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REVIEW

The Impact of Climate Change on the World's Marine Ecosystems

Ove Hoegh-Guldberg^{1*} and John F. Bruno^{1,2}

Marine ecosystems are centrally important to the biology of the planet, yet a comprehensive understanding of how anthropogenic climate change is affecting them has been poorly developed. Recent studies indicate that rapidly rising greenhouse gas concentrations are driving ocean systems toward conditions not seen for millions of years, with an associated risk of fundamental and irreversible ecological transformation. The impacts of anthropogenic climate change so far include decreased ocean productivity, altered food web dynamics, reduced abundance of habitat-forming species, shifting species distributions, and a greater incidence of disease. Although there is considerable uncertainty about the spatial and temporal details, climate change is clearly and fundamentally altering ocean ecosystems. Further change will continue to create enormous challenges and costs for societies worldwide, particularly those in developing countries.

Earth, with its life-filled ocean, is unusual among planets (1). Covering 71% of Earth's surface, the ocean nurtured life on our planet and continues to play a dominating role in regulating its climate. Change has been the norm as Earth has swung through a variety of states in which life has prospered, dwindled, or experienced calamitous declines. In the latter

case, intrinsic events (e.g., volcanic activity) or extrinsic events (e.g., large meteorite strikes) have sometimes resulted in hostile conditions that have increased extinction rates and driven ecosystem collapse. There is now overwhelming evidence that human activities are driving rapid changes on a scale similar to these past events (2). Many of these changes are already occurring within the world's oceans (Figs. 1 and 2), with serious consequences likely over the coming decades.

Our understanding of how climate change is affecting marine ecosystems has lagged behind that of terrestrial ecosystems. This is partly due to the size and complexity of the ocean, but also

to the relative difficulty of taking measurements in marine environments. Long-term studies of climate change in the oceans are rare by comparison to those on land (3). Here, we review the impacts of anthropogenic climate change on marine ecosystems, revealing that the majority are changing rapidly with an increased risk of sudden nonlinear transformations. Given the overwhelming importance of the ocean to life on our planet, these changes underscore the urgency with which the international community must act to limit further growth of atmospheric greenhouse gases and thereby reduce the serious risks involved.

Rates of Change

Rising atmospheric greenhouse gas concentrations have increased global average temperatures by ~0.2°C per decade over the past 30 years (4), with most of this added energy being absorbed by the world's oceans. As a result, the heat content of the upper 700 m of the global ocean has increased by 14×10^{22} J since 1975 (5), with the average temperature of the upper layers of the ocean having increased by 0.6°C over the past 100 years (2) (Fig. 1, A and B). These changes are ongoing; global ocean surface temperatures in January 2010 were the second warmest on record for the month of January, and the period June to August 2009 reached 0.58°C above the average global temperature recorded for the 20th century, 16.4°C (6).

In addition to acting as the planet's heat sink, the oceans have absorbed approximately one-third of the carbon dioxide produced by human activities. The absorption of anthropogenic CO₂ has acidified the surface layers of the ocean, with a

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Changing Oceans

steady decrease of 0.02 pH units per decade over the past 30 years and an overall decrease since the pre-industrial period of 0.1 pH units (7) (Fig. 1C). Although these increases appear small in terms of pH, they are associated with a substantial decline in the concentration of carbonate ions (Fig. 1D) and represent a major departure from the geochemical conditions that have prevailed in the global ocean for hundreds of thousands if not millions of years (Fig. 1C) (8, 9).

Increases in the heat content of the ocean have driven other changes. Thermal expansion of the oceans as well as increased meltwater and discharged ice from terrestrial glaciers and ice sheets have increased ocean volume and hence

ocean are likely to decrease as a consequence of increasing stratification (14); this is supported by recent observations (15). There is growing paleological evidence that declining oxygen concentrations have played a major role in at least four or five mass extinction events, driving large amounts of hydrogen sulfide into the atmosphere as a result of deep-ocean anoxia (16). In some situations, intensified upwelling resulting from changes in wind strength can lead to a greater flux of organic material into deeper shelf waters, leading to an increase in respiration, hypoxia, and in some cases the eruption of toxic gases such as methane and hydrogen sulfide from deep anoxic sediments (17). Changes to wind and

ocean. Slowing of the thermohaline or Meridional Overturning Circulation (MOC) as a result of disproportionate heating in Earth's polar regions has major implications for regional climates. It is very likely that the MOC is changing as a result of higher temperatures in polar regions and a decrease in the salinity of surface waters due to ice sheet melt, and will continue to do so (21). Natural variability within the ocean climate system also occurs at various time scales (seasonal to decadal), producing climatic phenomena such as the El Niño–Southern Oscillation (ENSO), North Atlantic Oscillation (NAO), and Pacific Decadal Oscillation (PDO) (20). Although our comprehension of how this variability

will change over the coming decades remains uncertain, the steady increases in heat content of the ocean and atmosphere are likely to have profound influences on the strength, direction, and behavior of the world's major current systems (21). Changes in the behavior of ocean currents have the potential to strongly influence the distribution and abundance of marine ecosystems, as demonstrated by recent impacts of ENSO variability on kelp forests (22) and coral reefs (23) (Box 1 and table S2).

Some of the most striking impacts of global climate change have appeared in polar oceans, where temperatures and acidities are changing at more than twice the global average (4, 21) (Fig. 1). As a result of the changes, the amount of Arctic sea ice is steadily decreasing, its area being 16.5 million km² in March 1979 but reduced to 15.25 million km² by March 2009 (Fig. 2D). Summer sea ice (measured in September each year) is projected to disappear completely by 2037 (24). The warming of the polar oceans also has important ramifications for the stability of continental ice sheets, such as

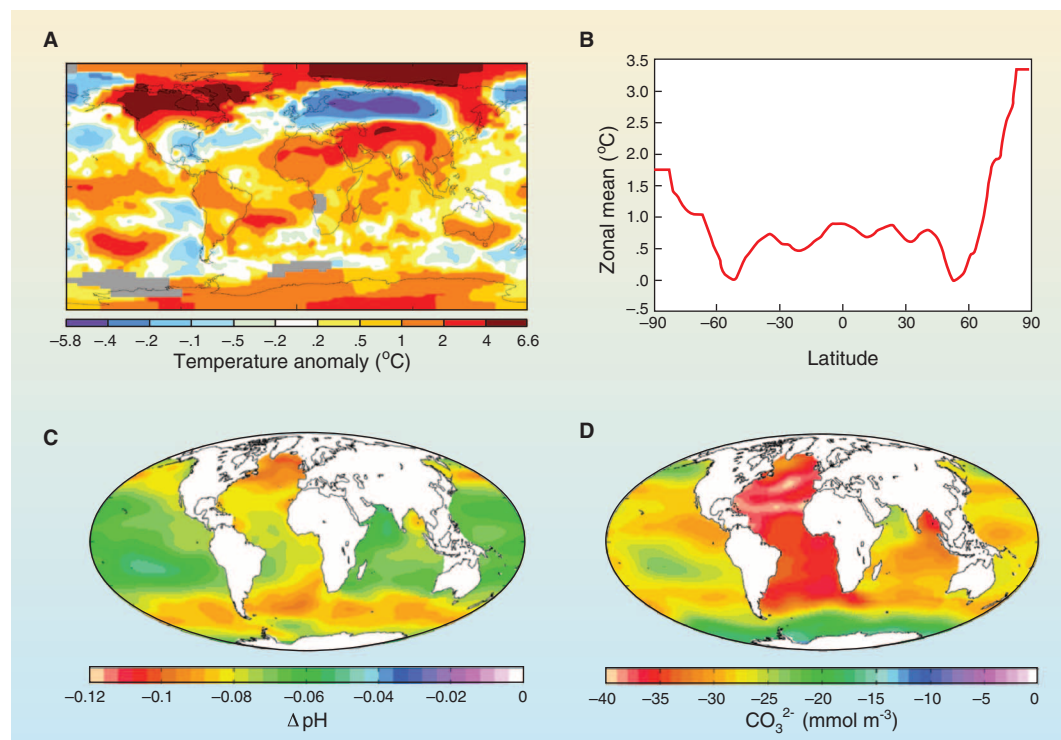


Fig. 1. Recent changes in ocean temperature, acidity, and carbonate ion concentration. **(A)** Surface temperature anomaly for January 2010 relative to the mean for 1951–1980. **(B)** The same data presented in **(A)** as a function of latitude. **(C)** Estimated change in annual mean sea surface pH between the pre-industrial period (1700s) and the present day (1990s). **(D)** Estimated change in annual mean sea surface carbonate ion concentration between the pre-industrial period (1700s) and the present day (1990s). [Credits: **(A)** and **(B)** NASA Goddard Institute for Space Studies; **(C)** and **(D)** Global Ocean Data Analysis Project (57)]

sea level (10) (Fig. 2, A and B). Warmer oceans also drive more intense storm systems (11) (Fig. 2C) and other changes to the hydrological cycle (12). The warming of the upper layers of the ocean also drives greater stratification of the water column, reducing mixing in some parts of the ocean and consequently affecting nutrient availability and primary production. These changes have increased the size of the nutrient-poor “ocean deserts” of the Pacific and Atlantic by 6.6 million km², or 15%, over the period 1998 to 2006 (13).

General circulation models also predict that oxygen concentrations in the upper layers of the

ocean currents driven by anthropogenic climate change are consequently likely to interact with overfishing and eutrophication, further increasing the incidence of hypoxic and anoxic events. These events are associated with an increased risk of mass mortalities among some deepwater benthic communities, as has recently been seen along the west coasts of North America (18) and southern Africa (19).

The uneven distribution of heating (Fig. 1, A and B) also strongly influences the behavior of ocean currents (20), which play critical roles in the dynamics, local climates, and biology of the

those in Greenland and in western Antarctica (WAIS), which are sensitive to small increases in global temperature (25). Changes in ice sheet volume have important implications for sea level rise, with an overall contribution of up to 12 m to mean sea levels if both Greenland and WAIS ice sheets were to melt completely (26). Satellite altimeter data (Fig. 2A) reveal that the average global sea level is changing at a rate of 3.3 ± 0.4 mm/year (over the period 1993–2006), which is consistent with tidal gauge data (26) and is tracking the highest projections of the fourth assessment report of the Intergovernmental Panel on

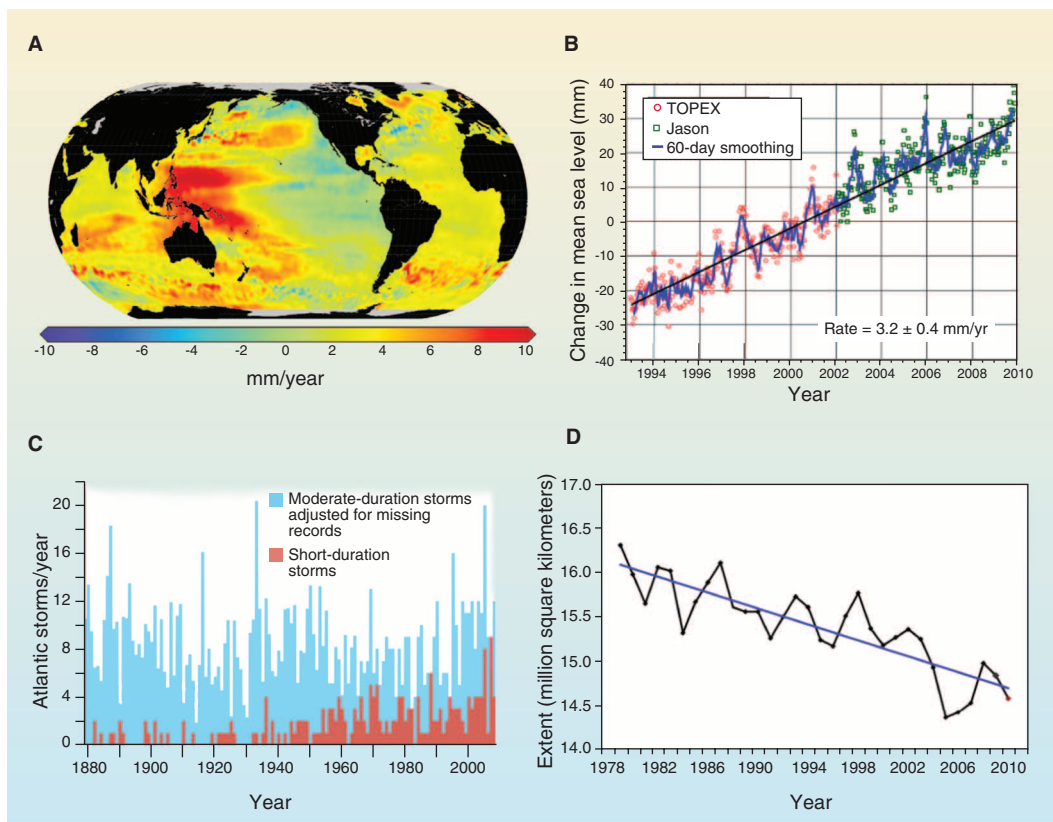


Fig. 2. (A and B) Average rate of global sea level rise (1993–2010) from TOPEX/Poseidon and Jason satellite altimetry data, shown as a map (A) and as a global mean sea level (B). (C) Trends in moderate-duration storms (lasting >2 days) and short-duration storms (<2 days) in the North Atlantic since 1880. (D) Average monthly Arctic sea ice extent from February 1979 to February 2010. [Credits: (A) NOAA/Laboratory for Satellite Altimetry; (B) Colorado Center for Astro-dynamics Research (<http://sealevel.colorado.edu>) (58); (C) adapted from (59) with permission; (D) National Snow and Ice Data Center, Boulder, CO]

Climate Change (IPCC). Current estimates of future sea level rise by 2100 range from 0.5 to 1.2 m (26).

Effects on Ecosystem Function

The scale and pace of change in the chemical and physical conditions within the world's oceans have set in motion a wide range of biological responses, with a corresponding rise in the number of studies reporting changes, from 319 published papers in 2000 to more than 1000 papers by 2009. However, papers reporting changes within marine ecosystems remain at only ~5% of the total publications on climate change (table S1 and fig. S1). Rather than revisiting the impacts of climate change on an ecosystem-by-ecosystem basis, here we focus on the impact of rapid anthropogenic climate change on general marine ecosystem processes and services.

Temperature has a fundamental effect on biological processes simply by its influence on molecular kinetic energy (i.e., Maxwell-Boltzmann energy distribution), which determines the rate of fundamental processes such as enzyme reactions, diffusion, and membrane transport (27). Moderate increases in temperature increase meta-

bolic rates, which ultimately determine life history traits, population growth, and ecosystem processes (28). In this regard, organisms tend to adapt to local environmental temperatures, with optimal physiological responses matching temperatures that are close to the environmental average. Organisms are able to acclimatize to a range of temperatures around these optimal values (27). Beyond this range, however, acclimatization fails, mortality risk increases, fitness is reduced, and populations decline or are driven to local extinction (27).

Variation in temperature can also have impacts on key biological processes. For example, the distribution and abundance of phytoplankton communities throughout the world, as well as their phenology and productivity, are changing in response to warming, acidifying, and stratifying oceans (7, 13). The annual primary production of the world's oceans has decreased by at least 6% since the early 1980s, with nearly 70% of this decline occurring at higher latitudes (29) and with large relative decreases occurring within Pacific and Indian ocean gyres (13). Climate variability strongly influences ocean productivity, such as seen in the anomalous conditions of 1998, which

that left a clear fingerprint on global ocean phytoplankton productivity and chlorophyll standing stocks (30). Overall, these changes in the primary production of the oceans have profound implications for the marine biosphere, carbon sinks, and biogeochemistry of Earth (31).

Animal metabolism is temperature-dependent (27), and consequently ecological processes such as predator-prey interactions are likely to be altered as warming occurs (32). Respiration is also more sensitive than photosynthesis to changes in temperature (33), resulting in the caloric demands of consumers being potentially more strongly influenced by increased temperature when compared to the temperature response of primary production (Fig. 3, A to F). Increasing temperatures in mesocosm experiments from 21° to 27°C have shown that the consumer control of primary production is substantially strengthened and reduces both total food web biomass and the ratio of plant to animal biomass (34). Large-scale field studies of North Atlantic plankton communities have documented similar temperature–food web relationships (Fig. 3, E and F) (35).

These findings have implications for the ability of pelagic systems to capture and store carbon dioxide, with the potential for these critical ocean processes to decline as temperature increases (33). Warming has also been found to decrease the size of individual phytoplankton (35), further altering the functioning and biogeochemistry of shallow pelagic ecosystems and, in particular, reducing their potential for carbon sequestration.

Changes to ocean conditions also have direct influences on the life history characteristics of marine organisms as varied as invertebrates and sea birds (Fig. 3, G to I, and table S2). The developmental rates of poikilotherms, where body temperatures vary with the environment, increase exponentially with temperature (28), with important consequences for a range of ecological attributes including larval dispersal, population connectivity, local adaptation, and speciation (28). Reduced developmental times may also result in phenological mismatches between developing larval organisms and the availability of suitable food (36), similar to phenological mismatches reported for terrestrial systems (37). When combined with changing patterns of primary productivity and metabolic rate, these fundamental

Changing Oceans

influences have the potential to substantially modify ocean food web dynamics, from coastal to open-ocean ecosystems.

Reduced Habitat Complexity

Among the most clear and profound influences of climate change on the world's oceans are its impacts on habitat-forming species such as corals, sea grass, mangroves, salt marsh grasses, and oysters. Collectively, these organisms form the habitat for thousands of other species. Although some resident species may not have absolute requirements for these habitats, many do, and they disappear if the habitat is removed. For example, mass coral bleaching and mortality, the result of increasing temperatures, is already reducing the richness and density of coral reef fishes and other organisms (23).

Coastal angiosperms such as mangroves, sea grass, and saltmarsh communities also face escalating threats from both local and global stresses

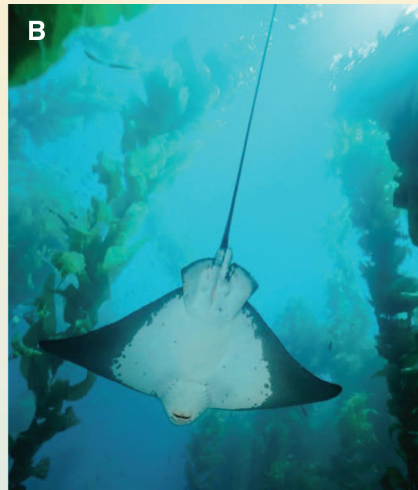
(table S2). Although mangrove deforestation (1 to 2% per year) represents a greater near-term threat, risks from sea level are increasing, with expected losses of 10 to 20% of mangroves by 2100 (38). Impacts on mangrove habitats vary with location; areas with steep coastal inclines or coastal human infrastructure that limit landward migration are most at risk. Mangroves in many areas can adapt to sea level rise by landward migration, but these shifts threaten other coastal habitats such as saltmarsh, which have other important biogeochemical and ecological roles.

Sea ice, like coral reefs and kelp forests, plays a critical role in structuring the biodiversity of polar oceans. The spring melt has a major role in determining the timing of phytoplankton blooms and consequently influences polar marine food web dynamics. In addition, the loss of sea ice will drive additional changes through reductions in food webs that are dependent on sea-ice algae (39), which may explain the recent $75 \pm 21\%$ per

decade decrease in krill (40). Sea ice also plays a critical role for a wide range of birds and mammals, functioning as a temporary or permanent platform from which crucial predatory, reproductive, or migratory activities are carried out (41). Many arctic mammals face serious declines, with polar bears projected to lose 68% (~700,000 out of 1 million km^2) of their summer habitat by 2100. Ice-dependent Antarctic organisms such as penguins and seals are declining and, in some cases, face an escalating risk of extinction under the current projections for Antarctic warming (42).

Ecologically Novel Assemblages, "Exotic" Species, and Disease

One of the inevitable outcomes of differing tolerances for changes in the environment among marine organisms is the development of novel assemblages of organisms in the near future. Such communities will have no past or contemporary counterparts (43) and consequently are



Box 1. Marine ecosystems are already responding to the rapid pace of change in the physical and chemical conditions that surround them (see table S2 for summary of recent literature). One of the most important impacts has been on the organisms and physical processes that create habitat for millions of other species. **(A)** Heron Island, southern Great Barrier Reef. Coral Reef ecosystems are declining because of anomalously warm sea temperatures, which are driving an increased frequency of coral bleaching and mortality. These impacts are combining with local impacts, as well as the slowing of reef accretion due to the impact of ocean acidification. Complex coral-dominated reef ecosystems like this one are likely to be rare by 2050. **(B)** Kelp forest (*Macrocystis pyrifera*, with California bat ray, *Myliobatis californica*) near San Clemente Island, California, USA. Warming ocean temperatures are driving a major contraction in the distribution of kelp forests worldwide. **(C)** Daintree River, northeastern Australia. Mangroves are critically important coastal habitat for numerous coastal species. The loss of 10 to 20% of mangroves is projected if sea levels rise by 1 m above today. **(D)** The loss of summer sea ice by 2040 in the Arctic will have a strong impact on a range of dependent organisms, both above and below the ice. [Credits: (A) and (C) O. Hoegh-Guldberg; (B) Philip Colla, www.Oceanlight.com; (D) Daniel J. Cox, www.NaturalExposures.com]

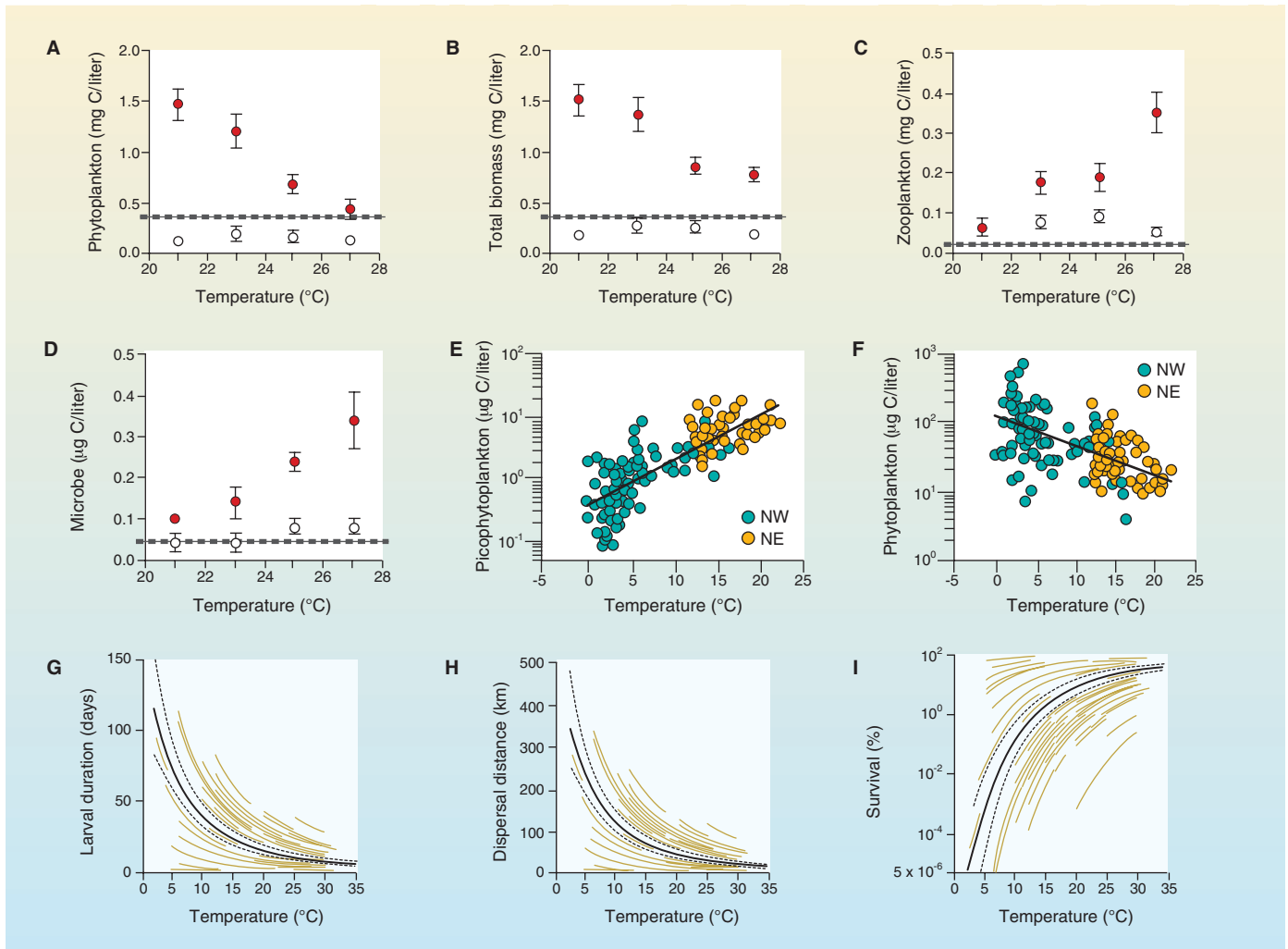


Fig. 3. Effects of climate change on biological processes in the ocean. **(A to D)** Experimental mesocosm results demonstrating the effect of temperature on different food web properties. Solid symbols indicate supplemental nutrient addition; open symbols indicate ambient (low) nutrient concentration; dashed horizontal lines denote initial conditions; error bars denote SE. **(E and F)** Relationship between temperature and abundance of small phytoplankton (E) and total phytoplankton biomass (F) from large-scale field sampling of the North Atlantic. Black lines are

regression lines. **(G)** Relationship between water temperature and planktonic larval duration from published experimental laboratory studies of 72 species (six phyla, including six fish and 66 invertebrates). **(H and I)** The predicted effects of temperature on larval dispersal distance (H) and larval survival (I). In (G) to (I), black lines represent the population-averaged responses; brown lines represent species-specific trajectories. [Credits: (A) to (D) from (34); (E) and (F) from (35); (G) to (I) from (28); all figures reprinted with permission of authors and journal]

likely to present serious challenges to marine resource managers and policy makers. The rising number of “exotic” marine species (table S2) provides some insight into the challenges ahead. Over the past several hundred years, the movement of ships and other transport vehicles around the globe has enabled the spread of a large number of marine species. Successful establishment, however, depends on conditions at the destination matching the tolerance range of invading organisms. Recent accelerated warming of high-latitude environments has increased the chances that species being transported from lower latitudes are able to establish themselves and spread (44). A rising number of species are expanding their ranges, often with large-scale impacts on ecosystems at the destination. For example, the southeastern Australian sea urchin

Centrostephanus rodgersii (Diadematae) has recently expanded its range into Tasmanian waters, where it has transformed macroalgal communities into taxonomically impoverished “urchin barrens” (22). Although barrens are a prominent feature of the southeastern Australian mainland normally occupied by *C. rodgersii*, they are relatively novel in Tasmanian waters (22).

Climate change has been implicated in recent variation in the prevalence and severity of disease outbreaks within marine ecosystems (45). These influences are likely to be a consequence of several factors, including the expansion of pathogen ranges in response to warming, changes to host susceptibility as a result of increasing environmental stress, and the expansion of potential vectors. There are numerous examples that illustrate this effect, including the spread of the oyster par-

asite *Perkinsus marinus* across a 500-km range of the northeastern United States during pronounced warming in 1990 and 1991 (46). Other examples are the strong association of thermal stress and coral cover in predicting disease within reef-building corals (47) and the temperature susceptibility of red abalone to a fatal rickettsial infection (48). A growing number of studies show a rise in marine diseases and has prompted some to conclude that “a warmer world would be a sicker world” (45). That said, there are large uncertainties about the interplay between ecological dynamics and potential vectors or disease-causing agents, making it difficult to predict whether the incidence of particular diseases will increase or decrease in a warmer and more acidic world. The potentially large costs of an increasing incidence and prevalence of dis-

ease, however, make a compelling reason for understanding and limiting these changes.

Local-Global Interactions, Synergies, and Thresholds

Although most of the ocean is undergoing impacts from multiple anthropogenic stressors (49), little is known about the potential for large-scale synergisms (or antagonisms) (50). Even additive effects have great potential to overwhelm key species and entire ecosystems. Coral reefs represent a prominent example where increasing mass coral bleaching and reduced calcification as a result of increasing atmospheric CO₂ are combining with the increasing inputs of sediments, nutrients, and pollution from disturbed coastlines to reduce the ability of these ecosystems to recover from natural and anthropogenic disturbances (47). Another example is that of open-ocean ecosystems, where a wide range of factors, including overfishing, increased ultraviolet light exposure, as well as warming and stratifying surface waters, are driving complex changes in community structure and food web dynamics.

Recent evidence suggests that there is now a growing risk that several thresholds will soon be exceeded (51). For example, increasing ocean temperatures and acidities associated with atmospheric CO₂ concentrations of 450 parts per million (ppm) represent a serious threat to ecosystems such as coral reefs. In the latter case, temperatures that exceed 2°C above pre-industrial temperatures are very likely to drive an unsustainable frequency of mass coral bleaching and mortality, whereas ocean acidification associated with atmospheric CO₂ above 450 ppm will push coral reefs into a negative carbonate balance (23). Similar thresholds (400 to 450 ppm or a +2°C increase in average global temperature above pre-industrial values) have been identified for key ocean components such as aragonite undersaturation of the Southern Ocean (52), loss of polar sea ice (24), and the melting of the Greenland (53) and Western Antarctic (54) ice sheets. Specific thresholds (or tipping points) are predicted to have large-scale consequences for coastal and oceanic ecosystems, as outlined above. These drivers add to the complex behavior of ecological systems, increasing the chance of triggering amplifying feedback loops and domino effects. Given the growing evidence that relatively small increases in the concentrations of atmospheric carbon dioxide will trigger a wide array of irreversible changes to critically important marine ecosystems, avoiding any further increases and aiming to reduce the atmospheric concentration of CO₂ below 350 ppm in the long term must be an international imperative (55, 56).

Managing Risk in a Changing World

The rapid ecological shifts that are occurring in the world's oceans present major challenges for managers and policy makers. Understanding

and reducing risk exposure will become increasingly important as conditions change and the likelihood of major ecological shifts increases. These changes will decrease the relevance of current models and practices for managing ecological resources and fisheries stocks, leading the management of many marine resources into "uncharted waters." Nonetheless, "no regret" management strategies that reduce the impact of local stresses while maintaining ecological resilience will play an increasingly important role as the climate changes. Actions that reduce the flow of nutrients and sediments from coastal catchments, for example, as well as those that reduce activities such as the deforestation of mangroves and the overfishing of key ecological species (e.g., herbivores), will become increasingly important as the impacts of climate change mount. Natural resource management must also remain flexible in order to absorb the sudden and nonlinear changes that are likely to characterize the behavior of most ecosystems into the future. Overall, however, reducing greenhouse gas emissions remains the priority, not only because it will reduce the huge costs of adaptation but also because it will reduce the growing risk of pushing our planet into an unknown and highly dangerous state.

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Supporting Online Material

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Fig. S1

Tables S1 and S2

References

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