

# Evolutionary Adaptation of Marine Zooplankton to Global Change

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## Keywords

reaction norm, phenotypic plasticity, harmful algal blooms, hypoxia, climate change, evolutionary rate

## Abstract

Predicting the response of the biota to global change remains a formidable endeavor. Zooplankton face challenges related to global warming, ocean acidification, the proliferation of toxic algal blooms, and increasing pollution, eutrophication, and hypoxia. They can respond to these changes by phenotypic plasticity or genetic adaptation. Using the concept of the evolution of reaction norms, I address how adaptive responses can be unequivocally discerned from phenotypic plasticity. To date, relatively few zooplankton studies have been designed for such a purpose. As case studies, I review the evidence for zooplankton adaptation to toxic algal blooms, hypoxia, and climate change. Predicting the response of zooplankton to global change requires new information to determine (*a*) the trade-offs and costs of adaptation, (*b*) the rates of evolution versus environmental change, (*c*) the consequences of adaptation to stochastic or cyclic (toxic algal blooms, coastal hypoxia) versus directional (temperature, acidification, open ocean hypoxia) environmental change, and (*d*) the interaction of selective pressures, and evolutionary and ecological processes, in promoting or hindering adaptation.

## 1. INTRODUCTION

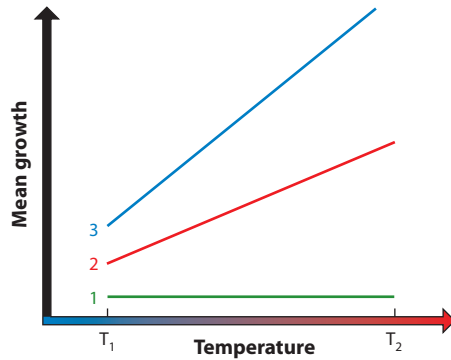
Among the major challenges for ocean scientists are understanding and predicting the response of the oceanic biota to global change. Some global change problems relevant to ocean biota include warming (Intergov. Panel Clim. Change 2007), ocean acidification (Doney et al. 2009), and the proliferation of harmful algal blooms (Hallegraeff 1993) as well as increasing pollution, eutrophication, and hypoxia (Cloern 2001, Breitbart et al. 2009, Rabalais et al. 2010). Zooplankton can respond to global change phenotypically (with alterations in their physiology or behavior) or evolutionarily (with a shifting genetic composition of populations). Here I argue that achieving the goals of understanding and predicting the response of zooplankton to global change requires that we pay more attention to evolutionary processes, particularly adaptation. Although recognition of the importance of adaptation is slowly growing, it has been relatively ignored in oceanographic studies (Sanford & Kelly 2011).

Because the variables associated with these global change problems—temperature, pH, toxins, pollutants, food quantity and quality, and dissolved oxygen—have the potential to affect organismal fitness either individually or in interactions with one another, they may be viewed as evolutionary selection pressures. Moreover, they vary in both time and space, creating selection gradients. Populations within a species also show genetic variability in their responses to selection pressures even if they all experience the same environment (Angilleta 2009). The combination of selection gradients and genetic variability among populations provides the necessary conditions for differential fitness among genotypes in a species. Thus, provided that traits are heritable, we should expect that local adaptation—via natural selection—should become manifest. Of course, natural selection may be overwhelmed by an influx of nonadapted genotypes, particularly in species with high levels of dispersal such as zooplankton. However, there is mounting evidence of considerable local adaptation in marine populations, especially in those with planktonic dispersal, despite the assumed high connectivity among populations in the ocean (Sanford & Kelly 2011). Therefore, adaptation cannot be outright ignored as an important response of the biota to global change.

Zooplankton are not just intellectual curiosities. The pivotal role of zooplankton in food webs (Banse 1995, Dam et al. 1995, Landry et al. 1997) makes their adaptive responses important to the entire ecosystem—up to fish and other consumers as well as down to phytoplankton and other prey. Zooplankton are also important in the biogeochemical cycles in the oceans (Longhurst et al. 1990, Longhurst 1991). In addition, zooplankton are excellent model organisms for studies of the responses of animals to global change because they have short generation times (typically weeks to months), making them amenable to rapid evolutionary change (Hairston et al. 1999). Many zooplankton species are also suitable for experimental manipulation in studies of adaptation (Lonsdale & Levinton 1985, Lee et al. 2003, Colin & Dam 2004). This review deals only with holoplanktonic taxa that can be cultured in the laboratory, for reasons that become evident in Section 2.

Recent reviews by Somero (2010, 2011, 2012) elegantly made the case for using the comparative physiology approach to provide a mechanistic understanding of adaptation at the organismal level, and addressed the strengths and limitations of this approach for understanding and predicting the responses of the biota to global change. The approach in this review is different and grounded in evolutionary ecology. Adaptation is viewed through the lens of the evolution of reaction norms—an approach that has a long and distinguished history (Schlichting & Pigliucci 1998, Angilleta 2009) but may not be familiar to most oceanographers. Thus, a modest goal of this review is to introduce (or perhaps reacquaint) oceanographers with this approach.

Global change is a multifaceted term, and by necessity I cover only a few issues. Those interested in the evolution of salinity tolerance in zooplankton can consult the work of Lee et al. (2003). A



**Figure 1**

Hypothetical reaction norms (also called performance curves) for the mean growth rates of three genotypes in a population. The slopes of the lines indicate the strength of phenotypic plasticity. The fact that the lines have different elevations indicates that there is a genetic component to plasticity. The differences in slope reveal gene-environment interactions that represent the genetic variation for phenotypic plasticity, which is necessary for the evolution of the reaction norms.

much-talked-about topic these days is ocean acidification, which I do not cover for two reasons. First, the effects of ocean acidification on marine zooplankton have been reviewed elsewhere (Fabry et al. 2008, Kurihara 2008). Second, and more important, I could not find any studies that actually attempted to test for the evolution of the CO<sub>2</sub> reaction norm in zooplankton populations.

In this review, I outline phenotypic and adaptive responses and how to experimentally discern one from the other. I briefly discuss why adaptation matters to predictions of the response of zooplankton to global change. As case studies, I summarize the evidence for zooplankton adaptation to toxic algal blooms, hypoxia, and climate change and the implications of adaptation for understanding and predicting the response of zooplankton to their changing environments. Finally, I outline some outstanding issues for zooplankton adaptation research and global change.

## 2. PHENOTYPIC PLASTICITY AND ADAPTATION

The response of a genotype across a range of environments, known as the reaction norm (**Figure 1**), is depicted by a plot of a phenotypic variable across two or more environments (Schlichting & Pigliucci 1998).<sup>1</sup> The environment in this case is either an abiotic variable (e.g., temperature, dissolved oxygen) or a biotic one (food concentration, toxic versus nontoxic prey). The total variance in a phenotypic variable,  $V_P$  (e.g., a life history trait such as body size or fecundity, or a physiological function such as ingestion or respiration rate), can be partitioned as  $V_P = V_G + V_E + V_{G \times E} + error$  (Falconer & Mackay 1996). The terms on the right side of the equation represent the proportions of total phenotypic variance ( $V_P$ ) attributable to genes ( $V_G$ ), the environment ( $V_E$ ), the interaction of genes and the environment ( $V_{G \times E}$ ), and unexplained variation (*error*) arising from measurement error, environmental noise, etc.

Phenotypic plasticity occurs when a genotype gives rise to different phenotypes in different environments (Pigliucci 2001, Whitman & Agrawal 2009). Phenotypic plasticity is easily visualized in a reaction norm. **Figure 1** depicts the hypothetical mean-growth-rate responses of three

<sup>1</sup>Here, I use the terms reaction norm and performance curve as synonyms. There are subtle differences between the two terms (Kingsolver et al. 2004), but the same quantitative genetic framework outlined here applies to both.

genotypes to temperature. Because the growth of genotype 1 is independent of temperature, this genotype displays no phenotypic plasticity. Plasticity in phenotype 2 is less than that in phenotype 3, and therefore the slope of its reaction norm is less steep (Angilleta 2009). The different growth rates among genotypes at a given temperature reveal  $V_G$ , the changes in the mean growth rates of genotypes 2 and 3 as temperature varies reveal  $V_E$ , and the different slopes of the reaction norms among genotypes reveal  $V_{G \times E}$ . This last term is important because it represents the genetic variation for genotypic plasticity (Roff 1997) and hence the potential evolution of the reaction norm for a population; that is, the effect of natural selection on genotypes can alter the shape and variance of the reaction norm in a population (see Angilleta 2009, Whitman & Agrawal 2009).

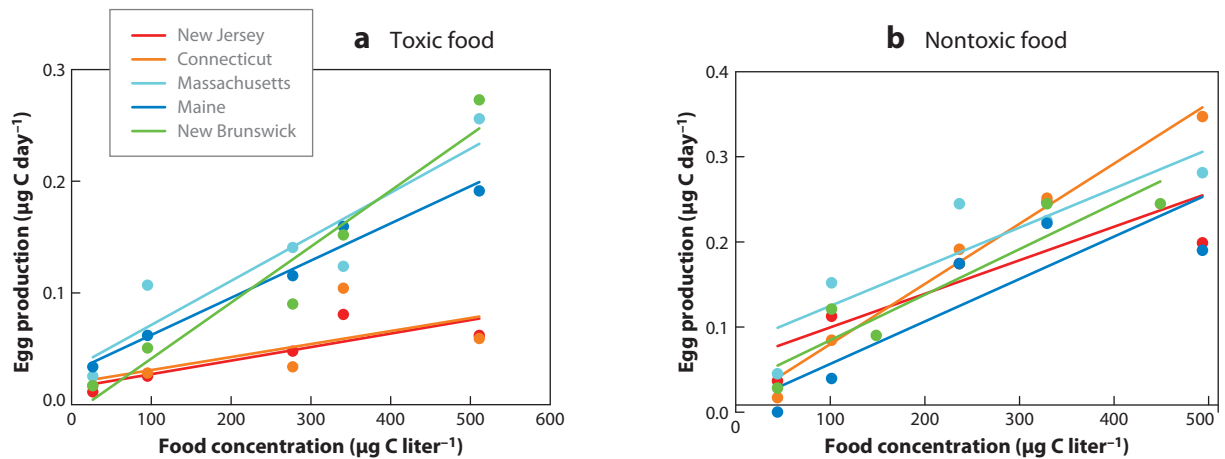
Significant gene-environment interactions for traits important to fitness have been demonstrated in marine zooplankton (Bradley & Ketzner 1982, Bradley 1986, Lee & Petersen 2002, Avery 2005). Of course, for the reaction norm to evolve, the phenotypic variable must be heritable. Properly designed experiments for the study of phenotypic plasticity also allow the quantification of heritability in phenotypic variables, or the fraction of the total phenotypic variability attributable to genes (Roff 1997). Heritable life history traits in marine zooplankton have been documented in relation to temperature (copepods; McLaren 1976, Bradley & Ketzner 1982, Bradley 1986, Avery 2005) and  $\text{CO}_2$  (echinoderm larvae; Sunday et al. 2011b).

Adaptation can be separated from phenotypic plasticity by comparing the reaction norms of different populations (Schlichting & Pigliucci 1998). Kawecki & Ebert (2004) reviewed the different approaches and their drawbacks as well as the requirements for rigorous experimental design in detecting local adaptation. In planktonic organisms, the typical approach is to use common garden experiments (Lonsdale & Levinton 1985; Boersma et al. 1999; Hairston et al. 1999, 2001; Colin & Dam 2002, 2004; Decker et al. 2003; Lee et al. 2003). Sanford & Kelly (2011) also recently reviewed the use of common garden experiments to study local adaptation in marine invertebrates.

Recall that  $V_P = V_G + V_E + V_{G \times E} + \text{error}$ . In properly designed common garden experiments, populations that come from environments that putatively experience differential selective pressures are brought to the laboratory and kept in large numbers (> 500 individuals) under the same conditions for at least two generations. Using large numbers of individuals minimizes genetic drift, and raising the populations in the same environment for several generations ensures that residual effects—such as maternal effects—from their source locations are removed or minimized (Falconer & Mackay 1996). Phenotypic variables that are correlated with fitness—survival, fecundity, developmental rate, etc.—are then compared in the same environment. Under the common environment condition,  $V_E$  is zero and hence  $V_{G \times E}$  must also be zero. Therefore, differences in the reaction norms among populations are assumed to be genetic. Furthermore, these differences are interpreted as evolution of the reaction norms (Angilleta 2009)—i.e., local adaptation (**Figure 2**). Common garden experiments have been used to demonstrate the adaptation of marine zooplankton to several environmental variables relevant to global change (**Table 1**).

Common garden experiments can also be used to document the local adaptation of zooplankton populations separated in time rather than space. The existence of diapause eggs that survive in sediments for decades to centuries (Hairston et al. 1999, 2001; Angeller 2007) makes this possible. In this approach, reaction norms are compared among populations that have originated from diapause eggs that were deposited in a system at different times. The approach has been used to demonstrate the evolution of cyanobacteria toxin tolerance (Hairston et al. 1999, 2001) and acid tolerance (Derry et al. 2010) in lakes, and could well be used in coastal environments because dormant zooplankton eggs are also found in the ocean (Marcus 1996).

A third approach, artificial selection experiments in the laboratory, can test for the potential for phenotypic variables to evolve. Laboratory selection experiments have shown the potential evolution of zooplankton life history traits as a function of temperature (Bradley & Ketzner 1982),



**Figure 2**

Reaction norms (also called performance curves) for populations of the copepod *Acartia budsonica* from the east coast of North America that were challenged with a diet of (a) the toxic dinoflagellate *Alexandrium fundyense* and (b) the nontoxic green flagellate *Tetraselmis* sp. The reaction norms are from common garden experiments in which populations were raised under the same conditions for several generations before the experiments were performed. The New Jersey and Connecticut populations either never or rarely experienced blooms of toxic *Alexandrium fundyense*, whereas the other three often did. The slopes of the regressions are not significantly different for the nontoxic diet. The slopes of the New Jersey and Connecticut populations are not different from each other but are significantly lower than those of the three other populations. The difference in slopes between these two groups represents the evolution of the reaction norms underlain by adaptation to toxic algae. Adapted from Colin & Dam (2007).

phytoplankton toxins (Colin & Dam 2004), and heavy metals (Tsui & Wang 2005, Medina et al. 2008, Kwow et al. 2012).

In summary, both phenotypic plasticity and adaptation are important mechanisms for organisms to cope with changes in the environment. The former can be viewed as changes in the reaction norms of populations within generations, and the latter as the changes between

**Table 1 Common garden experiments showing the adaptation of marine zooplankton to variables relevant to global change problems**

Species	Selective pressure	Trait(s) under selection	Reference(s)
<i>Scottolana canadensis</i>	Temperature	Development, body size, growth	Lonsdale & Levinton 1985
<i>Tigriopus californicus</i>	Temperature	Survival	Willet 2010
<i>Acartia budsonica</i>	Phytoplankton toxins	Ingestion, egg production	Colin & Dam 2002, 2007; Zheng et al. 2011
<i>Acartia budsonica</i>	Phytoplankton toxins	Development, survival, egg production	Colin & Dam 2004
<i>Acartia tonsa</i>	Phytoplankton toxins	Egg production	Jiang et al. 2011
<i>Acartia tonsa</i>	Hypoxia	Behavioral avoidance of hypoxic environment	Decker et al. 2003
<i>Eurytemora affinis</i>	Salinity	Salinity tolerance, survival, development	Lee et al. 2003

To remove maternal and other residual effects, all experiments were carried out after populations to be compared had been raised in the same environment for at least two generations.

generations (Whitman & Agrawal 2009). The heritable genetic component of phenotypic plasticity provides the conditions for adaptation. Well-established experimental approaches exist to distinguish phenotypic plasticity from adaptation.

### 3. ADAPTATION: TRADE-OFFS, COSTS, AND CURRENCY

A trade-off arises when a genotype cannot have maximal fitness in two environments (Fry 2003). Thus, a fitness improvement in one environment comes with a fitness loss in another. As a consequence, trade-offs result in negative correlation between traits—e.g., reproduction versus survival—in one environment (Stearns 1989). Organisms adapt to stress by either avoiding (resistance) or dealing with (tolerance) the negative effects of stress (Råberg et al. 2009). Both mechanisms involve expenditures for the organism and thus can incur fitness costs. A cost to adaptation is evident if there is a fitness penalty when the selective pressure is relaxed (Sibly & Calow 1986).

Here I define fitness in terms of the net reproductive rate  $N_{\tau}/N_0$ , where  $N$  is the number of individuals in a genotype, phenotype, or population and the subscripts  $\tau$  and  $0$  represent generation time and time zero, respectively. Therefore, fitness is a function of lifetime fecundity and survival (Roff 1997). Most studies of adaptation do not actually measure fitness, but rather measure correlates of fitness such as fecundity, survival, development rate, or somatic growth. However, because of the possibility of trade-offs, the evolution of a trait does not automatically equate to a fitness advantage. I discuss trade-offs further in the Section 5 case studies.

### 4. WHY ADAPTATION MATTERS

Recent reviews of the relationship between zooplankton and climate change, to choose one example, have emphasized responses in species distribution and phenology (Hays et al. 2005, Richardson 2008, Ji et al. 2010). These reviews implicitly espouse an ecological perspective, that is, one in which the responses of species to changes in temperature in their habitat are interpreted as reflecting changes in physiological rates, phenotypic plasticity, and migration. An alternate perspective is evolutionary, that is, one in which genetic changes in the population take place in response to a selective pressure and local adaptation ensues. For example, because the physiological and life history traits of ectotherms are strongly dependent on temperature, zooplankton in low-temperature habitats are expected to have reductions in life history traits—somatic growth, development time, and fecundity—and consequently a net reduction in fitness. Yet it is well established for all kinds of ectotherms that individuals from colder climates can grow as rapidly as those from warmer climates (Pörtner et al. 2006, Yamahira et al. 2007). This latitudinal or temperature compensation is interpreted as local adaptation.

The evolutionary responses of the biota to climate change are gaining recognition (Parmesan 2006). Calls have been made for future studies of the biota and climate change to (a) incorporate the ability of populations to adapt (Harley et al. 2006) and (b) discern the relative roles of ecological and evolutionary processes in determining the phenology and life history traits of populations (Gienapp et al. 2008, Ji et al. 2010). Some have even argued that the three main outcomes of the responses of the biota to climate change—persistence in situ if the changing climate remains within the species' tolerance limits, range shifts (migration) to regions where the climate is currently within the species' tolerance limits, and extinction—all involve evolutionary processes (Davis et al. 2005). In contrast, others have concluded that many responses perceived as adaptations to changing environmental conditions could be environmentally induced plastic responses rather than microevolutionary adaptations (Gienapp et al. 2008). Determining whether a response results from phenotypic plasticity or adaptation is important because the responses of species and

populations to climate change will be constrained by the particular mechanism at play (Chown et al. 2010, Sanford & Kelly 2011, Somero 2012). Essentially, phenotypic plasticity allows populations to deal with short-term environmental variation, and adaptation does the same for longer timescales.

Let us now consider some consequences of ignoring evolution in predicting the response of zooplankton to climate change. Current attempts at prediction combine coupled population–physical models with output from climate models under future temperature regimes (reviewed in Richardson 2008, Stegert et al. 2010). This approach does not consider genetic variation within a species (let alone a population) and assumes that the thermal reaction norm (say, growth versus temperature) does not evolve. Both of these implicit assumptions are in all likelihood incorrect: Evolution of the reaction norm could well increase the thermal optimum and thermal limit of the population (Angilletta 2009). Thus, by failing to account for adaptation, the current models would underpredict the growth rate in a warming environment. I discuss several other implications of thermal adaptation for our understanding and prediction of zooplankton response to climate change in Section 5.3.

Another example illustrates the importance of adaptation. Grazer populations with a history of exposure to toxic algal blooms have significantly higher fitness when challenged with toxic prey than those with little or no history of exposure (Colin & Dam 2002, 2004; Bricelj et al. 2005), demonstrating local adaptation. The consequences of such adaptation can be positive. For example, copepod populations adapted to toxic algae have the potential to keep toxic algal blooms in check (Colin & Dam 2007) and do not necessarily accumulate more toxins in their bodies (Dam & Haley 2011). However, the consequences can also be detrimental. Bivalve populations adapted to toxic algae accumulate much greater quantities of toxins in their bodies (Bricelj et al. 2005), potentially serving as strong vectors for toxin transfer up the food web.

Adaptation to rising temperatures and toxic algae are but two examples of the importance of zooplankton adaptive responses to global change problems. The former illustrates the need to consider adaptation when forecasting population behavior; the latter shows how adaptation modulates predator–prey interactions and toxin transfer. In the following section, I discuss the adaptive responses of zooplankton to some global change problems. I also outline the evidence for adaptation and the consequences of such adaptation for predicting the future responses of zooplankton.

## 5. CASE STUDIES

### 5.1. Toxic Algal Blooms

Several phytoplankton taxa, particularly dinoflagellates, produce toxins that negatively affect the physiological functions of grazers (Turner & Tester 1997). Many toxin-producing phytoplankton taxa have proliferated in distribution and abundance in the past half century (Hallegraeff 1993). Areas that not long ago had not experienced these blooms now do. Moreover, there are strong differences in the geographical distribution of these blooms, their frequency, and their intensity (e.g., Anderson 1997). Thus, for zooplankton, blooms of phytoplankton-producing toxins represent selection gradients in both time and space. Incidentally, similar temporal and spatial gradients for a different kind of toxin, heavy metals, should be expected as a result of industrialization. However, in the remainder of the discussion I deal only with phytoplankton toxins.

The evolution of grazer adaptation to phytoplankton toxins is now well established in both the ocean (Colin & Dam 2002, 2004, 2007; Jiang et al. 2011; Zheng et al. 2011) and freshwater (Hairston et al. 1999, 2001; Sarnelle & Wilson 2005). The pattern is similar in all cases:

Populations with a longer history of exposure to toxic algae have enhanced performance when challenged with toxic algae relative to those populations that have little or no exposure history—that is, naïve populations (**Figure 2**). The key point in **Figure 2** is that the reaction norms differ among populations only in the presence of toxic algae. For the toxic diet, the slopes of the reaction norms for populations with a history of toxin exposure are significantly higher than those for populations with no history of exposure; for the nontoxic diet, in contrast, there are no significant differences in the slopes. Had the pattern for both diets been similar, it could be argued that because the populations were sampled along a latitudinal (temperature) gradient, the measured response arose from countergradient variation (Conover & Schultz 1995), reflecting temperature compensation. Another line of evidence that supports the adaptation hypothesis is that animals from naïve populations failed to acclimatize to toxic algae (Colin & Dam 2002, figure 7). Altogether, the inference that the reaction norms have evolved owing to selective pressure exerted by algae is strong.

The reaction norms for ingestion also evolve in response to toxic algae, following a pattern similar to that of egg production (Colin & Dam 2007). Using a simple population dynamics model in which the grazing rate was parameterized with data from the reaction norms of the different populations, Colin & Dam (2007) showed that, on scales relevant to bloom duration, adapted zooplankton populations could keep toxic algal blooms in check but naïve ones could not. Another interesting outcome of adaptation is relevant to toxin transfer in the food web. Again using common garden experiments, Dam & Haley (2011) compared toxin uptake accumulation and depuration between copepod populations. Despite the much higher uptake rate of the adapted population, the toxin accumulation of this population was not different from that of the naïve population. As a consequence, the adaptation of copepods to toxic algae does not necessarily imply higher toxin transfer up the food web. This is in stark contrast to bivalves that consume the same toxins; in this case, individuals from adapted populations accumulate much higher levels of toxins than those from naïve populations (Bricelj et al. 2005).

Fitness involves the product of lifetime fecundity and survival (Roff 1997). Thus, almost no studies of reaction norms actually measure fitness. One exception is the study of Colin & Dam (2004), in which the common garden experiments were done for the entire life cycles of populations with and without a history of exposure to toxic algae (the Maine and New Jersey populations in **Figure 2**, respectively). This allowed the determination of survival and fecundity, and hence the estimation of population fitness, in the presence of toxic and nontoxic food. In the Maine population, fitness (defined as  $\lambda$ , the net reproductive rate during the experiment) did not differ between diets. In the New Jersey population, in contrast, fitness was significantly lower for the toxic diet than for the control diet. It was therefore evident that the naïve population, but not the historically exposed one, paid a fitness penalty when exposed to toxic algae.

Avery & Dam (2007) documented relative costs and trade-offs in copepod fecundity phenotypes related to phytoplankton toxin adaptation. Phenotype fitness was calculated based on survival and fecundity; phenotype fitness comparisons for a nontoxic diet (selection was relaxed) revealed costs, and those for a toxic diet revealed trade-offs. In four of five phenotypes, the costs were small (<10% reduction relative to the fittest phenotype), but one phenotype had an almost 50% fitness reduction. Trade-offs were also evident. The phenotype with the highest fitness had intermediate fecundity but the highest survival; this trade-off was interpreted as a form of heterozygote advantage that would lead to a polymorphism in the population, which in turn would prevent the fixation of toxin-tolerant alleles in the natural population.

This interpretation is important for understanding the dynamics of toxic algae and grazers and the fate of toxic algal blooms. These blooms are typically either stochastic or episodic. Therefore, during blooms there is selection for toxin-tolerant phenotypes, but these phenotypes are at a



disadvantage and are culled from the population after the blooms disappear. A logical consequence of this process is that the evolutionary clock for toxin-tolerant phenotypes is partly reset after blooms wane. Additional indirect evidence for this notion is the observation of the rapid loss of toxin-tolerant phenotypes in copepod populations when selection is relaxed in the laboratory (Jiang et al. 2011). The extent to which polymorphisms are prevalent in grazer populations is unknown, but a simple prediction can be made that the degree of polymorphism is inversely proportional to the temporal and spatial scale of toxic algal blooms. In any case, polymorphisms create challenges to building mechanistic and predictive models for grazer control of toxic algal blooms and toxin transfer in the food web.

## 5.2. Hypoxia

Hypoxia is the environmental condition in which dissolved oxygen concentrations are below roughly 2 mg liter<sup>-1</sup>. Large portions of the ocean are naturally hypoxic (Kamikowski & Zentara 1990, Helly & Levin 2004), but hypoxia is also quickly increasing in other parts of the ocean (Stramman et al. 2008) and in the coastal zone (Diaz & Rosenberg 2008, Breitbart et al. 2009, Rabalais et al. 2010). As warming (Intergov. Panel Clim. Change 2007) and eutrophication (Cloern 2001)—two of the factors that promote the depletion of oxygen in the ocean interior—are also increasing, the expansion of hypoxic zones in time and space is expected.

A thorough review of the literature (Ekau et al. 2010) showed that, not surprisingly, small crustacea such as copepods and euphausiids can tolerate much lower dissolved oxygen levels than larger zooplankton such as scyphozoans and ctenophores (see Ekau et al. 2010, table 2). In most cases, hypoxia negatively affects egg production (Sedlacek & Marcus 2005), survival (Roman et al. 1993, Stalder & Marcus 1997, Invidia et al. 2004, Auel & Verheye 2007), and egg hatching (Lutz et al. 1994, Invidia et al. 2004). Therefore, hypoxia can be a selective force for zooplankton.

Indirect evidence of hypoxia adaptation is provided by the observation that zooplankton from permanent oxygen minimum zones (OMZs) are less sensitive to hypoxia than zooplankton from coastal waters, where hypoxia is more seasonal (Marcus 2001). For example, the copepod *Lucicutia grandis* shows ontogenic vertical zonation in the OMZ that correlates to physiological (low oxygen tolerance) and ecological (predation and food availability) constraints (Wishner et al. 2000). Moreover, crustaceans inhabiting the OMZ have evolved a variety of physiological adaptations to enhance oxygen uptake: enhanced ventilatory capability, large gill surfaces, short diffusion distances, and respiratory proteins with very high oxygen affinity (Childress & Seibel 1998). However, the strategy of zooplankton inhabiting the OMZ appears to be a combination of short-term anaerobic metabolism coupled with vertical migration into well-oxygenated zones to repay the oxygen debt generated while in the OMZ (Marcus 2001 and references therein).

It appears that in coastal waters, the fitness costs of anaerobic metabolism are high for zooplankton, and adaptation is behavioral rather than physiological. For example, severe summertime hypoxia is a recurrent feature in the bottom waters of Chesapeake Bay. For most of this period, copepods are not found in the bottom waters. In contrast, during episodic events of mixing when hypoxia is relaxed, maximum copepod abundance often occurs in bottom waters (Roman et al. 1993). A genetic component is evident in this habitat selection. Common garden experiments in which a population of the copepod *Acartia tonsa* from Chesapeake Bay was compared with a population from the Florida coast, where hypoxia does not occur, showed that the former avoids hypoxic waters whereas the latter does not (Decker et al. 2003). This finding is consistent with the notion of local adaptation in the Chesapeake Bay population. Avoidance of hypoxic waters by Chesapeake Bay copepods likely increases fecundity; however, it is not clear that this behavior always increases survival, as the risk of death from visual predators also likely increases. Thus,

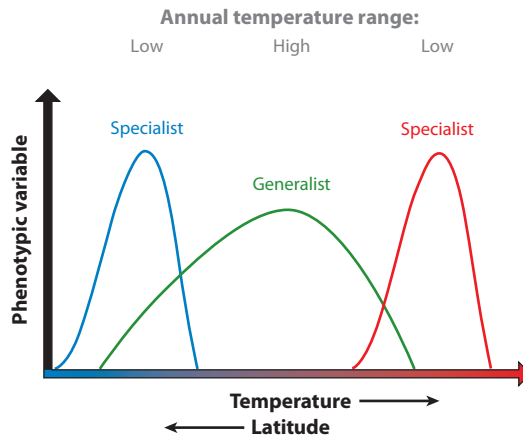
a trade-off between fecundity and survival may arise in this population. However, the trade-off cannot be such that population fitness would decrease for the population, or the behavior would not have evolved.

As in the case of toxin adaptation discussed in the previous section, the evolution of zooplankton habitat selection driven by hypoxia might involve polymorphisms owing to both trade-offs and the seasonality of coastal hypoxia. Again, an important issue is the degree of persistence of the adaptive behavior, which is a function of the strength of selection during the hypoxia season and the cost of adaptation. In areas in which selection is weak, such as those where hypoxia is sporadic, the behavior is unlikely to persist in the long term.

### 5.3. Climate Change

Zooplankton are ectotherms; hence, their physiological functions are strongly dependent on temperature (e.g., Mauchline 1998). Global increases in surface temperature of 2°C–4°C are expected within a century (Intergov. Panel Clim. Change 2007). Many questions arise from this observation: Will zooplankton thermally adapt to this directional increase in temperature? What type of adaptation will occur? How quickly can zooplankton adapt? Can adaptation keep up with the pace of temperature increase? What can keep adaptation from happening? To address these questions, I paraphrase and summarize several of the concepts presented in Angilleta's (2009) masterly textbook on thermal adaptation and apply them to zooplankton.

Will zooplankton adapt to changes in temperature? Consider the hypothetical thermal reaction norms shown in **Figure 3**. In the absence of evolution, the ability of organisms to thrive in an environment depends on whether the range of temperature they experience is within the envelope defined by the reaction norm—i.e., phenotypic plasticity. The risk of extinction increases as environmental temperatures move away from the optimum toward the tails of the reaction norm.



**Figure 3**

Hypothetical thermal reaction norms (also called performance curves) for three genotypes in the ocean. The temperature gradient is equivalent to the latitude gradient but in the opposite direction. The annual temperature range is low in tropical and polar regions but high at mid-latitudes (Clarke & Gaston 2006). The genotypes at high (e.g., tropical regions) and low (e.g., polar regions) temperatures are stenothermal, whereas the genotype at intermediate temperatures (subtropical and temperate regions) is eurythermal. The specialist-generalist trade-offs are clear, with the generalist genotype tolerating a wider range of temperatures but having lower performance at its optimum temperature.

If the reaction norm evolves in such a way that it tracks the changes in the environment, then adaptation ensues, and the risk of extinction diminishes.

In addition to the obvious latitudinal cline in temperature, we must consider several points to address whether zooplankton will adapt and, if so, how. First, the rate of temperature change is not spatially uniform. For the period 1976–2000, high latitudes in the Northern Hemisphere warmed twice as fast as the global mean; furthermore, some areas have actually cooled (Walther et al. 2002). Second, the annual range of temperature fluctuation varies dramatically with latitude: Surface waters in polar and tropical regions vary by 1°C to 3°C, whereas those in temperate regions vary by 5°C (Northern Hemisphere) to 10°C (Southern Hemisphere) (see Clarke & Gaston 2006, figure 1). The geographic clines in temperature and the mosaics in rates of warming and annual range of variation create selection gradients for zooplankton thermal adaptation. The local adaptation of marine zooplankton to temperature has been demonstrated in common garden experiments that compare the reaction norms of copepod populations from different latitudes and hence different temperatures (**Table 1**). The adaptations involve life history traits and thermal stress tolerance. Temperature compensation for growth has been shown in populations of the copepod *Scottolana canadensis*. Comparisons of five populations along the east coast of the United States from Florida (27° N) to Maine (43° N) showed that cold-water populations developed more rapidly, achieved a larger adult size, and had higher somatic growth at lower temperatures than at higher temperatures, whereas the opposite pattern was the case for warm-water populations (Lonsdale & Levinton 1985).

Similarly, the copepod *Tigriopus californicus* shows adaptation to thermal stress. Willet (2010) compared *T. californicus* populations inhabiting splash pools in rocky outcrops along the west coast of North America, from Baja California (32° N) to British Columbia (49° N). In this region, there is a clear, but not necessarily continuous, temperature gradient from south to north in maximum recorded values, yearly extreme high values, and average daily maximum and minimum values (Willet 2010, figure 2). In this case, both acute and chronic high-temperature stress tolerance clearly increase from north to south. This increase, although not monotonic, is consistent with the hypothesis of thermal stress adaptation. However, the adaptation is not without costs (a point I return to below). Moreover, not every trait is temperature-labile for this species. Edmands & Deimler (2004) were unable to find any differences in survival or development among three populations (two from California and one from Oregon) under two temperature and two salinity conditions.

Mesocosm experiments conducted in seminatural conditions to evaluate the responses of freshwater cladoceran species to warming have shown the evolution of survival, size and maturity, and reproduction (Van Doorslaer et al. 2007, 2010) but not intrinsic growth rate (fitness). Therefore, selected phenotypes could persist under projected scenarios of warming but would probably not predominate in the population.

Although the number of studies examining thermal adaptation is small, there is indeed evidence of such adaptation. Also recall that many traits show heritability for temperature (Section 2). As long as there are selection gradients, traits are heritable, and there is genetic variability in the population, we should expect adaptation to proceed. Below, I discuss some factors that could keep adaptation from becoming evident.

What kind of adaptation should we expect to see? Geographic variability in temperature might affect the type of thermal adaptation as a result of trade-offs (**Figure 3**). These trade-offs are predicated on the assumption that “a jack-of-all-temperatures is a master of none” (Huey & Hertz 1984). Under that assumption, optimality models (Lynch & Gabriel 1987, Gilchrist 1995) predict that natural selection would favor specialists in more thermally homogeneous environments and generalists in more thermally heterogeneous ones (but see Huey & Hertz 1984 for exceptions). If

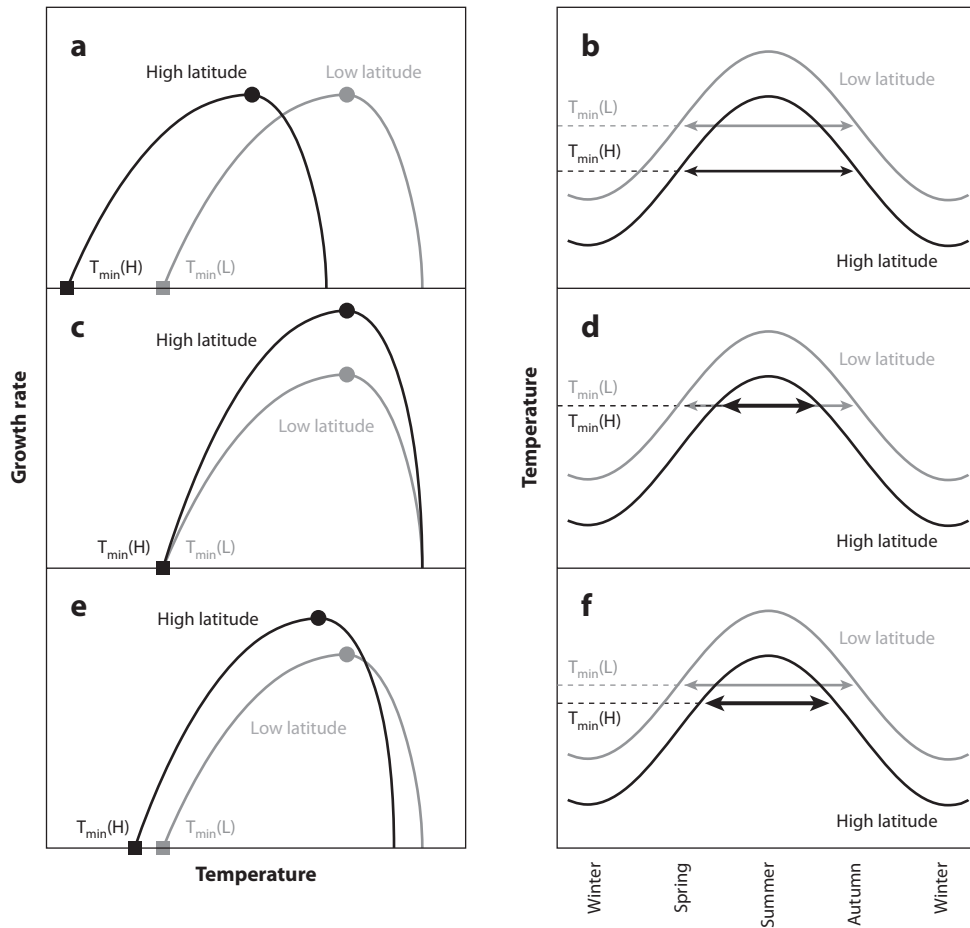
specialist-generalist trade-offs are at play in the ocean, then stenothermality is the rule for tropical and polar regions and eurythermality is the rule for subtropical and temperate regions (Sunday et al. 2011a).

Deutsch et al. (2008) predicted fitness changes of terrestrial insects from 40° S to 60° N as a function of temperature. They also reported stenothermality in tropical insects and eurythermality elsewhere. The predicted fitness changes were negative for tropical regions and positive elsewhere (Deutsch et al. 2008); therefore, in the absence of adaptation we would expect to see higher risks of zooplankton extinction in the tropical and polar regions. Furthermore, the capacity for thermal adaptation in these regions is not guaranteed for two reasons (Somero 2010): First, studies of thermal tolerance in a variety of invertebrates suggest that species in tropical regions may be living near their thermal limits, and second, polar species appear to have lost the biochemical machinery required to deal with warmer temperatures. The extent to which these findings apply to zooplankton remains an open question. The effects of warming would be worse for polar zooplankton because they have nowhere to go. However, acclimatization (or even slight adaptation) coupled with dispersion (the combined effect of diffusion and advection) toward cooler water could mitigate the negative effects of warming on tropical zooplankton. This hypothesis could explain the patterns observed by Beaugrand et al. (2002): Over a period of 40 years, warm-water zooplankton species of the eastern North Atlantic extended their range to the north by 10°, whereas cold-water species contracted their range by retracting to the north.

Changes in zooplankton phenology are also correlated with climate change (Richardson 2008, Ji et al. 2010). The timing of peak zooplankton abundance is now earlier in the season, and has continued to shift in this direction at a rate of 8 days per decade (see Richardson 2008, figure 5 and table 1; data compiled mostly from the North Atlantic). Although Ji et al. (2010) acknowledged the possibility of rapid evolution and local adaptation in their recent review, they interpreted the current changes in zooplankton phenology and distribution as largely ecological phenomena. Yet there is evidence that in zooplankton, natural selection can alter not only thermal physiology (Willet 2010) but also phenological mechanisms such as dormancy (Marcus 1984, Avery 2005). Bradshaw & Holzapfel (2006) also proposed a mechanism by which the photoperiodic thresholds for activity and dormancy can evolve in response to climate change.

Can the expected changes in development and growth associated with increased local temperatures account for the observed phenological shifts in zooplankton? The answer is no because the shifts are much greater than what would be expected from the increase in physiological rates alone (Mackas et al. 1998). For the sake of argument, I provide two evolutionary explanations, to complement the ecological ones, for the shifts in phenology. The first explanation is that increased temperature selects for fast-growing genotypes in the zooplankton populations. One way to test this hypothesis is to look for decreases in zooplankton body size that correlate with the phenology shifts, because there is typically a trade-off between body size and growth (Roff 1997). Indeed, a decrease in zooplankton body size has been observed in the past 40 years in some areas of the eastern North Atlantic (Pitois & Fox 2006). In addition, a generalized response of decrease in body size (within populations and across species) has been reported for aquatic systems (Daufresne et al. 2009). The second explanation is that zooplankton respond not only to temperature but also to phenological shifts in resources. Because the phenological shift for phytoplankton is twice as large as that for zooplankton (Edwards & Richardson 2004), selection for fast-growing zooplankton would alleviate the mismatch between zooplankton and their food.

Do zooplankton respond to climate change by thermal or seasonal adaptation? Zooplankton species that have wide latitudinal ranges and display latitudinal compensation may offer an opportunity to address this question. **Figure 4** compares three models for cold- and warm-adapted populations of a species (Yamahira et al. 2007). In the thermal adaptation model (**Figure 4a,b**),



**Figure 4**

Models for the evolution of latitudinal compensation in the growth rates of high- and low-latitude populations. (*Left*) Thermal reaction norms for models of (*a*) thermal adaptation, (*c*) seasonality adaptation, and (*e*) a mix of thermal and seasonality adaptation. (*Right*) The corresponding latitudinal variations in the length of the growing season (*arrow length*) and instantaneous growth rate (*arrow width*) for each model.  $T_{\min}(H)$  and  $T_{\min}(L)$  indicate the minimum temperatures for growth of the high- and low-latitude populations, respectively. Adapted from Yamahira et al. (2007) with permission from John Wiley and Sons.

the high- and low-latitude populations have equal maximum growth rates, but the maxima occur at different temperatures—that is, the thermal reaction norm of each population has been shaped by natural selection to span different windows of temperatures permitting growth. In the seasonal adaptation model (**Figure 4c,d**), the high-latitude organisms grow faster than the low-latitude organisms, but the temperatures of maximum growth and the minimum temperatures for growth are identical for both populations; as a result, the growing season of the high-latitude population is shorter than that of the low-latitude population (Yamahira et al. 2007). Because the thermal and seasonality adaptation models are not mutually exclusive, a third model (a mixture of the thermal and seasonality adaptation models) is possible (**Figure 4e,f**). Any of these three models may be responsible for part of the latitudinal compensation observed in any particular case. The three models outlined here might be particularly appropriate for testing in high-latitude

zooplankton, and would require comparison of thermal reaction norms among populations as well as corroborating evidence from phenological observations.

The thermal and seasonality models come with different trade-offs. In thermal adaptation, the trade-off is between thermal environments, whereas in seasonality adaptation, the trade-off is between traits—that is, fast growth, for example, must come at the expense of other traits, because otherwise all populations would grow equally fast. Understanding these trade-offs will be vitally important to understanding and predicting the effects of climate change on zooplankton.

Latitudinal adaptation in physiological traits is not inevitable. For example, studies of *Daphnia* did not find any evidence of thermal (Mitchell & Lampert 2000) or seasonal (Mitchell et al. 2004) adaptation. Mitchell and coworkers have argued that the trait of diapause, or dormancy, allows *Daphnia* to occupy a broad geographical range without latitudinal compensation. Copepods—the largest group of marine zooplankton—produce dormant eggs in response to temperature (Marcus 1996, Avery 2005), so they may respond in a manner similar to *Daphnia*. At present, however, copepod responses are virtually unknown. Fortunately, such questions are amenable to experimental manipulation.

How fast can adaptation evolve, and can it keep pace with climate change? The rate of phenotypic evolution is defined by  $R = b^2S$ , where  $b$  is the heritability of the phenotypic trait (see Section 2) and  $S$  is the selection gradient, or the change in fitness that results from a small change in the phenotype (Falconer & Mackay 1996). For the evolution of multiple traits,  $R$  and  $S$  become vectors of traits and selection gradients (Lande & Arnold 1983). The important point is that the rate of phenotypic evolution is proportional to heritability and hence proportional to genetic variance. Studies of heritability in marine zooplankton are quite limited (see examples in Section 2). I am aware of only one study that has attempted to measure selection gradients in marine zooplankton (Sunday et al. 2011a). Thus, at this point our ability to predict rates of zooplankton evolution is severely hampered by ignorance of these parameters.

I mentioned above that evolution of the reaction norm in the direction of environmental change can diminish the risk of extinction. The key question is whether the rate of evolution can keep pace with environmental change. One approach to addressing this question is predicated on the evolution of the thermal optimum. Based on the work of Lynch & Lande (1993), Chevin et al. (2010) derived, for a quantitative trait, an equation for the maximum rate of environmental change (e.g., warming) that allows the long-term persistence of the population:

$$\eta_c = \sqrt{\frac{2r_{max}\gamma}{T}} \frac{b^2\sigma^2}{|B - b|}.$$

This critical rate ( $\eta_c$ ) is directly proportional to the maximum growth rate of the population ( $r_{max}$ ), the strength of stabilizing selection ( $\gamma$ ), the phenotypic variance ( $\sigma$ ), and the heritability of the trait ( $b$ ). It is inversely proportional to generation time ( $T$ ) and the difference between the environmental sensitivity of selection ( $B$ , which measures how the optimum phenotype changes with the environment) and phenotypic plasticity ( $b$ ). Therefore, other factors being equal, populations with rapid growth and high genetic variance ( $b^2\sigma^2$ ) can withstand faster rates of warming. In contrast, populations with longer generation time and lower phenotypic plasticity have greater risk of extinction (lower  $\eta_c$ ).

A second approach to examining extinction risk is to consider the evolution of the breadth of the reaction norm. Again based on the work of Lynch & Lande (1993), Huey & Kingsolver (1993) determined the reaction norm breadth that maximizes the critical rate of warming (as defined above). The outcome depends on the relationship between the genetic variation in optimal temperatures and the breadth of the reaction norm. If they are independent of each other, then genotypes with intermediate breadths can withstand the fastest rate of warming; that is, when the

reaction norm is too narrow, even a slow rise in temperature can lead to extinction, whereas when the reaction norm is too wide, performance at the thermal optimum decreases because of specialist-generalist trade-offs (Figure 3). Moreover, if there is a trade-off between maximum performance and the breadth of the reaction norm, then thermal specialists are favored over thermal generalists in rapidly warming environments. In contrast, when the genetic variation in optimal performance increases with breadth, thermal generalists withstand the fastest rates of warming.

At this point, we know almost nothing about several of the parameters required to apply models of the evolution of the thermal optimum or the breadth of the reaction norm. Significant progress in our ability to predict the response of zooplankton to global warming will require knowledge of genetic variability, phenotypic plasticity, and the environmental sensitivity of selection (to characterize the evolution of the thermal optimum). Likewise, characterization of the breadth of the reaction norm and the genetic variation in the thermal optimum for different environments will allow us to predict whether adaptation occurs via changes in the breadth of the reaction norm.

## 6. INTERACTION OF EVOLUTIONARY PROCESSES

It is evident from the discussion to this point that our ability to understand zooplankton adaptation to single stressors such as warming or hypoxia is very limited. To make matters worse, several evolutionary agents are working simultaneously, potentially complicating our understanding even further. For example, warming and acidification are correlated (Doney et al. 2009), as are warming and hypoxia (see Section 5.2). The same may be the case for hypoxia and harmful algal blooms (Cloern 2001). Studying the synergistic or antagonistic interactions of these processes will present logistical and conceptual challenges to the study of the evolutionary adaptation of zooplankton to global change. The hypothesis of oxygen- and capacity-limited thermal tolerance in animals (Pörtner et al. 2006) is a good example of a conceptual framework that links simultaneous evolutionary stressors.

## 7. INTERACTION OF EVOLUTIONARY AND ECOLOGICAL PROCESSES

Adaptive responses can occur on the timescales over which climate change occurs (Davis et al. 2005, Parmesan 2006). In fact, it has been argued that some microevolutionary processes occur on timescales similar to those of ecological processes, which has been termed rapid evolution (Hairston et al. 2005). For example, rapid evolution has been well documented in the case of the interaction between zooplankton and toxic algae (Hairston et al. 1999, Colin & Dam 2004). More important, the timescale convergence for microevolutionary and ecological processes leads to feedbacks that are manifested at multiple levels of ecological organization, from populations to communities and ecosystems (Hairston et al. 2005, Post & Palkovacs 2009). Thus, evolution can alter ecological processes and vice versa: Although it is possible that selection for organismal traits could mitigate, for example, climate-related environmental shifts, the outcome of selection could be countered by ecological processes. Interactions between variables could lead to trade-offs or genetic correlations between traits that might limit the ability of species to adapt to climate change (Harley et al. 2006). As examples, I consider the interaction of thermal adaptation and two ecological processes: competition and overfishing-associated predation.

In a study discussed above (Willet 2010), copepod populations that faced the greatest thermal stress displayed the strongest high-temperature stress tolerance. However, in intraspecific competition assays, those populations were at a disadvantage at more moderate temperatures. A similar competitive disadvantage was shown for cladoceran populations that had adapted to warming relative to those that had not (Van Doorslaer et al. 2009b). Therefore, thermal adaptation could

lead to an ecological trade-off (competitive disadvantage) that may limit the ability of thermally adapted populations to spread to new habitats.

In a study of genetic adaptation to temperature in *Daphnia* under two culling regimes, an adaptive response was obvious after a few generations of selection in a thermal regime but in only one of the two culling regimes, suggesting that predation may affect the outcome of evolution (Van Doorslaer et al. 2009a).

One contemporary process that can have a strong bearing on the response of zooplankton to climate change is overfishing. There are now well-documented cases that overfishing leads to cascading trophic interactions that affect zooplankton. For example, in a four-level food chain on the eastern Scotian Shelf in the Northwest Atlantic, a decline in the aggregate biomass of top predators (groundfish) resulted in an explosion in both planktivore and macroinvertebrate abundances, which then precipitated declines in the abundance of large herbivorous copepods (Frank et al. 2005). Similarly, in the open Baltic Sea, reduction of the cod (*Gadus morhua*) population directly affected its main prey, the zooplanktivorous sprat (*Sprattus sprattus*), and indirectly affected the summer biomass of zooplankton (Casini et al. 2009). In addition, overfishing has led to trophic cascades and the proliferation of gelatinous zooplankton in the Black Sea (Daskalov et al. 2007). Thus, overfishing can lead to a preponderance of visual (e.g., fish) or nonvisual (ctenophores and jellyfish) zooplanktivores. The former tend to be size selective, but the latter do not.

Let us now consider the interaction of overfishing and thermal adaptation. For the sake of argument, we can posit that in a warming world the outcome of natural selection would be faster-growing individuals with shorter generation times. This typically results in a trade-off of reduced body size and fecundity (Roff 1997). Indeed, a reduction in body size is a recognized response to global warming (Sheridan & Bickford 2011). Now consider predation as an evolutionary force in combination with temperature. In the case of visual predators and a warming climate, predation mortality will be greater for larger individuals within a population, leading to further selection for small body size. In contrast, in the case of nonvisual predators (e.g., gelatinous zooplankton) and a warming climate, predation will be determined mostly by encounter rate; hence, the smaller, more abundant zooplankton will experience higher predation mortality, counteracting the effects of temperature selection for small body size. To the extent that the outcome of thermal adaptation will vary among zooplankton populations along a latitudinal gradient, so too will the effects of the interaction of temperature and predation on the zooplankton population dynamics. This interaction will then also affect prey availability for larval and small pelagic fishes. Such feedback mechanisms should be taken into account when oceanographers analyze the phenology and distribution of zooplankton in terms of climate change.

### SUMMARY POINTS

1. Zooplankton respond to global change problems such as toxic algal blooms, hypoxia, and climate change through both phenotypic plasticity and genetic adaptation. The evolution of reaction norms (also called performance curves) among populations provides a powerful conceptual framework to disentangle phenotypic plasticity from genetic adaptation. Common garden experiments are a suitable means to test for genetic adaptation in zooplankton in the ocean.
2. Although the number of studies that have rigorously tested for genetic adaptation in marine zooplankton is small, there is unequivocal evidence for genetic adaptation to a variety of environmental stresses and for genetic variation in the phenotypic plasticity related to these stresses. The latter is essential for the evolution of reaction norms.



3. Measurements of fitness in studies of marine zooplankton adaptation are extremely limited. Because of trade-offs, studies that measure only a single trait may lead to erroneous conclusions regarding adaptation.
4. The fixation of adapted genotypes in zooplankton populations facing stochastic or cyclic environmental stress (e.g., toxic algal blooms and coastal hypoxia) will depend on the fitness penalty (cost) incurred by those phenotypes in the absence of the environmental stressors. Such costs are poorly constrained. Zooplankton adaptation to directional selection (e.g., temperature, acidification) may be better understood based on specialist-generalist trade-off theory.
5. Evolutionary rates of adaptation in marine zooplankton are poorly constrained. This uncertainty severely limits our ability to predict whether zooplankton can adapt quickly enough to global environmental change.
6. We know almost nothing about the effects of the interaction of selective pressures on zooplankton adaptation. Interactions between adaptation and ecological processes such as competition and predation are gaining recognition as important factors in understanding the response of zooplankton to global change.

## FUTURE ISSUES

1. Studies that rigorously test for differences between phenotypic plasticity and genetic adaptation will remain a priority for understanding the response of zooplankton to global change.
2. Fitness is a composite measure of lifetime survival and fecundity. Because of trade-offs among life history traits, fitness should be the currency for studies of adaptation in marine zooplankton (e.g., Colin & Dam 2004). Measurements of fitness impose considerable logistical demands but overcome many of the interpretation problems common to most adaptation studies.
3. At least in the case of directional selection, there is a solid framework for comparing evolutionary rates to environmental change (Chevin et al. 2010), which is the key issue for predicting whether marine zooplankton will adapt quickly enough to global change. Progress in this area will require two types of efforts: (*a*) within-population studies to assess the genetic component of phenotypic variability and the heritability of traits correlated with fitness (survival, fecundity, developmental rate, and size and age at maturity) and (*b*) measurements of selection differentials.
4. Studies of the synergistic or antagonistic effects of selective pressures (e.g., warming and acidification, or warming and hypoxia) and of evolutionary (adaptation) and ecological (predation, competition, parasitism) processes can significantly advance our ability to forecast the response of zooplankton to global change. Progress in this area will require close collaboration between marine ecologists, evolutionary biologists, and modelers.

5. Arnold (1983) introduced evolutionary ecologists to the linkages between morphology, performance, and fitness. Paraphrasing Arnold, marine zooplanktologists should strive for an integrative view of genetics, physiology, performance, and fitness. To achieve this goal, the gap between molecular biology, physiology, and population genetics must continue to narrow (e.g., Bricelj et al. 2005, Somero 2012).

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## Errata

An online log of corrections to *Annual Review of Marine Science* articles may be found at <http://marine.annualreviews.org/errata.shtml>