

Will Climate Change and Ocean Acidification Lead to the Massive Death of Marine Organisms?

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Abstract

Ocean acidification represents a threat to marine species worldwide, and forecasting the ecological impacts of acidification is a high priority for science, management, and policy. As research on the topic expands at an exponential rate, a comprehensive understanding of the variability in organisms' responses and corresponding levels of certainty is necessary to forecast the ecological effects. More specifically, what stands to be understood from this review is an understanding of the effects of ocean acidification and whether marine organisms have sufficient physiological plasticity to adapt to the changes in their environment as pCO₂ concentration continues to rise. An experiment assessing the impact of ocean acidification on a given species, community, or ecosystem should include realistic changes for all environmental drivers (CO₂, temperature, salinity, food concentrations, light availability), and be long-term (i.e., several years) to allow for natural variability and multiple generations of each species under consideration. Single experimental approaches on single organisms often do not capture the true level of complexity of in situ marine environments, and multi-disciplinary approaches involving technological advancements and development are critically needed before a correct determination is made on the mortality of marine organisms.

Keywords: pCO₂, CO₂ concentration, ocean acidification (OA), pH, marine organisms

1. Introduction

The anthropogenic release of CO₂ into the atmosphere has two side effects; some of the CO₂ remains in the atmosphere contributing to climate change/global warming as CO₂ is one of the greenhouse gases while some of the CO₂ is absorbed by the plants during photosynthesis. Some of the CO₂ is absorbed by the ocean and seas causing what we call ocean acidification (OA). The combined effect of ocean acidification and global warming on marine organisms is a complex phenomenon [1, 2]. The understanding of how marine organisms will be affected by both climate change and ocean acidification is of primary importance. It has been documented in most research papers that olfaction is the most affected area in fish and once this area is affected it compromises several behavioral functions. Olfaction conveys critical environmental information to fishes, enabling activities such as mating, locating food, discriminating kin, avoiding predators, and homing. Sensory stimuli allow organisms to perceive their external environment. Perception of chemical, auditory, and visual cues play an integral role in the daily life and survival of marine organisms by influencing homing [3, 4], settlement, predator detection, and evasion, foraging [5], conspecific social interactions, and mating [6]. Additional senses—including the lateral line system, electro sense in elasmobranchs, and the ability to detect magnetic fields—offer unique conduits for perceiving the world to specialized marine species. All these behaviors can be impaired or lost because of exposure to acidified surface waters. Different biological responses to OA have been observed across multiple taxa, with sensitivity varying according to the measured trait, life stage, species, and exposure duration [7].

2. What Is Currently Known about Ocean Acidification

The pH indicates how acidic or basic (alkaline) a liquid is. It depends on the concentration of hydrogen ions in an aqueous solution. If the number of hydrogen ions decreases, the pH increases. If the number of hydrogen ions increases, the pH decreases. Since the beginning of the Industrial Revolution, the average pH of the global ocean surface has already fallen from 8.2 to 8.1, corresponding to an increase in acidity of about 26 percent. The pH values of 7.8 to 7.9 are expected by 2100, representing a doubling of acidity compared to the time before the industrial revolution (Biological Impact of Ocean Acidification [8] Fig. 1 below). It is unlikely that the open-ocean

surface layer will ever become truly acidic (drop below pH 7.0), because seawater is buffered by dissolved salts. That's why scientists emphasize it "acidifies" or becomes "more acidic", but not "acidic". The term "ocean acidification" refers to a pH shift towards the acidic end of the pH scale – like the way we would describe an increase in air temperature from minus -10 degrees Fahrenheit to minus -5 degrees Fahrenheit. The air is still cold, but we say, "It is "warming" [8]. Low pH has been shown to affect senses in fish including sight [9] and hearing [10], and especially the sense of smell, which is called olfaction [11]. It appears that the behavior of fish is compromised in acidified water. When we talk about fish behavior, we mean the muscle and body movements fish make in response to sensory cues. The way the fish moves in response to its environment, and how it behaves, is driven by its neural physiology. This is the system in the fish's body that allows it to sense and react to its environment. Behavior involves interactions among the brain, sensory organs, and muscles, which are all connected by nerves.

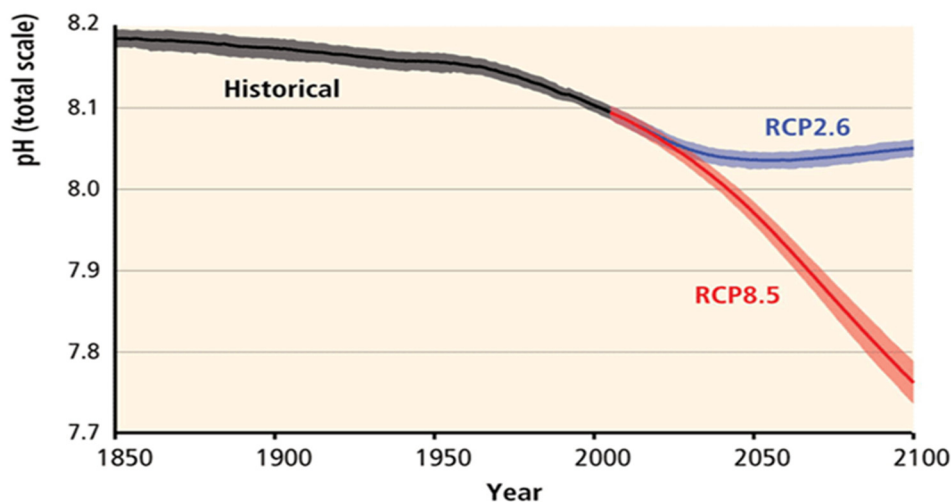


Figure 1. The world mean pH from 1850 to 2100 (climate model)
The trend is a decrease of about 0.1 pH units (in black).
Projections up to 2100 are indicated for high emissions scenarios (RCP8.5 red) and low emission scenarios (RCP2.6 blue)
Source: Gattuso et.al 2014, Fig OA1b.

3. The Previous Research on Ocean Acidification

Over the last two centuries, the intensification of human activities has led to a rise in the atmospheric concentration of carbon dioxide. Nowadays, this concentration is more than 400 ppm, a level that has never been reached in the past 800,000 years [12]. At the current rate of emissions, atmospheric CO₂ concentration is projected to reach between 750 and 1000 ppm by the end of the twenty-first century [13]. More severe scenarios even project an increase up to 1500 ppm [14]. Despite a growing understanding of species' vulnerabilities, however, it remains unclear how the direct effects of ocean acidification on marine organisms might impact different levels of marine species. Experiments examining the indirect effects of ocean acidification on individual marine species via altered species interactions are still rare, and the few multi-species studies available suggest that large-scale community shifts associated with ocean acidification are partly mediated by species interactions [15] [16] [17].

Emerging evidence suggests that elevated CO₂ can also reduce the capability of predatory fish to detect prey species [18], possibly through neurological pathways like those that can compromise chemoreceptors and behavior physiology in the prey. In addition, there is evidence that OA can cause an increase in the size of otoliths, important organs used to detect sounds, in fish [19] [20]; [21]. Sound detection could be magnified due to an increase in otolith size, but it is unclear whether increased sound detection improves or worsens fish's capability in detecting the prey (or predators). The outcome may depend on whether fish can discriminate useful sounds from background noise [22]. The initial research on the subject primarily focused on the importance of altered competition for space in high-CO₂ conditions, but the degree to which perturbed predator-prey dynamics influence community shifts remains unknown. The large number of studies that have now been conducted into the behavioral effects of elevated CO₂ in fish shows that there is considerable interspecific variation in sensitivity [23]; [24] and some species do not seem to be affected at all [25]; [26] [27], [28].

For example, the Estuaries are the interface between land and sea, and represent variable environments that are highly influenced by both oceanic and terrestrial processes. These dynamic systems are important in the life history of a diverse range of aquatic species. Estuarine conditions vary at sub-daily scales through the influence of tides and are also susceptible to the pulse and press effects of freshwater inflow from feeder tributaries and the catchments that they drain [29]. Terrestrial run-off and freshwater inflows greatly influence the physico-chemical conditions in estuaries and can carry contaminants from terrestrial habitats into estuarine systems which can subsequently impact the health of aquatic species. In coastal floodplain systems, the presence of acid sulfate soils in the catchment is a pervasive source of contaminants and poor water quality in adjacent estuaries [30]. Acid sulfate soils are common in some parts of the world, e.g. south-eastern Australia and contribute to a broad range of issues for estuaries that drain modified coastal floodplains in this area [30, 31]. This can lead to acidic conditions in estuaries, with changes to estuarine water quality potentially leading to the displacement or death of estuarine fish, or other potentially lethal or sub-lethal effects [32, 33]. One of the indirect effects of acid sulfate soils is the mobilization of metals naturally present in floodplain sediments and soils [34]. Decreases in pH can lead to the release of metal ions from clay minerals, particularly aluminum (Al), iron, sodium, potassium and magnesium [33]. Aluminum solubility increases with decreasing pH, and the resultant leachate can also drain into estuarine systems, often after heavy rainfall [35]. Generally, low pH can increase the bioaccumulation of metals in aquatic animals [36], since induces the dissociation of metals, thus increasing their solubility, and consequently their toxicity [37]. The pH and concentration of inorganic monomeric Aluminum are the key factors for toxicity in acid water, and despite that, there are marine organisms living in estuaries.

Over the past 15 years, biologists have documented substantial negative effects of ocean acidification on marine biota [7]. With more than 300 papers published per year from 2006 to 2015, the exponential growth of studies in this field is unprecedented in the marine sciences (4). In recent years, however, there has been increasing skepticism and uncertainty around the severity of ocean acidification's effects on marine organisms [38]. Some of the most profound reports are those concerning fish behavior, whereby a series of sentinel papers in 2009 and 2010 published in prestigious journals reported outstanding effects of laboratory-simulated ocean acidification [39, 40]. The severe negative impacts and drastic ecological consequences outlined in those studies were highly publicized in prominent media outlets [41, 42, 43, 44], perhaps partly due to the charismatic nature of the species studied. Not only were the findings alarming, but the extraordinarily clear and strong results also left little doubt that the effects were real.

The Representative Concentration Pathways (RCP8.5) 'business as usual' scenario, which predicts increases of 1000+ μatm pCO_2 and subsequent reductions in seawater pH by a further 0.3–0.4 pH units by the end of the century [45], has generally indicated negative biological and ecosystem effects [38, 7, 17, 46]. Although, as stated by Browman [38], a broader perspective is required as there are many gaps in our knowledge about compensatory responses, such as calcification, adaptive responses, and the interaction between simultaneous environmental changes, as well as the influence of life stages, season and nutritional condition. To date, it has been demonstrated that sensitivities to elevated pCO_2 concentrations vary among taxa, species, and populations [47, 48, 49]. It is thought that species living in environments that experience greater fluctuations in pH and temperature (e.g. vents, coastal shelf sea, and the intertidal) may be more resilient to future environmental change due to their pre-adapted physiological capacities and plasticity [50, 51].

The idea that low pH in ocean acidification would jeopardize the survival of calcifiers in the near future has become a common belief among marine scientists as it is widely written in textbooks and disseminated in media.[52] However, this view seems to focus disproportionately on the studies showing negative effects, while those showing neutral or positive effects are rarely emphasized. Negative results (i.e., showing minimal or no effects) are also less likely to be published than positive results. These reasons would create a perception bias about the effects of ocean acidification on calcifiers. On the other hand, some early studies infer the ecological consequences of ocean acidification from the biological responses shown at extreme CO_2 levels [53, 54, 55, 56]. Despite being not quite ecologically relevant, the implications made in these studies would generate a very negative perception of ocean acidification. When considering the plausible RCP6.0 scenario (≈ 700 ppm atmospheric CO_2), or even less plausible RCP8.5 scenario (≈ 1000 ppm atmospheric CO_2) by the year 2100, the impacts of ocean acidification on calcifiers may be less deleterious than initially thought. The global concern raised over ocean acidification has galvanized a substantial number of studies over the last two decades. Most of them were conducted in the laboratory, where calcifiers were typically exposed to CO_2 -manipulated seawater for a certain period, followed by measuring their biological responses. Physiological parameters, such as growth, calcification, photosynthesis, and respiration, were frequently measured to indicate the effects of ocean acidification. Despite the important insights offered, one of the major shortcomings of most previous studies is the lack of habitat complexity in the

experimental design (e.g., only seawater and calcifiers are included in the system), making the results less ecologically relevant. The static seawater pH manipulated in most previous studies is also unnatural and can elicit additional stress to marine organisms. Furthermore, a majority of previous experiments were short-term (typically less than 3 months), due to various reasons including logistical and financial constraints. These short-term studies might have overstated the negative effects of ocean acidification as the acclimation capacity of e.g., calcifiers, especially via transgenerational plasticity, was overlooked. To evaluate the impacts of ocean acidification on calcifiers or any other species more realistically with broader perspectives, the experimental design in future studies should incorporate more comprehensive sets of species, experimental duration, and environmental relevance. Coccolithophores, calcifying algae, corals, bivalves, and sea urchins have been intensively studied, whereas calcifiers that are considered tolerant to ocean acidification (e.g., barnacles, shrimps, crabs, and cephalopods) are underexplored by comparison. Without a more balanced number of observations across various taxa in the literature, it is premature to draw a general conclusion that ocean acidification is detrimental to calcifiers [57, 58]. More studies on tolerant taxa are needed to shed light on the potential mechanisms offering calcifiers with resistance to ocean acidification. Results from short-term CO₂ perturbation experiments represent poorly the effects of ocean acidification because calcifiers may be able to acclimate to the gradual change in seawater pH. Instead, these results indicate the shock response of calcifiers as their adaptive potential is neglected (e.g., via physiological or genetic adaptation). Although it is impractical to simulate the slow rate of pH change based on the predicted increase in CO₂ concentrations over time, the exposure duration of experiments should be lengthened (e.g., $\approx 40\%$ life span of organisms) to ensure that the acclimation capacity is taken into consideration. There is also increasing evidence that some species may be capable of maintaining calcified structures under conditions of OA, but that this maintenance requires more energy [59, 60]. When food or energy is abundant, some species may be able to simply acquire the additional energy necessary to maintain calcification by increasing feeding rates [61, 62], with no trade-off in growth or reproduction. However, when food is not plentiful or energy is otherwise limited, calcified species may confront two outcomes: (1) calcified structures may become thinner or weaker [63, 64, 65] or (2) net calcification may be maintained at the expense of growth, reproduction, or other defenses [66, 67, 68].

4. How the Recent Researchers Have Done Their Work and Their Findings

Many researchers have documented that the effects of ocean acidification vary among life stages or taxonomic groups of marine organisms [69, 7, 70]. More recently the compensatory responses that could occur during acid-base regulation were found to influence fish calcification, behavior, and ion transport [72, 73, 74]. Of late most studies documenting the effects of high levels of pCO₂ on fish have been performed in laboratory conditions, showing variable and sometimes contradictory results and in some cases underestimating the potential ability of fish to acclimatize and adapt to the predicted ocean acidification in the long term [71].

Upwelling is a physical process involving the wind-driven replacement of surface waters with denser, colder, nutrient-rich seawater from depth. Deep seawater contains higher nutrient, dissolved inorganic carbon (DIC), and CO₂ concentrations than the surface ocean [75, 76]. Macronutrient concentrations can increase severalfold during upwelling [77], which enhances productivity [78, 79]. The increase in dissolved inorganic carbon (DIC) and CO₂ is driven by high respiration rates in deep water masses and by increased CO₂ solubility with decreasing temperature [75]. In some upwelling regions, such as the northeastern Pacific Ocean, changes in carbonate chemistry result in extremely high pCO₂ values, exceeding 1,000 μatm near surface waters [76], making near-surface waters corrosive to carbonate minerals [76, 80]. The activity of protein and transporters currently involved in acid-base homeostasis of the fish larvae could be sufficient to reach the adjustment need of the projected acidification levels. The tolerance of sea bass larvae to projected levels of ocean acidification may be partially explained by the wide range of habitats this species occupies during its life cycle. The European Sea bass (as indicated by Jennings and Pawson) has a large distribution area and inhabits a broad range of habitats from offshore (as larvae) to inshore nurseries to coastal zones as adults [81]. Young sea bass experience strong environmental fluctuations that characterize coastal environments, such as wide qualitative and quantitative fluctuations in the food supply, salinity, dissolved oxygen, and even PCO₂ and pH due to water hydro-dynamism and eutrophication [82, 83]. The use of such fluctuating habitats may constitute a factor that permitted the evolution of the plasticity of sea bass larvae [84, 22, 85]. This broad range of conditions may have contributed to enlarging the physiological toolbox of the sea bass, allowing the larvae to better cope with environmental constraints including hypercapnia and related water acidification. Further investigations on the interactive effect of different stressors should therefore be promoted [86] in the scientific study of ocean acidification.

Most OA studies on fish physiology have been conducted in laboratories and were designed to exclude as many variables as possible and isolate the effects of OA on the fish. While this is necessary to understand how OA affects fish directly, it can make it difficult to translate results to the real world,

which is full of variables and in constant flux [87]. Scientists must begin to study fishes at natural CO₂ seeps, which may mimic future OA conditions, to see if behavioral changes noted in the lab translate to nature [88, 89, 90]. Multigenerational studies may also help to reveal what capacity fish have to adapt to OA across generations. Major questions that remain include (1) the ability of individual fish to acclimatize to lower pH over longer periods or move to areas of higher pH; (2) adaptive parental effects, or the possibility that parent fish exposed to OA produce offspring that are more resilient to this condition; and (3) the degree to which genetic variation and natural selection in fish will be affected by future OA conditions. Browman in 2016 introduced a set of articles that took a broader look at OA and how it might affect fish and marine ecosystems generally. While we understand a great deal about how OA affects specific fish species, we are just beginning to scratch the surface of predicting what it might mean for future global fisheries. These results demonstrate that rapid selection pressure of CO₂-tolerant phenotypes can occur in nature. If the individual variation in CO₂ tolerance in reef fish observed in previous studies [39, 10], is heritable then we might expect that fish populations will exhibit adaptation to elevated CO₂ through time. Like most marine species, coral-reef fishes are highly fecund, spawn repeatedly, reproduce over many seasons, and only a small fraction of offspring survive to become juveniles. Consequently, there is considerable potential for selection to favor populations dominated by CO₂-tolerant individuals over the coming decades. Furthermore, most reef fishes have very large populations, which increases genetic variation and the number of breeding individuals likely to produce favorable genotypes. Establishing that rapid selection pressure for CO₂ tolerance occurs in nature is an important step toward understanding the capacity for adaptation to rising CO₂ in the ocean. A necessary next step would be to show that the variation in CO₂ sensitivity observed here in juvenile fish is heritable. The variation in response to elevated CO₂ observed in the flume does appear to have at least some genetic basis, as full sibs reared under identical conditions in the laboratory exhibited the same variation in CO₂ sensitivity [39]. Nevertheless, quantitative genetic analyses, such as comparisons of parent-offspring or half-sib variation might be required to estimate heritability [91, 92].

Most marine organisms are not solitary but live in colonies or groups with conspecifics in their natural habitats. Most previous studies, however, determined the effects of ocean acidification on calcifiers without considering intraspecific interactions (e.g., only one or few individuals used in the system). Intraspecific interactions can modulate the physiology and behavior of calcifiers, possibly alleviating the impacts of ocean acidification [93]. Whether conspecific aggregations help calcifiers counter ocean acidification deserves more investigation. It is noteworthy that the same species from different populations or geographical locations can respond differently to ocean acidification (i.e., intraspecific variability), subject to the environmental conditions of their habitats [94, 95]. It is intriguing to understand if hybridization between populations can facilitate adaptation as gene flow is fundamental to adaptive evolution. Studying hybridization along with transgenerational effects would be a new frontier in ocean acidification research.

5. Conclusion

Experimental exposure to the ocean and freshwater acidification affects the behavior of multiple aquatic organisms in laboratory tests. Experimental designs must be made more ecologically relevant by taking into consideration all relevant factors that come into play in natural habitats e.g. fluctuations of pH, day-night cycles, substratum, habitat-forming species, and temperature variations. All these need to be incorporated into the research design to maximize habitat complexity. Such design is particularly important for studying coastal organisms that are constantly exposed to environmental fluctuations that can affect their adaptive abilities [96, 97]. In coastal areas or nearshore ecosystems, fish may already experience very high CO₂ concentrations, which are not predicted to occur in the open ocean even in the next centuries [98]. Interestingly, the large variability and the exposure to extreme CO₂ levels in natural settings may potentially modulate the specific tolerances of fish to OA, as observed for some invertebrate populations subjected to spatiotemporal environmental gradients [99].

Most previous studies have investigated the effects of ocean acidification on marine organisms by choosing RCP8.5 commonly known as the Business-as-usual scenario. This scenario is increasingly deemed impossible to be accurate because it does not have any mitigation policies to regulate CO₂ emissions [100] and as such overstates the impacts of ocean acidification. Finally, acclimation and adaptation plus gene plasticity of these marine organisms to ocean acidification may be consequential. In some marine organisms, their adaptation may be very quick resulting in their survival, while for other organisms their adaptations may be too slow, especially among long-lived species [101] and some potentially may meet their fate in the process. Hydro-dynamism, gene plasticity or adaptations, and intraspecific interactions between different species may save many marine organisms from mass extinction. Interdisciplinary studies of the coastal acidified oceans if undertaken could generate and provide a dataset on the abundance, growth, and fecundity of several intertidal invertebrates and vertebrate marine organisms. They may provide a greater ability to detect and project the biological impacts of ocean acidification.

An experiment assessing the impact of ocean acidification on a given species, community or ecosystem should include realistic changes for all environmental drivers (CO₂, temperature, salinity, food concentrations, light availability), and be long-term (i.e., several years) to allow for natural variability [6] and multiple generations of each species under consideration [102]. Single experimental approaches on single organisms often do not capture the true level of complexity of in situ marine environments, and multi-disciplinary approaches involving technological advancements and development are critically needed before a correct determination is made on the mortality of marine organisms.

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