

The Impacts of Ocean Acidification on Marine Ecosystems and Reliant Human Communities

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Keywords

carbon dioxide, ocean acidification, organism responses, marine ecosystems, natural resources, social-ecological systems

Abstract

Rising atmospheric carbon dioxide (CO₂) levels, from fossil fuel combustion and deforestation, along with agriculture and land-use practices are causing wholesale increases in seawater CO₂ and inorganic carbon levels; reductions in pH; and alterations in acid-base chemistry of estuarine, coastal, and surface open-ocean waters. On the basis of laboratory experiments and field studies of naturally elevated CO₂ marine environments, widespread biological impacts of human-driven ocean acidification have been posited, ranging from changes in organism physiology and population dynamics to altered communities and ecosystems. Acidification, in conjunction with other climate change–related environmental stresses, particularly under future climate change and further elevated atmospheric CO₂ levels, potentially puts at risk many of the valuable ecosystem services that the ocean provides to society, such as fisheries, aquaculture, and shoreline protection. This

review emphasizes both current scientific understanding and knowledge gaps, highlighting directions for future research and recognizing the information needs of policymakers and stakeholders.

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Carbon dioxide

(CO₂): a gas that is removed by photosynthesis and released by respiration and fossil fuel combustion

pH: a measure of the acidity of water where lower pH reflects more acidic conditions; reported on a log-scale such that a 1-unit drop in pH is equivalent to a factor of 10 increase in acidity

1. INTRODUCTION

Present-day (2020) atmospheric carbon dioxide (CO₂) levels of more than 410 ppm are nearly 50% higher than preindustrial concentrations, and the current elevated levels and rapid growth rates are unprecedented in the past 55 million years of the geological record (1). The source for this excess CO₂ is clearly established as human driven, reflecting a mix of anthropogenic fossil fuel, industrial, and land-use/land-change emissions (2). The concept that the ocean acts as a major sink for anthropogenic CO₂ has been present in the scientific literature since at least the late 1950s, and multiple lines of evidence, including direct observations of increasing dissolved inorganic carbon (DIC) inventories (3), support the finding that the ocean takes up roughly a quarter of total anthropogenic CO₂ emissions. It is also well understood that the additional CO₂ in the ocean results in a wholesale shift in seawater acid-base chemistry toward more acidic, lower pH conditions and lower saturation states for carbonate minerals used in many marine organism shells and skeletons (4). Extensive observational systems are now in place or being built for monitoring seawater CO₂ chemistry and acidification for both the global open ocean and some coastal systems (5, 6).

The potential for substantial biological responses to the excess CO₂ and ocean acidification has only started to be well appreciated in the past two decades, stimulated in part by a seminal

Royal Society meeting and report (7). Reported acidification effects span from changes in cellular metabolism, organism physiology, and sensory perception to population and community, biogeochemical, and ecosystem-level dynamics (8). Knowledge about organismal responses leverages a wealth of data from laboratory manipulative experiments. More limited information is available on community and ecosystem responses from mesocosm and field studies, natural high-CO₂ environments, and modeling exercises.

The implications for human society—for fishery and resource management, marine conservation, and impacts on communities reliant on the ocean—are just now coming into focus. Atmospheric CO₂ and the concurrent ocean acidification are projected to continue to rise through mid-century, if not longer, without deliberate and decisive international action on climate mitigation and emissions reductions. Thus, improved understanding is urgently needed on ocean acidification impacts from scientific, management, policy, and socioeconomic perspectives to develop adequate adaptation strategies.

This review focuses on the rapidly expanding body of knowledge on ocean acidification in the scientific literature over the past decade since a previous *Annual Reviews* article on the topic (9). It builds from numerous recent synthesis efforts in journal special issues (10) and national and international scientific assessments (11–14). There are also numerous excellent reviews on various topical aspects of ocean acidification, a selection including articles on physiological responses (15), effects on invertebrate and fish larvae (16), animal behavior (17), nitrogen cycle (18), coral reefs (19), ecological theory (20), and policy solutions (21).

The remainder of this review is partitioned into sections on acidification impacts on seawater chemistry from rising atmospheric CO₂ and coastal land use and pollution (Section 2); organismal responses to acidification (Section 3); community and ecosystem impacts on key food-web interactions such as competition and predator-prey interactions (Section 4); risks to human communities that rely on the natural resources provided by the ocean via fisheries, aquaculture, and cultural and social connections (Section 5); and a brief summary (Section 6).

2. SEAWATER CHEMISTRY

Aqueous carbon dioxide [CO₂(aq)] and the inorganic carbon system play a central role in seawater acid-base chemistry, and the addition of CO₂ from natural and anthropogenic sources causes acidification and shifts in the speciation of dissolved ions (4, 22). At seawater pH levels (~8), CO₂ added to seawater reacts with water to form bicarbonate (HCO₃⁻) and hydrogen ions (H⁺):



The release of H⁺ acts to increase acidity and lower seawater pH, defined as

$$\text{pH} = -\log_{10}[\text{H}^+], \quad 2.$$

and lower the concentration of carbonate ions (CO₃²⁻), via



Acidification impacts will depend on organism responses to multiple, simultaneous chemical changes—increasing CO₂(aq), HCO₃⁻, and H⁺ and decreasing CO₃²⁻ (23).

Many types of marine organisms that form shells and skeletons from calcium carbonate (CaCO₃) minerals are sensitive to acidification. The solubility of carbonate minerals,



Ocean acidification: changes in seawater chemistry including increased acidity, lower pH, and reduced carbonate ion levels caused by input of excess carbon dioxide, typically by human activities over an extended period of decadal and longer timescales

Carbonate ion (CO₃²⁻): an inorganic carbon molecule formed when carbon dioxide dissolves in seawater and a key building block for carbonate minerals used in organism biomineralization

can be expressed as a carbonate saturation state,

$$\Omega = \frac{[\text{CO}_3^{2-}][\text{Ca}^{2+}]}{K_{sp}}, \quad 5.$$

Calcite: a less soluble mineral form of calcium carbonate used by marine organisms in shell and skeleton formation via biomineralization

Aragonite: a more soluble mineral form of calcium carbonate used in marine biomineralization

where K_{sp} is the apparent equilibrium solubility product at a given temperature, salinity, and pressure for each particular CaCO_3 mineral form. A value of $\Omega < 1$ indicates undersaturation with respect to thermodynamic equilibrium, and under those seawater conditions, unprotected carbonate materials will dissolve. The multiple forms of carbonate minerals vary in K_{sp} and so have different solubilities, with calcite being less soluble than aragonite and amorphous calcium carbonate. As CO_2 increases, the CO_3^{2-} concentration declines because of consumption with H^+ (Equation 3) causing a decline in Ω (Equation 5).

The inorganic carbon acid-base reactions and carbonate mineral solubility are controlled by well-characterized, equilibrium thermodynamic relationships as a function of temperature, salinity, and pressure. The system is characterized fully from the physical state and any two of four chemical properties: pCO_2 , pH, DIC, and alkalinity. DIC is the total concentration of CO_2 gas and the inorganic carbon acid-base products resulting from hydration (Equations 1 and 3). Alkalinity is the acid buffering capacity of seawater that reflects the speciation of the carbonate and borate acid-base systems as well as minor trace species. The scientific community has developed best practices for the measurement of seawater carbonate chemistry in field and lab samples (24) as well as standardized approaches for mimicking acidification chemical changes in biological manipulation studies (25).

On a global scale, acidification of the surface ocean is occurring because of the rapid rise in atmospheric CO_2 . Driven primarily by fossil fuel combustion, contemporary human CO_2 emissions to the atmosphere of approximately 10 billion metric tons of carbon per year result in an increase in atmospheric CO_2 of roughly 2 ppm/year or 0.5% per year (2). Present-day CO_2 levels (~ 410 ppm) have not been experienced by life on Earth for several million years, and the human-induced CO_2 growth rate is nearly two orders of magnitude faster than what occurred during the large glacial-interglacial transitions (11).

Ocean surface waters exchange CO_2 with the overlying atmosphere via physical gas transfer, and the surface seawater partial pressure, pCO_2 , tends to track the growth of atmospheric CO_2 for much of the global ocean, as illustrated by long-term time series records at numerous open-ocean locations (26) and analysis of global surface ocean CO_2 observational networks (27). As a result, surface pH and CO_3^{2-} are declining (**Figure 1**), and surface ocean pH is estimated to have dropped on average globally by approximately 0.1 units from the preindustrial era to present, which is an $\sim 30\%$ increase in hydrogen ion concentration.

More acidified ocean conditions, found regionally due to natural processes and local human impacts, are exacerbated by the global acidification signal driven by CO_2 emissions. Coastal upwelling systems typically have elevated CO_2 and low O_2 levels because of the marine biological pump, the production of organic matter in the surface ocean via photosynthesis and subsequent transport of organic material to the subsurface ocean via particle sinking, zooplankton migration and related physical and biological processes and subsequent respiration of sinking organic matter at depth (28, 29). Similar high CO_2 –low O_2 conditions are found in many coastal and estuarine systems associated with excess nutrient and organic carbon inputs from land sources (29, 30). Coastal acidification can also occur because of low-alkalinity freshwater fluxes from rivers, groundwater, and ice melt (31–33). Coastal systems tend to exhibit large amplitude variations of seawater chemistry on smaller time and space scales (34).

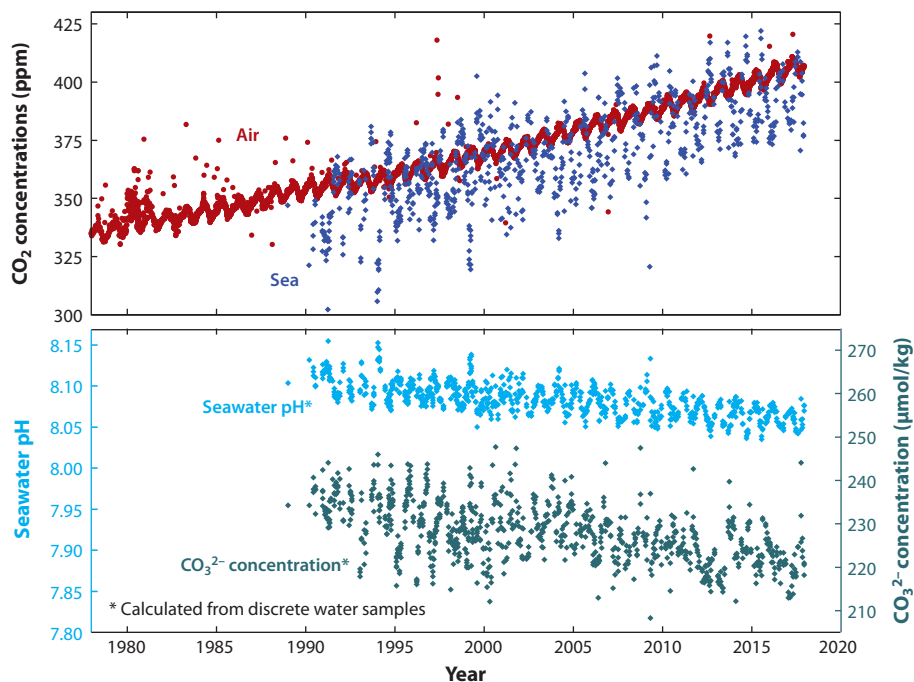


Figure 1

Trends in surface (<50 m) ocean carbonate chemistry calculated from observations obtained at the Hawai'i Ocean Time-series (HOT) Program in the North Pacific during 1988–2015. The upper panel shows the linked increase in carbon dioxide (CO_2) in the atmosphere (*red points*) and surface ocean (*blue points*), both presented in terms of CO_2 concentration in air (ppm). For seawater, the equivalent air concentration is computed assuming solubility equilibrium with the aqueous carbon dioxide concentration [$\text{CO}_2(\text{aq})$]. Ocean CO_2 concentration is often also reported in terms of a carbon dioxide partial pressure $p\text{CO}_2$ (μatm). The bottom panel shows a decline in seawater pH (*light blue points*, primary y-axis) and carbonate ion (CO_3^{2-}) concentration (*green points*, secondary y-axis). Ocean chemistry data were obtained from the Hawai'i Ocean Time-series Data Organization & Graphical System (HOT-DOGS; <http://hahana.soest.hawaii.edu/hot/hot-dogs/index.html>). Figure adapted from Jewett & Romanou (13), originally created by Dwight Gledhill, NOAA.

3. ORGANISMAL RESPONSES

The literature on organismal sensitivity to high- CO_2 conditions has expanded rapidly (35), and, in marine biology, ocean acidification has moved in a decade from being a frontier science to a mature subdiscipline exploring species sensitivity in fine detail. Research on how high- CO_2 conditions influence fishes exemplifies this trend. Although some fish appear able to compensate for disturbance to acid-base balance under high- CO_2 conditions, they express unexpected sensitivity to current and near future CO_2 levels in the growth of otoliths—calcium carbonate structures in fish ears that aid in balance—mitochondrial function, metabolic rate, larval yolk consumption, activity, neurosensory processes, and behavior, including settlement into specific habitat at the end of the early life stages (16, 36). Altered fish physiology in high- CO_2 conditions may disrupt systems related to the neurotransmitter GABA_A (37). GABA_A is involved in a wide variety of sensory and behavioral pathways in the nervous systems of animals; the consequences of GABA_A signaling disruption in fishes due to ocean acidification are still being determined. Substantial variation in sensitivity exists within and between fish species (38, 39), and acidification effects on sensory

perception should be considered in the context of a suite of other human alterations of the sensory landscape for marine animals (40).

As more detailed information on species sensitivity to ocean acidification conditions becomes available, generalizations about patterns in sensitivity are difficult to make. For example, copepod sensitivity currently defies simple characterization, as it is higher in earlier life stages than in the adult life stage, variable between species and within different populations of the same species, and dependent on co-stressors and processes of acclimatization and adaptation (41). Variation also exists within and between phytoplankton groups: Diazotrophs (nitrogen fixers), diatoms, and other large phytoplankton including dinoflagellates have higher growth rates in high-CO₂ conditions, whereas coccolithophores (calcium carbonate-plated phytoplankton), *Synechococcus*, and *Prochlorococcus* (both globally abundant picoplankton) do not, although there is wide variation in response within groups (42). While species that calcify are generally more sensitive to high-CO₂ conditions than those that do not calcify, this generalization is not uniformly applicable, and the form of CaCO₃ that species produce (i.e., calcite, aragonite) is not strongly linked to species sensitivity (43). In general, crustacea and echinoderms produce high-magnesium calcite structures and molluscs produce aragonite structures, although marine species produce structures with a variety of mineralogies, including amorphous CaCO₃, low-magnesium calcite, or a mix of multiple CaCO₃ forms (43).

Recent reviews emphasize how species sensitivity to various CO₂ conditions is influenced by exposure to other aspects of climate change. Negative additive effects typically occur with simultaneous exposure to high CO₂ and low dissolved oxygen (44). A trend toward lower survival, slower growth, and development is also evident with simultaneous exposure to high CO₂ and elevated temperature (45).

As **Figure 2** shows, a variety of experimental strategies are being used to characterize the sensitivity of species to acidification now and in the future (46, 47). Complementary approaches are needed because any one technique is limited by issues related to drawing inferences from short-term experiments or small-scale spatial range, choices about treatment conditions and study subjects, logistics related to engineering and animal husbandry, and other factors (35). Below we discuss recent experimental and field breakthroughs through the lens of three challenges or tensions in designing and interpreting organismal sensitivity studies.

3.1. Characterizing Present Versus Projected Future Sensitivity to Ocean Acidification

Ocean acidification is a perturbation of marine environmental conditions, a sustained and growing ecological press, with implications for marine ecosystems on the scale of decades, centuries, and longer. Similar to the marine heat wave events that punctuate the warming trend induced by climate change, the impacts of acidification may first be witnessed in coastal ecosystems that express more variability in carbonate chemistry and could episodically move across biological thresholds of sensitivity. Early work characterizing the sensitivity of marine species to ocean acidification focused on a stationary approach: the sensitivity of representative individuals of a species as they exist in the present (48, 49). Although useful, this approach does not necessarily yield information on how species in their future state will react to changes in seawater carbonate chemistry as acidification progresses in the environment. Predicting how marine populations will evolve in response to climate change and ocean acidification requires consideration of the flexibility of individuals in each generation to adjust to new environmental conditions (i.e., phenotypic plasticity) and natural selection across environments (50).

Discovery of individuals or populations more resilient to high-CO₂ conditions has arisen by testing the repeatability within and between identical sensitivity experiments (51, 52) and among

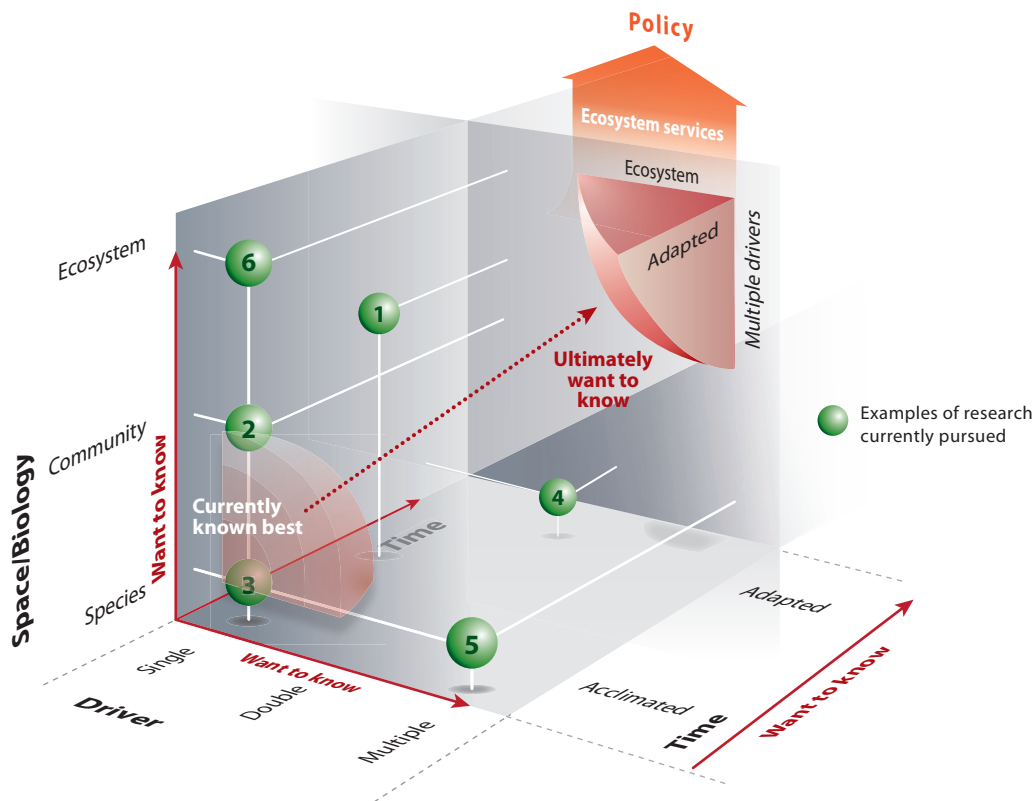


Figure 2

Various types of studies generate information about how ocean global change will influence marine life. The cube, a visualization developed by Riebesell & Gattuso (227), represents different scales of space and biological organization, time, and drivers of environmental change. It depicts schematically where information on ecosystem services that could inform policy would emerge and where currently pursued types of research are located in time/space dimensions: ❶ mesocosms, including free ocean carbon-dioxide enrichment (FOCE) experiments; ❷ competition experiments; ❸ typical acclimated species under acidification; ❹ long-term (>400 generations) microevolution studies; ❺ multiple driver studies; and ❻ sites of CO₂ natural enrichment such as CO₂ seeps. Figure adapted from Boyd et al. (47) with permission of John Wiley and Sons and originally developed by Riebesell & Gattuso (227).

populations of the same species. Some populations living in naturally high-CO₂ environments express less sensitivity to high-CO₂ experimental treatments (53–55). Others at the edge of a species' range can be more sensitive to high-CO₂ exposure, suggesting the influence of biogeographic processes beyond carbonate chemistry conditions (56).

Studying populations living in naturally high-CO₂ environments is another way to explore whether long-term exposure to high CO₂ can confer resistance to ocean acidification. Laboratory experiments on two zooplankton species collected from Puget Sound, an urbanized estuary in the northeast Pacific with high-CO₂ conditions due to both natural and human sources (30), find that individuals express sensitivity to carbonate chemistry conditions already experienced by local populations, suggesting a lack of resistance to the high-CO₂ conditions within their current range (57, 58). Field collections show that some species express sensitivity to the high-CO₂ conditions already observed along the western coast of the United States, whereas others express signs of potential adaptation (59–62, 229).

Organisms may evolve much more quickly than we recently thought possible (63), especially via epigenetics (64, 65). Groundbreaking work in the purple urchin *Strongylocentrotus purpuratus* has

Hypoxia: low oxygen conditions in the coastal and open ocean often associated with respiration of organic material that also elevates carbon dioxide

shown transgenerational plasticity in response to high-CO₂ exposure, with documented transgenerational impacts on the epigenome (chemical attachments to DNA, often heritable, that modify its function) (66), gene expression (67), and phenotype (68). Other work in the purple urchin has found evidence of response in larval size and genome-wide shifts to selection imposed by different CO₂ conditions (53, 69). Multigenerational experimental evolution studies are feasible for microbes and have indicated that adaption to high-CO₂ conditions is possible (70–72).

3.2. Designing Tractable Experiments Versus Aiming for Ecological Relevance

The ecological relevance of aspects of present-day experimental capabilities can be debated, and the resulting knowledge gaps limit our ability to project or model the potential direct and indirect impacts of acidification at the ecosystem level (49). For example, results from experiments that hold environmental conditions static may not be fully relevant to the dynamic conditions that organisms experience in nature (73). Also, sensitivity research tends to cluster on a limited group of taxa—driven by logistics, stakeholder concerns, and concentration of mechanistic studies on a limited set of target organisms—thus failing to reflect the diversity of marine species (49). Publication bias against sharing negative experimental results, that is cases with no or small CO₂ effects, also may limit the representativeness of available data for synthesis and modeling (35).

Ocean acidification should not be considered an isolated phenomenon but is instead part of a complex of changing ocean conditions that must be considered together if sensitivity studies are to have ecological relevance. Designing research studies to tackle the complexity of multiple changing parameters, while still being logistically feasible and interpretable, is a challenge. Boyd et al. (47) describe two complementary paths: (a) a mechanistic, reductionist approach in which the influence of each aspect of ocean change is considered alone and then in conjunction with other aspects of ocean change; and (b) a scenario-based approach in which multiple variables are altered together to match future projections of ocean conditions.

A well-recognized danger in the reductionist approach is that considering one factor alone can yield incorrect information related to how a species might fare in a future ocean. The response of species to various aspects of ocean change can be additive, synergistic, or antagonistic (47, 74). For example, the sensitivity of reproduction in kelp to pH sensitivity can depend on temperature conditions (55). Elevated CO₂ in coastal regions and the deep ocean typically co-occurs with low oxygen or hypoxia, both generated by respiration of organic matter (44). High CO₂ and reduced oxygen content can have opposite effects on otolith size in juvenile rockfish (75), while metabolomic response of juvenile Dungeness crabs indicates that exposure to low oxygen may drive the physiology of juvenile crabs more than CO₂ (76).

3.3. Sensitivity to High-CO₂ Conditions Versus Detecting Ocean Acidification Impacts in the Environment

Most studies to date focused on organismal responses to different seawater inorganic carbon chemistry conditions in either laboratory or field settings—valuable research, although not actually demonstration of ocean acidification impacts on marine species (77). In contrast, more limited research has attempted to detect change in marine species in the environment that can be attributed to ocean acidification and its progression. Studies correlating ocean carbonate chemistry to marine species abundance have mixed results, with some finding a signature of ocean acidification impacts (78) and many failing to do so (79–81). Historical records of pteropods and foraminifera show correlations of shell conditions with reconstructed carbonate chemistry conditions (82–85), although such correlations do not yet exist for coral reefs and are contradictory for coccolithophores (86, 87). Work from the western coast of the United States links

pteropod shell condition with anthropogenic CO₂ increase and reveals how acidification likely impacts pteropod shell condition, survival, and distribution (229–231).

Because ocean acidification co-occurs with other aspects of climate change and human impacts on ocean systems, disentangling ocean acidification impacts from those of other stressors is a challenge (88). It is also likely that the thresholds at which carbonate chemistry conditions will impact many species have not yet been crossed and that the signature of ocean acidification impacts may be weaker than those of other phenomena, and thus, harder to detect. For example, although the general expectation is that ocean acidification should have already negatively influenced shallow coral reefs and many reef properties vary with natural gradients in aragonite saturation state, the effects of anthropogenic ocean acidification on coral reefs have not yet been confidently isolated (89). Natural variation in carbonate chemistry in modern systems has been used to gain insight into the current and projected future effects of ocean acidification on marine species (60, 90). As understanding of the sublethal signatures of exposure to high-CO₂ conditions increases, such as alterations in molecular markers of stress (62), the immune system (91), or shell state (60), robust methods for detecting and monitoring the impacts of ocean acidification on marine species will emerge. The probability of detecting and attributing change to ocean acidification will likely increase as the chemical signature of ocean acidification emerges from the natural variation of carbonate chemistry in the coastal oceans (92).

4. COMMUNITY AND ECOSYSTEM EFFECTS

4.1. Introduction: Overall Patterns of Community Change

Studies examining how individual organismal effects of ocean acidification will affect communities and functioning ecosystems have received increasing recent attention (20). Results from both experiments and studies using natural gradients in carbonate chemistry strongly suggest that ocean acidification increases primary producer biomass and decreases taxonomic diversity (93–95), although many species are able to survive (or even thrive) in high-CO₂ conditions. The decreases in taxonomic diversity are likely to have functional consequences (96), although the effects on ecosystem function are just beginning to be explored. In general, there is a trend toward the homogenization of community structure in space and time, which has been attributed to altered competitive interactions (e.g., for food or space) (97, 98). Although functional redundancy, the number of species that provide a particular ecosystem function such as habitat formation or reef bioerosion and material recycling, is generally considered to be quite low in marine ecosystems (99), redundancy within trophic groups can limit community shifts associated with acidification if resilient species are able to compensate functionally for more vulnerable species (100).

Increased primary production associated with high pCO₂ can boost production across multiple trophic levels (101), if consumers are able to increase their consumption rates. However, it is unclear what controls the ability of a consumer to increase their consumption rate in high-CO₂ conditions. For example, in laboratory experiments consumers have been shown to compensate for increased primary producer biomass associated with acidification, thereby limiting the predicted shifts in community structure associated with the increased growth and competitive dominance of macroalgae (102, 103). However, in an observational study at natural high-CO₂ seeps, the increase in consumer consumption rates was insufficient to keep pace with increased algal productivity, and thus community structure associated with high-CO₂ conditions was dominated by fleshy macroalgae (101). Moreover, there are numerous examples of consumers demonstrating little to no change in their consumption rates in high-CO₂ conditions, including when decreases in prey quality caused by acidification require altered consumption rates for predator survival (104).

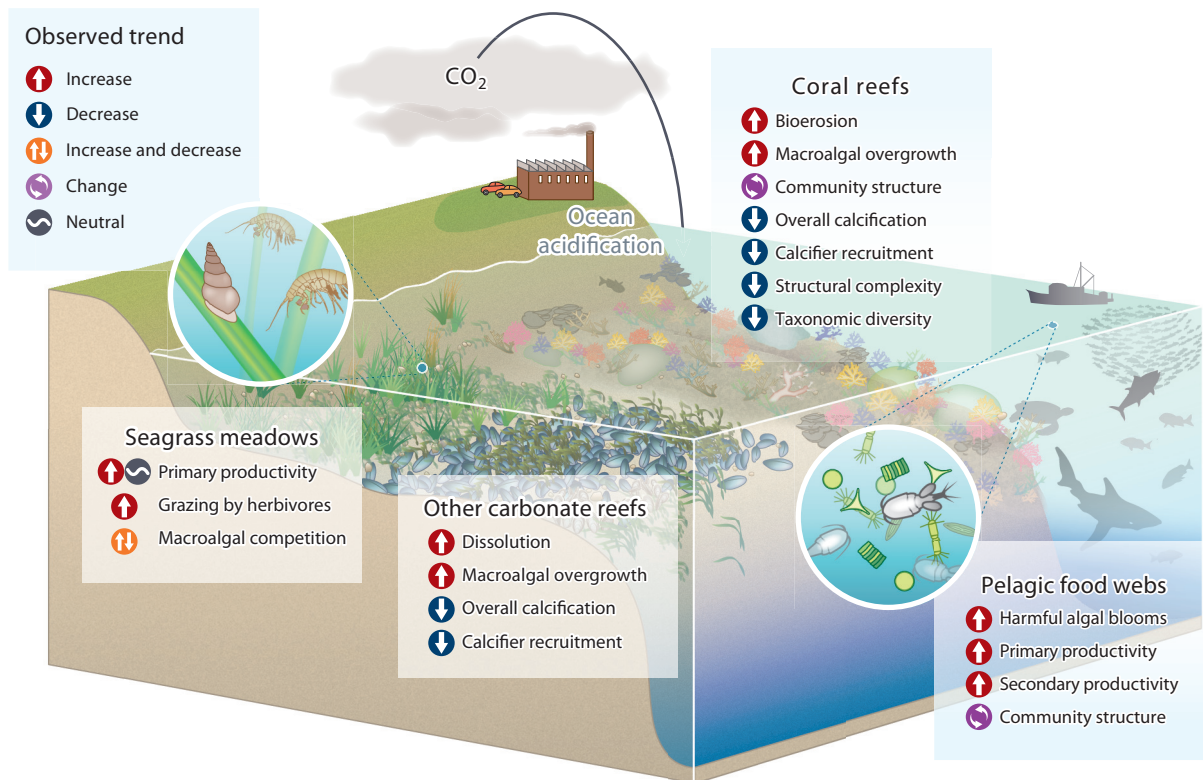


Figure 3

General trends in key community and ecosystem properties and processes in response to ocean acidification in seagrass meadows, coral reefs, other carbonate reef ecosystems, and pelagic food webs. Trends are primarily derived from studies of multiple-species experiments or observational studies in naturally acidified ecosystems. That is, these are not direct observations of anthropogenically driven change in nature. The literature cited for each system (see below) is not exhaustive but represents key studies highlighting the community and ecosystem effects in the critical habitats featured in this review. Recruitment is defined as the net outcome of the various processes needed to add new individuals to a population. Seagrass meadows: increase or no change in primary productivity (135, 136), grazing by herbivores (102, 141–143), competition between seagrass and macroalgae (93, 137, 140). Coral reefs: bioerosion (118), macroalgal overgrowth (94, 95, 120, 123), community structure (94, 95, 119, 125), overall, net ecosystem calcification (115, 116, 118), habitat-forming calcifier recruitment (122–124), structural complexity (127, 128), taxonomic diversity (94, 95, 128). Other carbonate reefs: carbonate dissolution (131), macroalgal overgrowth (134), overall, net ecosystem calcification (133, 134), habitat-forming calcifier recruitment (132, 133). Pelagic food webs: harmful algal blooms (112, 113), productivity of primary producers (109), productivity of secondary producers (107, 109, 110), community structure (106–108).

Altered behavior in marine consumers (e.g., predator avoidance) caused by exposure to conditions of ocean acidification can also weaken predator-prey links in marine food webs, causing cascading effects on community structure and function (105).

Below, we review the expanding literature on community and ecosystem effects of acidification on four critical habitats especially relevant for resource managers: pelagic food webs; coral reefs; oyster and other biogenic, carbonate reefs; and seagrass beds (**Figure 3**).

4.2. Pelagic Food Webs

The community structure of planktonic communities is very likely to change with acidification (106, 107), with cascading impacts on the productivity of the entire food web. An important caveat

to consider, however, is that the responses of phytoplankton will likely depend on other environmental conditions and factors, such as the nutrient availability, salinity, and the temperature regime (108), and these interactions have yet to be fully incorporated into whole-community mesocosm studies. Modeling work suggests that ocean acidification, warming, and increased stratification will drive changes in marine microbial community makeup (42), but it is not yet known whether microbial changes will alter global ecosystem functions such as net primary production and export or air-sea gas exchange.

Whole-community mesocosm studies have demonstrated increased productivity at the base of pelagic (water-column) food webs (106), leading to increased productivity of higher trophic levels (109), including enhanced survival and biomass of larval fish that are directly negatively impacted by acidification (110). However, not all zooplankton are expected to benefit from increased primary productivity. For example, some zooplankton taxa appear to be vulnerable directly to ocean acidification, regardless of the resources available (60). Field studies across upwelling gradients indicate that pteropods may already be experiencing shell dissolution in low-pH waters along the California Current (60). In addition, the nutritional quality of some zooplankton may suffer with ocean acidification, despite increased production or abundance (111). As such, models of pelagic food webs with ocean acidification have indicated that the effects on upper trophic-level species are likely to be complex and species specific, based on the specific food-web linkages in the ecosystem.

Ocean acidification could also disrupt pelagic food webs via the proliferation of toxic algal blooms (112). Ocean acidification can either increase the toxicity of the harmful algae (113) or increase the abundance of toxic bloom-forming species through altered competitive interactions (112). Again, it is less well understood how ocean acidification may interact with other factors, including changing ocean temperatures and nutrient concentrations to affect harmful algal blooms, but it is clear that increases in the toxicity or abundance of bloom-forming species could severely disrupt food webs.

4.3. Coral Reefs

The persistence of coral reefs depends on the balance of net accretion (carbonate production minus dissolution) and bioerosion by boring and scraping organisms at each reef. Numerous studies document declines in net calcification of different coral species and coral reef assemblages with lower carbonate saturation states. Moreover, retrospective studies from the Great Barrier Reef have highlighted large declines in the net calcification of corals over time (114). However, it has been difficult to attribute the declines in net accretion to ocean acidification due to the concurrent trends in ocean warming and coral bleaching. Using manipulative alkalinity enrichment at the scale of a reef flat, Albright et al. (115) recently demonstrated that net community calcification increases when the seawater carbonate saturation states are raised to preindustrial levels. This suggests that coral reefs have already suffered declines in net calcification associated with ocean acidification (115).

There is growing evidence that bioerosion may be more sensitive to changes in carbonate chemistry than carbonate production (116). This is potentially due to changes in the density or structural integrity of the coral skeletons produced in lower carbonate saturation states (117). Indeed, increased bioerosion has been demonstrated in naturally more acidic locations (95, 118, 119), which suggests minor shifts in biological species interactions may further tip the balance from net accretion to net erosion of coral reefs in future conditions.

As with other habitats, most observational studies of naturally acidified coral reefs indicate that diversity is depressed and macroalgal abundance is elevated in carbonate chemistry

Carbonate saturation state: a comparison of seawater carbonate and calcium ion concentrations relative to thermodynamic equilibrium, where saturation states below 1 reflect undersaturation and carbonate mineral dissolution

conditions comparable to those projected for the end of the century (94, 95). Potential shifts in the competitive balance between corals and macroalgae are especially important given the numerous studies documenting the detrimental effects of algal overgrowth of corals. Turf algal communities, in particular, are expected to increase in biomass and diversity in high-CO₂ conditions (120, 121), which could further impact community structure by limiting the recruitment of juvenile corals. Declines in the percent cover of crustose coralline algae, which are often used as recruitment substrates by corals, may also contribute to reduced coral settlement in high-CO₂ conditions (122). High-CO₂ effects on early succession dynamics lead to higher abundance of micro- and macroalgae and lower coral recruitment, although the mechanisms attributed to these shifts differ among studies: altered competitive interactions (123) versus chemical control (124).

Despite these observed shifts in coral reef community structure, corals do not disappear in naturally more acidic conditions. In several studies, the coral community shifts from relatively faster-growing, structurally complex corals to slower-growing, mounding corals (94, 95) or even soft corals (125) in conditions comparable to end of the century projections. Studies of coral reefs growing in the rock islands of Palau, however, documented slightly different shifts in coral community structure than other naturally acidified ecosystems (119). In this system, community composition of the coral species varies with carbonate chemistry, as in other systems, but the shifts in community composition are not associated with decreased diversity, structural complexity, or increased macroalgal abundance. Instead, distinct coral reef communities, with high coral cover, exist in the naturally more acidic bays. Lab studies of the corals growing in these environments suggest there may be some level of adaptation to lower saturation states or other co-occurring environmental covariates (126). Thus, the potential adaptive capacity of corals to projected future warming and acidification remains an important frontier that needs to be resolved better for understanding emergent community shifts.

Shifts in coral community structure associated with acidification can have indirect effects on reef-associated invertebrate and fish communities (127). For example, shifts from structurally complex corals to massive, mounding corals, as witnessed near natural CO₂ seeps, can reduce the structural complexity of the habitat and the associated invertebrate communities (94, 128). Alternatively, increased macroalgal abundance that provides shelter or habitat structure for prey can benefit fish populations, despite negative direct effects on fish behavior and predator avoidance (129). Although there have been several studies of fish behavior and population dynamics in naturally acidified conditions, the spatial scale of the affected areas in these studies is usually much smaller than the range of many fish species (130). Thus, our inference regarding the emergent effects on fish populations is generally limited to those with very small home ranges.

4.4. Oyster and Other Biogenic, Carbonate Reefs

Similar to coral reefs, ocean acidification is expected to increase dissolution rates of oyster shells that make up the structure of oyster reefs (131), and high-CO₂ impacts on oyster larvae may negatively influence oyster recruitment (132). Ocean acidification threatens the structure and ecosystem services provided by vermetid reefs, which are built in warm, subtropical waters by vermetid gastropods and cemented together by crustose coralline algae, because of reduced gastropod recruitment and enhanced shell dissolution (133). Maerl beds (also called rhodolith beds), a habitat formed by unattached, branching crustose coralline algae in the Mediterranean and along the Atlantic coast of Europe to the North Sea, are also threatened by acidification. Laboratory exposure of the community to more acidic conditions led to decreased calcification and increased dissolution of the habitat-forming species as well as to an increase in the biomass of competitive epiphytic algae. The dominant grazers in this ecosystem were not able to keep pace with the

increased biomass of epiphytic algae, potentially contributing to overgrowth of the habitat-forming species and the further deterioration of these ecosystems (134).

4.5. Seagrass Beds

Seagrasses may benefit from acidification based on the argument that elevated CO_2 will reduce energetic costs of carbon uptake for photosynthesis (135), but there is limited and sometimes contradictory evidence of CO_2 enrichment of seagrass productivity from field studies (136). The effects of acidification on associated species also could mediate the community and ecosystem effects for seagrass beds. Of concern is the response of marine epiphytes, organisms that grow on the surface of submerged aquatic vegetation, and macroalgae that compete with seagrasses (137). Additionally, seagrasses are sensitive to water quality and benthic light levels, so acidification effects on plankton dynamics may also play a role (138). While epiphytes that produce calcium carbonate structures are expected to decrease with acidification (93, 137), enhanced seagrass production may protect some calcareous species very close to the seagrass tissues in low flow environments (139). In contrast, fleshy epiphytic algae are largely expected to benefit from high pCO_2 (140). Experimental studies of temperate seagrass communities, dominated by fleshy epiphytes and macroalgae, suggest that grazers can keep epiphytic algae in check (102), and in some cases, acidification may actually increase top-down control (141). Despite having calcareous skeletons, many of the invertebrate grazers in seagrass ecosystems have high tolerance to acidification (142, 143).

5. RISKS TO HUMAN COMMUNITIES

The emergence of ocean acidification impacts on the Pacific oyster industry in the Pacific Northwest United States in the mid-2000s (144) immediately framed ocean acidification as a present-day concern with direct implications for small and large businesses and coastal communities. Since then, much ocean acidification research has focused on economically, culturally, and ecologically important species. Other studies have focused on how ocean acidification will ultimately alter the benefits that marine systems provide to human communities (also called ecosystem services, or nature's contributions to people).

Detecting changes in ecosystem services can be challenging, and attributing those changes to one long-term driver, such as ocean acidification, is even more difficult. Moreover, human and natural systems are constantly adapting and responding to ocean acidification in a multi-stressor context, while the risk of harmful changes to ecosystem services from climate change is increasing (145, 146). Multidisciplinary studies focused on social-ecological risks from ocean acidification are exploring economics, ecosystem services, and cultural and societal institutions. Researchers are also studying interventions that decrease vulnerability by either decreasing social-ecological systems' exposure to ocean acidification or increasing their adaptive capacity. In addition to strengthening fisheries and aquaculture, or improving the resilience of coastal environments, these actions have the cobenefit of improving management of marine systems and resources (Figure 4).

5.1. Fisheries and Food Webs

Both real-world and laboratory evidence suggest that ocean acidification is very likely to decrease harvests of several bivalve shellfish species, with lost revenue and cultural disruption to follow. During the mid-2000s, the Pacific oyster aquaculture industry in the Pacific Northwest, which is increasingly at risk from acute ocean acidification worsened by enhanced coastal

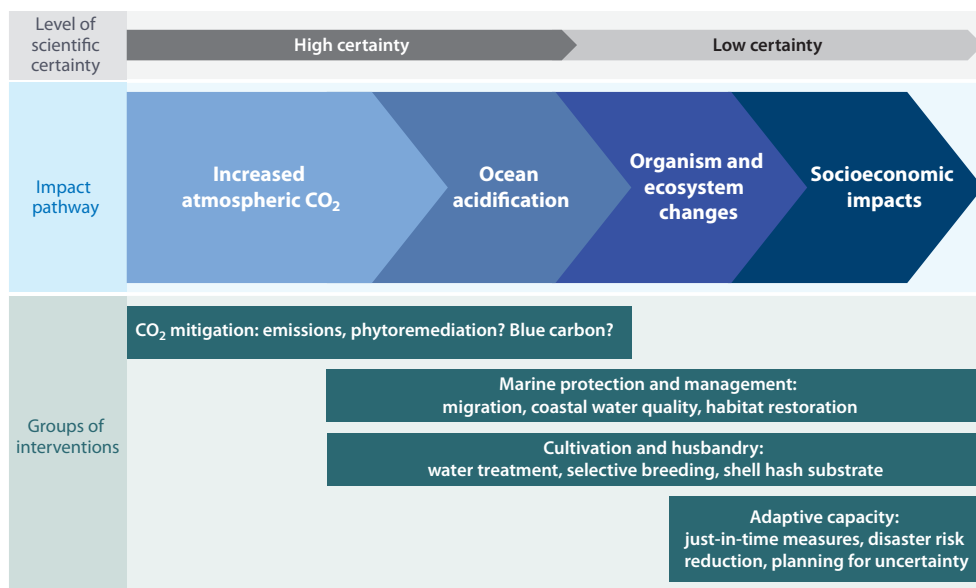


Figure 4

Impact pathway from increased atmospheric carbon dioxide (CO₂) to changes in social-ecological systems. Gray band indicates level of scientific certainty. Teal green blocks show the groups of interventions discussed in the text that are frequently proposed to directly decrease harm from ocean acidification on social-ecological systems. Figure adapted from Gattuso et al. (228) with permission of the Intergovernmental Panel on Climate Change (IPCC).

upwelling, supported more than 3,000 jobs and \$270 million in economic activity per year (144). Because marine mollusks comprise 9% of the total world fishery production by value (147), ocean acidification's potential effects on shellfish harvests and provisioning ecosystem services became a research theme (148).

Ocean acidification causes decreases in bivalve reproduction, survival of juvenile bivalves, or delayed maturation of adults and can alter recruitment, harvestable biomass, maximum sustainable yield, and economic value of shellfish fisheries (149). Other impacts such as alterations in the taste or other food qualities of shellfish (150, 151), or behavioral changes in finfish species (17, 152), have not yet been detected in nature or incorporated into models, so their socioeconomic implications have not been projected yet.

Studies with varying degrees of complexity have examined potential economic losses from associated shellfish harvest decreases. Models with simple CO₂-damage relationships for all bivalves and time discounting have projected losses of approximately 10–28% losses for both US and UK mollusk harvests annually (148, 153). Model estimates of welfare losses from ocean acidification impacts on shellfish range widely depending on estimates of per capita income and mollusk demand growth: US losses toward 2100 are estimated at \$400 million USD and global losses, dominated by China, from \$6 billion to \$100 billion USD annually (147), with an annual projected impact of more than \$1 billion USD for Europe by 2100 (154). For UK fisheries, ocean acidification and warming together are projected to decrease shellfish biomass by 30% by 2020, with overall employment losses related to shellfish and finfish declines from 3% to 20% by 2050 (155). United States economic damages by the end of the century for mollusk fishery losses are on the same order as those for increased hurricane damages (156).

Integrated assessment models (IAMs) are now being utilized to explore the possible combined impacts of climate change, acidification, harvest, fishery management, and social-economic factors on specific commercial fisheries. Cooley et al. (149) found a substantial decline in US northeast sea scallop harvests by 2050 under high CO₂ emission scenarios and contemporary harvest rules, if ocean acidification decreases recruitment and slows growth, although adjustments to management can help increase biomass somewhat (157). Another IAM projected a decrease in the Alaska-based southern Tanner crab fishery catch and profits by more than 50% in the next 20 years (158). A dynamic bioclimate envelope model examining ocean acidification and temperature effects together found that total fisheries revenue in the Arctic region may increase by 39% from 2000 to 2050 under SRES A2, because poleward movement of temperate fisheries will increase Arctic fishery revenues more than calcifier mortality will drive losses (159).

Ecosystem models and vulnerability assessments have also evaluated the interaction of ocean acidification with other drivers and fisheries. In the California Current, decreased pH is expected to most impact crabs, shrimps, benthic grazers, and bivalves, with indirect effects on specific demersal species that prey on these groups (160) and different consequences for port-based economies in the region (161). Using a suite of regional ecosystem models from around the world, Olsen et al. (162) explored the interaction of ocean acidification, marine protection, and fishing pressure, finding that marine protection and ocean acidification have greater overall effects on the ecosystem than adjusting fishing pressure. Seijo et al. (163) recommend considering possible ocean acidification effects when defining fisheries management strategies, and Olsen et al. (162) and Talloni-Álvarez et al. (164) suggest that ocean acidification should also be considered when developing protection strategies and ecosystem-based management. Regional vulnerability to potential losses in shellfish harvests from ocean acidification is greater for indigenous groups and rural communities in the United States (165, 166) and developing nations with artisanal fishing fleets in the Mediterranean (167). Minimizing overall community vulnerability to losses from ocean acidification requires addressing community and environmental factors such as overall economic well-being, access to job alternatives, coastal hypoxic events, and more as well as ocean acidification impacts on marine species.

5.2. Coral Reefs

Potential economic and cultural losses of coral reef—provided ecosystem services—coastal protection, habitat and biodiversity, fisheries, recreational and tourism opportunities, and existence and amenity values—have been considered since the earliest days of ocean acidification research. Approximately 500 million people derive food, income, coastal protection, and other services from coral reefs (168). The worldwide value of coral reefs, however, is difficult to pin down; published estimates range from \$29.8 billion/year (169) to \$376 billion/year (170), although Pendleton et al. (171) find that data are insufficient to allow rigorous evaluation. Ocean acidification combined with erosion and other disturbances have lowered the seafloor around carbonate platform environments in the Florida Keys, Caribbean, and near Hawai‘i, accelerating the rate of relative sea-level rise (172) and endangering human safety and property (173). Without coastal protection from reefs, specifically, flood damages from 100-year storm events would nearly double, rising to \$272 billion (173). Brander et al. (174) examined the economic impact of ocean acidification on coral reefs, concluding that economic effects of reef scarcity and increasing global wealth would keep tourism and economic value of reefs strong, despite net loss of coral reefs from acidification.

Other analyses use noneconomic methods to evaluate risks posed by changes in coral reef health or coverage. Pendleton et al. (171) showed that overlapping risk of reef loss from warming and acidification and social and economic vulnerability puts Southeast Asia at particular combined

risk, yet most places there have minimal data on ocean acidification exposure. A similar approach around the Great Barrier Reef concluded that a suite of ecological and social measures is needed to decrease risk of harm from climate-associated reef loss (175).

Vermetid and shellfish reefs suffer from ocean acidification as well as coastal disturbances such as trampling, sedimentation, dredging, and pollutants or poisons (133, 176, 177). Both types of reefs are “ecosystem engineers” that stabilize sediments, provide habitat for benthic ecosystems, and store organic carbon (133, 176). Oyster reefs provide an estimated value of \$5,500–\$99,000 per hectare per year via shoreline stabilization, habitat creation, and water filtration (178). Ocean acidification’s economic ramifications for vermetid and shellfish reefs have not been explored, but the reefs’ important noneconomic environmental roles have made them focal areas for preservation and restoration.

5.3. Coastal Systems and Submerged Aquatic Vegetation

Many near-shore, coastal systems contain submerged aquatic vegetation, such as seagrass beds or kelp forests, that are increasingly mentioned as a solution to address ocean acidification (21, 179). Submerged aquatic vegetation’s ability to create habitat and slow water flow in coastal regions is better established (180–182) than its ability to consistently capture and sequester CO₂ or modulate local pH swings, where evidence is mixed (183–185). Nevertheless, restoring and preserving submerged aquatic vegetation is increasingly seen as a widely useful marine conservation step that will help sustain marine provisioning and regulating services (186) and may help mitigate ocean acidification in localized areas (21). This overall approach is frequently termed phytoremediation (Figure 4).

Similar to submerged aquatic vegetation, coastal systems including wetlands, mangroves, and nearshore sediments are thought to help mitigate ocean acidification by sustaining regulating services and capturing carbon or releasing alkalinity (187–189). However, local details strongly influence the amount and duration of carbon captured (188, 190). Estimates of the economic value of this blue carbon (carbon sequestered in wetlands, mangroves, sediments, macroalgae, and submerged aquatic vegetation) are functions of these environments’ carbon drawdown, their spatial coverage, and the social cost of carbon (191, 192). Conservation and restoration of coastal systems to sequester carbon are being evaluated and promoted as part of overall carbon mitigation efforts (193, 194), which may indirectly benefit ocean acidification.

5.4. Biodiversity and Environmental Health

All healthy ocean and coastal systems, including the environments mentioned above, sustain biodiversity. The reduced biodiversity associated with acidified conditions observed in many coastal systems (195) decreases ecosystem resilience and compromises regulating services, including habitat provision, nutrient cycling, and carbon storage (196). For example, slower growth and survival of a widespread mussel species (*Mytilus edulis*) under ocean acidification could substantially decrease its ability to regulate coastal water quality by filtering water (197). Ocean acidification could strongly affect critical or unique environments such as coral reefs, deep-sea systems, and high-latitude systems, which depend on highly endemic species and may not have much functional redundancy within species groups (196). Outcomes for pelagic food webs are harder to anticipate, because ocean acidification and other drivers reshuffle species composition (196), and it is difficult to determine how ecosystem function will change. Gascuel & Cheung (198) caution that loss of ocean biodiversity that decreases regulating functions and functional redundancy can decrease not only system productivity, but also stability and resiliency; additionally, it can raise the risk of large-scale ecosystem shifts in ecosystem structure and decrease resilience.

Losses of marine biodiversity from ocean acidification impacts on marine systems can also affect cultural services (199–202). Cultural services comprise activities from supporting individual recreational activities to sustaining multi-generational, community-wide religious and cultural identities. There is broad agreement that the actual effects and modes of action of ocean acidification and other ocean changes on cultural services are insufficiently understood (203–206). Encouragingly, however, Koenigstein et al. (199) report that human communities recognize the potential implications of lost marine biodiversity, especially regarding extinctions and losses in ecosystem function, and this can spark meaningful, conservation-oriented multi-stakeholder discussions.

5.5. Interventions and Adaptations

Nearly every study that identifies potential harm from ocean acidification to ecosystem services also identifies possible interventions (**Figure 4**). There is consensus across the scientific community that the foremost solution to ocean acidification is to cut atmospheric CO₂ emissions (14, 207–211). At present, the international body of climate policy [within the United Nations Framework Convention on Climate Change (UNFCCC)] does not explicitly address ocean acidification, although numerous analyses agree that ocean acidification falls within UNFCCC-relevant concerns (210, 212, 213).

Adaptive management of marine systems, where management interventions are implemented to achieve particular ecosystem function goals, evaluated, and adjusted in response to new information or cumulative effects of change, is often cited as a possible intervention. Multi-stakeholder ocean planning, where shared objectives are set and ocean uses are coordinated among interest groups, shows promise for allowing many ocean uses to continue in a sustainable way. But acidification, oxygen loss, and the gradual redistribution of species across management boundaries to higher latitudes from ocean warming already confound current and future management decisions (168) and make projecting future conditions even more difficult. A critical challenge is maintaining an ongoing balance of protection versus sustainable human resource use for impacted systems (214). In coastal zones, ocean acidification interacts with other anthropogenic and natural drivers such as pollution, freshwater runoff, and coastal plankton blooms (215), but many existing water quality regulatory policies can start to help address coastal acidification locally (216).

Husbandry of captive or wild species also offers intervention opportunities. Encouraging shellfish aquaculture industry growth, despite the trade-offs associated with aquaculture, has been proposed as an adaptation to ocean acidification and warming (217). Shellfish hatcheries have enhanced water quality monitoring, improved water quality, and expanded selective breeding and strategic feeding to adapt to acidification, and this has stabilized or improved yields and economic revenues (144). Amending tidal flats where shellfish grow to maturity with ground CaCO₃ shell material provides substrate for larval settlement and may modulate ocean acidification locally (218–220). Submerged aquatic vegetation may also capture CO₂ locally through photosynthesis while providing habitat (185). Active interventions are being piloted to support coral species and restore coral reef environments, including selective breeding and carefully protected outplanting, as a key conservation tactic to maintain biodiversity (221). As with water quality, existing management levers might also improve resilience to ocean acidification and hypoxia (222).

The least well-developed group of interventions involves increasing the adaptive capacity of human communities that depend on marine resources. Just-in-time adaptations do work, as demonstrated by industry-science partnerships undertaken by the US Pacific oyster shellfish fishery. Personal networks were leveraged to identify and address ocean acidification through ocean monitoring and active water quality management by shellfish hatcheries adding calcium

carbonate to culture tanks (6, 144). An alternative adaptation approach that also shows promise is planned, end-to-end structures that support communities that may experience future losses from ocean change (6). This must reach beyond ocean acidification, as extreme ocean events including harmful algal blooms, hypoxia, and marine heat waves have recently tested management systems and stressed marine-dependent socioeconomic systems (223). Emphasizing disaster risk reduction (224) and rigorously incorporating uncertainty (225) in marine policy and governance can greatly improve outcomes for both social and ecological systems affected by ocean change (226).

6. SUMMARY

The scientific study of seawater chemistry changes due to rising atmospheric CO₂ and the sensitivity of marine life to elevated CO₂ have advanced dramatically in the past two decades. Major challenges remain, however, in understanding the implications of the ongoing long-term, press perturbation of ocean acidification for marine species, ocean biological communities and ecosystems, and the risks to human communities that depend on marine resources and ecosystem services. Efforts to understand the sensitivity of marine species to projected future ocean acidification are delving into detailed characterization and mechanisms of species sensitivity, consideration of acclimation and adaptation, greater ecological relevance including consideration of multiple stressors, and detection and attribution of the impacts for ocean ecosystems. Front-line risks to human communities have been identified, including loss of shellfish harvests and decline in coastal protection by coral reefs, and more risks are being investigated. Several existing policies used to regulate water quality and marine species conservation can also help address acidification, with no or minimal amendments. Likewise, many adaptive actions used to address other issues, such as strengthening the shellfish aquaculture industry overall, can have cobenefits in addressing acidification. Current management practices must be adjusted, however, to allow marine governance to remain nimble in the face of both global-scale changes such as acidification and climate change and local-scale concerns.

SUMMARY POINTS

1. Human CO₂ emissions alter surface seawater acid-base chemistry globally, with additional coastal acidification from nutrient pollution and other factors.
2. Biological impacts reflect multiple, simultaneous chemical changes—increasing CO₂(aq), HCO₃⁻, and H⁺ and decreasing CO₃²⁻ and carbonate saturation state.
3. Laboratory and field studies indicate a wide range of biological responses to high CO₂ on organism-level physiology, biomineralization, growth, reproduction, sensory perception, and behavior.
4. New research fronts involve characterization and mechanisms of species sensitivity, acclimation and adaptation, ecological relevance, multiple stressors, and detection and attribution of the ocean ecosystem impacts.
5. Propagation of organism-level effects into community and ecosystem responses is being elucidated through mesocosm and field manipulation experiments and studies of naturally acidified marine environments.
6. A suite of multiple stressors including acidification, climate change, and other environmental alterations must be considered when determining the emergent ecological effects and any adaptation-focused intervention.

7. Acidification likely will impact aquaculture, fisheries, shoreline protection, and other valuable marine ecosystem services, resulting in vulnerabilities and risks to human communities, but interventions designed to address other issues (e.g., biodiversity loss, water quality, governance) may also help address harm from ocean acidification.
8. The ultimate solution to ocean acidification involves global-scale reductions in human CO₂ emissions, with local adaptation strategies also needed to minimize harm from the impacts that are inevitable.

FUTURE ISSUES

1. Enhanced monitoring of ocean acidification is possible by leveraging improved autonomous ocean platform and sensor, remote sensing, data analysis, and modeling technologies.
2. Targeted observing systems, process studies, and modeling efforts are needed to evaluate acidification impacts in the marine environment across biological scales from populations to ecosystems.
3. Experimental studies of ecological effects of ocean acidification that explicitly incorporate environmental context (e.g., temporal variability in pCO₂/pH and concurrent exposure to multiple, relevant drivers) are needed to improve forecasts of emergent ecological effects.
4. Increased monitoring and data synthesis efforts aimed at detecting species and ecosystem change and understanding what portion of the change can be attributed to ocean acidification will help guide living marine resource management and the scientific efforts that support it.
5. Development and evaluation of adaptation solutions for ocean acidification are key priorities that will likely require coproduction of knowledge and close cooperation by scientists, resource managers, and stakeholders.
6. Marine management strategies need updating to balance protection and sustainable human uses in the face of overlapping global-scale changes like acidification, warming, and oxygen loss.
7. Adaptive management systems must be developed to move beyond the assumption of steady-state environmental conditions, to accommodate geographic and temporal shifts in living marine resources, and to nimbly address extreme events in ways that minimize harm to both marine systems and ocean-dependent human communities.

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