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## The Impacts of Climate Change in Coastal Marine Systems

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### REVIEWS AND SYNTHESES

# The impacts of climate change in coastal marine systems

### Abstract

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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 (CO<sub>2</sub>), coastal oceanography, community structure, distributional shifts, marine ecosystems, ocean pH, population dynamics, synergistic effects, temperature.

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### 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



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



### 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 multimillenial-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  $CO_2$ ) emissions. Together, elevated  $CO_2$  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<sup>-1</sup> (IPCC 2001). Because warming trends will be stronger over continental interiors than over oceans, the atmospheric





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 CO<sub>2</sub> released by 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.

human activities between 1800 and 1994 is now stored in the ocean (Sabine et al. 2004), and about 30% of modern CO<sub>2</sub> emissions are taken up by oceans today (Feely et al. 2004). Continued uptake of atmospheric CO<sub>2</sub> 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 proximal 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, longlived 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 CO<sub>2</sub> 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  $CO_2$  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  $CO_2$  concentrations has profound implications for physiological processes in marine organisms. Short-term experimental elevation of  $CO_2$  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  $CO_2$  and pH.

Longer-term, climatically realistic manipulations of CO<sub>2</sub> 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  $CO_2$  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 CO<sub>2</sub> 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 CO<sub>2</sub> (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 parksii 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 (Wethey 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 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 & Lejeusne 2003). Because many coastal marine ecosystems such as kelp forests and coral reefs feature low functional redundancy

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