Living on the Edge of Two Changing Worlds: Forecasting the Responses of Rocky Intertidal Ecosystems to Climate Change

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Abstract

Long-term monitoring shows that the poleward range edges of intertidal biota have shifted by as much as 50 km per decade, faster than most recorded shifts of terrestrial species. Although most studies have concentrated on species-range edges, recent work emphasizes how modifying factors such as regional differences in the timing of low tide can overwhelm large-scale climatic gradients, leading to a mosaic of environmental stress. We discuss how changes in the mean and variability in climatic regimes, as modified by local and regional factors, can lead to complex patterns of species distribution rather than simple range shifts. We describe how ecological forecasting may be used to generate explicit hypotheses regarding the likely impacts of different climatic change scenarios on the distribution of intertidal species and how related hindcasting methods can be used to evaluate changes that have already been detected. These hypotheses can then be tested over a hierarchy of temporal and spatial scales using coupled field and laboratory-based approaches.

INTRODUCTION

Anthropogenic increases in greenhouse-gas production and changes in land use have led to significant changes in global climate, and these trends are expected to continue far into the foreseeable future (Intergovernmental Panel on Climate Change 2001, Stainforth et al. 2005). Subsequently, understanding and forecasting the impacts of climatic change on the abundance and distribution of native and invasive species have become important endeavors in the fields of ecology and conservation biology (McCarty 2001, Parmesan & Galbraith 2004, Root & Schneider 1995, Wiens & Graham 2005).

This review summarizes research on the effects of climate change on rocky intertidal habitats, which are among the most-intensively experimentally studied ecosystems globally (Paine 1994), and sets forth an agenda for how and where the ecological effects of future changes in climate may be quantified. Rocky intertidal habitats (the regions between the high- and low-tide lines of coastlines) exist at the margins of both the terrestrial and marine realms; thus animals and algae in this ecosystem are subject to environmental challenges posed by both aquatic and aerial climatic regimes. As a result, rocky-shore organisms and assemblages may serve as early warning systems for the impacts of climate change (Barry et al. 1995; Harley et al. 2006; Hawkins et al. 2003; Mieszkowska et al. 2006; Sagarin et al. 1999; Southward et al. 1995; Thompson et al. 2002, 2004).

We draw upon insights from long-term monitoring studies (Hawkins et al. 2003, Southward 1991, Southward et al. 1995) and resurveys (Barry et al. 1995, Mieszkowska et al. 2005, Sagarin et al. 1999, Zacherl et al. 2003) carried out in the intertidal as an initial attempt to answer some of the key questions posed by ecologists faced with the dilemma of current global warming:

1. Which intertidal taxa show evidence of climatic impacts?
2. What is the rate and nature of change observed in intertidal systems?
3. Which elements of biological change must we investigate to detect and forecast past and future responses to climate change?

We highlight the importance of studies encompassing multiple spatial and temporal scales for the detection and quantification of biological responses to climatic shifts (Denny et al. 2004, Helmuth et al. 2002, Holtmeier & Broll 2005), emphasizing the necessity of considering physiological performance within the context of environmental regime (Helmuth et al. 2005, Hofmann et al. 2005). We then discuss the complementary application of ecological forecasting (Clark et al. 2001, Gilman et al. 2006) as a means of mechanistically predicting the physiological and ecological effects of future climate change scenarios on this sensitive ecosystem. Specifically, we address how forecasting (and related hindcasting) approaches can be used to generate hypotheses regarding the potential impacts of climate, and climate change, on the distribution of intertidal species, which can then be tested using coupled field and laboratory-based approaches. We argue that by generating explicit predictions of the direct physiological and ecological impacts of climate change and its indirect influences on biotic interactions, we will be better prepared to face future challenges. We emphasize the necessity of generating explicit hypotheses that can then be tested not just at poleward- and equatorial-range boundaries, but also at multiple locations within the ranges of species.

THE ROCKY INTERTIDAL ZONE

Intertidal invertebrates and algae are ectotherms that evolutionarily are of marine origin but must regularly contend with the terrestrial environment during each low tide. As such they provide a unique perspective on the relationships between both aquatic and terrestrial climatic regimes and organismal physiology and ecology. Indeed, largely because of the steep gradient in thermal and desiccation stresses that occurs during low tide, the rocky intertidal zone has long served as a natural laboratory for examining relationships between abiotic stresses, biotic interactions, and ecological patterns in nature (Bertness et al. 1999, Connell 1972, Hatton 1938, Orton 1929, Paine 1994, Somero 2002, Southward 1958, Wethey 1984). The upper limits of zonation of many intertidal organisms (i.e., their upward extent from the low-tide level) can be set directly by thermal and desiccation stresses (Connell 1972, Davenport & Davenport 2005, Somero 2002). Biotic interactions and behavior can also play an important role (Southward 1958, Underwood & Jernakoff 1981, Wolcott 1973), but such processes ultimately are dictated by the underlying environmental gradient (Raffaelli & Hawkins 1996; but see Wolcott 1973). Many intertidal organisms are therefore expected to display strong responses to changes in terrestrial climatic conditions (Fields et al. 1993, Lubchenco et al. 1993, Somero 2002). Specifically, if and when the zonational limit of a species is set by stresses related to terrestrial climate (such as increases in aerial body temperature), then we should observe a downward shift in upper limit of zonation as these stresses are magnified (Harley & Helmuth 2003, Wethey 1983). We should, however, only observe mortality events in locations where the upper limit is set by some factor related to terrestrial climate (as opposed to, for example, feeding or immersion time) (Davenport & Davenport 2005, Harley & Helmuth 2003, Southward 1958, Wolcott 1973).

Species can therefore be eliminated altogether from an intertidal region by changes in water temperature, upwelling regimes (Leslie et al. 2005) or oxygen levels (Service 2004), or when the upper limit of a prey species is squeezed down to the upper limit of its predator (Harley 2003). In these cases, we expect to observe contractions in species geographic distributions as climatic conditions exceed the species physiological threshold of tolerance. Conversely, when environmental conditions at a site become physiologically tolerable for the first time, we expect to see range expansions as new individuals are able to colonize. Understanding the impacts of climate change on the intertidal ecosystem thus requires an integrated approach that links changes in multiple environmental parameters to the physiological and ecological responses of organisms over a range of temporal and spatial scales and within a hierarchy of biological organization.

WEATHER, CLIMATE, AND CLIMATE CHANGE

Ecologists have long recognized the impacts of both weather and climate on natural ecosystems. Short-term localized atmospheric conditions (weather) fluctuate from hour to hour and day to day and encompass local air temperature, solar radiation, cloud cover, precipitation, and wind (Stenseth et al. 2003). Intertidal and subtidal organisms are also exposed to short-term fluctuations when the tide is in as a result

of internal wave formation, upwelling, and changes in wave action, salinity, sedimentation, and oxygen availability (Dahlhoff & Menge 1996, Leichter et al. 1996, Leslie et al. 2005, Service 2004, Witman & Smith 2003). Although short-term fluctuations in the marine environment are often less variable in magnitude compared with those in the terrestrial environment, they have been shown to have significant physiological impacts (Dahlhoff 2004, Dahlhoff & Menge 1996, Leichter et al. 1996, Leslie et al. 2005). For example, rapid fluctuations in phytoplankton associated with upwelling can have significant influences on the growth of intertidal invertebrates (Dahlhoff & Menge 1996), and even moderately protracted periods of low oxygen can result in significant levels of mortality (Service 2004).

Climate is typically defined in the meteorological community as the mean of weather over a large temporal scale (30 years or more). The important distinction is therefore that weather is a much more temporally variable measure of what organisms experience at specific times. Moreover, climatic variables are often grouped over large spatial scales into climatic indices, such as the El Niño Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO), which tend not only to lump multiple environmental variables, but also tend to smooth small-scale and short-term changes in climate into large-scale patterns (Hallett et al. 2004, Stenseth et al. 2003). When considering environmental change there is therefore a trade-off (Stenseth et al. 2003) between manageability in terms of understanding, identifying, and predicting trends (climatic indices) and documenting the variability actually experienced by an organism or population at any given point in space and time (weather). In the next section, we examine the evidence for the impacts of climatic change on intertidal organisms, focusing on the utility of long-term monitoring programs conducted over nested spatial scales. We then discuss the need for an understanding of local patterns of environmental variables (Hallett et al. 2004) coupled with ecological and physiological responses of organisms to those environmental conditions (Hofmann 2005, Hofmann et al. 2005, Somero 2002).

HISTORY OF MARINE BIOGEOGRAPHICAL STUDIES

Many of the early biogeographic studies correlated species distributions with temperature (Andrewartha & Birch 1954, Hutchins 1947, Orton 1920) and still form the basis of ecological principles today. Hutchins (1947) provided a comprehensive synthesis of pioneering work and explicitly separated out the likely causes of poleward and equatorial limits. He emphasized the important role of reproduction and recruitment (termed repopulation) in setting distributions, building on work by Orton (1920). Hutchins (1947) argued that isotherms of sea surface temperature (SST) were correlated with the worldwide distribution of mussels (*Mytilus edulis*) and barnacles (*Semibalanus balanoides*), and he used these correlations to develop a general model to explain the role of thermal tolerance in setting range boundaries in coastal species.

Species distribution limits were grouped into four main zonal types: (*a*) the setting of poleward limits by survival during winter (cold stress) and equatorial limits by survival during summer (heat stress) (Southward 1958); (*b*) poleward limits determined

by the inability to repopulate in summer and equatorial limits set by the inability to repopulate during winter (Bowman & Lewis 1986, Moore & Kitching 1939); (*c*) summer temperatures setting limits both by reducing survival at equatorial margins and repopulation at poleward margins (Ritchie 1927); and (*d*) winter temperatures setting limits by reducing survival at poleward margins and repopulation at equatorial margins (Hutchins 1947). Transient populations could occur beyond these margins, but these populations are often seasonal, only surviving until the extreme temperature event (cold winter or hot summer) occurs. Relic populations are occasionally found beyond range limits when a year class has survived a period of less-extreme climate, but these populations quickly become extinct when exposed to conditions that are too extreme for repopulation or survival. A more-recent extension of this theory is that population abundances are expected to be highest near the center of the species' distribution, where levels of physiological stress are assumed to be lowest, and then to decrease toward the range margins (Brown 1984).

The records collected during these early biogeographic studies provide baseline and time-series data for intertidal species prior to the onset of the current period of rapid warming. Surveys of the distribution and abundance of intertidal organisms made by various researchers in the region of Point Conception (northeast Pacific) were assimilated into a data set stretching back 18 decades (Smith & Gordon 1948). Hewatt (1937) made small-scale abundance surveys in the 1930s on the California coastline, but work was not as prolific as that in the northeast Atlantic, where Orton (1920) inspired a generation of researchers in postwar Britain. Detailed mapping of individual species followed in Europe (e.g., Crisp & Southward 1958, 1959; Fischer-Piette 1933, 1955; Fischer-Piette & Prenant 1956; Lewis 1964; Moore & Kitching 1939; Southward 1980, Southward & Crisp 1954b).

These pioneering surveys and somewhat ethically dubious transplantation experiments charted the distributions of intertidal species and investigated the factors setting species distributions. This work on the intertidal zone became integrated into a broader approach to understanding fluctuations in ecosystems of the western English Channel (Crisp & Southward 1958; Mieszkowska et al. 2006; Russell et al. 1971; Southward 1963, 1991; Southward et al. 1995, 2005). Southward & Crisp (1954a,b) resurveyed earlier work (Moore 1936, Moore & Kitching 1939) and showed that between the 1930s and 1950s, the northern barnacle *S. balanoides* had become rarer in the United Kingdom while the southern barnacle *Chthamalus stellatus* (later split into *C. stellatus* and *C. montagui*) had become more common (Southward & Crisp 1956). By the early 1960s, the role of climatic fluctuations in driving marine ecosystem responses, including those of intertidal zones, was well appreciated (Southward 1967). The extremely cold winter of 1962–1963 (Crisp 1964) and a shift to colder climatic conditions for the next two decades gave researchers further impetus.

At the assemblage level, Ballantine (1961) showed how the balance between algal domination in shelter and sessile invertebrates (particularly barnacles and mussels) on exposed shores shifted geographically on the European coastline, mediated by limpet grazing (Hawkins & Hartnoll 1983, Hawkins et al. 1992). Broitman et al. (2001) also observed this latitudinal pattern of changes in functional group dominance in Chile.

Research shifted focus from the ultimate and underlying factor of temperature and its influence on ectothermic species to the proximate causes of species-range edges. Processes proposed included a lack of consistent recruitment (Lewis 1986), barriers to dispersal (Kendall 1987), a lack of suitable habitat (Crisp & Southward 1958), and extreme events causing adult mortality (Crisp 1964). There was also a growing appreciation of the correlation between the fluctuations in climate (Southward & Crisp 1954b, 1956) and in the abundance of animals within ranges and at boundaries (Crisp & Southward 1958). As early as 1954, Southward & Crisp (1954b) proposed *S. balanoides* and *Chthamalus* spp. as indicator organisms to investigate species responses to changes in the general environment, as both taxa were likely sensitive to even small changes in temperature.

By the late 1980s, it became apparent that patterns driven by solar flux (using the sun-spot index) were beginning to break down, and anthropogenic influences were suggested (Southward 1991). From the late 1980s onward, conditions were obviously becoming much warmer, with consequent responses shown by intertidal species in Europe (Southward 1991, Southward et al. 1995).

EVIDENCE FOR THE IMPACTS OF CLIMATE CHANGE ON INTERTIDAL COMMUNITIES

An increasing number of recent studies have documented the impacts of climate change on intertidal invertebrates and algae, and these studies are summarized in **Table 1**. Studies carried out at the northern range edge of the southern neogastropod *Kelletia kelletii* in the California region of the northeast Pacific, for example, demonstrated that the boundary had shifted north from the late 1970s/early 1980s to the 2000s (Herrlinger 1981, Zacherl et al. 2003) (**Table 1**). Data from fossil records (Arnold 1903, Lohnhart & Tupen 2001), and surveys ranging from 1830s until modern times (Zacherl et al. 2003), showed that this was the first-recorded extension north of Point Conception. The range extension coincided with the steady increase in regional coastal SST that occurred during the second half of the twentieth century (Zacherl et al. 2003).

The blue mussel *M. edulis* has recently jumped a historic oceanographical barrier from the Norwegian mainland to the Svalbard archipelago, extending its distribution north by 500 km to Bear Island between 1977 and 1994 (Weslawski et al. 1997). By 2002, *M. edulis* had extended its range a further 500 km north to Isfjorden on Svalbard island, where it had not been recorded for 1000 years (Berge et al. 2005, Salvigsen et al. 1992). This 1000-km poleward extension of northern distributional limits over the course of the past three decades is thought to have arisen from the dispersal of planktonic larvae from a source population on the Norwegian mainland by an anomalously large northward transport of warm Atlantic water into the Greenland Sea region in recent years (Berge et al. 2005).

Northern and eastern range extensions have been identified around the British coastline for the southern trochid gastropods *Gibbula umbilicalis* and *Osilinus lineatus* (Mieszkowska et al. 2005, 2006) (**Table 1**) between the mid-1980s and the 2000s, in contrast to static range limits observed during the 1970s and early 1980s (Kendall

1987, Kendall & Lewis 1986). The ranges of the southern barnacles (*Chthamalus* spp. and *Balanus perforatus*) have also extended in Britain since the previous surveys in the 1950s (Herbert et al. 2003; Mieszkowska et al. 2005, 2006) (**Table 1**), and have also increased in abundance at survey sites along the English Channel coastline (Herbert et al. 2003). The eastern limit of the southern alga *Bifurcaria bifurcata* has re-extended along the English Channel in the past four decades (N. Mieszkowska, unpublished data) (**Table 1**). The previous record of *B. bifurcata* at its current range edge at Portland was in 1902. This was immediately prior to a sudden change in the marine climate in the English Channel from a warm phase into one of the coolest periods in modern record, and *B. bifurcata* was restricted to southwest England during this time (E. Burrows, unpublished data).

In general, the southern boundaries of cold-water species have shown less movement (e.g., range contractions of two species have been recorded) in Britain compared with northern boundaries of warm-water species (e.g., eight species have recorded range extensions), which may reflect that many species with northern ranges reach their absolute range limits further south in Europe, particularly in Portugal (Southward et al. 1995). The northern alga *Alaria esculenta* has, however, disappeared from the coastline of northeast Britain since the 1990s (R. Bowman, personal communication), and although present at some locations in southwest Britain, no survival occured in transplant experiments to locations where it was previously recorded before the 1950s (Vance 2004). Water temperatures greater than 16°C are fatal to mature sporophytes of *A. esculenta* (Widdowson 1970). Increases in sea and air temperatures in both the North Sea and English Channel have occurred between the original surveys and resurveys, and the poleward-range contraction of *A. esculenta* at its southern limits in Britain during this time has mirrored the poleward shift of the summer 16°C SST isotherm.

Abundances of many southern intertidal species (e.g., Chthamalid barnacles, trochids, *Patella depressa* and *B. perforatus*) have increased in the region of the biogeographic boundary in southwest England since the 1980s (Crisp & Southward 1958, Herbert et al. 2003, Mieszkowska et al. 2005). In contrast, many of the northern species have shown decreases in abundance (e.g., *Semibalanus balanoides* and *Patella vulgata*), although not to the same degree (Mieszkowska et al. 2006, Southward 1991, Southward et al. 1995). In general, where northern and southern pairs of species with similar ecological niches co-occur, a general shift in the abundance ratios in favor of southern species has been observed in Britain. Similar patterns have been observed in Monterey Bay, California, where researchers compared abundance data for over 130 species between the 1930s (Hewatt 1937) and the 1990s (Barry et al. 1995, Sagarin et al. 1999). This comparison showed a significant increase in the abundance of southern species of gastropods, anthozoans, and barnacles; a significant decrease in the abundance of northern anthozoan and limpet species; and no apparent trend for species classified as cosmopolitan in their distribution (Barry et al. 1995, Sagarin et al. 1999). These changes occurred in parallel to increases in summer coastal SST of ∼2°C and led to large alterations in local community structure.

Although factors including the overfishing of urchins and groundfish have affected coastal-community composition in the Gulf of Maine since the 1980s (Harris &

Table 1 Summary of major shifts in the biogeographic distributions of rocky intertidal species, and population-level changes observed within species ranges in response to the current period of climate warming. Southern species spread northward and eastward around the British Isles, including paradoxically southward around the cooler North Sea coastlines

Species	Geographic region	Impact	Survey	Resurvey
Mytilus edulis	Bear Island, Svalbard	Range extension 500 km N,[a] range extension 500 km N[b]	1979 (first record in 1000 years)	1994, 2004
Gibbula umbilicalis	North Scotland, south England, north Wales, south England	Range extension 55 km N, range extension 125 km E; increased recruitment success near range edges[c,d]	1985, 1985	2001–2004 2001–2004
Osilinus lineatus	North Wales, south England	Re-extension 40 km N, range extension 55 km E; increased recruitment success near range edges[d,e]	1964, 1980s, 1986	2001–2004 2001–2004
Chthamalus montagui	North Scotland	Range extension 75 km along cooler North Sea coast[d,f]	1980s	2001–2004
Chthamalus stellatus	North Scotland	Range extension 40 km along cooler North Sea coast[d,f]	1980s	2001–2004
Patella depressa	South England	Range extension 30 km E[d]	1964, 1980s	2001–2004
Patella ulyssiponensis	South England	Range extension 120 km E[d]	1964, 1980s	2004
Balanus perforatus	South England	Range extension 170 km E[g]	1960s	1993–2001
Bifurcaria bifurcata	South England	Re-extension 150 km E[d]	1902, 1936	2002
Patella rustica	North Portugal	Infilling of gap 39.3° N–43.2° N at southern end of range[h]	1950s	2003
Kelletia kelletii	California	Range extension 400 km N[i]	1970s	1980s
Codium fragile	Gulf of Maine	Range extension N; warmer summers facilitating reproduction[j]	1975–present	1990

Species	Location	Observation		
Alaria esculenta	North England, south England	Range contraction >120 km N[d]; range contraction 120 km E[f]	1950s	1990s, 2004
Tectura tessulata	Irish Sea	Loss of species from south of Isle of Man[d]	1980s	2001–2004
Fissurella crassa	Chile	Range contraction 3° latitude N[k]	1962	1998–2000
Enoplochiton niger	Chile	Range contraction 3.5° latitude N[k]	1962	1998–2000
Echinolittorina peruviana	Chile	Range contraction 5° latitude N[k]	1962	1998–2000
Thais haematoma	Chile	Range contraction 8° latitude N[k]	1962	1998–2000
Gastropods, anthozoans, barnacles	California	Increases in abundance of warm-water species[l]	1930s	1998–2000
Anthozoans and limpets	California	Decreases in abundance of cold-water species[l]	1930s	1998–2000
Asterias forbesi	Gulf of Maine	Increase in abundance[m]	1979	1998
Asterias vulgaris	Gulf of Maine	Decrease in abundance[m]	1979	1998

[a] Weslawski et al. 1997.
[b] Berge et al. 2005.
[c] Kendall & Lewis 1986.
[d] Mieszkowska et al. 2005.
[e] Kendall 1987.
[f] Crisp & Southward 1958.
[g] Herbert et al. 2003.
[h] Lima et al. 2006.
[i] Zacherl et al. 2003.
[j] Harris & Tyrrell 2001.
[k] Rivadeneira & Fernandez 2005.
[l] Sagarin et al. 1999.
[m] Harris et al. 1998.

Tyrrell 2001), increasing sea temperatures are the driving factor behind the increases in abundance of the warm-water starfish *Asterias forbesi* and the concurrent decline in the cold-water congener *A. vulgaris* (Harris et al. 1998). Increasing sea temperatures have also facilitated the range extension of the warm-water alga *Codium fragile* into the Gulf owing to summer temperatures sufficient to allow successful reproduction since the mid-1970s (Harris & Tyrrell 2001).

Natural climatic phenomena such as fluctuations in the strength and direction of the ENSO index or the NAO index—where temperature, currents, sea level, and storm frequency may all be altered (Allison et al. 1998, Strub & James 2002)—can also be used as a proxy for the likely effects of anthropogenic climate change. Rising temperatures and altered currents as a result of ENSO events have been linked with changes in species distributions (Fields et al. 1993), including introduced species such as *Carcinus maenas* on the west coast of the United States (Yamada et al. 2005). Increased sea temperatures that result from ENSO-mediated relaxation of upwelling events have been used to document changes in the interaction strength between a keystone predator and its prey (Sanford 1999).

In summary, the locations of range edges of many intertidal species have shifted by as much as 50 km per decade (**Table 1**), much faster than most recorded shifts of terrestrial species (e.g., Parmesan & Galbraith 2004). Contractions in the equatorial-range limits have also been seen, but the rate and extent are less than the changes observed at the poleward limits of distribution. These biogeographic shifts have been accompanied by increases in the abundance of many species close to their poleward-range limits and changes in the relative abundances of warm- and cold-water species at long-term monitoring sites.

However, these records of fluctuating densities of warm- and cold-water species, and alterations in assemblage composition, highlight two important points. First, not all evidence of change has occurred at poleward and equatorial margins of species-range boundaries. Recently the range of the southern limpet *Patella rustica* has expanded in northern Portugal, bridging a historic distributional gap within the species distributional range during a period when the regional cold coastal upwelling was seen to weaken (Lima et al. 2006).

Second, although the evidence is clear that climate has had, and will continue to have, large impacts on at least some species in rocky intertidal ecosystems (**Table 1**), we should not expect to see impacts of climate change everywhere. For example, the distributional limits of many intertidal species are not all exhibiting the same trend or extent of poleward expansions, with some species showing little or no change despite exposure to warming sea and air temperatures (Rivadeneira & Fernandez 2005). Importantly, only through continuous monitoring can many of these potential changes in abundance and distribution be detected, as these responses can occur rapidly. Moreover, the challenge before us is not simply to monitor these responses, but to build on this existing knowledge in an attempt to forecast future changes and to understand how and when such responses are linked to climatic variability. Importantly, we must first understand the mechanisms by which organisms are impacted by their ambient physical environment, both directly through physiological performance and indirectly through mediation of biotic interactions.

PHYSIOLOGICAL RESPONSES TO CLIMATE FACTORS BY INTERTIDAL ORGANISMS

Intertidal invertebrates and algae live at the interface of the marine and terrestrial worlds. Many studies, for example, have shown that the production of heat shock proteins occurs after exposure to temperatures experienced during low tide and have suggested that the production of these proteins incurs some metabolic cost (Dahlhoff 2004, Hofmann 2005, Sanders et al. 1991, Somero 2002, Tomanek & Sanford 2003). The upper limits of zonation of many species of invertebrates have been correlated with maximum aerial temperatures (Davenport & Davenport 2005, Kennedy 1976, Somero 2002, Williams & Morritt 1995), and experimental manipulations of aerial body temperature by shading have resulted in changes in mortality, rates of predation, relative competitive ability, and species zonation patterns (Harley & Lopez 2003, Hatton 1938, Wethey 1984). Other studies have documented natural mortality events resulting from both high- and low-temperature extremes experienced during aerial exposure (Carroll & Highsmith 1996, Tsuchiya 1983).

When these upper limits of an organism are squeezed down to the upper limit of a predator or dominant competitor (Harley 2003), the subordinate or prey species is eliminated from the intertidal zone, and species are geographically limited by physiological stresses related to aerial exposure (Harley & Helmuth 2003). This observation is key because organisms are differentially affected by terrestrial climate and by the characteristics of the organism itself. As a result, two organisms exposed to the same climatic conditions can exhibit markedly different body temperatures and hence different levels of physiological stress (Helmuth 2002, Helmuth et al. 2005, Gilman et al. 2006; but see Wethey 1983). Such interspecific variation may be particularly important when considering the impacts of climate on predator/prey pairs, competitors, or native versus invasive species. For example, Helmuth (2002) has shown that at low tide, the predatory seastar *Pisaster ochraceus* may be up to 10° cooler than the prey (*Mytilus californianus*) that it is feeding on. Differences in the body temperature of species pairs may have implications for biogeographic boundaries. For example, if the upper limit of a prey species is shifted downward by climate change, but the upper limit of its predator remains unaffected, the prey species may be eliminated from the ecosystem (Harley 2003).

Numerous studies have also focused on the important role of water temperature, usually measured as SST, in setting species distributional limits (Frank 1975, Hutchins 1947). Water temperature has been shown to have strong effects on the metabolism and growth (Bayne et al. 1973, Phillips 2005), feeding behavior (Petraitis 1992; Sanford 1999, 2002), and reproduction (Hutchins 1947, Philippart et al. 2003) of intertidal and subtidal organisms. Water temperature also can have significant impacts on rates of larval development (Anil et al. 2001, Hoegh-Guldberg & Pearse 1995, Luppi et al. 2003).

Importantly, however, although various aspects of both terrestrial and aquatic climate drive the physiological performance and survival of coastal organisms, these factors often alternate with one another, and with nonclimate-related factors, in setting distributional limits. Many factors, such as temperature and food, and temperature

and desiccation, are often interactive in their effects (Gilman 2006, Li & Brawley 2004). Harley & Helmuth (2003) correlated the upper zonation limits of mussels and barnacles with measurements of maximum body temperature at multiple sites in northwestern Washington State (United States) and found that local distributional limits were tightly correlated with temperature at some sites, but at others the correlation was weak. Their results suggest maximum body temperature alternated with some other environmental factor, such as feeding time, in setting upper zonation heights of these species in this region and again argue that limiting factors must be considered on a spatially explicit basis. In contrast, Sanford (1999, 2002) showed that the foraging behavior of the keystone predator *P. ochraceus* was driven predominantly by water temperature experienced during submersion at high tide and appeared to be uncorrelated with air temperature.

Taken collectively, these studies show that although climate is likely to have significant impacts on the local and geographic distributions of intertidal species, the specific climatic drivers that contribute to these patterns are likely complex and must be tested experimentally. In the above example, a predator (*Pisaster*) appears most susceptible to changes in water temperature, whereas its prey (*Mytilus* spp.) may be affected by both the aerial and aquatic climatic regimes. Moreover, these climatic drivers are likely to alternate in their importance as limiting factors from location to location, and simple statistical correlations between environmental factors and species-range limits are likely to yield poor results, especially when made over large geographic scales (Holtmeier & Broll 2005). In other words, it may be naïve to expect single environmental variables such as water temperature or air temperature to be correlated with population abundances and range limits at all sites and at all scales examined. Similarly, we should not expect environmental variables to be physiologically limiting at all range edges, as is commonly assumed by many environmental niche models; i.e., range edges are not always indicative of an organism's fundamental niche space.

In addition, researchers must also investigate the potential variation in the physiological and ecological responses of organisms to climatic and nonclimatic factors at different stages of their life history (**Figure 1**). For example, the onset of gametogenesis has been linked to increases or decreases in environmental temperature in many intertidal species, with duration and frequency of gonad activity also regulated by local thermal regimes (Bode et al. 1986, Kendall & Lewis 1986). Owing to the variation in reproductive mode between species, spawning, fertilization and larval release may respond to either thermal, physical, or biological cues including temperature changes (Bowman & Lewis 1986, Hawkins 1982, Lewis 1986), wave action, storminess (Carrington 2002, Lewis 1986), photoperiod (Brockington & Clarke 2001), and the timing of phytoplankton blooms (Clarke 1988, Connell 1961), all of which vary on local as well as regional scales (**Figure 1**). Many intertidal invertebrate species have a planktonic larval phase, the duration of which can be altered by water temperature (Hoegh-Guldberg & Pearse 1995). Dispersal of larvae is controlled by both local and regional hydrographic regimes, wave action, the length of time spent as a pelagic veliger, larval feeding mode, and larval size and shape (Pechenik 1999).
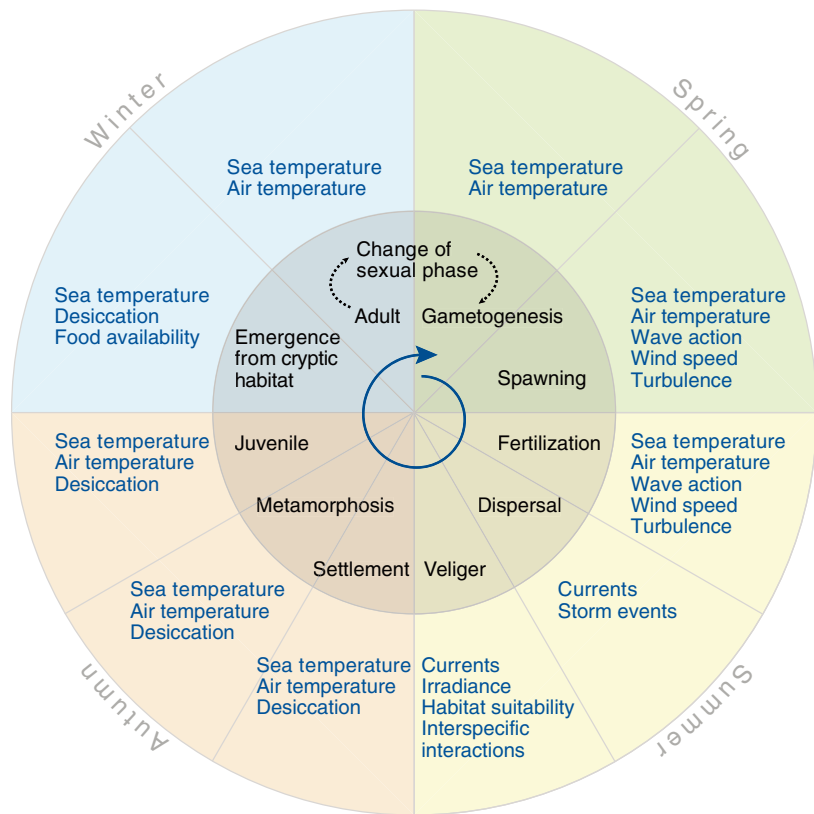
Settlement may also occur in response to temperature changes (Pineda et al. 2002), but nonthermal cues including habitat suitability, irradiance, and intra- and interspecific interactions can also mediate or determine when and where larvae commence the sessile phase of the life cycle (Bertness et al. 1999, Wethey 1986). Postsettlement survival has also been shown to be affected by large-scale terrestrial climatic changes, as experienced during the cold winter of 1962–1963 (Crisp 1964, Kendall & Lewis 1986) and 1979 (Wethey 1985) and by the marine climate at the regional scale (Southward & Crisp 1956; N. Mieszkowska, unpublished data), but idiosyncratic species responses can modulate survival rates at the local scale and affect the extent of range contractions on a regional scale.

The interactive effects of climate must therefore be considered with respect to both the life history of each species and the variation in life-stage sensitivity to both climatic and nonclimatic environmental factors. This must be done within a spatially explicit context that includes aspects of local environmental variability (Schoch & Dethier 1996), as well as variability in physiological and genetic responses to those environmental signals (Hilbish 1981, Stillman 2003).

THE BASIS OF WEATHER AND CLIMATE IN DRIVING SPECIES DISTRIBUTIONS

Hutchins' (1947) general argument that large-scale climatic regimes determine the latitudinal distributions of marine species remains a baseline assumption in many ecological studies related to climatic change. It is obvious that polar communities experience colder conditions than tropical communities and that large-scale gradients in climate exist when looking over very large segments of latitude (Stenseth et al. 2003). Moreover, large-scale, integrative indices of climate can in some cases serve as a far more synthetic tool for looking at broad-scale patterns than individual weather records (Stenseth et al. 2003). To this end, most meta-analyses of the impacts of climate change on natural ecosystems have looked for evidence of latitudinal shifts in species-range boundaries at the northern and southern edges of their distributions (Parmesan & Yohe 2003).

Indeed, in many cases there is strong evidence of multispecies faunal breaks that appear to coincide with changes in climatic variables (Briggs 1974, Morris et al. 1980, Zacherl et al. 2003). Two factors in this assumption, however, tend to be ignored when considering the likely impacts of climate change, particularly when employing climate envelope–type approaches. First, not all latitudinal boundaries are set by climate. Discontinuities in larval dispersal may act to set distributional limits (Crisp & Southward 1958, Gaylord & Gaines 2000), which may be caused by localized hydrographic features such as the strong offshore currents that occur at Portland in the English Channel (Maddock & Pingree 1977), or by larger, basin-scale features such as increases in offshore Eckman transport along sections of the eastern Pacific seaboard (Connolly & Roughgarden 1998, Broitman et al. 2001).

Alternatively, range edges may be set by a lack of unsuitable habitat. For example, the eastern range edge of southern species of barnacles, limpets, topshells, and winkles in Europe has been limited to the western English Channel from the 1930s to the 1980s owing to the lack of rocky intertidal habitat as well as strong offshore currents at various headlands (Crisp & Southward 1958, Kendall 1987). Thus we should not expect to observe species-range shifts at all latitudinal boundaries because not all may be directly set by some aspect of climate. Key areas where climate change likely has large impacts are thus the transitional zones bounding those biogeographic provinces primarily delimited by climate. Such sharp faunal breakpoints corresponding to changes in thermal provinces occur on the western Atlantic at Cape Hatteras (Johnson 1934); the eastern Atlantic in the Bay of Biscay (Sauvageau 1897, Fischer-Piette 1955); southwest England, Wales, and Ireland (Forbes 1853); the east Pacific at Point Conception (Briggs 1974); the west Pacific at the East Cape (Schiel 2004); and the Cook Straight (Knox 1960) of New Zealand. Range shifts of cold- and warm-adapted species have already been documented in many of these regions (Herbert et al. 2003; Lima et al. 2006; Mieszkowska et al. 2005, 2006; Zacherl et al. 2003).

Second, spatial patterns of climatic conditions within species ranges are often far more complex than generally appreciated, so organisms may be presented with a mosaic pattern of environmental stress, rather than a simple latitudinal gradient. In other words, although latitudinal trends in climate may exist over very large spatial

scales, considerable spatial variability may occur at scales that are biogeographically meaningful. Organisms respond physiologically not to some generic aspect of climate measured over large scales, but to the localized environmental conditions in which they live (Hallett et al. 2004). Especially in the case of sessile organisms, this sphere of influence may be exceedingly restricted and may be significantly affected by factors ranging in scale from the angle of the substratum on which the organism sits to the character of the local weather system (e.g., coastal fog) and patterns of local tides and waves (Helmuth & Hofmann 2001, Schoch & Dethier 1996). Although some degree of heterogeneity along broad-scale climatic gradients is certainly not surprising, several recent studies suggest that species and ecosystem responses to climate are far more complex than previously appreciated. Specifically, in some cases, the effects of climatic gradients may be subsumed by those of local modifying factors, even over large areas. In other words, patterns of weather may be more important than climate, and we need to pay close attention to how localized patterns of weather are averaged into large-scale climatic indices (Hallett et al. 2004).

For example, Holtmeier & Broll (2005) argue that large-scale descriptors of climate are a poor predictor of the sensitivity of treeline distribution to climate change and that the influence of local modifying factors such as recent land use and substratum aspect can override those of climate. Likewise, Helmuth et al. (2002) have shown that patterns of local weather, wave height, and tidal regime interact to create a thermal mosaic along the west coast of the United States, so maximum aerial body temperatures of intertidal mussels at sites in northern Washington and Oregon can exceed those of animals living 100–1000s of kilometers farther to the south, in southern California. Their results suggest that because of the influence of the timing of low tide, coupled with the impacts of wave splash and local weather, patterns of mussel body temperature do not become increasingly colder moving northward from California to Washington. As a result, mortality events at hot spots where periods of summertime low tides coincide with hot terrestrial climatic conditions should be expected rather than simple latitudinal range shifts. These results fit well with the observation that many intertidal species along the west coast of the United States do not display an abundant center distribution, as would be predicted by Brown's (1984) principle if levels of physiological stress were lowest in the center of their distribution and highest near their range edges (Gilman 2005, Sagarin & Gaines 2002, Sagarin & Somero 2006). Instead these species show a pattern where population numbers (Sagarin & Gaines 2002) and physiological indicators of stress (Sagarin & Somero 2006) wax and wane along the length of the species distribution. Such patterns strongly suggest that we require local patterns of intertidal organism temperature, and temperature anomalies, to decipher changes in assemblages over time.

Similarly, Hallett et al. (2004) correlated patterns of mortality in Soay sheep against records of local weather, and against broad-scale patterns of climate (the NAO index). They found that when they used a mechanistic relationship between local weather and mortality, patterns of local weather proved to be a much better predictor of population trends than did the large-scale NAO index. In other words, once the relationship between local weather variables such as rainfall and air temperature was considered within the context of the physiological response of the organism, local

descriptors of weather served as a far better predictor of population response than did the NAO index (Hallett et al. 2004).

Taken cumulatively, these results indicate a need for clearer understanding of the relative importance of climatic indices versus localized factors in driving the responses of intertidal populations to climate change, and we should not expect to see evidence of climate change only at poleward- and equatorial-range margins (Gilman et al. 2006; Helmuth et al. 2002, 2005; Holtmeier & Broll 2005; Sagarin & Somero 2006). Thus, when local and regional factors are sufficiently large, they may create holes in species distributions, especially when they occur adjacent to habitat that is already unsuitable (for example, sections of muddy substratum uninhabitable by rocky intertidal organisms).

The question, therefore, is do micro- and mesoscale heterogeneity in the physical environment as driven by local modifying factors matter in terms of biogeographic responses to climate change? Microscale variability introduced by factors such as substratum angle may serve as an effective means of detecting early signs of the impacts of climate change, and this scale of heterogeneity may have important consequences for maintaining genetic polymorphism (Schmidt & Rand 2001). At larger scales, factors such as tidal regime may be sufficiently large in spatial extent to have significant biogeographic consequences (Helmuth et al. 2002).

Overall, the importance of heterogeneity in the physical environment is determined largely by the ability of populations to recover from disturbance events, which in turn is driven by the interaction between the life history of the larval stage and local and regional dispersal patterns (Broitman et al. 2005, Sotka et al. 2004). For example, if a mortality event occurs on a section of coastline, but larvae or gametes are able to bypass or repopulate that dead zone, then the presence of this small-scale hot spot has few or no biogeographic consequences. If, in contrast, a persistent dead zone is sufficiently large, or occurs adjacent to an area of unsuitable habitat such that propagules are no longer able to disperse across this gap, then barriers to genetic dispersal may be created. Similar arguments may be made in the case of range expansions. For example, the topshell *G. umbilicalis*, which has a short larval stage, has extended and consolidated its northern range limits to a greater extent than the barnacles *C. montagui* and *C. stellatus*, which have much longer planktonic dispersal times. This appears to be a result of high densities of recruits settling locally, facilitating colonization of neighboring shores, and rapidly increasing the range by small increments (N. Mieszkowska, unpublished data). The relative importance that larval dispersal and reproduction play in the regulation of heterogeneity within species distributions therefore depends on the spatiotemporal magnitude of the disturbance and the location of disturbance within the species range.

Predators and competitors may also play a key role in these patterns by restricting subordinate intertidal species from subtidal environments; if an intertidal population is eliminated owing to a heat-stress event, for example, but a healthy subtidal population remains, then the subtidal population may serve as a reservoir. If there are no subtidal populations, then the elimination of a species from the intertidal could have significant biogeographic consequences, but only if its absence creates gaps that cannot be spanned by larvae over time. The processes of reproduction, dispersal,

larval mortality, and postrecruitment mortality, which can drive range expansions and contractions, must be therefore examined on a spatially explicit basis, encompassing areas within the range as well as the range edges. Specifically, whereas physiological responses to climate drive patterns of reproductive success, mortality, and species interactions, oceanographic regimes and coastal geomorphology determine levels of connectivity between habitats that are made suitable or unsuitable by climatic change (Broitman et al. 2005, Lima et al. 2006, Sotka et al. 2004). To this end, the application of ecological-forecasting techniques may potentially serve as an effective means of predicting patterns in environmental variables.

ECOLOGICAL FORECASTING

Ecological forecasting (and related hindcasting) uses first principles to relate patterns in environmental variables to the physiological responses of organisms. For example, weather data can be used to generate heat-budget models, which in turn can generate spatially and temporally explicit maps of aquatic and aerial body temperature (Helmuth 1999, Porter et al. 2002, Wethey 2002). From these patterns, and given explicit measurements of physiological responses of organisms to relevant environmental variables and of the indirect impacts of these responses on species interactions, we can then quantitatively anticipate effects on natural assemblages given various scenarios of global climate change. Specifically, forecasting the impact of climate change on the distribution and abundance of organisms requires that the following questions be addressed:

1. How are relevant environmental factors such as air and water temperature, food supply, and oxygen availability likely to change over appropriate temporal and spatial scales under future climate-change scenarios?

2. How are environmental factors such as air temperature and water temperature translated into physiologically relevant factors such as body temperature (Gilman et al. 2006, Helmuth 2002, Helmuth et al. 2002, Wethey 2002)? In many cases, organisms perceive and respond to environmental signals such as water velocities, air temperatures, and oxygen availabilities in different ways depending on factors such as organism size, morphology, and behavior. It may thus be impossible to decipher environmental patterns without considering the role of the organism in integrating and responding to these environmental signals (Helmuth et al. 2005).

3. How close are individuals living to the limits of their physiological tolerance within each portion of each species range (Chown et al. 2004, Hofmann 2005, Somero 2002, Southward 1958), and in cases where distributional limits (both local and geographic) are set directly by physiological limitation, what environmental factor(s) drives these limits? Namely, it is necessary to understand when and where organisms are living at the limits of their fundamental niche (i.e., are limited by some aspect of physiological tolerance) in contrast to when their patterns of distribution are affected by the presence of predators, competitors, and facilitators (i.e., species boundaries are representative of realized niche space) (Davis et al. 1998, Hampe 2004, Hutchins 1947). How do

multiple environmental factors (e.g., food availability, temperature, and pH) interact to drive susceptibility to climatic change (Dahlhoff 2004, Harley et al. 2006, Helmuth et al. 2005)?

4. In cases where species distributions are determined by biotic interactions, how are such interactions indirectly affected by climate (Burnaford 2004; Sanford 1999, 2002; Southward 1991; Wethey 1983, 2002)? Specifically, can mechanistic forecasts be made of the indirect impacts of climatic change on species interactions?

5. How rapidly can populations evolve in response to environmental changes (and interactions among them) (Clarke 2003)?

6. When cases of mortality and reproductive failure do occur, how do patterns of fertilization success and propagule dispersal affect the probability of successful recolonization (Broitman et al. 2005, Gaylord & Gaines 2000, Palumbi et al. 2003, Sotka et al. 2004)? Similarly, when sites become newly habitable, how does propagule dispersal affect the colonization of these sites or affect the invasibility by nonnative species? Finally, when large dead zones are created in the centers of species distributions, how do larval and gamete dispersal and organism life history interact with the size of the dead zone to affect the creation of disjunct populations (Sotka et al. 2004)? What impact does this have on the capacity of populations to evolve in response to rapid climate change (Clarke 2003)?

Satisfactorily answering these questions is clearly not a straightforward or easy task for any ecosystem, although significant progress has been made in most of these arenas. Answering them all for any one ecosystem is an incredibly ambitious challenge and likely impossible to enact for every species within an assemblage. However, by applying such techniques to keystone and habitat-forming species, considerable insight can be gained into the likely impacts of climatic change on population and community levels of organization. Moreover, a failure to include these aspects into a forecasting approach does not allow us to mechanistically predict where and when damage to ecosystems is likely to occur.

For example, as pointed out by several authors (Davis et al. 1998, Hampe 2004), most niche modeling approaches have assumed that all observed range boundaries are representative of a species' fundamental niche space. These studies have also assumed that physiological tolerance remains constant across a species range, a pattern shown to be inaccurate (Stillman 2003). Similarly, many studies assume that indicators of physiological stress such as aerial body temperature become increasingly stressful with decreasing latitude and often neglect both the importance of cold stress incurred at higher latitudes (Gilman 2005) and the importance of local and mesoscale processes on geographic patterns of intertidal stress in the middle of species ranges (Helmuth et al. 2002, 2005; Sagarin & Somero 2006). In many cases, studies have failed to provide a mechanistic link between environmental parameters such as air temperature and physiologically relevant metrics such as body temperature (Gilman et al. 2006), making it difficult to explicitly forecast how future changes in climate will impact the distribution and abundance of marine organisms.

As a result, the potential for committing both Type I errors (observing change where none truly exists) or, conversely, failing to see expected change in response to

climatic variation can be large and is particularly great when physiological mechanisms are not taken into account (Helmuth et al. 2005). Many studies, for example, attempt to correlate changes in the abundance or distribution of a species with a single environmental parameter (for example, air or water temperature) along a broad-scale latitudinal gradient. There are several reasons why this approach is likely to fail. First, there is no a priori reason to expect a single environmental parameter to always act as the limiting factor at all locations along a species range. For example, for intertidal organisms, water temperature may alternate with aerial temperature stress or feeding time in setting species distributions along the species range (Harley & Helmuth 2003), and factors such as body temperature and food supply are often interactive in their effects (Gilman 2006). Second, the parameter in question may not always serve as an effective proxy for physiological stress; for example, air temperature is often a poor proxy for body temperature (Helmuth 2002, Gilman et al. 2006). It is therefore not surprising that attempts to correlate changes in water temperature with changes in intertidal species abundances have sometimes yielded mixed results (e.g., Schiel et al. 2004) because water temperature may in some cases be less important than aerial body temperature in driving physiological stress. Third, environmental measurements only have relevance within the context of an organism's tolerance to those environmental factors (Southward 1958, Stillman 2003).

Importantly, by explicitly predicting where lethal and sublethal stress should occur, researchers can avoid looking for evidence of climate change in the wrong place and at the wrong time. Ecological-forecasting approaches (the prediction of patterns of environmental stress using climatic databases, remote sensing data, global climate change models, and techniques such as heat-budget modeling) can be used to generate explicit hypotheses regarding where climate change is most likely to impact organisms and populations and where it is not. Similarly, hindcasting techniques can be used to generate maps of environmental stress that can be compared against historical records of species-range shifts to explicitly test hypotheses regarding the impacts of past climatic changes on marine communities. However, these techniques are only useful when they are combined with information on the indirect and direct effects of climate on physiological performance and population dynamics.

These approaches can be used to predict patterns of physiological stress in a spatially and temporally explicit manner and to generate explicit hypotheses that can then be tested under field conditions. The important distinction between this type of forecasting and larger-scale correlative approaches is that there is no a priori expectation of a simple relationship between a single environmental variable and the response of individuals, populations, or communities to climatic change. Instead, predictions can be tested on a spatially and temporally explicit basis, and environmental and biotic factors can alternate with one another in setting distributional limits across a cascade of scales.

An important potential weakness in the climate envelope approach that has been highlighted is that as currently used, it tends to ignore the indirect effects of climate on species interactions. Davis et al. (1998) rekindled the debate regarding the role of biotic versus abiotic factors in determining the geographic range of species. Most climate envelope (environmental niche modeling) approaches estimate species

distribution patterns on the basis of environmental variables and then map suitable climate (niche) space, often ignoring the effects of species interactions and dispersal capabilities (Davis et al. 1998). Importantly, however, although these factors have not been addressed previously using such approaches, the inclusion of indirect effects in ecological-forecasting approaches is not precluded.

Instead of selection for either abiotic or biotic parameters, we argue for the incorporation of both types of data at local as well as regional spatial scales. Specifically, we suggest physiological and behavioral responses of biota to microclimate and local weather (Sanford 1999, 2002; Southward 1958) should be integrated into existing models of climate-driven biogeographic distribution (Helmuth et al. 2005, Hodkinson 1999, Porter et al. 2002). Together, this approach can be used to explicitly generate hypotheses as to when and where climate-mediated interactions, or climate alone, may set geographical distributions (Helmuth et al. 2005, Wethey 2002). For example, forecasting techniques can be used to generate spatially explicit maps of both subtidal and intertidal body temperatures of keystone species over a cascade of spatial and temporal scales. These maps can then be compared against lethal limits generated by physiological studies (Somero 2002) and studies exploring the indirect biotic influence of these impacts (Sanford 1999, Wethey 1983). These overlain maps can then be used to test the potential role of extreme temperatures and cumulative measures such as degree hours, as is currently used in subtidal environments such as coral reefs (Gleeson & Strong 1995), in setting present, past, and future range boundaries.

Such a mechanistic framework therefore recognizes that species interactions can both modify the effects of and be modified themselves by climate change (Burnaford 2004, Pincebourde & Casas 2006). Where species of cold- and warm-water origins coexist, changes in climate can alter the relative dominance of species and force competitively inferior species into refugia (Connell 1961; Southward 1967, 1991; Southward & Crisp 1954b; Wethey 1983, 1984) or cause localized extinctions to occur. The strength of predator-prey and facilitation interactions may also be affected by shifts in climate (Bertness et al. 1999; Sanford 1999, 2002; P. Moore, unpublished data), resulting in trophic mismatches and ecosystem destabilization (Power et al. 1999, Richardson & Schoeman 2004).

Importantly, such a framework can be used to predict the potential movement of invasive species. The introduction of invasive species has become more common throughout the twentieth century with the intensification of aquaculture and increased global maritime transport (Carlton & Geller 1993). The proliferation of invasive species may be aided by climatic change as local environmental conditions become suitable for initial survival and promote the earlier settlement and increased reproductive success of invasive species (Stachowicz et al. 2002). This competitive advantage may lead to reductions in the abundance or total extinction of native species from sites.

SUMMARY

A large body of evidence has conclusively demonstrated that Earth's climate is changing and that these changes in some cases have devastating impacts on natural

ecosystems. Importantly, the results of long-term monitoring have shown that these changes are evident across a wide range of marine taxa and can be rapid, with major shifts in biogeographic distributions occurring on a subdecadal scale. Unless we continuously track changes in ecological communities alongside concomitant changes in key environmental variables, measured at scales relevant to organisms, we may miss important signature events such as extreme freezes that can leave their marks on assemblages for decades.

The challenge before biologists is to understand the mechanisms underlying the role of climate in driving physiological and ecological performance and the subsequent impacts on species distributions. An important consideration, however, is that climatic factors do not affect all ecological interactions, and not all impacts are negative. Moreover, when mortality events occur, they may be overwhelmed by patterns of larval dispersal. We should therefore not expect to see evidence of the impacts of climatic change everywhere we look. Conversely, we should be prepared to look beyond simple range shifts for impacts of climate change on intertidal organisms.

Subsequently, it is important to shift our emphasis away from the search for the impacts of climate change and toward a hypothesis-driven approach that recognizes the interactions between climatic and nonclimatic factors in determining patterns of species abundance and distribution (Parmesan et al. 2005). Clearly, climate change is having and will continue to have a large impact on many natural assemblages; the challenge is to forecast where and when such effects are most likely to occur, given our best estimates of future climatic change. For example, by comparing physiological tolerances against patterns of environmental variables in the field, we can determine where species are living at their realized versus fundamental niche spaces and therefore determine how close to the edges of their tolerance limits these organisms are likely to be (Somero 2002). Similarly, by looking for rapid changes in past climatic conditions— for example, inflection points where sudden cooling or heating events occurred (e.g., Crisp 1964)—we can compare our predictions of changes in faunal communities against the results of monitoring to test our understanding of community responses to climate change using hindcasting approaches. Importantly, such an approach dictates that we look not only at species-range boundaries, but also at multiple sites within species distributions.

Such a program is ambitious and difficult to attain for even a few species, much less all species over a large geographic region. Beginning with keystone and habitat-forming species may serve to explain much of the ecological impacts of climate change where they occur. To this end, the use of large-scale meta-analysis on the impacts of climate on natural ecosystems must continue, for it allows us to detect general patterns over large scales and is vital for informing policy. However, if we are to move forward in predicting the impacts of climate change, we must move beyond the search for more proof and toward methods that permit the explicit forecasting of where damage is likely to occur. Ecological forecasting is only one piece in an exceedingly large and complex puzzle, but it may serve as an effective means of initial triage, helping to determine which sites are most likely to sustain damage in coming years. Although the pioneers envisaged such an approach (Crisp & Southward 1958, Fischer-Piette 1933, Hutchins 1947, Lewis 1964, Orton 1920, Southward & Crisp 1954a), it is only

with recent technological advances that we can expand on this knowledge to move from qualitative prediction to quantitative forecast.

SUMMARY POINTS

1. Long-term monitoring has shown that changes in the distribution, abundance, and range limits of intertidal species can occur rapidly, and that poleward-range edges have shifted by as much as 50 km per decade.

2. Climate change impacts intertidal species at multiple life history stages. Factors such as water temperature, aerial body temperature, and food supply are likely to alternate in their importance in space and time in setting species-range boundaries.

3. Recent evidence suggests that environmental heterogeneity along species distributions may be higher than expected. As a result, species may display responses to climate change at multiple sites within their ranges, and not just at poleward- and equatorial-range boundaries.

4. Many studies rely on environmental proxies for physiological stress (e.g., air or water temperature) and fail to consider the environment at the scale of the organism; often these patterns in air or water temperature can be misleading.

5. Although large-scale climate envelope approaches provide an initial approximation of the potential effects of climate change, they often ignore the indirect effects of warming and the influence of nonclimate factors in setting range boundaries.

6. Ecological-forecasting approaches provide a means of generating explicit hypotheses regarding the effects of climate change on species distribution patterns.

FUTURE ISSUES

1. Our understanding of the future effects of climate change mandates that we validate our hypotheses by the comparison of historical changes in climate with the resulting responses of ecological communities. The continuation of long-term monitoring projects is thus an essential part of any future forecasting program.

2. Our understanding of the indirect effects of climate change, for example, on rates of foraging and sublethal levels of physiological stress, is still limited.

3. The interaction between multiple physiological stressors related to climate change (e.g., aerial and aquatic body temperatures, pH) is still poorly understood for most intertidal organisms.