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

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Abstract

Rising atmospheric carbon dioxide (CO_2) levels, from fossil fuel combustion and deforestation, along with agriculture and land-use practices are causing wholesale increases in seawater CO_2 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 CO_2 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 CO_2 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.

Contents

Carbon dioxide (CO_2): 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 (CO_2) 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 CO_2 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 CO_2 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 CO_2 emissions. It is also well understood that the additional CO_2 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 CO_2 chemistry and acidification for both the global open ocean and some coastal systems (5, 6).

The potential for substantial biological responses to the excess CO_2 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-CO_2 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 CO_2 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 CO_2 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).

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 (CO_3^{2-}): an inorganic carbon molecule formed when carbon dioxide dissolves in seawater and a key building block for carbonate minerals used in organism biomineralization

2. SEAWATER CHEMISTRY

Aqueous carbon dioxide [$CO_2(aq)$] and the inorganic carbon system play a central role in seawater acid-base chemistry, and the addition of CO_2 from natural and anthropogenic sources causes acidification and shifts in the speciation of dissolved ions (4, 22). At seawater pH levels (~8), CO_2 added to seawater reacts with water to form bicarbonate (HCO_3^-) and hydrogen ions (H^+):

$$CO_2 + H_2O \rightarrow HCO_3^- + H^+. \quad 1.$$

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

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

and lower the concentration of carbonate ions (CO_3^{2-}), via

$$CO_3^{2-} + H^+ \rightarrow HCO_3^-. \quad 3.$$

Acidification impacts will depend on organism responses to multiple, simultaneous chemical changes—increasing $CO_2(aq)$, HCO_3^-, and H^+ and decreasing CO_3^{2-} (23).

Many types of marine organisms that form shells and skeletons from calcium carbonate ($CaCO_3$) minerals are sensitive to acidification. The solubility of carbonate minerals,

$$CaCO_3(s) \leftrightarrow CO_3^{2-} + Ca^{2+}, \quad 4.$$

can be expressed as a carbonate saturation state,

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

$$\Omega = \frac{[CO_3^{2-}][Ca^{2+}]}{K_{sp}}, \qquad 5.$$

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 ~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).

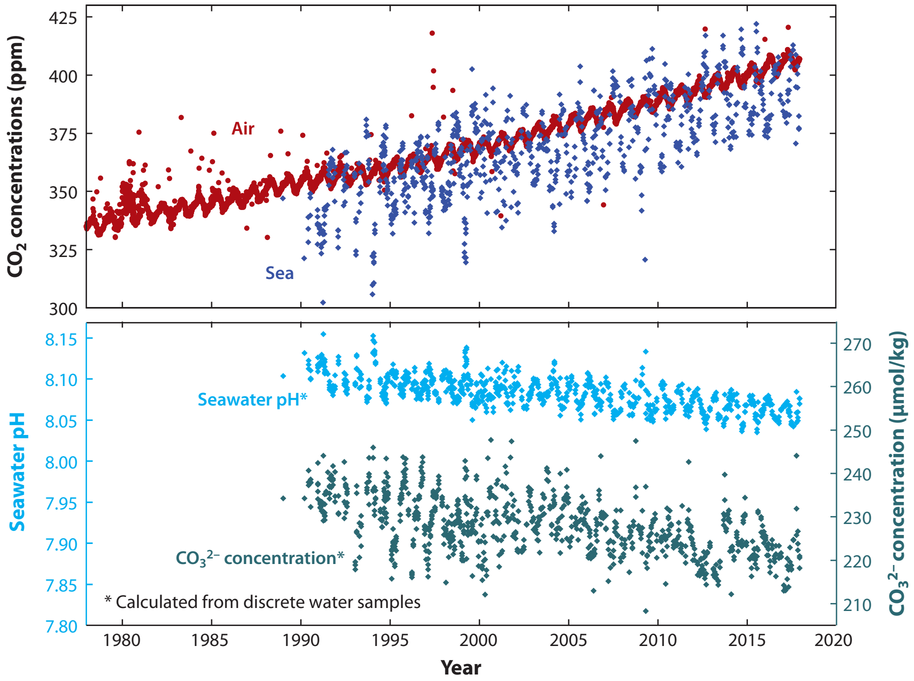

Figure 1

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 [CO_2(aq)]. Ocean CO_2 concentration is often also reported in terms of a carbon dioxide partial pressure pCO_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-CO_2 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-CO_2 conditions than those that do not calcify, this generalization is not uniformly applicable, and the form of $CaCO_3$ 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 $CaCO_3$, low-magnesium calcite, or a mix of multiple $CaCO_3$ forms (43).

Recent reviews emphasize how species sensitivity to various CO_2 conditions is influenced by exposure to other aspects of climate change. Negative additive effects typically occur with simultaneous exposure to high CO_2 and low dissolved oxygen (44). A trend toward lower survival, slower growth, and development is also evident with simultaneous exposure to high CO_2 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-CO_2 conditions has arisen by testing the repeatability within and between identical sensitivity experiments (51, 52) and among

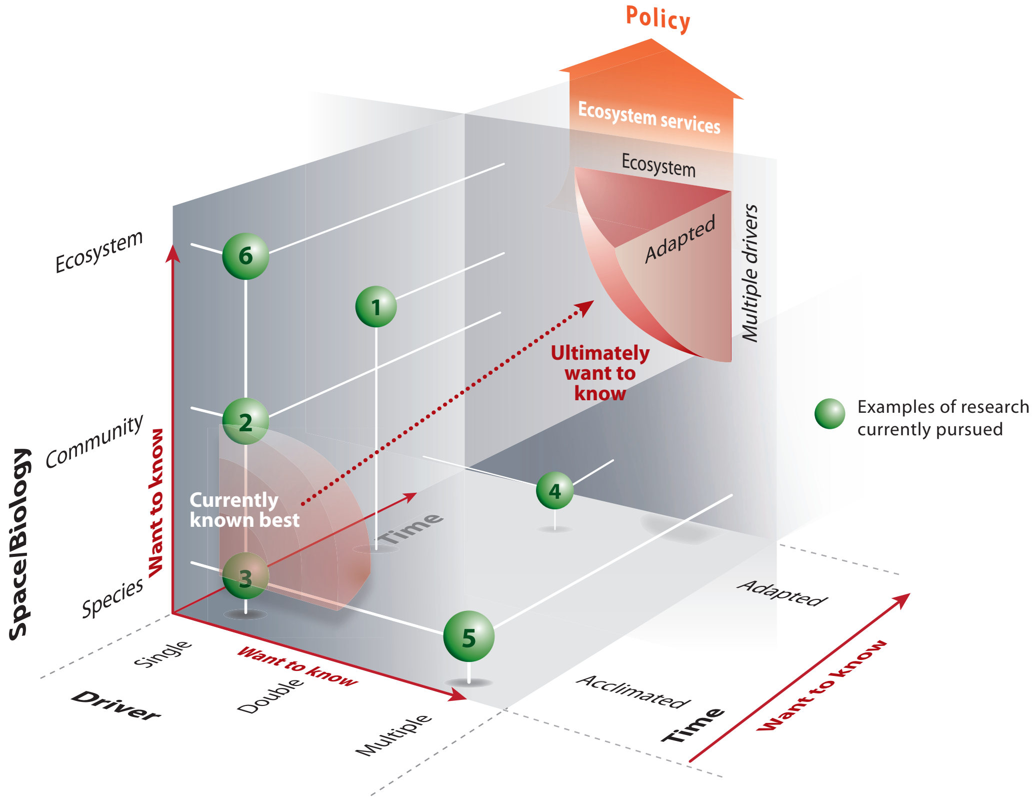

Figure 2

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 CO_2 natural enrichment such as CO_2 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-CO_2 environments express less sensitivity to high-CO_2 experimental treatments (53–55). Others at the edge of a species' range can be more sensitive to high-CO_2 exposure, suggesting the influence of biogeographic processes beyond carbonate chemistry conditions (56).

Studying populations living in naturally high-CO_2 environments is another way to explore whether long-term exposure to high CO_2 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-CO_2 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-CO_2 conditions within their current range (57, 58). Field collections show that some species express sensitivity to the high-CO_2 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-CO_2 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 CO_2 conditions (53, 69). Multigenerational experimental evolution studies are feasible for microbes and have indicated that adaption to high-CO_2 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 CO_2 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 CO_2 in coastal regions and the deep ocean typically co-occurs with low oxygen or hypoxia, both generated by respiration of organic matter (44). High CO_2 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 CO_2 (76).

3.3. Sensitivity to High-CO_2 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 CO_2 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-CO_2 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-CO_2 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 pCO_2 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-CO_2 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-CO_2 seeps, the increase in consumer consumption rates was insufficient to keep pace with increased algal productivity, and thus community structure associated with high-CO_2 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-CO_2 conditions, including when decreases in prey quality caused by acidification require altered consumption rates for predator survival (104).

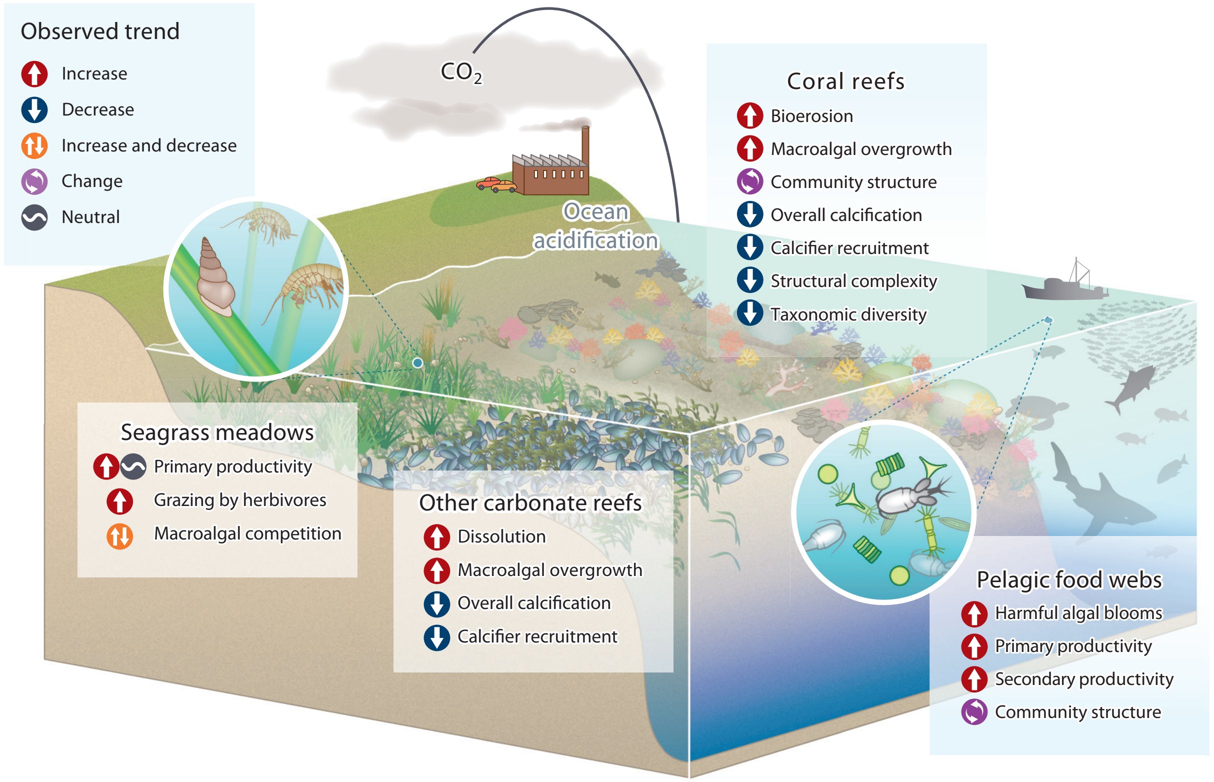

Figure 3

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.

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

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 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-CO_2 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-CO_2 conditions (122). High-CO_2 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).

Ecosystem services: benefits that people accrue from natural marine ecosystems such as fisheries and aquaculture

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 CO_2 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-CO_2 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

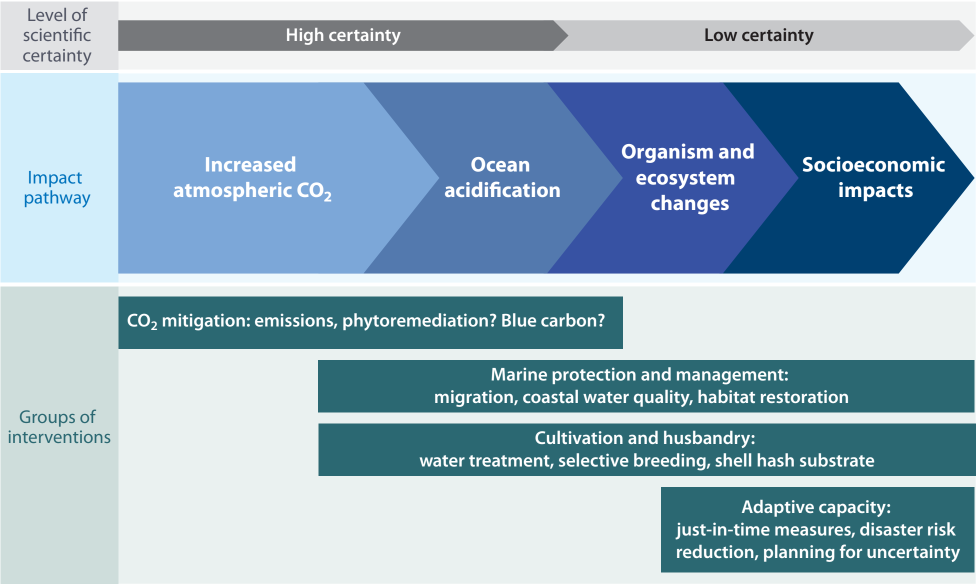

Figure 4

Impact pathway from increased atmospheric carbon dioxide (CO_2) 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 CO_2-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 CO_2 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 CO_2 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 CO_2 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 $CaCO_3$ shell material provides substrate for larval settlement and may modulate ocean acidification locally (218–220). Submerged aquatic vegetation may also capture CO_2 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 CO_2 and the sensitivity of marine life to elevated CO_2 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 CO_2 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 $CO_2(aq)$, HCO_3^-, and H^+ and decreasing CO_3^{2-} and carbonate saturation state.
3. Laboratory and field studies indicate a wide range of biological responses to high CO_2 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 CO_2 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 pCO_2/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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LITERATURE CITED

1. Gingerich PD. 2019. Temporal scaling of carbon emission and accumulation rates: modern anthropogenic emissions compared to estimates of PETM onset accumulation. *Paleoceanogr. Paleoclim.* 34:329–35
2. Le Quéré C, Andrew RM, Friedlingstein P, Sitch S, Hauck J, et al. 2018. Global Carbon Budget 2018. *Earth Syst. Sci. Data* 10:2141–94
3. Gruber N, Clement D, Carter BR, Feely RA, van Heuven S, et al. 2019. The oceanic sink for anthropogenic CO_2 from 1994 to 2007. *Science* 363:1193–99
4. Zeebe RE, Wolf-Gladrow D. 2001. *CO_2 in Seawater: Equilibrium, Kinetics, Isotopes*. Amsterdam: Elsevier Sci.
5. Tilbrook B, Jewett EB, DeGrandpre MD, Hernandez-Ayon JM, Feely RA, et al. 2019. An enhanced ocean acidification observing network: from people to technology to data synthesis and information exchange. *Front. Mar. Sci.* 6:337
6. Cross JN, Turner JA, Cooley SR, Newton JA, Azetsu-Scott K, et al. 2019. Building the knowledge-to-action pipeline: connecting ocean acidification research and actionable decision support. *Front. Mar. Sci.* 6:356
7. **Royal Society. 2005. *Ocean acidification due to increasing atmospheric carbon dioxide*. Policy Doc. 12/05, R. Soc., London**
8. **Gattuso J-P, Hansson L, eds. 2011. *Ocean Acidification*. Oxford, UK: Oxford Univ. Press**
9. Doney SC, Fabry VJ, Feely RA, Kleypas JA. 2009. Ocean acidification: the other CO_2 problem. *Annu. Rev. Mar. Sci.* 1:169–92
10. Mathis JT, Cooley SR, Yates KK, Williamson P. 2015. Introduction to this special issue on ocean acidification: the pathway from science to policy. *Oceanography* 28(2):10–15
11. Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, et al. 2013. Carbon and other biogeochemical cycles. In *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. TF Stocker, D Qin, G-K Plattner, M Tignor, SK Allen, et al., pp. 465–570. Cambridge, UK: Cambridge Univ. Press
12. Hoegh-Guldberg O, Cai R, Poloczanska ES, Brewer PG, Sundby S, et al. 2014. The ocean. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. VR Barros, CB Field, DJ Dokken, MD Mastrandrea, KJ Mach, et al., pp. 1655–731. Cambridge, UK: Cambridge Univ. Press
13. Jewett L, Romanou A. 2017. Ocean acidification and other ocean changes. In *Climate Science Special Report: Fourth National Climate Assessment*, Volume I, ed. DJ Wuebbles, DW Fahey, KA Hibbard, DJ Dokken, BC Stewart, TK Maycock, pp. 364–92. Washington, DC: US Glob. Change Res. Progr.
14. Bindoff NL, Cheung WWL, Kairo JG, Arístegui J, Guinder JA, et al. 2019. Changing ocean, marine ecosystems, and dependent communities. In *Special Report on the Ocean and Cryosphere in a Changing Climate*. Geneva, Switz.: Int. Panel Clim. Change
15. Falkenberg LJ, Dupont S, Bellerby RGJ. 2018. Approaches to reconsider literature on physiological effects of environmental change: examples from ocean acidification research. *Front. Mar. Sci.* 5:453
16. Espinel-Velasco N, Linn Hoffmann L, Agüera A, Byrne M, Dupont S, et al. 2018. Effects of ocean acidification on the settlement and metamorphosis of marine invertebrate and fish larvae: a review. *Mar. Ecol. Prog. Ser.* 606:237–57
17. Nagelkerken I, Munday PL. 2016. Animal behaviour shapes the ecological effects of ocean acidification and warming: moving from individual to community-level responses. *Glob. Change Biol.* 22(3):974–89
18. Wannicke N, Frey C, Law CS, Voss M. 2018. The response of the marine nitrogen cycle to ocean acidification. *Glob. Change Biol.* 24(11):5031–43

7. Seminal interdisciplinary report that raised the visibility of ocean acidification and galvanized new research.

8. First authoritative book on the subject with comprehensive set of edited chapters.

19. Kleypas JA. 2019. Climate change and tropical marine ecosystems: a review with an emphasis on coral reefs. *UNED Res. J.* 11(1):S24–S35

20. Gaylord B, Kroeker KJ, Sunday JM, Anderson KM, Barry JP, et al. 2015. Ocean acidification through the lens of ecological theory. *Ecology* 96(1):3–15

21. Gattuso J-P, Magnan AK, Bopp L, Cheung WWL, Duarte CM, et al. 2018. Ocean solutions to address climate change and its effects on marine ecosystems. *Front. Mar. Sci.* 5:337

22. Millero FJ. 2007. The marine inorganic carbon cycle. *Chem. Rev.* 107:308–41

23. Hurd CL, Beardall J, Comeau S, Cornwall CE, Havenhand JN, et al. 2019. Ocean acidification as a multiple driver: how interactions between changing seawater carbonate parameters affect marine life. *Mar. Freshwater Res.* 71:263–74

24. Dickson AG, Sabine CL, Christian JR, eds. 2007. *Guide to Best Practices for Ocean CO_2 Measurements*. Sidney, BC, Can.: PICES, Spec. Publ. 3

25. Riebesell U, Fabry VJ, Hansson L, Gattuso J-P, eds. 2010. *Guide to Best Practices for Ocean Acidification Research and Data Reporting*. Luxembourg: Publ. Off. Eur. Union

26. Benway HM, Lorenzoni L, White AE, Fiedler B, Levine NM, et al. 2019. Ocean time series observations of changing marine ecosystems: an era of integration, synthesis, and societal applications. *Front. Mar. Sci.* 6:393

27. Bakker DCE, Pfeil B, Landa CS, Metzl N, O'Brien KM, et al. 2016. A multi-decade record of high-quality fCO_2 data in version 3 of the Surface Ocean CO_2 Atlas (SOCAT). *Earth Syst. Sci. Data* 8:383–413

28. Feely RA, Sabine CL, Hernandez-Ayon JM, Ianson D, Hales B. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. *Science* 320(5882):1490–92

29. Feely RA, Okazaki RR, Cai W-J, Bednaršek N, Alin SR, et al. 2018. The combined effects of acidification and hypoxia on pH and aragonite saturation in the coastal waters of the California current ecosystem and the northern Gulf of Mexico. *Cont. Shelf Res.* 152:50–60

30. Feely RA, Alin SR, Newton J, Sabine CL, Warner M, et al. 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. *Estuar. Coast. Shelf Sci.* 88:442–49

31. Gledhill DK, White MM, Salisbury J, Thomas H, Mlsna I, et al. 2015. Ocean and coastal acidification off New England and Nova Scotia. *Oceanography* 8(2):182–97

32. Rheuban JE, Doney SC, McCorkle DC, Jakuba RW. 2019. Quantifying the effects of nutrient enrichment and freshwater mixing on coastal ocean acidification. *J. Geophys. Res. Oceans.* 124:9085–9100

33. Evans W, Mathis JT, Cross JN. 2013. Calcium carbonate corrosivity in an Alaskan inland sea. *Biogeosciences* 11:365–79

34. Waldbusser GG, Salisbury JE. 2014. Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. *Annu. Rev. Mar. Sci.* 6:221–47

35. Browman HI. 2016. Applying organized scepticism to ocean acidification research. *ICES J. Mar. Sci.* 73:529–36

36. Heuer RM, Grosell M. 2014. Physiological impacts of elevated carbon dioxide and ocean acidification on fish. *Am. J. Physiol.-Regul. Integr. Comp. Physiol.* 307:R1061–84

37. Tresguerres M, Hamilton TJ. 2017. Acid-base physiology, neurobiology and behaviour in relation to CO_2-induced ocean acidification. *J. Exp. Biol.* 220:2136–48

38. Cattano C, Claudet J, Domenici P, Milazzo M. 2018. Living in a high CO_2 world: a global meta-analysis shows multiple trait-mediated fish responses to ocean acidification. *Ecol. Monogr.* 88:320–35

39. Esbaugh AJ. 2018. Physiological implications of ocean acidification for marine fish: emerging patterns and new insights. *J. Comp. Physiol. B* 188:1–13

40. Nagelkerken I, Doney SC, Munday PL. 2019. Consequences of anthropogenic changes in the sensory landscape of marine animals. *Oceanogr. Mar. Biol.* 57:229–64

41. Wang M, Jeong C-B, Lee YH, Lee J-S. 2018. Effects of ocean acidification on copepods. *Aquat. Toxicol.* 196:17–24

42. Dutkiewicz S, Morris JJ, Follows MJ, Scott J, Levitan O, et al. 2015. Impact of ocean acidification on the structure of future phytoplankton communities. *Nat. Clim. Chang.* 5:1002–6

20. Connects acidification to fundamental ecological principles and conceptual models of population- and community-level effects.

21. Systematic assessment of a dozen different ocean-based mitigation and adaptation solutions to climate change.

25. Authoritative guide to improve reproducibility and consistency of ocean acidification experiments and data across communities.

39. Synthesis covering marine fish respiratory acid-base, early-life, metabolic, reproductive, and neurosensory physiological impacts.

43. Busch DS, McElhany P. 2017. Using mineralogy and higher-level taxonomy as indicators of species sensitivity to pH: a case-study of Puget Sound. *Elementa* 5:53
44. Gobler CJ, Baumann H. 2016. Hypoxia and acidification in ocean ecosystems: coupled dynamics and effects on marine life. *Biol. Lett.* 12:20150976
45. **Kroeker KJ, Kordas RL, Crim R, Hendriks IE, Ramajo L, et al. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. *Glob. Change Biol.* 19:1884–96**
46. Sunday JM, Calosi P, Dupont S, Munday PL, Stillman JH, Reusch TBH. 2013. Evolution in an acidifying ocean. *Trends Ecol. Evol.* 29(2):117–25
47. Boyd PW, Collins S, Dupont S, Fabricius K, Gattuso JP, et al. 2018. Experimental strategies to assess the biological ramifications of multiple drivers of global ocean change—a review. *Glob. Change Biol.* 24:2239–61
48. Kroeker KJ, Kordas RL, Crim RN, Singh GG. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. *Ecol. Lett.* 13:1419–34
49. Busch DS, McElhany P. 2016. Estimates of the direct effect of seawater pH on the survival rate of species groups in the California Current ecosystem. *PLOS ONE* 11:e0160669
50. Chevin L-M, Collins S, Lefèvre F. 2013. Phenotypic plasticity and evolutionary demographic responses to climate change: taking theory out to the field. *Funct. Ecol.* 27:967–79
51. Murray C, Baumann H. 2018. You better repeat it: complex CO_2 × temperature effects in Atlantic silverside offspring revealed by serial experimentation. *Diversity* 10:69
52. Guscelli E, Spicer JI, Calosi P. 2019. The importance of inter-individual variation in predicting species' responses to global change drivers. *Ecol. Evol.* 9:4327–39
53. Kelly MW, Padilla-Gamiño JL, Hofmann GE. 2013. Natural variation, and the capacity to adapt to ocean acidification in the keystone sea urchin *Strongylocentrotus purpuratus*. *Glob. Change Biol.* 19:2536–46
54. Vargas CA, Lagos NA, Lardies MA, Duarte C, Manríquez PH, et al. 2017. Species-specific responses to ocean acidification should account for local adaptation and adaptive plasticity. *Nat. Ecol. Evol.* 1:0084
55. Hollarsmith JA, Buschmann AH, Camus C, Grosholz ED. 2020. Varying reproductive success under ocean warming and acidification across giant kelp (*Macrocystis pyrifera*) populations. *J. Exp. Mar. Biol. Ecol.* 522:151247
56. Calosi PS, Melatunan S, Turner LM, Artioli Y, Davidson RL, et al. 2017. Regional adaptation defines sensitivity to future ocean acidification. *Nat. Comm.* 8:13994
57. Busch DS, Maher M, Thibodeau P, McElhany P. 2014. Shell condition and survival of Puget Sound pteropods are impaired by ocean acidification conditions. *PLOS ONE* 9:e105884
58. McLaskey AK, Keister JE, McElhany P, Olson MB, Busch DS, et al. 2016. Development of *Euphausia pacifica* (krill) larvae is impaired under pCO_2 levels currently observed in the Northeast Pacific. *Mar. Ecol. Prog. Ser.* 555:65–78
59. Pespeni MH, Chan F, Menge BA, Palumbi SR. 2013. Signs of adaptation to local pH conditions across an environmental mosaic in the California Current Ecosystem. *Integr. Comp. Biol.* 53:857–70
60. Bednaršek N, Feely RA, Reum JCP, Peterson B, Menkel J, et al. 2014. *Limacina helicina* shell dissolution as an indicator of declining habitat suitability due to ocean acidification in the California Current Ecosystem. *Proc. R. Soc. B* 281:20140123
61. Bednaršek N, Feely RA, Beck MW, Glippa O, Kanerva M, Engström-Öst J. 2018. El Niño-related thermal stress coupled with upwelling-related ocean acidification negatively impacts cellular to population-level responses in pteropods along the California Current System with implications for increased bioenergetic costs. *Front. Mar. Sci.* 5:486
62. Engström-Öst J, Glippa O, Feely RA, Kanerva M, Keister JE, et al. 2019. Eco-physiological responses of copepods and pteropods to ocean warming and acidification. *Sci. Rep.* 9:4748
63. Sanford E, Kelly MW. 2011. Local adaptation in marine invertebrates. *Annu. Rev. Mar. Sci.* 3:509–35
64. Moore RS, Kaletsky R, Murphy CT. 2019. Piwi/PRG-1 argonaute and TGF-β mediate transgenerational learned pathogenic avoidance. *Cell* 177:1827–41.e1812

45. Comprehensive meta-analysis synthesizing the results of 228 studies examining biological responses to ocean acidification.

65. Perez MF, Lehner B. 2019. Intergenerational and transgenerational epigenetic inheritance in animals. *Nat. Cell Biol.* 21:143–51
66. Strader ME, Wong JM, Kozal LC, Leach TS, Hofmann GE. 2019. Parental environments alter DNA methylation in offspring of the purple sea urchin, *Strongylocentrotus purpuratus*. *J. Exp. Mar. Biol. Ecol.* 517:54–64
67. Wong JM, Johnson KM, Kelly MW, Hofmann GE. 2018. Transcriptomics reveal transgenerational effects in purple sea urchin embryos: Adult acclimation to upwelling conditions alters the response of their progeny to differential pCO_2 levels. *Mol. Ecol.* 27:1120–37
68. Wong JM, Kozal LC, Leach TS, Hoshijima U, Hofmann GE. 2019. Transgenerational effects in an ecological context: conditioning of adult sea urchins to upwelling conditions alters maternal provisioning and progeny phenotype. *J. Exp. Mar. Bio. Ecol.* 517:65–77
69. **Pespeni MH, Sanford E, Gaylord B, Hill TM, Hosfelt JD, et al. 2013. Evolutionary change during experimental ocean acidification. *PNAS* 110:6937–43**
70. Collins S. 2011. Competition limits adaptation and productivity in a photosynthetic alga at elevated CO_2. *Proc. R. Soc. B* 278:247–55
71. Lohbeck KT, Riebesell U, Reusch TBH. 2012. Adaptive evolution of a key phytoplankton species to ocean acidification. *Nat. Geosci.* 5:346–51
72. Schaum CE, Collins S. 2014. Plasticity predicts evolution in a marine alga. *Proc. R. Soc. B* 281:20141486
73. Wahl M, Saderne V, Sawall Y. 2016. How good are we at assessing the impact of ocean acidification in coastal systems? Limitations, omissions and strengths of commonly used experimental approaches with special emphasis on the neglected role of fluctuations. *Mar. Freshwater Res.* 67:25–36
74. **Przeslawski R, Byrne M, Mellin C. 2015. A review and meta-analysis of the effects of multiple abiotic stressors on marine embryos and larvae. *Glob. Change Biol.* 21:2122–40**
75. Hamilton SL, Kashef NS, Stafford DM, Mattiasen EG, Kapphahn LA, et al. 2019. Ocean acidification and hypoxia can have opposite effects on rockfish otolith growth. *J. Exp. Mar. Biol. Ecol.* 521:151245
76. Trigg SA, McElhany P, Maher PM, Perez D, Busch DS, Nichols KM. 2019. Uncovering mechanisms of global ocean change effects on the Dungeness crab (*Cancer magister*) through metabolomics analysis. *Sci. Rep.* 9:10717
77. McElhany P. 2016. CO_2 sensitivity experiments are not sufficient to show an effect of ocean acidification. *ICES J. Mar. Sci.* 74:926–28
78. Rivero-Calle S, Gnanadesikan A, Del Castillo CE, Balch WM, Guikema SD. 2015. Multidecadal increase in North Atlantic coccolithophores and the potential role of rising CO_2. *Science* 350:1533–37
79. Beare D, McQuatters-Gollop A, van der Hammen T, Machiels M, Teoh SJ, Hall-Spencer JM. 2013. Long-term trends in calcifying plankton and pH in the North Sea. *PLOS ONE* 8:e61175
80. Howes EL, Stemmann L, Assailly C, Irisson JO, Dima M, Bijma J, Gattuso JP. 2015. Pteropod time series from the North Western Mediterranean (1967–2003): impacts of pH and climate variability. *Mar. Ecol. Prog. Ser.* 531:193–206
81. Thibodeau PS, Steinberg DK, Stammerjohn SE, Hauri C. 2019. Environmental controls on pteropod biogeography along the Western Antarctic Peninsula. *Limnol. Oceanogr.* 64:S240–56
82. de Moel H, Ganssen GM, Peeters FJC, Jung SJA, Kroon D, et al. 2009. Planktic foraminiferal shell thinning in the Arabian Sea due to anthropogenic ocean acidification? *Biogeosciences* 6:1917–25
83. Wall-Palmer D, Hart MB, Smart CW, Sparks RSJ, Le Friant A, et al. 2012. Pteropods from the Caribbean Sea: variations in calcification as an indicator of past ocean carbonate saturation. *Biogeosciences* 9:309–15
84. Howes EL, Eagle RA, Gattuso J-P, Bijma J. 2017. Comparison of Mediterranean pteropod shell biometrics and ultrastructure from historical (1910 and 1921) and present day 2012 samples provides baseline for monitoring effects of global change. *PLOS ONE* 12:e0167891
85. Osborne EB, Thunell RC, Gruber N, Feely RA, Benitez-Nelson C. 2020. Climatic modulation of anthropogenic ocean acidification in the California Current. *Nature* 13:43–49
86. Beaufort L, Probert I, de Garidel-Thoron T, Bendif EM, Ruiz-Pino D, et al. 2011. Sensitivity of coccolithophores to carbonate chemistry and ocean acidification. *Nature* 476:80–83

69. Experiments with purple sea urchins showing rapid evolution at genetic level in response to acidification.

74. Meta-analysis of multi-stressor studies of temperature, salinity, and pH targeting marine embryos to larvae.

87. Krumhardt KM, Lovenduski NS, Freeman NM, Bates NR. 2016. Apparent increase in coccolithophore abundance in the subtropical North Atlantic from 1990 to 2014. *Biogeosciences* 13:1163–77

88. Silbiger NJ, Donahue MJ, Brainard RE. 2017. Environmental drivers of coral reef carbonate production and bioerosion: a multi-scale analysis. *Ecology* 98:2547–60

89. Doo S, Kealoha A, Andersson AJ, Cohen A, Hicks TL, et al. 2020. The challenges of detecting and attributing ocean acidification impacts on marine ecosystems. *ICES J. Mar. Sci.* 2020:fsaa094

90. Silbiger NJ, Guadayol Ò, Thomas FIM, Donahue MJ. 2014. Reefs shift from net accretion to net erosion along a natural environmental gradient. *Mar. Ecol. Prog. Ser.* 515:33–44

91. Meseck SL, Alix JH, Swiney KM, Long WC, Wikfors GH, Foy RJ. 2016. Ocean acidification affects hemocyte physiology in the tanner crab (*Chionoecetes bairdi*). *PLOS ONE* 11:e0148477

92. Sutton AJ, Feely RA, Maenner-Jones S, Musielwicz S, Osborne J, et al. 2019. Autonomous seawater pCO_2 and pH time series from 40 surface buoys and the emergence of anthropogenic trends. *Earth Syst. Sci. Data* 11:421–39

93. Hall-Spencer JM, Rodolfo-Metalpa R, Martin S, Ransome E, Fine M, et al. 2008. Volcanic carbon dioxide vents show ecosystem effects of ocean acidification. *Nature* 454:96–99

94. Fabricius KE, Langdon C, Uthicke S, Humphrey C, Noonan S, et al. 2011. Losers and winners in coral reefs acclimatized to elevated carbon dioxide concentrations. *Nat. Clim. Chang.* 1(3):165–69

95. Enochs IC, Manzello DP, Donham EM, Kolodziej G, Okano R, et al. 2015. Shift from coral to macroalgae dominance on a volcanically acidified reef. *Nat. Clim. Chang.* 5:1083–88

96. Teixidó N, Gambi MC, Parravacini V, Kroeker K, Micheli F, et al. 2018. Functional biodiversity loss along natural CO_2 gradients. *Nat. Commun.* 9(1):5149

97. Kroeker KJ, Micheli F, Gambi MC. 2013. Ocean acidification causes ecosystem shifts via altered competitive interactions. *Nat. Clim. Chang.* 3(2):156–59

97. Experiments on acidification-driven competition for substrate between recruitment of calcareous species and fleshy seaweeds.

98. Brustolin MC, Nagelkerken I, Moitinho Ferreira C, Urs Goldenberg S, Ullah H, Fonseca G. 2019. Future ocean climate homogenizes communities across habitats through diversity loss and rise of generalist species. *Glob. Chang. Biol.* 25(10):3539–48

99. Micheli F, Halpern BS. 2005. Low functional redundancy in coastal marine assemblages. *Ecol. Lett.* 8(4):391–400

100. Baggini C, Issaris Y, Salomidi M, Hall-Spencer J. 2015. Herbivore diversity improves benthic community resilience to ocean acidification. *J. Exp. Mar. Bio. Ecol.* 469:98–104

101. Doubleday ZA, Nagelkerken I, Coutts MD, Goldenberg SU, Connell SD. 2019. A triple trophic boost: how carbon emissions indirectly change a marine food chain. *Glob. Chang. Biol.* 25(3):978–84

102. Alsterberg C, Eklöf JS, Gamfeldt L, Havenhand JN, Sundbäck K. 2013. Consumers mediate the effects of experimental ocean acidification and warming on primary producers. *PNAS* 110(21):8603–8

103. Ghedini G, Russell BD, Connell SD. 2015. Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances. *Ecol. Lett.* 18(2):182–87

104. Harvey BP, Moore PJ. 2017. Ocean warming and acidification prevent compensatory response in a predator to reduced prey quality. *Mar. Ecol. Prog. Ser.* 563:111–22

105. Jellison BM, Gaylord B. 2019. Shifts in seawater chemistry disrupt trophic links within a simple shoreline food web. *Oecologia* 190(4):955–67

106. Bach LT, Alvarez-Fernandez S, Hornick T, Stuhr A, Riebesell U. 2017. Simulated ocean acidification reveals winners and losers in coastal phytoplankton. *PLOS ONE* 12(11):e0188198

107. Taucher J, Haunost M, Boxhammer T, Bach LT, Algueró-Muñiz M, Riebesell U. 2017. Influence of ocean acidification on plankton community structure during a winter-to-summer succession: an imaging approach indicates that copepods can benefit from elevated CO_2 via indirect food web effects. *PLOS ONE* 12(2):e0169737

108. Boyd PW, Lennartz ST, Glover DM, Doney SC. 2015. Biological ramifications of climate-change-mediated oceanic multi-stressors. *Nat. Clim. Chang.* 5(1):71–79

109. Boxhammer T, Taucher J, Bach LT, Achterberg EP, Algueró-Muñiz M, et al. 2018. Enhanced transfer of organic matter to higher trophic levels caused by ocean acidification and its implications for export production: a mass balance approach. *PLOS ONE* 13(5):e0197502

110. Sswat M, Stiasny MH, Taucher J, Algueró-Muñiz M, Bach LT, et al. 2018. Food web changes under ocean acidification promote herring larvae survival. *Nat. Ecol. Evol.* 2(5):836–40

111. Rossoll D, Bermúdez R, Hauss H, Schulz KG, Riebesell U, et al. 2012. Ocean acidification-induced food quality deterioration constrains trophic transfer. *PLOS ONE* 7(4):e34737

112. Riebesell U, Aberle-Malzahn N, Achterberg EP, Algueró-Muñiz M, Alvarez-Fernandez S, et al. 2018. Toxic algal bloom induced by ocean acidification disrupts the pelagic food web. *Nat. Clim. Chang.* 8(12):1082–86

113. Fu FX, Tatters AO, Hutchins DA. 2012. Global change and the future of harmful algal blooms in the ocean. *Mar. Ecol. Prog. Ser.* 470:207–33

114. De'ath G, Lough JM, Fabricius KE. 2009. Declining coral calcification on the Great Barrier Reef. *Science* 323(5910):116–19

115. Albright R, Caldeira L, Hosfelt J, Kwiatkowski L, Maclaren JK, et al. 2016. Reversal of ocean acidification enhances net coral reef calcification. *Nature* 531(7594):362–65

116. Silbiger NJ, Guadayol Ò, Thomas FIM, Donahue MJ. 2016. A novel μCT analysis reveals different responses of bioerosion and secondary accretion to environmental variability. *PLOS ONE* 11:e0153058

117. Mollica NR, Guo W, Cohen AL, Huang K-F, Foster GL, et al. 2018. Ocean acidification affects coral growth by reducing skeletal density. *PNAS* 115(8):1754–59

118. Enochs IC, Manzello DP, Kolodziej G, Noonan SHC, Valentino L, Fabricius KE. 2016. Enhanced macroboring and depressed calcification drive net dissolution at high-CO_2 coral reefs. *Proc. R. Soc. B* 283(1842):20161742

119. Shamberger KEF, Cohen AL, Golbuu Y, McCorkle DC, Lentz SJ, Barkley HC. 2014. Diverse coral communities in naturally acidified waters of a Western Pacific reef. *Geophys. Res. Lett.* 41:499–504

120. Connell SD, Kroeker KJ, Fabricius KE, Kline DI, Russell BD. 2013. The other ocean acidification problem: CO_2 as a resource among competitors for ecosystem dominance. *Philos. Trans. R. Soc. Lond. B* 368(1627):20120442

121. Ober GT, Diaz-Pulido G, Thornber C. 2016. Ocean acidification influences the biomass and diversity of reef-associated turf algal communities. *Mar. Biol.* 163(10):204

122. Doropoulos C, Ward S, Diaz-Pulido G, Hoegh-Guldberg O, Mumby PJ. 2012. Ocean acidification reduces coral recruitment by disrupting intimate larval-algal settlement interactions. *Ecol. Lett.* 15(4):338–46

123. Crook ED, Kroeker KJ, Potts DC, Rebolledo-Vieyra M, Hernandez-Terrones LM, Paytan A. 2016. Recruitment and succession in a tropical benthic community in response to in-situ ocean acidification. *PLOS ONE* 11(1):e0146707

124. Noonan SHC, Kluibenschedl A, Fabricius KE. 2018. Ocean acidification alters early successional coral reef communities and their rates of community metabolism. *PLOS ONE* 13(5):e0197130

125. Inoue S, Kayanne H, Yamamoto S, Kurihara H. 2013. Spatial community shift from hard to soft corals in acidified water. *Nat. Clim. Chang.* 3(7):683–87

126. Barkley HC, Cohen AL, Golbuu Y, Starczak VR, DeCarlo TM, Shamberger KEF. 2015. Changes in coral reef communities across a natural gradient in seawater pH. *Sci. Adv.* 1(5):e1500328

127. Sunday JM, Fabricius KE, Kroeker KJ, Anderson KM, Brown NE, et al. 2016. Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. *Nat. Clim. Chang.* 7:81–85

128. Fabricius KE, De'ath G, Noonan S, Uthicke S. 2014. Ecological effects of ocean acidification and habitat complexity on reef-associated macroinvertebrate communities. *Proc. Biol. Sci.* 281(1775):20132479

129. Nagelkerken I, Russell BD, Gillanders BM, Connell SD. 2015. Ocean acidification alters fish populations indirectly through habitat modification. *Nat. Clim. Chang.* 6:89–93

130. Munday PL, Cheal AJ, Dixson DL, Rummer JL, Fabricius KE. 2014. Behavioural impairment in reef fishes caused by ocean acidification at CO_2 seeps. *Nat. Clim. Chang.* 4(6):487–92

131. Waldbusser GG, Steenson RA, Green MA. 2011. Oyster shell dissolution rates in estuarine waters: effects of pH and shell legacy. *J. Shellfish Res.* 30(3):659–69

132. Waldbusser GG, Hales B, Langdon CJ, Haley BA, Schrader P, et al. 2015. Ocean acidification has multiple modes of action on bivalve larvae. *PLOS ONE* 10(6):e0128376

133. Milazzo M, Rodolfo-Metalpa R, Chan VBS, Fine M, Alessi C, et al. 2014. Ocean acidification impairs vermetid reef recruitment. *Sci. Rep.* 4:4189

134. Legrand E, Riera P, Lutier M, Coudret J, Grall J, Martin S. 2017. Species interactions can shift the response of a maerl bed community to ocean acidification and warming. *Biogeosciences* 14(23):5359–76

135. Koch M, Bowes G, Ross C, Zhang X-H. 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. *Glob. Change Biol.* 19(1):103–32

136. Berg P, Delgard ML, Polsenaere P, McGlathery KJ, Doney SC, Berger AC. 2019. Dynamics of benthic metabolism, O_2, and pCO_2 in a temperate seagrass meadow. *Limnol. Oceanogr.* 64:2586–604

137. Campbell JE, Fourqurean JW. 2014. Ocean acidification outweighs nutrient effects in structuring seagrass epiphyte communities. *J. Ecol.* 102(3):730–37

138. Zimmerman RC, Hill VJ, Gallegos CL. 2015. Predicting effects of ocean warming, acidification, and water quality on Chesapeake region eelgrass. *Limnol. Oceanogr.* 60:1781–804

139. Cox TE, Díaz-Castañeda V, Martin S, Alliouane S, Mahacek P, et al. 2017. Effects of in situ CO_2 enrichment on epibiont settlement on artificial substrata within a *Posidonia oceanica* meadow. *J. Exp. Mar. Bio. Ecol.* 497:197–211

140. Martínez-Crego B, Olivé I, Santos R. 2014. CO_2 and nutrient-driven changes across multiple levels of organization in *Zostera noltii* ecosystems. *Biogeosciences* 11(24):7237–49

141. Burnell OW, Russell BD, Irving AD, Connell SD. 2013. Eutrophication offsets increased sea urchin grazing on seagrass caused by ocean warming and acidification. *Mar. Ecol. Prog. Ser.* 485:37–46

142. Eklöf JS, Havenhand JN, Alsterberg C, Gamfeldt L. 2015. Community-level effects of rapid experimental warming and consumer loss outweigh effects of rapid ocean acidification. *Oikos* 124(8):1040–49

143. Hughes BB, Lummis SC, Anderson SC, Kroeker KJ. 2018. Unexpected resilience of a seagrass system exposed to global stressors. *Glob. Chang. Biol.* 24(1):224–34

144. Barton A, Waldbusser G, Feely R, Weisberg S, Newton J, et al. 2015. Impacts of coastal acidification on the Pacific Northwest shellfish industry and adaptation strategies implemented in response. *Oceanography* 25(2):146–59

145. Gosling SN. 2013. The likelihood and potential impact of future change in the large-scale climate-earth system on ecosystem services. *Environ. Sci. Policy* 27(Suppl. 1):S15–S31

146. Scholes RJ. 2016. Climate change and ecosystem services. *WIREs Clim. Change* 7(4):537–50

147. Narita D, Rehdanz K, Tol RSJ. 2012. Economic costs of ocean acidification: a look into the impacts on global shellfish production. *Clim. Change* 113(3):1049–63

148. Cooley SR, Doney SC. 2009. Anticipating ocean acidification's economic consequences for commercial fisheries. *Environ. Res. Lett.* 4(2):024007

149. Cooley SR, Rheuban JE, Hart DR, Luu V, Glover DM, et al. 2015. An integrated assessment model for helping the United States sea scallop (*Placopecten magellanicus*) fishery plan ahead for ocean acidification and warming. *PLOS ONE* 10(5):e0124145

150. Dupont S, Hall E, Calosi P, Lundve B. 2014. First evidence of altered sensory quality in a shellfish exposed to decreased pH relevant to ocean acidification. *J. Shellfish Res.* 33(3):857–61

151. Lemasson AJ, Hall-Spencer JM, Kuri V, Knights AM. 2019. Changes in the biochemical and nutrient composition of seafood due to ocean acidification and warming. *Mar. Environ. Res.* 143:82–92

152. Ashur MM, Johnston NK, Dixson DL. 2017. Impacts of ocean acidification on sensory function in marine organisms. *Integr. Comp. Biol.* 57(1):63–80

153. Mangi SC, Lee J, Pinnegar JK, Law RJ, Tyllianakis E, Birchenough SNR. 2018. The economic impacts of ocean acidification on shellfish fisheries and aquaculture in the United Kingdom. *Environ. Sci. Policy* 86:95–105

154. Narita D, Rehdanz K. 2017. Economic impact of ocean acidification on shellfish production in Europe. *J. Environ. Plan. Manag.* 60(3):500–18

155. Fernandes JA, Papathanasopoulou E, Hattam C, Queirós AM, Cheung WWWL, et al. 2017. Estimating the ecological, economic and social impacts of ocean acidification and warming on UK fisheries. *Fish Fisheries* 18(3):389–411

156. Moore C. 2015. Welfare estimates of avoided ocean acidification in the U.S. mollusk market. *J. Agric. Resour. Econ.* 40(1):50–62

157. Rheuban JE, Doney SC, Cooley SR, Hart DR. 2018. Projected impacts of future climate change, ocean acidification, and management on the US Atlantic sea scallop (*Placopecten magellanicus*) fishery. *PLOS ONE* 13(9):e0203536

158. Punt AE, Foy RJ, Dalton MG, Long WC, Swiney KM. 2016. Effects of long-term exposure to ocean acidification conditions on future southern Tanner crab (*Chionoecetes bairdi*) fisheries management. *ICES J. Mar. Sci.* 73(3):849–64

159. Lam VWY, Cheung WWL, Sumaila UR. 2016. Marine capture fisheries in the Arctic: winners or losers under climate change and ocean acidification? *Fish Fisheries* 17(2):335–57

160. Marshall KN, Kaplan IC, Hodgson EE, Hermann A, Busch DS, et al. 2017. Risks of ocean acidification in the California Current food web and fisheries: ecosystem model projections. *Glob. Chang. Biol.* 23(4):1525–39

161. Hodgson EE, Kaplan IC, Marshall KN, Leonard J, Essington TE, et al. 2018. Consequences of spatially variable ocean acidification in the California Current: Lower pH drives strongest declines in benthic species in southern regions while greatest economic impacts occur in northern regions. *Ecol. Model.* 383(10):106–17

162. Olsen E, Kaplan IC, Ainsworth C, Fay G, Gaichas S, et al. 2018. Ocean futures under ocean acidification, marine protection, and changing fishing pressures explored using a worldwide suite of ecosystem models. *Front. Mar. Sci.* 5:64

163. Seijo JC, Villanueva-Poot R, Charles A. 2016. Bioeconomics of ocean acidification effects on fisheries targeting calcifier species: a decision theory approach. *Fish. Res.* 176:1–14

164. Talloni-Álvarez NE, Sumaila UR, Le Billon P, Cheung WWL. 2019. Climate change impact on Canada's Pacific marine ecosystem: the current state of knowledge. *Mar. Policy* 104:163–76

165. Mathis JT, Cooley SR, Lucey N, Colt S, Ekstrom J, et al. 2015. Ocean acidification risk assessment for Alaska's fishery sector. *Prog. Oceanogr.* 136:71–91

166. Ekstrom JA, Suatoni L, Cooley SR, Pendleton LH, Waldbusser GG, et al. 2015. Vulnerability and adaptation of US shellfisheries to ocean acidification. *Nat. Clim. Chang.* 5:207–14

167. Hilmi N, Allemand D, Cinar M, Cooley S, Hall-Spencer JM, et al. 2014. Exposure of Mediterranean countries to ocean acidification. *Water* 6(6):1719–44

168. Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S. 2017. Coral reef ecosystems under climate change and ocean acidification. *Front. Mar. Sci.* 4:158

169. Cesar H, Burke L, Pet-Soede L. 2003. *The economics of worldwide coral reef degradation*. Tech. Rep., Cesar Environ. Econ. Consult., Arnhem, Neth.

170. Costanza R, d'Arge R, de Groot R, Farber S, Grasso M, et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387(6630):253–60

171. Pendleton LH, Thébaud O, Mongruel RC, Levrel H. 2016. Has the value of global marine and coastal ecosystem services changed? *Mar. Policy* 64:156–58

172. Yates KK, Zawada DG, Smiley NA, Tiling-Range G. 2017. Divergence of seafloor elevation and sea level rise in coral reef ecosystems. *Biogeosciences* 14(6):1739–72

173. Beck MW, Losada IJ, Menéndez P, Reguero BG, Díaz-Simal P, Fernández F. 2018. The global flood protection savings provided by coral reefs. *Nat. Commun.* 9(1):2186

174. Brander LM, Rehdanz K, Tol RSJ, Van Beukering PJH. 2012. The economic impact of ocean acidification on coral reefs. *Clim. Change Econ.* 3:1–29

175. Pendleton L, Hoegh-Guldberg O, Albright R, Kaup A, Marshall P, et al. 2019. The Great Barrier Reef: vulnerabilities and solutions in the face of ocean acidification. *Reg. Stud. Mar. Sci.* 31:100729

176. Lemasson AJ, Fletcher S, Hall-Spencer JM, Knights AM. 2017. Linking the biological impacts of ocean acidification on oysters to changes in ecosystem services: a review. *J. Exp. Mar. Bio. Ecol.* 492:49–62

177. Milazzo M, Fine M, La Marca EC, Alessi C, Chemello R. 2017. Drawing the line at neglected marine ecosystems: ecology of vermetid reefs in a changing ocean. In *Marine Animal Forests*, Vol. 8, ed. S Rossi, L Bramanti, A Gori, C Orejas, pp. 345–67. Cham, Switz.: Springer Int. Publ.

178. Grabowski JH, Brumbaugh RD, Conrad RF, Keeler AG, Opaluch JJ, et al. 2012. Economic valuation of ecosystem services provided by oyster reefs. *Bioscience* 62(10):900–9

162. End-to-end ecosystem modeling examining ocean acidification in context of marine ecosystem-based management.

179. California Ocean Protection Council. 2018. *State of California Ocean Acidification Action Plan*. California Ocean Protection Council, Sacramento, CA
180. Hurd CL. 2015. Slow-flow habitats as refugia for coastal calcifiers from ocean acidification. *J. Phycol.* 51(4):599–605
181. Macreadie PI, Jarvis J, Trevathan-Tackett SM, Bellgrove A. 2017. Seagrasses and macroalgae: importance, vulnerability and impacts. In *Climate Change Impacts on Fisheries and Aquaculture*, Vol. 52, ed. BF Phillips, M Pérez-Ramírez, pp. 729–70. Chichester, UK: Wiley
182. Morris RL, Graham TDJ, Kelvin J, Ghisalberti M, Swearer SE. 2020. Kelp beds as coastal protection: wave attenuation of *Ecklonia radiata* in a shallow coastal bay. *Ann. Bot.* 125(2):235–46
183. Gao K, Beardall J, Häder D-P, Hall-Spencer JM, Gao G, Hutchins DA. 2019. Effects of ocean acidification on marine photosynthetic organisms under the concurrent influences of warming, UV radiation, and deoxygenation. *Front. Mar. Sci.* 6:322
184. Garrard SL, Beaumont NJ. 2014. The effect of ocean acidification on carbon storage and sequestration in seagrass beds; a global and UK context. *Mar. Pollut. Bull.* 86(1–2):138–46
185. Kapsenberg L, Cyronak T. 2019. Ocean acidification refugia in variable environments. *Glob. Chang. Biol.* 25(10):3201–14
186. Herr D, Galland GR. 2009. *The Ocean and Climate Change: Tools and Guidelines for Action*. Gland, Switz.: Int. Union Conserv. Nature
187. Howard J, McLeod E, Thomas S, Eastwood E, Fox M, et al. 2017. The potential to integrate blue carbon into MPA design and management. *Aquat. Conserv.* 27:100–15
188. Pacella SR, Brown CA, Waldbusser GG, Labiosa RG, Hales B. 2018. Seagrass habitat metabolism increases short-term extremes and long-term offset of CO_2 under future ocean acidification. *PNAS* 115(15):3870–75
189. Sippo JZ, Maher DT, Tait DR, Holloway C, Santos IR. 2016. Are mangroves drivers or buffers of coastal acidification? Insights from alkalinity and dissolved inorganic carbon export estimates across a latitudinal transect: mangroves buffer coastal acidification. *Glob. Biogeochem. Cycles* 30(5):753–66
190. Sabine CL. 2018. Good news and bad news of blue carbon. *PNAS* 115(15):3745–46
191. Luisetti T, Turner RK, Andrews JE, Jickells TD, Kröger S, et al. 2019. Quantifying and valuing carbon flows and stores in coastal and shelf ecosystems in the UK. *Ecosyst. Serv.* 35:67–76
192. Beaumont NJ, Jones L, Garbutt A, Hansom JD, Toberman M. 2014. The value of carbon sequestration and storage in coastal habitats. *Estuar. Coast. Shelf Sci.* 137:32–40
193. Lavery PS, Mateo M-Á, Serrano O, Rozaimi M. 2013. Variability in the carbon storage of seagrass habitats and its implications for global estimates of blue carbon ecosystem service. *PLOS ONE* 8(9):e73748
194. Pendleton L, Donato DC, Murray BC, Crooks S, Jenkins WA, et al. 2012. Estimating global "blue carbon" emissions from conversion and degradation of vegetated coastal ecosystems. *PLOS ONE* 7(9):e43542
195. Hall-Spencer JM, Harvey BP. 2019. Ocean acidification impacts on coastal ecosystem services due to habitat degradation. *Emerging Top. Life Sci.* 3(2):197–206
196. Barry JP, Widdicombe S, Hall-Spencer JM. 2011. Effects of ocean acidification on marine biodiversity and ecosystem function. In *Ocean Acidification*, ed. J-P Gattuso, L Hansson, pp. 192–209. Oxford, UK: Oxford Univ. Press
197. Broszeit S, Hattam C, Beaumont N. 2016. Bioremediation of waste under ocean acidification: reviewing the role of *Mytilus edulis*. *Mar. Pollut. Bull.* 103(1–2):5–14
198. Gascuel D, Cheung WWL. 2019. Marine biodiversity and ecosystem services: the large gloomy shadow of climate change. In *Predicting Future Oceans*, ed. AM Cisneros-Montemayor, WWL Cheung, Y Ota, pp. 79–85. Amsterdam: Elsevier
199. Koenigstein S, Ruth M, Gößling-Reisemann S. 2016. Stakeholder-informed ecosystem modeling of ocean warming and acidification impacts in the Barents Sea region. *Front. Mar. Sci.* 3:93
200. Rodrigues LC, van den Bergh JCJM, Ghermandi A. 2013. Socio-economic impacts of ocean acidification in the Mediterranean Sea. *Mar. Policy* 38:447–56
201. Ruckelshaus M, Doney SC, Galindo HM, Barry JP, Chan F, et al. 2013. Securing ocean benefits for society in the face of climate change. *Mar. Policy* 40:154–59

202. Urquhart J, Acott T. 2014. A sense of place in cultural ecosystem services: the case of Cornish fishing communities. *Soc. Nat. Resour.* 27(1):3–19

203. Pörtner H-O, Karl DM, Boyd PW, Cheung W, Lluch-Cota SE, et al. 2014. Ocean systems. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. VR Barros, CB Field, DJ Dokken, MD Mastrandrea, KJ Mach, et al., pp. 411–84. Cambridge, UK: Cambridge Univ. Press

204. Arctic Monitoring and Assessment Programme (AMAP). 2018. *AMAP Assessment 2018: Arctic Ocean Acidification*. Tromsø, Norway: AMAP

205. Garcia Rodrigues J, Conides AJ, Rivero Rodriguez S, Raicevich S, Pita P, et al. 2017. Marine and coastal cultural ecosystem services: knowledge gaps and research priorities. *One Ecosyst.* 2:e12290

206. Klain SC, Chan KMA. 2012. Navigating coastal values: participatory mapping of ecosystem services for spatial planning. *Ecol. Econ.* 82:104–13

207. Billé R, Kelly R, Biastoch A, Harrould-Kolieb E, Herr D, et al. 2013. Taking action against ocean acidification: a review of management and policy options. *Environ. Manag.* 52(4):761–79

208. Cooley SR, Ono CR, Melcer S, Roberson J. 2016. Community-level actions that can address ocean acidification. *Front. Mar. Sci.* 2:128

209. Gattuso J-P, Magnan A, Billé R, Cheung WWL, Howes EL, et al. 2015. Contrasting futures for ocean and society from different anthropogenic CO_2 emissions scenarios. *Science* 349(6243):aac4722

210. Magnan AK, Billé R, Cooley SR, Kelly R, Pörtner HO, et al. 2015. *Intertwined ocean and climate: implications for international climate negotiation*s. Policy Brief 04/15, Inst. Sustain. Dev. Int. Relat., Paris

211. Strong AL, Kroeker KJ, Teneva LT, Mease LA, Kelly RP. 2014. Ocean acidification 2.0: managing our changing coastal ocean chemistry. *Bioscience* 64(7):581–92

212. Harrould-Kolieb ER, Herr D. 2012. Ocean acidification and climate change: synergies and challenges of addressing both under the UNFCCC. *Clim. Policy* 12(3):378–89

213. Potts T. 2018. Climate change, ocean acidification and the marine environment. In *International Marine Environmental Law and Policy*, ed. D Hassan, S Karim, pp. 87–100. London: Taylor & Francis

214. Pratchett MS, Hoey AS, Wilson SK. 2014. Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. *Curr. Opin. Environ. Sustain.* 7:37–43

215. Kelly RP, Foley MM, Fisher WS, Feely RA, Halpern BS, et al. 2011. Mitigating local causes of ocean acidification with existing laws. *Science* 332:1036–37

216. Kelly RP, Caldwell MR. 2013. Ten ways states can combat ocean acidification (and why they should). *Harvard Environ. Law Rev.* 37:57–103

217. Alleway HK, Gillies CL, Bishop MJ, Gentry RR, Theuerkauf SJ, Jones R. 2019. The ecosystem services of marine aquaculture: valuing benefits to people and nature. *Bioscience* 69(1):59–68

218. Doyle B. 2018. *Tsleil-Waututh Nation: restoring shellfish harvest opportunities in Burrard Inlet, Canada*. Paper presented at the 2018 Salish Sea Ecosystem Conference, Seattle, WA, April 4–6

219. Green MA, Waldbusser GG, Reilly SL, Emerson K, O'Donnell S. 2009. Death by dissolution: sediment saturation state as a mortality factor for juvenile bivalves. *Limnol. Oceanogr.* 54(4):1037–47

220. Waldbusser GG, Powell EN, Mann R. 2013. Ecosystem effects of shell aggregations and cycling in coastal waters: an example of Chesapeake Bay oyster reefs. *Ecology* 94(4):895–903

221. Nat. Acad. Sci. Eng. Med. 2019. *A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs*. Washington, DC: Nat. Acad. Press

222. Kroeker KJ, Carr MH, Raimondi PT, Caselle JE, Washburn L, et al. 2019. Planning for change: assessing the potential role of marine protected areas and fisheries management approaches for resilience management in a changing ocean. *Oceanography* 32(3):116–125

223. Ritzman J, Brodbeck A, Brostrom S, McGrew S, Dreyer S, et al. 2018. Economic and sociocultural impacts of fisheries closures in two fishing-dependent communities following the massive 2015 U.S. West Coast harmful algal bloom. *Harmful Algae* 80:35–45

224. Munang R, Thiaw I, Alverson K, Liu J, Han Z. 2013. The role of ecosystem services in climate change adaptation and disaster risk reduction. *Curr. Opin. Environ. Sustain.* 5(1):47–52

225. Carriger JF, Yee SH, Fisher WS. 2019. An introduction to Bayesian networks as assessment and decision support tools for managing coral reef ecosystem services. *Ocean Coast. Manag.* 177:188–99

226. Silver JM, Arkema KK, Griffin RM, Lashley B, Lemay M, et al. 2019. Advancing coastal risk reduction science and implementation by accounting for climate, ecosystems, and people. *Front. Mar. Sci.* 6:556
227. Riebesell U, Gattuso J-P. 2015. Lessons learned from ocean acidification research. *Nat. Clim. Chang.* 5:12–14
228. Gattuso J-P, Brewer PG, Hoegh-Guldberg O, Kleypas JA, Pörtner H-O, Schmidt DN. 2014. Cross-chapter box on ocean acidification. In *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, ed. VR Barros, CB Field, DJ Dokken, MD Mastrandrea, KJ Mach, et al., pp. 129–31. Cambridge, UK: Cambridge Univ. Press
229. Bednaršek N, Feely RA, Tolimieri N, Hermann AJ, Siedlecki SA, et al. 2017. Exposure history determines pteropod vulnerability to ocean acidification along the US West Coast. *Sci. Rep.* 7:4526
230. Bednaršek N, Ohman MD. 2015. Changes in pteropod distributions and shell dissolution across a frontal system in the California Current System. *Mar. Ecol. Prog. Ser.* 523:93–103
231. Feely RA, Alin SR, Carter B, Bednaršek N, Hales B, et al. 2016. Chemical and biological impacts of ocean acidification along the west coast of North America. *Estuar. Coast. Shelf Sci.* 183A:260–70

RELATED RESOURCES

Feely RA, Doney SC. 2014. Ocean acidification: the other CO_2 problem. *Limnol. Oceanogr. Web Lect.* 3(1):1–59. **https://doi.org/10.4319/lol.2011.rfeely_sdoney.5**

Global Ocean Acidification Observing Network (GOA-ON). **http://www.goa-on.org/**

International Atomic Energy Agency (IAEA). 2020. Ocean Acidification International Coordination Centre (OA-ICC). *International Atomic Energy Agency (IAEA)*. **https://www.iaea.org/services/oa-icc**

International Ocean Carbon Coordination Project (IOCCP). **http://www.ioccp.org/**

NOAA Ocean Acidification Program (OAP). **https://oceanacidification.noaa.gov/**

Northeast Coastal Acidification Network (NECAN). **http://www.necan.org/**

Ocean Conservancy Ocean Acidification Program. 2020. Confronting ocean acidification: The chemistry of our ocean is changing. *Ocean Conservancy*. **https://oceanconservancy.org/ocean-acidification/**

United Nations Development Programme (UNDP). 2020. Goal 14: Life Below Water. *United Nations Development Programme (UNDP).* **https://www.undp.org/content/undp/en/home/sustainable-development-goals/goal-14-life-below-water.html**

United Nations Development Programme (UNDP). 2020. Sustainable Development Goal 14: Conserve and sustainably use the oceans, seas and marine resources for sustainable development. *United Nations Development Programme (UNDP)*. **https://sustainabledevelopment.un.org/sdg14**