

Climate Change Impacts on Marine Ecosystems

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Abstract

In marine ecosystems, rising atmospheric CO₂ and climate change are associated with concurrent shifts in temperature, circulation, stratification, nutrient input, oxygen content, and ocean acidification, with potentially wide-ranging biological effects. Population-level shifts are occurring because of physiological intolerance to new environments, altered dispersal patterns, and changes in species interactions. Together with local climate-driven invasion and extinction, these processes result in altered community structure and diversity, including possible emergence of novel ecosystems. Impacts are particularly striking for the poles and the tropics, because of the sensitivity of polar ecosystems to sea-ice retreat and poleward species migrations as well as the sensitivity of coral-algal symbiosis to minor increases in temperature. Midlatitude upwelling systems, like the California Current, exhibit strong linkages between climate and species distributions, phenology, and demography. Aggregated effects may modify energy and material flows as well as biogeochemical cycles, eventually impacting the overall ecosystem functioning and services upon which people and societies depend.

INTRODUCTION

Marine ecosystems are maintained by the flow of energy from primary producers at the base of food webs through to intermediate consumers, top predators (including humans), and pathogens, and then back again through decomposition and detrital pathways. Thus, marine communities are biological networks in which the success of species is linked directly or indirectly through various biological interactions (e.g., predator-prey relationships, competition, facilitation, mutualism) to the performance of other species in the community. The aggregate effect of these interactions constitutes ecosystem function (e.g., nutrient cycling, primary and secondary productivity), through which ocean and coastal ecosystems provide the wealth of free natural benefits that society depends upon, such as fisheries and aquaculture production, water purification, shoreline protection, and recreation.

However, growing human pressures, including climate change, are having profound and diverse consequences for marine ecosystems. Rising atmospheric carbon dioxide (CO₂) is one of the most critical problems because its effects are globally pervasive and irreversible on ecological timescales (Natl. Res. Council 2011). The primary direct consequences are increasing ocean temperatures (Bindoff et al. 2007) and acidity (Doney et al. 2009). Climbing temperatures create a host of additional changes, such as rising sea level, increased ocean stratification, decreased sea-ice extent, and altered patterns of ocean circulation, precipitation, and freshwater input (**Figure 1a**). In addition, both warming and altered ocean circulation act to reduce subsurface oxygen (O₂) concentrations (Keeling et al. 2010). In recent decades, the rates of change have been rapid and may exceed the current and potential future tolerances of many organisms to adapt. Further, the rates of physical and chemical change in marine ecosystems will almost certainly accelerate over the next several decades in the absence of immediate and dramatic efforts toward climate mitigation (Natl. Res. Council 2011).

Direct effects of changes in ocean temperature and chemistry may alter the physiological functioning, behavior, and demographic traits (e.g., productivity) of organisms, leading to shifts in the size structure, spatial range, and seasonal abundance of populations. These shifts, in turn, lead to altered species interactions and trophic pathways as change cascades from primary producers to upper-trophic-level fish, seabirds, and marine mammals, with climate signals thereby propagating through ecosystems in both bottom-up and top-down directions. Changes in community structure and ecosystem function may result from disruptions in biological interactions. Therefore, investigating the responses of individual species to single forcing factors, although essential, provides an incomplete story and highlights the need for more comprehensive, multispecies- to ecosystem-level analyses.

The effects of rising CO₂ do not act in isolation. Additional regional pressures on ocean ecosystems (**Figure 1b**) include intensive use of fertilizers, coastal and benthic habitat degradation, overexploitation of fish stocks, rising aquaculture production, and invasive species (Halpern et al. 2008). Coastal hypoxia is increasing and expanding globally (Diaz & Rosenberg 2008). Ecosystem deterioration is intense and increasing, particularly for coastal systems, with 50% of salt marshes, 35% of mangroves, 30% of coral reefs, and 29% of seagrasses already either lost or degraded worldwide (Jackson 2010). Thus, the integrated and synergistic effects of these multiple stressors on marine ecosystems—both CO₂ and non-CO₂ related—must be considered in total, not as independent issues (Doney 2010).

There have been few systematic reviews of the impacts of rising CO₂ and climate change on marine ecosystems (e.g., Hoegh-Guldberg & Bruno 2010). Here, we document the emerging science in this field, cutting across biological scales from organisms to ecosystems and illustrating general points with three case studies—sea-ice-dependent polar ecosystems, shallow tropical and

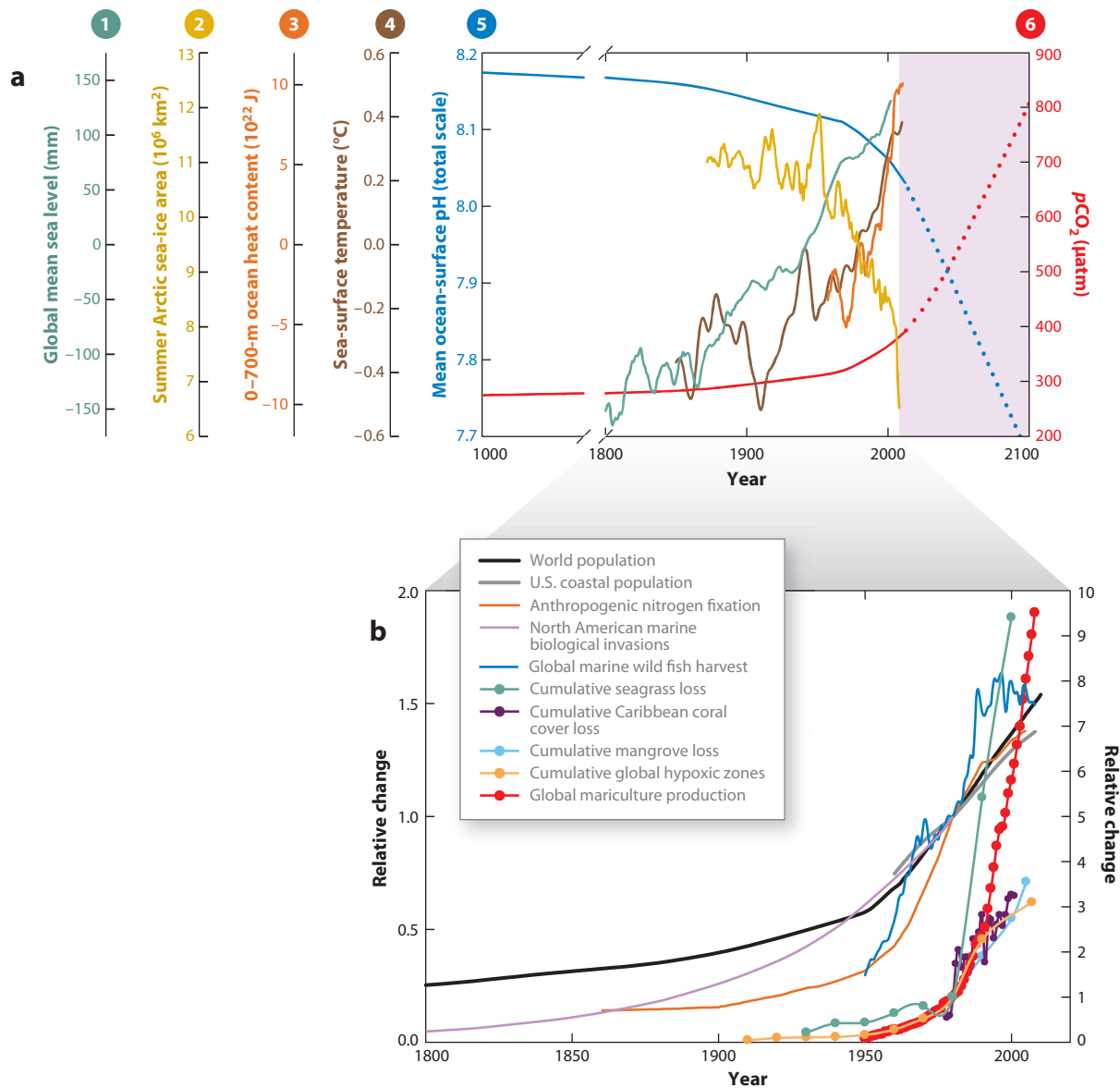


Figure 1

(a) Changes in ① global mean sea level (teal line; Jevrejeva et al. 2008), ② summer Arctic sea-ice area (yellow line; Walsh & Chapman 2001), ③ 0–700-m ocean heat content (orange line; Levitus et al. 2009), ④ sea-surface temperature (brown line; Rayner et al. 2006), ⑤ mean ocean-surface pH (blue line; Natl. Res. Council 2010), and ⑥ atmosphere $p\text{CO}_2$ (red line; Petit et al. 1999). Light purple shaded region denotes projected changes in pH and $p\text{CO}_2$ consistent with the Intergovernmental Panel on Climate Change's twenty-first-century A2 emissions scenario with rapid population growth. (b) Time series (as identified in figure key): trends in world population (Goldewijk 2005), U.S. coastal population (Wilson & Fischetti 2010), anthropogenic nitrogen fixation (Davidson 2009), North American marine biological invasions (Ruiz et al. 2000), global marine wild fish harvest (Food Agric. Org. U.N. 2010), cumulative seagrass loss (Waycott et al. 2009), cumulative Caribbean coral cover loss (Gardner et al. 2003), cumulative mangrove loss (Food Agric. Org. U.N. 2007), cumulative global hypoxic zones (Diaz & Rosenberg 2008), and global mariculture production (Food Agric. Org. U.N. 2010). All time series in panel b are normalized to 1980 levels. Trends with <1.5-fold variation are depicted as solid lines (left axis), and trends with >1.5-fold variation are depicted as dotted lines (right axis).

IPCC:

Intergovernmental Panel on Climate Change

SST: sea-surface temperature

ENSO: El Niño/Southern Oscillation

WAP: western Antarctic Peninsula

EBCS: Eastern Boundary Current system

subtropical regions (coral reef systems), and an upwelling system (the California Current)—where substantial change is evident already and susceptibility to further change is likely.

CLIMATE AND GLOBAL CHANGE

Humans influence climate primarily through fossil-fuel, industrial, agricultural, and other land-use emissions that alter atmospheric composition. Long-lived, heat-trapping greenhouse gases (CO_2 , CH_4 , N_2O , tropospheric ozone, and chlorofluorocarbons) warm the planet's surface globally, whereas shorter-lived aerosols can either warm or cool regionally. Direct radiative warming is amplified through a series of positive climate feedbacks (e.g., water vapor and sea ice); best estimates of projected global mean surface temperature increase over the twenty-first-century range from approximately 1.8°C to 4.0°C , depending on emission scenario (Solomon et al. 2007). Fossil-fuel CO_2 emissions for the past decade have been at the high-end of Intergovernmental Panel on Climate Change (IPCC) scenarios owing to rapid economic growth in developing countries (Le Quéré et al. 2009). Moreover, the climate system exhibits considerable inertia, and temperatures will likely continue to increase decades to centuries after greenhouse gas levels stabilize.

Significant ocean physical changes are documented in the most recent IPCC assessment (Bindoff et al. 2007) (**Figure 1**). Upper-ocean heat content has grown substantially since the 1950s, with mean global sea-surface temperature (SST) increasing by approximately 0.4°C during this interval (Levitus et al. 2009). Warming is not spatially uniform owing to ocean circulation, spatially variable changes in winds, and interaction with natural modes of climate variability such as El Niño/Southern Oscillation (ENSO) and the North Atlantic Oscillation (Ishii et al. 2006). Upper-ocean salinity is trending fresher in low-salinity regions and saltier in high-salinity regions, patterns consistent with a warmer atmosphere and SSTs driving elevated evaporation and precipitation rates (Boyer et al. 2005, Bindoff et al. 2007, Durack & Wijffels 2010). Broad-scale warming and mid- to high-latitude freshening increase water-column vertical stratification, which in turn alters ocean currents, mixing, and ventilation.

Sea-ice extent has declined dramatically in the Arctic (Stroeve et al. 2007, Polyakov et al. 2010) and along the western Antarctic Peninsula (WAP) (Stammerjohn et al. 2008), particularly during summer. The Arctic is expected to be sea-ice free during summer starting in the mid- to late twenty-first century (Holland et al. 2008), if not earlier, and thick, multiyear Arctic ice is being replaced with thin, first-year ice (Maslanik et al. 2007). Owing to thermal expansion and melting of landfast ice (glaciers and ice caps and sheets), warming is causing sea level to rise, with a current rate of approximately 3 mm per year (Cazenave et al. 2008). Locally, sea-level rise can differ substantially from the global mean because of heterogeneity in upper-ocean warming, changes in atmosphere and ocean circulation, and local geological uplift or subsidence.

Climate warming affects regional wind patterns and thus ocean circulation in multiple dimensions. A strengthening of midlatitude westerlies in the Southern Hemisphere promotes spin-up of subtropical circulations and a poleward shift in the Antarctic Circumpolar Current (Roemmich et al. 2007). Warmer SSTs may affect the frequency and strength of tropical storms, increasing the vulnerability of coastal habitats. Recent analyses, however, suggest only a modest increase, or even a decrease, in the frequency and intensity of future Atlantic cyclones (Kerr 2008). Upwelling winds in Eastern Boundary Current systems (EBCSs) are generated by pressure differences between continental thermal lows and oceanic highs; as warming intensifies pressure gradients between land and sea, upwelling winds are predicted to intensify (Bakun et al. 2010). Regional-scale projections generally converge on increased upwelling and/or changes to the seasonality of upwelling winds (Snyder et al. 2003). In some instances, projected upwelling increases may overcome the countervailing effects of upper-ocean warming and stratification to cause regional cooling (Auaud et al.

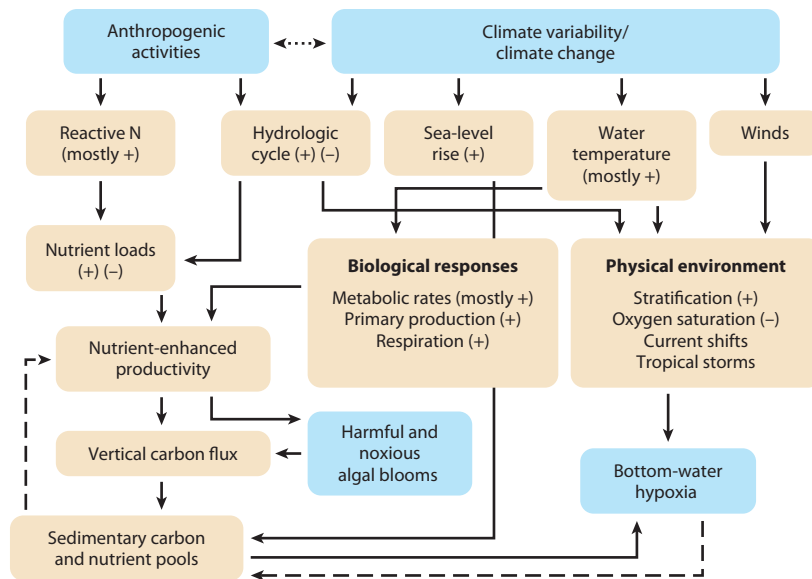


Figure 2

Conceptual diagram of human and climate interactions on nutrient-enhanced productivity, harmful and noxious algal blooms, and formation of hypoxia. Positive (+) interactions designate a worsening of conditions related to algal blooms and hypoxia, and negative (–) interactions designate fewer algal blooms and lessening of hypoxia symptoms. Dashed lines indicate negative feedback processes to nutrient-enhanced production and subsequent hypoxia. Dotted line between anthropogenic activities and climate variability/ climate change indicates that current climate change is driven largely by humans, but that climate change can certainly affect human activities. Modified from Rabalais et al. (2010).

2006). Available time series point to broad trends of increased wind-driven upwelling across many of the ocean's major EBCSs (García-Reyes & Largier 2010, Patti et al. 2010).

Projected declines in ocean oxygen levels reflect the combined effects of reduced oxygen solubility from warming and reduced ventilation from stratification and circulation changes (Keeling et al. 2010). Deoxygenation is also possible because of shifts in the magnitude and composition of sinking organic material (Hofmann & Schellnhuber 2009). Stramma et al. (2008) reported vertical expansion of the intermediate-depth low-oxygen zones in the eastern tropical Atlantic and the equatorial Pacific during the past 50 years, and Whitney et al. (2007) documented persistent oxygen declines in the eastern subarctic Pacific between the 1950s and 2000s. Such events related to warming are not well documented in coastal waters, but the number of coastal hypoxic regions has grown dramatically with time (Diaz & Rosenberg 2008), in large part because of human activities that increase the amount of bioavailable nitrogen that reaches the coastal ocean. Future levels of coastal hypoxia will be modulated by climate change via alterations in vertical stratification (temperature, precipitation, freshwater runoff), winds, and mixing (Rabalais et al. 2010; Figure 2).

In the open ocean, rising atmospheric CO₂ and the resulting increased oceanic CO₂ uptake are the predominant factors driving ocean acidification (Dore et al. 2009). Ocean acidification reflects a series of chemical changes: elevated aqueous CO₂ and total inorganic carbon as well as reduced pH, carbonate ion, and calcium carbonate saturation states (Doney et al. 2009). Sea-surface pH is estimated to have dropped by 0.1 pH units since the preindustrial era, a 26% increase in acidity over the past 150 years, mostly in the past several decades. Future projections suggest declines of

an additional 0.2–0.3 pH units over this century (Feely et al. 2009). Polar regions may be especially sensitive because of a transition to undersaturated conditions for aragonite in surface water within the next several decades (Steinacher et al. 2009). In eutrophic coastal systems, surface water is usually higher in pH because of primary production, whereas water below the pycnocline has reduced pH because of respiratory demand and CO₂ production. Furthermore, changing land use and river flow can alter river alkalinity and, in turn, influence coastal inorganic carbon balance; for example, Raymond et al. (2008) documented a large anthropogenic increase in Mississippi bicarbonate and water fluxes.

BIOLOGICAL PROCESSES AND STRUCTURE

Physical and chemical changes have strong direct and indirect effects on the physiology and behavior of marine organisms, which can translate to population- and community-level changes. Consequently, changes in ocean conditions and key biological interactions can alter the underlying dynamics that govern ecosystem structure and function.

Physiological Responses

Physiological performance is the principal determinant of a species' tolerance to environmental variability and change. As climate or other conditions shift, organisms initially respond based on physiological and behavioral adaptations molded through their evolutionary history (Somero 2012). New conditions may be physiologically tolerable, allowing acclimatization (an adjustment of physiology within individuals) or adaptation (increased abundance and reproduction of tolerant genotypes over generations), or may be intolerable, promoting migration (by individuals or populations), change in phenology (timing of annual events), or death and local extinction if adaptation is not possible (Parmesan 2006).

Environmental change may benefit some species or populations, owing to greater availability of food or nutrients, reduced physiological costs of maintenance (e.g., energy used for respiration, acid-base balance, calcification), or reduced competition or predation. Such species may experience higher survival, growth, and reproduction, and may thus be “winners” in a changing world. In many cases, however, a shift toward environmental conditions outside the normal range of variability is stressful, causing suboptimal physiological performance and thus creating the “losers” of environmental change. For such individuals, more stressful conditions may lead to higher mortality, reduced growth, smaller size, and reduced reproduction.

Generally, metabolic rates of ectothermic organisms rise exponentially with temperature, leading to higher rates for most physiological processes, including photosynthesis and respiration, within the range of temperatures that an organism tolerates. This relationship is formalized in the concept of Q_{10} , which is the rate increase resulting from a 10°C rise in temperature. For example, Eppley (1972) reported an average Q_{10} of 1.9 for growth rates among ~130 species and clones of phytoplankton, yielding a 37% increase in growth rate for a 2°C warming. On this basis, it might be expected that primary production, as well as the growth rates of ectothermic animals and pathogens, will increase in a warmer ocean. However, nutritional status, thermal tolerance, oxygen availability, environmental chemistry, food availability, or other factors may limit growth and production, or other biological processes, regardless of metabolic rate.

In heterotrophic organisms, warmer temperatures raise basal metabolic rates but can also raise respiratory demand, potentially reducing their aerobic scope for activity (e.g., feeding, predator avoidance, digestion) and leaving less energy for growth and reproduction (Pörtner & Knust 2007). For example, salmon swimming through warmer ocean waters in the North Pacific experience elevated metabolic and respiratory rates, which in turn increase energy requirements. In addition,

warmer surface waters generally have lower prey and oxygen levels. Consequently, energy demand can exceed energy intake and is thought to have contributed to reduced growth, survival, and spawning success of salmon in the Pacific Northwest (Welch et al. 1998, Farrell et al. 2008).

The expansion and intensification of hypoxic regions, particularly along productive ocean margins (Diaz & Rosenberg 2008), are increasingly stressful for many marine organisms. Severe hypoxia has led to mass mortalities of organisms in several areas. Even mild hypoxia can have strong effects on the physiology and activity levels. Low-oxygen conditions can initiate compensatory respiratory changes, including higher blood flow and ventilation or increased concentration of respiratory proteins or binding affinity (Wu 2002). Oxygen conservation (through reduced activity and/or reduced cellular function) and anaerobic metabolism are invoked to cope with reduced oxygen levels. Consequently, hypoxia can lead to reduced feeding, growth, reproduction, and survival, with highly variable responses among species.

By lowering carbonate ion levels and increasing carbonate solubility, ocean acidification is thought to increase the energetic cost of calcification (Fabry et al. 2008). This idea is supported by observations of mostly negative effects of higher CO₂ on calcification rates for a variety of marine invertebrates (Kroeker et al. 2009, Hofmann et al. 2010). Acidification, therefore, could have major impacts on biogenic habitat (e.g., coral reefs, oyster beds), food webs (e.g., pteropods and other mollusks), and planetary geochemical cycles (e.g., pelagic coccolithophore algae). For carbon-limited autotrophs (including seagrasses and some phytoplankton), increased CO₂ may promote photosynthesis, whereas for others (particularly calcifying taxa), photosynthesis may be either reduced or unaffected (Kroeker et al. 2009). In some taxa, including some fishes and mollusks, lower pH reduces the oxygen-binding capacity of respiratory proteins (e.g., hemocyanin), limiting their aerobic scope for activity unless acclimation or behavioral changes can compensate for respiratory loss. Thus, acidification and hypoxia may have synergistic effects. Immersion in more acidic waters can also disturb the internal acid-base balance of organisms, which in turn can affect a wide variety of metabolic processes (Pörtner 2010). Some organisms, particularly those with well-developed respiratory systems (e.g., fishes), can maintain or restore internal acid-base balance with some degree of change in ocean chemistry, whereas less physiologically flexible taxa (e.g., sea urchins) may be more vulnerable.

Population and Community Responses

Physiological responses to climate change will manifest at the population level as shifts in abundance, timing of annually recurring events (phenology), and the spatial organization (distribution and dispersion) of organisms. Suboptimal conditions and poor individual performance can cause reduced abundance and population productivity as well as reduced resilience to disturbance. Well-documented biological impacts from climate change include shifts in population range and distributions, which reflect the product of several interacting processes (see sidebar Long-Term Ocean Observations). First, the dispersal capacity of species from a regional species pool determines whether they will have the opportunity to invade or inhabit a site. Second, the range of abiotic environmental conditions that are physiologically tolerable to a species defines its fundamental niche, and thus niche boundaries can change as climate changes the ocean environment. Third, biological interactions (predation, competition, and others) may constrain, or in some cases expand (Bruno et al. 2003), the habitable range of conditions or the realized niche of a species. A set of species with overlapping realized niches constitutes a community, and by affecting all of these processes, climate change can alter the composition and function of marine communities.

One example of changes to dispersal patterns is that many boreal species currently restricted to either the North Atlantic or North Pacific are separated because of dispersal inhibition by harsh Arctic conditions. As this Arctic barrier weakens with warming and sea-ice retreat,

LONG-TERM OCEAN OBSERVATIONS

Although relatively few in number, long-term ocean biological data sets are essential for understanding climate change impacts on marine ecosystems (Ducklow et al. 2009). Ocean time-series and spatial surveys can be used to elucidate temporal trends and empirical relationships between biological variables and environmental forcing. Complementing more mechanistic laboratory and field process studies, field records provide information on the biological responses of natural populations and communities over longer timescales and larger spatial scales than are typically accessible to direct manipulation. Multidecadal time spans are often needed to detect climate change signals from substantial natural variability. Commonly, long-term data records were originally collected for different purposes and have been adapted for climate research. For example, information on geographic range shifts for fish populations has been determined from routine commercial fishery surveys. Other seminal biological data sets include the Continuous Plankton Recorder survey established in 1931 and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program initiated in 1949. In the 1980s and 1990s, national and international ocean research programs created new time series such as the Hawaii Ocean Time-Series and the marine Long-Term Ecological Research sites. Though somewhat shorter in length, satellite remote-sensing records of ocean color are emerging as important tools for studying trends and patterns in lower trophic levels and primary production (McClain 2009). Maintaining long-term ocean sampling is challenging in terms of logistics, personnel, and sustained funding. Future time series may rely on a combination of limited ship-based sampling integrated with cost-effective autonomous sensors and platforms.

large-scale trans-Arctic exchange between the two oceans seems likely over the coming decades, as has occurred in the past (Vermeij & Roopnarine 2008). For example, the diatom *Neodenticula seminae*, a dominant primary producer in North Pacific pelagic ecosystems, became abundant in 1999 in the Atlantic for the first time in 800,000 years following an exceptional year of ice-free water in the Canadian Arctic (Reid et al. 2007).

Climate change also causes shifts in ranges as species align their distributions to match their physiological tolerances under changing environmental conditions. Species' distributions along environmental gradients can provide key information on how they will respond to climate forcing (Hillyer & Silman 2010). Empirical and theoretical studies suggest that in response to warmer conditions, marine fishes and invertebrates tend to shift their distributions to higher latitudes and/or into deeper depths (Mueter & Litzow 2008, Spencer 2008), consistent with observational evidence for the North Sea (Perry et al. 2005) and Mid-Atlantic Bight (Nye et al. 2009, Lucey & Nye 2010). Climate-driven range shifts also may be accompanied by changes in demographics and organism abundance and size, as suggested by coupled climate-population models (Hare et al. 2010).

Climate-related distribution shifts contribute to observed alterations in community composition and biodiversity for many systems and organism groups, from rocky intertidal invertebrates (Barry et al. 1995) to seabirds (Hyrenbach & Veit 2003). Warming has been shown to decrease the diversity of salt marsh plant communities via increased evapotranspiration and soil drying (Gedan & Bertness 2009). In the North Sea, fish species richness increased by ~50% between 1986 and 2005 as temperatures rose, with a general trend toward greater representation of small-bodied southern species (Perry et al. 2005). Bioclimate envelope models predict that invasion intensity (the number of invasions relative to current species richness) may reach a global average of 55% by 2050 (Cheung et al. 2009). Warming is not the only driver of such changes; in a northeast Pacific rocky shore community, declining pH over eight years corresponded with gradual shifts from the mussel-dominated communities typical of such temperate shores to communities more dominated

by fleshy algae and barnacles (Wootton et al. 2008). In shallow benthic communities near natural CO₂ seeps, calcareous corals and algae are replaced by noncalcareous algae, and juvenile mollusks are sharply reduced in number or absent altogether (Hall-Spencer et al. 2008).

Multiple factors beyond climate change influence changes in marine community composition and trophic structure, and synergistic effects may arise among climate, exploitation, and the introduction of invasive species. A survey of four well-studied marine regions found that invasions are shifting food webs toward domination by suspension and deposit feeders low in the food chain, presumably reflecting the widespread transport of small fouling organisms and the decline of large fishes caused by human harvesting (Byrnes et al. 2007). Molecular genetic techniques are emerging as powerful tools for deciphering the history of species invasions caused by human transport (Geller et al. 2010) and may be equally valuable for understanding climate-driven shifts. Evidence from the Atlantic (Stachowicz et al. 2002) and Pacific (Sorte et al. 2010) coasts of North America indicates that nonnative species in fouling invertebrate communities are favored over native species in warmer waters. In this way, warming may tend to homogenize the composition of marine communities.

Climate-mediated community effects also involve alterations in trophic interactions. Given that physiological responses to climate change are species specific, changes in timing of life-history events (phenology) induced by climate change will often differ between interacting species at different trophic levels, leading to mismatches in trophic synchrony and effects on consumer-prey relationships (Brander 2010). In aquatic mesocosms and terrestrial ecosystems, higher trophic levels are often more affected, resulting in more variability and higher extinction risks, than lower ones (Petchey et al. 1999, Voigt et al. 2003). Warming can also increase the consumption rates and interaction strengths of consumers, as shown for intertidal sea stars (Sanford 1999), leading to stronger top-down effects of benthic herbivores feeding on seaweeds (O'Connor 2009), zooplankton feeding on phytoplankton (O'Connor et al. 2009), and benthic predators feeding on bivalves (Philippart et al. 2003). Climate change and acidification will undoubtedly affect microbial food webs as well, although there are many uncertainties (Sarmiento et al. 2010, Joint et al. 2011). The complex networks of interactions among species mean that climate-mediated changes at the community level can be difficult to predict and sometimes counterintuitive.

Increasingly, climate-mediated shifts in species distributions are creating novel or emerging no-analog ecosystems consisting of species with little or no shared evolutionary history (Hobbs et al. 2006, Williams & Jackson 2007). There is growing evidence that the climate-mediated invasions mentioned above are biased taxonomically or by functional traits such as life history and trophic level (Byrnes et al. 2007). Some studies indicate that grazing pressure tends to be stronger at low latitudes, resulting in elevated plant and sponge investments in chemical defenses (Bolser & Hay 1996, Pennings & Silliman 2005), and warming-driven range shifts may strengthen species interactions at temperate latitudes. Other studies suggest that a warming climate aggravates the prevalence of marine diseases (Harvell et al. 2002).

Ecosystem Structure and Function

Ecosystems integrate the responses of organism physiologies and ecological interactions to changes in climate and CO₂. As a consequence, the mechanisms that link changes in populations and communities to alterations in ecosystem-level properties such as trophic structure, food-web dynamics, energy flow, and biogeochemical cycles are diverse. Disruptions of existing biological interactions can occur through asynchronous shifts in the seasonal phenologies of interacting predator and prey populations (i.e., the match-mismatch hypothesis); biogeographic reorganizations, leading to changes in community composition and biodiversity; and loss of functionally prominent species.

These processes can be expressed through bottom-up impacts such as declines in water-column primary production and/or shifts toward smaller cells in planktonic communities, as well as through top-down impacts that cascade down from the losses or gains of ecologically dominant consumers. Alterations in biogeochemical cycling can occur because of the replacement of functional groups (e.g., calcifiers) even if overall productivity and diversity remain approximately constant.

The actual extent of ecosystem changes faced by individual systems will likely depend on factors such as functional redundancy, the rate and sequence of community change, and other features of population and community organization. Some studies suggest that geographic variability may modulate ecosystem response to climate-induced structural changes. Navarrete et al. (2005), for example, found that a southern part of the upwelling region along the western coast of Chile exhibited top-down control; in the north, communities were recruitment limited, so predators had negligible effects on community composition. Considerable progress has been made on methods for identifying reliable indicators (i.e., measurable characteristics of ecosystems, such as mean length of fish or proportion of predatory fish in a community) of marine ecosystem function and resistance to perturbations (Gaichas et al. 2009, Samhuri et al. 2009, Bundy et al. 2010).

Numerous studies have addressed the response of open-ocean primary productivity to climate forcing on local to global scales. Retrospective studies show that increases in upper-ocean temperature, and hence vertical stratification, result in decreases in phytoplankton and primary production, especially in mid- to low latitudes (Behrenfeld et al. 2006). Warming also may cause the fraction of small phytoplankton (picophytoplankton) to increase, reducing the energy flow to higher trophic levels (Moran et al. 2010). Declines in historical phytoplankton abundance are detectable on scales from decades to the past century (Antoine et al. 2005, Boyce et al. 2010). Steinacher et al. (2010) report results from four climate models indicating reductions in global primary production from 2% to 20% by 2100 with declines in mid- to low latitudes due to reduced nutrient input into the euphotic zone, and gains in the Southern Ocean and (in three of the four models) the Arctic due to warmer temperatures and less sea ice.

Further, entire biomes may expand or contract, with the potential for the emergence of new regions with combined biotic and abiotic conditions that have not been observed before. Polovina et al. (2011) forecast a 30% areal increase of the North Pacific subtropical biome by 2100, owing to northward expansion by as much as 100 km per decade, as well as growth in the area where tropical SSTs permanently exceed 30°C from a negligible amount to over 25 million km². Such warmer, more nutrient-poor oligotrophic conditions typically lead to lower primary productivity and greater dominance of a microbial food web with increased recycling, reduced export flux of sinking organic matter, and greater production of dissolved organic matter.

Climate-driven impacts on keystone and foundation species may be especially important. Some critical habitat-forming marine benthic species, such as oysters or corals, appear sensitive to CO₂ and climate change both directly and through pathogens. In oyster populations within Delaware Bay, United States, the protistan parasite *Perkinsus marinus* (which causes the disease Dermo) proliferates at high water temperatures and high salinities, and epidemics followed extended periods of warm winter weather; these trends in time are mirrored by the northward spread of Dermo up the eastern seaboard as temperatures warmed (Ford 1996). Similarly, corals on the Great Barrier Reef showed more infections by the emerging disease “white syndrome” in warmer than normal years (Bruno et al. 2003). These processes and others resulting from altered species composition will likely have important rippling affects through ecosystems.

Climate change and altered ocean circulation may change organism dispersal and the transport of nutrient and organic matter that provide important connectivity across marine ecosystems. If species dispersal is disrupted by climate-induced thermal blocks or shifts in currents carrying larvae, both species and community dynamics will be altered. For example, Gulf menhaden transported

5%–10% of primary production of estuaries in Louisiana to deeper communities in the Gulf of Mexico (Deegan 1993). Energy exchanges between habitats such as mangroves–coral reefs and coral reefs–seagrasses can be disrupted in complex ways as fish abundances decline (e.g., Mumby & Hastings 2008, Valentine et al. 2008). Many studies have found that altering the metapopulation dynamics of a species can reduce its ability to withstand pressures because rescue and recolonization dynamics are disrupted (e.g., Lipcius et al. 2008). However, the net effect of climate-induced changes on the distribution of habitats and species' ability to maintain energy flows between them has not been examined in great detail.

ECOSYSTEM CASE STUDIES

No ecosystem is untouched by the effects of increasing CO₂ in the atmosphere and climate change; although the effects are felt initially at the surface, perturbations associated with the changing climate have already been detected in the deep sea, with consequences for the global carbon cycle (Smith et al. 2009). Using the following three case studies, we illustrate the complex interplay of physical and chemical forcing with physiological and behavioral responses of individual organisms that can result in changes to ecosystem structure and function.

Ice-Dominated Polar Systems

Currently, the physical climate of the poles is changing as fast or faster than anywhere on Earth, and thus the poles serve as both a bellwether of climate change and an illustration of the complex ecosystem-level consequences that we can expect elsewhere. As a result, polar marine ecosystems are experiencing large shifts in species size, spatial range, and seasonality of production that can cascade directly to valued ecosystem services, such as the health of large marine mammals and seabirds as well as fisheries (see sidebar Climate Impacts on Ecosystem Services from the Sea).

Polar marine ecosystems are intimately tied to sea-ice extent and seawater temperatures, which together influence food sources, organismal growth and reproduction, and biogeochemical cycles. Many polar fishes and invertebrates are adapted to contemporary cold conditions and have limited tolerance to seemingly small increases in water temperature (Somero 2012). Life cycles and

CLIMATE IMPACTS ON ECOSYSTEM SERVICES FROM THE SEA

Climate change puts at risk many of nature's benefits, or ecosystem services, that humans derive from the sea. These impacts will have repercussions for society's dependence on the ocean for wild-caught and farmed food, recreation, nutrient cycling, waste processing, protection from natural hazards, climate regulation, and other services. For example, climate-induced sea-level rise could put added pressure on coastal infrastructure and thus the health and safety of human communities. Natural habitats such as wetlands, mangroves, coral and oyster reefs, and seagrasses buffer coastlines from erosion and inundation, providing important protective services. One of the many advantages of nature-based protection is that those same habitats also provide other benefits, including nursery grounds for commercial and recreationally valued species, filtration of sediment and pollutants, and carbon storage and sequestration. The social values of these services are broad and include those reflected in markets, avoided damage costs, maintenance of human health and livelihoods, and cultural and aesthetic sustenance. Understanding how human activities and a changing climate are likely to interact to affect the delivery of these ecosystem services is of the utmost importance as we make decisions now that affect the health of marine and coastal systems and their ability to sustain future generations.

physiological requirements of many polar organisms are closely tied to the annual cycles of sea ice and available sunlight. The early ice-edge bloom supports underlying benthic communities, often initiating reproductive processes in the spring. Model projections reveal that greater light availability caused by a reduction in sea ice may increase open-water phytoplankton primary production (Arrigo et al. 2008, Steinacher et al. 2010), although nutrient limitation could ultimately limit the magnitude of this increase (Grebmeier et al. 2010). Changes in community composition may complicate this picture—a recent study documented a shift to smaller-celled algal species due to freshening in the western Arctic Ocean (Li et al. 2009), with the potential for reduced overall productivity. Sea ice also provides an important habitat for seabirds and mammals (e.g., polar bears, walrus, seals) that use the ice as a foraging platform or breeding habitat, suggesting that these species will face problems with warming. A recent review evaluating Arctic ecosystem responses to climate change (Wassmann et al. 2011) documented marine species range shifts; changes in abundance, growth, condition, behavior, and phenology; and community and regime shifts as key components of change. Thus, climate change can drive changes in both abiotic and biotic interactions, including nonlinear impacts within the food-web structure that can have unexpected results that may move current marine ecosystems to a new state.

An example of an Arctic ecosystem already undergoing change is the seasonally ice-covered northern Bering shelf ecosystem, which is dependent on spring ice-edge production. With limited zooplankton grazing early in the spring season, the high primary production sinks and is exported to the shallow sediments, supporting a large and diverse benthic community that is critical for benthic-feeding marine mammals and seabirds (Grebmeier et al. 2006). Seasonal ice coverage and cold waters have typically limited pelagic fish predation, allowing diving seabirds, bearded seals, walrus, and gray whales to harvest the high benthic production. But distributions of many polar organisms are changing, with rippling consequences through the food web. Recent warming and variability in sea-ice retreat coincided with declines in clam populations, which in turn co-occur with dramatic declines in diving sea ducks, more northerly migrations of large vertebrate predators (walrus and gray whales), and potentially poleward-expanding ranges for pelagic fishes (cf. Grebmeier et al. 2010). Further north, the rapid loss of sea ice in the Chukchi Sea has resulted in the relocation of thousands of walrus to land in both Russia and Alaska (Fischbach et al. 2009). These community structure changes are also influencing traditional subsistence hunting by native communities, who must now travel longer distances in open water to hunt.

In the Antarctic, winter air temperatures along the WAP have warmed by 6°C since the 1950s, seasonal sea-ice duration has declined by nearly 90 days since the beginning of satellite-based measurements in 1978, and increased upwelling of warm Antarctic Circumpolar Current water has occurred (Schofield et al. 2010). Coincident water-column warming and increased freshwater input from melting glaciers in the WAP are forcing changes throughout the marine ecosystem (Schofield et al. 2010). Time-series satellite ocean color records for the northern regions of the WAP indicate that phytoplankton stocks have declined by over 80%, owing to sea-ice loss reducing the meltwater-induced water-column stratification that is necessary for plant growth (Montes-Hugo et al. 2009). By comparison, phytoplankton standing stocks have increased in the south in the present seasonal marginal ice zone.

As in the Arctic, warming has especially significant impacts on cold- and ice-adapted species as suitable habitats contract toward the poles. The decline of Antarctic sea ice may be the cause of a major regime shift in the pelagic community, where krill have declined by an order of magnitude in the Atlantic sector since 1950, with a corresponding increase in the abundance of salps, leading to important consequences for the pelagic food web (Atkinson et al. 2004, Schofield et al. 2010). Owing to these cascading responses to sea-ice loss, reduced krill availability, and elevated late-spring snowfalls, the population of Adélie penguins has declined by 80% in the Palmer

Station region, similar to observed declines in crabeater seals in the region (Ducklow et al. 2007). Conversely, in a case of opening niche space and species expansion, the ice-avoiding or ice-tolerant gentoo penguins and fur seals are now migrating into the region and establishing new breeding colonies (Schofield et al. 2010). This example of species range expansion is similar to the northward range migration of the gray whales in the Chukchi Sea occurring because of reduced sea-ice extent and duration (Moore 2008). Thus, in both polar marine regions, the reduction of sea ice, warming seawater, and increasing freshwater content are impacting species composition, productivity, phenology, and predator-prey interactions. The impacts of these changes on biodiversity and marine biogeochemical cycling can have both known and unknown consequences to the world ocean and internal feedbacks to climate. With continued warming, we can expect poleward species migrations that could reorganize traditional cold-adapted biomes, change biodiversity, and increase food-web complexity, with direct impacts on carbon transfer within the polar ecosystem and enhanced connectivity with the global ocean system.

Coral Reef Systems

Because one-quarter of all marine species associate with coral reefs, the ecological impacts of changing climates and chemistry on overall marine biodiversity are potentially severe and widespread. The ability of the coral animal to create massive and complex reef structures, on which the rest of the ecosystem depends, is sensitive to relatively small changes in temperature and pH (Kleypas et al. 2006, Hoegh-Guldberg et al. 2007). Because the effects of climate change are already apparent on coral reefs, this ecosystem is often called the canary in the coal mine for warming and acidification. Concerns about reefs are heightened by the fact that most coral reefs today are also severely impacted by multiple stressors such as overfishing, destructive fishing, pollution, sedimentation, nutrient overenrichment, and invasive species.

Warming of as little as 1°C causes coral bleaching, a state in which the tissues of the coral become colorless because of the loss of the zooxanthellae, the symbiotic dinoflagellates that through their photosynthesis fuel the growth of their coral hosts (Hoegh-Guldberg et al. 2007, Donner 2009). Moderate bleaching results in stress that causes reduced growth rates and reproductive output, whereas severe bleaching results in coral death. Bleaching also appears to make corals more vulnerable to disease, so that some death occurs after a time lag (e.g., Muller et al. 2007). Genetic diversity in hosts and symbionts leads to a diversity of responses to mild temperature increases, but severe temperature anomalies almost always lead to widespread bleaching and death. Reefs are likely to become dominated in the future by symbiotic associations with warm-tolerant zooxanthellae, allowing some corals to survive moderate temperature increases. However, these more robust zooxanthellae may be less suitable as partners from the perspective of other aspects of coral health, such as growth (Jones & Berkelmans 2010).

Ocean acidification makes it more difficult for corals to secrete and maintain their skeletons (Salvat & Allemand 2009). Some coral species lose their skeletons altogether (Fine & Tchernov 2007), and skeletal growth of recent recruits can be disrupted (Cohen et al. 2009). Growth rates of adult corals may be reduced, or their skeletons may be less dense (which would make storm damage more serious). However, as with zooxanthellae and temperature, some coral species are likely to be more resistant to the effects of low pH.

Many other reef organisms can also be negatively affected by changing temperatures and pH. A particularly worrying possibility is the reduction of cover by coralline algae, which are preferred recruitment surfaces for coral larvae but are highly sensitive to low pH because of the chemical composition of their calcareous skeletons (Doney et al. 2009). Ocean acidification also disrupts the sensory abilities of coral reef fishes (Munday et al. 2009) and likely has reproductive impacts

on external spawners. The impact that seemingly countless small changes in the fitness of many individual species have on the function of entire coral reef ecosystems is currently impossible to estimate, but potentially substantial.

In addition to the direct negative effects of warming and acidification, many reef-associated species are also expected to decline because of the decline in their coral-constructed habitat. Preliminary studies indicate a loss in both fish diversity and invertebrate diversity (Jones et al. 2004, Idjadi & Edmunds 2006), with loss of coral cover and structure. Some coral-associated species are able to live in other habitats (e.g., rocky reefs), but others are specialized coral associates restricted to reefs.

Coral reefs are particularly vulnerable to future temperature increases and acidification because of the losses they have already suffered, amounting to reductions of coral cover of ~80% in the Caribbean and ~50% in the Pacific, much of it due to local human impacts (Jackson 2010). In the long run, low growth rates caused by a combination of factors may make it difficult for the growth of coral reefs to keep up with rising sea levels, losses due to storm damage, and bioerosion, as ultimately, the existence of reefs depends on net positive accretion. Viewed more positively, protection from local stressors can make reefs more resilient in the face of global change (Knowlton & Jackson 2008).

The literature of coral reef degradation makes frequent reference to tipping points and thresholds. For example, overfishing can make the effects of mortality from mass coral mortality via bleaching much worse, as the liberation of bare space can result in algal blooms that overwhelm local herbivores, leading ultimately to domination by distasteful algae that inhibit reef recovery (a phase shift). Recently, Hoegh-Guldberg et al. (2007) have argued that specific concentrations of CO₂ in the atmosphere represent thresholds for the existence of reefs in any substantial form. In fact, there are a series of tipping points and thresholds relating coral reef health and CO₂ concentrations via the frequency of bleaching events, the likelihood of phase shifts, and the loss of the corals' ability to build reefs (Mumby et al. 2011). Coral recovery was faster in the Caribbean in areas where mangrove connections to reefs were intact (Mumby & Hastings 2008), which may also influence the resilience of coral reefs to climate change and CO₂.

The most serious consequence of rising temperatures and dropping pH would be extinction. Although marine species have traditionally been viewed as less vulnerable to extinction, the combination of global change and local stressors may change this. Recent analyses suggest that one-third of all coral species may be at risk of extinction (Carpenter et al. 2008). Reef fish are also vulnerable (Graham et al. 2011); however, there is relatively little overlap between the fishes most vulnerable to climate change (primarily due to loss of coral habitat) and those most vulnerable to overfishing. Thus, these two stressors may have synergistic negative effects on fish diversity.

Upwelling Systems: The California Current

EBCSs characterize the eastern margins of both the Pacific and Atlantic Oceans, and support high production throughout the food web owing in large part to persistent coastal upwelling of nutrient-rich water. The California Current is one of four highly productive EBCSs that collectively support as much as one-fifth of the global marine fish harvest. Exceptional, yet variable, productivity arises from transport of subarctic water from the north via the California Current itself and wind-driven coastal upwelling flows that supply nutrients to the sunlit upper ocean (Checkley & Barth 2009). Ecosystem structure and function within the California Current are strongly influenced by the natural basin-scale modes of interannual to interdecadal climate variability, including ENSO, the Pacific Decadal Oscillation (PDO), and the North Pacific Gyre Oscillation (Chavez et al. 2011). By modulating gyre circulation, current flows, sea level, and depths of the thermocline

and upwelling cells, these modes of oceanic and atmospheric variability play fundamental roles in structuring the flow of energy and nutrients through food webs across the California Current. Although strong interannual and interdecadal climate variability pose inherent challenges in the attribution of ecological changes in the California Current to climate change, multidecadal time series of climate variability and ecosystem responses have provided important insights into the suite of dynamics that will likely govern future changes.

Climate change is expected to have several far-reaching consequences for the California Current, stemming from alterations in water-column stability, timing and intensity of upwelling-favorable winds, and the sources and chemical properties of water that is advected horizontally and vertically into the system. A warming ocean is projected to reduce nutrient inputs and primary productivity as the thermocline deepens and stratification intensifies. There is considerable evidence of significant warming (Schwing et al. 2010) and concomitant changes in water-column stratification (Palacios et al. 2004) across the California Current over the past century. The longest ecological time series starts not with phytoplankton but with zooplankton in the southern California Current. There, zooplankton biomass has declined dramatically over the past 60 years in concert with increases in ocean temperature (Roemmich & McGowan 1995), a trend that continues to this day. Reductions in pelagic tunicates are largely responsible for this decline from the 1950s to early 1990s, possibly as warm-water taxa were favored by a shift toward greater relative abundance of small prey (picoplankton) (Lavaniegos & Ohman 2003). Hsieh et al. (2009) report a similar declining trend for nongelatinous zooplankton in the region. Because a shift toward less abundant, smaller, and lipid-poor subtropical copepods accompanied the transition into warm phase of the PDO (Peterson & Schwing 2003), continued warming of the California Current is predicted to translate up the food chain to reduce juvenile survivorship in salmonid fishes.

Extended time series of primary productivity or phytoplankton biomass are surprisingly rare, but illustrate some of the complexity of pelagic ecosystem responses to warming-induced changes in physical forcing. Continuous records available for the central and southern California Current since the 1980s indicate shoaling of high-nutrient subsurface waters and increasing primary productivity (Aksnes & Ohman 2009, Chavez et al. 2011). This runs counter to expected nutrient declines from a warming ocean surface, as shoaling of nutrient-rich water has occurred despite increased stratification (Aksnes & Ohman 2009). The California Current spans strong physical gradients in the circulation and water-column structure that mediate spatial variation in ecosystem response to climate change (King et al. 2011). As a consequence, the rate of warming is spatially heterogeneous, and increases in upwelling-favorable winds have slowed or reversed warming trends in some nearshore regions (García-Reyes & Largier 2010). In this manner, nutrient declines associated with water-column warming can be countered by strengthening of winds that drive coastal and curl-driven upwelling flows (Aquad et al. 2006). In the southern California Current, shoaling of nutrient-rich water is consistent with an increase in wind-stress curl since the 1980s (Ryckaczewski & Checkley 2008) and may be countering the first-order effects of surface warming. Whether observed changes in wind forcing reflect secular trends or decadal-scale variability in the climate system of the California Current, and what net impacts warming and upwelling increases will have on future production (Di Lorenzo et al. 2005), have emerged as two critical questions for further research.

The likely impacts of a warming California Current on ecosystem function and upper-trophic-level consumers can be estimated by using observed declines in nutrient supply and primary production as proxies. Both of these changes were observed during strong El Niños and as the system transitioned into the 1977–1998 warm phase of the PDO (McGowan et al. 2003), and in both instances, declines in primary production propagated up the food web from zooplankton to upper-trophic-level consumers, including seabirds (Veit et al. 1996, Sydeman et al. 2009). There

is also strong evidence that the trophic impacts of climate change can extend from changes in both the mean and variance of production at the base of the food web. In the southern California Current, Kim et al. (2009) demonstrated increasing chlorophyll *a* concentrations as well as an advancement in the timing of the spring bloom. In the northern California Current, the peak biomass of *Neocalanus plumchrus*, a large copepod, has both narrowed and advanced by nearly 6 weeks over 30 years (Mackas et al. 2007). Asynchronies between prey availability and demand can have particularly strong consequences for consumers such as migrating juvenile salmon, or breeding seabirds that undergo critical life-history transitions over narrow phenological windows. For example, seabird reproductive failures have been attributed to spatial and temporal mismatches in the availability of and demand for prey (Sydeman et al. 2006). In some cases, seabird breeding success has become more variable while average values have remained largely unchanged (Sydeman et al. 2009).

Climate change has also altered community structure via nontrophic pathways. In the Santa Barbara Basin, Field et al. (2006) showed an increasing abundance of foraminifera with subtropical zoogeographic affinities as the system warmed over the past century. Similarly, in nearshore regions, Barry et al. (1995) documented a shift toward increased abundance of southern taxa and decreased abundance of northern taxa in intertidal communities that experienced long-term warming between the 1930s and 1990s. Hsieh et al. (2009) showed long-term changes in the abundance of fish (25 of 34 species) in the oceanic region, as well as redistributions (16 of 34 species). Field et al. (2010) showed long-term declines in the relative abundance of young rockfish (*Sebastes* spp.). In the Southern California Bight, the conservation habitat for cowcod rockfish (*Sebastes levis*) is projected to be reduced by 18% over the next 20 years should present trends in the shoaling of the hypoxia horizon continue (McClatchie et al. 2010). In the northern California Current, reduced oxygen content in water masses that feed coastal upwelling flows, in combination with strengthened upwelling-favorable winds, has resulted in oxygen declines (Grantham et al. 2004, Chan et al. 2008) to hypoxic levels where fishery catch can be suppressed (Keller et al. 2010). Changing ocean conditions also may allow highly mobile predators (e.g., jumbo squid; Field et al. 2007) to expand their range and exploit new ecosystems. Therefore, observational evidence confirms climate-related changes across multiple trophic levels in the California Current.

In the future, transitions across climate regimes may provide critical insights into the likely responses of the California Current to continued climate changes. Such insights may prove particularly valuable if future changes are expressed through increased variance in ENSO or North Pacific Gyre Oscillation activity, as Di Lorenzo et al. (2010) have predicted. At the same time, the value of past climate-ecosystem dynamics as analogs for future changes becomes less certain (Chavez et al. 2011). For example, warm ENSO events have involved both thermocline deepening and upwelling reductions. In contrast, future climate scenarios are predicted to involve both increased thermocline depth and upwelling wind stress (King et al. 2011; **Figure 3**). Similarly, future warming in the California Current will be accompanied by increases in nutrient supply (and decreases in dissolved oxygen and pH) if basin-scale warming increases the age and preformed nutrient content of upwelled water (Rykaczewski & Dunne 2010). Additional changes in carbonate chemistry due to continued ocean uptake of anthropogenic CO₂ will further represent challenges to ecosystem structure and function that are largely unpredictable from past dynamics.

FINAL THOUGHTS

As illustrated in the case studies, evidence is mounting that the physical and chemical conditions present in different ocean regions are changing with time, and that climate and CO₂ can have

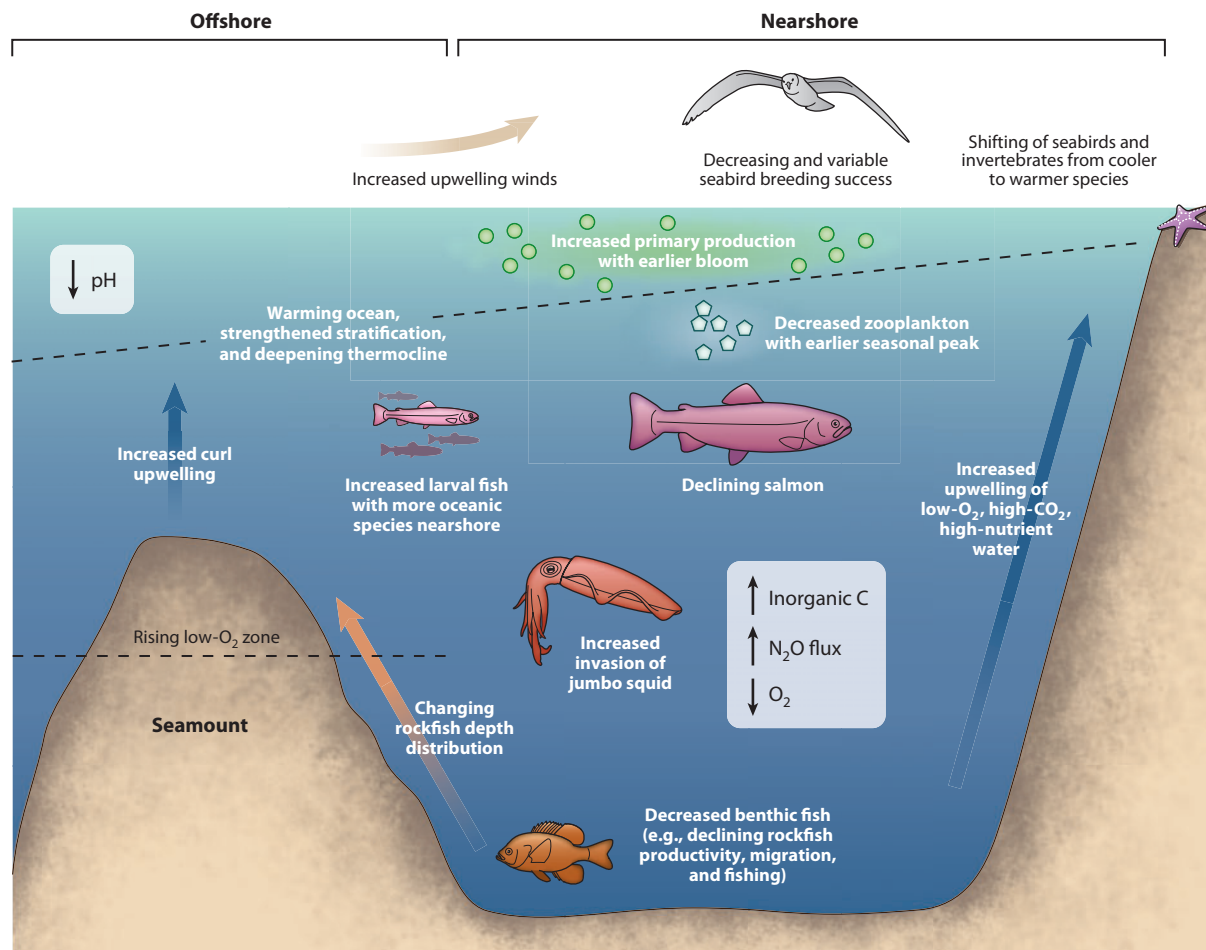


Figure 3

Summary of climate-dependent changes in the California Current. Observed physical changes include surface warming, strengthened stratification, and a deepening thermocline that is superimposed on strengthened upwelling wind stress and resultant increases in coastal and curl-driven upwelling. Long-term declines in dissolved oxygen have resulted in intensification of shelf hypoxia and vertical displacement of the hypoxia horizon, reducing the habitat for certain oxygen-sensitive demersal fish species and increasing the inorganic carbon burden and potential for N₂O flux. The surface inorganic carbon load has also increased because of anthropogenic CO₂ uptake. Time series from the past two to three decades indicate increasing trends in phytoplankton biomass; longer time series for zooplankton indicate decreasing biovolumes over the past six decades as well as shifts toward an earlier and narrower window of peak abundance. Increases in oceanic larval fish have been observed, as have declines in salmon and rockfish productivity. Seabirds have experienced more variable and in some cases declining breeding success. Distributional shifts toward species with subtropical or southern ranges (warmer) and away from species with subarctic or north ranges (cooler) have been evident in intertidal invertebrate, zooplankton, and seabird communities.

substantial effects on organism physiology, populations of individual species, and community composition and biodiversity. Somewhat less is known about the consequences of these climate-induced shifts for ecosystem structure and aggregated ecosystem functions, such as energy flow from primary production through to upper trophic levels, connections across habitats via dispersal and transport, sequestration of organic carbon, and biogeochemical cycling. Research is also just starting to define and quantify the large range of potential synergistic impacts that could arise

from co-occurring climate, CO₂, and nonclimate stressors, thus amplifying human environmental pressures. In many cases, existing data records are too short to clearly attribute the mechanism causing observed biological changes or to differentiate between the effects of natural climate variability and secular climate trends.

Drawing lessons from existing ecological studies, we can generate useful hypotheses about future climate impacts that can be tested with empirical information and models. For example, as both the polar and California Current case studies illustrate, we should expect continued shifts in the abundance, phenology, and distribution of individual species in response to further warming and sea-ice retreat. Differential responses across species assemblages may also become more pronounced as the strength of anthropogenic forcing grows, leading to the increasing possibility of substantial disruptions in biological interactions and existing community composition. In the future, climate and CO₂ impacts may grow large enough to create no-analog ecosystems whose behavior will be more difficult to forecast based on historical patterns. Nonlinear responses, thresholds, and counterintuitive effects may also arise.

The current state of knowledge highlights the need for a more comprehensive, multispecies approach to ecosystem-level analyses in order to better track and forecast changing marine ecosystems. Research needs span laboratory and field process studies, manipulative experiments, observational networks, historical data synthesis, and modeling from small-scale process simulations to large-scale coupled biophysical models. Especially important is the establishment of long-term, biologically oriented, and ecosystem-based observational systems. These sustained networks are essential for detecting and attributing ecological changes in response to rising CO₂, climate change, and other human pressures. Research should also feed into improving ecological forecasting capabilities to support climate adaptation strategies and policy decisions.

SUMMARY POINTS

1. Rising atmospheric CO₂ is causing increasing atmosphere and ocean temperatures, which in turn drive rising sea levels, increased vertical stratification, retreating sea ice, and altered precipitation, runoff, and wind patterns. Warming and altered ocean circulation reduce subsurface oxygen concentrations, and rising atmospheric CO₂ leads to ocean acidification.
2. Regional pressures on ocean ecosystems arise from runoff from intensive fertilizer use, coastal and benthic habitat degradation, fish stock overexploitation, growing aquaculture production, and invasive species. These factors interact in complex and sometimes synergistic ways such that these multiple stressors on marine ecosystems—both CO₂ and non-CO₂ related—must be considered in total, not as independent issues.
3. Climate and CO₂ changes influence many levels of ocean biological organization and function. Direct temperature and chemical effects alter organism physiology and behavior, leading to population-level impacts such as poleward shifts in spatial ranges as well as changes in population size, population growth rates, and seasonal variation.
4. Community-level impacts of climate change stem from altered physiology that translates to changing interactions among species such as competition, grazing, predation, and disease dynamics. Together with local climate-driven invasion and extinction, these processes result in altered community structure and diversity, including emergence of novel ecosystems.

5. No ecosystem is unaffected by the diverse effects of rising CO₂ levels. The effects of climate change are particularly striking for the poles and the tropics, because of the sensitivity of polar ecosystems to sea-ice retreat and poleward species migration as well as the sensitivity of coral-algal symbiosis to minor increases in temperature. Ocean acidification may hasten the decline of tropical coral ecosystems.
6. Intra- and interdecadal climate variability in midlatitude upwelling systems, like the California Current, reveals strong linkages between climate forcing and species distributions, phenology, and demography. This coupling highlights the sensitivity of the California Current to further changes in the climate system that regulates ocean stratification, upwelling wind stress, and basin-scale circulation.
7. Rising CO₂ and climate change may modify overall ecosystem properties such as trophic structure, food-web dynamics, and aggregated functioning such as energy and material flows and biogeochemical cycles, eventually impacting the ecosystem services upon which people and societies depend.

FUTURE ISSUES

1. To what extent will climate change be expressed through changes in the temporal variability and amplitude of key modes of natural ocean climate cycles?
2. What effects will interactions between natural climate cycles and anthropogenic climate change have on marine ecosystem structure and function?
3. How will the possible emergence of ecosystem states with no analog in the past impact our ability to forecast future dynamics of marine ecosystems?
4. How will marine ecosystems respond to the interactions between climate-dependent and climate-independent stressors?
5. How do ecosystem tipping points scale from physiological-, population-, and community-level processes? What information is critical for predicting approaching tipping points?
6. Which aspects of marine ecosystem structure are most important for conferring resilience against climate stressors and most amenable to management?
7. What role will biological acclimatization and adaptation play in modulating the rate of climate-driven marine ecosystem change?
8. How will climate change effects on marine ecosystem structure and function impact society's ability to rely on the flow of goods and services from the sea?

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LITERATURE CITED

- Aksnes DL, Ohman MD. 2009. Multi-decadal shoaling of the euphotic zone in the southern sector of the California Current System. *Ecol. Res.* 54:1272–81
- Antoine D, Morel A, Gordon HR, Banzon VF, Evans RH. 2005. Bridging ocean color observations of the 1980s and 2000s in search of long-term trends. *J. Geophys. Res.* 110:C06009
- Arrigo KR, van Dijken G, Pabi S. 2008. Impact of a shrinking Arctic ice cover on marine primary production. *Geophys. Res. Lett.* 35:L19603
- Atkinson A, Siegel V, Pakhomov E, Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432:100–3
- Auad G, Miller A, Di Lorenzo E. 2006. Long-term forecast of oceanic conditions off California and their biological implications. *J. Geophys. Res.* 111:C09008

- Bakun A, Field D, Redondo-Rodriguez A, Weeks S. 2010. Greenhouse gas, upwelling-favorable winds, and the future of coastal ocean upwelling ecosystems. *Glob. Change Biol.* 16:1213–28
- Barry JP, Baxter CH, Sagarin RD, Gilman SE. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267:672–75
- Behrenfeld MJ, O'Malley RT, Siegel DA, McClain CR, Sarmiento JL, et al. 2006. Climate-driven trends in contemporary ocean productivity. *Nature* 444:752–55
- Bindoff NL, Willebrand J, Artale V, Cazenave A, Gregory JM, et al. 2007. Observations: oceanic climate change and sea level. In *Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. S Solomon, D Qin, M Manning, Z Chen, M Marquis, et al., pp. 385–432. Cambridge: Cambridge Univ. Press
- Bolser RC, Hay ME. 1996. Are tropical plants better defended? Palatability and defenses of temperate versus tropical seaweeds. *Ecology* 77:2269–86
- Boyce DG, Lewis MR, Worm B. 2010. Global phytoplankton decline over the past century. *Nature* 466:591–96
- Boyer TP, Levitus S, Antonov JI, Locarnini RA, Garcia HE. 2005. Linear trends in salinity for the World Ocean, 1955–1998. *Geophys. Res. Lett.* 32:L01604
- Brander K. 2010. Impacts of climate change on fisheries. *J. Mar. Syst.* 79:389–402
- Bruno JF, Stachowicz JJ, Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18:119–25
- Bundy A, Shannon LJ, Rochet MJ, Neira S, Shin YJ, et al. 2010. The good(ish), the bad, and the ugly: a tripartite classification of ecosystem trends. *ICES J. Mar. Sci.* 67:745–68
- Byrnes JE, Reynolds PL, Stachowicz JJ. 2007. Invasions and extinctions reshape coastal marine food webs. *PLoS One* 2:e295
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, et al. 2008. One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science* 321:560–63
- Cazenave A, Lombard A, Llovel W. 2008. Present-day sea level rise: a synthesis. *C. R. Geosci.* 340:761–70
- Chan F, Barth JA, Lubchenco J, Kirincich A, Weeks H, et al. 2008. Emergence of anoxia in the California Current large marine ecosystem. *Science* 319:920
- Chavez F, Messie M, Pennington J. 2011. Marine primary production in relation to climate variability and change. *Annu. Rev. Mar. Sci.* 3:227–60
- Checkley DM, Barth JA. 2009. Patterns and processes in the California Current System. *Prog. Oceanogr.* 83:49–64
- Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, Pauly D. 2009. Projecting global marine biodiversity impacts under climate change scenarios. *Fish Fish.* 10:235–51
- Cohen AL, McCorkle DC, de Putron S, Gaetani GA, Rose KA. 2009. Morphological and compositional changes in the skeletons of new coral recruits reared in acidified seawater: insights into the biomineralization response to ocean acidification. *Geochem. Geophys. Geosyst.* 10:Q07005
- Davidson E. 2009. The contribution of manure and fertilizer nitrogen to atmospheric nitrous oxide since 1860. *Nat. Geosci.* 2:659–62
- Deegan LA. 1993. Nutrient and energy-transport between estuaries and coastal marine ecosystems by fish migration. *Can. J. Fish. Aquat. Sci.* 50:74–79
- Diaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–29
- Di Lorenzo E, Cobb KM, Furtado JC, Schneider N, Anderson BT, et al. 2010. Central Pacific El Niño and decadal climate change in the North Pacific Ocean. *Nat. Geosci.* 3:762–65
- Di Lorenzo E, Miller A, Schneider N, McWilliams J. 2005. The warming of the California Current System: dynamics and ecosystem implications. *J. Phys. Oceanogr.* 35:336–62
- Doney SC. 2010. The growing human footprint on coastal and open-ocean biogeochemistry. *Science* 328:1512–16
- Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO₂ problem. *Annu. Rev. Mar. Sci.* 1:169–92
- Donner SD. 2009. Coping with commitment: projected thermal stress on coral reefs under different future scenarios. *PLoS One* 4:e5712

- Dore JE, Lukas R, Sadler DW, Church MJ, Karl DM. 2009. Physical and biogeochemical modulation of ocean acidification in the central North Pacific. *Proc. Natl. Acad. Sci. USA* 106:12235–40
- Ducklow HW, Baker K, Martinson DG, Quetin LB, Ross RM, et al. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philos. Trans. R. Soc. B Biol. Sci.* 362:67–94
- Ducklow HW, Doney SC, Steinberg DK. 2009. Contributions of long-term research and time-series observations to marine ecology and biogeochemistry. *Annu. Rev. Mar. Sci.* 1:279–302
- Durack PJ, Wijffels SE. 2010. Fifty-year trends in global ocean salinities and their relationship to broad-scale warming. *J. Clim.* 23:4342–62
- Eppley R. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* 70:1063–85
- Fabry VJ, Seibel BA, Feely RA, Orr JC. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES J. Mar. Sci.* 65:414–32
- Farrell A, Hinch S, Cooke S, Patterson D, Crossin G, et al. 2008. Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict the success of spawning migrations. *Physiol. Biochem. Zool.* 81:697–708
- Feely RA, Doney SC, Cooley SR. 2009. Ocean acidification: present conditions and future changes in a high-CO₂ world. *Oceanography* 22:36–47
- Field DB, Baumgartner TR, Charles CD, Ferreira-Bartrina V, Ohman MD. 2006. Planktonic foraminifera of the California Current reflect 20th-century warming. *Science* 311:63–66
- Field JC, Baltz K, Phillips AJ, Walker WA. 2007. Range expansion and trophic interactions of the jumbo squid, *Dosidicus gigas*, in the California Current. In *CalCOFI Rep.* 48, pp. 131–46. La Jolla, CA: Calif. Coop. Ocean. Fish. Investig.
- Field JC, MacCall AD, Bradley RW, Sydeman WJ. 2010. Estimating the impacts of fishing on dependent predators: a case study in the California Current. *Ecol. Appl.* 20:2223–36
- Fine M, Tchernov D. 2007. Scleractinian coral species survive and recover from decalcification. *Science* 315:1811
- Fischbach AS, Monson DH, Jay CV. 2009. Enumeration of Pacific walrus carcasses on beaches of the Chukchi Sea in Alaska following a mortality event, September 2009. *Open File Rep. 2009-1291*, US Geol. Surv., Reston, VA
- Food Agric. Org. U.N. 2007. The world's mangroves 1980–2005. *FAO For. Pap.* 153, Food Agric. Org. U.N., Rome
- Food Agric. Org. U.N. 2010. Fishery and aquaculture statistics. *FAO Yearb.*, Food Agric. Org. U.N., Rome
- Ford SE. 1996. Range extension by the oyster parasite *Perkinsus marinus* into the northeastern United States: response to climate change? *J. Shellfish Res.* 15:45–56
- Gaichas S, Skaret G, Falk-Petersen J, Link JS, Overholtz W, et al. 2009. A comparison of community and trophic structure in five marine ecosystems based on energy budgets and system metrics. *Prog. Oceanogr.* 81:47–62
- García-Reyes M, Largier J. 2010. Observations of increased wind-driven coastal upwelling off central California. *J. Geophys. Res.* 115:C04011
- Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science* 301:958–60
- Gedan KB, Bertness MD. 2009. Experimental warming causes rapid loss of plant diversity in New England salt marshes. *Ecol. Lett.* 12:842–48
- Geller JB, Darling JA, Carlton JT. 2010. Genetic perspectives on marine biological invasions. *Annu. Rev. Mar. Sci.* 2:367–93
- Goldewijk KK. 2005. Three centuries of global population growth: a spatial referenced population (density) database for 1700–2000. *Popul. Environ.* 26:343–67
- Graham NAJ, Chabanet P, Evans RD, Jennings S, Letourneur Y, et al. 2011. Extinction vulnerability of coral reef fishes. *Ecol. Lett.* 14:341–48
- Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, et al. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429:749–54
- Grebmeier JM, Cooper LW, Feder HM, Sirenko BI. 2006. Ecosystem dynamics of the Pacific-influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog. Oceanogr.* 71:331–61

- Grebmeier JM, Moore SE, Overland JE, Frey KE, Gradinger R. 2010. Biological response to recent Pacific Arctic sea ice retreats. *Eos* 91:161–63
- Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E, Fine M, et al. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454:96–99
- Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, et al. 2008. A global map of human impact on marine ecosystems. *Science* 319:948–52
- Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD. 2010. Forecasting the dynamics of a coastal fishery species using a coupled climate-population model. *Ecol. Appl.* 20:452–64
- Harvell CD, Mitchell CE, Ward JR, Altizer S, Dobson AP, et al. 2002. Ecology: climate warming and disease risks for terrestrial and marine biota. *Science* 296:2158–62
- Hilley R, Silman MR. 2010. Changes in species interactions across a 2.5 km elevation gradient: effects on plant migration in response to climate change. *Glob. Change Biol.* 16:3205–14
- Hobbs RJ, Arico S, Aronson J, Baron JS, Bridgewater P, et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Glob. Ecol. Biogeogr.* 15:1–7
- Hoegh-Guldberg O, Bruno JF. 2010. The impact of climate change on the world's marine ecosystems. *Science* 328:1523–28
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, et al. 2007. Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–42
- Hofmann GE, Barry JP, Edmunds PJ, Gates RD, Hutchins DA, et al. 2010. The effect of ocean acidification on calcifying organisms in marine ecosystems: an organism-to-ecosystem perspective. *Annu. Rev. Ecol. Evol. Syst.* 41:127–47
- Hofmann M, Schellnhuber H-J. 2009. Oceanic acidification affects marine carbon pump and triggers extended marine oxygen holes. *Proc. Natl. Acad. Sci. USA* 106:3017–22
- Holland MM, Serreze MC, Stroeve J. 2008. The sea ice mass budget of the Arctic and its future change as simulated by coupled climate models. *Clim. Dyn.* 34:185–200
- Hsieh C-H, Kim H, Watson W, Di Lorenzo E, Sugihara G. 2009. Climate-driven changes in abundance and distribution of larvae of oceanic fishes in the southern California region. *Glob. Change Biol.* 15:2137–52
- Hyrenbach K, Veit R. 2003. Ocean warming and seabird communities of the southern California Current System (1987–98): response at multiple temporal scales. *Deep-Sea Res. Part II* 50:2537–65
- Idjadi JA, Edmunds PJ. 2006. Scleractinian corals as facilitators for other invertebrates on a Caribbean reef. *Mar. Ecol. Prog. Ser.* 319:117–27
- Ishii M, Kimoto M, Sakamoto K, Iwasaki SI. 2006. Steric sea level changes estimated from historical ocean subsurface temperature and salinity analyses. *J. Oceanogr.* 62:155–70
- Jackson JBC. 2010. The future of the oceans past. *Philos. Trans. R. Soc. B Biol. Sci.* 365:3765–78
- Jevrejeva S, Moore JC, Grinsted A, Woodworth PL. 2008. Recent global sea level acceleration started over 200 years ago? *Geophys. Res. Lett.* 35:8–11
- Joint I, Doney SC, Karl DM. 2011. Will ocean acidification affect marine microbes? *ISME J.* 5:1–7
- Jones A, Berkelmans R. 2010. Potential costs of acclimatization to a warmer climate: growth of a reef coral with heat tolerant versus sensitive symbiont types. *PLoS One* 5:e10437
- Jones G, McCormick M, Srinivasan M, Eagle J. 2004. Coral decline threatens fish biodiversity in marine reserves. *Proc. Natl. Acad. Sci. USA* 101:8251–53
- Keeling RF, Körtzinger A, Gruber N. 2010. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* 2:199–229
- Keller AA, Simon V, Chan F, Wakefield WW, Clarke ME, et al. 2010. Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fish. Oceanogr.* 19:76–87
- Kerr RA. 2008. Global warming: Hurricanes won't go wild, according to climate models. *Science* 320:999
- Kim H-J, Miller A, McGowan J, Carter M. 2009. Coastal phytoplankton blooms in the Southern California Bight. *Prog. Oceanogr.* 82:137–47
- King JR, Agostini VN, Harvey CJ, McFarlane GA, Foreman MGG, et al. 2011. Climate forcing and the California Current ecosystem. *ICES J. Mar. Sci.* 68:1199–216
- Kleypas JA, Feely RA, Fabry VJ, Langdon C, Sabine C, Robbins L. 2006. Impacts of ocean acidification on coral reefs and other marine calcifiers: a guide for future research. *Rep., Natl. Sci. Found., Natl. Ocean. Atmos. Adm., and US Geol. Surv., Washington, DC*

- Knowlton N, Jackson JBC. 2008. Shifting baselines, local impacts, and global change on coral reefs. *PLoS Biol.* 6:e54
- Kroeker KJ, Kordas RL, Crim RN, Singh GG. 2009. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 13:1419–34
- Lavaniegos B, Ohman M. 2003. Long-term changes in pelagic tunicates of the California Current. *Deep-Sea Res. Part II* 50:2473–98
- Le Quéré C, Raupach MR, Canadell JG, Marland G, Bopp L, et al. 2009. Trends in the sources and sinks of carbon dioxide. *Nat. Geosci.* 2:831–36
- Levitus S, Antonov JI, Boyer TP, Locarnini RA, Garcia HE, Mishonov AV. 2009. Global ocean heat content 1955–2008 in light of recently revealed instrumentation problems. *Geophys. Res. Lett.* 36:L07608
- Li WKW, McLaughlin FA, Lovejoy C, Carmack EC. 2009. Smallest algae thrive as the Arctic Ocean freshens. *Science* 326:539
- Lipcius RN, Eggleston DB, Schreiber SJ, Seitz RD, Shen J, et al. 2008. Importance of metapopulation connectivity to restocking and restoration of marine species. *Rev. Fish. Sci.* 16:101–10
- Lucey SM, Nye JA. 2010. Shifting species assemblages in the Northeast US Continental Shelf Large Marine Ecosystem. *Mar. Ecol. Prog. Ser.* 415:23–33
- Mackas D, Batten S, Trudel M. 2007. Effects on zooplankton of a warmer ocean: recent evidence from the Northeast Pacific. *Prog. Oceanogr.* 75:223–52
- Maslanik JA, Fowler C, Stroeve J, Drobot S, Zwally J, et al. 2007. A younger, thinner Arctic ice cover: increased potential for rapid, extensive sea-ice loss. *Geophys. Res. Lett.* 34:L24501
- McClain CR. 2009. A decade of satellite ocean color observations. *Annu. Rev. Mar. Sci.* 1:19–42
- McClatchie S, Goericke R, Cosgrove R, Auad G, Vetter R. 2010. Oxygen in the Southern California Bight: multidecadal trends and implications for demersal fisheries. *Geophys. Res. Lett.* 37:1–5
- McGowan J, Bograd S, Lynn R, Miller A. 2003. The biological response to the 1977 regime shift in the California Current. *Deep-Sea Res. Part II* 50:2567–82
- Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, et al. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323:1470–73
- Moore SE. 2008. Marine mammals as ecosystem sentinels. *J. Mammal.* 89:534–40
- Moran XAG, Lopez-Urrutia A, Calvo-Diaz A, Li WKW. 2010. Increasing importance of small phytoplankton in a warmer ocean. *Glob. Change Biol.* 16:1137–44
- Mueter FJ, Litzow MA. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. *Ecol. Appl.* 18:309–20
- Muller EM, Rogers CS, Spitzack AS, van Woesik R. 2007. Bleaching increases likelihood of disease on *Acropora palmata* (Lamarck) in Hawksnest Bay, St. John, US Virgin Islands. *Coral Reefs* 27:191–95
- Mumby PJ, Hastings A. 2008. The impact of ecosystem connectivity on coral reef resilience. *J. Appl. Ecol.* 45:854–62
- Mumby PJ, Iglesias-Prieto R, Hooten AJ, Sale PF, Hoegh-Guldberg O, et al. 2011. Revisiting climate thresholds and ecosystem collapse. *Front. Ecol. Environ.* 9:94–96
- Munday PL, Dixon DL, Donelson JM, Jones GP, Pratchett MS, et al. 2009. Ocean acidification impairs olfactory discrimination and homing ability of a marine fish. *Proc. Natl. Acad. Sci. USA* 106:1848–52
- Natl. Res. Council. 2010. *Ocean Acidification: A National Strategy to Meet the Challenges of a Changing Ocean*. Washington, DC: Natl. Res. Council.
- Natl. Res. Council. 2011. *Climate Stabilization Targets: Emissions, Concentrations and Impacts over Decades to Millennia*. Washington, DC: Natl. Res. Council.
- Navarrete SA, Wieters EA, Broitman BR, Castilla JC. 2005. Scales of benthic–pelagic coupling and the intensity of species interactions: from recruitment limitation to top-down control. *Proc. Natl. Acad. Sci. USA* 102:18046–51
- Nye JA, Link JS, Hare JA, Overholtz WJ. 2009. Changing spatial distribution of fish stocks in relation to climate and population size on the Northeast United States continental shelf. *Mar. Ecol. Prog. Ser.* 393:111–29
- O’Connor MI. 2009. Warming strengthens an herbivore–plant interaction. *Ecology* 90:388–98
- O’Connor MI, Pihler MF, Leech DM, Anton A, Bruno JF. 2009. Warming and resource availability shift food web structure and metabolism. *PLoS Biol.* 7:e1000178

- Palacios DP, Bograd SJ, Mendelssohn R, Schwing FB. 2004. Long-term and seasonal trends in stratification in the California Current, 1950–1993. *J. Geophys. Res.* 109:C10016
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.* 37:637–69
- Patti B, Guisande C, Riveiro I, Thejll P, Cuttitta A, et al. 2010. Effect of atmospheric CO₂ and solar activity on wind regime and water column stability in the major global upwelling areas. *Estuar. Coast. Shelf Sci.* 88:45–52
- Pennings SC, Silliman BR. 2005. Linking biogeography and community ecology: latitudinal variation in plant-herbivore interaction strength. *Ecology* 86:2310–19
- Perry AL, Low PJ, Ellis JR, Reynolds JD. 2005. Climate change and distribution shifts in marine fishes. *Science* 308:1912–15
- Petchey OL, McPhearson PT, Casey TM, Morin PJ. 1999. Environmental warming alters food-web structure and ecosystem function. *Nature* 402:69–72
- Peterson WT, Schwing FB. 2003. A new climate regime in northeast Pacific ecosystems. *Geophys. Res. Lett.* 30:1896
- Petit JR, Raynaud D, Basile I, Chappellaz J, Davisk M, et al. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature* 399:429–36
- Philippart CJM, van Aken HM, Beukema JJ, Bos OG, Cadee GC, Dekker R. 2003. Climate-related changes in recruitment of the bivalve *Macoma baltica*. *Limnol. Oceanogr.* 48:2171–85
- Polovina JJ, Dunne JP, Woodworth PA, Howell EA. 2011. Projected expansion of the subtropical biome and contraction of the temperate and equatorial upwelling biomes in the North Pacific under global warming. *ICES J. Mar. Sci.* 68:986–95
- Polyakov IV, Timokhov LA, Alexeev VA, Bacon S, Dmitrenko IA, et al. 2010. Arctic ocean warming contributes to reduced polar ice cap. *J. Phys. Oceanogr.* 40:2743–56
- Pörtner HO. 2010. Oxygen and capacity limitation of thermal tolerance: a matrix for integrating climate related stressors in marine ecosystems. *J. Exp. Biol.* 213:881–93
- Pörtner HO, Knust R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315:95–97
- Rabalais NN, Diaz RJ, Levin LA, Turner RE, Gilbert D, Zhang J. 2010. Dynamics and distribution of natural and human-caused hypoxia. *Biogeosciences* 7:585–619
- Raymond PA, Oh N-H, Turner RE, Broussard W. 2008. Anthropogenically enhanced fluxes of water and carbon from the Mississippi River. *Nature* 451:449–52
- Rayner NA, Brohan P, Parker DE, Folland CK, Kennedy JJ, et al. 2006. Improved analyses of changes and uncertainties in sea surface temperature measured in situ since the mid-nineteenth century: the HadSST2 dataset. *J. Clim.* 19:446–69
- Reid PC, Johns DG, Edwards M, Starr M, Poulin M, Snoeijs P. 2007. A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800 000 years. *Glob. Change Biol.* 13:1910–21
- Roemmich D, Gilson J, Davis R, Sutton P, Wijffels S, Riser S. 2007. Decadal spinup of the South Pacific Subtropical Gyre. *J. Phys. Oceanogr.* 37:162–73
- Roemmich D, McGowan J. 1995. Climatic warming and the decline of zooplankton in the California Current. *Science* 267:1324–26
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. *Annu. Rev. Ecol. Evol. Syst.* 31:481–531
- Rykaczewski RR, Checkley DM. 2008. Influence of ocean winds on the pelagic ecosystem in upwelling regions. *Proc. Natl. Acad. Sci. USA* 105:1965–70
- Rykaczewski RR, Dunne JP. 2010. Enhanced nutrient supply to the California Current Ecosystem with global warming and increased stratification in an earth system model. *Geophys. Res. Lett.* 37:L21606
- Salvat B, Allemand D. 2009. *Acidification and Coral Reefs*. New Caledonia, France: Coral Reef Initiat. Pac.
- Samhuri JF, Levin PS, Harvey CJ. 2009. Quantitative evaluation of marine ecosystem indicator performance using food web models. *Ecosystems* 12:1283–98
- Sanford E. 1999. Regulation of keystone predation by small changes in ocean temperature. *Science* 283:2095–97

- Sarmento H, Montoya J, Vazquez-Domingues E, Vaquer D, Gasol J. 2010. Warming effects on microbial food web processes: How far can we go when it comes to predictions? *Philos. Trans. R. Soc. B Biol. Sci.* 365:2137–49
- Schofield O, Ducklow HW, Martinson DG, Meredith MP, Moline MA, Fraser WR. 2010. How do polar marine ecosystems respond to rapid climate change? *Science* 328:1520–23
- Schwing FB, Mendelssohn R, Bograd SJ, Overland JE, Wang M, Ito S-I. 2010. Climate change, teleconnection patterns, and regional processes forcing marine populations in the Pacific. *J. Mar. Syst.* 79:245–57
- Smith KJ, Ruhl H, Bett B, Billett D, Lampitt R, Kaufmann R. 2009. Climate, carbon cycling, and deep-ocean ecosystems. *Proc. Natl. Acad. Sci. USA* 106:19211–18
- Snyder M, Sloan L, Diffenbaugh N, Bell J. 2003. Future climate change and upwelling in the California Current. *Geophys. Res. Lett.* 30:1823
- Solomon S, Qin D, Manning M, Chen Z, Marquis M, et al. 2007. *Climate Change 2007: The Physical Science Basis: Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge Univ. Press
- Somero G. 2012. The physiology of global change: linking patterns to mechanisms. *Annu. Rev. Mar. Sci.* 4:39–61
- Sorte CJB, Williams SL, Zerebecki RA. 2010. Ocean warming increases threat of invasive species in a marine fouling community. *Ecology* 91:2198–204
- Spencer P. 2008. Density-independent and density-dependent factors affecting temporal changes in spatial distributions of eastern Bering Sea flatfish. *Fish. Oceanogr.* 17:396–410
- Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW. 2002. Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions. *Proc. Natl. Acad. Sci. USA* 99:15497–500
- Stammerjohn SE, Martinson DG, Smith RC, Yuan X, Rind D. 2008. Trends in Antarctic annual sea ice retreat and advance and their relation to El Niño–Southern Oscillation and Southern Annular Mode variability. *J. Geophys. Res.* 113:C03S90
- Steinacher M, Joos F, Froelicher TL, Bopp L, Cadule P, et al. 2010. Projected 21st century decrease in marine productivity: a multi-model analysis. *Biogeosciences* 7:979–1005
- Steinacher M, Joos F, Froelicher TL, Plattner GK, Doney SC. 2009. Imminent ocean acidification in the Arctic projected with the NCAR global coupled carbon cycle–climate model. *Biogeosciences* 6:515–33
- Stramma L, Johnson GC, Sprintall J, Mohrholz V. 2008. Expanding oxygen–minimum zones in the tropical oceans. *Science* 320:655–58
- Stroeve J, Holland MM, Meier W, Scambos T, Serreze M. 2007. Arctic sea ice decline: faster than forecast. *Geophys. Res. Lett.* 34:L09501
- Sydeman W, Bradley R, Warzybok P, Abraham C, Jahncke J, et al. 2006. Planktivorous auklet *Ptychoramphus aleuticus* responses to ocean climate, 2005: unusual atmospheric blocking? *Geophys. Res. Lett.* 33:L22S09
- Sydeman W, Mills K, Santora J, Thompson S. 2009. Seabirds and climate in the California Current: a synthesis of change. In *CalCOFI Rep.* 50, pp. 82–104. La Jolla, CA: Calif. Coop. Ocean. Fish. Investig.
- Valentine JF, Heck KL, Blackmon D, Goecker ME, Christian J, et al. 2008. Exploited species impacts on trophic linkages along reef–seagrass interfaces in the Florida keys. *Ecol. Appl.* 18:1501–15
- Veit RR, Pyle P, McGowan JA. 1996. Ocean warming and long-term change in pelagic bird abundance within the California Current System. *Mar. Ecol. Prog. Ser.* 139:11–8
- Vermeij GJ, Roopnarine PD. 2008. Ecology: the coming Arctic invasion. *Science* 321:780–81
- Voigt W, Perner J, Davis AJ, Eggers T, Schumacher J, et al. 2003. Trophic levels are differentially sensitive to climate. *Ecology* 84:2444–53
- Walsh JE, Chapman WL. 2001. 20th-century sea-ice variations from observational data. *Ann. Glaciol.* 33:444–48
- Wassmann P, Duarte CM, Agusti S, Sejrk MK. 2011. Footprints of climate change in the Arctic marine ecosystem. *Glob. Change Biol.* 17:1235–49
- Waycott M, Duarte CM, Carruthers TJB, Orth RJ, Dennison WC, et al. 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. *Proc. Natl. Acad. Sci. USA* 106:12377–81
- Welch D, Ishida Y, Nagasawa K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* 55:937–48

- Whitney F, Freeland H, Robert M. 2007. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* 75:179–99
- Williams JW, Jackson ST. 2007. Novel climates, no-analog communities, and ecological surprises. *Front. Ecol. Environ.* 5:475–82
- Wilson S, Fischetti T. 2010. Coastline population trends in the United States: 1960 to 2008. *Curr. Popul. Rep.*, US Census Bur., Washington, DC
- Wootton JT, Pfister CA, Forester JD. 2008. Dynamic patterns and ecological impacts of declining ocean pH in a high-resolution multi-year dataset. *Proc. Natl. Acad. Sci. USA* 105:18848–53
- Wu R. 2002. Hypoxia: from molecular responses to ecosystem responses. *Mar. Pollut. Bull.* 45:35–45



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Errata

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