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Metabolic Ecology: A Scaling Approach

Chapter · March 2012

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Chapter 15

MARINE INVERTEBRATES

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Text

SUMMARY

1 Ocean temperature strongly controls metabolic rates of marine invertebrates. A highly conserved, nonlinear scaling of metabolic rate with temperature explains variation in metabolic rate and associated ecological and evolutionary processes over depth and latitudinal gradients.

2 Body mass and temperature explain most variation in metabolic rate with depth in accordance with the metabolic theory of ecology, although predators in sunlit surface waters appear to have evolved higher resting rates.

3 General temperature-dependence models also explain the duration of a key demographic life stage – planktonic larval development – over temperature

gradients. Within a species, larval development is faster in warmer water, and the rate of acceleration is predicted by metabolic theory.

4 Comparisons of larval development rate among species reveal that effects of temperature within species are stronger than patterns among species. The among-species pattern possibly reflects adaptations to compensate for the strong effect of temperature on development.

5 The metabolic theory of ecology offers a powerful, unifying approach to explain biogeographic patterns in marine life histories and responses to climate change.

15.1 INTRODUCTION

Most animals on Earth are marine invertebrates. Across this ecologically and phylogenetically diverse group, there is clear evidence of temperature- and mass-dependence of metabolic rates. The metabolic theory of ecology (MTE; Brown and Sibly, Chapter 2) provides a conceptual framework for applying general models of mass- and temperature-dependence of metabolic rates to understanding mechanistic drivers of variation in life-history traits and metabolic rates over environmental gradients in the ocean. Though rela-

tionships between temperature, mass, and metabolic rate have been studied among species and closely related taxa for decades (Thorson 1950; Childress 1971; Emlet et al. 1987; Pearse and Lockhart 2004), the generality of the models in MTE (Brown and Sibly, Chapter 2) have inspired synthesis of scaling relationships across broader taxonomic groups and geographic regions (Hirst and Lopez-Urrutia 2006; Lopez-Urrutia et al. 2006; Seibel and Drazen 2007). These syntheses have allowed new tests of old hypotheses (Seibel and Drazen 2007), and have provided a quantitative framework for considering biological impacts of future

climate change (Hirst and Lopez-Urrutia 2006; Lopez-Urrutia et al. 2006; O'Connor et al. 2007; see also Anderson-Teixeira, Smith, and Ernest, Chapter 23).

This chapter provides an overview of several themes in the studies of metabolic ecology of marine invertebrates that pre-date the Metabolic Theory, and considers these themes in the context of the recent conceptual and empirical syntheses. After an outline of hypotheses for how abiotic conditions in the ocean limit metabolic rates in extreme environments, the primary focus of this chapter is how size- and temperature-scaling of metabolism in marine invertebrates has provided new insight into their ecology and evolution. Specifically, metabolic scaling theory has provided a framework that allows identification of general allometric and temperature-scaling relationships and exceptions to these patterns, and points to patterns in life-history traits and community structure that may reflect indirect effects of environmental temperature gradients. In this way, a theory of metabolic scaling in the ocean sheds new light on old problems, and points a way forward for understanding changing ocean ecosystems.

15.2 OVERVIEW OF METABOLIC THEMES IN MARINE INVERTEBRATE ECOLOGY AND EVOLUTION

Of the over one million described animal species, 95% are invertebrates, and every major animal phylum is represented in the oceans (Ruppert and Barnes 1994). The only common characteristics that all marine invertebrates share are that they live in the ocean, do not internally regulate body temperatures (are ectotherms), and their bodies lack a backbone (i.e., they do not belong to the subphylum *Chordata*). The body masses of adult marine invertebrates span 11 orders of magnitude, from the smallest metazoans – planktonic rotifers (10^{-8} g) – to the colossal squid (*Mesonychoteuthis hamiltoni*, 500 kg) (Rosa and Seibel 2010) which even outweighs the giant squid (*Architeuthis dux*). Marine invertebrates have exploited every ocean environment, including rocky shores, sunlit tropical surface waters and dark, hypoxic, cold water 5 km below sea level.

Across these environments, geographic patterns in invertebrate abundance, diversity and life-history traits have attracted the interest of scientists (Thorson 1936, 1950; Thiel 1975; Witman et al. 2004; Tittensor et al. 2010). Some of these patterns have been dubbed “rules”: Thorson’s rule describes the trend in numer-

ous phyla toward greater parental investment per offspring in the form of larger offspring, brooding or enhanced nutritional provisions, with increasing depth and latitude (Thorson 1950; Pearse and Lockhart 2004). At the community level, diversity declines with increasing latitude and depth, such that communities of extremely cold environments are characterized by low diversity, low abundance, slow biological rates, and large size (Witman et al. 2004; Etter et al. 2005; Rex et al. 2006). In stark contrast, warm environments are characterized by high diversity, high abundance, and a fast pace of life. Though hypotheses to explain these patterns in terms of metabolic constraints are not new, they have lacked a general framework that would unify patterns across taxa through a fundamental, quantifiable biological mechanism.

A metabolic theory of ecology that transcends system (marine, terrestrial) and taxon provides a powerful approach to understanding ecology and evolution, not only in the ocean but in all systems. Testing and developing such a theory in different cases involving unique taxa and systems allows us to explore deviations from predictions, and potentially expand the theory (Duarte 2007). Historically, marine invertebrate (and vertebrate) ecological research has emphasized the role of constraints on metabolism. Major research foci have been the roles of food limitation, oxygen limitation, and temperature limitation in driving geographic variation in life histories, size, abundance, and diversity. In the next paragraphs we outline three major hypotheses for how abiotic conditions limit metabolic rates in the oceans.

15.2.1 Resource limitation hypotheses: food limitation

The vast majority of the ocean houses consumers that feed on primary production from surface waters. Primary production in the sunlit ocean is limited by nutrient availability, and one common fate of primary production is to sink to deep, dark water where it may be consumed by deep-sea animals. In polar environments where winter months are dark and cold, food chains are sustained by primary productivity from the preceding growing season. Many adaptations toward slower rates of growth and secondary production have been interpreted as consequences of long periods without adequate supply of food (Childress 1971; Clarke 1983). Certainly food limitation is an important

ecological constraint, and the biomass of higher trophic levels is ultimately constrained by primary production. The hypothesis that food limitation can act as a selective force for lower metabolic rates has received much attention, but has been rejected in several recent studies (Cowles et al. 1991; Pearse and Lockhart 2004; Seibel and Drazen 2007).

15.2.2 Resource limitation hypotheses: oxygen limitation

Though marine animals live in water, they still require oxygen for respiration. In midwater depths and in the deep sea, waters are hypoxic, meaning very low in concentration of dissolved oxygen. It has been suggested that low metabolic rate (oxygen consumption rate) has evolved to facilitate persistence in low-oxygen environments (Childress and Seibel 1998). Though some adaptations to low-oxygen habitats have been shown, including elevated gill surface areas, high ventilation volumes, and respiratory proteins with a high affinity for oxygen (Pauly 2007), it is not clear that low metabolic rate is an adaptation to low-oxygen concentration zones (Childress and Seibel 1998).

15.2.3 Metabolic constraints of cold temperatures

Declines in metabolic rate as temperature decreases ("scaling of metabolic rate with temperature") are well appreciated in marine ecological studies. Typically, this effect is approximated by a Q_{10} value of 2–3, and is equivalent to an activation energy of approximately $E = 0.5\text{--}1.0\text{ eV}$. Early research suggested that metabolic rates in cold water were acclimated such that they occurred at rates comparable to those observed in warm water (Krogh 1916; Pearse and Lockhart 2004). This type of acclimation is termed "metabolic cold adaptation," and has been postulated to occur in other groups including insects (Addo-Bediako et al. 2002). More recently, it has been shown and argued that metabolic cold adaptation does not occur among marine invertebrates, and at cold temperatures metabolic processes are generally very slow, as would be predicted based on fundamental constraints imposed by temperature (Clarke 1983; Pearse and Lockhart 2004). Therefore, the prevailing effect of temperature on biogeographic patterns in metabolic rates in marine invertebrates is one of scaling, and tests of the Arrhenius

relationship between temperature and rates have supported the use of the Gillooly et al. (2001) MTE model for broad groups of marine invertebrates (Hirst and Lopez-Urrutia 2006; Lopez-Urrutia et al. 2006; O'Connor et al. 2007; Lopez-Urrutia 2008).

15.2.4 An opportunity for synthesis

Each of these hypotheses reflects a constraint of the environment on fundamental metabolic processes. Yet, so far, they have not been integrated into a single framework. Such a framework would relate the effects of temperature on oxygen consumption rates and resource use rates, potentially explaining patterns that appear to be exceptions to any single limitation hypothesis. The remainder of this chapter explores how metabolic theory can be used to identify unusual conditions that point to selection for higher metabolic rates when fast movement is required to catch prey, as well as selection of life-history traits that can compensate for extreme effects of temperature in cold climates. Selection for unusually high metabolic rates for a particular temperature or size effectively integrates into a gene pool the results of ecological and evolutionary processes that produce the diversity of life in the ocean. Finally, general, direct and indirect effects of temperature on metabolism may explain community-level patterns in the ocean corresponding to temperature gradients. In this way, metabolic ecology of marine invertebrates has already made unique contributions to a broader metabolic theory (Duarte 2007), and much more work remains to be done.

15.3 PATTERNS IN METABOLIC RATE WITH DEPTH, AND SELECTION FOR HIGH RATES IN SURFACE WATERS

The marine habitat extends from sunlit waters in the upper 100–200 m of the ocean to dark, cold (–1 to –4 °C) waters over 4000 m deep. Environmental conditions change dramatically over the uppermost few hundred meters, and below that pressure is high, and light and temperature are very low and decline gradually with depth. It has been suggested that environmental differences between warm, light surface water and the cold dark water below 1000 m severely constrain metabolic processes and thus limit the performance, abundance, and body size of deep-sea animals

(Thiel 1975; Rex et al. 2006). Ideas about how this gradient should impact ecology and evolution via constraints on metabolic processes preceded sufficient data to test whether and how metabolic rates actually vary with depth.

One commonly cited pattern is a reduction in metabolic rate with depth. Recently, Seibel and Drazen (2007) reviewed metabolic rates of marine animals across a range of depths to explore potential explanations for this pattern. Most of their samples were measured at 5 °C, and those that were not were standardized to 5 °C using a $Q_{10} = 2$ ($E = \sim 0.5$ eV in the Arrhenius equation; Gillooly et al. 2001). Controlling for temperature in this way, metabolic rate still declined with increasing depth (Fig. 15.1A). The strong effect of temperature on metabolic rate means that animals living in cold (<5 °C) polar or deep water use oxygen at rates up to 27-fold lower than some animals living in surface waters in the tropics (Gillooly et al. 2001; Seibel and Drazen 2007), and may explain how some can persist in low-oxygen environments.

For marine invertebrates, mass-specific metabolic rate varies with body size, and the slope of this relationship across all taxa was -0.22 in Seibel and Drazen's (2007) dataset, consistent with quarter-power scaling. For any given body size, there is substantial variation among taxa in metabolic rate. Despite this variability, comparison of nested, general linear models that allowed for variation in slopes, intercepts, or both among taxonomic orders shows that the same slope (-0.20) applies to all orders (Fig. 15.1B). When body size variation was accounted for in the full dataset, the trend in metabolic rate with depth was eliminated (Fig. 15.1C), possibly reflecting a trend toward smaller body sizes in deeper water (Fig. 15.1D) (Rex et al. 2006). For most groups in the study, body size and temperature explain observed declines in metabolic rate with depth among marine invertebrates.

In some groups a depth gradient in metabolic rate persists even after controlling for size and temperature (Fig. 15.1E). Some cephalopods and crustaceans (and fish) living near the ocean surface have much higher metabolic rates than expected based on their size and temperature (Seibel and Drazen 2007) (Fig. 15.1F). It is possible that an evolutionary "arms race" (or in this case, a speed race) has occurred in which selection favors speedier prey to escape predation, and speedier predators to catch prey in warm, clear water (Seibel and Drazen 2007). The visual predation hypothesis formalizes the idea that selection has favored high

metabolic rates in groups of cephalopods, fish, and crustaceans that use image-forming eyes to identify and locate prey in clear, refuge-free waters (Childress 1995; Seibel and Drazen 2007). When Seibel and Drazen (2007) analyzed their data and partitioned taxa based on whether they were visual predators, the visual predators had elevated metabolic rates above what would be indicated by body-size and temperature-based expectations, and these rates did not decline with body size as steeply as in other groups (Fig. 15.1F).

In sum, across a broad thermal gradient, metabolic rate in marine invertebrates scales with temperature across species. Most deviations from this temperature-scaling expectation occur not at low temperatures, where it had been hypothesized that rates should be higher than predicted due to thermal acclimation and adaptation, but at *high* temperatures in sunlit surface waters. The work of Childress, Seibel, and their colleagues suggests that selection favors high metabolic rates in certain groups in light, warm water. Such adaptation can cause large deviations from predictions based on simple scaling theory. But for the majority of marine invertebrates and fish in the dataset, allometric and temperature-scaling relationships are sufficiently informative to explain variation in metabolic rate over environmental gradients spanning 4000m from the surface of the ocean to the deep sea.

15.4 TEMPERATURE DEPENDENCE OF DEVELOPMENT, AND RELATED PHENOTYPIC COMPENSATION

For most marine invertebrates, the distinct life stages of egg and larval development are characterized by very small size, high risk of mortality, and passive dispersal away from adult habitats in a moving pelagic environment (Levin and Bridges 1995; Kinlan and Gaines 2003). Often, the larval period is the only opportunity for long-distance dispersal among populations and habitats. Survival and dispersal during this period contribute to spatial patterns in demography, genetic connectivity, and biogeography of marine invertebrates (Shanks et al. 2003; Siegel et al. 2003; Kinlan et al. 2005), and is critical to assessments of the potential effectiveness of conservation measures such as marine protected areas (Hart 1995; Shanks et al. 2003; Lester and Ruttenberg 2005; Laurel and Bradbury 2006).

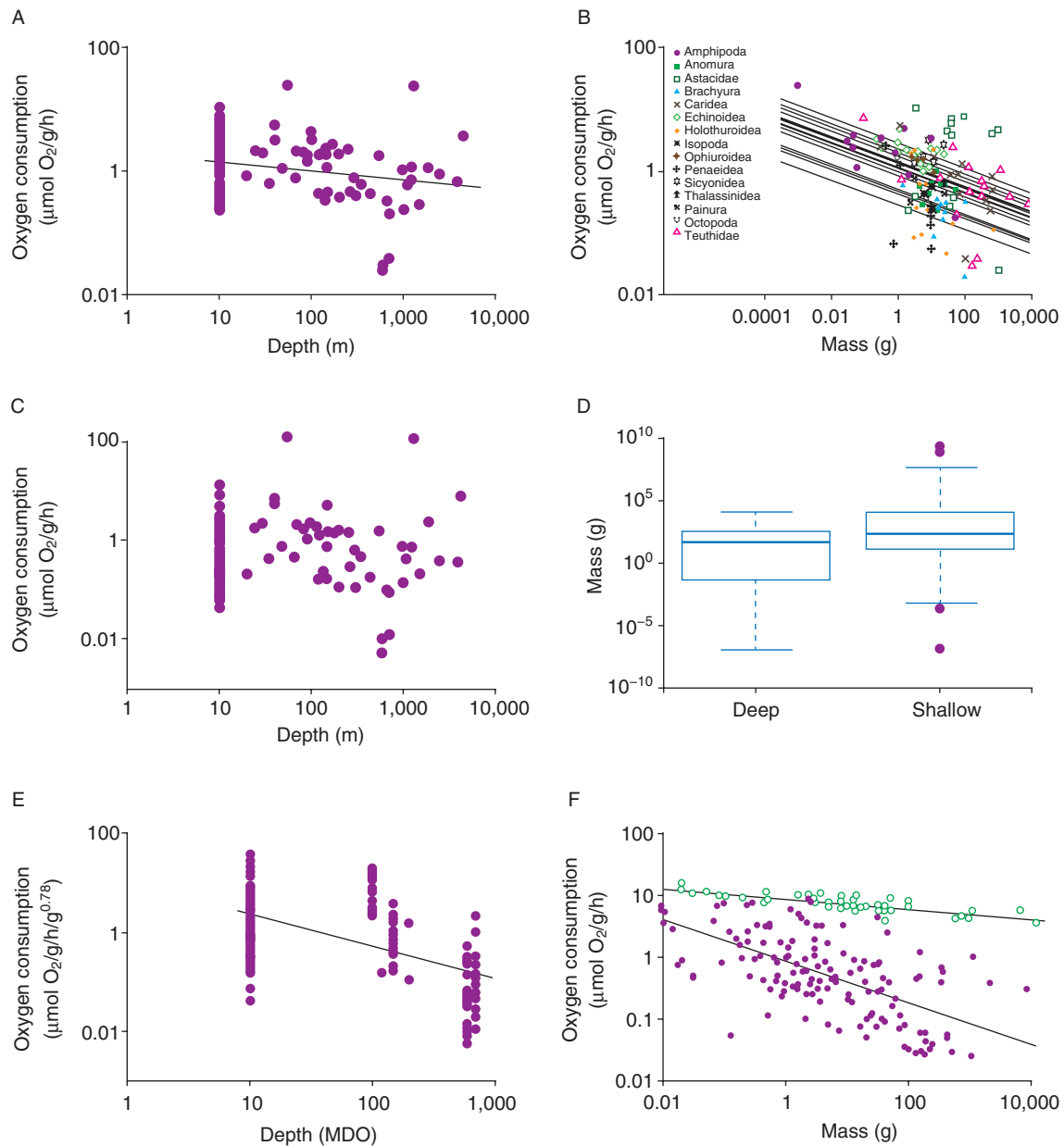


Figure 15.1 Across marine invertebrate species ($n = 145$), resting metabolic rate varies with body size and temperature (data replotted and reanalyzed from Seibel and Drazen 2007). (A) Temperature-corrected oxygen consumption rate declines with depth (minimum depth of occurrence) across a broad taxonomic group of in marine invertebrates (slope = -0.13 , $p = 0.03$, $r^2 = 0.05$). (B) Temperature-corrected, mass-specific oxygen consumption rate declines with body mass within 14 taxonomic orders of marine invertebrates (slope = -0.31 within taxonomic order, and intercepts vary among orders). (C) After correcting for body size, oxygen consumption rate does not decline with depth across entire dataset. (D) The sample of deep-sea animals in this dataset suggests smaller size in deep water ($p = 0.01$). (E) Even after controlling for effects of size and temperature, metabolic rate declines with depth (minimum depth of occurrence) among cephalopods ($p < 0.001$). (F) Temperature-corrected, mass specific metabolic rate declines with increasing size more strongly for cephalopods that are not visual predators (filled symbols, slope = -0.33 , $p < 0.001$) than for visual predators in surface waters (open symbols, slope = -0.08 , $p < 0.001$).

15.4.1 Temperature dependence of a critical demographic life stage links metabolic ecology at the individual level to community-level processes

The egg and larval development periods are highly sensitive to temperature. For offspring collected from a single population, development occurs faster and the

larval period is shorter in warmer water (O'Connor et al. 2007). The near exponential effect of temperature within a non-stressful range is well known, but a comparison of the scaling effect of temperature across a diverse set of species that spanned six phyla showed that the temperature dependence of larval duration is highly consistent with predictions from MTE (Hirst and Lopez-Urrutia 2006; O'Connor et al. 2007) (Fig. 15.2).

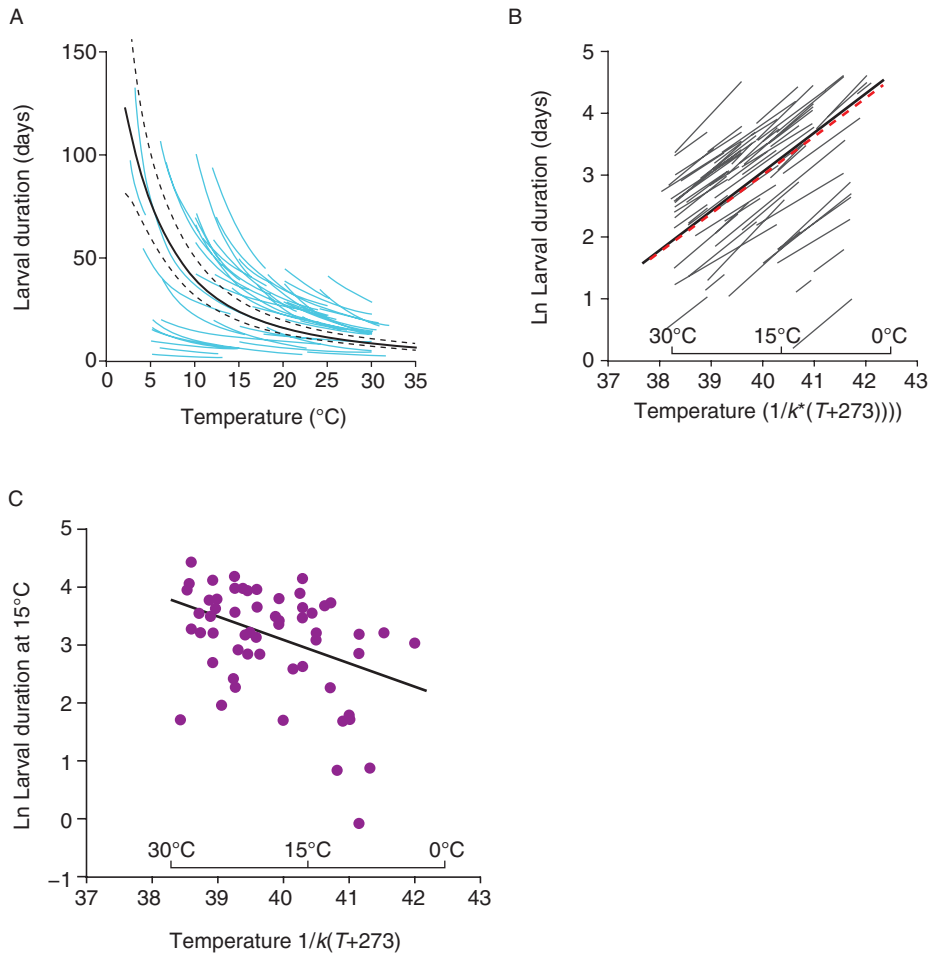


Figure 15.2 Planktonic larval duration (the inverse of development rate) is strongly and consistently affected by temperature. (A) Blue lines represent curves fit to data on individual species, and the black line is the population averaged trajectory and 95% confidence intervals (O'Connor et al. 2007). (B) Data in A replotted on Arrhenius axes (warmer temperatures to the left) and statistical model (black line) compared with MTE prediction of a slope of 0.62 eV ($p < 0.001$, red dashed line). At a single temperature, there is still variation among species (e.g., variation among blue lines at 15°C in (A)). (C) When larval duration is normalized to 15°C for each species, there is a much weaker relationship between temperature and the normalized larval duration (slope = -0.40 , $p < 0.001$). Points in (C) reflect larval duration at 15°C for each species in (A). All data from O'Connor et al. (2007).

The generality of the effect of warming on larval duration implies potentially predictable effects of temperature on processes that scale with larval duration, including adaptation, dispersal distance, survival, and population connectivity for benthic marine invertebrates and fish (Hirst and Lopez-Urrutia 2006; Duarte 2007; O'Connor et al. 2007; Munday et al. 2009; Cheung et al. 2010).

Evolution and connectivity depend on the success of dispersing larvae, and their rates of survival and settlement. Larval settlement success depends on the probability that a larva released from a certain point (e.g., a benthic parent population) will settle at any other point. Settlement probability depends on dispersal distance and can be represented as a dispersal kernel (Fig. 15.3A). Predictable variation in dispersal

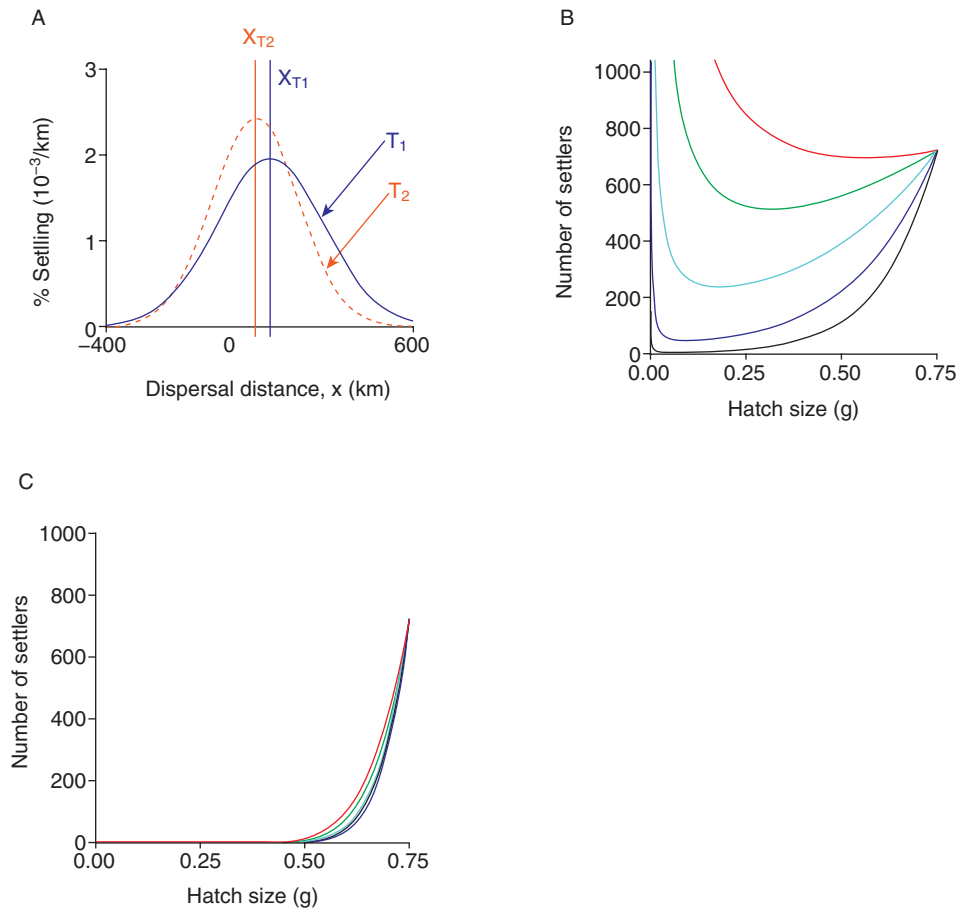


Figure 15.3 (A) A dispersal kernel representing the probability of larvae settling along a coastline (x -axis). Larvae were released from a parental population at 0 on the x -axis, and this model assumes directional alongshore currents with cross-shore transport and random diffusion (Siegel et al. 2003). Kernels are compared for two temperatures (a cool temperature T_1 in blue, and a warmer temperature $T_2 = T_1 + 2^\circ\text{C}$, in red). The only difference between the kernels is the effect of temperature on planktonic larval dispersal, shown in Figure 2A. (B) Results of a temperature-dependent optimal hatch size model that assumes a trade-off between offspring size and number, and predicts optimal size in terms of the number of settlers (Kiflawi 2006). At warmer temperatures (red line), producing larvae that hatch at smaller sizes will produce the highest number of settlers. At cooler temperatures (blue and black lines), producing larger hatchlings results in the most settlers. In this model, development scales with size as $b = -0.25$, while mortality is independent of temperature and size. (C) When mortality is negatively size-dependent and positively temperature-dependent, the effect of temperature on number of settlers is eliminated in the model, and large larvae result in the most settlers at all temperatures.

with temperature might translate to quantifiable change in the probability of settlement at a particular site. In the case of a coastline with directional flow, cross-shore transport and eddies, the duration of larval development in the plankton influences the mean dispersal distance, the variance about the mean, and the survival of larvae (Fig. 15.3) (Siegel et al. 2003). By changing the development period, a small change in temperature alone could shift the dispersal kernel, therefore affecting both short- and long-distance dispersal and the associated demographic processes of population connectivity and gene flow (Kinlan et al. 2005; O'Connor et al. 2007; Munday et al. 2009). If unmodified by ecological or evolutionary processes (see section 15.4.2), temperature scaling of planktonic larval duration could lead to broader dispersal kernels in colder climates, or narrower kernels with ocean warming (Fig. 15.3A). Greater population connectivity and reduced community dispersal limitation at higher latitudes are also consistent with broader dispersal kernels in colder regions (Witman et al. 2004; Etter et al. 2005).

15.4.2 The effect of temperature on metabolic processes is generally stronger at colder temperatures

Stronger effects of a change in temperature at colder temperatures (Fig. 15.2A) suggest geographic variation in the ecological effects of temperature. At warmer temperatures (above 15–20 °C), the temperature constraint on planktonic larval duration effectively disappears for many taxa, because the nonlinear temperature-dependence relationship is nearly flat (Fig. 15.2A, temperature above approximately 25 °C).

15.4.3 The general pattern of within-species scaling of development time does not imply a pattern among species

Most tests of metabolic theory have examined patterns across species, where one datum in the analysis represents the rate and body size or temperature of an entire species (e.g., Gillooly et al. 2001; Savage et al. 2004a; Hirst and Lopez-Urrutia 2006). In contrast, the general pattern of temperature scaling of planktonic larval development is seen most clearly within species, and this effect is shared among species (Fig. 15.2A,B).

When examined among species, however, the slope of the relationship between planktonic development period and temperature is much shallower (Fig. 15.2C). Hirst and Lopez-Urrutia (2006) found even shallower slopes of $E = -0.074$ to -0.127 for planktonic egg development times.

One explanation for the absence of a strong trend among species is evolutionary compensation. The slow development rates at extremely cold temperatures would require such long larval durations that cumulative mortality could be unsustainable (Hirst and Lopez-Urrutia 2006; O'Connor et al. 2007), and could select for traits that would reduce the *planktonic* larval duration (Emlet et al. 1987). Direct reduction of development rate is constrained by extremely limited options for the fundamental biochemical components of metabolism (Gillooly et al. 2002). Instead, shorter development times can be achieved by life-history strategies that produce larvae provisioned with greater nutritional stores, or by altering traits such as size at hatch relative to size at settlement or metamorphosis, or by protecting offspring (Havenhand 1993; Charnov and Gillooly 2004; Hirst and Lopez-Urrutia 2006). Such traits are consistent with increased parental investment per offspring.

The hypothesis that selection should favor increased parental investment per offspring in very cold climates, and that this could eliminate a temperature-driven latitudinal trend in absolute development time, rests on the premise that there is a trade-off between offspring size and number if the total allocation to reproduction is not increased; larger eggs or larvae require more nutritional resources and therefore come at a predictable cost to the parent in terms of number of offspring (fecundity) (Lack 1954; Smith and Fretwell 1974; Emlet et al. 1987). In many taxa, increased offspring mortality shifts the balance of this trade-off toward increased parental investment and lower fecundity (Vance 1973; Kolding and Fenchel 1981). Therefore, producing fewer, larger offspring may be favorable at cold temperatures (Pearse et al. 1991; Yampolsky and Scheiner 1996). Indeed, for numerous marine invertebrate taxa, parental investment per offspring increases with latitude. Eggs and larvae in cold water tend to be larger, better provisioned, or partially or completely brooded (Thorson 1950; Mileikovskiy 1971; Pearse et al. 1991; Clarke 1992; Laptikhovskiy 2006), all minimizing the planktonic period.

The hypothesis that compensation for mortality during the planktonic stage selects for traits that minimize larval duration demands a reason for why

selection would not favor such traits at all temperatures. Two factors suggest that the fitness gain of increased investment per offspring at the expense of offspring number can be beneficial at cold temperatures and not at warm temperatures. First, the nonlinear effect of temperature results in a weak effect of a change in temperature on development in warm climates, but a strong effect in cold climates (Fig. 15.2A). In warm ocean regions, temperature only weakly constrains development rate or related traits reflecting parental investment. Second, through an analysis of an optimal size model, Kiflawi (2006) showed that when planktonic larval duration scales with temperature according to MTE, the optimal larval size is large at cold temperatures and small at warm temperatures (Fig. 15.3B). Therefore, if the temperature constraint were the most important factor determining larval hatch size, in cold water each parent should release a few, large offspring that reach their settlement size quickly and spend a short time in the plankton, while at warm temperatures numerous, small hatching larvae would be more common because development times are faster (Fig. 15.3B). This model suggests that the negligible fitness benefit of increased larval hatch size to shorten the larval duration is likely not worth the cost of increased investment in warmer climates, and small offspring sizes should be most common at all temperatures except the coldest temperatures (Fig. 15.3B). Latitudinal patterns in larval and egg size within several closely related taxa are consistent with this model (Thorson 1950; Mileikovsky 1971; Pearse et al. 1991; Clarke 1992; Laptikhovsky 2006).

Kiflawi (2006) also showed that when larval mortality rates are size- and temperature-dependent, the effect of temperature on optimal hatch size is nullified (Fig. 15.3C). So, stronger predation in warmer water (Seibel and Drazen 2007) could impose a much stronger selection on larval traits than temperature constraints on development time. At warm temperatures when development is fast, larger larvae may be more likely to escape predation, and survival conferred by this size escape may outweigh the fecundity cost of increased parental investment. This prediction is consistent with comprehensive reviews of invertebrate egg size distributions (Levitán 2000; Collin 2003). Thus, a life-history model that incorporates metabolic theory predicts that the ecological factors influencing selection on larval size shift from temperature in high latitudes to predation or food availability in warmer environments (i.e., lower latitudes).

In summary, comparison of within- and among-species trends in how temperature affects development time illustrates that applying the metabolic theory of ecology to biogeographic patterns is not necessarily a straightforward endeavor. Similar findings have emerged from tests of latitudinal variation in primary production in terrestrial plant communities (Kerkhoff et al. 2005; Enquist et al. 2007a), where it appears that adaptation and acclimatization of plant physiological processes compensate for shorter growing seasons and lower temperatures to elevate annual primary production and eliminate any trend toward lower primary production in colder climates. For marine invertebrates, strong temperature-dependence of planktonic larval duration implies predictable effects of changes in temperature, on ecological timescales, on processes that scale with development. Over evolutionary timescales, adaptation of traits related to dispersal and survival during the planktonic period may compensate for the underlying metabolic scaling of development rate. Metabolic theory therefore provides a conceptual framework for uniting short- and long-term metabolic effects of temperature on population and community ecology.

15.5 MOVING FORWARD: A NEW GENERATION OF MARINE METABOLIC ECOLOGY IN A TIME OF GLOBAL CHANGE

Metabolic theory can inform population- and community-level patterns when metabolism is tightly related to a demographically critical rate, such as a larval development rate. The strategy of identifying critical rates and exploring their temperature dependence has been applied to herbivory as well (O'Connor 2009). A stronger general temperature dependence of herbivores (zooplankton and heterotrophic protists) relative to primary producers (phytoplankton) drives shifts in the structure and carbon cycling of pelagic planktonic food webs (Lopez-Urrutia et al. 2006; O'Connor et al. 2009). A similar approach in other systems could quite likely provide additional insights into how temperature affects complex ecological processes and the resulting patterns.

Scaling of metabolic rate with temperature implies predictable responses to ocean change associated with climate change. But to understand impacts of climate change, metabolic scaling theory will need to be integrated with another major theme in marine metabolic

ecology—the ecology of physiological stress. Differences among interacting species in their tolerance of temperature change can strongly influence species distribution, interactions, and food webs (Harley 2003; Gilman et al. 2006; Gooding et al. 2009; Kordas et al. 2011). Through a combined approach, general effects of scaling with temperature can be related to species-dependent responses to temperature change, such as range shifts (e.g., Cheung et al. 2010).

As environmental temperature regimes change with global climate change, we must marshal our best ecological and evolutionary theory to anticipate how eco-

logical systems will respond. The scaling models of the metabolic theory of ecology explain substantial variation within and among ecological communities with variation in temperature. Patterns not directly explained by metabolic scaling with temperature, such as trends in metabolic rate with pelagic cephalopods or offspring size in marine larvae, might be explained by integrating evolutionary theory with scaling theory. Such a united theory would provide a powerful approach to understanding the ecological consequences of abiotic environmental change for populations and communities.