REVIEW

Effects of temperature change on mussel, *Mytilus*

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Abstract
An increasing body of research has demonstrated the often idiosyncratic responses of organisms to climate-related factors, such as increases in air, sea and land surface temperatures, especially when coupled with non-climatic stressors. This argues that sweeping generalizations about the likely impacts of climate change on organisms and ecosystems are likely less valuable than process-based explorations that focus on key species and ecosystems. Mussels in the genus *Mytilus* have been studied for centuries, and much is known of their physiology and ecology. Like other intertidal organisms, these animals may serve as early indicators of climate change impacts. As structuring species, their survival has cascading impacts on many other species, making them ecologically important, in addition to their economic value as a food source. Here, we briefly review the categories of information available on the effects of temperature change on mussels within this genus. Although a considerable body of information exists about the genus in general, knowledge gaps still exist, specifically in our ability to predict how specific populations are likely to respond to the effects of multiple stressors, both climate and non-climate related, and how these changes are likely to result in ecosystem-level responses. Whereas this genus provides an excellent model for exploring the effects of climate change on natural and human-managed ecosystems, much work remains if we are to make predictions of likely impacts of environmental change on scales that are relevant to climate adaptation.

Key words: climate change, mussels, *Mytilus*, organismal responses, temperature

PREDICTING IMPACTS OF CLIMATE CHANGE USING MODEL SPECIES

An increasing number of studies have recognized the difficulties inherent in predicting the likely impacts of climate change on natural ecosystems (Hampe 2004; Kearney & Porter 2009). Because many environmental conditions under climate change are likely to be novel, it is unclear how well extrapolations from observations of contemporary communities will serve as a guide for future responses to environmental change. Moreover, even when we understand the physiological and demographic influence of single environmental parameters, the interaction of multiple stressors on organisms and communities can be difficult to predict (Crain et al. 2008). Recent studies have further suggested that local adaptation and acclimatization are key factors in predicting
climate-related impacts (Kuo & Sanford 2009). Finally, indirect effects, such as impacts on trophic cascades and competitive ability, are also known to be affected by environmental conditions that are undergoing significant change (Wethey 2002; Edwards & Richardson 2004; Pincebourde et al. 2008; Broitman et al. 2009).

Therefore, exploring these intertwined issues represents a significant challenge, and suggests that a diversity of approaches, including statistically-based/correlative and mechanistic methods (and hybrids and ensembles thereof) are needed if we are to prepare for current and forthcoming climate change impacts (Brown et al. 2011; Burrows et al. 2011). One way forward is to focus on model species for which considerable existing information is known. Especially important are species that have a large impact on other species in their assemblage; for example, keystone predators and structural species (Monaco & Helmuth 2011).

As part of this volume on the biological effects of climate change, we focus on marine mussels in the genus Mytilus. Given the ecological (Seed & Suchanek 1992) and economic (FAO 2010) importance of this species, an enormous amount is known about its physiology, genetics and ecology. Our goal is not to provide an exhaustive review of all that is known. Not only would that be impractical, but several excellent overviews of this genus already exist (Bayne 1976; Bayne et al. 1976a,b; Gosling 1984; Seed & Suchanek 1992). Rather, our intent is to provide examples of what types of information are known about thermal stress-related effects on mussels in this genus, and to identify where knowledge gaps still exist.

It is also critical to note that here we focus primarily on the impacts of thermal stress on Mytilus populations, despite the fact that there are multiple stressors simultaneously acting upon a given organism at a particular time (Table 1). Although significant progress has been made in exploring the independent effects of these stressors (Table 1), there is still a significant knowledge gap in our understanding of how multiple stressors affect organisms and ecosystems. For example, a recent review by Crain et al. (2008) of marine ecosystem studies found that the interaction of environmental temperature with stressors ranging from pH to disease to overfishing could be additive (effects reflect sum of individual stressors), synergistic (effect greater than sum of individual stressors) or antagonistic (overall effect less than sum of individual stress effects). Many of these observations likely resulted from differential impacts operating at different trophic levels (Crain et al. 2008).

Table 1 Interactive effects of biotic and abiotic stressors on Mytilus spp.

<table>
<thead>
<tr>
<th>Species</th>
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<tbody>
<tr>
<td>M. californianus</td>
<td>Jones et al. (1993)</td>
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<tr>
<td>M. edulis</td>
<td>Berge et al. (2006); Bibby et al. (2008); Beckmann et al. (2011)</td>
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<tr>
<td>M. galloprovincialis</td>
<td>Michaelidis et al. (2005); Kurihara et al. (2008)</td>
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<td>M. edulis</td>
<td>Solle et al. (2016); Combue et al. (2016)</td>
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<td>M. galloprovincialis</td>
<td>Platt et al. (2002); Carrington et al. (2009); Wallin et al. (2011)</td>
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<td>M. edulis</td>
<td>Menge et al. (2008)</td>
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<tr>
<td>M. galloprovincialis</td>
<td>Schneider et al. (2010)</td>
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<td>M. edulis</td>
<td>Dallhoff &amp; Meng (2002)</td>
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<tr>
<td>M. californianus</td>
<td>Fisher et al. (1992); de Zwaan et al. (1995); Ferran et al. (1996); Parry et al. (2004); Baijens et al. (2011)</td>
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<tr>
<td>M. galloprovincialis</td>
<td>Sunlu (2006); Besada et al. (2011), Maria &amp; Bebianno (2011)</td>
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<td>M. edulis</td>
<td>Eufemia &amp; Epel (2000)</td>
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<tr>
<td>M. californianus</td>
<td>Hernandez et al. (1994); Luedeking &amp; Kohler (2004); Apitz et al. (2006); Hong et al. (2009)</td>
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<tr>
<td>M. galloprovincialis</td>
<td>Fernandez et al. (2010); Fernandez-Abalos et al. (2011); Guerguen et al. (2011)</td>
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Effects of temperature change on Mytilus
2008). At the individual level, physiological stress imposed by one factor may reduce the organism’s resistance to other stressors (Pörtner 2010) or the synergistic effect of multi-stressors may be irreversible and lead to negative consequences. For example, changes in sea surface temperature can alter the salinity concentration of the open ocean, which has been shown to influence the immune response of Mytilus edulis Linnaeus, 1758 (Bussell et al. 2008), thereby increasing the susceptibility to other stressors, such as physical disturbances. As projected with climate change, an increase in storm frequency and flooding could lead to extended periods of reduced salinity, thus significantly jeopardizing the well-being of this keystone species and ultimately altering the marine ecosystem (e.g. changes in biodiversity and aquaculture (Williams et al. 2011)). Similarly, M. trossulus Gould, 1850 and M. galloprovincialis Lamarck, 1819 show lowered resistance to elevated temperatures in low food regimes (Schneider et al. 2010). Therefore, although the long history of physiological and ecological studies of this genus will provide considerable insight into future responses to climate change, the interaction of multiple stressors within an ecological context, the varying vulnerability of populations to changing environmental conditions and the subsequent impacts of population changes on ecosystems remain relatively unexplored areas.

The mussel Mytilus

Mussel beds occur worldwide, inhabiting soft bottoms in cold and temperate waters and rocky substrates along the coast (Paine 1966; Seed & Suchanek 1992). Mytilid species are considered ecologically dominant organisms of the intertidal zone by overgrowing their competitors (Paine 1994; Robles & Desharnais 2002) and having the ability to physically alter their environment by attaching byssal threads to the substrate and conspecifics (Gutiérrez et al. 2003). They also serve as a food source for many other organisms, including humans (Seed & Suchanek 1992; FAO 2010). These ecosystem engineers (Crooks 2002; Gutiérrez et al. 2003) are very important to their environment by creating diverse species assemblages (Seed & Suchanek 1992; Seed 1996; Smith et al. 2006; Büttger et al. 2008; Buschbaum et al. 2009). Furthermore, these voracious filter feeders provide ecosystem services by filtering toxins and bacteria that may be in the water column at a rapid speed of 3–5 l/h (Van Duren 2007).

The California mussel M. californianus Conrad, 1837 has a broad latitudinal distribution spanning from the Aleutian Islands of Alaska to northern Mexico of Baja California (Morris et al. 1980). Its vertical zonation is centrally located in the mid intertidal zone and found in dense aggregated beds where wave action is most intense. In contrast, the bay mussel, M. edulis, commonly inhabits soft bottom mussel beds with calmer waters in the North Atlantic and North Pacific coasts of the USA, Europe and even polar waters around the world. M. edulis also are found on hard substrata, and when exposed to wave action tend to grow more slowly with thicker shells. The European blue mussel M. galloprovincialis displays the most global distribution from the Mediterranean, western Australia, Tasmania and New Zealand, and was introduced to Great Britain, Ireland, France, Japan and southern California (Lee & Morton 1985; Geller 1999; Branch & Steffani 2004). This dominant invader has been successful in replacing the native mussel M. trossulus, in many parts of the world (Brannock et al. 2009), including the west coast of North America, where it is thought to have invaded in the early 1900s via commercial shipping transport (Geller et al. 1994). M. trossulus exists in the northern Pacific from Siberia to central California, in the Canadian Maritimes, and in the Baltic Sea. These 2 congeners have co-evolved to establish a hybrid population in and around San Francisco Bay, California (McDonald & Koehn 1988; Rason & Hilbish 1995; Geller 1994; Geller et al. 1994).

The patchiness and complexity of distribution patterns reflects ecological and biophysical drivers ranging from broad biogeographic to microgeographical scales. For example, M. galloprovincialis can tolerate high saline conditions, warmer water temperatures and more wave action (Skibinski et al. 1983) than its lower salinity, cooler adapted and less wave-exposed counterpart (Sarver & Foltz 1993; Wonham 2004; Braby & Somero 2006a). Such abiotic factors likely impact the distribution and performance patterns of the 2 species, and could induce physiological stress affecting their competitive ability in the field.

For almost 12 000 years, Native Americans along the west coast of the USA harvested mytilid mussels as a food source. To this day, they are considered a staple for some seafood dishes around the world (e.g. Spanish, Portuguese, French, Dutch, Belgian and Italian) and, according to the Food and Agriculture Organization of the United Nations (FAO 2010), in 2009, over 60 000 tons were harvested. Until the early 1990s, M. edulis was the most common mussel for consumption, but, recently,
M. galloprovincialis has become popular. Market value for mytid mussels ranged from US $400 to US $1700 per ton in the year 2000, with an estimated average net worth of US $2 480 000 to US $102 000 000.

**PHYSIOLOGICAL EFFECTS**

Temperature, one of the most studied abiotic factors, is a primary driver in setting species’ ranges in terrestrial and marine systems, and has pervasive effects at the molecular level of an organism that can be transduced to influence their distribution, abundance and fitness (Hochachka & Somero 2002; Pörtner 2002; Somero 2005). Changes in environmental temperature are thought to be the cause of observed biogeographic shifts in many taxa (Thomas & Lennon 1999; Parmesan & Yohe 2003; Root et al. 2003; Parmesan 2007) including mussels (e.g. Jones et al. 2009). Understanding the effects of environmental temperature on Mytilus can be complex, especially for intertidal populations that are exposed to the aerial environment at low tide, often for many hours. Given their relatively low metabolic rate, when submerged, a mussel’s body temperature closely approximates that of the surrounding water. In contrast, during aerial exposure at low tide, the body temperatures of mussels are driven by multiple, interacting environmental factors, of which air temperature is but one. Thus, aerial body temperatures of mussels are often considerably higher than the temperatures of the surrounding air and substrate, so much so that air temperature can be a poor predictor of animal temperature (Helmuth et al. 2011).

To date, the majority of studies of thermal responses has examined the effects of water temperature, or have used experiments in water to characterize temperature effects at low tide. An increasing number of studies are examining the potential importance of aerial body temperature, and have suggested very different responses in these 2 media. For example, Jones et al. (2009) found that the LT$_{50}$ of M. edulis from the east coast of the USA ranged from 25 to 37 °C depending on the number of exposures and time of year at which measurements were made. In summer (June), thermal tolerances were similar in air and water, but differed by up to 5 °C (lower in water) in fall (November). These results are generally consistent with those of earlier studies. For example, Read and Cumming (1967) estimate the upper tolerance level of M. edulis as 28 °C, and Ritchie (1927) shows that exposures to water temperatures in excess of 28.9 °C leads to death within 14 h. Wallis (1975) found that the lethal temperature of M. edulis varies with acclimation and body size, as well as with photoperiod and salinity levels.

Denny et al. (2011) report aerial LT$_{50}$ for M. californianus that range between 36 to 41 °C depending on thermal history, which is consistent with the observation that these mussels regularly experience body temperatures that exceed 30 °C at several sites along the west coast of North America during low tide (Elvin & Gonor 1979; Helmuth et al. 2006a). In Europe, mussels acclimated to ecologically relevant water temperatures (20–25 °C) had an LT$_{50}$ of 30–31 °C (Jansen et al. 2007). M. edulis, from Australia, had an upper lethal temperature of 28.2 °C when acclimated to 20 °C (Wallis 1975). Tsuchoya (1983) reports mass death (>50% of the population) of M. edulis following exposure to air temperatures >40 °C, and Harley (2008) reports death in intertidal M. californianus following unusually warm aerial temperatures.

Therefore, although the relative importance of body temperature during submergence and aerial exposure remains unclear, results suggest that both have impacts on survival and physiological performance, and that interactions between aerial and aquatic temperature affect mussel physiology (Schneider 2008). Because solar energy is a dominant driver of aerial body temperature (Marshall et al. 2010), much of the variability in thermal regimes within rocky intertidal sites is driven by substratum angle (Denny et al. 2011), with non-shaded surfaces exposing mussels to much higher temperatures than shaded vertical surfaces (Helmuth & Hofmann 2001). As a result, intra-site variability in aerial body temperature can easily exceed that observed over latitudinal scales (Helmuth et al. 2006a; Denny et al. 2011). These intra-site variations can contribute to spatial variability in mortality events. For example, when the timing of the low tide and weather conditions resulted in widespread death of M. californianus in Bodega Bay, CA in 2004 (Harley 2008), death primarily occurred on southern (equator-ward) facing slopes. Similarly, Schneider and Helmuth (2007) found that levels of death in M. trossulus and M. galloprovincialis were higher on non-shaded surfaces, and found overall lower levels of survival by M. trossulus, which is less thermal tolerant (Lockwood & Somero 2011a).

One way to quantify responses to thermal stress is with a temperature coefficient, $Q_{10}$. An organism’s $Q_{10}$ reflects the rate of change for a biological, chemical or physiological processes as a consequence of a 10 °C increase in temperature. This metric varies depending on levels of acclimation and the temperature range exam-
ined, and, therefore, can vary between seasons (e.g. Jansen et al. 2007). For most reactions under ‘non-stressful’ conditions, the $Q_{10}$ ranges from 1 to 3. In contrast, some energy intensive reactions show $Q_{10}$ between 4 and 6. Low $Q_{10}$ values illustrate temperature independence where no significant acclimation to a temperature change is evident.

Measurements of the effects of temperature on respiratory function can provide an understanding of an organism’s tolerance to the environment (Jansen et al. 2007). When exposed to non-stressful temperatures (13–22 °C), the oxygen consumption of *M. californianus* in the field has been shown to be relatively temperature independent, with a $Q_{10}$ of 1.20, although the filtration rate is more temperature-dependent ($Q_{10} = 2.10$) (Bayne et al. 1976a). Similarly, Widdows (1976) reports a $Q_{10}$ for *M. edulis* of 1.5–2.1 after cycling between 11 and 19 °C for 30 days. Van der Veer et al. (2006) report an Arrhenius temperature in *M. edulis* of 5800 K, which corresponds to a $Q_{10}$ of 2. Respiration rate increases with temperature in the Mediterranean mussel (*M. galloprovincialis*) with $Q_{10}$ values $>$2, with good acclimatization between 6 and 19 °C (Barbariol & Razouls 2000). Filtration rate and heart beat frequency in *Mytilus* spp. are also completely temperature dependent (Bayne et al. 1976a), such that differences in thermal tolerance of cardiac function in *Mytilus* may reflect a temperature-compensation adaptation, and help to explain the successful replacement of native species by invasive species (Braby & Somero 2006b).

Physiological responses of mussels exposed to stressful temperatures are more complex, especially when considering the interactions between physiological stress experienced by intertidal mussels alternating between aerial and aquatic habitats. *Mytilus* spp. show a reduction in aerobic capacity at high and low temperatures (Bayne et al. 1976a; Anestis et al. 2007) and display tissue-specific anaerobic activities (Lockwood & Somero 2011a). For example, during short periods of aerial exposure accumulation of alanine and malate, end-products of anaerobic metabolism, were elevated in the adductor muscle of *M. californianus* (Bayne et al. 1976b), probably an attempt to maintain redox balance and to make up for energy deficiency from oxygen deprivation. Diffusion of oxygen into water trapped by the mantle cavity during periods of aerial exposure is common among intertidal bivalves; however, congeneric differences in aerial rates of oxygen consumption have been reported for mussels. For example, *M. californianus*, a species with marked shell gaping in air, consumes a high rate of oxygen between 30 and 80% of the immersed rate (Bayne et al. 1976b) compared to *M. edulis* and *M. galloprovincialis*, whose shell valves are typically closed in air and consume much less oxygen, 4–17% of the immersed rate (Widdows et al. 1979; Widdows & Shick 1985). Different species of mussels utilize different metabolic processes as a means to conserve energy during aerial exposure by decreasing their metabolic activity when shifting from aerobic to anaerobic metabolism (Page et al. 1998; Anestis et al. 2007; Anestis et al. 2010). Results by Bayne et al. (1976a) suggest an interaction between stress experienced during aerial exposure and during submergence, in which a ‘debt’ accrued during low tide is then ‘paid’ at high tide (Bayne et al. 1976b). Schneider (2008) shows that mussels acclimated to warmer water temperatures (18 °C) were less susceptible to death during aerial exposure (30 °C). However, when animals were grown in cooler (12 °C) water temperatures, *M. trossulus* showed higher death and lower growth than compared to *M. galloprovincialis*.

Temperature can have a major effect on organismal performance and growth by influencing filtration rates, absorption and utilization of available food (Widdows 1976; Kittner & Riisgard 2005; Jansen et al. 2007). Mussel growth has been linked to temperature and food availability (Page & Hubbard 1987; Blanchette et al. 2007; Schneider et al. 2010), where mussels are more likely to grow faster or larger at warmer climatic sites when food abundances are greater (Lesser et al. 2010) from phytoplankton blooms, upwelling events and/or coastal currents (Menge et al. 2008). The costs associated with acclimatizing to thermal stress could be offset by the availability of significantly higher concentrations of food (Lesser et al. 1994; Dahlhoff et al. 2002), consequently compounding physiological trade-offs by allocating energy from reproduction towards physiological defenses (Bayne 2004).

The timing and success of reproduction is heavily weighed upon temperature and food availability (Sastry 1966; Suarez et al. 2005; Lemaire et al. 2006; Okaniwa et al. 2010). For example, mussels (*M. californianus*) near the high edge of the mussel bed invested less energy into reproduction and spawned early in the summer compared to those in the lower edge, where food availability was high and reproduction occurred throughout the year (Petes et al. 2008). Thus, by mobilizing more energy to reproduction, less energy is devoted to physiological defenses (Petes et al. 2008). These trade-offs become economically important when temperature influences *Mytilus* in aquaculture and hatchery facili-
ties (LeBlanc et al. 2005, Ruiz et al. 2008) by reducing the capacity for growth and the maturation of gametes (Fearman & Moltschaniwskyj 2010). Similarly, in natural populations, reproduction and growth are vital to the formation of stable populations. More recently, biophysical approaches (e.g. dynamic energy budget models) have been tested on different Mytilus spp. to predict how much energy is assimilated and assigned to physiological processes (i.e. growth, development and reproduction) under fluctuating environmental conditions, such as thermal variation and food availability (Cardoso et al. 2006; van der Veer et al. 2006; Freitas et al. 2009; Sará et al. 2011). The functionality of these models could provide an understanding of the possible constraints on current intertidal distribution and abundance, while forecasting how they might be altered under predicted climate change scenarios (Kearney et al. 2010).

A host of new molecular and biochemical techniques have opened the door to a deeper understanding of the subcellular level responses that ultimately result in whole-organism responses to stress, such as growth (Dahlhoff 2004; Somero 2011). A commonly used approach has been to measure the heat shock response, a complex of molecular chaperones that mitigate cellular damage and restore cellular homeostasis (Hochacha & Somero 2002; Kültz 2005). Molecular chaperones, collectively known as heat shock proteins (Hsps), stabilize the unfolding of proteins to prevent further denaturation and assist in the refolding to its native stable state. Hsps play an important role in protein homeostasis and are strong indicators of stress-induced protein damage. Mytilus spp. show changes in cellular response to thermal stress across geographic scales (Place et al. 2008, 2012; Dutton & Hofmann 2009; Lesser et al. 2010) and seasonal changes have been demonstrated as well (Chaple et al. 1998; Jansen et al. 2007; Gracey et al. 2008; Ioannou et al. 2009; Banni et al. 2011). Measurement of the heat shock response at small spatial scales has revealed the importance of microhabitat (Hofmann & Somero 1995; Buckley et al. 2001; Halpin et al. 2004). For example, the body temperatures of M. californianus are consistently higher on horizontal (non-shaded) surfaces than on vertical shaded surfaces, which is reflected in the amount of inducible Hsp70 that they produce (Helmuth & Hofmann 2001). Differences in protein homeostasis have also been measured using ubiquitin, a regulatory protein that covalently binds to degraded and miss-folded proteins (Glickman & Ciechanover 2002); M. galloprovincialis exhibits more warm adapted proteins, while M. trossulus are more cold-adapted (Hofmann & Somero 1995, 1996; Dutton & Hofmann 2008).

More recently, some physiologists investigating cellular stress are turning their attention to ‘omic’ experimentation to understand how the ‘whole’ organism confronts these environmental factors and how it may affect energy allocation. Studying the expression of thousands of genes at the transcriptional level, known as transcriptomics, is a tool that has begun to translate the understanding of how environmental signals affect physiological responses. In M. californianus, transcriptional differences have been seen across spatial (Place et al. 2008, 2012) and temporal (Gracey et al. 2008; Banni et al. 2011) scales, while also revealing a comparative response between invader and native blue mussels (Lockwood et al. 2010; Lockwood & Somero 2011b). Similarly, proteomics have provided more information about the temperature-dependent patterning between congeners of Mytilus (Lopez et al. 2002; Tomanek & Zuzow 2010) by analyzing the changes in protein pool composition. Investigating sublethal thermal stress at the cellular level can reveal important information about the subtle patterns of cellular damage and repair, while providing physiologists with molecular ‘biomarkers’ for characterizing the degree of stress and sensitivity among species and how it may impact the energy allocation of an organism. Importantly, recent studies have also demonstrated the presence of circadian rhythms in transcription of proteins in intertidal animals, potentially complicating interpretations of field measurements (Gracey et al. 2008; Connor & Gracey 2011).

INDIRECT EFFECTS OF TEMPERATURE-TROPHIC CASCADES AND RATES OF COMPETITION

Changes in environmental conditions have a direct impact on an organism’s physiology; however, indirect effects that operate through impacts on an organism’s prey, predators and competitors may be equally as important (e.g. Wethey 2002). Sanford (1999, 2002) shows that predation rates by the sea star Pisaster ochraceus (Brandt, 1835) on M. californianus are significantly affected by water temperature. Pincebourde et al. (2008) shows that aerial (low tide) body temperatures also affect rates of predation by Pisaster, but that this effect differs markedly depending on the duration of exposure to elevated aerial temperatures.

Because body temperature can be affected by an organism’s morphology and behavior, the thermal niche of a predator (e.g. a sea star) and its prey (mussel) can
be significantly different even though they occupy identical microhabitats in the intertidal zone (Briotman et al. 2009). The predator–prey interactions between Pisaster and Mytilus can be sensitive to slight shifts in temperature due to the timing and intensity of seasonal events (Sanford 1999; Pincebourde et al. 2008, 2009; Harley 2011), and this could ultimately change the intertidal ecosystem by altering the food web of the community assemblage (Paine 1966). For example, whether ‘prey stress’ or ‘consumer stress’ models apply (Menge & Olson 1990) will likely vary from site to site, as well as between seasons (Monaco & Helmuth 2011).

The ability for an organism to invade a new region may be closely linked to its thermal adaptation (Stachowicz et al. 2002), and understanding the attributes that facilitate or interfere with the success of an invasion is vital to predict and forecast future invasions. In the USA and Japan, invasion by Mytilus galloprovincialis has replaced the naturally occurring M. trossulus (Wilkens et al. 1983; Geller 1999), and hybrids between M. galloprovincialis and both M. edulis (Hilbish et al. 1994) and M. trossulus (Suchanek et al. 1997) are common. This effect can be observed over geographic scales (Hilbish et al. 2010) as well as within sites due to high thermal heterogeneity (Schneider & Helmuth 2007). Currently, on the west coast of the USA, the cold-water adapted mussel (M. trossulus) resides primarily in northern California and Oregon, while the warm-adapted mussel (M. galloprovincialis) is almost exclusively in southern California (Sarver & Foltz 1993; Suchanek et al. 1997). At smaller scales, both species coexist at central California sites, but M. galloprovincialis is most common on sunny intertidal substrata and M. trossulus is more common on shaded surfaces (Schneider & Helmuth 2007). Substantial evidence supports that these species differ in their thermal physiology, including cellular processes (Hofmann & Somero 1996; Fields et al. 2006; Braby & Somero 2006b; Evans & Somero 2010), enzymatic activity (Lockwood & Somero 2011a), molecular function (Lockwood et al. 2010; Tomanek & Zuzow 2010), growth rate (Braby & Somero 2006a; Schneider 2008; Shinen & Morgan 2009) and survival (Matson et al. 2003; Schneider 2008). Differences found between these two species suggest that climate change might facilitate species invasion, with the invader species (M. galloprovincialis) having a higher capacity to cope with elevated temperatures, therefore having a competitive advantage over the native species. Recent data suggest that current environmental conditions, such as temperature, could be preventing M. galloprovincialis from further invading northward into California (Hilbish et al. 2010). How these patterns will likely be altered by climate change remains an open question (Jones et al. 2010).

OBSERVED CHANGES IN NATURE

Range shifts in nature can occur either through gradual change in average conditions or through rare but extreme events (Cury & Shannon 2004; Wooster & Zhang 2004; Wetney et al. 2011). Compared to terrestrial ecosystems, marine organisms tend to have larger range distributions, and marine distribution patterns also appear to be changing much more rapidly than terrestrial range edges (Helmuth et al. 2006b). Often, these distribution patterns are far more complicated than simple poleward range shifts. For example, M. californianus along the west coast of the USA experience thermal mosaics rather than latitudinal gradients (Hilbish et al. 2006a) in aerial body temperature, which is reflected in their physiological performance (Place et al. 2008, 2012). For example, Place et al. (2008) show that mussels in central Oregon, where local conditions can lead to high temperatures, exhibit higher levels of upregulation in genes related to thermal stress than do mussels several thousand kilometers to the south. Similarly, changes in distribution are not monotonic in time, and reversals have been observed (Hilbish et al. 2010), in accordance with the overlay of increases in temperature resulting from climate change with temporally varying patterns such as the El Niño-Southern Oscillation (ENSO). Regions influenced by ENSO can cause rapid warm episodes and ‘set backs’ during cool periods (Wather et al. 2002). Populations can shift their competitive abilities at their northern and southern boundaries and at the upper vertical distributional boundary (Denny & Paine 1998) where temperatures may be too high or too low for growth, reproduction and/or survival. This marginal shift could lead to a downward swing, resulting in local extinction, poleward expansion or range retraction. Range shifts vary greatly between species, and the distributions of Mytilus populations all over the world are responding differently to climate change. For example, M. californianus along the Strait of Juan de Fuca near Washington state have decreased their vertical distribution by 51% over the past 52 years (Harley 2011), and along the western coast of North America, M. galloprovincialis has contracted southward over 540 km over the past 10 years (Hilbish et al. 2010).
FORECASTING FUTURE RESPONSES

Global climate change is now the backdrop against which all ecological interactions occur. As a result, understanding the processes by which temperature and other climate-related environmental factors drive organismal biology and population and community ecology have taken on a new urgency. In particular, because climate change in many cases will present organisms with conditions never before experienced, the ability to project changes in nature from studies conducted under controlled conditions that reflect those novel environments is becoming increasingly vital (Chown & Gaston 2008). Several approaches have been used to project future changes. Climate envelope models (predictions of future shifts in range edges produced by correlating environmental conditions at existing range boundaries) have become useful tools for making broad-scale predictions about how climate change is likely to affect species boundaries (Hampe 2004). However, a number of recent reviews have criticized these methods because: (i) they often extrapolate from current environmental conditions to novel conditions; (ii) they ignore indirect effects, such as biotic interactions (although these might be implicit in the observed correlations); (iii) they are unable to account for local adaptation and/or acclimatization (Kuo & Sanford 2009); and (iv) they do not incorporate non-climatic factors that might change on local and regional scales (Mustin et al. 2007). As a result, the ‘stationarity’ of these models (i.e. the ability to predict changes in one part of the world from measurements made in another part of the world) is a serious issue. Alternative approaches base future projections on physiological performance (Chown & Gaston 2008). These mechanistic, or process-based, models are inherently much more time consuming than statistically-based models, but have been shown to produce different predictions than envelope models (Kearney et al. 2008). By comparing physiological limits made via measurements under controlled conditions against future conditions estimated at local or regional scales, these models can predict changes in range boundaries that are much more reflective of the actual mosaics that are being observed (as opposed to monotonic range shifts [Helmuth et al. 2006a; Burrows et al. 2011]).

Newer approaches have begun to connect biophysical models with energetics models to predict not only changes in range boundaries, but also to predict altered growth and reproduction (Kearney et al. 2010; Sará et al. 2011). These models fully incorporate what is known about physiological responses to changing environmental conditions using energetics approaches, such as Dynamic Energy Budget models (Kooijman 2009). For example, Sará et al. (2011) apply this approach to M. galloprovincialis in the Mediterranean; their results suggest that while range limitations in the intertidal zone were set by lethal limits at some sites, at others the absence of mussels was more likely set by conditions that led to reproductive failure.

The obvious drawback of these latter approaches is that they require considerable detail about the organism in question and, therefore, are not practical for examining large numbers of species. In this regard, model species such as Mytilus might serve as an excellent focal point because of their economic and ecological importance, and the extensive knowledge compiled about animals in this genus. Nevertheless, a host of challenges remain, including a better understanding of the roles of acclimatization and local adaptation in determining the sensitivity of animals to either gradual or abrupt change; the role of indirect effects on community-level processes, and especially the role of interacting stressors, both climatic and non-climatic in nature. An understanding of all of these processes will be key if we are to project the likely impact of climate change on this animal.

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