temperature and hemisphere with regard to aplanktonic development—temperature covaried with the incidence of aplanktonic development in the Southern Hemisphere but not in the Northern Hemisphere [16].

The relationship between temperature and the relative proportion of species with aplanktonic development (in the Southern Hemisphere) is described by the equation (as analysed in [16], though the equation was not presented there):

$$P_{\mathrm{aplanktonic}} = \frac{e^{(-0.096T-0.151)}}{1+e^{(-0.096T-0.151)}}, \tag{2.1}$$

where $P_{\mathrm{aplanktonic}}$ is the predicted probability of a species having aplanktonic development and T is temperature.

Similarly, the relationship between temperature and the prevalence of larval feeding is described by the equation (as analysed in [16], though the equation was not presented there):

$$P_{\mathrm{nonfeeding}} = \frac{e^{(-0.895T-0.059)}}{1+e^{(-0.895T-0.059)}}. \tag{2.2}$$

Once we established the relationships between temperature and developmental modes based on current patterns (or, more precisely, current and historical patterns, as some life-history data are from over 50 years ago), we then explored how predicted temperature increases for 80 years in the future (i.e. 2100) would change current distributions, according to these relationships. Our predictions for the developmental mode were made irrespective of longitude and were based on a simple temperature function, so we kept our approach to future temperatures equally simple.

We based our temperature projections on the Fifth Assessment Report CMIP5 ensemble means from the KNMI Climate Explorer (http://climexp.knmi.nl) [30]. We calculated the change in temperature from 1986–2005 to 2100 under RCP2.6 or RCP8.5. RCP2.6 is a low greenhouse gas emissions scenario with warming of about 1°C. RCP8.5 is a high greenhouse gas emission scenario with around 4°C warming. We used annual mean surface temperature for the 10° latitudinal bands across the entire range of longitudes. We used this coarse mean because across our database of marine invertebrates, some species reproduce in summer, others in winter. Furthermore, our relationships between the temperature and the developmental mode are not longitude-specific, so we could not apply any higher resolution temperature data to our life-history data.

To make our projections, we assumed that the relationship between the temperature and the developmental mode will not change over the next 80 years, though this is certainly possible. Further, we assumed no systematic differences in the thermal sensitivity of the species considered here beyond their developmental mode—we essentially assume that thermal tolerance is random with respect to the developmental mode. It is unclear whether this assumption is wholly reasonable or not. On the one hand, the developmental mode is extremely evolutionarily labile in marine invertebrates—congeners can have very different developmental modes [31]—implying that the developmental mode is not phylogenetically constrained [32]. On the other hand, some taxonomic groups show only one developmental mode and if that group is more or less vulnerable to change than species on average, then our predictions may mis-estimate changes in the distribution of developmental modes.

We calculated the current and future distribution of each developmental mode across latitudes, and for ease of comparison, calculated the relative change in the prevalence of each developmental mode across latitude.

(b) The temperature-dependence of temperature-dependence

We sought to formally estimate how the temperature-dependence of development varied systematically with the temperature regime that the species experienced in nature. This approach differs from more comprehensive studies examining the relationship between temperature and developmental duration *among* species to estimate how temperature affects development time (e.g. [33]). Rather we were interested in how the temperature-dependence of development (a *within-species* measure) specifically covaried with the temperature that species experienced (a covariance that is estimated at an *among-species* level). For example, a tropical species might have a low temperature-dependence (a within-species measure) and a polar species might have a high temperature-dependence. For this example, we would therefore estimate a negative relationship between temperature and temperature-dependence at the among-species level.

There are a number of compilations of how temperature affects development time in marine invertebrates (e.g. [13,25]). We used these compilations to find the original source material for some of these species and augmented these compilations based on searches of our own. Our compilation is relatively smaller than these earlier studies because we needed a larger temperature range with more resolution so as to estimate within-species temperature ranges effectively. As the literature is scattered, we used a variety of search terms to locate papers and so we could not follow formal meta-analytical techniques, but it is worth noting that our estimates here are very similar to more formal meta-analyses [25]. Because we were particularly interested in species that developed in very cold water, and because such estimates are exceedingly rare in marine invertebrates, we augmented our dataset with marine fish data. We focused on finding studies that were reasonably well replicated and presented temperature-dependence of development for cold-water species in particular. Importantly, our results were qualitatively identical whether these data were included or not.

We were able to compile data on the relationship between temperature and development for 35 species from five phyla (electronic supplementary material, table 1).

To estimate how temperature affected developmental duration, we fitted a standard function using nonlinear regression [29]:

$$D(T) = de^{-bT} + c, \tag{2.3}$$

where developmental duration, $D(T)$, is described by an exponential function with a constant. This function has a long history of being used to describe the relationship between temperature and development [34,35] and shows a better fit to developmental data than a simple exponential function [29]. The key parameter for describing the temperature-dependence of development is parameter b—larger values of b indicate a sharper decline in developmental duration with increasing temperatures. We estimated b for all 35 species and then examined how b varied with the temperature in which that species typically occurred.

To estimate the temperature in which these species live, we used the midpoint temperature (T_{mid}) from the assembled developmental data. For example, if development was examined from 18 to 30°C for a species, then its T_{mid} would be 24°C. This is a crude way of characterizing the temperature of a species and many more sophisticated methods could be used. For example, if detailed information on the length and timing of the breeding season is known, plus the full range of a species, as well as whether spawning phenology shows spatial variation, then the precise temperature at which development occurs could be calculated. The problem is that for most species, such data are largely unavailable. Reassuringly, T_{mid} is a good predictor of both the maximum and minimum temperature that species experience [29] and, across such a wide range of temperatures, almost certainly does a reasonable job of representing the temperature regime experienced by that species.

Once we had calculated both b and T_{mid}, we analysed the relationship between the two using a phylogenetically controlled analysis. We fitted the temperature-dependent parameter b as a function of T_{mid} using the package 'MCMCglmm' v. 2.26 [36] in R v. 3.5.2 [37]. T_{mid} was $\log_{10}$-transformed; as there were negative T_{mid} values, we added a constant value (a) to all T_{mid} such that the logarithm of the lowest mid-range value would be defined ($a = 2.3$). To correct for non-independence between observations owing to phylogenetic relatedness between species, we included species as a random effect and specified a variance–covariance matrix based on the phylogenetic tree. We extracted the phylogenetic tree from the Open Tree of Life with the R package 'rotl' v. 3.0.6 [38]. Because branch lengths for the phylogeny were unknown, we assigned branch length using [39] the method with the package 'ape' v. 5.2 [40]. In Grafen's method, each node is given a height equal to the number of descendant tips minus one. Node height is then scaled relative to the height of the root and each branch length is computed as the difference in height between the upper and lower nodes. The phylogenetic signal—equivalent to Pagel's λ—was estimated as the proportion of the variance that was explained by the phylogeny (the variance explained by the phylogeny divided by the sum of the residual variance plus the variance explained by the phylogeny).

(c) Current versus future developmental durations

We used our estimate of how temperature affects the temperature dependency of the developmental mode to project how temperature increases will affect planktonic durations in the future. To illustrate our results, we parametrized (equation (2.3)) to consider two hypothetical species—a species with feeding larvae and a species with non-feeding larvae, and set their developmental duration parameters as follows. For the feeding larvae: $d = 80$; $c = 20$. For the non-feeding larvae, $d = 80$ and $c = 3$. The values give asymptotic larval periods of 3 and 20 days for the non-feeding and feeding 'species', respectively. We then recalculated the predicted developmental durations for these two hypothetical species under future warming conditions, with latitude-specific increases in the temperature based on Fifth Assessment Report CMIP5 projections as before.

There are profound uncertainties regarding how temperature-dependence might change under future conditions, so we explore three different scenarios that hopefully encompass the full range of possibilities. First, we explore a simplified scenario where the temperature-dependence of development is not temperature-dependent (i.e. b from equation (2.3) is constant). As a conservative approach, we used a relatively low value of b (0.26), which represents the minimum temperature-dependence that we observed in our analysis. This approach tends to predict that developmental durations are shortened by relatively small amounts with a global change, the shortened durations are more homogeneous across latitudes (see Results), and it makes predictions that are similar to earlier explorations of this topic [13].

We then explored a scenario where we allow b to show temperature-dependence as suggested by our results, but we applied temperature-dependent b's in two different ways for our second and third approaches. For both species, we set b according to the local temperature regime using the equation:

$$b = 0.66(T + 2.3)^{-0.51} \tag{2.4}$$

which reflected the best-fit function for b across a range of temperatures (see Results).

In our second approach, we assumed that b evolves to track warming temperatures perfectly. In other words, whatever the future temperature regime is, the species living there immediately takes on the value of b that is appropriate to the temperature. This approach makes relatively conservative predictions in that it reduces the impact of temperature-dependence being temperature-dependent on developmental durations. However, it assumes that temperature-dependence is perfectly plastic (or evolves instantaneously), which is not particularly realistic given what we know about plasticity and adaptation more generally [2].

For our third approach, we allowed b to be temperature-dependent but we introduced a 'lag' in the rate at which b changed to track the warming environment. In essence, we forced our hypothetical species to retain the b from the temperature regime that they previously experienced such that their developmental durations were much more temperature-sensitive than they were under our second approach. We believe that this approach is the most realistic in that it reflects the temperature-dependent nature b as supported by data, and it reflects the fact that this trait is unlikely to evolve instantaneously (though it could be plastic). This approach predicts the greatest reductions in developmental durations, particularly in high latitudes (see Results).

3. Results

(a) Current versus future distribution of developmental modes

Global warming is predicted to reduce the prevalence of species with aplanktonic development by between 1 and 5% in the Southern Hemisphere, with the greatest reductions predicted for species near the poles (figure 1). Species with non-feeding planktonic larvae will become less prevalent overall, except near the poles, where they are predicted to show a slight increase (figure 2; confidence intervals for per cent change overlap 0, but the mean value is still positive above 60°). Higher emission scenarios yield greater predicted changes across all latitudes.

Species with non-feeding larvae or aplanktonic development that are lost under higher temperatures are predicted to be replaced by species with planktotrophic larvae (figure 2). Planktotrophs are predicted to increase in prevalence across all latitudes fairly uniformly in an absolute sense (prevalence will increase by approx. 5% across all latitudes). In a relative sense, different regions will experience different amounts of changes. The tropics are predicted to lose approximately 25% of their (already rare) aplanktonic species. By contrast, planktotrophs are currently uncommon near the poles but may increase their relative prevalence by 25% in the future (figure 2).

(b) The temperature-dependence of temperature-dependence

The temperature-dependence of development is itself dependent on temperature. In our phylogenetically controlled

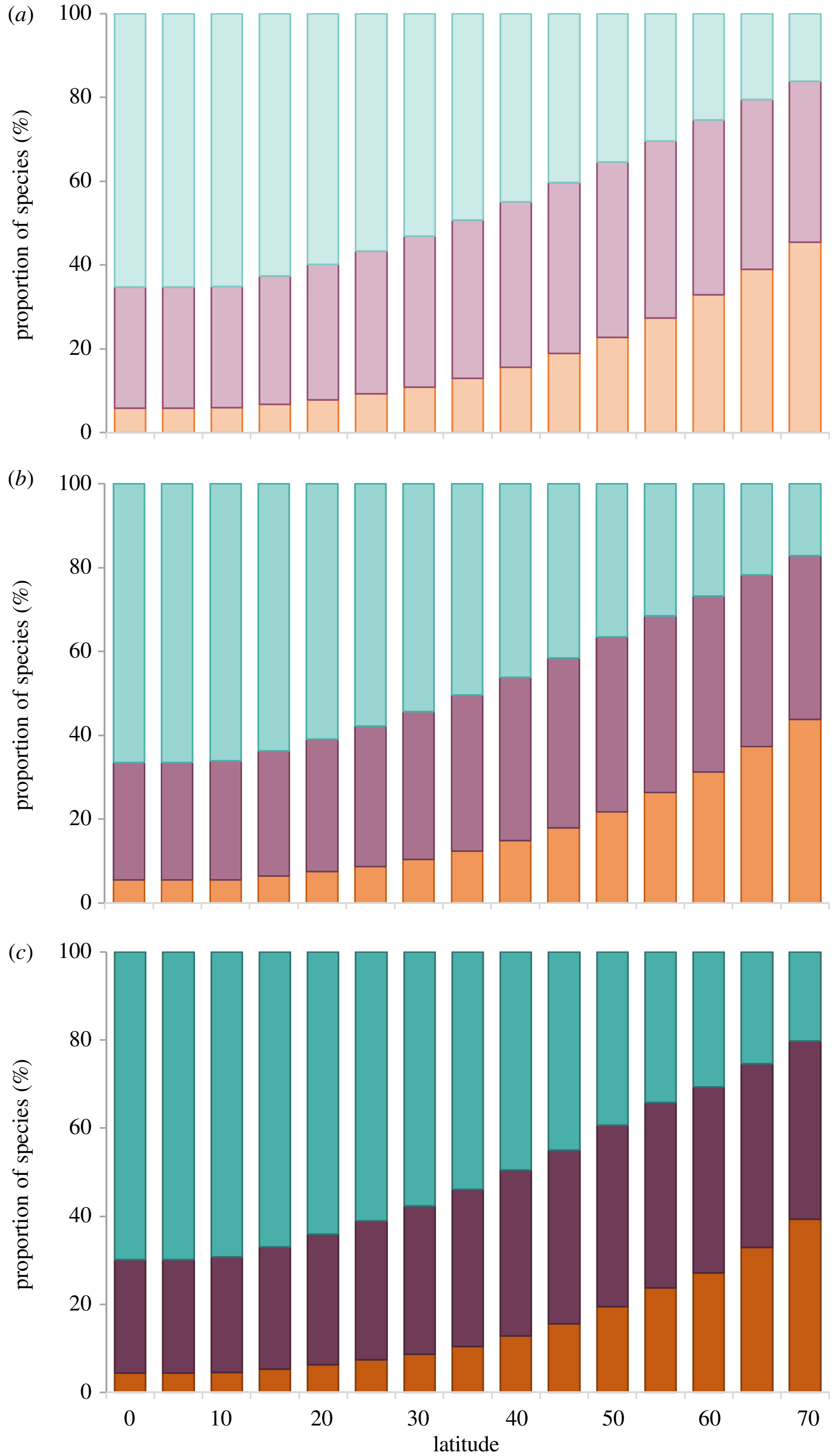

Figure 1. Prevalence of species with different developmental modes. (*a*) Recent conditions (where orange represents aplanktonic larvae, purple represents non-feeding planktonic larvae and blue represents feeding planktonic larvae); (*b*) future (2100) conditions under RCP2.6 and (*c*) future (2100) conditions under RCP8.5. Only projections for the Southern Hemisphere are shown because for the Northern Hemisphere there is no systematic latitudinal pattern in aplanktonic development. (Online version in colour.)

analysis, the parameter that describes temperature-dependence, b, decreases with an increasing temperature:

$$\log_{10}(b) = -0.177 - 0.515\log_{10}(T_{\text{mid}} + 2.3),$$

(lower confidence interval (CI): −0.996; upper CI: −0.094) with the probability of the posterior distribution of the coefficient including zero $[p(\text{MCMC})] = 0.0236$, it was associated with a reasonably strong phylogenetic signal $\lambda = 0.80$ (95% CI: 0.65–0.92). In other words, the temperature-dependence of development was greatest for cold-water species and smallest for warm-water species (figure 3).

(c) Current versus future developmental durations

Developmental durations are likely to be shorter under future climates, particularly if emissions remain high (figures 4 and 5). Around the equator, regardless of which

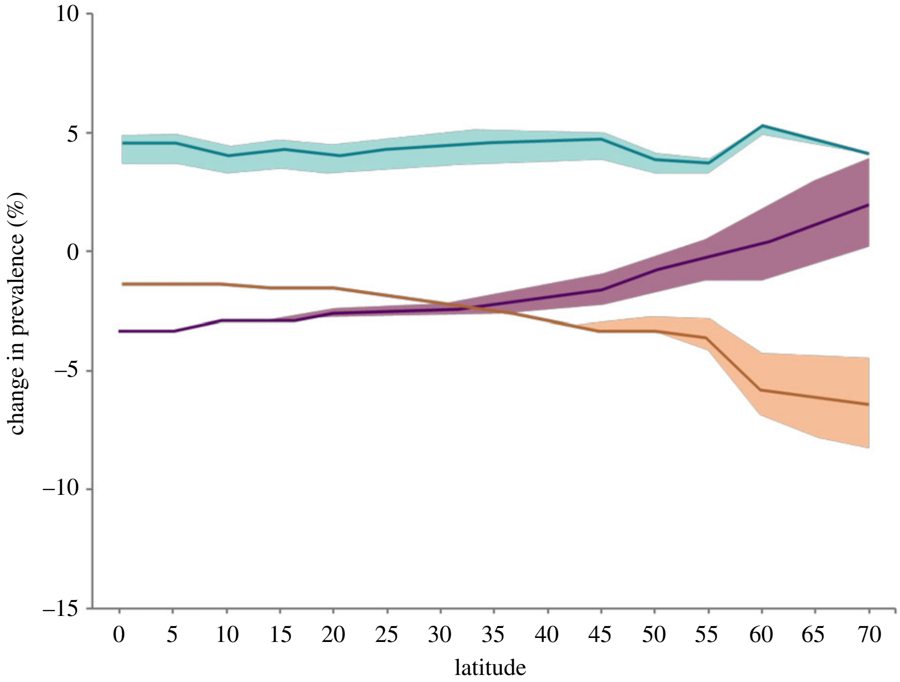

Figure 2. Predicted changes in the developmental mode prevalence under RCP8.5 for the Southern Hemisphere only. Lines show model best-fit ± CI. Orange represents aplanktonic larvae, blue represents feeding planktonic larvae and purple represents non-feeding planktonic larvae. (Online version in colour.)

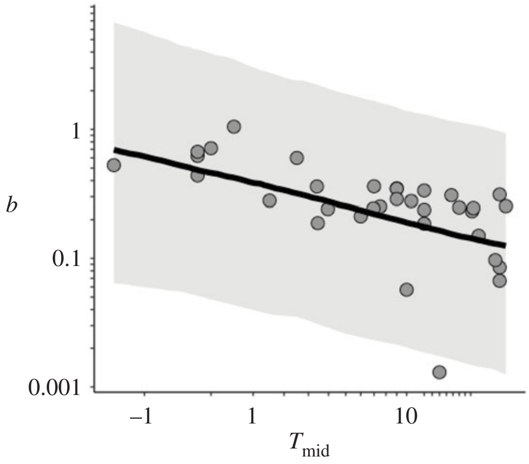

Figure 3. The relationship between the parameter describing the temperature-dependence of development (*b*; in log-scale) and the temperature in which species live (T_{mid} in log[°C])). Each point is a species, the black line shows the fitted model and the grey ribbon shows the 95% credible intervals.

scenario (in terms of both emissions and temperature dependency) and developmental mode is considered, developmental durations are predicted to change very little. For all other latitudes, the degree to which developmental durations are predicted to decline varies according to the developmental mode, emission scenario and the temperature dependency of development.

If temperature dependency of development is assumed to be constant, then reductions in the developmental mode start to occur at around 40° of latitude for species with feeding larvae and 20° for species with non-feeding larvae (figures 4 and 5). Under low emissions, the greatest reductions in developmental durations (which occur near the poles) are predicted to be around 55% for non-feeding larvae and approximately 20% for feeding larvae. Under higher emissions and greater warming, the greatest reductions in developmental duration are approximately 75% for non-feeding larvae and exceed 40% for feeding larvae.

If temperature-dependence of development is assumed to be temperature-dependent itself, then substantial reductions in planktonic duration are not predicted for latitudes less than 45°. However, at the highest latitudes, durations are predicted to be extremely curtailed (figures 4 and 5). Under high emission scenarios, feeding larvae will have 60% shorter planktonic durations, while non-feeding larvae will have durations that are around 90% shorter. The reductions are predicted to be very similar regardless of whether an instantaneously changing *b* or a lagged *b* is considered, although using lagged *b* tends to yield greater reductions in the planktonic period, particularly at higher latitudes.

Overall, our results predict that warmer oceans have far less diversity in the planktonic durations that species exhibit. Under current conditions, larval durations are predicted to vary between 3 and 54 days for non-feeding larvae, and 20 and 71 days for feeding larvae. Under the greatest warming we considered, this range drops to 3–4.7 days for non-feeding larvae and 20–23 days for feeding larvae.

4. Discussion

Our simple simulations suggest that rising ocean temperatures will alter the distribution of marine life histories and dispersal potential in profound ways. Near-future temperature increases are likely to cause a reduction in the prevalence of species with aplanktonic development (in the Southern Hemisphere) and species with non-feeding larvae (globally). Meanwhile, species with feeding larvae are predicted to become more prevalent everywhere, with significant increases in the relative prevalence of such species near the poles. Simultaneously, for species with pelagic larvae, dispersal potentials are predicted to decrease dramatically. Previous studies anticipated that climate change will reduce marine dispersal, but

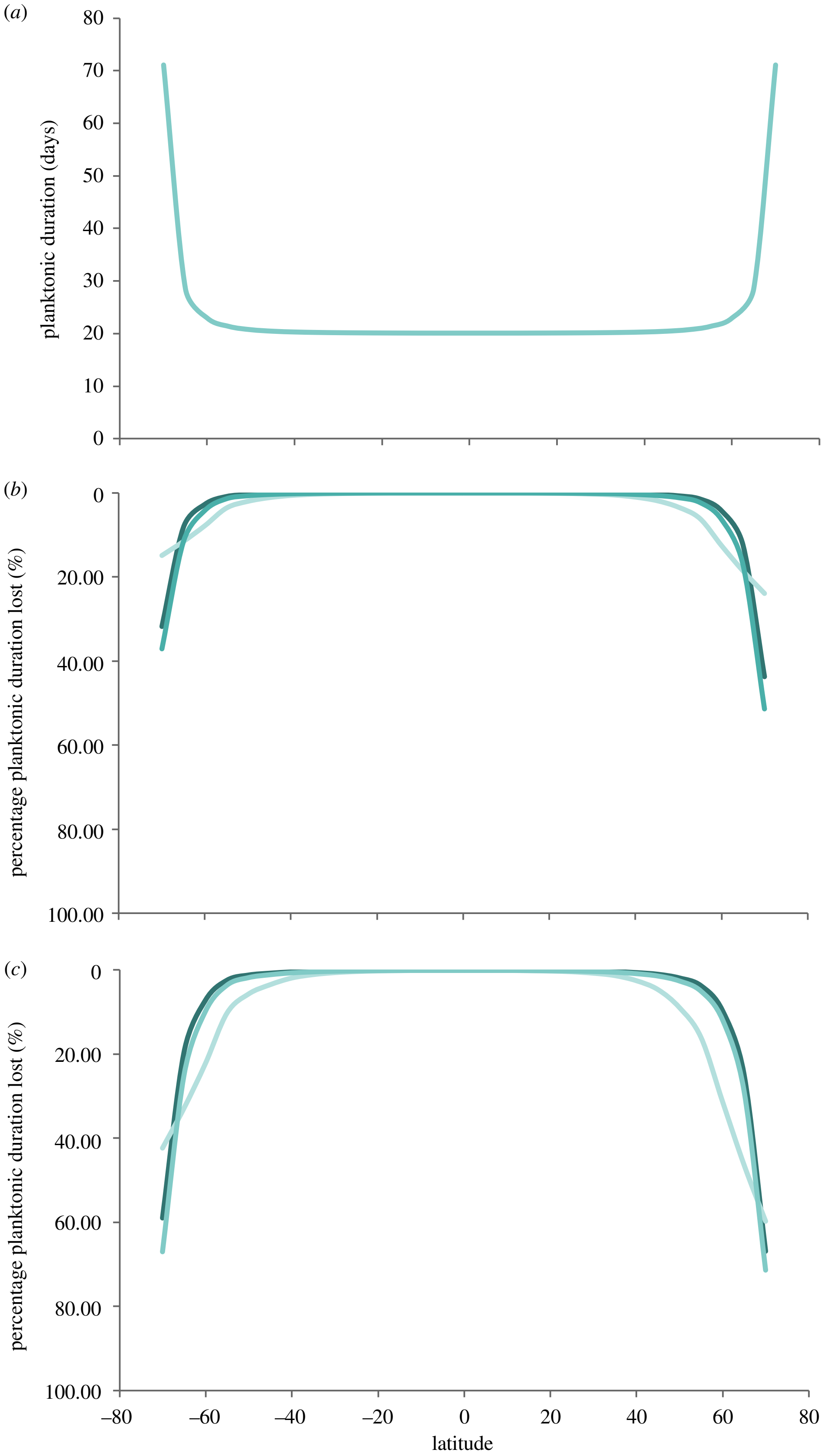

Figure 4. (*a*) Planktonic duration for a hypothetical species with feeding larvae across latitudes (Southern Hemisphere on the left). (*b*) Predicted percentage of planktonic duration lost under RCP2.6. (*c*) Predicted percentage of planktonic duration lost under RCP8.5. Lightest colour shows a predicted percentage under a constant temperature dependency of development, medium shading under temperature-dependent, temperature dependency of development and perfect matching of *b*. Darkest shading shows predictions for under temperature-dependent temperature dependency of development with a lagged *b*. (Online version in colour.)

these studies focused on tropical and temperate regions [13,26]. Here, we find further support for such projections, but predict that high latitudes in particular will experience the greatest reduction in dispersal potential—larval periods could be reduced by more than 90% in polar seas. While uncertainties exist, our results suggest that global warming could reduce the viability of entire developmental modes and reduce the connectivity of marine populations.

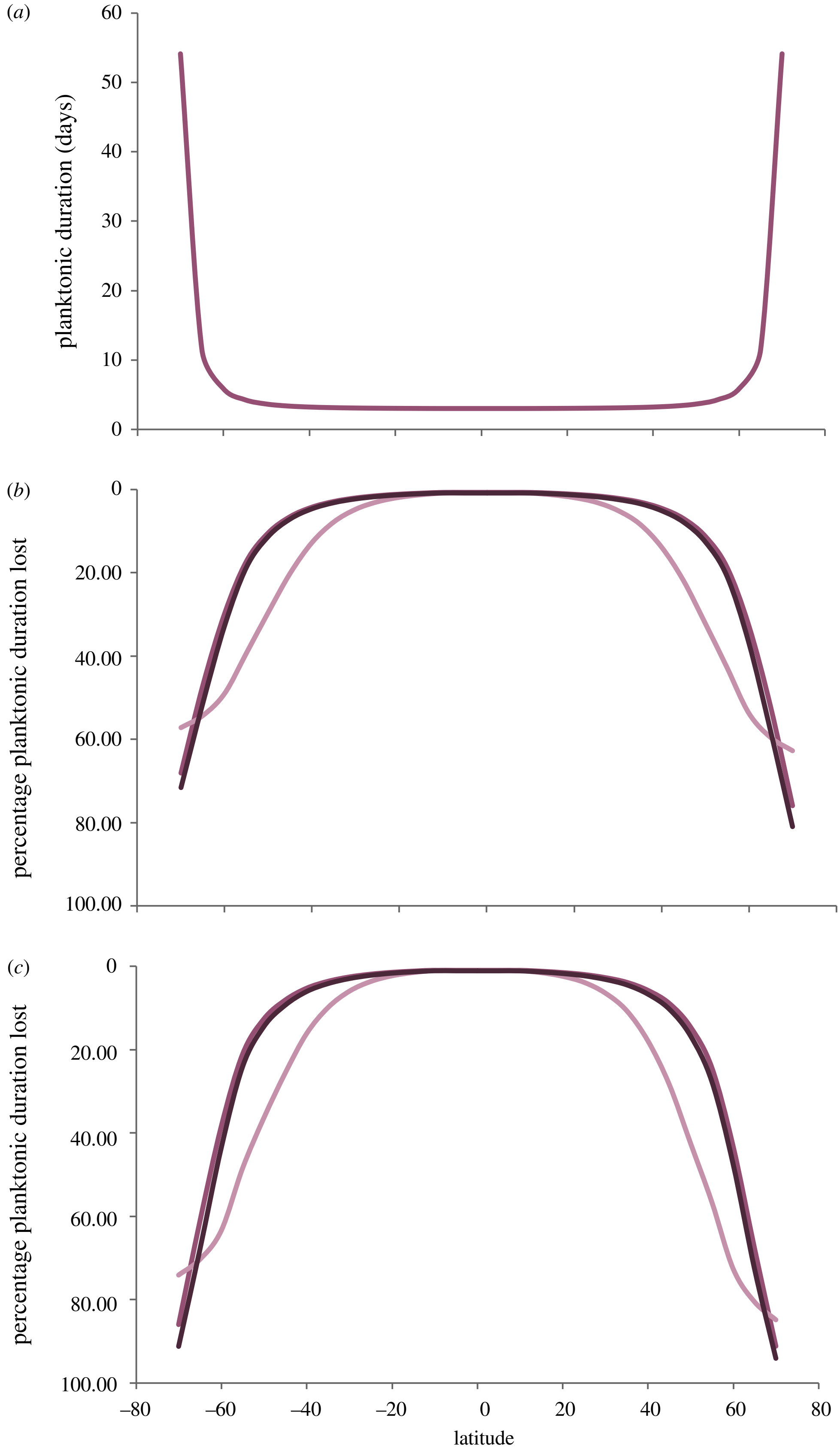

Figure 5. (*a*) Planktonic duration for a hypothetical species with non-feeding larvae across latitudes (Southern Hemisphere on the left). (*b*) Predicted percentage of planktonic duration lost under RCP2.6. (*c*) Predicted percentage of planktonic duration lost under RCP8.5. Lightest colour shows a predicted percentage under a constant temperature dependency of development, medium shading under temperature-dependent, temperature dependency of development and perfect matching of *b*. Darkest shading shows predictions for under temperature-dependent, temperature dependency of development with a lagged *b*. (Online version in colour.)

(a) Developmental diversity in future oceans

A loss of developmental diversity, particularly at higher latitudes, seems likely as oceans warm. Our developmental mode-specific approach, rather than species-specific approach, allows us to make some generalizations about the types of species that may benefit or suffer from climate change. Our results predict that species with aplanktonic development or non-feeding planktonic larvae are likely losers under future climates, whereas the prevalence of species with feeding larvae is predicted to increase. A poleward expansion of some planktotrophs may already be occurring [41,42], but as far as we are aware, accelerated range contractions of species, specifically with non-feeding larvae or aplanktonic development, have not been explored [43]. We believe this would be an interesting next step.

Our results imply specific groups are under more threat than others, particularly in groups that show a single developmental mode. For example, whelks tend to show aplanktonic development exclusively and crinoids lack feeding larvae [16]. Both groups are predicted to suffer under ocean warming, or at least they seem particularly vulnerable to further warming given their developmental modes. This increased vulnerability might not be apparent if only adult distributions are considered—we recommend future studies that predict range shift changes consider the role of developmental mode specifically.

We focused exclusively on mean temperature as a driving factor in the distribution of developmental modes but other factors, notably the predictability of temperature and primary productivity, also shape the distribution of developmental modes [17]. Projections about the future predictability of temperatures are less specific at this stage and so we cannot make quantitative statements about how this factor will alter the relative prevalence of different developmental modes. However, if ocean temperatures become less predictable, then we might anticipate that this would exacerbate an increase in the prevalence of species with feeding larvae [17]. On the other hand, increased thermal stratification associated with rising temperatures is predicted to reduce the productivity of the world's oceans [44]. Reduced productivity would favour an increase in the prevalence of aplanktonic species, all else being equal [17]. Marine life histories are shaped by multiple factors simultaneously [17,45], all of which are likely to change under climate change, hampering precise predictions about future distributions. Nevertheless, it seems highly likely that global distributions of developmental modes will change, particularly at higher latitudes, with concomitant systematic losses of species with some developmental modes over others.

(b) The temperature-dependence of temperature-dependence

We found that the relationship between developmental duration and temperature within species was dependent on the temperature in which species lived—species in colder water are much more sensitive to minor changes in temperature than species in warmer water. This finding is at odds with among-species explorations of how developmental duration is affected by temperature—such studies tend to emphasize the consistency of the effect of temperature on development ([33] but see [13,46]). Importantly, our study addresses a different scale of biological organization—how *within-species* development–temperature relationships covary with temperature *among species*, so from this perspective, the different findings are not incompatible. However, given that studies exploring among-species patterns often invoke fundamental mechanistic drivers as explanations [47], these same processes should apply within species. Instead, we see systematic covariation between the within-species temperature-dependence and the temperatures in which these species occur. Interestingly, this same temperature-dependence of temperature-dependent development has recently been detected in terrestrial and freshwater ectotherms [29] and similar patterns have also been noted in trematodes [48]. Finally, the temperature-dependence of the metabolic rate also seems to be temperature-dependent in ectotherms—species living in warmer temperature tend to have metabolic rates that are less affected by changes in temperature than species living in cooler temperatures [29]. The fact that these patterns are repeated across a wide variety of taxa and at least two key rates (development and metabolic) implies that there is some common factor that drives the evolution of different temperature dependencies according to the local thermal regime and deserves much more exploration. For now, we are at a loss to explain this pattern. Nevertheless, finding that cold-water species have much greater temperature dependencies than warmer water species has critical implications for how future climate change will affect developmental durations and dispersal potentials in the sea.

(c) Dispersal potential and the future connectivity of marine populations

We found that temperature increases are predicted to reduce the developmental durations of marine organisms across all of the world's oceans, but particularly in the polar seas. At latitudes greater than 55°, developmental durations in 2100 will be shorter by at least 20% regardless of what assumptions are used and could be up to 90% shorter under some conditions. The effects are particularly pronounced for species with non-feeding larvae, which, unfortunately, are the most abundant species in polar regions. The dramatic reduction in dispersal potential will alter the degree to which populations are demographically connected with implications for species persistence and population dynamics.

Shortened dispersal distances will reduce genetic exchange among populations, therefore decreasing genetic variation and limiting the population's ability to cope with changing environmental conditions [49]. Limited dispersal also hampers metapopulation persistence by reducing the 'rescue effect', where immigration from distant patches reduces the risk of local extinctions [50,51]. On the other hand, genetic isolation facilitates adaptation to local conditions and consequently increases speciation rates [7,52,53]. Reductions in dispersal will also alter density-dependent processes within populations (e.g. [54]): individuals in source populations are likely to experience more competition as larvae are more likely to settle nearby.

(d) Sources of uncertainty regarding developmental predictions

There are several sources of uncertainty that could affect our predictions regarding future development durations. First, we focus on development to the completion of the larval stage, but larvae can remain competent to metamorphose for days or even weeks after completing development, so our results pertain to minimum dispersal durations. However, non-feeding larvae in particular cannot delay metamorphosis indefinitely, as they rely on finite stores, which will be consumed at higher rates under higher temperatures [25]. The duration of the competency period, in which larvae are capable of settlement and metamorphosis and have sufficient stores to successfully metamorphose, is likely to decrease with higher temperatures, shortening dispersal further.

Second, we assume that marine organisms do not alter the size of their eggs in response to higher temperatures. However, a recent study suggested that cold-water species will decrease the size of their eggs under slight temperature increases, in response to lower developmental costs [25]. By contrast, warm (greater than 22°C) water species should increase the size of their offspring as developmental costs will increase with temperature increases [25,29]. If egg sizes do change as predicted, changes in developmental duration will be relatively slight (egg size effects on development, though significant, are less strong than temperature effects [55,56]). In warm-water species, where feeding larvae are most common, an increase in egg size will decrease developmental durations slightly (because larvae will need to spend less time in the plankton in order to reach a critical size; [56]). In cold-water species, where non-feeding larvae are most common, decreases in egg size will reduce planktonic duration slightly because smaller eggs take less time to complete developing into a non-feeding larva [11]. Therefore, incorporating any changes in egg size would exacerbate the reductions in larval duration that we discuss above, albeit via very different mechanisms depending on the larval type.

Third, we do not consider changes in seasonality and the abundance of phytoplankton—larval food—that might counteract the effects of increases in the mean temperature. Previous studies have shown that species with feeding larvae are less prevalent in more seasonal seas [17]. Polar seas are more seasonal than temperate or tropical seas, particularly with regard to temperature. The degree to which seasonality will change in the future, and the relative influence of mean temperatures versus seasonality is unclear (but see [30]), and a source of significant uncertainty.

Warmer, more stratified seas are predicted to be less productive—potentially reducing the availability of larval food. When feeding larvae are grown in food limited conditions, they take longer to reach metamorphic competence [57]. Incorporating larval food effects could therefore offset the minor reductions in the planktonic period predicted for species with feeding larvae in warmer waters. On the other hand, recent studies make conflicting predictions about algal biomass in future seas, particularly in the tropics [58]. Given the current uncertainty regarding the productivity of future oceans, we refrain from speculating about how changes in larval food will alter larval durations in feeding larvae.

Fourth, we do not consider the temperature-dependence of larval mortality. Larval predation and larval starvation are thought to be the principle sources of larval mortality, and we would predict that both would increase under higher temperatures. Higher larval mortality rates would reduce effective dispersal kernels further, exacerbating the effects of reduced larval durations on population connectivity. So overall, while we do not formally incorporate several sources of uncertainty with regard to estimates of how temperature affects dispersal durations and connectivity, for the most part these factors would further reduce connectivity.

Fifth, ocean currents are predicted to change under future climate regimes [30]. Larval transport is the product of both net current velocity and larval duration [59]—we have only focused on larval duration here. An important next step will be to explore how current regimes differ at a global scale [30], and how these are likely to change.

(e) The rise of the planktotrophs

Our two findings: (i) that higher temperatures favour the poleward expansion of species with feeding larvae, and (ii) that higher temperatures will reduce the developmental durations of cold-water species in particular, taken together, have some worrying implications for how species range shifts will (and more importantly, will not) occur. Consider the following scenario. As oceans warm, planktotrophs, suited to warm water, will extend their ranges poleward. Meanwhile, species with non-feeding larvae will also shift their ranges poleward but such species already have shorter planktonic periods at a given latitude than species with feeding larvae, so their range shifts are likely to be slower. Worse, species with non-feeding larvae originating from cooler temperature regimes will have much higher temperature dependencies of development relative to planktotrophs. Non-feeding larval developmental durations will be shortened much more relative to planktotrophs, even if they experience the exact same temperature increase. In other words, the ‘invading’ planktotrophs will have their planktonic periods affected minimally, while the ‘retreating’ species with non-feeding larvae will have their (already shorter) planktonic durations greatly reduced. We would therefore predict that planktotrophs will move and expand their range poleward more quickly than species with non-feeding larvae. In the Southern Hemisphere, aplanktonic species (which are naturally poorer dispersers already) are common at high latitudes, but these species have nowhere left to expand their range (the analogue of a montane terrestrial species), such that they will be lost disproportionately. Overall, it seems that multiple factors will combine to expand the prevalence of plankotrophs at the expense of species with non-feeding larvae or aplanktonic development.

Shifting life-history compositions also may have consequences for marine food webs. Non-feeding larvae tend to be larger, more resource rich and are more likely to be chemically defended relative to feeding larvae [16]. It is likely that these different developmental modes have different predators, though we are unaware of any studies that have explored this issue. Similarly, phytoplankton-feeding larvae that are likely to be more prevalent could have consequences for primary production, though again this is highly speculative. Regardless, systematic changes in the prevalence of different developmental modes as seas warm will probably have consequences that extend beyond the species directly affected.

Data accessibility. Most of the data upon which the analyses are based are currently available online and the only new data here are included in the electronic supplementary material.

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