CHAPTER THREE

TIPPING POINTS, THRESHOLDS AND THE KEYSTONE ROLE OF PHYSIOLOGY IN MARINE CLIMATE CHANGE RESEARCH

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Abstract

The ongoing and future effects of global climate change on natural and human-managed ecosystems have led to a renewed interest in the concept of ecological thresholds or tipping points. While generalizations such as poleward range shifts serve as a useful heuristic framework to understand the overall ecological impacts of climate change, sophisticated approaches to management require spatially and temporally explicit predictions that move beyond these oversimplified models. Most approaches to studying ecological thresholds in marine ecosystems tend to focus on populations, or on non-linearities in physical drivers. Here we argue that many of the observed thresholds observed at community and ecosystem levels can potentially be explained as the product of non-linearities that occur at three scales: (a) the mechanisms by which individual organisms interact with their ambient habitat, (b) the non-linear relationship between organismal physiological performance and

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variables such as body temperature and (c) the indirect effects of physiological stress on species interactions such as competition and predation. We explore examples at each of these scales in detail and explain why a failure to consider these non-linearities — many of which can be counterintuitive — can lead to Type II errors (a failure to predict significant ecological responses to climate change). Specifically, we examine why ecological thresholds can occur well before concomitant thresholds in physical drivers are observed, i.e. how even small linear changes in the physical environment can lead to ecological tipping points. We advocate for an integrated framework that combines biophysical, ecological and physiological methods to generate hypotheses that can be tested using experimental manipulation as well as hindcasting and nowcasting of observed change, on a spatially and temporally explicit basis.

1. Introduction

Anthropogenic climate change is among the most critical threats facing the world’s natural and human-managed ecosystems (Rockstrom et al., 2009). Numerous studies have documented geographic shifts in species range boundaries (Beaumont and Hughes, 2002; Parmesan and Yohe, 2003; Zacherl et al., 2003), alterations in phenology (Parmesan, 2006; Mitchell et al., 2008) and episodes of mass mortality (Harley, 2008; Harley and Paine, 2009) related to climate change. While temperature is one of the more obvious drivers of these patterns (Tomanek, 2008; Pörtner, 2010; Somero, 2010), stressors such as ocean acidification (OA) (Fabry, 2008; Hoegh-Guldberg and Bruno, 2010) have also been shown to have significant ecological impacts. The biological effects of climate change in turn have enormous economic and societal implications (Climate Change Science Program, CCSP, 2008; Millennium Ecosystem Assessment, 2005). Subsequently, and as highlighted recently by Hoegh-Guldberg and Bruno (2010), there has been an increase in the number of peer-reviewed papers examining climate change and its consequences to the natural world and to human society (Fig. 3.1).

While generalizations such as poleward migrations of species range boundaries or upward shifts in altitudinal distribution in mountain environments have served as a useful heuristic framework for exploring the ecological impacts of climate change, recent evidence suggests that these generalizations may be violated in nature more often than has previously been appreciated. For example, Crimmins et al. (2011) found that despite increases in ambient air temperature, the distribution of 64 plant species shifted downward in elevation during the last ca. 75 years. This pattern was explainable because the negative physiological impacts of increased temperature were overridden by the positive impacts of increases in precipitation, which had also occurred during this time period. Similarly,
numerous studies have now shown that geographic patterns of physiological stress do not always follow simple latitudinal gradients, but rather exhibit ‘mosaic’ patterns over geographic scales (Helmuth et al., 2002, 2006; Holtmeier and Broll, 2005; Finke et al., 2007; Place et al., 2008;
Mislán et al., 2009; Pearson et al., 2009), suggesting that our expectation of what to expect in coming decades may not always be poleward shifts in species range boundaries, but at least in some cases may be localized extinctions even well within range boundaries. Moreover, recent studies have documented geographic variability in physiological tolerance (Pearson et al., 2009) and have experimentally shown evidence of local adaptation (Kuo and Sanford, 2009). All of these studies suggest that a detailed understanding of the mechanisms underlying the complex interaction between changes in the physical environment and organismal and ecological responses is vital if we are to predict future patterns of biodiversity, distribution and abundance, and that simple generalizations are not always effective as working null hypotheses.

Moreover, increasingly sophisticated adaptation planning by a wide array of decision makers demands quantitative predictions of ecological impacts of climate change, often at fine spatial and temporal resolutions, along with associated estimates of uncertainty. For example, the emplacement of protected areas (Hoffinan, 2003), predictions of fishery, crop and livestock productivity (CCSP, 2008) and estimates of the spread of disease and invasive species (Chown and Gaston, 2008; Kearney et al., 2008; US EPA, 2008) all demand quantitative, spatially and temporally explicit predictions of how climate change is likely to impact organisms and ecosystems (Ludwig et al., 2001). Predictions that are based on simple generalizations are highly unlikely to be able to capture the spatial and temporal complexity of the real world in order to effectively plan and prepare for ongoing and future climate change impacts.

Furthermore, the public’s perception of climate change, and their trust in the scientific community’s understanding of climate change, is significantly affected by the frequency by which scientific predictions are borne out. Simple generalizations, while logically tractable, are not always the expected outcome, as shown by Crimmins et al. (2011). Nevertheless, when patterns contrary to sweeping generalizations are reported, they are often viewed by ‘climate skeptics’ as evidence of the falsehood of climate change or, worse, of the duplicity of scientists. In a recent opinion piece, Parmesan et al. (2011) stated that any attempts to attribute individual responses to climate change were ‘ill advised,’ suggesting that because such cause and effect linkages were too complex, the scientific community should instead focus on overarching trends. In stark contrast, however, data collected by communication experts have shown that when scientists make explicit predictions that can then be tested in a transparent manner, even at the risk of failure, this builds trust between the public and the scientific community (Goodwin and Dahlstrom, 2011). Thus, explicit, testable predictions made using mechanistic approaches (Helmuth et al., 2005) not only provide useful information to decision makers, and potentially elucidate important principles by which weather and climate affect organisms.
and ecosystems, but may also play an important role in discourse between scientists and the public.

While several recent authors have highlighted the importance and power of cross-disciplinary research when exploring the ecological impacts of climate change (Wiens and Graham, 2005; Stenseth, 2007; Chown and Gaston, 2008; Denny and Helmuth, 2009; Hofmann et al., 2010), in many ways such collaborations have yet to be fully realized. To a large extent, environmental data are collected, archived and disseminated with little or no thought given to their potential biological applications (Helmuth et al., 2010). Similarly, many physiological studies are conducted with only a limited ecological context, and vice versa (Denny and Helmuth, 2009). When such studies are used in the decision-making process, they also frequently fail to take the needs of end-users into consideration (Agrawala et al., 2001).

Here we discuss some of the underlying reasons why an understanding of the detailed mechanisms by which weather and climate (both terrestrial and oceanic) affects organisms and ecosystems can fundamentally alter our predictions of the ecological impacts of climate change. We focus primarily on coastal marine invertebrates using the concept of ‘tipping points’ (ecological thresholds) to explore the importance of these details. We advocate for an interdisciplinary, mechanistic approach, explicitly embedded within a collaborative framework that combines assessments of physiological performance, organismal biology and population and community ecology performed at different scales. Specifically, we argue that many of the observed instances of tipping points are explainable given non-linearities in how environmental signals are translated into physiological responses, and subsequently how those physiological responses drive species interactions and population dynamics that affect ecosystem-level patterns. We divide these non-linearities into three broad categories: (a) the translation of environmental parameters (‘habitat’, as in Kearney, 2006) into niche-level processes such as body temperature; (b) the physiological consequences of these niche-level processes and (c) the indirect, ecological effects of physiological stress on species interactions.

The goal of this chapter is not to provide an exhaustive review of studies of ecological thresholds in marine ecosystems: a recent special issue of Marine Ecology Progress Series (Osman et al., 2010) provides an excellent overview of the current state of the field. Nor is it our intention to imply that studies or approaches that focus on populations or ecosystems rather than on individual organisms and physiological responses are flawed. For example, catastrophic physical disturbance such as damage from hurricanes obviously can play a large role in driving phase shifts and may have no connection to physiological performance (although, physiological performance may contribute to recovery from such events, sensu Highsmith et al., 1980). However, current discussions of the concept of ecological thresholds/tipping points seldom incorporate the physiological performance of the constituent organisms, despite an increasing number of studies focused on ecological thresholds in
the context of global climate change (Fig. 3.1B). For example, the CCSP of the United States, recently released the Synthesis and Assessment Product 4.2 (SAP 4.2), *Thresholds of Climate Change in Ecosystems*, a comprehensive report that specifically elaborates on our current knowledge of ecological thresholds at the ecosystem level and provides guidelines for resource managers who are forced to contend with the uncertain scenarios presented by global climate change. The document lists areas where further research is needed to fill the many gaps in our current understanding of the causes and consequences of ecological thresholds (CCSP, 2009), and advocates for an integrative approach as a means for dealing with cross-scale interaction processes. Notably, however, because the report primarily focuses on large-scale ecosystem responses, it generally fails to recognize the importance of examining the impacts of weather and climate at organismal scales (Somero, 2010). Our goal is therefore to demonstrate how much can potentially be learned through an integrated approach that includes an understanding of the mechanisms underlying thresholds, including biophysical interactions between organisms and their environment, and physiological consequences of climate change at organismal scales (Sanford, 2002a; Pörtner et al., 2006).

1.1. Non-Linearities, tipping points and concepts of scale

A system is said to be non-linear when its inputs and outputs are disproportionate to one another (Hilbert, 2002). Within an ecosystem context, the term input thus refers to any relevant abiotic variable, e.g. precipitation or air temperature, or a biotic component such as a keystone predator (Menge et al., 1994), and the output is any physiological or ecological process such as an organism's phenology, reproductive output or ecological interactions (Sanford, 2002a; Pincebourde et al., 2008). The CCSP SAP 4.2 report defines an ecological threshold (tipping point) as 'the point where there is an abrupt change in an ecosystem quality, property, or phenomenon or where small changes in an environmental driver produce large, persistent responses in an ecosystem, which is not likely to return to the previous more stable state’ (CCSP, 2009).

Studies of ecological thresholds are extremely valuable for planning conservation strategies, as they can shed light on an ecosystems’ sensitivity to environmental change (Littler and Littler, 2007; Briske et al., 2010). Studies performed at the community and ecosystem levels of organization have also detected the presence of tipping points that set the boundary between different ecological states (Scheffer et al., 2001), although other authors have suggested that the simple dichotomy between alternative stable states, while intellectually appealing, may be an oversimplification of a much more complicated process (Dudgeon et al., 2010). Long-term observations of community-level dynamics have allowed for both empirical and theoretical descriptions of major phase shifts and/or alternative
stable states (Hare and Mantua, 2000; Casini et al., 2009; Dudgeon et al., 2010) in marine systems such as coral reefs (Idjadi et al., 2006) and rocky intertidal communities (Petraitis et al., 2009). Characterizing these higher-level changes has proven useful for ecologists and wildlife managers, since they provide an overall understanding of the main environmental variables shaping natural systems.

So far, most studies of threshold effects in marine systems have measured and modelled processes at community and ecosystem scales. Empirical studies that only concentrate on higher-level dynamics can seldom tease apart the underlying factors driving systems to change, which often restricts conclusions to pure documentations of the observed patterns. Of course, a focus on community- and ecosystem-level processes does not mean that authors do not recognize the importance of underlying biological processes at the scale of the organism (Hewitt and Thrush, 2010). For example, Norkko et al. (2010) manipulated disturbance via hypoxia at scales ranging from 1 to 16 m² and monitored recovery by infaunal and epifaunal organisms living in soft substrate communities. Their results highlighted the importance of considering life-history characteristics (epifaunal/infaunal) and mobility (dispersal) of the organisms in driving the resilience and recovery of the benthic community. There are also excellent examples of the power of considering physiological performance in the context of ecological thresholds (Littler and Littler, 2007; Hofmann et al., 2010). Most notably, recent studies of OA squarely place an emphasis on measuring the effects of decreases in pH on growth and survival of ecologically key species when attempting to understand and predict ecological consequences at large scales (Fabry, 2008, Hofmann et al., 2010). For example, McNeil and Matear (2008) measured and modelled levels of carbonate (CO$_3^{2-}$) and pH in the southern ocean, and then projected the impact on rates of calcification by key plankttonic species. Their results suggested that the pteropod *Limacina helicina* Philps, 1774, was likely to be severely impacted during larval development. This species is ecologically important, comprising up to ~65% of the total zooplankton in the Ross Sea, and the thecosome shells of this and other pteropod species are thought to be a major contributor to the carbonate flux of the deep ocean south of the Polar Front (Hunt et al., 2008).

Understanding the physiological responses of calcifying organisms such as pteropods, corals (Hoegh-Guldberg et al., 2007) and coccolithophores (Fabry, 2008) to changes in ocean pH thus clearly has significant ecological consequences, and therefore physiological performance is likely to have a direct impact on the probability of phase transitions/ecological thresholds occurring.

Many recent studies have further emphasized the importance of considering physiological performance in determining local and biogeographic patterns of distribution (Somero, 2005; Helmuth et al., 2006; Pörtner et al., 2006; Gedan and Bertness, 2009), an approach often termed
‘macrophysiology’ (Chown et al., 2004; Chown and Gaston, 2008). For example, Wethey and Woodin (2008) compared long-term records of sea surface temperature against known physiological thresholds of the barnacle *Semibalanus balanoides* and showed that observed range shifts were consistent with winter temperatures known to cause reproductive failure in this species. However, studies that span scales from molecular to biogeographical remain rare (Pörtner et al., 2006; Denny and Helmuth, 2009; Pearson et al., 2009; Hofmann et al., 2010). Moreover, a number of studies have shown that organisms may be living close to their physiological tolerances even well within their range limits (Sagarin and Somero, 2006; Place et al., 2008; Beukema et al., 2009), and have warned that, conversely, physiological stress is not always the limiting factor at species range edges (Davis et al., 1998a,b). Thus, while understanding the relationship between the physiological performance of key species and ecological thresholds may not always be simple (Hutchins et al., 2007; Crain et al., 2008), a failure to consider these effects can potentially lead to Type II errors, i.e. we may be surprised by sudden phase shifts due to non-linearities that ultimately originate at (sub)organismal scales. Understanding when such events are likely to occur, and the mechanisms that lead to their occurrence, is therefore critical. Perhaps even more importantly, as recently discussed by Mумby et al. (2011), tipping points may be preceded by significant alterations in ecosystem function that, while not meeting the definition of a ‘threshold’, nevertheless may have catastrophic ecological, economic and societal implications. For example, declines in ecosystem services may occur well before threshold events are observed. As a result, Mумby et al. (2011) argue that while threshold events are important, we must not lose focus on the importance of predicting declines in other metrics of ecosystem performance. In this review we explore how small, often linear changes in physical drivers may potentially lead to large, non-linear responses in ecological systems. As a result, ecological tipping points may theoretically occur long before any comparable changes in the physical environment are observed. However, such methods may also be applied to the agenda set forth by Mумby et al. (2011), in that they provide a mechanistic framework that can be used to predict potential ‘trouble areas’ not just in terms of threshold events but also in terms of declining ecosystem function.

### 2. Weather, Climate and Climate Change from the Viewpoint of a Non-Human Organism

Climate change is a global phenomenon, but to an organism the ‘world’ can be exceedingly small. Consider for example an intertidal barnacle. As a cyprid floating in the water column, only the immediate
conditions of pH, temperature and food surrounding the animal affect its physiology. To that larval animal, it does not matter if it is entrained in a gyre or in the nearshore swash zone per se, but rather what its location within either of those larger-scale phenomena means to its immediate physical and biological environment. As the animal moves onshore, it encounters levels of turbulence, temperature, pH and nutrients different from those in the immediate nearshore environment (Pineda and Lopez, 2002; Pfister et al., 2007; Wootten et al., 2008). Importantly, those conditions likely could not have been predicted given measurements made just offshore (Pfister et al., 2007). Eventually, as the larva reaches the intertidal zone where it settles, metamorphoses and grows into an adult barnacle, it experiences not only the conditions of the subtidal environment, but also those of the terrestrial environment during low tide, conditions which can vary markedly with intertidal zonation height (Wethey, 1983). Perhaps not surprisingly, all point to the fact that the physical environment for these animals, like that for many others, is highly spatially and temporally heterogeneous (Denny et al., 2004, 2011).

Nevertheless, in many cases, measurements conducted at moderate to large spatial scales, e.g. by satellite and buoy, appear to provide considerable insight into large-scale ecological processes (Schoch et al., 2006; Blanchette et al., 2008; Gouhier et al., 2010). Similar concordance appears over large temporal scales, and when looking at the ecological influences of climate indices such as the El Niño Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and the Pacific Decadal Oscillation (PDO; Stenseth et al., 2002, 2003; Forchhammer and Post, 2004). However, as pointed out by Hallet et al. (2004), the seemingly superior ability of these large-scale indices to predict biological responses than higher frequency weather data may lie in a failure to take mechanism into account. Using detailed data from a population of Soay sheep, Hallet et al. (2004) showed that high rainfall, high winds or low temperatures could all contribute to the mortality of sheep, either immediately or with a lag. In other words, the association between each of these variables and the timing of mortality varied significantly between years, so that overall there appeared to be no pattern. Without an understanding of the underlying physiological mechanistic drivers, simple correlations between any single variable such as rainfall and mortality failed to uncover any relationship, giving the false impression that climatic indices were a better predictor of ecological response than were weather variables. However, when variables such as rainfall and air temperature were used in an integrated context that considered not only their direct physiological effects but also their indirect effects on food, etc., a highly significant relationship emerged (Hallet et al., 2004) that had greater explanatory power than did climatic indices. Such may be the case for many environmental factors that are often dismissed as irrelevant due to their apparent lack of
concordance with biological processes: by assuming a direct relationship between variables such as solar radiation, air and water temperature, or food availability and population responses, we fail to consider that these variables interact in non-linear ways, and are filtered through the functional traits of the organisms that they are affecting (Kearney, 2006; Kearney et al., 2010).

A case in point is how weather variables are translated into physiologically and ecologically relevant terms such as body temperature (Kearney, 2006). While we may be interested in climate change, it is weather (as affected by climate) that drives physiological responses. Global climate change encompasses change in numerous ‘environmental signals’ (Helmuth, 2009) including ocean pH, sea level, salinity and temperature. Importantly, however, the only environmental signals that matter to an organism directly are those that the organism experiences, i.e. those at the level of the niche (Kearney, 2006). The physiological niche of an organism is driven by the interaction of an organism’s morphology, size and behaviour with its local microhabitat, and is therefore often very different from measurements of large-scale, habitat-level parameters such as air or water temperature (Marshall et al., 2010; Helmuth et al., 2006, 2011). Thus, two species inhabiting the same microhabitat may experience radically different physiological drivers such as body temperature. For example, as has been shown for many species in both terrestrial and intertidal environments, the flux of heat is driven by the interaction of multiple environmental factors, including solar radiation, wind speed, air temperature and relative humidity (Porter and Gates, 1969; Bell, 1995; Marshall et al., 2010). Moreover, the characteristics of the organism — mass, colour, surface wetness, etc. — significantly alter heat flux so that two organisms exposed to identical environmental parameters can experience markedly different body temperatures (Broitman et al., 2009). In some cases, the difference between body temperature and environmental temperature can be fairly minor, e.g. when animals continually live in the shade or in deep water environments.

In other cases, the difference in temperature between an ectothermic organism and its surroundings is quite remarkable. The body temperatures of ectothermic animals in the sun are generally significantly hotter than the temperature of the surrounding air (Marshall et al., 2010). Only in cases where animals lose heat through the evaporation of water, or through infrared radiation at night, is body temperature likely to be significantly lower than that of air or surface temperature (Bell, 1995; Helmuth, 2002). These observations are significant, because they suggest that for many organisms (e.g. those that are unable to evaporatively cool or for which desiccation is a limitation), air temperature is likely to set the lower limit to body temperature during the day, and solar radiation then increases body temperature above that minimum. Critically, this also means that convective heat transfer serves to bring the temperature of the
animal closer to that of the surrounding air, i.e. cooler, even in the absence of evaporation. For example, recent modelling suggests that predicted increases in the mean wind field along the west coast of the United States may in some cases counteract the effect of increases in ambient air temperature on animal body temperature, at least for animals with dry surfaces (Helmuth et al., 2011). In contrast, for animals with wet surfaces (seastars, seaweeds), the forecasted increase in mean wind may have a greater physiological impact through increased desiccation stress (Bell, 1995). Importantly, this does not mean that changes in parameters such as air temperature are unimportant; if all other environmental factors remain unchanged, increases in air temperature will lead to increases in body temperature (Fig. 3.2). However, in some cases the importance of variability or long-term change in air temperature can be overridden by other factors such as wind speed, wave splash (Helmuth et al., 2011) or the timing of when low tide occurs (Mislan et al., 2009).

Moreover, these results indicate that increases in body temperature cannot be based on changes in any one environmental parameter. Figure 3.2 shows the results of a simple heat budget model for a generic ectotherm, in which all parameters are identical except for wind speed. In the three simplified scenarios shown, body temperature increases linearly with air temperature, i.e. the coefficient of determination is 1.0. However, the y intercept varies markedly depending on which value of wind speed is used. In the first scenario (wind speed = 0.25 m s⁻¹), an increase in air temperature from 15°C to 20°C leads to an increase in body temperature from 33°C to 38°C; in the second scenario, the same change in air

![Figure 3.2](image-url) Translation of habitat-level parameters such as air temperature to niche-level parameters (which drive physiology) such as body temperature. The figure shows a steady-state heat budget for a generic ectotherm under identical conditions of solar radiation and cloud cover, over a range of air temperatures, and with wind speeds of (A) 0.25 m s⁻¹, (B) 1.0 m s⁻¹ and (C) 2.5 m s⁻¹. In this simplified example, body temperature increases linearly with increasing air temperature. Notably, the y intercept varies with wind speed, so that a 5°C increase in air temperature results in shifts between very different magnitudes of body temperature.
temperature, but with a wind speed of 1.00 m s\(^{-1}\), leads to a change in body temperature from 30°C to 35°C; in the third scenario, with a wind speed of 2.50 m s\(^{-1}\), the same change in air temperature leads to a change in body temperature from 26°C to 31°C. Clearly, simply measuring the temperature of the habitat (air), or even the change in the air temperature, is not sufficient to assess how the changing environment will impact the organism.

In the steady-state scenario shown in Fig. 3.2, all parameters except wind speed are held constant, and body temperature increases linearly with air temperature. Under natural field conditions it is unclear how often this holds true, but in the few cases where explicit comparisons have been made it appears that the relationship between air and body temperature can be extremely poor. Marshall et al. (2010) compared maximum air temperature at low tide to the body temperature of intertidal snails and found that there was no correlation between the two temperatures; at times the temperature of the animal could be 22°C above that of the air. Helmuth et al. (2011) compared maximum air temperature at low tide to the temperature of biomimetic loggers designed to mimic the temperature of intertidal mussels and reported a coefficient of determination of only 0.14, with differences of up to 19°C between air and animal temperature. They also showed that mussel (logger) temperatures were frequently high even on days when air temperatures were low and vice versa. Broitman et al. (2009) compared the temperatures of predators (*Pisaster ochraceus* Brandt, 1835) to those of their prey (*Mytilus californianus* Conrad, 1837) under identical microclimatic conditions at four sites, two on each end of Santa Cruz Island, CA. They found that on the west side of the island, the temperatures of predators and prey were very similar, but on the east side of the island, the body temperatures of the predator and prey were very different from one another, even though in all cases both species were exposed to identical weather conditions at each site. Again, these results point to the interaction between multiple weather variables, and between weather and the functional traits of the organism (Kearney et al., 2010) in driving the body temperature of ectotherms and demonstrate the highly non-linear nature of the relationship between ‘habitat’ and ‘niche’ (Kearney, 2006).

While arguments regarding heat flux apply most directly to terrestrial organisms and intertidal organisms exposed to air at low tide, studies have shown that in shallow water, solar radiation can raise the temperature of coral tissue by several degrees when rates of convection (i.e. water flow) are sufficiently low (Fabricius, 2006; Jimenez et al., 2008). Analogous arguments can also be made for the exchange of gas and nutrients in subtidal environments, where the flux of these substances is driven not only by concentration gradients but also by fluid flow (Lesser et al., 1994). As elegantly discussed by Patterson (1992), the characteristics of fluid flow
around the respiratory and feeding structures of subtidal organisms determine rates of exchange of oxygen, bicarbonate and nutrients through their effects on the diffusion boundary layer (Shashar et al., 1996). A generic equation to describe the exchange of any mass item thus includes a mass transfer coefficient \( h_m \), an empirically derived parameter that describes the interaction of an organism with the surrounding flow:

\[
d_m/dt = h_m A (C_o - C_i)
\]  

(3.1)

where \( dm/dt \) is the rate of mass flux; \( h_m \) is the mass transfer coefficient, \( A \) is the area over which exchange occurs, and \( C_o \) and \( C_i \) are the concentrations of the mass item of interest (e.g. \( O_2 \)) outside and inside of the organism, respectively. The mass transfer coefficient changes non-linearly with increasing flow (Fig. 3.3), and is lower for ‘streamlined’ animals than for animals with a bluff body. (The equation for convective heat exchange is functionally identical, except that a heat transfer coefficient, \( h_c \), is used to describe the effect of morphology on the rate of heat exchange, which is affected by a temperature gradient rather than a concentration gradient.)

Numerous studies have documented the important role of mass flux in driving the physiological ecology of benthic organisms. Both laboratory (Nakamura et al., 2003) and field studies (Nakamura and van Woesik, 2001; Finelli et al., 2006) have shown that increased mass flux reduces the rate of coral bleaching through the removal of excess oxygen, which reduces oxidative stress (Lesser, 1996, 1997, 2004). As with heat exchange in the terrestrial environment, the morphology of an organism can significantly affect fluid flow, so that two organisms exposed to identical flows,
and/or identical concentrations of gases, can experience very different rates of passive gas uptake. Lenihan et al. (2008) showed an effect of reef structure (height and morphology) on rates of bleaching in Moorea, French Polynesia. At a much smaller scale, Finelli et al. (2007) found that intracolony variability in coral bleaching could be explained by differences in flow, which in turn was affected by coral morphology. Thomas and Atkinson (1997) showed that rates of flow and surface roughness controlled rates of ammonium uptake by corals. These results demonstrate why simply measuring the concentration of oxygen, bicarbonate or ammonium is not sufficient to estimate rates of exchange; two organisms exposed to identical ‘habitats’ (gas or nutrient concentrations) will experience markedly different rates of uptake depending on how their functional traits/morphology interact with local flow.

Directly analogous studies have shown the non-linear relationship between water flow and the risk of dislodgement by sessile organisms, especially those in wave-swept environments (Denny and Gaylord, 2010). The force of drag acting upon an organism varies as the square of water velocity, so that small changes in flow can result in large changes in the force of drag acting on an organism:

\[
\text{Drag} = \frac{1}{2} \rho A C_d U^2
\]

where \(A\) is the area upon which the fluid acts, \(\rho\) is fluid density, \(C_d\) is the drag coefficient, and \(U\) is fluid velocity. As above, the \(C_d\) is a function of organism morphology, and a bluff body has a much higher \(C_d\) than does a streamlined organism. Similarly, the force of lift also scales with the square of \(U\) (Denny and Gaylord, 2010). Numerous studies have examined the interactions between the fluid environment and the risk of dislodgement of sessile organisms, noting that one prediction of climate change in many regions is an increase in wave height (Boller and Carrington, 2007; Carrington et al., 2009). While some studies have suggested that the relationship between increasing wave height and onshore wave velocity may be more complex than expected due to the tendency of larger waves to break farther offshore (Helmuth and Denny, 2003) and because of the overwhelming importance of small-scale topography in affecting local flows (Denny et al., 2004), these results nevertheless point to the potentially important, highly non-linear relationship between small increases in wave height, water flow and the risk of dislodgement.

Thus, almost never are interactions between organisms and their physical environment, or interactions between the physical parameters acting on organisms, linear in their impacts. For example, heat and mass transfer coefficients, which describe the interactions between the morphology of an organism (or colony) and the surrounding fluid in driving heat or mass (e.g. gases and nutrients), are usually a nearly asymptotic function, in which small changes in fluid velocity initially lead to a large change in
exchange of mass or heat. After a point, however, further increases in flow lead to very little change in heat or mass flux (Fig. 3.3). Small increases in wind speed initially have a large effect of cooling through convection, but once wind serves to bring the temperature of an organism close to the temperature of the surrounding air, very little change occurs with further increases in wind speed. Likewise, small increases in water flow can initially lead to large increases in gas or nutrient flux, but past some threshold make little difference. Conversely, when conditions of wind or flow decrease, initial changes may result in little change when the range of conditions corresponds to the ‘plateau’ region of the curve, but below some threshold, rapid changes may ensue with even subtle drops in flow. Note that these relationships starkly contrast with the relationship between water flow and drag, which increases exponentially. In essence, therefore, these non-linearities thus create tipping points as environmental parameters at the habitat level are translated into changes at the niche level (Kearney, 2006): linear changes in parameters such as flow speed, wave height or air temperature can lead to non-linear changes in physiologically relevant parameters such as body temperature or gas flux, and thus to the likelihood of reproductive failure and mortality of key species.

3. Physiological Response Curves

Although changes in niche-level responses such as body temperature and oxygen exchange are the proximal drivers of physiological response, ultimately cellular- and subcellular-level reactions will determine the consequences of those environmental changes (Somero, 2010). For example, Carrington (2002) has shown that the attachment strength of mussels (Mytilus edulis Linnaeus, 1758) varies seasonally, and is twofold higher in winter than in summer. However, the match between wave force and attachment strength is not perfect, and during hurricane season mussels are only weakly attached. Their results suggest a potential energetic trade-off between the production of byssal threads and energy devoted to reproduction (Carrington, 2002), and emphasize the critical importance of measuring not only environmental variables but also the vulnerability of organisms to their physical environment (Helmuth et al., 2005).

One of the best ways to describe an organism’s response to changing environmental conditions is through the use of physiological performance curves. Physiological performance curves have long been used to define the complex relationships between organism responses related to fitness, such as growth, reproduction and survival and factors such as body temperature (although, notably, many studies mistakenly have used habitat
temperature as the independent axis, incorrectly assuming that it is equivalent to body temperature). Performance curves describe both an organism’s physiological limits to survival and the conditions under which that organism can survive and reproduce (Huey and Stevenson, 1979; Angilletta et al., 2002, 2003). Importantly, these curves are almost always ‘left skewed’ in that fairly large increases in body temperature (or other factor) above some lower threshold generally lead to only modest changes in performance (Fig. 3.4) until a maximal level of performance ($P_{\text{max}}$) is reached, at body temperature $T_{\text{max}}$ (or $T_{\text{opt}}$; Dewitt and Friedman, 1979; Angilletta, 2009). Above that optimum, however, performance declines rapidly with increasing temperature. Thus, at temperatures above $T_{\text{max}}$, small changes in body temperature can have significant impacts on survival and reproduction.

Returning to the scenario presented in Fig. 3.2, when a biophysical approach using a heat budget model is combined with a physiological performance curve, the importance of considering the non-linearities involved in how habitat-level parameters are translated into physiological responses becomes apparent. Under conditions of wind speed $= 2.5 \text{ m s}^{-1}$, a 5°C increase in air temperature from 15°C to 20°C leads to an increase in body temperature from 26°C to 31°C (Fig. 3.5A). When this change in body (not air) temperature is translated to a physiological (thermal) performance
curve, this leads to an increase in physiological performance, as the temperature of this hypothetical animal is brought closer to $T_{\text{max}}$ (Fig. 3.5B). In contrast, an increase in air temperature from 15°C to 20°C but coupled with a wind speed of 0.25 m s$^{-1}$ leads to an increase in animal body temperature from 33°C to 38°C — enough to shift the animal's temperature from a point near its optimum to its lethal limit (Fig. 3.5, in red).

3.1. Thermal physiology of marine organisms

Describing an organism’s physiological performance curve under a range of physical conditions is considered a fairly straightforward analysis that can provide valuable information on how individual organisms respond to their environment, the energetic trade-offs that emerge from specific responses (Angilletta et al., 2003), and the evolutionary consequences of such responses (Kingsolver et al., 2004). However, while this approach has been used with great success by terrestrial ecologists, marine ecologists have rarely described a species’ performance throughout its entire thermal range, especially for invertebrates. Although some excellent examples of marine species performance curves can be found in the literature (Table 3.1), marine invertebrate physiologists have primarily focused either on identifying thermal limits ($C_{T\text{max}}$ and $C_{T\text{min}}$), or on contrasting the effects of a few habitat temperatures covering only portions of a species’ whole thermal range. Here we follow Angilletta’s (2009, p. 36)
<table>
<thead>
<tr>
<th>Phylum</th>
<th>Species</th>
<th>Performance trait</th>
<th>$P_{\text{max}}$</th>
<th>$T_{\text{max}}$</th>
<th>$T_{\text{min}}$</th>
<th>$T_{\text{CT}_{\text{max}}}$</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mollusca</td>
<td><em>Nucella lamellosa</em> adult</td>
<td>Crawling rate</td>
<td>40 cm h$^{-1}$</td>
<td>20</td>
<td>0</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>Mollusca</td>
<td><em>Nucella lamellosa</em> juvenile</td>
<td>Crawling rate</td>
<td>30 cm h$^{-1}$</td>
<td>5—20</td>
<td>0</td>
<td>30</td>
<td>1</td>
</tr>
<tr>
<td>Mollusca</td>
<td><em>Nucella ostrina</em></td>
<td>Crawling rate</td>
<td>23 cm h$^{-1}$</td>
<td>5—10</td>
<td>0</td>
<td>25</td>
<td>1</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Mytilus</em> sp.</td>
<td>Speed of cilia</td>
<td>334 mm s$^{-1}$</td>
<td>32.5</td>
<td>&lt;0</td>
<td>40</td>
<td>2</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Semibalanus balanoides</em></td>
<td>Cirral activity</td>
<td>0.63 beats s$^{-1}$</td>
<td>21</td>
<td>&lt;2.3</td>
<td>31</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Semibalanus balanoides</em></td>
<td>Cirral activity</td>
<td>0.56 beats s$^{-1}$</td>
<td>18.4</td>
<td>&lt;1.8</td>
<td>31.5</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Chthamalus stellatus</em></td>
<td>Cirral activity</td>
<td>1 beats s$^{-1}$</td>
<td>30</td>
<td>4.6</td>
<td>37.5</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus perforatus</em></td>
<td>Cirral activity</td>
<td>0.9 beats s$^{-1}$</td>
<td>25.2</td>
<td>6</td>
<td>36</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus perforatus</em></td>
<td>Cirral activity</td>
<td>0.94 beats s$^{-1}$</td>
<td>30.3</td>
<td>6</td>
<td>35.2</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus crenatus</em></td>
<td>Cirral activity</td>
<td>1 beats s$^{-1}$</td>
<td>21.3</td>
<td>&lt;4.3</td>
<td>25.5</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Elminius modestus</em></td>
<td>Cirral activity</td>
<td>2.2 beats s$^{-1}$</td>
<td>24.2</td>
<td>2</td>
<td>33</td>
<td>3</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Lepas anatifera</em></td>
<td>Cirral activity</td>
<td>0.28 beats s$^{-1}$</td>
<td>19.8</td>
<td>0.5</td>
<td>33</td>
<td>4</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus improvisus</em></td>
<td>Cirral activity</td>
<td>0.11 beats s$^{-1}$</td>
<td>30</td>
<td>−2</td>
<td>35.5</td>
<td>4</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus amphitrite</em></td>
<td>Cirral activity</td>
<td>0.14 beats s$^{-1}$</td>
<td>29.9</td>
<td>6</td>
<td>38.4</td>
<td>4</td>
</tr>
<tr>
<td>Arthropoda</td>
<td><em>Balanus balanus</em></td>
<td>Cirral activity</td>
<td>0.48 beats s$^{-1}$</td>
<td>20.2</td>
<td>−2</td>
<td>30</td>
<td>4</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Botryllus schlosseri</em></td>
<td>Reproductive output</td>
<td>2 larvae colony$^{-1}$ week$^{-1}$</td>
<td>25</td>
<td>15</td>
<td>&gt;25</td>
<td>5</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Botryllus schlosseri</em></td>
<td>Growth rate</td>
<td>28 zooids colony$^{-1}$ 70 day$^{-1}$</td>
<td>20</td>
<td>5</td>
<td>&gt;25</td>
<td>5</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Botrylloydies violaceus</em></td>
<td>Growth rate</td>
<td>20 zooids colony$^{-1}$ 70 day$^{-1}$</td>
<td>20</td>
<td>5</td>
<td>&gt;25</td>
<td>5</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Salmo trutta</em> juvenile</td>
<td>Growth rate</td>
<td>0.3 g day$^{-1}$ (1 g fish)</td>
<td>16.8</td>
<td>1.24</td>
<td>24.74</td>
<td>6</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Salmo trutta</em> juvenile</td>
<td>Feeding rate</td>
<td>1.25 attempts min$^{-1}$</td>
<td>17.3</td>
<td>&lt;2.6</td>
<td>&gt;24</td>
<td>6</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Oncorhynchus nerka</em> juvenile</td>
<td>Growth</td>
<td>25% wet weight day$^{-1}$</td>
<td>15</td>
<td>&lt;1</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Oncorhynchus nerka</em> adult</td>
<td>Growth</td>
<td>15% wet weight day$^{-1}$</td>
<td>15</td>
<td>&lt;1</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>Chordata</td>
<td><em>Oncorhynchus nerka</em></td>
<td>Food intake</td>
<td>27% body dry weight</td>
<td>17</td>
<td>&lt;5</td>
<td>24</td>
<td>7</td>
</tr>
</tbody>
</table>

Temperatures are in °C.
References:
(1) Bertness and Schneider (1976), (2) Gray (1923), (3) Southward (1955a,b), (4) Southward (1957), (5) Epelbaum et al. (2009), (6) Ojanguren et al. (2001) and (7) Brett (1971).
definition of performance as ‘any measure of the organism’s capacity to function, usually expressed as a rate or probability’. The decision of which specific trait(s) to evaluate is of great importance for the conclusions that one can draw from response curves. In essence, one should consider the species’ niche-dependent requirements and measure those traits that most closely contribute to fitness (i.e. lifetime reproductive success). For instance, foraging rates and/or success are considered proxies of an organism’s fitness, but the way these are estimated is entirely dependent upon the organism’s life history. For example, the adult seastar *Leptasterias polaris* Müller and Troschel, 1842, a major subtidal predator inhabiting soft sediments in the northern Gulf of St. Lawrence (Canada), relies on its ability to sense the odour of infaunal prey to guide its digging efforts and to forage efficiently (Thompson et al., 2005). Using odour sensitivity as a performance trait for *L. polaris* is consistent with its ecological niche; this trait would reflect a potential for survival and reproduction under different environmental conditions (e.g. current speed and water temperature). In contrast, for predators that rely on other traits to forage efficiently such as vision or speed, measuring odour sensitivity as a performance trait would not tell us anything about the mechanisms that drive their ecological responses.

Recent studies with marine species of crabs, fish, bivalves and polychaetes have used the concept of oxygen and capacity-limited thermal tolerance (Pörtner et al., 1999; Sommer and Pörtner, 1999; Frederich and Pörtner, 2000; Pörtner and Farrell, 2008; Kassahn et al., 2009;) to explain the mechanism that regulates both an organism’s thermotolerance windows (CTs) and thermal optima (*T*_max). The theory states that detrimental temperatures bring about insufficient oxygen supply and transport to tissues, which coupled with high baseline oxygen demand at elevated temperatures likely shapes the typical ‘left-skewed’ thermal performance curve (Fig. 3.4; Angilletta, 2009).

Traditional life-history traits used to describe physiological performance curves include lifetime reproduction (e.g. fecundity and reproductive output), growth (e.g. change in size or body mass), feeding/assimilation (e.g. feeding rate and chemosensory ability), development rate and locomotion (e.g. speed and distance covered). Some investigators have also included survival probability — or any proxy for it such as righting response or burrowing capacity (Angillette, 2009); we believe such studies are necessary for identifying temperature critical limits, but because they do not provide quantifiable information of an organism’s potential reproductive contribution (other than zero or ‘maybe’), we opt not to consider them as strict fitness-related performance traits.

From the traditionally measured traits listed above, lifetime reproduction is considered the most closely related to fitness; unfortunately quantifying the lifetime contribution of an individual through
reproduction is not an easy task (Angilletta, 2009), especially for broadcasting species with pelagic life-cycle stages, which are common in coastal marine ecosystems (Thorson, 1950). An example of a reproductive performance curve is given by Epelbaum et al. (2009) (Table 3.1), who tested the interactive effects of water temperature and salinity on two invasive species of colonial ascidians now present throughout much of the northeast Pacific, Botryllus schlosseri Pallas, 1766, and Botryllus violaceus Oka, 1927 (Lambert, 2005). The study included virtually the entire thermotolerance window, of the species (Brunetti et al., 1980), and captured the conditions where reproduction and growth would be maximized (Table 3.1). It is worth noting that, for B. schlosseri, CTmin is greater when reproduction is used as the performance trait than when growth is used (Table 3.1). This occurs because reproductive output, unlike growth, is stalled when temperatures are lower than 20°C, a trade-off commonly observed in marine invertebrates (Sebens, 2002; Sibly and Atkinson, 1994).

Because body size is a relatively straightforward parameter to measure, growth is commonly used as a performance trait. In addition, growth is regarded as a fairly accurate proxy for fitness. An organism’s growth represents a net yield, which results from the difference between energy costs (metabolic cost) and benefits (ingestion/assimilation rate) (Levinton, 1983; Sanford, 2002a). Thus, aquaculture-driven research has dedicated a considerable amount of effort to understanding energetic constraints on a number of marine and freshwater species of interest (e.g. salmon and trout species). For example, Ojanguren et al. (2001) elegantly describe thermal performance curves for juvenile activity levels, feeding attempts and growth rates (Table 3.1).

Feeding and/or assimilation rates have also been extensively used as proxies for temperature-dependent fitness. The ecological importance of feeding rates is overarching as it not only provides an organism-specific condition index but also sheds direct light on processes that occur at higher (i.e. population and community) levels (Paine, 1966). Southward (1955a,b, 1957) studied cirral activity, a proxy for feeding rates of different intertidal barnacle species that inhabit rocky shores of the United Kingdom. He provided extensive data on the effects of temperature throughout their thermotolerance windows (Table 3.1), revealing a clear fit with a typical performance curve’s shape (Fig. 3.6). Furthermore, his research draws attention to differences in performance in relation to additional sources of variability, including geographic origin of the species and populations (including the potential for thermal adaptation and acclimation) and intertidal height. For example, he showed how the species Balanus perforatus and Chthamalus stellatus exhibited higher Pmax and Tmax than S. (Balanus) balanoides, in accordance with their more southern distribution (Southward 1955a,b). Notably, as highlighted above, studies that only concentrate on feeding rates
may not be sufficient to explain the entire story. Although feeding rates are known to increase with temperature — presumably allowing for higher growth, reproduction and fitness — the energetic costs (metabolic rate) are known to rise exponentially with temperature as well, compromising the overall contribution of increased feeding rates shown by the organism (Levinton, 1983; Sanford, 2002a).

In sum, while many examples exist in the literature of the effects of environmental factors on traits related to fitness and performance, in relatively few cases do we have complete performance curves for marine organisms, and especially non-commercial invertebrates. Many studies have focused on extremes of temperature, or (especially in the case of aquaculture studies) on optima. This area thus represents a major gap in our knowledge, but is one that could be filled relatively easily. It is a critical area. For example, the outcome of field manipulations that compare the influence of environmental parameters on physiological or ecological performance depends entirely on where the conditions of the two sites lie on the performance curve; e.g. an increase in habitat temperature could lead to an increase in performance, a decrease in performance, or no change at all depending entirely on what combination of conditions were used (Fig. 3.5). While axiomatic in hindsight, often field manipulations fail to take such relationships into consideration or, when they do, they do not measure the conditions of the organism directly, but rather rely on proxies such as air or water temperature that may or may not accurately represent the physiological status of the organism (Figs 3.2 and 3.5).

Figure 3.6 Performance curve based on barnacle cirral beat frequency, as reported by Southward (1955a,b).
4. INDIRECT EFFECTS OF CLIMATE CHANGE: SPECIES INTERACTIONS AND TIPPING POINTS

Key to our argument is the concept that changes in the population dynamics of one or a few species can lead to community-level phase shifts/tipping points, and that the reproductive failure or large-scale mortality of a species will not simply result in its replacement by a functional equivalent. Clearly this argument will not apply to all organisms or ecosystems. For example, there are many discussions in the literature of functional redundancy, especially in planktonic communities, and of the role of guilds. However, many examples of the important role played by a few key species have been shown, as in the case of organisms at the base of food webs such as the Antarctic pteropod (example given earlier).

The concept of keystone species, first introduced by Paine (1969), has become a cornerstone of ecological theory (Power et al., 1996), and while its universality has been questioned (Strong, 1992), experimental manipulations have shown that it serves as a useful heuristic tool for examining interaction strengths within food webs (Menge et al., 1994), and the disproportionately large importance that some species have in relation to their abundance, i.e. the definition of a keystone species (Power et al., 1996). In some definitions, the keystone species concept is remarkably similar to that of a tipping point. For example, in his criticism of the keystone species concept, Strong (1992) defines keystone species as ‘taxa with such top-down dominance that their removal causes precipitous change in the [eco]system’.

In a now-famous experiment Paine (1974) experimentally removed the predatory seastar *Pisaster* over a period of 5 years from a rocky intertidal shore. The removal of this keystone predator resulted in the competitive dominance of the primary space occupier *M. californianus*, which then excluded over 25 other species of invertebrates and benthic algae from the shore (although, as noted by Suchanek (1992), the presence of mussel beds also increases the diversity of fauna living within the bed). Estes and Palmisano (1974) have shown that the removal of sea otters results in rapid expansion of sea urchin populations, which in turn destroy macroalgae, resulting in urchin barrens. On coral reefs, the presence of herbivores determines whether reefs undergo a phase shift from a coral-dominated reef to an algal-dominated reef (but see Dudgeon et al., 2010). Hoey and Bellwood (2009) quantified rates of browsing on *Sargassum* on the Great Barrier Reef and found that despite the fact that the reef supported 50 herbivorous fish species and 6 macroalgal browsing species, a single species, *Naso unicorns* Forsskål, 1775, was responsible for ~95% of the algae removed via grazing. Thus, this single species determined to a large extent the phase transition from a coral-dominated to a macroalgal-dominated reef.
Forty years after the introduction of the term, the definition of a keystone species is still debated, and has taken on new urgency given its implications for conservation management (Clemente et al., 2010; Navarrete et al., 2010). The discussion over whether keystone species should receive special management status continues, and several authors have suggested that the concept be expanded to include any species that has a large impact on their assemblage, whether out of proportion to their biomass or not (Mills et al., 1993; Davic, 2003). For example, in a 1993 review, Mills et al. described five different types of keystone species: keystone predators, keystone prey, keystone mutualists, keystone hosts and keystone modifiers. Keystone predators typically act by removing competitive dominants or other consumers, as described above. Keystone prey species affect community diversity through their impacts on the populations of their predators; via high rates of reproduction, these species are able to sustain populations of predators, thereby reducing the density of other prey species (Holt, 1977). Keystone mutualists are species that are critical to mutualistic relationships, e.g. pollinators and seed dispersers. Keystone hosts are the organisms that in turn support those pollinators and dispersers, e.g. plants. While Mills et al. (1993) did not list any marine examples of these latter two categories, zooxanthellae and their coral hosts may potentially lend themselves to these definitions.

Finally, Mills et al. (1993) defined keystone modifiers as species that significantly altered the physical habitat without necessarily having any trophic relationship with other species. The archetypical example given was that of North American beavers, which through the creation of dams flood the landscape, thereby impacting all other members of the assemblage. Jones et al. (1994) expanded on this latter definition to explore the concept of organisms as physical ecosystem engineers. Ecosystem engineers physically modify, maintain or create habitat, and in doing so directly or indirectly control the availability of resources to other species. Thus, for example, ecosystem engineers such as trees, corals, tube worms and bed-forming animals such as mussels and oysters all create living space for other organisms. Suchanek (1992) noted 135 species living in beds of the mussel M. californianus. Some polychaete species (e.g. Diopatra neapolitana Delle Chiaje, 1841) can build large emergent tubes that can alter flow regimes, stabilize sediment, and drive patterns of biodiversity by providing refugia for other species from predation (Woodin, 1981). Other species (e.g. Arenicola marina Linnaeus, 1758) are bioturbators that create disturbance that leads to decreases in biodiversity (Berke et al., 2010).

In all of these examples, one species has a large effect on the ecological community, and thus any sudden change in levels of physiological stress, reproduction or mortality that affect the behaviour and/or population dynamics of those species is likely to have a cascading ecological impact (Connell et al., 2011; Kordas et al., 2011). In many cases these impacts are likely to exhibit a threshold effect as well. Below critical population
densities, populations can exhibit an Allee effect (depensation) in which negative rates of per capita growth begin to occur (Stoner and Ray-Culp, 2000). For example, below critical densities spawning success of urchins has been shown to decline (Levitan et al., 1992). Recent work has shown that small populations, especially those at the edge of species ranges (‘frayed edges’), are more highly susceptible to environmental change (i.e. less physiologically resilient) due to lower genetic variance (Pearson et al., 2009). Results such as these are worrisome, because they suggest that thresholds may occur even more rapidly once some minimum threshold in genetic variance, and hence a lower adaptive capacity, is surpassed. Cumulatively these studies point to the need for a better understanding not only of the direct physiological effects of climate change but also the indirect effects on species interactions.

Multiple studies have examined the indirect effects of changes in climate-related factors on species interactions (Poloczanska et al., 2008; Yamane and Gilman, 2009; Connell et al., 2011; Kordas et al., 2011). Wetney (1984) experimentally altered the outcome of competitive interactions by shading two species of intertidal barnacles, demonstrating that the dominant competitor was restricted from the more physiologically challenging high intertidal zone by thermal and/or desiccation stress. Schneider et al. (2010) compared the survival of two species of mussels (Mytilus trossulus Gould, 1850, and Mytilus galloprovincialis Lamarck, 1819) under varying conditions of aerial exposure and food availability and reported differential survival under stressful aerial conditions, suggesting a role of environmental stress in driving the distribution of these two species, one of which (M. galloprovincialis) is an invasive. Sanford (1999, 2002a) showed that rates of predation by the seastar P. ochraceus on the intertidal mussel M. californianus were positively correlated with water temperature. Pincebourde et al. (2008) expanded upon this work and showed that the aerial body temperature of Pisaster also affected feeding rates. Following short (1–2 day) exposures to elevated temperatures, increasing aerial body temperatures led to higher feeding rates. However, following longer (8 day) exposures to temperatures that were high yet still realistic when compared to what was observed in the field, feeding rates decreased by up to 40%, and led to decreases in seastar growth (Pincebourde et al., 2008).

5. Putting the Pieces Together: Where Do We Go from Here?

Given the complicated interactions between organisms and their physical environments, the physiological mechanisms by which environmental factors drive organism behaviour, fitness and survival, and the indirect effects of
these impacts on species interactions, is there any hope for a mechanistic framework? Multiple models have been proposed to explore the relationship between abiotic stressors and species interactions. For example, consumer stress models posit that top predators are more affected by physiological stress than are their prey (Menge and Sutherland, 1987). In contrast, prey stress models suggest that prey experience higher levels of physiological stress than do their predators (Menge and Olson, 1990). A quantitative understanding of relative physiological stress levels of predator and prey under both normal and extreme field conditions is thus vital to the application of these theories (Petes et al., 2008). Critically, the concepts presented in this chapter suggest not only that patterns in the field may be more complex than anticipated, but they also may be highly context dependent. That is, a site that is physiologically stressful for one species may not necessarily be so for another, for several reasons (Fig. 3.7). For example, a prey species may be physiologically more stressed than its predator because the predator has a thermal performance curve with higher optimum and lethal temperature limits. However, a prey species may also be more stressed than its predator simply because, under the same environmental conditions, the predator maintains a lower body temperature (Fig. 3.7). This appears to be the case with the intertidal seastar *P. ochraceus* and its mussel prey *M. californianus* (Petes et al., 2008). Largely because of its wet surface and large thermal inertia (Pincebourde et al., 2009), *Pisaster* appears to maintain a temperature that is either the same or lower than that of its prey (Broitman et al., 2009). Even if the two species have similar performance curves (e.g., *Pisaster* and *Mytilus* appear to have similar lethal limits: Pincebourde et al., 2008; Denny et al., 2011), they will experience very different levels of stress under identical field conditions simply because the predator is able to maintain a lower body temperature. Thus, neither measurements of performance curves nor measurements of body temperature alone are enough to determine relative (or even absolute) stress levels in the field; and certainly measurements of habitat alone are insufficient.

Predicting physiological stress levels under field conditions is of course no simple matter due to potential interactions between multiple stressors. Crain et al. (2008) reviewed 171 studies that manipulated two or more stressors in marine ecosystems. Their meta-analysis showed an overall synergistic interaction effect, suggesting that the cumulative effects of multiple stressors are likely to be worse than expected based on the independent impacts of each stressor. Moreover, they found that cumulative effects could be additive, synergistic or antagonistic. Thus, in some cases, stressors either ameliorated one another, or one stressor had such a large effect the addition of a second stressor had no additional impact.

Still, some studies have shown that when there is an overwhelming effect of one stressor, explicit predictions can be made that can then be tested under field conditions. Hofmann et al. (2010) outlined an approach that links differential susceptibility to OA, including physiological plasticity,
to spatially explicit measurements of ocean pH in order to assess global patterns of calcification. Terrestrial ecologists have long used mechanistic heat budget models to generate temporally and spatially explicit maps of body temperature that can then be compared against known tolerance limits derived from controlled laboratory and field studies (Kearney and Porter, 2009). More recently these approaches have been applied to
intertidal ecosystems (Gilman *et al.*, 2006; Kearney *et al.*, 2010; Denny *et al.*, 2011; Helmuth *et al.*, 2011). Such studies hold a distinct advantage over correlative (‘climate envelope’) models in that they can potentially incorporate local adaptation (Kuo and Sanford, 2009) and acclimation (Somero, 2010); however, they also are much more time- and data intensive.

Most recently, biophysical models have been connected to Dynamic Energy Budget (DEB) models (Kooijman, 2009) as a means of accurately estimating the effects of changing levels of food and temperature on growth, reproductive output and survival (Kearney *et al.*, 2010; Sará *et al.*, 2011). Unlike other conceptual models, DEB models recognize that organisms live, as the name implies, in a dynamic environment. Thus, for example, Fig. 3.4 implies that it is a simple matter to define performance level at any given temperature (or combination of food and temperature, etc.). In reality, however, except for organisms in environments such as the deep sea or polar waters, organisms seldom live at a fixed temperature. Even in relatively thermally stable environments such as coral reefs, water temperatures fluctuate by up to several degrees due to solar heating of surface waters (Leichter *et al.*, 2006; Castillo and Lima, 2010). Fluctuations in body temperature of 25°C or more are not uncommon in intertidal environments (Finke *et al.*, 2009; Marshall *et al.*, 2010). In reality, therefore, organismal performance changes throughout the course of the day as body temperature changes, although mobile organisms can potentially ameliorate much of that variability through microhabitat selection. As a corollary, the cumulative effects of thermal variability have been shown to significantly affect an organism’s long-term performance. For example, Sanford (2002b) compared feeding and growth rates of the intertidal predators *P. ochraceus* and *Nucella canaliculata* Duclos, 1832, held in tanks at three temperature treatments: constant ‘cold’ (9°C), constant ‘warm’ (12°C), and a 14-day fluctuating regime (9–12°C) simulating recurrent upwelling conditions. His experiments revealed greater growth under a fluctuating thermal environment, which led him to speculate that a continuous displacement in body temperature around the $T_{\text{max}}$ of a thermal performance curve would explain such results. Importantly, as theoretical models (Katz *et al.*, 2005) and empirical studies (Easterling *et al.*, 2000) have demonstrated that climate change involves increases in temperature variability, models designed to forecast organisms’ response to climate change need to explicitly consider scenarios with different thermal amplitudes (Folguera *et al.*, 2009). The use of a single temperature to represent the physiological state of an animal over the course of a day (or even longer time period) is therefore generally untenable, especially when average values are used. DEB bypasses such limitations through a dynamic approach.
Kearney et al. (2010) successfully combined a biophysical heat budget model with a DEB model to study the effects of aerial and aquatic temperature on the intertidal mussel *M. californianus*. While they did not use the model to explore potential future effects of climate change, they did demonstrate the efficacy of the approach in predicting patterns of reproductive output and growth. Thus, the model could easily be combined with projections of future climate scenarios to predict the conditions under which this major space occupier would be most likely to experience mortality and/or reproductive failure, thus leading to a major phase shift in the intertidal ecosystem. Alternatively, it could be used as part of a sensitivity analysis to determine which environmental parameters are most likely to impact this key species (Helmuth et al., 2011).

Mechanistic forecasting approaches such as these thus hold considerable promise, especially if and when they can begin to incorporate indirect effects such as predation (Sanford, 2002a; Petes et al., 2008; Pincebourde et al., 2008; Yamane and Gilman, 2009). However, their ability to predict such complex interactions can only be assessed empirically; and because it is imperative that we test such models now rather than wait to see what will happen under future climate scenarios, our best option is thus to use nowcasting and hindcasting as hypothesis-testing frameworks (Helmuth et al., 2006; Wetney and Woodin, 2008). Specifically, using our understanding of the sensitivity of organisms to changes in environmental parameters, we can develop much more sophisticated predictions of the likely effects of changes in the physical environment that can then be tested using experimental manipulations (Firth and Williams, 2009). The combination of both organismal- and sub-organismal scale measurements and models with studies at population and community scales will provide a much more comprehensive view of the drivers of ecological thresholds than will simple correlations between environmental change and community responses. More to the point, an understanding of the world as viewed by the organisms we study will place us in a much better stead if we are to have any hope of predicting, and hopefully averting, some of the most severe impacts of anthropogenic change in coming decades.

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Tipping Points and the Keystone Role of Physiology


