



Marine ecology warms up to theory

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A recent report by O'Connor *et al.* demonstrates that planktonic larval duration time declines with temperature, as predicted from metabolic theory. This observation enabled the authors to develop a unified model predicting the effects of temperature on planktonic larval duration and, therefore, dispersal potential in the marine environment. These results show metabolic theory to be a unifying ecological principle that bridges the marine and terrestrial divide, helping to address fundamental problems in marine biodiversity and conservation, as well as to understand the response of marine organisms to climate change.

Ecological theory across the land–ocean divide

The transfer of ecological theory and knowledge across the land–ocean interface is challenging because many of the underlying principles are specific only to one of these biomes or their inhabitants; however, when successfully transferred, such knowledge can advance our general understanding of, and novel perspectives on, the alternative biome [1]. Marine biodiversity research lags behind that on land, with only 10% of overall biodiversity research devoted to marine biodiversity [2] and exhibits a general neglect of developments in general ecological theory. Recent reports have identified this knowledge gap and the associated disciplinary divide between terrestrial and marine ecology as key factors in determining the poor success rate of marine biodiversity conservation [2].

The metabolic theory of ecology (MTE), which draws from first principles of biophysics to formulate predictions across a range of key ecological phenomena (Box 1), has emerged as a powerful, unifying ecological principle [3]. Most applications of metabolic theory focus on terrestrial organisms and ecosystems; however, studies applying the MTE to fundamental problems in marine ecology are now emerging [4–7]. The recent work of O'Connor *et al.* [7] demonstrates that the temperature dependency of planktonic larval duration time (PLD) is consistent with the expectations of MTE. This observation enabled the authors to develop a unified model that predicts the effects of temperature on PLD and, therefore, dispersal potential in the marine environment, a fundamental problem in marine ecology and conservation. Their work provides a clear demonstration of the progress that applying MTE can bring to marine ecology research.

Predicting planktonic stage duration

Most marine organisms rely on planktonic phases for dispersal, enabling disjoint adult populations to be

connected by planktonic propagules [8]. In particular, PLD constrains the potential dispersal distances of fish and invertebrates, affecting the neighbourhood size of marine populations and the potential connectivity among disjoint populations [8–10]. Despite its important consequences for the management of marine protected areas and fish stocks [8–10], our ability to predict larval dispersal has remained limited to order-of-magnitude approximations [8,10]. Present knowledge has indicated that larvae that develop in the plankton over weeks or months disperse across tens to thousands of kilometers during that time [8,10]. Parallel research has provided evidence of an exponential decline in the PLD with increasing temperature for a large number of species [7]. However, these relationships were assumed to represent idiosyncratic, species-specific responses. In a new paper [7], O'Connor *et al.* show that the exponential decline in PLD with increasing temperature is accurately predicted from MTE (Box 1) and that the predictions of MTE hold across species.

In a previous paper, Hirst and López-Urrutia [6] demonstrated a similar relationship between temperature and the time to hatching of eggs of marine organisms [12]. Eggs that are freely released into the water column represent a major dispersal agent of many marine animals, with continuity into the larval dispersal phase as eggs hatch. When combined, these findings [6,7] provide a framework that can be used to predict the distances that marine organisms disperse from egg release to juveniles, and validate the predictions of MTE in different ways.

O'Connor *et al.* [7] demonstrate that PLD is similarly scaled to temperature across and within species, a test that was not possible for planktonic egg duration time (PED) owing to the lack of comparable data on its temperature dependence. The analysis of PED enabled the effects of egg mass (M) to be examined, with PED increasing with egg mass, as predicted by the MTE (i.e. $M^{\frac{1}{3}}$; Box 1 [6]). A paucity of reports on larval mass precluded a similar test for PLD [7]. Both analyses identified significant life-history and evolutionary effects on the duration of the egg and larval stages, as planktonic larvae that feed in the plankton have longer development times for any one temperature than do non-feeding ones [7]; similarly, eggs that are protected or attached show longer hatching times for any one temperature than do those that are freely released into the water column [6].

The most striking aspect of these two independent analyses is the similarity between the average PLD and mass-corrected fish PED predicted from temperature (Figure 1). This suggests that a single equation, derived from the first principles of MTE, can predict the rate of

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Box 1. The metabolic theory of ecology

Metabolism, the biological processing of energy and materials, determines the rates of biological activities, from those of cell machinery to ecosystem processes [3]. The dependence of metabolic rates on temperature and body size ranks among the most robust empirical laws in ecology [14,15]: whole-organism metabolic rate (I) scales as the 3/4 power of body mass (M), as described by the allometric equation I [14]:

$$I = I_0 M^{3/4}, \quad [\text{Eqn I}]$$

and metabolic rates increase exponentially with temperature, as described by the Boltzmann factor or the Van't Hoff-Arrhenius relation (Equation II),

$$I = e^{-\frac{E}{kT}}, \quad [\text{Eqn II}]$$

where E is the activation energy, k is Boltzmann's constant, and T is absolute temperature in K [3].

The MTE combines these general laws into a single law that formulates the joint effects of M and T on the whole-organism

metabolic rate, as described by Equation III [3,11]:

$$I = i_0 M^{3/4} e^{-\frac{E}{kT}}, \quad [\text{Eqn III}]$$

or by Equation IV:

$$I = i_0 M^{-1/4} e^{-\frac{E}{kT}}, \quad [\text{Eqn IV}]$$

for mass-specific rates. Biological times, such as the time to larval hatching, are the reciprocal of rates and, therefore, scale as (Equation V),

$$I = i_0 M^{1/4} e^{\frac{E}{kT}}. \quad [\text{Eqn V}]$$

Equations III–V, which represent the basis of the MTE, hold for a range of metabolic and life-history processes and times at various scales, from molecular to the ecosystem, and over the biologically relevant temperature range of 0 to 40 °C for organisms ranging from microbes to trees and the largest mammals [3,11,12]. The MTE formulates quantitative predictions based on first principles that apply across a broad range of processes [3–7] and can be used to predict organismal responses to environmental changes, such as those derived from climate change.

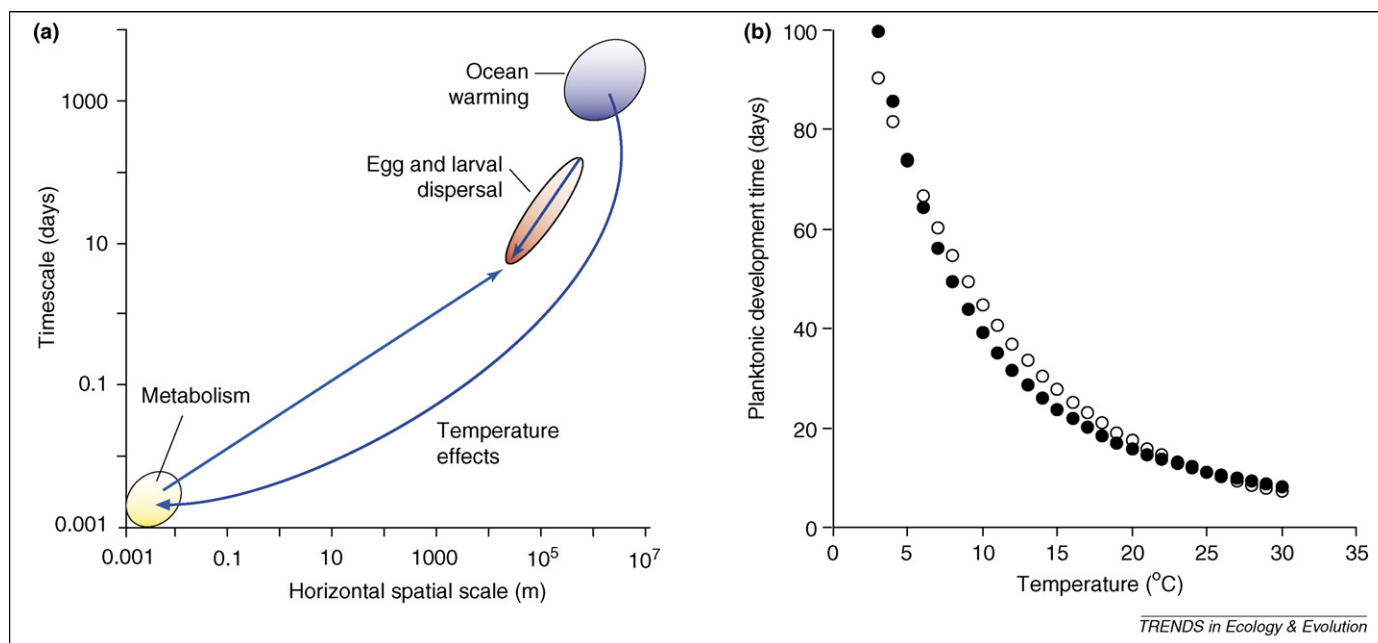


Figure 1. Effects of temperature and ocean warming on planktonic egg and larval development times and associated dispersal distances. **(a)** Temperature forcing (blue arrows) of processes occurring on different time and spatial scales in the ocean. Ocean warming (blue oval) occurs over ocean basin-wide spatial scales and decadal timescales. Increased sea temperature accelerates metabolic processes, occurring over short (<1 s) and small (<<1 mm) time and spatial scales (yellow oval). These, in turn, affect planktonic egg and larval development times and dispersal scales (red oval), which occur at intermediate time and spatial scales. The blue arrow within the red oval indicates the predicted reduction in dispersal spatial and timescales with increasing temperature over the 2–30 °C range. **(b)** shows the predicted planktonic larval development time (filled circles) (population-averaged equation from Figure 2 in Ref. [7]) and mass-corrected hatching time of planktonic fish eggs (open circles) (from Table 1 in Ref. [6]) with increasing temperature. The red oval in (a) encompasses the planktonic egg and larval dispersal timescales predicted from the temperature dependence of development times using the relationships shown in (b) and the corresponding spatial dispersal scales predicted from development time using the model introduced in Ref. [7].

change in the duration of egg and larval dispersal stages with changing temperature. This observation identifies MTE as a solid foundation on which to predict the dispersal timescales of marine organisms.

Predicting planktonic dispersal distances and ocean warming

The significance of the ability to predict the duration times of planktonic eggs and larvae is related to their importance in constraining the horizontal dispersal distances of the organisms. O'Connor *et al.* [7] showed that the horizontal dispersal distances of larvae are expected to shorten by almost 30 times with increasing temperature across the 3–35 °C range owing to the acceleration of larval development with

increasing temperature. The predicted horizontal dispersal scales are consistent with the tens to thousands of kilometers inferred previously [8,10]. Whereas the individual predictions depend on the parameterization of the dispersal model used [7], the relative effect of temperature on horizontal dispersal scales is likely to be robust, and should be similar to its effect on the horizontal dispersal scales of planktonic fish eggs, because of the similar temperature dependence of PED (Figure 1).

Conclusions

These results show that the effects of temperature on enzymatic processes, which operate at time and spatial scales that are less than seconds and millimetres, respect-

ively, impact on planktonic larval and egg duration times and, thus, dispersal distance, which occur over longer temporal (days to months) and spatial (tens to thousands of kilometers) scales (Figure 1). Furthermore, climatic changes occur over basin-wide spatial scales and decadal timescales, affecting metabolic processes and, hence, planktonic egg and larval duration time and dispersal scales. These propagule development and dispersal scales are, therefore, strongly constrained by cooperative, synergistic processes between climate change and its metabolic effects, occurring over much larger and much smaller time and spatial scales, respectively, than the dispersal process itself (Figure 1). In particular, global warming is projected to elevate ocean temperatures by an estimated 4 °C over the course of the 21st century [13]. The temperature dependence of planktonic egg and larval duration time [6,7] implies a reduction in the dispersal distances (calculated using the approach in Ref. [7]) by, on average, 45% with a 4 °C warming. This reduction, which could be compounded by other possible effects of temperature (e.g. changes in ocean currents and mixing, mortality and fecundity), suggests that marine populations that are already fragmented will become even more disjoint, rendering stepping-stone processes connecting distant populations [8] less effective; in addition, the density of networks of marine protected areas that are designed to link across present-day dispersal scales might have to increase to remain effective [7]. These inferences show the far-reaching implications of these results [6,7] for our understanding of processes that maintain marine biodiversity and our capacity to forecast future changes, and should draw immediate attention to the use of newly available models.

Most importantly, these models do not derive from blind statistical fits through data, but from the applications of the first principles embedded in the MTE. Along with recent demonstrations that MTE helps predict the impacts of temperature and organismal size structure on marine metabolism [4,5], the results presented by O'Connor *et al.* [7] provide evidence that it can also help

address fundamental problems in marine biodiversity and conservation, such as dispersal, its consequences for population connectivity and the design of marine protected areas and responses to ocean warming. The application of MTE to pelagic ecosystems might, in turn, help move this theory in new directions. Thus, MTE is emerging as the first unifying ecological principle bridging the marine–terrestrial divide.

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