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Abstract (Maximum of 150 words; currently 149 words)

Rising atmospheric 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. Based on 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. Emphasis in this review is on both current scientific understanding and knowledge gaps, highlighting directions for future research and recognizing the information needs of policymakers and stakeholders.

Main Text

(target 10,000 words; currently ~8900 words, excluding references, and ~1200 additional word equivalents from 3 moderately sized figures and 1 table estimated at ~300 words each)

(target 150 references; currently ~220. Note that references numbered by appearance in text, but with author names left in text for now to ease editing and revisions; will be removed for final version)

1. INTRODUCTION

Present-day atmospheric carbon dioxide (CO_2) levels of more than 410 ppm in 2020 are nearly 50% higher than pre-industrial concentrations, and the current elevated levels and rapid growth rates are unprecedented in the past several million years of the geological record. 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 (1) (Le Quéré et al., 2018). 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 inventories (2) (Gruber et al., 2019), document ocean uptake of 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 towards more acidic, lower pH conditions and lower saturation states for carbonate minerals used in many marine organism shells and skeletons (3) (Zeebe and Wolf-Gladrow, 2001). Extensive observational systems are now in place or being built for monitoring seawater CO_2 chemistry and acidification both for the global open-ocean and some coastal systems (4, 5) (Tilbrook et al., 2019, Cross et al., 2019).

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 (6) (Royal Society, 2005). Reported acidification effects span from changes in cellular metabolism, organism physiology, and sensory perception to population and community, biogeochemical, and ecosystem-level dynamics (7) (Gattuso and Hannson, 2011). 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 socio-economic 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 (8) (Doney et al., 2009). It builds from a number of recent synthesis efforts in journal special issues (9) (Mathis et al., 2015a) and national and international scientific assessments (10, 11, 12, 13) (Ciais et al., 2013, Hoegh-Guldberg et al., 2014, Jewett and Romanou, 2017; Bindoff et al., 2019). There are also a number of excellent review papers on various topical aspects of ocean acidification, a selection including articles on physiological responses (14) (Falkenberg et al., 2018), effects on invertebrate and fish larvae (15) (Espinel-Velasco et al., 2018), animal behavior (16) (Nagelkerken and Munday, 2016), nitrogen cycle (17) (Wannicke et al., 2018), coral reefs (18) (Kleypas, 2019), ecological theory (19) (Gaylord et al., 2015), and policy solutions (20) (Gattuso et al., 2018).

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 effects of acidification (Section 3), community and ecosystem impacts on key food-web interactions such as competition, predator-prey interactions, and disease (Section 4), risks to human communities that rely on the natural resources provided by the ocean via fisheries, aquaculture, and culture and social connections (Section 5), and a brief summary (Section 6).

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 (3, 21) (Zeebe and Wolf-Gladrow 2001, Millero 2007). At seawater pH levels (~8), CO_2 added to seawater reacts with water to form bicarbonate, HCO_3^-, and hydrogen ions, H^+:

$$CO_2 + H_2O \rightarrow HCO_3^- + H^+ \qquad \text{(Eq 1)}$$

The release of hydrogen ions acts to increase acidity and lower seawater pH, defined as:

$$pH = -log_{10}[H^+] \quad \text{(Eq 2)}$$

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

$$CO_3^{2-} + H^+ \rightarrow HCO_3^- \quad \text{(Eq 3)}$$

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-} (22) (Hurd et al. 2019).

Acidification has been shown to affect many types of marine organisms that form shells and skeletons from calcium carbonate minerals ($CaCO_3$). The solubility of carbonate minerals:

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

can be expressed as a saturation state:

$$\Omega = \frac{[CO_3^{2-}][Ca^{2+}]}{K_{sp}} \quad \text{(Eq. 5)}$$

where $\Omega<1$ indicates undersaturation with respect to thermodynamic equilibrium and the expectation that unprotected carbonate materials will dissolve. There are multiple forms of carbonate minerals with different solubilities, with calcite being less soluble than aragonite and amorphous carbonate.

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, dissolved inorganic carbon (DIC), and alkalinity. DIC is the total concentration of CO_2 gas and the inorganic carbon acid-base products resulting from hydration (Eq. 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 as well as standardized approaches for mimicking acidification chemical changes in biological manipulation studies (23) (Riebesell et al. 2010).

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 about 10 billion metric tons carbon per year result in an increase in atmospheric CO_2 of roughly 2 ppm/year or 0.5% per year (1) (Le Quéré et al., 2018). 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 (10) (Ciais et al., 2013).

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 a number of open-ocean locations (24) (Benway et al., 2019) and analysis of global surface ocean CO_2 observational networks (25) (Bakker et al., 2016). As a result, surface pH and carbonate ion are declining (Figure 1), and surface ocean pH is estimated to have dropped on average globally by about 0.1 units from the pre-industrial era to present.

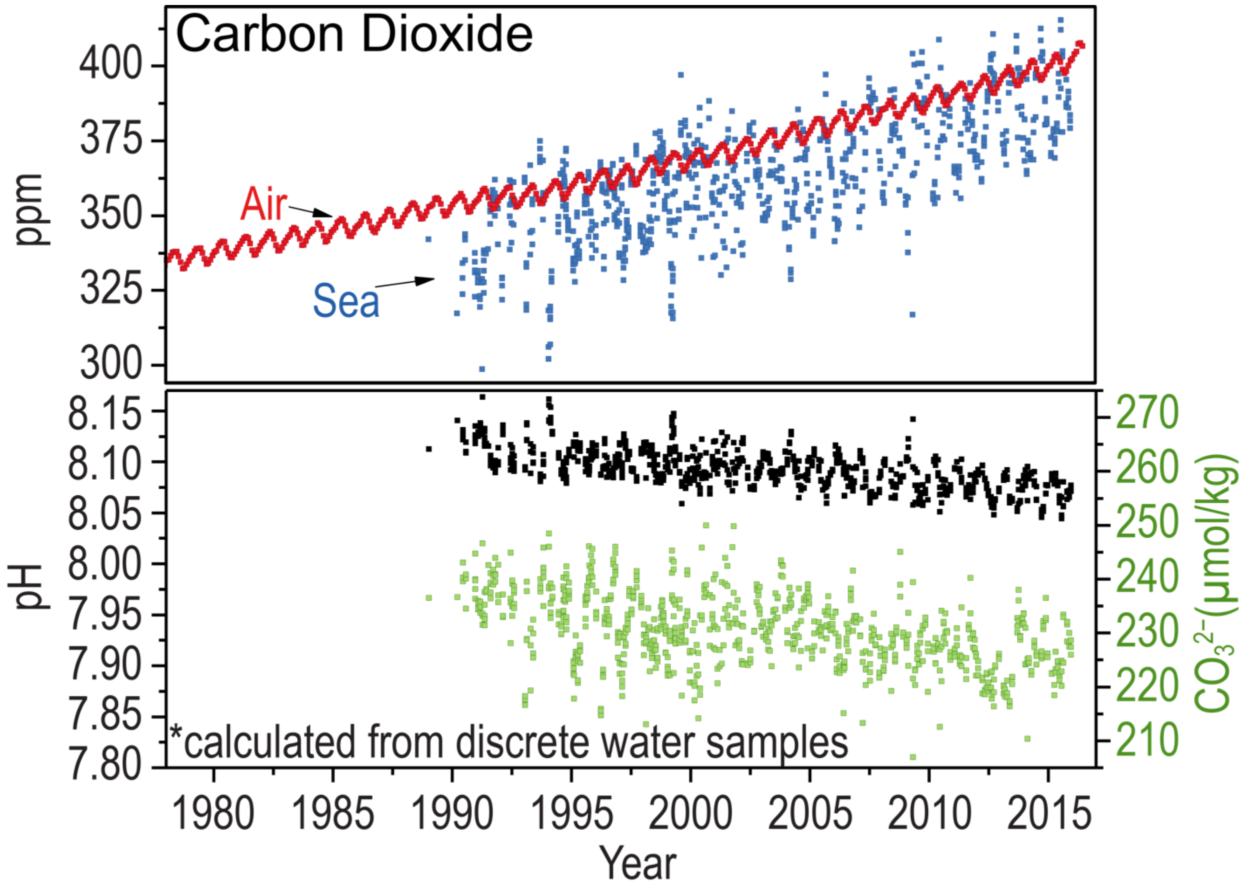


Figure 1. Trends in surface (<50m) ocean carbonate chemistry calculated from observations obtained at the Hawai‘i Ocean Time-series (HOT) Program in the North Pacific over 1988–2015. The upper panel shows the linked increase in atmospheric (red points) and seawater (blue points) CO_2 concentrations. The bottom panel shows a decline in seawater pH (black points, primary y-axis) and carbonate ion 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 source: NOAA and Jewett and Romanou, 2017). Note: final version of published figure shown here is slightly different than the electronic version shared from authors so that file will need minor redrafting to match published version.

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 and subsequent respiration of sinking organic matter at depth (26, 27) (Feely et al., 2008; Feely et al., 2018). 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 (27, 28) (Feely et al., 2010; Feely et al., 2018). Coastal acidification can also occur because of low-alkalinity freshwater fluxes from rivers, groundwater, and ice melt (29, 30, 31) (Gledhill et al., 2015; Rheuban et al., 2019; Evans et al., 2013). Coastal systems tend to exhibit large amplitude variations of seawater chemistry on smaller time and space scales (32) (Waldbusser and Salisbury, 2014).

3. ORGANISMAL RESPONSES

The literature on organismal sensitivity to high CO_2 conditions has expanded rapidly (33) (Browman, 2016), and, in marine biology, ocean acidification has moved from being a frontier science to a mature sub-discipline exploring species sensitivity at finer detail than a decade ago. Research on how high-CO_2 conditions influence fishes exemplifies this trend. While some fish appear able to compensate for disturbance to acid-base balance under high-CO_2 conditions, they express unexpected sensitivity in otolith growth, mitochondrial function, metabolic rate, larval yolk consumption, activity, and neurosensory and behavioral endpoints, including settlement and post-settlement processes, to current and near future CO_2 levels (15, 34) (Espinel-Velasco et al. 2018, Heuer and Grosell 2014). Altered fish physiology in high CO_2 conditions may disrupt systems related to the neurochemical $GABA_A$ (35) (Tresguerres and Hamilton 2017). Substantial variation in sensitivity exists within and between fish species (36, 37) (Cattano et al. 2018, Esbaugh 2018).

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 (38) (Wang et al. 2018). Variation also exists within and between phytoplanton groups: diazotrophs, diatoms, and other large photoplankton including dinoflagellates have higher growth rates in high CO_2 conditions, while coccolithophores, *Synechoccucus*, and *Prochlorococus* do not, though there is wide variation in response within groups (39) (Dutkiewicz et al. 2015). 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 calcium carbonate that species produce (i.e., calcite, aragonite) is not strongly linked to species sensitivity (40) (Busch and McElhany 2017).

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 (41) (Gobler and Baumann 2016). A trend toward slower survival, growth, and development is also evident with simultaneous exposure to high CO_2 and elevated temperature (42) (Kroeker et al. GCB 2013).

As displayed in Figure 2, a variety of experimental strategies are being used to characterize the sensitivity of species to acidification now and in the future (43, 44) (Sunday et al. 2013; Boyd et al. 2018). 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 (33) (Browman 2016). Below we discuss recent experimental and field breakthroughs through the lens of three challenges or tensions in designing and interpreting organismal sensitivity studies.

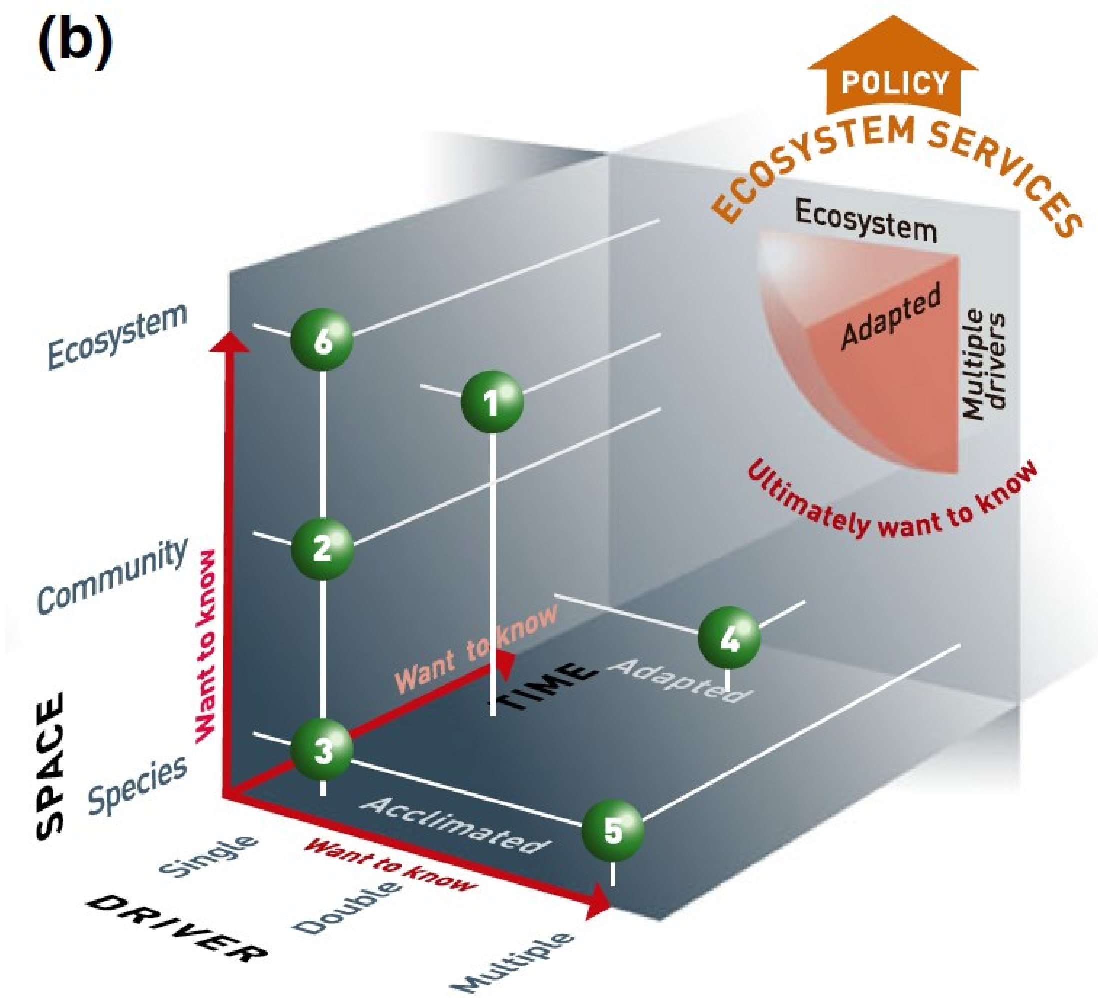


Figure 2. Progress in studies of ocean global change overlaid on the property-property space (termed the "RG cube") developed by (45) Riebesell and Gattuso (2015). The cube represents different experimental strategies: 1 mesocosms, including FOCE experiments; 2 competition experiments; 3 typical acclimated species under acidification; 4 long-term (>400 generations) microevolution studies; 5 multiple driver studies; 6 sites of CO_2 natural enrichment such as CO_2 seeps. Figure from (44) Boyd et al. 2018. Note: final version of published figure shown here from .png file is slightly different than the electronic eps and pdf versions shared from authors; those files will need some redrafting.

3.1 Characterizing present versus projected future sensitivity to ocean acidification

Ocean acidification is a long-term, press perturbation on marine ecosystems that will play out on the scale of decades, centuries, and longer. 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 (46, 47) (Kroeker et al. 2010, Busch and McElhany 2016). While 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 the evolutionary demographic responses to climate change and ocean acidification requires consideration of phenotypic plasticity and natural selection across environments (48) (Chevin et al. 2013).

Discovery of individuals or populations more resilient to high CO_2 conditions has arisen by testing the repeatability within and between identical sensitivity experiments (49, 50) (Murray and Baumann 2018, Guscelli et al. 2019) and among populations of the same species. Some populations living in naturally high CO_2 environments express less sensitivity to high CO_2 experimental treatments (51, 52, 53) (Kelly et al. 2013, Vargas et al. 2017, Hollarsmith et al. 2020). 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 (54) (Calosi et al. 2017).

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 (28) (Feely et al. 2010), finds that individuals are negatively impacted by carbonate chemistry conditions already experienced by local populations (55, 56) (Busch et al. 2014, McLaskey et al. 2016). Field collections show that some species express sensitivity to the high CO_2 conditions already observed along the western coast of the United States, while others express signs of potential adaptation (57, 58, 59, 60) (Pespeni et al. 2013 Int. Comp. Biology, Bednaršek et al. 2014, Bednaršek et al. 2018, Engström-Öst et al. 2019).

Organisms may evolve much more quickly than we recently thought possible (61) (Sanford and Kelly 2011), especially via epigenetics (62, 63) (Moore et al. 2019, Perez and Lehner 2019). Groundbreaking work in the purple urchin *Strongylocentrotus purpuratus* has shown transgenerational plasticity in response to high CO_2 exposure, with documented transgenerational impacts on the epigenome (64) (Strader et al. 2019), gene expression (65) (Wong et al. 2018), and phenotype (66) (Wong et al. 2019). Other work in the purple urchin has found evidence of additive genetic variance for size and genome-wide selection under different CO_2 conditions (51, 67) (Kelly et al. 2013, Pespeni et al. 2013b). Multigenerational experimental evolution studies are feasible for microbes and have indicated that adaption to high CO_2 conditions is possible (68, 69, 70) (Collins 2011, Lohbeck et al. 2012, Schaum and Collins 2014).

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 (47) (Busch and

McElhany 2016). For example, results from experiments that hold environmental conditions static may not be fully relevant to the dynamic conditions that organisms experience in nature (71) (Wahl et al. 2016). 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 (47) (Busch and McElhany 2016). 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 (33) (Browman 2016).

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. (44) (Boyd et al. 2018) describe two complementary paths: 1) 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 2) 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 (44, 72) (Boyd et al. 2018; Przeslawski et al. 2015). For example, the sensitivity of reproduction in kelp to pH sensitivity can depend on temperature conditions

(53) (Hollarsmith et al. 2020). 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 (41) (Gobler and Baumann 2016). High CO_2 and reduced oxygen content can have the opposite effects on otolith size in juvenile rockfish (73) (Hamilton et al. 2019).

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, but not actually demonstration of ocean acidification impacts on marine species (74) (McElhany 2016). 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 (75) (Rivero-Calle et al. 2015) and many failing to do so (76, 77, 78) (Beare et al. 2013, Howes et al. 2015, Thibodeau et al. 2019). Historical records of pteropods and foraminfera show correlation of shell conditions with reconstructed carbonate chemistry conditions (79, 80, 81, 82) (de Moel et al. 2009, Wall-Palmer et al. 2012, Howes et al. 2017, Osborne et al. In press), though such correlations do not yet exist for coral reefs and are contradictory for coccolithophores (83, 84) (Beaufort et al. 2011, Krumhardt et al. 2016).

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 (85) (Silbiger et al. 2017). It is also likely that the thresholds at which carbonate chemistry conditions will impact many species have not yet been crossed. 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 (58, 86) (Bednaršek et al. 2014, Silbiger et al. 2014). As understanding of the sublethal signatures of exposure to high-CO_2 conditions increases, such as alterations in molecular markers of stress (60) (Engström-Öst et al. 2019), the immune system (87) (Meseck et al. 2016), or shell state (58) (Bednaršek et al. 2014), 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 (88) (Sutton et al. 2019).

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 (19) (Gaylord et al. 2015). Results from both mesocosm experiments and studies using natural gradients in carbonate chemistry strongly suggest ocean acidification increases primary producer biomass and decreases taxonomic diversity (89, 90, 91) (Hall-Spencer et al. 2008, Fabricius et al. 2011, Enochs et al. 2015), although many species are able to survive in high CO_2 conditions. The decreases in taxonomic diversity are likely to have functional consequences (92) (Teixidó et al. 2018), although the effects on ecosystem function are just beginning to be explored. In general, there is a trend towards the homogenization of community structure in space and time, which has been attributed to altered competitive interactions (93, 94) (Kroeker et al. Nat. Clim. 2013; Brustolin et al. 2019). Although functional redundancy is generally considered to be quite low in marine ecosystems (95) (Micheli & Halpern 2005), redundancy within trophic groups can limit community shifts associated with acidification if resilient species are able to compensate functionally for more vulnerable species (96) (Baggini et al. 2015).

Increased primary production associated with high pCO_2 can boost production across multiple trophic levels (97) (Doubleday et al. 2019), 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, 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 (98, 99) (Alsterberg et al. 2013; Ghedini et al. 2015). 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 (97) (Doubleday et al. 2019). 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 it for predator survival (100) (Harvey and Moore 2017). Altered behavior in marine consumers (e.g., predator avoidance) caused by exposure to conditions of ocean acidification can also weaken indirect trophic linkages (e.g., trophic cascades), causing cascading effects on community structure and function (101) (Jellison and Gaylord 2019).

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 (Table 1).

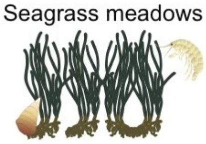
Critical habitat	**Community/Ecosystem Property or Process**	**Trend**	**References**
Pelagic foodwebs 	Community structure	Δ	102, 103, 104
	Primary productivity	⇧	105
	Secondary productivity	⇧	103, 105,106
	Harmful algal blooms	⇧	108,109
Coral Reefs 	Community structure	Δ	90, 91,115, 121
	Net ecosystem calcification	⬇	111, 112, 114
	Bioerosion of habitat forming species	⇧	114
	Recruitment of habitat forming species	⬇	118-120
	Competition of habitat forming species with macroalgae	⇧	90, 91, 116, 119
	Structural complexity	⬇	123,124
	Taxonomic diversity	⬇	90, 91, 124
Other carbonate reefs 	Net calcification	⬇	129, 130
	Dissolution	⇧	127
	Recruitment of habitat forming species	⬇	128, 129
	Competition of habitat forming species with macroalgae	⇧	130
Seagrass meadows 	Primary productivity	⇧	131
	Competition of habitat forming species with macroalgae	⇧⬇	89, 132, 135
	Top-down control/grazing	⇧	98, 136-138

Table 1: General trends in key community and ecosystem properties and processes in response to ocean acidification from the primary literature. Triangle = change (neither increase or decrease), upward arrow = increase, downward arrow = decrease. Trends are primarily derived from studies of multiple-species mesocosm experiments or observational studies in naturally acidified ecosystems. The literature cited is not

exhaustive but represents key studies highlighting the community and ecosystem effects in the critical habitats featured in this review.

4.2 Pelagic food webs

The community structure of planktonic communities is very likely to change with acidification (102, 103) (Bach et al. 2017; Taucher et al. 2017), 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 (104) (Boyd et al. 2015), 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 (39) (Dutkiewicz et al. 2015), but it is not yet known whether microbial changes will alter global ecosystem functions such as net primary production and export or air-sea gas exchange.

Whole-community mesocosm studies have demonstrated increased productivity at the base of pelagic food webs (102) (Bach et al. 2017), leading to increased productivity of higher trophic levels (105) (Boxhammer et al. 2018), including enhanced survival and biomass of larval fish that are directly negatively impacted by acidification (106) (Sswat et al. 2018). 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 (58) (Bednarsek et al. 2014). Field studies across upwelling gradients indicate that pteropods may already be experiencing shell dissolution in low pH waters along the California Current (58) (Bednarsek et al. 2014). In addition, the nutritional quality of some zooplankton may suffer with ocean acidification, despite increased production or abundance (107) (Rossoll et al. 2012). 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 (108) (Riebesell et al. 2018). Ocean acidification can either increase the toxicity of the harmful algae (109) (Fu et al. 2012) or increase the abundance of toxic bloom forming species through altered competitive interactions (108) (Riebesell et al. 2018). 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 (e.g., carbonate production minus dissolution) and bioerosion of the habitat-forming coral species. 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 (110) (De’ath et al. 2009). 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. (2016) (111) recently demonstrated that net community calcification increases when the seawater carbonate saturation states are raised to pre-industrial levels. This suggests that coral reefs have already suffered declines in net calcification associated with ocean acidification (111) (Albright et al. 2016).

There is growing evidence that bioerosion may be more sensitive to changes in carbonate chemistry than carbonate production (112) (Silbiger et al. 2016). This is potentially due to changes in the density or structural integrity of the coral skeletons produced in lower carbonate saturation state (113) (Mollica et al. 2018). Indeed, increased bioerosion has been demonstrated in naturally more acidic locations (91, 114, 115) (Enochs et al. 2015, Enochs et al. 2016; Shamberger et al. 2014), which suggests minor shifts in 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 (90, 91) (Fabricius et al. 2011, Enochs et al. 2015). Potential shifts in the competitive balance between corals and macroalgae is 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 (116, 117) (Connell et al. 2013, Ober et al. 2016), 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 (118) (Doropoulos et al. 2012). 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 (119) (Crook et al. 2016) versus chemical control (120) (Noonan et al. 2018).

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 (90, 91) (Fabricius et al. 2011, Enochs et al. 2015) or even soft corals (121) (Inoue et al. 2013) 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 (115) (Shamberger et al. 2014). 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 (122) (Barkley et al. 2015). 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 (123) (Sunday et al. 2016). 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 (90, 124) (Fabricius et al. 2011; Fabricius et al. 2014). 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 (125) (Nagelkerken et al. 2015). While 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 (126) (Munday et al. 2014). 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 (127) (Waldbusser et al. 2011), and high CO_2 impacts on oyster larvae may negatively influence oyster recruitment (128) (Waldbusser et al. 2015). Vermetid reefs, built by vermetid gastropods cemented together via crustose coralline algae, and the habitat structure and ecosystem services the reefs provide are threatened by ocean acidification, which reduces the recruitment and enhances shell dissolution for the gastropods (129) (Milazzo et al. 2014). Maerl beds (also called Rhodolith beds), in which the habitat forming species is an unattached, branching crustose coralline algae, 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 (130) (Legrand et al. 2017).

4.5 Seagrass beds

Seagrasses are largely expected to benefit from acidification (131) (Koch et al. 2013), but the effects on associated species could mediate the community and ecosystem effects. Of concern is the response of epiphytic and macroalgae that compete with seagrasses (132) (Campbell and Fourqurean 2014). Additionally, seagrasses are sensitive to water quality and benthic light levels, so acidification effects on plankton dynamics may also play a role (133) (Zimmermann et al. 2015). While calcareous epiphytes are expected to decrease with acidification (89, 132) (Hall-Spencer et al. 2008, Cambpell and Fourquerean 2014), enhanced seagrass production may protect some calcareous species in the diffusive boundary layer in low flow environments (134) (Cox et al. 2017). In contrast, fleshy epiphytic algae are largely expected to benefit from high pCO_2 (135) (Martinez-Crego et al. 2014). Mesocosm studies of temperate seagrass communities, dominated by fleshy epiphytic and macroalgae, suggest that grazers can keep epiphytic algae in check (98) (Alsterberg et al. 2013), and in some cases, acidification may actually increase top-down control (136) (Burnell et al. 2013). Despite the calcareous skeletons of several of the grazers in seagrass ecosystems, evidence suggests high tolerance of the macroinvertebrate taxa (137, 138) (Eklof et al. 2015, Hughes et al. 2018).

5. Risks to Human Communities

5.1 Introduction – Impacts on socially and ecologically important marine resources, environments, and people

The emergence of ocean acidification impacts on the Pacific oyster industry in the Pacific Northwest United States in the mid-2000s (139) (Barton et al. 2015) 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, like 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 (140, 141) (Gosling 2013, Scholes 2016). 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 co-benefit of improving management of marine systems and resources (Figure 3).

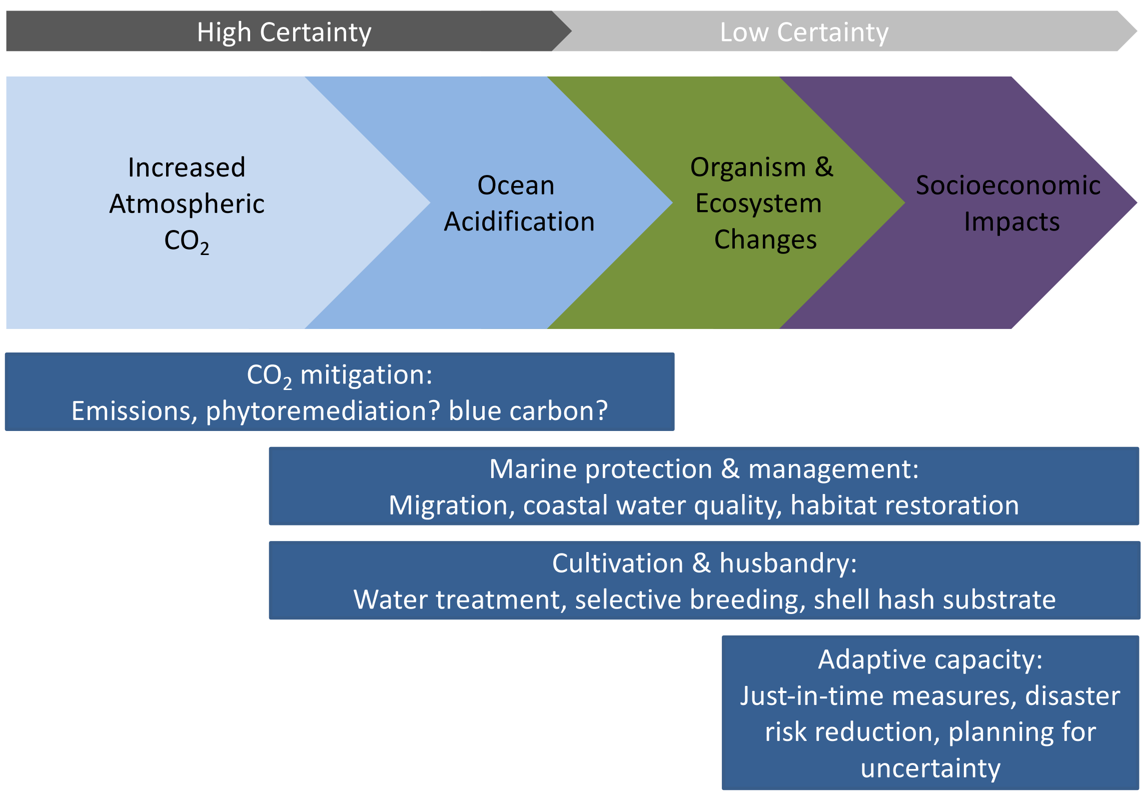


Figure 3. Impact pathway from increased atmospheric CO_2 to changes in social-ecological systems. Gray band indicates level of scientific certainty. Dark blue blocks show the groups of interventions that are frequently proposed to directly decrease harm from ocean acidification on social-ecological systems. Adapted from (142) (Pörtner et al. 2014)

5.2 Fisheries and food webs

Both real-world and laboratory evidence suggests 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 upwelling, supported over 3,000 jobs and $270 million in economic activity per year (139) (Barton et al. 2015). Because marine mollusks comprise 9% of the total world fishery production by value (143) (Narita et al. 2012), ocean acidification's potential effects on shellfish harvests and provisioning ecosystem services became a research theme (144) (Cooley & Doney 2009).

Ocean acidification caused decreases in bivalve reproduction, survival of juvenile bivalves, or delayed maturation of adults can alter recruitment, harvestable biomass, maximum sustainable yield, and economic value of shellfish fisheries (145) (Cooley et al. 2015). Other impacts such as alterations in the taste or other food qualities of shellfish (146, 147) (Dupont et al. 2014, Lemasson et al. 2019), or behavioral changes in finfish species (16, 148) (Nagelkerken and Munday, 2016; Ashur et al. 2017), 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 about 10-28% losses for both US and UK mollusk harvests annually (144, 149) (Cooley & Doney 2009, Mangi et al. 2018). Model estimates of welfare losses from ocean acidification impacts on shellfish range widely: US losses are estimated at $400 million USD and global losses from $6 billion-$100 billion USD annually (143) (Narita et al. 2012), with an annual projected impact of over $1 billion USD for Europe by 2100 (150) (Narita & Rehdanz 2017). Ocean acidification and warming together on UK fisheries are projected to decrease shellfish biomass by 30% by 2020, with overall employment losses related to shellfish and finfish declines from 3-20% by 2050 (151) (Fernandes et al. 2017). United State economic damages by the end of the century for mollusk fishery losses are on the same order as those for increased hurricane damages (152) (Moore 2015).

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. (145) (Cooley et al. 2015) found for the United States northeast sea scallop a substantial decline in harvests by 2050 under business-as-usual CO_2 emissions and contemporary harvest rules, if ocean acidification decreases recruitment and slows growth, although adjustments to management can help increase biomass somewhat (153) (Rheuban et al. 2018). 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 (154) (Punt et al. 2016). 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 2000-2050 under SRES A2, because poleward movement of temperate fisheries will increase Arctic fishery revenues more than calcifier mortality will drive losses (155) (Lam et al. 2016).

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 (156) (Marshall et al. 2017) and different consequences for port-based economies in the region (157) (Hodgson et al. 2018). Using a suite of regional ecosystem models from around the world, Olsen et al. (158) (Olsen et al. 2018) 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. (159) (Seijo et al. 2016) recommend considering possible ocean acidification effects when defining fisheries management strategies, and Olsen et al. (158) (Olsen et al. 2018) and Talloni-Alvarez et al. (160) (Talloni-Alvarez et al. 2019) 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 (161, 162) (Mathis et al. Prog. Oceanogr. 2015; Ekstrom et al. 2015) and developing nations with artisanal fishing fleets in the Mediterranean (163) (Hilmi et al. 2014). 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.

5.3 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 (164) (Hoegh-Guldberg et al. 2017). The worldwide value of coral reefs, however, is difficult to pin down; published estimates range from $29.8 billion/year (165) (Cesar et al. 2003) to $376 billion/year (166) (Costanza et al. 1997), although Pendleton et al. (167) (Pendleton et al. 2016) 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 (168) (Yates et al. 2017) and endangering human safety and property (169) (Beck et al. 2018). Without coastal protection from reefs, specifically, flood damages from 100-year storm events would nearly double, rising to $272 billion (169) (Beck et al. 2018). Brander et al. (170) (Brander et al. 2012) 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 non-economic methods to evaluate risks posed by changes in coral reef health or coverage. Pendleton et al. (167) (Pendleton et al. 2016) 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 are needed to decrease risk of harm from climate-associated reef loss (171) (Pendleton et al. 2019).

Vermetid and shellfish reefs suffer from ocean acidification as well as coastal disturbances like trampling, sedimentation, dredging, and pollutants or poisons (129, 172, 173) (Milazzo et al. 2014, Lemasson et al. 2017, Milazzo et al. 2017). Both types of reefs are "ecosystem engineers" that stabilize sediments, provide habitat for benthic ecosystems, and store organic carbon (129, 172) (Milazzo et al. 2014, Lemasson et al. 2017). Oyster reefs provide an estimated value of $5500–$99,000 per hectare per year via shoreline stabilization, habitat creation, and water filtration (174) (Grabowski et al. 2012). Ocean acidification's economic ramifications for vermetid and shellfish reefs have not been explored, but the reefs' important non-economic environmental roles have made them focal areas for preservation and restoration.

5.4 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 (20, 175) (Gattuso et al. 2018, California Ocean Protection Council 2018). Submerged aquatic vegetation's ability to create habitat and slow water flow in coastal regions is better established (176, 177, 178) (Hurd 2015, Macreadie et al. 2017, Morris et al. 2019) than its ability to consistently capture and sequester carbon dioxide or modulate local pH swings, where evidence is mixed (179, 180, 181) (Gao et al. 2019, Garrard & Beaumont 2014, Kapsenberg & Cyronak 2019). 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 (182) (Herr 2009) and may help mitigate ocean acidification in localized areas (20) (Gattuso et al. 2018).

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 (183, 184, 185) (Howard et al. 2017, Pacella et al. 2018, Sippo et al. 2016). However, local details strongly influence the amount and duration of carbon captured (184, 186) (Pacella et al. 2018, Sabine 2018). 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 (187, 188) (Luisetti et al. 2019; Beaumont et al. 2014). Conservation and restoration of coastal systems to sequester carbon are being evaluated and promoted as part of overall carbon mitigation efforts (189, 190) (Lavery et al. 2013, Pendleton et al. 2012), which may indirectly benefit ocean acidification.

5.5 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 (191) (Hall-Spencer & Harvey 2019) decreases ecosystem resilience and compromises regulating services including habitat provision, nutrient cycling, and carbon storage (192) (Barry et al. 2011). 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 (193) (Broszeit et al. 2016). Ocean acidification could strongly affect critical or unique environments like 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 (192) (Barry et al. 2011). Outcomes for ecosystems like phytoplankton populations are harder to anticipate, because ocean acidification and other drivers reshuffle species composition (192) (Barry et al. 2011), and it is difficult to determine how ecosystem function will change. Gascuel and Cheung (194) (Gascuel and Cheung 2019) caution that loss of ocean biodiversity that decreases regulating functions and functional redundancy can decrease not only system productivity, but also stability and resiliency; and it can raise the risk of large-scale ecosystem shifts in ecosystem structure and decrease the resilience.

Losses of marine biodiversity from ocean acidification impacts on marine systems can also affect cultural services (195, 196, 197, 198) (Koenigstein et al. 2016, Rodrigues et al. 2013, Ruckelshaus et al. 2013, Urquhart & Acott 2014). 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 (142, 199, 200, 201) (Pörtner et al. 2014, AMAP 2018, Garcia Rodrigues et al. 2017, Klain & Chan 2012). Encouragingly, though, Koenigstein et al. (195) (Koenigstein et al. 2016) 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.

5.6 Interventions and adaptations

Nearly every study that identifies potential harm from ocean acidification to ecosystem services also identifies possible interventions (Figure 3). There is consensus across the scientific community that the foremost solution to ocean acidification is to cut atmospheric CO_2 emissions (202, 203, 204, 205, 206) (Billé et al. 2013, Cooley et al. 2016, Gattuso et al. 2015, Magnan et al. 2015, Strong et al. 2014). At present, the international body of climate policy (within the U.N. Framework Convention on Climate Change, or UNFCCC) does not explicitly address ocean acidification, although numerous analyses agree that ocean acidification falls within UNFCCC-relevant concerns (205, 207, 208) (Magnan et al. 2015, Harrould-Kolieb & Herr 2012, Potts 2018).

Adaptive management of marine systems is often cited as a possible intervention. 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 (164) (Hoegh-Guldberg et al. 2017), and a critical challenge is the balance of protection versus sustainable human resource use for impacted systems (209) (Pratchett et al. 2014). In coastal zones, the ocean acidification interacts with other anthropogenic and natural drivers like pollution, freshwater runoff, and coastal plankton blooms (210) (Kelly et al. 2011), but many existing water quality regulatory policies can start to help address coastal acidification locally (211) (Kelly & Caldwell 2013).

Husbandry of captive or wild species also offers intervention opportunities. Encouraging shellfish aquaculture industry growth has been proposed as an adaptation to ocean acidification and warming (212) (Alleway et al. 2019). 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 (139) (Barton et al. 2015). Amending tidal flats where shellfish grow to maturity with ground shell material provides substrate for larval settlement and may modulate ocean acidification locally (213, 214, 215) (Doyle 2018, Green et al. 2009, Waldbusser et al. 2013). Submerged aquatic vegetation may also capture CO_2 locally through photosynthesis while providing habitat (181) (Kapsenberg and Cyronak 2019). 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 (216) (National Academies of Sciences, Engineering, and Medicine et al. 2019). As with water quality, existing management levers might also improve resilience to ocean acidification and hypoxia (217) (Kroeker et al. 2019 Oceanography).

The least well-developed group of interventions involves increasing the adaptive capacity of human communities that depend on marine resources. Just-in-time adaptations such as the industry-science partnerships undertaken by the United States Pacific oyster shellfish fishery to identify and address ocean acidification do work (5, 139) (Cross et al. 2019, Barton et al. 2015), but so do planned, end-to-end structures that support communities that may experience future losses from ocean change (5) (Cross et al. 2019). 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 socio-economic systems (218) (Ritzman et al. 2018). Emphasizing disaster risk reduction (219) (Munang et al. 2013) and rigorously incorporating uncertainty (220) (Carriger et al. 2019) in marine policy and governance can greatly improve outcomes for both social and ecological systems affected by ocean change (221) (Silver et al. 2019).

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 co-benefits 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 like acidification and climate change and local-scale concerns.

KEY TERMS (glossary and acronyms lists)

CO_2: Carbon dioxide gas that is removed by photosynthesis and released by respiration and fossil fuel combustion

CO_3^{2-}: Carbonate ion, an inorganic carbon molecule formed when CO_2 dissolves in seawater and a key building block for carbonate minerals used in organism biomineralization

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

Ocean acidification: Changes in seawater chemistry including increased acidity, lower pH, and reduced carbonate ion levels caused by input of excess carbon dioxide

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

Aragonite and calcite: Two of the mineral forms of calcium carbonate ($CaCO_3$) used by marine organisms for shell and skeleton formation via biomineralization

Hypoxia: Low oxygen conditions in the coastal and open ocean often associated with respiration of organic material that also elevates CO_2

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

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, etc.) 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 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 co-production 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 assumption of steady-state environmental, 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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