

The impacts of climate change in coastal marine systems

Christopher D. G. Harley,^{1,2*}
A. Randall Hughes,³ Kristin M.
Hultgren,³ Benjamin G. Miner,¹
Cascade J. B. Sorte,¹ Carol S.
Thornber,^{3,4} Laura F. Rodriguez,³
Lars Tomanek^{3,5} and Susan
L. Williams¹

¹*Bodega Marine Laboratory,
University of California-Davis,
Bodega Bay, CA 94923, USA*

²*Department of Zoology,
University of British Columbia,
Vancouver, BC, Canada V6T 1Z4*

³*University of California, Davis,
CA 95616, USA*

⁴*University of Rhode Island,
Kingston, RI 02881, USA*

⁵*California Polytechnic State
University, San Luis Obispo,
CA 93407-0401, USA*

Abstract

Anthropogenically induced global climate change has profound implications for marine ecosystems and the economic and social systems that depend upon them. The relationship between temperature and individual performance is reasonably well understood, and much climate-related research has focused on potential shifts in distribution and abundance driven directly by temperature. However, recent work has revealed that both abiotic changes and biological responses in the ocean will be substantially more complex. For example, changes in ocean chemistry may be more important than changes in temperature for the performance and survival of many organisms. Ocean circulation, which drives larval transport, will also change, with important consequences for population dynamics. Furthermore, climatic impacts on one or a few ‘leverage species’ may result in sweeping community-level changes. Finally, synergistic effects between climate and other anthropogenic variables, particularly fishing pressure, will likely exacerbate climate-induced changes. Efforts to manage and conserve living marine systems in the face of climate change will require improvements to the existing predictive framework. Key directions for future research include identifying key demographic transitions that influence population dynamics, predicting changes in the community-level impacts of ecologically dominant species, incorporating populations’ ability to evolve (adapt), and understanding the scales over which climate will change and living systems will respond.

Keywords

Anthropogenic climate change, carbon dioxide (CO₂), coastal oceanography, community structure, distributional shifts, marine ecosystems, ocean pH, population dynamics, synergistic effects, temperature.

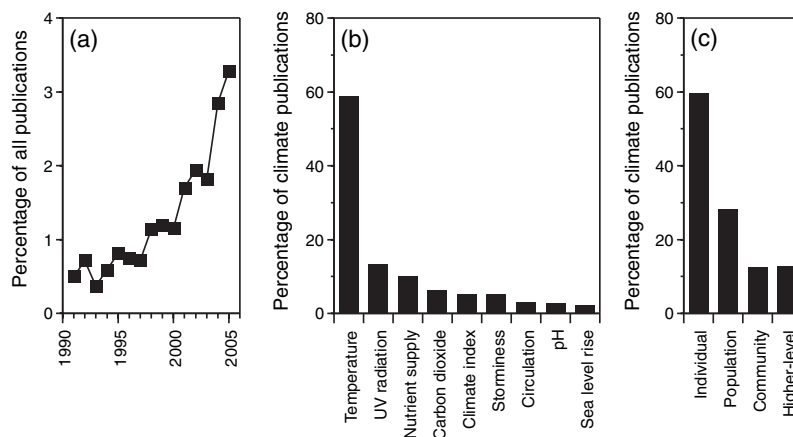
INTRODUCTION

Coastal marine systems are among the most ecologically and socio-economically vital on the planet. Marine habitats from the intertidal zone out to the continental shelf break are estimated to provide over US\$14 trillion worth of ecosystem goods (e.g. food and raw materials) and services (e.g. disturbance regulation and nutrient cycling) per year, or *c.* 43% of the global total (Costanza *et al.* 1997). However, there is a strong scientific consensus that coastal marine ecosystems, along with the goods and services they provide, are threatened by anthropogenic global climate change (IPCC 2001). Recent climatic trends, which are only a fraction of the magnitude of predicted changes in the coming centuries, have already triggered significant

responses in the Earth’s biota (IPCC 2001). As these changes continue, we risk serious degradation of marine ecosystems, with far-reaching consequences for human health and welfare.

Given their global importance, coastal marine environments are a major focus of concern regarding the potential impacts of anthropogenic climate change. A pair of seminal reviews in the early 1990s (Fields *et al.* 1993; Lubchenco *et al.* 1993) summarized the then-current understanding of climate change impacts on marine systems. In both cases, the authors focused on the effects of rising temperatures on organismal- and to a lesser extent population-level processes, and they used natural cycles such as the El Niño–Southern Oscillation (ENSO) and the Pleistocene–Holocene transition as proxies for future change. The basic

Figure 1 Climate-related publication trends in the marine ecology literature (see Appendix 1 for methodological details). (a) The rate of publication on marine climate change, expressed as a percent of the entire marine ecological literature. (b) Trends in the abiotic variables considered. (c) Trends in the level of biological response considered. Because some papers considered multiple variables or levels, the bars in b and c sum to more than 100%.



predictions can be summarized as follows: as temperature rises in the future, the distribution and abundance of species will shift according to their thermal tolerance and ability to adapt.

Since 1993, the literature on climate change impacts in marine systems has grown exponentially (Fig. 1a). Perhaps not surprisingly, the topics emphasized in the early 1990s continue to dominate the literature; most climate-related research in the marine environment focuses on temperature (Fig. 1b), and most work is conducted at the level of individual organisms (Fig. 1c). To some degree, this focus is entirely appropriate; many recent studies do indeed support the predictions of Fields *et al.* (1993) and Lubchenco *et al.* (1993). However, a growing body of work is demonstrating that these simplistic relationships between temperature and the biota are inadequate in predicting many important aspects of future biological change. Patterns of temperature change in space and time, and biological responses to them, are not as straightforward as once envisioned. More importantly, temperature is only one of a suite of potentially interacting climatic variables that will drive future ecological change in marine systems. Finally, studies conducted on population- and community-level processes suggest that climatic impacts on individual organisms do not necessarily translate directly into changes in distribution and abundance.

Here, we review recent advances in our understanding of the physical and chemical nature of climate change in coastal oceans. Next, we examine the likely ecological responses to climate change at two basic levels. We first address the proximate effects of environmental change, including impacts on individuals, populations and communities. We then consider the broader ecological responses that will emerge from these proximal impacts; emergent responses include alterations in biologically and socio-economically important patterns and processes ranging from primary productivity to biogeography to evolution. Finally, we highlight areas in which information is lacking, in hopes that continuing research efforts will fill these gaps and thus

improve our ability to predict and mitigate the effects of climate change. If we aim to successfully manage and conserve coastal marine species and habitats, improving our predictive power is imperative.

ABIOTIC CHANGE IN COASTAL MARINE ENVIRONMENTS

The earth's climate system varies naturally across a range of temporal scales, including seasonal cycles, inter-annual patterns such as the ENSO, inter-decadal cycles such as the North Atlantic and Pacific Decadal oscillations, and multimillennial-scale changes such as glacial to inter-glacial transitions. This natural variability is reflected in the evolutionary adaptations of species and large-scale patterns of biogeography. Over the past several centuries, human activities have become an additional, important component to the climate system (Fig. 2). Anthropogenic climatic forcing is mediated primarily by greenhouse gas (predominantly CO₂) emissions. Together, elevated CO₂ and the resultant increases in global mean temperature will result in a cascade of physical and chemical changes in marine systems.

Physically driven changes

Atmospheric greenhouse gases trap some of the heat energy that would otherwise re-radiate to space, helping to warm the planet. Owing in large part to increasing greenhouse gas concentrations, global air and sea surface temperatures have risen in the past century by 0.4–0.8 °C (IPCC 2001). These warming trends are expected to accelerate in the current century (IPCC 2001), with implications for several additional abiotic variables. For example, as a result of warming seawater, the world oceans are expanding. Coupled with freshwater input from ice-melt, thermal expansion of the oceans is causing sea level to rise at *c.* 2 mm year⁻¹ (IPCC 2001). Because warming trends will be stronger over continental interiors than over oceans, the atmospheric

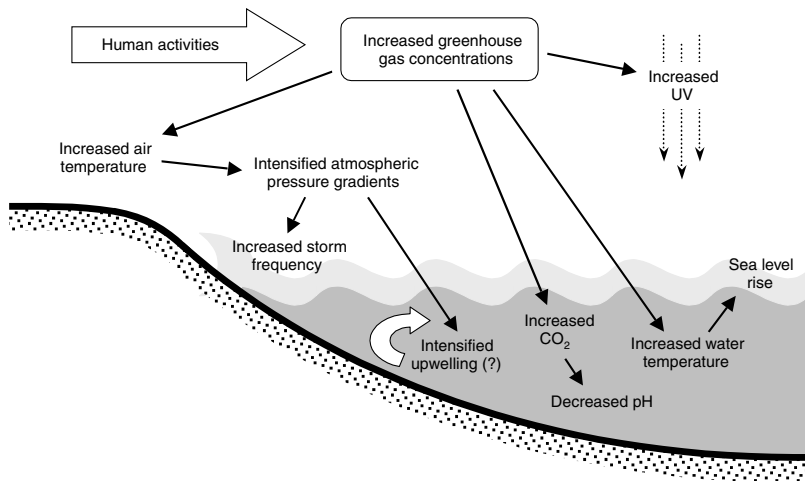


Figure 2 Important abiotic changes associated with climate change. Human activities such as fossil fuel burning and deforestation lead to higher concentrations of greenhouse gases in the atmosphere, which in turn leads to a suite of physical and chemical changes in coastal oceans. The question mark indicates that the relationship between climate change and upwelling is uncertain. See text for details.

pressure gradient, and thus wind fields, along ocean margins will intensify. Stronger wind fields might lead to enhanced upwelling in eastern boundary currents (Bakun 1990), which could increase nutrient availability at the surface. Paleoclimatic data suggest that upwelling in the California current system is positively correlated with temperature over millennial timescales (Pisias *et al.* 2001). Furthermore, upwelling along the California coast has increased over the past 30 years, and these increases are expected to continue (Snyder *et al.* 2003). However, stronger thermal stratification and a deepening of the thermocline could prevent cool, nutrient-rich waters from being upwelled (Roemmich & McGowan 1995). Because upwelling is of fundamental importance in coastal marine systems, further elucidation of the relationship between climate and upwelling is a high research priority. Changes in atmospheric circulation might also change storm frequency; an increase in the frequency of winter storms has already been observed in coastal oceans (Bromirski *et al.* 2003), and the trend is expected to continue (IPCC 2001). Atmospheric circulation changes will also influence precipitation patterns that will affect coastal salinity, turbidity, and inputs of terrestrial-derived nutrients and pollutants. Climate change could also alter large-scale ocean circulation; previous warm periods were associated with reduced advection within the California Current system (Pisias *et al.* 2001). Finally, future warming is predicted to lead to more frequent El Niño-like conditions (Timmermann *et al.* 1999).

Chemically-driven changes

Increasing greenhouse gas concentrations will have important and often overlooked impacts on ocean biogeochemistry. Atmospheric carbon dioxide concentrations are expected to rise from a pre-industrial level of 280 to 540–970 ppm by the year 2100, depending on future emission scenarios (IPCC 2001). Roughly half of the CO₂ released by

human activities between 1800 and 1994 is now stored in the ocean (Sabine *et al.* 2004), and about 30% of modern CO₂ emissions are taken up by oceans today (Feely *et al.* 2004). Continued uptake of atmospheric CO₂ is expected to substantially decrease oceanic pH over the next few centuries, changing the saturation horizons of aragonite, calcite, and other minerals essential to calcifying organisms (Kleypas *et al.* 1999; Feely *et al.* 2004). Model estimates of pH reduction in the surface ocean range from 0.3 to 0.5 units over the next 100 years and from 0.3 to 1.4 units over the next 300 years, depending on the CO₂ emission scenario used (Caldeira & Wickett 2005). While many marine organisms have adapted to thermal fluctuations in the last few million years, the expected changes in pH are higher than any other pH changes inferred from the fossil record over the past 200–300 million years (Caldeira & Wickett 2003; Feely *et al.* 2004). Finally, increasing CO₂ levels in the atmosphere have been postulated to deplete the ozone layer (Austin *et al.* 1992), potentially leading to enhanced levels of ultraviolet radiation at the earth's surface.

Additional complexities

The potential for biogeochemical feedback cycles makes it difficult to precisely predict future temperatures and carbon dioxide concentrations. For example, cloud cover, ultraviolet radiation, planktonic productivity, and the release of dimethyl sulphide (DMS) by marine algae are all linked via complex feedback mechanisms (IPCC 2001; Larsen 2005). The ecological implications of these biogeochemical feedbacks are beyond the scope of this review.

ECOLOGICAL RESPONSES TO CLIMATE CHANGE

The magnitude and variety of climatically forced changes in the physical environment will provoke substantial proximate and emergent responses in the biosphere (Fig. 3). The

proximate ecological responses to climate change depend upon the relationships between the abiotic environment, organismal-level processes, population dynamics and community structure. The direct effects of climate change (Fig. 3, yellow boxes) impact the performance of individuals at various stages in their life history cycle (shown in green) via changes in physiology, morphology and behaviour. Climate impacts also occur at the population level via changes in transport processes that influence dispersal and recruitment. Community-level effects (in blue) are mediated by interacting species (e.g. predators, competitors, etc.), and include climate-driven changes in both the abundance and the *per capita* interaction strength of these species. The combination of these proximate impacts (upper box) result in emergent ecological responses (lower oval), which include alterations in species distributions, biodiversity, productivity and microevolutionary processes.

In the sections below, we first focus on the proximate impacts that various aspects of climate change will have on organismal-level processes and population dynamics, and how these factors will play out in local communities. Because the existing literature is somewhat better integrated across levels of biological organization than across multiple climatic drivers (see *Future directions*), we break our discussion down by climate variable rather than by level of biological organization. After discussing the likely proximate impacts of climate change, we turn our attention to emergent ecological responses such as biogeographical range shifts and changes in productivity and diversity.

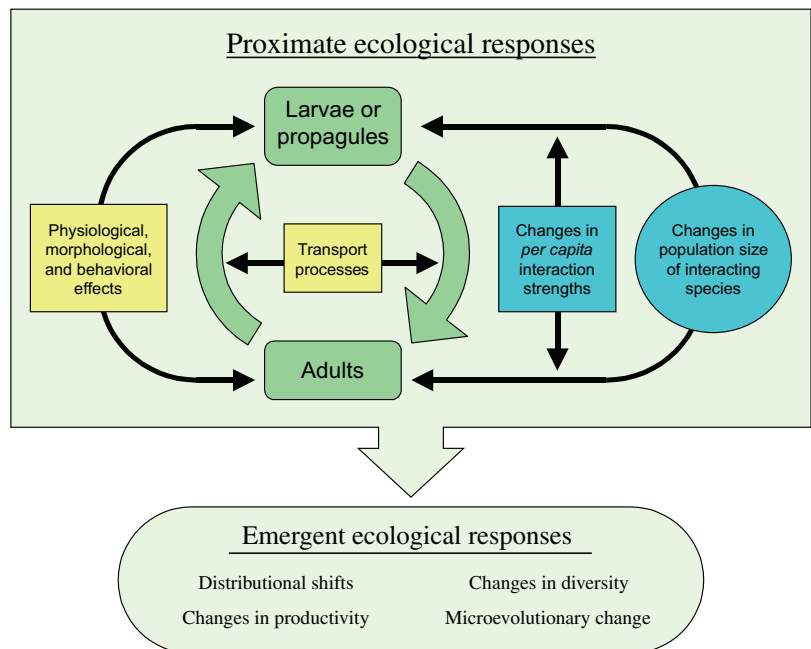
Proximal ecological responses to changing environmental conditions

Responses to temperature

Temperature affects physiological processes ranging from protein damage to membrane fluidity to organ function (Hochachka & Somero 2002). Because many marine organisms already live close to their thermal tolerances (Somero 2002; Hughes *et al.* 2003), increases in temperature can negatively impact the performance and survival of marine organisms. For example, many reef-building corals live very close to their upper thermal tolerances, and warm episodes have resulted in widespread coral bleaching and mortality (Hughes *et al.* 2003; McWilliams *et al.* 2005).

The biological importance of rising temperature varies within and among species. It has long been known that different ontogenetic stages are differentially susceptible to environmental stress. For example, certain planktonic larval stages are particularly susceptible to thermal effects (Pechenik 1989), and the young benthic stages of many organisms are more vulnerable to stress than are adults (Foster 1971). However, recent work has identified unexpected differences in climate change vulnerability among species. For example, although mid-intertidal porcelain crabs and turban snails are more thermotolerant than their subtidal congeners, the mid-intertidal species also live closer to their physiological temperature limits, and have a relatively limited ability to adjust their physiology (e.g. heart rates and heat-shock protein synthesis) with increasing acclimation temperature (Tomanek & Somero 1999; Still-

Figure 3 Potential ecological responses to climate change. The life cycle of a generic marine species is shown in green. Abiotic changes in the environment have direct impacts (yellow boxes) on dispersal and recruitment, and on individual performance at various stages in the life cycle. Additional effects are felt at the community level via changes in the population size and per capita effects of interacting species (in blue). The proximate ecological effects of climate change thus include shifts in the performance of individuals, the dynamics of populations, and the structure of communities. Taken together, these proximate effects lead to emergent patterns such as changes in species distributions, biodiversity, productivity, and microevolutionary processes. See text for details.



man 2003). Surprisingly, the more eurythermal and specifically heat-tolerant mid- to high-intertidal species might actually be more vulnerable to climate change than the less heat-tolerant species. This pattern also holds at the latitudinal scale: low-latitude species live nearer to their thermal limits than higher-latitude species (Tomanek & Somero 1999; Stillman 2002).

Temperature also affects the timing of ontogenetic transitions. Climate change may decouple changes in the larval environment from the cues used by the adult population (Edwards & Richardson 2004). For example, the timing of *Macoma balthica* spawning in north-western Europe is temperature dependent. Recent warming trends have led to earlier spawning but not earlier spring phytoplankton blooms, resulting in a temporal mismatch between larval production and food supply (Philippart *et al.* 2003). The intensity of predation on juvenile *Macoma* by seasonally abundant shrimp has also increased because the peak of shrimp abundance has advanced to coincide more closely with the arrival of vulnerable spat (Philippart *et al.* 2003).

Rising temperatures will drive other important changes at the community level. For example, the strength with which the sea star *Pisaster ochraceus*, a keystone predator, interacts with its principal prey (habitat forming mussels) varies with water temperature (Sanford 1999). Exposure to warmer waters increases both *Pisaster's* mid-intertidal abundance and per capita consumption rate (Sanford 1999). Sanford's results suggest that warming could allow *Pisaster* to progressively eliminate large sections of mussel beds and secondarily displace hundreds of species that inhabit the mussel matrix. Climatic effects on one or a few key species may drive community-level change in a variety of nearshore assemblages: for example, invertebrate responses to elevated sea surface temperatures near a power plant thermal outfall appear to be mediated indirectly by thermally forced decreases in the abundance of canopy-forming macrophytes such as subtidal kelps and intertidal foliose red algae (Schiel *et al.* 2004).

Responses to sea level rise

The most obvious consequence of sea level rise will be an upward shift in species distributions. Most species are expected to be able to keep pace with predicted rates of sea level rise, with the exception of some slow-growing, long-lived species such as many corals (see Knowlton 2001 for review). However, dramatic ecological changes could result from decreased habitat availability within a particular depth zone. For example, intertidal habitat area may be reduced by 20–70% over the next 100 years in ecologically important North American bays, where steep topography and anthropogenic structures (e.g. sea walls) prevent the inland migration of mudflats and sandy beaches (Galbraith *et al.*

2002). Sea level rise may also reduce the spatial extent of biogenic habitat by outpacing the accretion rates of marshes and coral reefs (Knowlton 2001; Scavia *et al.* 2002).

Responses to changes in circulation

Marine systems are expected to respond to changes in both the mean wind fields and extreme wind events. Increasing frequency of extreme winds and associated storm waves has obvious implications for intertidal and shallow subtidal systems that are vulnerable to hydrodynamic disturbance. Caribbean coral reefs require over 8 years to recover from damage incurred by storms (Gardner *et al.* 2005), and increasing storm frequency will reduce the odds of recovery between disturbance events. Changes in the mean wind velocity will also be important, particularly as it relates to upwelling intensity. Although researchers disagree on the exact nature of climate-induced changes in upwelling, shifts in nutrient supply are likely in the future. Upwelled nutrients fuel growth and reproduction in benthic and planktonic algae, and future changes in upwelling could have important consequences for productivity (see *Emergent ecological responses*).

Marine systems, which are often dominated by organisms with planktonic life history stages, are also sensitive to alteration in coastal oceanographic patterns. Upwelling and alongshore advection patterns are strong determinants of dispersal and recruitment in marine systems (Gaylord & Gaines 2000; Connolly *et al.* 2001). Modelling work suggests that increased offshore advection is often negatively correlated with adult population size, and very strong upwelling could theoretically prevent a species from maintaining an adult benthic population at particular sites (Connolly & Roughgarden 1999). Although such a scenario has not been conclusively demonstrated in the field, it is conceivable that altered patterns of mass transport could tip the balance of larval recruitment to adult mortality and lead to local population extinctions (Svensson *et al.* 2005). Intriguingly, a species' response to upwelling intensity could depend on community dynamics. Modelling work suggests that, by reducing the population sizes of predators and dominant competitors, increased offshore advection actually increases the adult population sizes of planktonically dispersing prey and subordinate competitors (Connolly & Roughgarden 1999) – a trend opposite that which would be predicted in the absence of interspecific interactions.

Responses to CO₂ and pH change

When compared with physically driven changes such as warming and sea level rise, the impacts of chemical changes in the ocean are poorly understood. While increases in CO₂ are expected to have positive impacts on many terrestrial plants because of increases in photosynthesis (Ainsworth & Long 2005), most marine plants (with the exception of

seagrasses) are carbon-saturated (Gattuso & Buddemeier 2000), and enhanced growth is not expected. However, the reduction in pH that will accompany elevated CO₂ concentrations has profound implications for physiological processes in marine organisms. Short-term experimental elevation of CO₂ results in reductions in subcellular processes such as protein synthesis and ion exchange (for review, see Pörtner & Langenbuch 2005). These physiological effects are more pronounced for invertebrates than for fish (Pörtner & Langenbuch 2005), suggesting that certain taxa may be disproportionately affected by changes in CO₂ and pH.

Longer-term, climatically realistic manipulations of CO₂ are extremely rare, but the few available results are sobering. A 3-month, 0.7-unit pH reduction lowered metabolic rate and growth in mussels (Michaelidis *et al.* 2005). A 6-month elevation of CO₂ by a conservative 200 ppm, which lowered pH by a mere 0.03 units, reduced both growth and survivorship in gastropods and sea urchins (Shirayama & Thornton 2005). Some of the measured reduction in growth described above may be a response to decreased rates of shell formation. Indeed, the future acidification of the oceans could severely impact the many marine invertebrates and algae that build carbonate structures. Decreased calcification rates in response to increased CO₂ has been shown in taxa including coccolithophorid zooplankters, coralline algae, reef-building scleractinian corals and pteropod molluscs (Kleypas *et al.* 1999; Riebesell *et al.* 2000; Feely *et al.* 2004). Rates of calcification in corals and coralline red algae are likely to drop by *c.* 10–40% with a climatically realistic doubling of the pre-industrial partial pressure of CO₂ (Feely *et al.* 2004). The population- and community-level impacts of such changes remain largely unknown. Considering that the expected pH drop may be unprecedented over the last several hundred million years, more research on the ecological implications of pH change is desperately needed.

Responses to UV

The depletion of the ozone layer because of increasing carbon dioxide concentrations (Austin *et al.* 1992) will likely result in increased ultraviolet radiation at the earth's surface, which would in turn have negative effects on invertebrate larvae and algae (Bischof *et al.* 1998; Hoffman *et al.* 2003; Peachey 2005). Recent work now suggests that the negative impacts of UV on a particular species depends on the presence of interacting species. For example, marine phytoplankton were protected from UVB damage when co-cultured with marine viruses (Jacquet & Bratbak 2003). The impact of UV radiation on benthic algae can depend on the presence of grazing invertebrates (Lotze *et al.* 2002). These results suggest that future work must move beyond single-factor experiments, as these simplistic studies might

greatly under- or over-estimate the importance of future increases in ultraviolet radiation.

Emergent ecological responses

Distributional shifts: zonation patterns

Intertidal and near-shore benthic habitats are characterized by strong vertical patterns in the distribution of organisms. Biological zonation reflects the sharp local gradients in physical stress, and zonation patterns are likely to shift as the environment changes (Lubchenco *et al.* 1993). Long-term data suggest that upper vertical limits, particularly of sessile intertidal organisms, are inversely correlated with temperature (Mathieson *et al.* 1998). Several North Atlantic fishes have also undergone shifts in their mean depth distribution in response to warming (Perry *et al.* 2005). In systems such as giant kelp forests where hydrodynamic disturbance from storm waves sets upper distributional limits (Graham 1997), species intolerant to such disturbance may become restricted to deeper water. Laboratory and observational evidence suggest that increased UV would also cause a downward shift for some species of algae (Bischof *et al.* 1998), although definitive field experiments have yet to be conducted. Finally, sea level rise will have obvious consequences for the vertical position of marine organisms (see above).

Although zonation shifts are local (vertical) phenomena, they can lead to patterns at a variety of alongshore (horizontal) scales. For example, some latitudinal range limits appear to be set where the vertical range of a species collapses to zero. This 'squeeze effect' arises when abiotic stress shifts the vertical range of one species into the vertical range of a consumer or competitor. The intertidal alga *Mazzaella parkesii* is restricted to environmentally benign, north-facing slopes by the combined influence of aspect-dependent abiotic stress and aspect-independent herbivory (Harley 2003). Conversely, the barnacle *Chthamalus fragilis* is excluded from an environmentally benign region (the Gulf of Maine) where there is no vertical thermal refuge from a dominant competitor (Wetthey 1983). The extent to which similar squeeze effects, operating through time rather than space, will result in local and geographic range shifts remains unknown.

Distributional shifts: biogeographical ranges

Widespread biogeographical range shifts clearly occur in association with changing climatic conditions in marine environments. Abundant fossil evidence demonstrates that marine faunas shifted polewards as sea surface temperatures rose, e.g. during the Pleistocene–Holocene transition (reviewed in Fields *et al.* 1993). Short-term pulses of increased temperatures, such as those during ENSO events, can also impact species' distributional limits (Keister *et al.* 2005). Pelagic species and those with pelagic larval stages are highly represented in the suite of species that have shifted

their distributions in the past and might be especially likely to experience range shifts with global climate change.

Historical records have identified recent, decadal-scale changes in species' distributions. Actual documentation of latitudinal range shifts is relatively rare, but recent work has identified warming-associated poleward range shifts for a Californian gastropod (Zacherl *et al.* 2003), a Caribbean coral (Precht & Aronson 2004), and North Sea fishes (Perry *et al.* 2005). In lieu of searching for the expansion or contraction of range boundaries, which are often difficult to determine with certainty, many researchers have investigated changes in species' relative abundances at a single location as a proxy for spatial shifts. Perhaps the most comprehensive study to date is that of Southward *et al.* (1995), which demonstrated changes in the abundance of Northeast Atlantic taxa ranging from kelps to barnacles and from zooplankton to fish. The local abundance of southern taxa increased while northern taxa decreased during periods of warming, and the reverse occurred during a period of cooling. Several additional studies have demonstrated a shift from higher-latitude to lower-latitude species during periods of warming (Barry *et al.* 1995; Holbrook *et al.* 1997; Hawkins *et al.* 2003). Interestingly, this seemingly general pattern of abundance shifts in accordance with 'warm' vs. 'cold' biogeographical distributions was not found in a study of artificial warming near a power plant (Schiel *et al.* 2004). It is unclear whether this discrepancy indicates that biogeographical designations are an overly simplistic predictor of change, or if ecological responses to spatially limited warming may not be accurate predictors of larger-scale impacts associated with climate change.

Predicting future distributional shifts requires additional attention to species' range boundaries and to the factors that determine them. In terrestrial environments, range edges are generally thought to be set where environmental conditions exceed the tolerances of individuals. Given this assumption, the 'bioclimate envelope' approach has been used with some success to predict range shifts through time (Pearson & Dawson 2003). In marine environments, direct climatic effects on individuals are also important. Many organisms are more stressed near their species' range boundaries (Sorte & Hofmann 2004), and the distributions of these species can be expected to shift as environmental conditions change. However, environmental processes which impact population dynamics (e.g. flow-mediated dispersal) are extremely important in marine environments, where they play a greater role than in terrestrial habitats. Current-mediated dispersal limitation can define many biogeographical boundaries in coastal oceans, despite potentially suitable habitat beyond the dispersal barrier (Gaylord & Gaines 2000). Thus, many marine species' range limits may remain stationary even as conditions in extra-limital habitats become suitable (Fields *et al.* 1993). Conversely, we suggest

that a warming-associated weakening of alongshore advection (Pisias *et al.* 2001) could actually break down certain marine biogeographical barriers that currently prevent range expansions.

Interactions among species at the community level could also influence range boundaries. This effect has been demonstrated in the laboratory (Davis *et al.* 1998), and has long been suspected to hold true in natural environments (Darwin 1859). Indeed, herbivory and competition play roles in setting local and regional range limits for the alga *Mazzaella parksii* and the barnacle *Chthamalus fragilis*, respectively (see above). Although definitive examples of interspecifically forced shifts in range boundaries are currently lacking, recent population declines and local extinctions near the southern limits of the mussel *Mytilus trossulus* and the abalone *Haliotis cracherodii* in California might have been driven by the expansion of a competitor and a parasite, respectively (Geller 1999; Raimondi *et al.* 2002). Although both examples involve putatively invasive species, both invasives are warm-water taxa whose present poleward expansion might be linked to rising temperatures.

Finally, it is important to consider the present and future patterns of environmental stress. Present temperatures and predicted near-future increases in thermal stress do not necessarily vary consistently with latitude in coastal marine systems (Helmuth *et al.* 2002), and organisms could be most at risk in 'hotspots' well removed from the range edge.

Changes in species composition, diversity and community structure

Climate change, along with exploitation, habitat alteration, and pollution, is reducing the abundance of many marine species and increasing the likelihood of local (and in some cases global) extinction. Although we know of no present-day extinction of a marine species definitively linked to climate change, climatically driven extinction risk is now extremely high for some species such as the Mediterranean mysid *Hemimysis speluncola* (Chevaldonne & Lejeune 2003). Because many coastal marine ecosystems such as kelp forests and coral reefs feature low functional redundancy (Micheli & Halpern 2005), the local loss of even one species could have important community- and ecosystem-level consequences. Conversely, climate change will play a role in the determining the rate at which new species are added to communities. In addition to allowing natural range expansions (see above), warming temperatures can facilitate the establishment and spread of deliberately or accidentally introduced species (Carlton 2000; Stachowicz *et al.* 2002b). More generally, climatically driven changes in species composition and abundance will alter species diversity, with implications for ecosystem functions such as productivity (Duffy 2003) and invasion resistance (Stachowicz *et al.* 2002a; Duffy 2003). The one study we are aware of that simultaneously manipulated diversity and thermal stress

found that more diverse algal assemblages were less resistant but more resilient to disturbance imparted by extreme temperatures (Allison 2004). Understanding linkages between species diversity and ecosystem function is a general research gap in marine ecology and is wide-open to investigations in the context of climate change.

Even if species composition is not altered by climate change, the strength or sign of interspecific interactions might change. Because species respond individually to climate change (e.g. Schiel *et al.* 2004), shifts in community dynamics are guaranteed as the abundance, phenology and per capita impacts of interacting species change. Although climate-forced shifts in species interactions are likely to be highly idiosyncratic, certain generalizations might apply. As environmental conditions become more stressful, competitive interactions in intertidal communities can shift to facilitative interactions (Leonard 2000). Conversely, the negative effects of disease are likely to become more severe, as pathogens are generally favoured by warmer temperatures relative to their hosts (Harvell *et al.* 2002). The strength of trophic interactions can change when climate change differentially affects consumer and resource species (Philippart *et al.* 2003). Importantly, direct climatic impacts on one or a few 'leverage' species could drive the response of an entire system (Sanford 1999; Schiel *et al.* 2004). As Sanford (1999) has demonstrated, changes in both population size and per capita effects can be important drivers of ecological change.

Changes in primary and secondary production

Changes in the distribution of habitat types because of global climate change and the concomitant rise in sea level will likely have significant ecosystem consequences via changes in primary production. Increasing temperature, UV radiation and storm disturbance could restrict the latitudinal and bathymetric ranges of important primary producers such as kelps (Graham *et al.* 1997; Bischof *et al.* 1998; Steneck *et al.* 2002). Although other producers might replace these climatically sensitive species, reductions in kelp production will have important consequences for other near-shore habitats that depend on the export of kelp detritus (Duggins *et al.* 1989).

Fluctuations in primary production in coastal systems will depend largely on variation in nutrient concentrations caused by changes in ocean current patterns and upwelling regimes. Although the exact direction of this change is difficult to predict because of complex oceanography, variation in nutrients will have significant impacts on benthic macroalgal abundance and evenness, with subsequent effects on overall production (Lotze & Worm 2002; Nielsen 2003). Furthermore, as dissolved carbon concentrations increase, macroalgae could be replaced in some localities by seagrasses. Seagrasses, which evolved during the

Cretaceous when CO₂ concentrations were much higher, exhibit carbon-limited photosynthesis under recent concentrations. Macroalgae, on the contrary, are currently carbon-saturated (Beardall *et al.* 1998). An increase in the relative abundance of seagrasses would result in a more detritus-based food web (Williams & Heck 2001).

Changes in primary production can in turn be ameliorated or exacerbated by climatic effects on the metabolic processes and population dynamics of consumers. Although increases in water temperature can positively affect macroalgal recruitment, the impacts of invertebrate consumers also tend to increase with temperature (Lotze & Worm 2002). The balance of climatic forcing at different trophic levels is clearly important, as the influence of nutrients on primary production often depends upon grazer abundances (Lotze & Worm 2002; Nielsen 2003). Individualistic phenological responses to climate change among marine functional groups will impact secondary production as the synchrony of successive trophic peaks decays (Edwards & Richardson 2004). The relative response of primary and secondary producers to upwelling dynamics can also be critical. In the Benguela upwelling system, high rates of offshore transport are proposed to favour producers by transporting herbivorous zooplankton out of the near-shore system (Bakun & Weeks 2004). The deposition and decomposition of surplus phytoplankton biomass on the seafloor have been linked to large eruptions of methane and hydrogen sulphide gas, which in turn lead to hypoxia and increased mortality of near-shore animals such as rock lobsters and Cape hake. Future global intensification of near-shore upwelling could drive additional coastal systems into a similar state (Bakun & Weeks 2004). Given the dramatic nature of this prediction, additional attention should be focused on the assumed relationship between climate change and upwelling dynamics.

Population dynamics and evolution

While 'contemporary evolution' in response to factors such as over-harvesting have been addressed (Stockwell *et al.* 2003), few studies have directly assessed how adaptation might mediate climatic impacts in marine systems (but see Berteaux *et al.* 2004). Selection for organismal-level traits has the potential to mitigate some of the climate-related environmental shifts predicted to occur (Fields *et al.* 1993). A growing body of evidence from phylogeographic (Marko 2004; Hickerson & Cunningham 2005) and contemporary studies (Kingsolver *et al.* 2001; Stockwell *et al.* 2003; Berteaux *et al.* 2004) indicates that adaptive and/or evolutionary responses can take place on the rapid temporal scales over which climate is expected to change. However, species with long-generation times are expected to have a slower response to rapid changes in climate (Berteaux *et al.* 2004), and clonal organisms may be especially sensitive to

change because, despite high numbers of individuals, they often have low effective population size and a little potential to adapt to rapid changes (Lasker & Coffroth 1999).

Dispersal is integral to gene flow and local adaptation among populations, and the ability of populations to adapt to changing selective forces will depend on species' dispersal mode, climate-related changes in abundance and distribution of organisms, and larval transport (Jump & Peñuelas 2005). For example, low gene flow between populations can increase the potential for local adaptation [(Holt & Gomulkiewicz 1997), see (Sanford *et al.* 2003) for a marine example]. However, climatically forced reductions in population size and subsequent genetic drift could restrict a species' potential for adaptation by eliminating heritable traits of ecological importance (Stockwell *et al.* 2003; Berteaux *et al.* 2004). Intense selection on single loci is likely to decrease variability in the rest of the genome (Jump & Peñuelas 2005), and lower population genetic variation can lead to a reduced ability to respond to climatic stress even on ecological time scales (Reusch *et al.* 2005). In addition to effects of neutral variation, variation in loci such as mannose phosphate isomerase (Mpi) (Rand *et al.* 2002) and heat-shock protein Hsp70 (Sorte & Hofmann 2005) can mediate which individuals tolerate thermal stress at different intertidal locations. However, a very little is known about how organisms might respond to multiple climate stressors (e.g. pH and temperature), and such responses are important to examine since trade-offs (Breeman *et al.* 2002) and/or genetic correlations (Etterson & Shaw 2001; reviewed in Jump & Peñuelas 2005) among physiological traits may limit the ability of species to adapt to contemporary climate change.

DIRECTIONS FOR FUTURE RESEARCH

Non-linearities and non-independent effects

One of the fundamental challenges facing ecologists is understanding how natural systems will respond to environmental conditions that have no analogue at present or in the recent past. This gap in our experience creates two ways in which future ecological change may surprise us. First, we risk being caught off guard by non-linearities in the climate system that are specific to climatic conditions we have not yet experienced. A prime example is the potential shut-down of thermohaline circulation in the North Atlantic. Our confidence in predicting such an event is severely limited by the simple fact that we have not witnessed conditions similar to those predicted to emerge over the next few centuries. Important non-linearities are likely to arise in biological systems as well. One recent study has demonstrated that biological responses to shifting climatic conditions (e.g. phytoplank-

ton abundance and salmon returns) are non-linear – appearing as ‘regime shifts’ – even though the underlying abiotic changes (e.g. sea surface temperature) are linear stochastic (Hsieh *et al.* 2005). This suggests that gradual changes in future climate may provoke sudden and perhaps unpredictable biological responses as ecosystems shift from one state to another.

The challenge of predicting the outcomes of climate change is made even more difficult when the combined effects of two or more variables cannot be predicted from the individual effect of each. Non-independent effects are common in nature, and may arise in one of two principle ways: (1) the impact of one factor is either strengthened or weakened by variation in another factor; and (2) the combined influence of two stressors pushes an individual or population beyond a critical threshold that would not be reached via variation in either forcing variable operating in isolation. Of the papers we considered in our literature review, a respectable 14.7% incorporated statistical designs that could detect non-independent effects of multiple forcing variables. However, the vast majority of these studies manipulated temperature and either salinity or food supply; only 2.2% of all studies were designed to test non-independent effects of more than one variable directly related to climate change.

Although the extent to which specific abiotic factors and biological responses will behave non-independently under future climate scenarios is largely unknown, there is a growing body of evidence that suggests that a variety of non-independent effects will be important. For example, Hoffman *et al.* (2003) found a non-independent relationship between temperature and UV; algal spores survived all levels of UV when water was relatively warm, whereas spores died in treatments with high levels of UV in relatively cool water. There is also a striking interaction between temperature and the partial pressure of CO₂ with regards to coral calcification rates; experimental *p*CO₂ increase did not affect calcification at 25 °C, but reduced it by nearly 50% at 28 °C (Reynaud *et al.* 2003). More broadly, elevated CO₂ is postulated to narrow the thermal tolerance limits of organisms via depression of vital physiological pathways (Pörtner & Langenbuch 2005). Because the cumulative effects of multiple stressors may lead to greater (or lesser) changes in marine systems than expected from studies that focus on a single stressor, future work must determine which variables are most likely to interact and why.

Interactions with additional anthropogenic stressors

Synergisms between climate change and anthropogenic factors are a special case of non-independent effects – we discuss them separately because they are much more readily

managed by altering human behaviour. The ways in which human activities interact with climate are multi-fold. For example, increasing exposure to polycyclic aromatic hydrocarbon pollutants (PAHs) did not significantly influence larval crab mortality in the absence of UV radiation, but the combination of UV radiation and high PAH exposure resulted in high mortality (Peachey 2005). Anthropogenic structures such as sea walls will influence the severity of habitat loss in response to sea level rise (Galbraith *et al.* 2002). Nearshore zones of hypoxia and anoxia are created in part by agricultural runoff (National Research Council 2000), and the physiological effects of hypoxia vary with temperature and CO₂ concentration (Pörtner & Langenbuch 2005). Most importantly, marine ecological responses to climate change will hinge on human fishing pressure. For example, it is possible for fishing and climate change acting in concert to reduce exploited populations below a population size from which they cannot easily recover (Scavia *et al.* 2002). Furthermore, the removal of important consumers through fishing alters community dynamics, which may increase a system's susceptibility to climate-induced changes (Hughes *et al.* 2003). Finally, complex feedbacks among fishing effort, stock size, and climate can drive changes in human socio-economic systems. For example, the combined influence of fishing pressure and changing environmental conditions led to the collapse of the cod fishery off western Greenland in the early 1990s (Hamilton *et al.* 2000). In response, local fishers redirected their effort to shrimp (which had not previously been exploited in the area), and the distribution of the human population along the Greenland coast is shifting to reflect the accessibility of this new resource (Hamilton *et al.* 2000). These examples illustrate the general point that human responses to changing environmental conditions (e.g. shifts in fishing effort or land use practices) will likely mediate many of the ecological outcomes of climate change.

Synthesis and model development

Linking individuals and populations to communities and ecosystems, and relating local-scale impacts to broader-scale changes, will improve our understanding of the biological consequences of climate change. Recent publication patterns (Fig. 1c) demonstrate that most studies have dealt with individual-level changes (e.g. physiology) with relatively few studies at the community level or higher. This pattern no doubt reflects the difficulty of manipulating and measuring responses at higher levels of biological organization. Consequently, we still know little about how climatic stresses, which are imparted upon individuals, translate into ecologically and socio-economically important changes in populations, communities, and ecosystems. Nevertheless, the evidence which has accumulated over the past several years clearly indicates that integrating different levels of

biological organization will be essential to predicting the responses of even simple ecosystems to climate change.

Determining how climate change will affect all levels of biological organization requires predictive mathematical models. An important advantage of models is that the underlying assumptions are typically explicit, and in some cases confidence intervals can be placed on predictions. In addition, investigators can use sensitivity and elasticity analyses to explore which parameters might strongly influence populations, communities and ecosystems. Within the marine literature, fisheries biologists have already developed mathematical models to predict the population level effects of climate change (Clark *et al.* 2003; Tian *et al.* 2004). However, predictive models for marine benthic invertebrates and algae are much less common (but see Svensson *et al.* 2005). Fisheries models can provide a valuable starting point for developing predictive models for a wide variety of marine population-, community-, and ecosystem-level responses to climate change.

A more complete synthesis will require active collaboration across additional disciplines. Within the biological sciences, communication among physiologists, geneticists, population biologists and community ecologists will help provide a more holistic image of biological change. Climatologists and oceanographers will help refine our understanding of where and how climate change will impact coastal systems. Finally, the inclusion of resource managers and economists will help to prioritize research efforts on those areas of highest socio-economic relevance.

CONCLUSIONS

The Earth's radiative heat balance is currently out of equilibrium, and mean global temperatures will continue to rise for several centuries even if greenhouse gas emissions are stabilized at present levels (IPCC 2001). Over the long-term, a reduction in greenhouse gas emissions will be necessary if we are to slow and eventually reverse global warming. The recent implementation of the Kyoto Protocol, which calls for developed countries to reduce their emissions on average by 5.2% below 1990 levels, is an important step towards this long-term goal. However, because it will be essentially impossible to halt or reverse warming within the next 100 years (or conceivably much longer), additional strategies must be adopted to mitigate the potentially harmful effects of climate change in coastal marine systems.

One such strategy is the establishment of marine protected areas and no-take reserves. Because stable populations and intact communities appear to be more resilient to climatic disturbances such as episodic heat waves and storms, such protective measures may help to minimize the risk of population collapses, community disruption, and

biodiversity loss (Hughes *et al.* 2003). The designation of protected areas should be based at least in part on known spatial and temporal refuges that can act as buffers against climate-related stress (Allison *et al.* 1998). Fisheries managers must also incorporate climate change into consideration when determining fishery management plans (Jurado-Molina & Livingston 2002). Additional research with explicit relevance to policy decisions will help evaluate the effectiveness of these conservation and management strategies.

Much recent scientific progress will be central to meeting current and future conservation and management goals. However, several key areas require additional study. In addition to temperature, the consequences of climate-related variables such as CO₂ and pH must be more fully considered. Crucially, ecologists must determine when, where, and how the role of any given climatic driver is dependent upon other forcing variables. Furthermore, the links between individuals, populations, and communities require further attention if we are to translate direct climatic impacts on individuals into their ultimate ecological outcomes. The daunting scope of this research should be managed by careful prioritization of key species (by their functional role in marine communities). Demographic modelling to identify life history stages critical to population persistence will provide a second level of prioritization within key species. Finally, improvements to climate models at the regional scale will be necessary if we are to apply our understanding of bioclimatic linkages to specific cases of concern for conservation and management. If approached with care, research in the coming decade should provide much of the additional information necessary to assess and mitigate the potential impacts of climate change in coastal marine ecosystems.

ACKNOWLEDGEMENTS

Early phases of this project were greatly enhanced by the participation of Andy Chang, Steven Morgan, Brian Steves, and Heidi Weiskel. Constructive criticism from Matt Bracken, Jane Hill, Eric Sanford, Jay Stachowicz, and four anonymous referees improved the manuscript. Molly Engelbrecht assisted with the literature review. C.S.T. was supported by an NIGMS MORE Institutional Research and Academic Career Development Award to UC Davis and San Francisco State University, grant no. K12GM00679. This is contribution no. 2290 of the Bodega Marine Laboratory, University of California at Davis.

REFERENCES

Ainsworth, E.A. & Long, S.P. (2005). What have we learned from 15 years of free-air CO₂ enrichment (FACE)? A meta-analytic

- review of the responses of photosynthesis, canopy properties and plant production to rising CO₂. *New Phytol.*, 165, 351–372.
- Allison, G. (2004). The influence of species diversity and stress intensity on community resistance and resilience. *Ecol. Monogr.*, 74, 117–134.
- Allison, G.W., Lubchenco, J. & Carr, M.H. (1998). Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.*, 8, S79–S92.
- Austin, J., Butchart, N. & Shine, K.P. (1992). Possibility of an Arctic ozone hole in a doubled-CO₂ climate. *Nature*, 360, 221–225.
- Bakun, A. (1990). Global climate change and intensification of coastal ocean upwelling. *Science*, 247, 198–201.
- Bakun, A. & Weeks, S.J. (2004). Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecol. Lett.*, 7, 1015–1023.
- Barry, J.P., Baxter, C.H., Sagarin, R.D. & Gilman, S.E. (1995). Climate-related, long-term faunal changes in a California rocky intertidal community. *Science*, 267, 672–675.
- Beardall, J., Beer, S. & Raven, J.A. (1998). Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Botanica Marina*, 41, 113–123.
- Berteaux, D., Reale, D., McAdam, A.G. & Boutin, S. (2004). Keeping pace with fast climate change: can Arctic life count on evolution? *Integr. Comp. Biol.*, 44, 140–151.
- Bischof, K., Hanelt, D. & Wiencke, C. (1998). UV-radiation can affect depth-zonation of Antarctic macroalgae. *Mar. Biol.*, 131, 597–605.
- Breeman, A.M., Oh, Y.S., Hwang, M.S. & van den Hoek, C. (2002). Evolution of temperature responses in the *Cladophora vagabunda* complex and the *C. albida/sericea* complex (Chlorophyta). *Eur. J. Phycol.*, 37, 45–58.
- Bromirski, P.D., Flick, R.E. & Cayan, D.R. (2003). Storminess variability along the California coast: 1858–2000. *J. Climate*, 16, 982–993.
- Caldeira, K. & Wickett, M.E. (2003). Anthropogenic carbon and ocean pH. *Nature*, 425, 365.
- Caldeira, K. & Wickett, M.E. (2005). Ocean model predictions of chemistry changes from carbon dioxide emissions to the atmosphere and ocean. *J. Geophys. Res.*, 110, C09S04, doi:10.1029/2004JC002671.
- Carlton, J.T. (2000). Global change and biological invasions in the oceans. In: *Invasive Species in a Changing World* (eds Mooney, H.A. & Hobbs, R.J.). Island Press, Covelo, CA, pp. 31–53.
- Chevaldonne, P. & Lejeune, C. (2003). Regional warming-induced species shift in north-west Mediterranean caves. *Ecol. Lett.*, 6, 371–379.
- Clark, R.A., Fox, C.J., Viner, D. & Livermore, M. (2003). North Sea cod and climate change – modelling the effects of temperature on population dynamics. *Global Change Biol.*, 9, 1669–1680.
- Connolly, S.R. & Roughgarden, J. (1999). Theory of marine communities: competition, predation, and recruitment-dependent interaction strength. *Ecol. Monogr.*, 69, 277–296.
- Connolly, S.R., Menge, B.A. & Roughgarden, J. (2001). A latitudinal gradient in recruitment of intertidal invertebrates in the Northeast Pacific Ocean. *Ecology*, 82, 1799–1813.
- Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B. *et al.* (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.
- Darwin, C. (1859). *The Origin of Species by Means of Natural Selection*. John Murray, London.

- Davis, A.J., Jenkinson, L.S., Lawton, J.H., Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783–786.
- Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.
- Duggins, D.O., Simenstad, C.A. & Estes, J.A. (1989). Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science*, 245, 170–173.
- Edwards, M. & Richardson, A.J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, 430, 8811–8884.
- Etterson, J.R. & Shaw, R.G. (2001). Constraint to adaptive evolution in response to global warming. *Science*, 294, 151–154.
- Feely, R.A., Sabine, C.L., Lee, K., Berelson, W., Kleypas, J., Fabry, V.J. *et al.* (2004). Impact of anthropogenic CO₂ on the CaCO₃ system in the oceans. *Science*, 305, 362–366.
- Fields, P.A., Graham, J.B., Rosenblatt, R.H. & Somero, G.N. (1993). Effects of expected global climate change on marine faunas. *Trends Ecol. Evol.*, 8, 361–367.
- Foster, B.A. (1971). On the determinants of the upper limit of intertidal distribution of barnacles (Crustacea: Cirripedia). *J. Anim. Ecol.*, 40, 33–48.
- Galbraith, H., Jones, R., Park, R., Clough, J., Herod-Julius, S., Harrington, B. *et al.* (2002). Global climate change and sea level rise: potential losses of intertidal habitat for shorebirds. *Waterbirds*, 25, 173–183.
- Gardner, T.A., Côté, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2005). Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. *Ecology*, 86, 174–184.
- Gattuso, J.-P. & Buddemeier, R.W. (2000). Calcification and CO₂. *Nature*, 407, 311–312.
- Gaylord, B. & Gaines, S.D. (2000). Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.*, 155, 769–789.
- Geller, J.B. (1999). Decline of a native mussel masked by sibling species invasion. *Conserv. Biol.*, 13, 661–664.
- Graham, M.H. (1997). Factors determining the upper limit of giant kelp, *Macrocystis pyrifera* Agardh, along the Monterey Peninsula, central California, USA. *J. Exp. Mar. Biol. Ecol.*, 218, 127–149.
- Graham, M.H., Harrold, C., Lisin, S., Light, K., Watanabe, J.M. & Foster, M.S. (1997). Population dynamics of giant kelp *Macrocystis pyrifera* along a wave exposure gradient. *Mar. Ecol. Prog. Ser.*, 148, 269–279.
- Hamilton, L., Lyster, P. & Otterstad, O. (2000). Social change, ecology and climate in 20th-century Greenland. *Climatic Change*, 47, 193–211.
- Harley, C.D.G. (2003). Abiotic stress and herbivory interact to set range limits across a two-dimensional stress gradient. *Ecology*, 84, 1477–1488.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. *et al.* (2002). Climate warming and disease risks for terrestrial and marine biota. *Science*, 296, 2158–2162.
- Hawkins, S.J., Southward, A.J. & Genner, M.J. (2003). Detection of environmental change in a marine ecosystem - evidence from the western English Channel. *Sci. Total Environ.*, 310, 245–256.
- Helmuth, B., Harley, C.D.G., Halpin, P.M., O'Donnell, M., Hofmann, G.E. & Blanchette, C.A. (2002). Climate change and latitudinal patterns of intertidal thermal stress. *Science*, 298, 1015–1017.
- Hickerson, M.J. & Cunningham, C.W. (2005). Contrasting Quaternary histories in an ecologically divergent sister pair of low-dispersing intertidal fish (*Xiphister*) revealed by multilocus DNA analysis. *Evolution*, 59, 344–360.
- Hochachka, P.W. & Somero, G.N. (2002). *Biochemical Adaptation: Mechanism and Process in Physiological Evolution*. Oxford University Press, New York.
- Hoffman, J.R., Hansen, L.J. & Klinger, T. (2003). Interactions between UV radiation and temperature limit inferences from single-factor experiments. *J. Phycol.*, 39, 268–272.
- Holbrook, S.J., Schmitt, R.J. & Stephens, J.S. Jr (1997). Changes in an assemblage of temperate reef fishes associated with a climate shift. *Ecol. Appl.*, 7, 1299–1310.
- Holt, R.D. & Gomulkiewicz, R. (1997). How does immigration influence local adaptation? A reexamination of a familiar paradigm. *Am. Nat.*, 149, 563–572.
- Hsieh, C., Glaser, S.M., Lucas, A.J. & Sugihara, G. (2005). Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature*, 435, 336–340.
- Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C. *et al.* (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.
- IPCC (2001). *Climate Change 2001, Synthesis Report. A Contribution of Working Groups I, II, and III to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK.
- Jacquet, S. & Bratbak, G. (2003). Effects of ultraviolet radiation on marine virus-phytoplankton interactions. *FEMS Microbiol. Ecol.*, 44, 279–289.
- Jump, A.S. & Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecol. Lett.*, 8, 1010–1020.
- Jurado-Molina, J. & Livingston, P. (2002). Climate-forcing effects on trophically linked groundfish populations: implications for fisheries management. *Can. J. Fish. Aquat. Sci.*, 59, 1941–1951.
- Keister, J.E., Johnson, T.B., Morgan, C.A. & Peterson, W.T. (2005). Biological indicators of the timing and direction of warm-water advection during the 1997/1998 El Niño off the central Oregon coast, USA. *Mar. Ecol. Prog. Ser.*, 295, 43–48.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E. *et al.* (2001). The strength of phenotypic selection in natural populations. *Am. Nat.*, 157, 245–261.
- Kleypas, J.A., Buddemeier, R.W., Archer, D., Gattuso, J.-P., Langdon, C. & Opdyke, B.N. (1999). Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, 284, 118–120.
- Knowlton, N. (2001). The future of coral reefs. *Proc. Natl. Acad. Sci.*, 98, 5419–5425.
- Larsen, S.H. (2005). Solar variability, dimethyl sulphide, clouds, and climate. *Global Biogeochem. Cycles*, 19, GB1014, 1–12.
- Lasker, H.R. & Coffroth, M.A. (1999). Responses of clonal reef taxa to environmental change. *Am. Zool.*, 39, 92–103.
- Leonard, G.H. (2000). Latitudinal variation in species interactions: a test in the New England rocky intertidal zone. *Ecology*, 81, 1015–1030.
- Lotze, H.K. & Worm, B. (2002). Complex interactions of climatic and ecological controls on macroalgal recruitment. *Limnol. Oceanogr.*, 47, 1734–1741.

- Lotze, H.K., Worm, B., Molis, M. & Wahl, M. (2002). Effects of UV radiation and consumers on recruitment and succession of a marine macrobenthic community. *Mar. Ecol. Prog. Ser.*, 243, 57–66.
- Lubchenco, J., Navarrete, S.A., Tissot, B.N. & Castilla, J.C. (1993). Possible ecological responses to global climate change: near-shore benthic biota of Northeastern Pacific coastal ecosystems. In: *Earth System Responses to Global Climate Change: Contrasts between North and South America* (eds Mooney, H.A., Fuentes, E.R. & Kronberg, B.I.). Academic Press, San Diego, CA, pp. 147–166.
- Marko, P.B. (2004). 'What's larvae got to do with it?' Disparate patterns of post-glacial population structure in two benthic marine gastropods with identical dispersal potential. *Mol. Ecol.*, 13, 597–611.
- Mathieson, A.C., Dawes, C.J. & Hehre, E.J. (1998). Floristic and zonation studies of seaweeds from Mount Desert Island, Maine. *Rhodora*, 100, 333–379.
- McWilliams, J.P., Côté, I.M., Gill, J.A., Sutherland, W.J. & Watkinson, A.R. (2005). Accelerating impacts of temperature-induced coral bleaching in the Caribbean. *Ecology*, 86, 2055–2060.
- Michaelidis, B., Ouzounis, C., Paleras, A. & Pörtner, H.O. (2005). Effects of long-term moderate hypercapnia on acid-base balance and growth rate in marine mussels *Mytilus galloprovincialis*. *Mar. Ecol. Prog. Ser.*, 293, 109–118.
- Micheli, F. & Halpern, B.S. (2005). Low functional redundancy in coastal marine assemblages. *Ecol. Lett.*, 8, 391–400.
- National Research Council (2000). *Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution*. National Academy Press, Washington, DC.
- Nielsen, K.J. (2003). Nutrient loading and consumers: agents of change in open-coast macrophyte assemblages. *Proc. Natl. Acad. Sci.*, 100, 7660–7665.
- Peachey, R.B.J. (2005). The synergism between hydrocarbon pollutants and UV radiation: a potential link between coastal pollution and larval mortality. *J. Exp. Mar. Biol. Ecol.*, 315, 103–114.
- Pearson, R.G. & Dawson, T.P. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecol. Biogeogr.*, 12, 361–371.
- Pechenik, J.A. (1989). Environmental influences on larval survival and development. In: *Reproduction of Marine Invertebrates* (eds Giese, A.C., Pearse, J.S. & Pearse, V.B.). Blackwell Scientific Publications, Palo Alto, CA, pp. 551–608.
- Perry, A.L., Low, P.J., Ellis, J.R. & Reynolds, J.D. (2005). Climate change and distribution shifts in marine fishes. *Science*, 308, 1912–1915.
- Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C. & Dekker, R. (2003). Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnol. Oceanogr.*, 48, 2171–2185.
- Pisias, N.G., Mix, A.C. & Heusser, L. (2001). Millennial scale climate variability of the northeast Pacific Ocean and northwest North America based on radiolaria and pollen. *Q. Sci. Rev.*, 20, 1561–1576.
- Pörtner, H.O. & Langenbuch, M. (2005). Synergistic effects of temperature extremes, hypoxia, and increases in CO₂ on marine animals: From Earth history to global change. *J. Geophys. Res.*, 110, C09S10, doi:10.1029/2004JC002561.
- Precht, W.F. & Aronson, R.B. (2004). Climate flickers and range shifts of reef corals. *Front. Ecol. Environ.*, 2, 307–314.
- Raimondi, P.T., Wilson, C.M., Ambrose, R.F., Engle, J.M. & Minchinton, T.E. (2002). Continued declines of black abalone along the coast of California: are mass mortalities related to El Niño events? *Mar. Ecol. Prog. Ser.*, 242, 143–152.
- Rand, D.M., Sackton, T.B., Spaeth, P.S. & Schmidt, P.S. (2002). Ecological genetics of Mpi and Gpi polymorphisms in the acorn barnacle and the spatial scale of neutral and non-neutral variation. *Integr. Comp. Biol.*, 42, 825–836.
- Reusch, T.B.H., Ehlers, A., Hämmerli, A. & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci. U.S.A.*, 102, 2826–2831.
- Reynaud, S., Leclercq, N., Romaine-Lioud, S., Ferrier-Pagès, C., Jaubert, J. & Gattuso, J.-P. (2003). Interacting effects of CO₂ partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. *Global Change Biol.*, 9, 1660–1668.
- Riebesell, U., Zondervan, I., Rost, B., Tortell, P.D., Zeebe, R.E. & Morel, F.M.M. (2000). Reduced calcification of marine plankton in response to increased atmospheric CO₂. *Nature*, 407, 364–367.
- Roemmich, D. & McGowan, J.A. (1995). Climatic warming and the decline of zooplankton in the California current. *Science*, 267, 1324–1326.
- Sabine, C.L., Feely, R.A., Gruber, N., Key, R.M., Lee, K., Bullister, J.L. *et al.* (2004). The oceanic sink for anthropogenic CO₂. *Science*, 305, 367–371.
- Sanford, E. (1999). Regulation of keystone predation by small changes in ocean temperature. *Science*, 283, 2095–2097.
- Sanford, E., Roth, M.S., Johns, G.C., Wares, J.P. & Somero, G.N. (2003). Local selection and latitudinal variation in a marine predator–prey interaction. *Science*, 300, 1135–1137.
- Scavia, D., Field, J.C., Boesch, D.F., Buddemeier, R.W., Burkett, V., Cayan, D.R. *et al.* (2002). Climate change impacts on U.S. coastal and marine ecosystems. *Estuaries*, 25, 149–164.
- Schiel, D.R., Steinbeck, J.R. & Foster, M.S. (2004). Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, 85, 1833–1839.
- Shirayama, Y. & Thornton, H. (2005). Effect of increased atmospheric CO₂ on shallow water marine benthos. *J. Geophys. Res.*, 110, C09S08, doi:10.1029/2004JC002618.
- Snyder, M.A., Sloan, L.C., Diffenbaugh, N.S. & Bell, J.L. (2003). Future climate change and upwelling in the California Current. *Geophys. Res. Lett.*, 30, 1823.
- Somero, G.N. (2002). Thermal physiology and vertical zonation of intertidal animals: optima, limits, and costs of living. *Integr. and Comp. Biol.*, 42, 780–789.
- Sorte, C.J.B. & Hofmann, G.E. (2004). Changes in latitudes, changes in aptitudes: *Nucella canaliculata* (Mollusca: Gastropoda) is more stressed at its range edge. *Mar. Ecol. Prog. Ser.*, 274, 263–268.
- Sorte, C.J.B. & Hofmann, G.E. (2005). Thermotolerance and heat-shock protein expression in Northeastern Pacific species with different biogeographical ranges. *Mar. Biol.*, 146, 985–993.
- Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002a). Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, 83, 2575–2590.
- Stachowicz, J.J., Terwin, J.R., Whitlatch, R.B. & Osman, R.W. (2002b). Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci.*, 99, 15497–15500.
- Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. *et al.* (2002). Kelp forest ecosystems: bio-

- diversity, stability, resilience and future. *Environ. Conserv.*, 29, 436–459.
- Stillman, J.H. (2002). Causes and consequences of thermal tolerance limits in rocky intertidal porcelain crabs, genus *Petrolisthes*. *Integ. and Comp. Biol.*, 42, 790–796.
- Stillman, J.H. (2003). Acclimation capacity underlies susceptibility to climate change. *Science*, 301, 65.
- Stockwell, C.A., Hendry, A.P. & Kinnison, M.T. (2003). Contemporary evolution meets conservation biology. *Trends Ecol. Evol.*, 18, 94–101.
- Svensson, C.J., Jenkins, S.R., Hawkins, S.J. & Åberg, P. (2005) Population resistance to climate change: modelling the effects of low recruitment in open populations. *Oecologia*, 142, 117–126.
- Tian, Y., Akamine, T. & Suda, M. (2004). Modeling the influence of oceanic-climatic changes on the dynamics of Pacific saury in the northwestern Pacific using a life cycle model. *Fish. Oceanogr.*, 13 (Suppl. 1), 125–137.
- Timmermann, A., Oberhuber, J., Bacher, A., Esch, M., Latif, M. & Roeckner, E. (1999). Increased El Niño frequency in a climate model forced by future greenhouse warming. *Nature*, 398, 694–697.
- Tomanek, L. & Somero, G.N. (1999). Evolutionary and acclimation-induced variation in the heat-shock responses of congeneric marine snails (genus *Tegula*) from different thermal habitats: implications for limits of thermotolerance and biogeography. *J. Exp. Biol.*, 202, 2925–2936.
- Wetley, D.S. (1983). Geographic limits and local zonation: the barnacles *Semibalanus* (*Balanus*) and *Chtbamalus* in New England. *Biol. Bull.*, 165, 330–341.
- Williams, S.L. & Heck, K.L. Jr (2001). Seagrass community ecology. In: *Marine Community Ecology* (eds Bertness, M.D., Gaines, S.D. & Hay, M.E.). Sinauer Associates, Inc., Sunderland, MA, pp. 317–337.
- Zacherl, D., Gaines, S.D. & Lonhart, S.I. (2003). The limits to biogeographical distributions: insights from the northward range extension of the marine snail, *Kelletia kelletia* (Forbes, 1852). *J. Biogeogr.*, 30, 913–924.

APPENDIX

In an effort to capture recent trends in the literature, we analysed recently published papers in the field of marine ecology. Our literature survey was divided into two parts: (1) changes in the publication rate of climate change-related science as a percentage of all marine ecology literature; and (2) a more in-depth look at research topics in recent years.

To assess the frequency of marine climate change-related papers, we ran a search on the Web of Science for the years 1991 (the first year in which abstracts were included for many journals) through 2004 (the most recent complete year). We also included all 2005 publications available in the database as of 31 October 2005. Our search terms were ‘marine’ plus any of the following: physiolog*, development, growth, reproduc*, mortality, population*, dispersal, evolution, community, competition, predation, parasitism, mutualism, facilitation, productivity, diversity, invasi*, extinction,

biogeograph*, or zonation. We then re-ran the search with the added term ‘climate change’. Changes in journal space devoted to climate change were identified by calculating the percentage of papers in the larger search that also contained the term ‘climate change’ on a year-by-year basis. Although no effort was made to verify the relevance of the 585 climate-related papers found, the patterns were indistinguishable from those arising from the more detailed search.

Our more detailed analysis was restricted to nine journals that span the spectrum of the primary literature: Ecology, Ecology Letters, Evolution, Global Change Biology, the Journal of Experimental Marine Biology and Ecology, Limnology & Oceanography, Marine Ecology Progress Series, Nature and Science. We searched within the years 2000–2004, inclusive. Our keywords included pH, CO₂, temperature, upwelling, sea level rise, UV, salinity, phenology, larvae, range shifts, zonation, life cycle, current, dispersal, recruitment and climate change, along with wildcards that allowed for alternate spellings and tenses. For non-marine journals, we restricted our analysis to those papers also containing one of the following terms: marine, ocean, sea, benthic, pelagic, subtidal and intertidal. For one journal (MEPS), our search yielded over 1000 hits; therefore, we further restricted the search within MEPS to words appearing in the title. All abstracts were checked to verify the paper’s relevance. In the end, our analysis included 360 references. These papers were binned into abiotic variable(s) investigated and level(s) of biological response investigated. The abiotic variables were temperature, CO₂, pH, nutrient supply, circulation (advection or upwelling papers unrelated to nutrient supply), storminess (including hydrodynamic disturbance), sea level rise, UV radiation and climate index (e.g. the ENSO or the North Atlantic Oscillation). Levels of biological response were individual (including physiology, growth, behaviour, development and mortality), population (including dispersal, inter-generational changes in abundance, population genetics and evolution), community (competition, predation, parasitism, mutualism and facilitation), and ‘higher level’ (productivity, diversity, species invasions, zonation and biogeography). Finally, we noted whether or not the statistical design would allow for the identification of non-independent effects (e.g. a factorial manipulation of both temperature and CO₂).