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Impacts of Climate Change on Marine Organisms and Ecosystems

Review

Andrew S. Brierley[1,*] **and Michael J. Kingsford**[2]

Human activities are releasing gigatonnes of carbon to the Earth's atmosphere annually. Direct consequences of cumulative post-industrial emissions include increasing global temperature, perturbed regional weather patterns, rising sea levels, acidifying oceans, changed nutrient loads and altered ocean circulation. These and other physical consequences are affecting marine biological processes from genes to ecosystems, over scales from rock pools to ocean basins, impacting ecosystem services and threatening human food security. The rates of physical change are unprecedented in some cases. Biological change is likely to be commensurately quick, although the resistance and resilience of organisms and ecosystems is highly variable. Biological changes founded in physiological response manifest as species range-changes, invasions and extinctions, and ecosystem regime shifts. Given the essential roles that oceans play in planetary function and provision of human sustenance, the grand challenge is to intervene before more tipping points are passed and marine ecosystems follow less-buffered terrestrial systems further down a spiral of decline. Although ocean bioengineering may alleviate change, this is not without risk. The principal brake to climate change remains reduced CO_2 emissions that marine scientists and custodians of the marine environment can lobby for and contribute to. This review describes present-day climate change, setting it in context with historical change, considers consequences of climate change for marine biological processes now and in to the future, and discusses contributions that marine systems could play in mitigating the impacts of global climate change.

Introduction

When Earth formed about 4.5 billion years ago there were no oceans. Since then, as surface water has accumulated, the filling ocean basins have been the reaction chamber for the development of life on Earth and have played a fundamental role in the ongoing evolution of the planet's climate. No credible discussion of physical climatic processes on Earth can be conducted without consideration of the seas and oceans, and it is becoming increasingly apparent that — rather than just being passive occupants that are impacted by physical change — life forms in the ocean make active and climate-influencing contributions to planetary function. For example, marine organisms have important roles in the cycling of carbon (the 'biological pump'), nitrogen and other key elements, turbulent mixing and the production of cloud condensation nuclei [1–5]: there are numerous interactions between climate, physical oceanographic processes and marine biology that should not be ignored.

There is broad consensus that contemporary global climate change is reality, and that much of the ongoing change is a direct result of human activity [6,7]. In particular, burning fossil fuels, making cement and changing land use have driven atmospheric carbon dioxide concentrations ($CO_{2[atm]}$) up from a pre-industrial value of about 280 parts per million (ppm) to 385 ppm in 2008 [8] (Figure 1). Annual increases are now exceeding 2 ppm, an emission trend that exceeds the worst case scenario of the Intergovernmental Panel on Climate Change (IPCC) [9]. There is a direct link between global temperature and $CO_{2[atm]}$ [6]. The increased heating in the lower atmosphere/Earth's surface (radiative forcing) resulting from the 'greenhouse' effect caused by increasing atmospheric CO_2, methane and other gasses (at a value of about 3 W m^{-2} [10]) is unprecedented in at least the last 22,000 years [11] and has already had direct physical consequences for the marine environment and organisms living there. These include increases in mean global sea surface temperature, by 0.13°C per decade since 1979 [10], and ocean interior temperature, by >0.1°C since 1961 [10], increasing wind velocity and storm frequency, changes in ocean circulation, vertical structure and nutrient loads [10], as well as rising sea level — by more than 15 cm in the last century [12] (Figure 1) and presently by a mean of about 3.3 mm per year. Because the oceanic and atmospheric gas concentrations tend towards equilibrium, increasing $CO_{2[atm]}$ drives more CO_2 in to the ocean, where it dissolves forming carbonic acid (H_2CO_3) and thus increases ocean acidity: ocean pH has dropped by 0.1 (a 30% increase in hydrogen$^+$ ion concentration) in the last 200 years [13] (Figure 1).

Because rates of physical change are unprecedented in many instances, the impacts on marine organisms and ecosystems are likely also to be unprecedented. It has been suggested that a $CO_{2[atm]}$ of 450 ppm is a critical threshold beyond which catastrophic and irreversible change might occur [7] — this would bring a global mean temperature rise of 2°C above pre-industrial values. At present rates, this threshold will be passed by 2040, but climate-related systems are notoriously non-linear [14]. By 2040, some particularly sensitive marine ecosystems such as coral reefs and ice-covered polar seas could already have been lost, and other unexpected consequences may arise [15].

In this review, we first describe some key interactions between the physical marine and climate systems and marine life. Second, we consider briefly climate variability over geological time: it is important to understand the scale of historic change to appreciate the enormity of present and predicted change. Third, we touch upon physical-driven changes over the wide range of temporal, spatial and biological-organizational scales that pervade marine biology. A major challenge for marine scientists, fisheries and

[1]Pelagic Ecology Research Group, Gatty Marine Laboratory, School of Biology, University of St Andrews, Fife, KY16 8LB, Scotland, United Kingdom. [2]School of Marine and Tropical Biology, and ARC Center of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia.
*E-mail: asb4@st-and.ac.uk

ecosystem managers — and indeed for us in this review — is to reconcile impacts significant at the cellular to ecosystem scale, from rock pools to ocean basins, and over time scales relevant to organism lifecycles, establishment of annual fishery quotas, the tenure of a government administration, a career, a lifespan or a grandchild's lifespan and beyond. Assimilating these into a coherent whole, yet maintaining finer-scale local relevance [16], is a lot to ask but is consistent with the move towards the holistic ecosystem approach [17] to fisheries management. Fourth, to illustrate key principles, we describe climate-related changes in selected marine ecosystems. Finally, we contemplate the challenge of dealing with the confounding effects of multiple impacts (climate change, fishing pressure, pollution), and discuss how we might respond to and mitigate against the effects of climate change. As one referee of this review pointed out, it is telling that the 'physical' sections of the review describe what will happen, whereas the 'biological' sections largely speculate on what *might* happen: this is generally indicative of the present state of knowledge. The oceans presently provide about 16% of human animal-protein food [18] and contribute about 63% in financial terms to global ecosystem services [19]: understanding interactions and feedbacks between climate and marine systems is a vital step towards predicting and dealing with the consequences of change for the coupled biosphere-geosphere-humanosphere.

Oceans, Life and Planetary-Scale Processes

Life and water are inextricably linked. Life on Earth began in water. The 1.3 billion cubic kilometers of sea water now on Earth cover 71% of the planet's surface and make up about 300 times more habitable volume than the terrestrial habitats [20]. The oceans contribute about 46% to global annual primary production, house a biomass of at least 2.6 billion tonnes and contain 36 of the 38 known metazoan animal phyla [21–23]. Compared to land, seawater is a stable habitat [24]. Most marine locations experience narrower ranges of daily and annual temperature variation than their terrestrial equivalents. Oceans do, however, exhibit physical variability over a range of vertical, horizontal and temporal scales. This variability influences nutrient availability, physiology, production, larval dispersal, species migration, biodiversity and biogeography. There are four distinct biomes in the world ocean (Polar, Westerlies, Trades and Coastal Boundary Zone) [25] and numerous ecosystems ranging from highly productive mangrove forests and estuaries in the intertidal, to food-impoverished abyssal depths: all of these are vulnerable to changing climate [26].

But the oceans are not just a mosaic of habitats that support life [27]. They are huge reservoirs for nutrients and gasses, including CO_2, and ocean currents redistribute heat around the planet, impacting atmospheric circulation, regional weather patterns and rainfall distribution. Changes in ocean circulation bring fundamental physical changes, with major accompanying biological ramifications. When continental drift separated Antarctica from South America, for example, about 30 million years ago, the Drake Passage opened and the Antarctic Circumpolar Current developed, leading to the effective isolation of the Southern Ocean. The waters south of the Antarctic Circumpolar Current became decoupled from warmer waters to the north, and temperatures around Antarctica fell rapidly. The Polar Frontal Zone associated with the Antarctic Circumpolar Current formed a biogeographic barrier between thermal

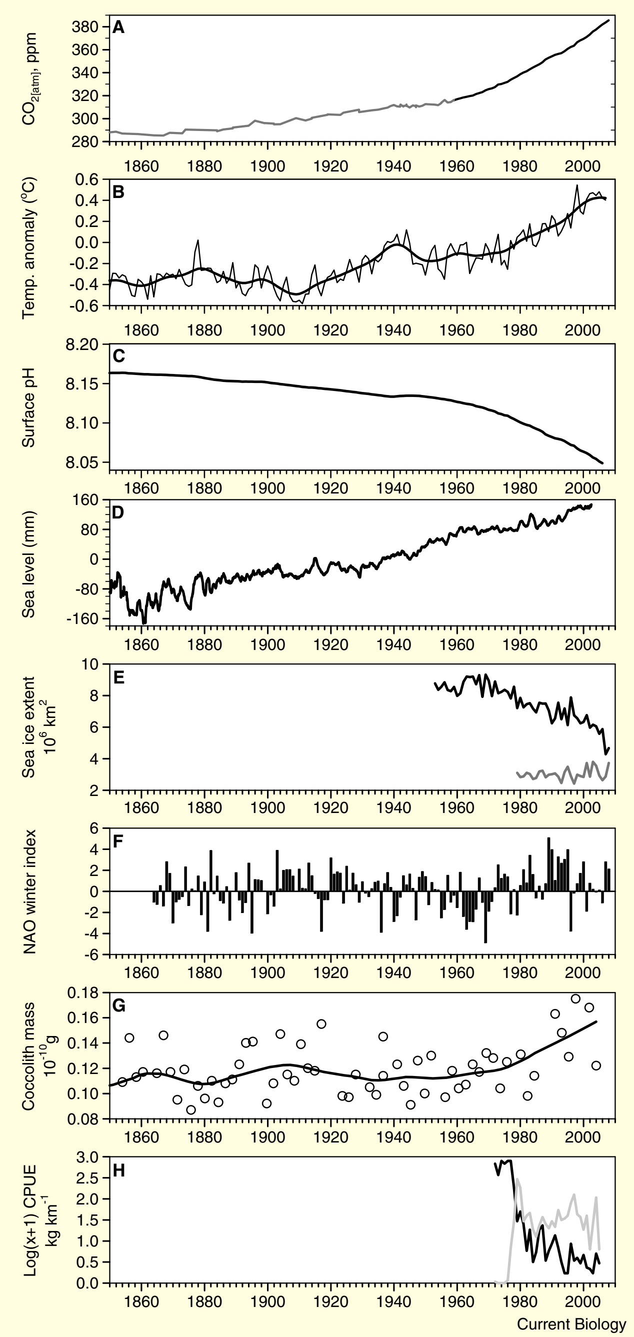

Figure 1. Indices of physical climate change relevant to marine systems, and two examples of biological change.

(A) $CO_{2[atm]}$ from Law Dome ice cores (grey line [8]) and Mauna Loa direct observations (black line [www.esrl.noaa.gov/gmd/ccgg/trends/]). (B) Annual and smoothed combined global land and marine surface temperature anomaly (http://www.cru.uea.ac.uk/cru/info/warming/). (C) Ocean surface pH calculated from $CO_{2[atm]}$. (D) Relative global sea level [148]. (E) Summer sea ice extent in the Arctic (black line; September, combined UK Hadley Center and US NSIDC chart and satellite data) and Antarctic (grey line; February, US NSIDC satellite data only). (F) Winter index of the North Atlantic Oscillation (www.cgd.ucar.edu/cas/jhurrell/indices.html). (G) Mean coccolithophore mass [62], and (H) catch per unit effort for Pacific cod (grey line) and pink shrimp (*Pandalus borealis*, black line) in Pavlof Bay, Alaska, showing the 1976/7 regime shift [93] (see also Figure 4).

Table 1. Timescales of change and approximate values of change pertinent to marine environments.

	Time scale						
	Geological	Oscillatory change		Secular change			
	(Cenozoic -)	Orbital/ Milankovitch	Recent Decadal	0 to industrial revolution, 1850	Post-industrial to present	Present to 2100	2100–4000
No. years	10^6 to 10^7	10^4 to 10^5	10s	c. 2k	c. 150	c. 100	c. 2k
Temp. at end, °C cf. 1850	'Icehouse' to 'greenhouse'	Glacial-interglacial; -8 to +5 [149]	+/- 2 (detrended) [40]	Stable between -1.2 to +0.4 [32]	+0.75 [6]	+2.5 to +5.5 [136]	+10 [150]
$CO_{2[atm]}$ ppm	150 to 3500 [36]	172 to 300 [149]	+/- 1 (detrended) [40]	Stable between ~274 and 282 [149]	385 (in 2008) [42]	450 to 1000 [136]	1700 to >2000 [150]
pH	7.3 to 8.3 [36]	Varies by 0.16 [13]	Stable	Stable around 8.2 (+/- 0.3) [13]	-0.1 [13]	-0.3 to -0.5 [13]	-0.77 [57]
Sea ice coverage, %	0 to mid latitude [31]	High latitude to mid latitude	Regionally variable [118,151]	Stable, c. 7% Earth's surface [152, 153]	Antarctic stable to -25% Arctic -20% [112, 152]	-40% cf. 1999 [111]	-90% [150]
Sea level, m		-130 to 0 [154]	Stable	Stable	+0.2 [12]	+0.5 to +1.4 [12]	+100
AMO circulation	Direction reversals	-40% to +40% [37]	Variable [155]	Variable	Variable 18.7 +/- 5.6 Sv [29]	-50% [155]	3 Sv to collapse [100,150]
Suboxic volume	Highly variable	Variable	Stable	Stable	Expanding [56]	+50% [66]	+300% [150]
Species events	Range changes & extinctions	Range changes	Regime shifts	Stable	Range changes	Range changes & extinctions [156]	Mass extinctions

regimes, and many Southern Ocean species evolved subsequently in isolation [28]. Seawater that is cooled around Antarctica is a major driver of today's global thermohaline circulation. Contemporary climate change has the potential to perturb ocean circulation on a time-scale far shorter than that of continental drift: a reduction in the North Atlantic Current [29] could have major implications for northern Europe and beyond during this century. The cooling that this might bring — reduced North Atlantic Current flow would deliver less heat northwards — runs counter to the 'global warming' paradigm, and emphasizes the importance of regional considerations verses global generalization.

Timescales of Temperature Change

Earth's climate has changed [30], and will likely continue to change [31], over multiple time scales (Table 1). Temperature change is apparent in the existing instrument record, and numerous proxies enable past temperature variations to be reconstructed [32]. Temperature is hugely influential on physiological processes [33] and fluid physics: biochemical reaction rates can double with a 10°C rise, and the density of water has a peculiar non-linear dependency on temperature that results in cold seawater sinking but ice floating. Although global mean sea-surface temperatures are rising at only about half the rate as that for land, 0.13°C per decade compared to 0.27°C per decade since 1979 [10], increasing temperature is the most pervasive of present-day impacts on marine systems [34].

The geological record is punctuated by numerous abrupt changes in temperature. These discontinuities — for example, the Paleocene-Eocene Thermal Maximum 56 million years ago when global temperatures rose by 6°C in 20,000 years — define boundaries between epochs of more consistency lasting tens of millions of years. During the Paleocene-Eocene Thermal Maximum 1500 to 2000 gigatonnes of carbon were released to the atmosphere in just 1,000 years; however, that rate is less than that at which carbon is being released now through anthropogenic activity [13]. Temperatures fell after the Paleocene-Eocene Thermal Maximum perhaps because of prolific growth of marine *Azolla* ferns [35], which reduced atmospheric carbon dioxide concentrations dramatically from 3500 ppm to 650 ppm [36], switching Earth from 'greenhouse' to 'icehouse'. This switch illustrates well the power of marine biological influences on global climate.

Variations in solar activity and Earth's orbit bring cyclical changes in temperature over tens to hundreds of thousands of years (Milankovitch cycles [37]). Feedback mechanisms involving greenhouse gasses, ocean circulation and ice extent, which in turn influences albedo — the fraction of incoming solar radiation reflected back to space — interact with Milankovitch cyclicity to provoke the Quaternary cycles of glaciation (c. 10°C change with c. 100,000 year periodicity) that have persisted for the past 2.5 million years [31]. The last glaciation ended 12,000 years ago and Earth is presently in a warm period. Climatic changes have also occurred at higher frequencies (stadials/interstadials), but these changes are not necessarily global. In the north Atlantic region, for example, Dansgaard-Oeschger and Bond events [38] occur roughly every 1500 years, and include the beginning of the Younger Dryas and the Little Ice Age. Fluctuating ocean circulation and associated greenhouse gas variations are implicated in these climate oscillations [39].

More frequent still are multi-decadal climatic oscillations and decadal-scale cycles including the El Niño Southern

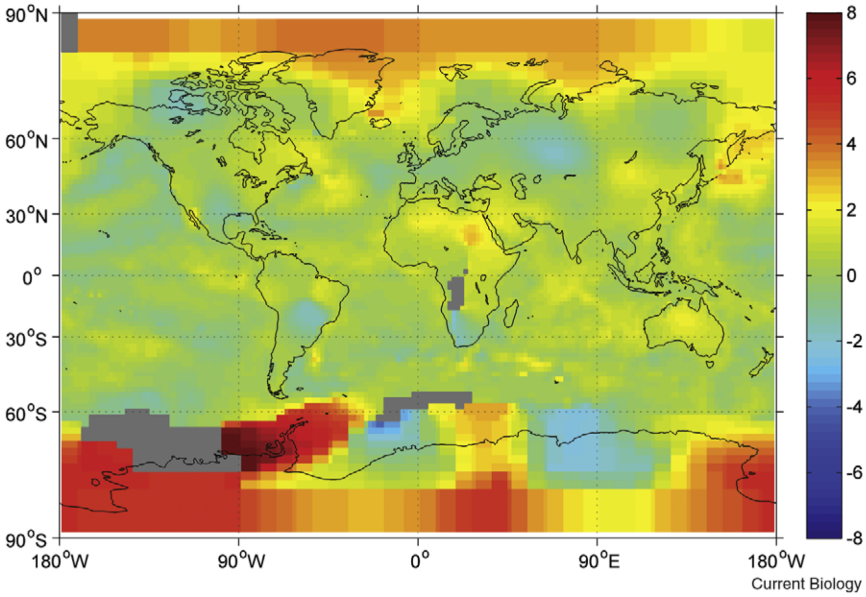

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Figure 2. Spatial variability in surface warming.

In this example map showing surface warming, the temperature anomaly (°C) is colour-coded for September 2008 compared to the 1951 to 1980 mean. Grey pixels indicate missing data. Data are from http://data.giss.nasa.gov/gistemp/maps/.

Oscillation and the North Atlantic Oscillation. These cycles are driven by large-scale atmospheric changes, but have oceanic impacts because winds drive horizontal ocean currents and upwelling which, in turn, impact on heat distribution. Because the modern era of direct scientific observation extends over multiple ten-year cycles, there is a growing body of work on the consequences of these cycles for marine biological processes around the world. For example, fluctuations in abundances of pelagic fish in the Pacific that are characterized by change in dominance between sardine and anchovy coincide with El Niño periodicity [40], and in the North Sea the abundance of some jellyfish is strongly correlated with an index of the North Atlantic Oscillation [41].

Given these multiple timescales of change, it can be difficult to distinguish a signal of secular change from the noise of background variability. However, recent change is so great that it stands out like the blade of a hockey stick [32]. $CO_{2[atm]}$ is now probably higher and rising faster than at any time in the past 20 million years [32,42] and global average temperatures are 0.76°C higher than in the second half of the 1800s [6] (Table 1). This unprecedented change has led to suggestions that the Earth is entering a new era, the Anthropocene. Boundaries between eras are often marked by mass extinctions: if present-day change remains unchecked, the impact on marine systems could be as great as at the boundaries between previous geological epochs, and extinctions are likely here [43]. Temperature influences physiological rates and physical boundaries of tolerance [44]. Although mobile marine species can shift distribution in response to changes [45,46], for sedentary organisms and many endemic species with narrow ranges of thermal tolerance (stenotherms), such as corals, the rate of local change may be more rapid than biological/evolutionary response times [47]. Unless annual carbon emissions fall below 5 gigatonnes [6], the 21st century will likely be characterized by fundamental and deleterious changes to marine organisms and ecosystems [43].

Spatial Scales of Temperature Change

Although global mean temperature is rising, and other physical factors are changing (Figure 1), the scale of impact is not and will not be distributed evenly geographically [7] (Figure 2). Temperatures throughout the Arctic Ocean have risen since the 1950s, by more than 4°C in some places, whereas around Antarctica some locations have warmed while others have cooled (sea surface temperatures in the Weddell Sea have decreased by 2°C but have warmed by 2°C at South Georgia [48]). The East Australia Current has increased its southward penetration by about 360 km over the last 60 years, and average temperatures in affected regions have increased by more than 2°C in that time [49]. These regional variations will be of major importance to local inhabitants.

The ocean depths are perhaps the most thermally-stable of Earth's habitats, and organisms there are likely to be among the last to be impacted directly by direct warming, but temperatures are rising and, as a result of thermal inertia, temperatures will continue to rise for many decades even if carbon emissions were to cease immediately [50]. In the Drake Passage, warming of 0.6°C has been observed to 700 m over the past 30 years, whereas surface waters have cooled by 2.1°C over the same time [51]. There is historic evidence for decoupling between surface and deep-water temperature changes, with deep-water extinctions occurring at the end of the Paleocene whilst processes in the near-surface plankton remained apparently unaffected [52]. Intertidal habitats are potentially subject to the greatest impact [53] and, in locations where peaks of increased daytime temperatures coincide with exposure at low spring tide, die-offs are to be expected despite the high stress-tolerance of some intertidal organisms. Reducing biodiversity in rock pools, as elsewhere, may impact ecosystem function [54], but colonization dynamics at the scale of rock pools, and variable resistance, may increase community stability for some species [55]: there will be winners and losers in the face of change, and those are often difficult to predict.

Other Key Physical Changes

Widespread changes in sea level, ocean pH and the extent of oxygen-deficient dead-zones (Table 2) are underway [12,13,56]. In many instances these and other factors will impact together [43], creating negative synergistic effects to which organisms and ecosystems may have little resistance.

Acidification

There is a direct relationship between $CO_{2[atm]}$ and ocean pH [13,57] (Figure 1): as $CO_{2[atm]}$ increases, pH drops. This poses a great threat to many marine organisms and ecosystems. Over the past 200 years, the oceans have absorbed approximately half of the anthropogenically-generated

Table 2. Key direct climate-related threats to major marine ecosystems up to the year 2025, and some consequences. Based on [26] and references therein.

Ecosystem	Threat	Consequence
Coastal		
Salt marshes/Mangroves	Sea level rise	Landward progression or habitat loss; altered productivity
	Rising temperature and $CO_{2[atm]}$	Changing growth rates; photosynthetic change; increasing C3 cf. C4 species
	Increasing storm frequency	Physical damage; choking or flooding channels; salinity changes
Estuaries	Sea level rise	Landward progression/basin modification
	Increasing storm frequency	Fluctuating freshwater inflow brings fluctuating nutrient and sediment input
	Rising temperature	Increased desiccation stress at low tide
	Mitigation: flooded for barrages	Ecosystem loss
Rocky substrates		
Rocky intertidal	Sea level rise	Altered zonation; compression on vertical engineered defenses
	Rising temperature	Increased thermal stress/desiccation at low tide; latitudinal species abundance/distribution changes
	Increasing storm frequency	Increasing effective exposure; shifts from grazers to filter feeders; shifts in direction of trophic control
Kelp forests	Rising temperature	Physiological impacts on growth and photosynthesis; latitudinal shifts in distribution
	Increasing storm frequency	Upper and near-shore limits affected negatively
Coral reefs	Rising temperature	Bleaching; distribution range contraction; overgrowth by algae
	Increasing acidity	Reducing calcification and skeletal structure compromise
	Rising sea level	Drowning reefs; habitat loss; human abandonment of flooding atolls may reduce fishing pressure
	Increasing storm frequency	Physical damage and runoff/silting increase
	Altered circulation and connectivity	Larval transport disrupted and nutrient availability altered
Soft substrates		
Sandy shores	Increasing storm frequency	Changing beach structure, loss of habitat, and perturbed interspecies competition
	Rising temperature	Changing productivity; species range changes
	Rising sea level	Loss of habitat; changing sand transport
Seagrass meadows	Rising temperature	Metabolic stress; range changes
	Increasing storm frequency	Increased nutrient loading; decreased water clarity; increasing runoff/sedimentation
	Rising $CO_{2[atm]}$	Increased growth rates; increased competitive advantage cf. algae; increased productivity
	Sea level rise	Loss of habitat
Shelf sea benthos	Rising temperature	Species distributional shifts
	Decreasing $[O_2]$	Expanding anoxic dead zones
Vast systems		
Pelagic	Rising temperature	Changing species distributions; timing of peak production; regime shifts; reduced fish production
	Rising $CO_{2[atm]}$	Increased primary production
	Increasing acidity	Altered planktic calcification
	Altered circulation/upwelling/stratification	Nutrient limitation and increasing bottom-up control on food chains
	Increasing storm frequency	Increased nutrient availability and production
	Decreasing $[O_2]$	Expanding anoxic dead zones
Polar and ice-edge	Rising temperature	Sea ice (habitat) loss; increasing primary production and associated trophic responses; physiological impacts leading to species range changes/extinctions;
	Ice reduction	Habitat loss; increasing Diel vertical migration (DVM)/CO_2 drawdown
	Increasing acidity	Detrimental carbonate conditions for plankton, and foodweb consequences
Deep sea	Rising temperature and changing nutrient availability	Changes in carbon flux from surface impact deep sea community composition
	Increasing acidity	Reducing carbonate availability
	Decreasing $[O_2]$	Expanding anoxic dead zones

$CO_{2[atm]}$ [13] and at present a further approximately 1 million tonnes of CO_2 diffuse in to the world ocean per hour. The rate of decreasing pH, 0.1 units in the last 200 years and an expected drop of 0.3 to 0.5 units by 2100, is more than 100 times as rapid as at any time over the past hundreds of millennia [13].

Rates of oceanic CO_2 absorption vary regionally as a function of wind strength and temperature. Colder waters can accommodate more dissolved CO_2 than warm waters and are, therefore, more prone to acidification [58]. The Southern Ocean might, however, already be saturated with CO_2 [59], which is worrying because it alone has absorbed about 7% of anthropogenic $CO_{2[atm]}$, and reduced capacity for future absorption means more CO_2 will remain in the atmosphere, provoking more warming. Ocean warming may partly counteract the acidification process, but the scale of impact will be insufficient to provide long-term reprieve from increased $CO_{2[atm]}$ [47].

One of the main impacts of ocean acidification on marine life arises because of interactions between acidity and carbonate availability. A taxonomically diverse array of marine organisms, including tiny coccolithophores (a type of phytoplankton), pelagic and benthic mollusks, fist-sized starfish and urchins, as well as massive corals, require calcium carbonate for their skeletons, and others have key carbonate rich structures (e.g. fish otoliths). All of these are likely to suffer as increasing acidity reduces carbonate availability, and impacts at the species level may cascade through to widespread community change [60].

At present, shallow waters are generally saturated with carbonate ions, but dissolution increases with depth [61]. The lysocline — the depth at which dissolution begins — will shallow as oceans become more acidic, reducing the depth range that offers suitable habitat for calcifying organisms. Even for shallow waters, a $CO_{2[atm]}$ greater than c. 490 ppm will compromise the capabilities of corals to make strong skeletons and loss of coral reefs will ensue [47]. The direction of change in calcification that acidification will bring is, however, questionable [47]: studies of the coccolithophore *Emiliania huxleyi* suggest both thickening and wasting of calcareous shells [62,63], and excretion of precipitated carbonates by teleost fish is predicted to rise with ambient CO_2 [3]. There is, thus, an urgent requirement for improved understanding of the effects of acidification from the cellular to ecosystem level.

Reducing Dissolved Oxygen Concentration

Low oxygen concentrations render compartments of the world ocean inhospitable to multicellular life [64]. Oxygen solubility in seawater is a function of temperature, and O_2 availability in the world ocean has been declining since the 1950s [65] as the ocean has warmed. Over a range from 0 to 15°C, dissolved oxygen concentration in seawater is related approximately linearly to temperature, and will decline by about 6% per one degree rise. Ongoing warming together with rising $CO_{2[atm]}$ will see an expansion of low oxygen zones, perhaps by more than 50% of their present volume by the end of the century [56,66]. These expansions will affect some of the world's most productive regions in terms of fisheries, so there could be economic as well as ecological consequences. Fish schooling behaviour is known to respond to varying oxycline depth [67], and krill swarms may be oxygen-limited [68]. Changes in group behaviour forced by reducing oxygen availability may impact predators that target aggregated pelagic prey [69]. Furthermore, coastal eutrophication resulting from increased riverine run-off of fertilizers and increases in sea level will bring further accumulations of particulate organic matter and increased microbial activity that consumes dissolved oxygen [56]. Mobile organisms are able to avoid low oxygen concentrations, but sedentary organisms have little choice but to tolerate low oxygen concentrations or die. Those that are able to tolerate hypoxic conditions might, paradoxically, benefit from reduced predation if predators are themselves excluded [70].

Sea Level Rise

Global temperature influences water and ice volumes and, hence, sea level [12]. Sea level influences the inundation and establishment of coastal habitats and ecosystems [27,71]. The rate of sea level rise during the 20th century was proportional to the warming above pre-industrial temperatures [12], and extrapolation suggests further rises of between 0.5 and 1.4 m above 1990 levels by 2100. Sea level changes impact habitat space, drive speciation, influence biodiversity [27] and alter local nutrient flux. Whilst rising sea levels could mean the end of some island nations, they could bring some respite to coral reefs as abandonment by humans of some atolls may lead to reduced fishing pressure. Elsewhere rising waters may force organisms towards steep, artificial sea defenses, with implications for intertidal sediment-dwelling organisms, zoned rocky-shore ecosystems and nursery habitats [72,73].

Impacts of Climate Change — from Genes to Ecosystems

Appraisal of the vulnerability of marine organisms and ecosystems to climate change needs to consider potential impacts across all levels of biological organization. These include gene expression, cellular and whole-organism physiology, skeletal structure, behaviour of individuals, population dynamics, community- and ecosystem-structure, and trophic interactions. In line with ecological niche theory, the ranges of tolerance of species simultaneously reflect physiology, environmental factors, interspecific competition and dispersal. Sensitivities to climate change may vary between levels of organization, and responses to the moving baselines of global stressors may be independent between levels or critically linked. Uneven sensitivities to climate change of competing species may disrupt competitive interactions, and complex indirect responses may become manifest at community levels [74].

Responses to climate change will depend on the rate and duration of the change, as well as the tolerance of the level of organization [33]. Rare, extreme events will play a different role in evolutionary dynamics than slow, secular change. 'Pulse' events have limited duration [75], and could include sporadic warming brought in to habitually cool regions by transient penetrating filaments of warm water [49]. Such pulses might be precursors to 'press' events that are more persistent and long-lasting, such as widespread warming. 'Resistant' systems are able to avoid displacement in the face of change: from a physiological point of view, they may be able to tolerate a broad range of temperatures and salinities, or from an ecological point of view resistant species may be habitat generalists. 'Resilient' systems, by contrast, are able to revert to the pre-disturbance state once a stress has passed [76]. Biodiversity influences ecosystem function [77], and ecosystems with a higher degree of functional redundancy — where pivotal roles are fulfilled by more than one species — are expected to be more resilient. However, in the case of ongoing secular climate change, resilience would have to be very great indeed given the temperature rise to which Earth is already committed (at least 2.4°C) and the likely persistence of that rise even following the (unlikely) immediate cessation of CO_2 emissions [50].

Temperature is the most pervasive climate-related influence on biological function [78]. Gene expression may vary within a species throughout its distributional range as a function of temperature [79], but the variation may not follow simple latitudinal clines; thus, predicting responses to climate change may be difficult. Genetic selection under environmental forcing can lead to rapid shifts in allele frequencies in populations of short-lived organisms [80]. For instance, muscle development can vary with temperature [81], and temperature change may thus have adverse implications for mobile organisms because muscle development impacts movement capability and reduced speed may lead to changing predator–prey interactions [69]. Sub-lethal temperature changes can impair physical function, and mortality can result from quite minor warming because organisms become unable to perform basic but imperative tasks [82]. Likewise, growth is temperature-dependent and, in the initial phases of warming, changing temperature may lead to changing community size structure and biomass [83]. Warming will not, however, necessarily increase growth rates [84]. The timing of reproduction, reproductive output and the condition of juveniles and larvae are also subject to variability [85]. Juveniles of marine organisms can be particularly susceptible to changes in temperature, salinity and pH, and larvae may succumb to elevated temperatures that their adult stages are able to survive [86]. The hatching times of eggs may affect the survival chances of larvae if larval appearance does not coincide with food availability. Changes in the timings of plankton blooms [87], including temperature-driven phenological changes [88], may lead to breaks in food chains [89,90], and wholesale departures of prey species in the face of warming may impact remaining predators, including commercially important fish species [91]. Some of these species will themselves shift ranges as a consequence of warming, but this will not necessarily lead to community decline: fish species richness in the North Sea increased over the last two decades of the 20th century as the region warmed [92]. That change was in line with expectations that species richness decreases generally with increasing latitude and the fact that local warming is in some respects effectively equivalent to latitude reduction.

A consequence of altering demographic characteristics, mortality rates and even allele frequencies — all of which may be consequences of climate change — is that the growth, size, resistance and resilience of whole populations may be altered. If population sizes change, interactions among species may also be perturbed, and ultimately ‘regime shifts’ may occur, with ecosystems undergoing rapid and perhaps irreversible transition from one phase to another [93]. For instance, bleaching and storm-induced structural damage to coral reefs and coral death can lead to proliferation of macroalgae. Algal domination may persist as an ‘alternative stable state’ if rates of algal grazing are low: in the Caribbean, death from disease of the sea urchin *Diadema antillarum*, an important grazer, had major consequences for entire coral reef ecosystems because the interaction between grazing pressure and coral cover was driven beyond a critical threshold at which ecosystem resilience was lost [94]. In the pelagic ecosystem off the Pacific coast of the USA wholesale changes across multiple trophic levels, that were evident in indices of 31 physical and 69 biological parameters, occurred during regime shifts in 1977 and 1989 [95].

Impacts of Climate Change on Ecosystems: Selected Case Studies

It is beyond the scope of this review to examine the impacts of climate change on all marine ecosystems. Others have accomplished that task with regard to change expected by 2025 [26], and their conclusions are summarized in Table 2. Instead, by focusing on ecosystems that are most familiar to us, we hope to illustrate some key concerns.

Open Ocean Environments

The oceans generate about half of Earth’s annual global primary production in terms of fixed carbon (48.5 Petagrams (Pg) of 104.9 Pg C [21]), but since 1999 global ocean primary production has fallen by 0.19 Pg C per year [96]. The majority of this reduction has occurred in the permanently-stratified low latitude oceans (roughly 45°N to 45°S) because warming and strengthened stratification have caused nutrient limitation. Phytoplankton and seaweeds require nutrients, including phosphate, silicate and nitrate, as well as trace elements such as iron [97], and reduced mixing brings fewer nutrients to the illuminated near-surface zone. In polar regions, increased wind strength — leading to increased mixing and nutrient replenishment — and reduced ice extent could lead to increased open ocean primary production [98], but these increases (e.g. 0.03 Pg C per year since 2003 in the Arctic [99]) will probably not counteract the mid-latitude reductions.

Mixed-layer depth and nutrient availability are also influenced by large-scale ocean circulation. Modeling studies [100] suggest that surface freshening after warming-induced melt of the Greenland ice cap would reduce Atlantic meridional overturning circulation by more than a factor of 5 (from 16×10^6 m^3 s^{-1} to 3×10^6 m^3 s^{-1} over the 500 year model run), similar to the change associated with Dansgaard-Oeschger oscillations [101]. Because of the key role Atlantic meridional overturning circulation has in global thermohaline circulation, this reduction would lead, on average, to a shallowing of the mixed layer globally, imposing a nutrient restriction that would cause a 20% reduction in carbon export production. In the North Atlantic, phytoplankton biomass might collapse by half [100] and, because most zooplankton populations there are subject to bottom-up control (limited by availability of their phytoplankton food) [90], secondary production would be much reduced. Fisheries production would also be expected to decline [102].

Increasing $CO_{2[atm]}$ and temperature may increase phytoplankton growth rates, but, at the same time, may lead to physiological responses that render cells more susceptible to UV damage [103]. Ongoing change might be expected to impact primary production, particularly in coastal seas where river runoff supplements nutrient availability [104] and where sea level rise might also impact nutrient loading.

In addition to fueling food chains, phytoplankton growth draws CO_2 down from the atmosphere, driving the biological pump that transports carbon to the ocean interior [1]. This flux will change as temperatures increase because nutrient reduction leads to smaller sized cells that sink more slowly [105]. Reduced photosynthetic carbon fixation may reduce $CO_{2[atm]}$ drawdown [106], with further climate consequences. Plankton from surface waters fall to the deep sea as an important source of nutrition for the deep benthos: temperature induced change of epipelagic plankton assemblages could, therefore, affect the deep sea [107].

Changing open ocean temperatures have brought major biogeographic shifts in species ranges. In the North Atlantic, plankton communities have changed distribution by more than 10 degrees of latitude since the 1960s [45]. Warming in the Arctic has enabled trans-polar invasion of the Atlantic by Pacific plankton species [108]. Baleen whales, which are amongst the largest, widest ranging and longest-lived marine organisms, might be expected to weather change, but some are impacted on short time scales because their short-lived prey — zooplankton at low trophic levels — responds rapidly to climate change [109,110].

Polar Seas and Sea Ice Systems

Sea ice covers up to 7% of the Earth’s surface and is one of the planet’s largest and most dynamic biomes [111]. The

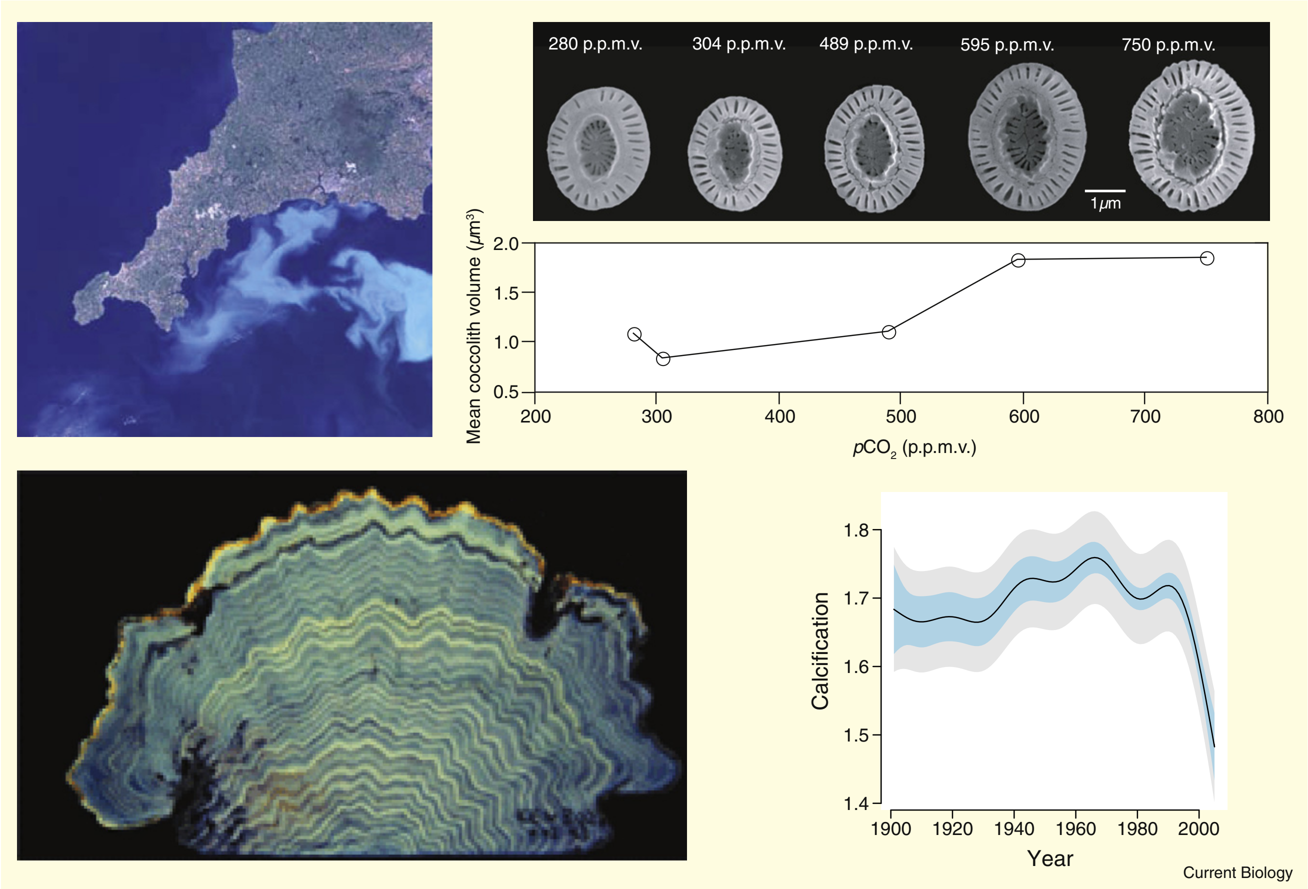

Figure 3. Contrasting climate-related variability in calcification in plankton and corals.

Top left: true colour satellite image of a bloom of the coccolithophore *Emiliania huxleyi* south of Plymouth, UK on the 30 July 1999 showing the spatial extent, and hence ecological importance, of the bloom (image from Remote Sensing Data Analysis Service (RSDAS) www.npm.ac.uk/rsdas/ of the UK Plymouth Marine Laboratory http://www.sanger.ac.uk/Info/Press/2005/050811.shtml). Top right: graph of coccolith volume, and scanning electron microscope images of typical coccoliths, from cultures at simulated $CO_{2[atm]}$ from 280 to 750 ppm. Reproduced with permission from [62]. Laboratory experiments are consistent with historic observations (Figure 1G) of mass increasing with increasing $CO_{2[atm]}$. Bottom left: annual growth bands in a slice of coral (photograph courtesy of Eric Matson, Australian Institute of Marine Science). Bottom right: variation in calcification (g cm^{-2} y^{-1}) in massive *Porites* corals over time. Light blue bands indicate 95% confidence intervals for comparison between years, and grey bands indicate 95% confidence intervals for the predicted value for any given year. Calcification declines by 14.2% from 1990–2005 [122] in a direction of change opposite to coccolithophores. Reproduced with permission from [122].

geographic extent, temporal duration and mean thickness of Arctic sea ice has decreased significantly since the 1960s, and summer extent is decreasing at 7.4% per decade [10]. 2007 saw the least Arctic summer sea ice on record. The total extent of Antarctic sea ice seems at present to be stable [10], although there is regional variability between years, but the possibility of a major circum-Antarctic decline in the mid-1960s remains [112]. For both hemispheres, sea ice is predicted to decline throughout the 21st century, and the Arctic Ocean may be ice-free in summer by 2030. The loss of Arctic sea ice may be one of the first climate tipping points [113]. Ice loss leads to a vicious circle of more rapid warming — and ever more rapid ice loss — because ice loss reduces albedo: dark ocean surfaces absorb more heat than reflective ice-covered seas, and warmer seas grow less ice.

Sea ice is a habitat in its own right, housing rich and diverse microbial communities within and beneath that form the base of ice-related water-column ecosystems, and is a platform for breeding and hunting vertebrates (e.g. penguins, seals and polar bears). Ice loss thus equates to habitat loss but, as elsewhere, there will be winners and losers. Polar bears are suffering because earlier ice melt reduces the time they can hunt at sea [114] whereas Adelie penguins can benefit from reduced extent of some ice types because of associated reductions in journey times from breeding sites to open-water feeding grounds [115].

Sea ice impacts the underlying water column, reducing light penetration and influencing stratification. Reducing the extent of ice may lead to increased primary production [99], particularly in the Arctic because ice loss is most pronounced in nutrient-rich coastal regions. In turn, this could lead to increased zooplankton and fisheries production [116]. Because of its impact on light attenuation, sea ice modifies the vertical migration behaviour of zooplankton beneath [117]. Initially, ice loss in the Arctic might lead to increased draw down of $CO_{2[atm]}$ because reduction in shading will provoke greater vertical migrations by zooplankton, and zooplankton feeding near the surface and defecating at depth will export increased primary production to deeper waters.

Impacts of ice loss are not simple to predict because the timing of ice melt may influence community development

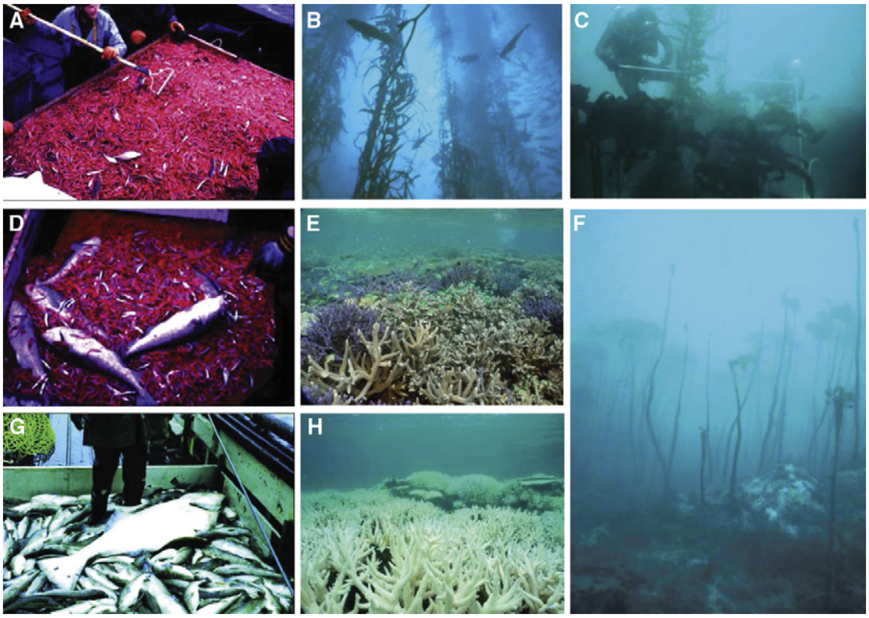

Figure 4. Climate-related changes in tropical and temperate marine ecosystems.

(A,D,G) Changes from shrimp-dominated (top) to cod-dominated (bottom) catches in small-meshed bottom trawls in Pavlof Bay, Alaska, through the 1976/7 regime shift. Reproduced with permission from [17] (also see Figure 1H). (B) Forest of giant kelp (*Macrocystis pyrifera*) with a well-developed canopy and associated fish in 1978 before the 1983 El Niño; from ~12 m at Stillwater Cove, Carmel Bay, California. The kelp provides structure and foraging opportunities for fish and invertebrates such as urchins. (C) Forest understory of *Pterygophora californica* before El Niño. (F) In June 1983, about 3 months after the big El Niño storms ended; all *Macrocystis pyrifera* was removed and *P. californica* had all its blades removed and they have just begun to regenerate. Northern California is affected by storms during El Niño while southern California is more affected by low nutrients that kill kelps (photographs courtesy of M. Foster, California State University). (E) Pristine *Acropora* reef. (H) Bleached corals in the shallows, Middle Island Keppels (copyright Great Barrier Reef Marine Park Authority) showing the dramatic impact of elevated temperature: sustained high temperatures can result in coral death and a phase shift to algae dominated reefs.

[118]. In the Bering Sea, late sea ice retreat leads to an early phytoplankton bloom in cold water at the ice edge, whereas following early ice retreat the bloom occurs later in warmer open water. Zooplankton production in the Bering Sea is influenced predominantly by water temperature, so when ice retreats early and the bloom occurs in warmer water zooplankton abundance is elevated and recruitment of planktivorous fish benefits. In the southern hemisphere, the lifecycle of Antarctic krill (*Euphausia superba*) is coupled tightly to sea ice, and reduced ice brings reduced krill recruitment [119]. There is evidence for a steep decline in krill abundance from the 1970s [120], and this could have had adverse effects for the suite of higher predators that depend upon krill for food [121].

Coral Reefs

Coral reefs are among the most diverse and economically important ecosystems on Earth. They are threatened by a variety of climate-related changes, including rising sea temperatures and levels as well as acidification. Corals require calcium carbonate (in the form of aragonite) to build skeletons, but acidification is driving availability down. Calcification of Great Barrier Reef corals has declined by 14.2% since 1990 [122] (Figure 3). At the present rate of $CO_{2[atm]}$ increase, carbonate accretion is expected to be further compromised such that corals will become increasingly rare beyond 2050 [47]. Corals and, in particular, their symbiotic zooxanthellae algae are highly sensitive to increases in temperature. Above 31°C, zooxanthellae are ejected and coral bleaching ensues [47] (Figure 4). The intensity and scale of bleaching has increased since the 1960s, and major bleaching events in 1998 and 2002 affected entire reef systems [123]. Waters of the Great Barrier Reef are expected to warm by between 1 and 3°C over the next 100 years, so the risk of high temperature press events that could be fatal to corals is increasing.

The ability of scleractinian corals to adapt to change is unclear, but modern genotypes and phenotypes probably do not have the capacity to adapt quickly enough to global climate change to guarantee local persistence [47,124] (but see [125]). Weakened skeletons, which are prone to storm damage, mean that coral reef architecture will be compromised and that regime shift to algal domination may become more likely with an associated loss of key functional groups [47,126]. As coral reefs are habitats for many animal species, loss of coral will cause changes in diversity and abundance of such species [127] and may lead to local extinctions of reef specialists [85,128]. In addition to bringing adverse ecosystem effects, losses of fish and invertebrates have major implications for fisheries, tourism and other human uses of reefs.

Combined Effects of Climate Change and Other Impacts

Most marine species and ecosystems are presently under numerous simultaneous threats [34]. In addition to climate change, these include fishing, elevated UV exposure, pollution, alien introductions and disease [43]. The resistance of individual species to single threats may be reduced in the face of multiple stressors, and perturbed ecosystems suffer diversity loss that can compromise ecosystem function and resistance to further change. For instance, drops in pH may interfere with ion exchange, depressing metabolism and leading to a narrower window of thermal tolerance [129]. Polar bears are not only struggling in the face of ice loss, but are also weakened by accumulation of polychlorinated biphenyls [114]; the Black Sea suffered a regime shift after prolonged heavy fishing pressure, a jellyfish invasion and eutrophication [130]; many coral reefs are suffering from rising temperatures, acidification, disease, fishing and tourist impact as well as silting and excess nutrients from river runoff [131]. Analysis of several north Atlantic fish stocks suggests that declining recruitment is climatically-driven

[132], and that fishing on its own cannot explain observed downward trends. The claim that "climate findings let fishermen off the hook" does not, however, tell the whole story [133], and excessive fishing will certainly not assist ecosystems stressed by climate change. There is growing acceptance of the requirement for an ecosystem approach to marine fisheries and environment management: this approach should take account of the whole gamut of anthropogenic and natural threats to ecosystems, including climate change [134].

Responding to Climate Change

Given the geographic variation in change in temperature, acidity and other factors, and the varying sensitivity of marine organisms and ecosystems, it is unlikely that any single strategy will alleviate impacts of climate change everywhere [16]. A series of regionally-tailored response plans under local governance [135] are required. However, on a global scale, an immediate reduction in CO_2 emissions is essential to minimize future human-induced climate change. Emissions to date have already committed the planet to a warming of 2.4°C above pre-industrial levels, i.e. beyond the 2°C threshold for 'dangerous anthropogenic influence' [50]. If emissions continue, it is not outrageous to expect $CO_{2[atm]}$ to reach 1000 ppm, with an associated warming of 5.5°C, by the end of this century, which would bring about the extinction of many species [136]. In the face of such terrifying change, even large scale interventions such as establishment of very large networks of Marine Protected Areas [137] — zones within which damaging activities such as fishing are prohibited — are unlikely to be effective.

A direct way to reduce warming is to reduce $CO_{2[atm]}$. The *Azolla* event illustrates how oceanic primary production can contribute significantly to this goal, and biomanipulation could perhaps invoke a similar response for the present age. Fertilization of the ocean with micronutrients, including iron, stimulates phytoplankton growth. On a large scale, this could draw substantial quantities of $CO_{2[atm]}$ to the ocean interior [138], and in theory the biological pump could sequester this carbon in the deep sea. There are, however, considerable uncertainties about this approach [139], and international restrictions are being put in place to limit ocean fertilization experiments [140]. Whilst direct injection of CO_2 to the deep ocean could offer storage for very large quantities, acidification and other pollution by impurities bring considerable threats to marine ecosystems: small scale experimental disposals were cancelled in 2002 because of environmental concerns [141].

Offshore wind farms and tidal barrages are two of several options for generating electricity without emitting CO_2 [142], yet ironically both have the potential to affect marine ecosystems adversely, bringing additional indirect climate-related degradation [143,144]. 'Spill over' of species and biomass from Marine Protected Areas can bring benefits to adjacent unprotected areas [145]: the extent of benefit is thus greater than the extent of constraint. Wind farms and barrages need perhaps to be viewed in this context: sacrificing some carefully-chosen areas may bring benefits in terms of emission reduction that are greater than the localized costs of habitat loss or environmental degradation. Such tradeoffs are likely to be emotive, particularly for local populations living alongside power-generation developments. But tough choices are going to have to be made, and made soon, if we are to avoid crossing the critical $CO_{2[atm]}$ 450 ppm threshold. Although the ocean has so far buffered climate change, absorbing about 50% of anthropogenically generated CO_2, if climate change continues unchecked the ocean could also be the source of additional woes. Methane hydrates in the ocean could become unstable with rising temperature, and large scale liberation of gaseous methane could send the planet on a runaway warming trajectory [146].

Improving models are increasing our ability to predict physical changes in the ocean [147] that will impact marine and terrestrial biology, but we need to progress beyond prediction and monitoring of decline and act to halt degradation. Despite options for intervention, it may already be too late to avoid major irreversible changes to many marine ecosystems. As history has shown us, these changes in the ocean could have major consequences for the planet as a whole.

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