

# Host–parasite interactions: a litmus test for ocean acidification?

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**The effects of ocean acidification (OA) on marine species and ecosystems have received significant scientific attention in the past 10 years. However, to date, the effects of OA on host–parasite interactions have been largely ignored. As parasites play a multidimensional role in the regulation of marine population, community, and ecosystem dynamics, this knowledge gap may result in an incomplete understanding of the consequences of OA. In addition, the impact of stressors associated with OA on host–parasite interactions may serve as an indicator of future changes to the biodiversity of marine systems. This opinion article discusses the potential effects of OA on host and parasite species and proposes the use of parasites as bioindicators of OA disturbance.**

## Increased CO<sub>2</sub>, seawater chemistry, and marine life

Anthropogenic emissions of carbon dioxide (CO<sub>2</sub>) since the beginning of the industrial revolution (ca. 1780) have caused atmospheric CO<sub>2</sub> to increase at an unprecedented rate and have resulted in a corresponding increase in dissolved CO<sub>2</sub> in the global ocean [1]. This addition of CO<sub>2</sub> has altered the carbonate chemistry of seawater, increasing hydrogen ion (H<sup>+</sup>) and bicarbonate ion (HCO<sub>3</sub><sup>-</sup>) concentrations, and reducing the concentration of carbonate ions (CO<sub>3</sub><sup>2-</sup>) (Box 1). The predominant consequences of these changes to seawater chemistry, now known as ocean acidification (OA) [2], are a reduction in the average environmental pH experienced by all marine organisms and a decrease in the availability of calcium carbonate (CaCO<sub>3</sub>) for calcifying marine species.

Calcification involves the concentration of CaCO<sub>3</sub> precursors in the extracellular compartment and could require increased metabolic energy as a consequence of OA [3]. In addition, all living organisms maintain an internal pH within an optimal range through acid–base regulation, a process that also requires metabolic energy. Therefore, a decrease in ambient pH caused by OA could increase the metabolic demands of acid–base regulation and reduce the amount of energy available to marine organisms for respiration, growth, reproduction, and, ultimately, survival (reviewed in [4]). Consequently, the changes to seawater chemistry caused by OA have the potential to affect the physiological performance of all marine organisms. Furthermore, as it is unlikely that all organisms will be affected equally by the changing demands of acid–base regulation or calcification, OA also has the potential to

highlight differences in physiological plasticity between coexisting species, potentially disrupting interspecific interactions.

As a biotic stressor, parasites regulate host populations, community biodiversity, and ecosystem function [5–7]. As a taxonomically diverse group of marine organisms, parasites are exposed to the abiotic stressors associated with OA. It is the duality of the role of parasites, as biotic stressors and stressed organisms, that may provide insights into the effects of OA on host organisms [8]. The parasitic infection of host species is a quantifiable stressor, which can be incorporated into experimental design to test the physiological limits of organisms expending increased metabolic energy on acid–base regulation or calcification. In addition, parasite density and abundance can be quantified in observational studies, and these parameters provide data regarding the presence or absence of a wide range of host organisms [9]. It seems clear, therefore, that parasitology could potentially become a valuable tool in understanding the current and future effects of OA on marine organisms and that parasites may also serve as bioindicators of the impact of OA on marine ecosystems.

This brief opinion article summarises the known impacts of OA on free-living marine organisms, highlights the potential synergy between OA and parasitism, and discusses the promising role of parasites as indicators of OA disturbance.

## Physiological consequences of OA

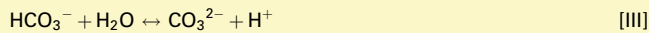
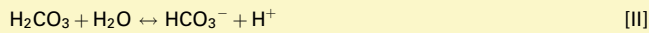
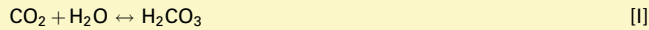
As described in Box 1, the addition of CO<sub>2</sub> to seawater alters the concentrations of hydrogen (H<sup>+</sup>), bicarbonate (HCO<sub>3</sub><sup>-</sup>), and carbonate (CO<sub>3</sub><sup>2-</sup>) ions. These chemical species play important roles in fundamental physiological processes such as protein function, enzyme activity, ion transport, and calcification. Protein function and enzyme activity are responsible for many important physiological processes, including growth and the generation of metabolic energy. A change in the electrochemical state of proteins or enzymes, caused by an increase in the extracellular concentration of charged ions, can affect binding and reaction rate properties, respectively (e.g., [10]). As the increase in atmospheric CO<sub>2</sub> over the past 200 years has already changed the concentration of dissolved ions in seawater (30% increase in H<sup>+</sup>, 5.6% increase in HCO<sub>3</sub><sup>-</sup>, and a 17.8% decrease in CO<sub>3</sub><sup>2-</sup> [11]), OA may alter the metabolic efficiency of marine organisms that possess poor ionoregulatory mechanisms [1].

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**Box 1. Fundamentals of ocean acidification**

Carbon dioxide (CO<sub>2</sub>) in the atmosphere is in equilibrium with CO<sub>2</sub> dissolved in the oceans. When CO<sub>2</sub> is added to the atmosphere, the concentration of CO<sub>2</sub> in seawater also increases. Once absorbed by the oceans, CO<sub>2</sub> undergoes several interrelated chemical reactions, which alter the speciation of dissolved carbon and cause a decrease in oceanic pH:



CO<sub>2</sub> is added to the atmosphere through the growth and decay of organic matter and, at a much faster rate, through fossil fuel combustion and cement production. Altogether, 118 Pg of CO<sub>2</sub>, or one-third of anthropogenically produced CO<sub>2</sub>, has been absorbed by the global ocean over the past 200 years [11].

Over the past 400 000 years, atmospheric CO<sub>2</sub> has varied between 200 ppm and 280 ppm. Since the industrial revolution began in the late 18th century, atmospheric CO<sub>2</sub> has increased to 390 ppm, and is currently increasing at a rate of ~0.5% per year [63]. This rate and magnitude of increase are unprecedented in the past million years [64,65].

The increase in atmospheric CO<sub>2</sub> over the past 200 years translates into a decrease in average oceanic pH of 0.1 units and a continuing decrease of ~0.02 pH units per decade [66]. The current oceanic pH is ~8.1 units [11] and is predicted to drop to ~7.7 units by the year 2100 and to ~7.3 units by 2300 [13].

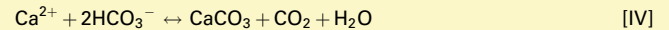
Calcification (Box 2) is the process through which calcifying organisms, such as molluscs, crustaceans, corals, echinoderms, and many species of plankton, synthesise CaCO<sub>3</sub> structures from dissolved calcium (Ca<sup>2+</sup>) and CO<sub>3</sub><sup>2-</sup> ions in seawater [12]. Predicted decreases in CO<sub>3</sub><sup>2-</sup> concentrations caused by OA may reduce the rate of calcification in many marine organisms by reducing the availability of inorganic carbon [13]. Furthermore, all calcifying organisms possess a biological mechanism to concentrate Ca<sup>2+</sup> and CO<sub>3</sub><sup>2-</sup> in extracellular compartments prior to biomineralisation [12]. A decrease in ambient levels of CO<sub>3</sub><sup>2-</sup> in seawater may increase the amount of energy required by calcifiers to maintain the concentrations required for biosynthesis [14]. In addition, changes to the ambient concentrations of dissolved CaCO<sub>3</sub> will reveal interspecific differences in the efficiency of Ca<sup>2+</sup> and CO<sub>3</sub><sup>2-</sup> concentrating mechanisms, potentially disrupting competitive relationships between coexisting species.

**Current OA research**

The effect of altered environmental pH on marine systems and organisms has been investigated as a basic biological and biogeochemical parameter since the early 20th century (reviewed in [15]). Recently, however, investigations into decreased pH in the context of OA have become the focus of increased scientific attention. Other than a few isolated studies, the majority of research on OA has been conducted since the late 1980s, with 79% of OA articles published since 2004 (see bibliometric analysis in [15]). To date, OA research has focussed on plankton, corals, molluscs, and macroalgae (reviewed in [1,15]), and has found that the overall biological impact of OA will be negative [4]. Observational and experimental studies conducted in the past decade have documented a wide variety of biological

**Box 2. Fundamentals of calcification**

Calcification is the process through which calcifying organisms cause the precipitation of calcium carbonate (CaCO<sub>3</sub>) from seawater and synthesise it into biomineral structures such as shells. The formation of CaCO<sub>3</sub> in seawater is described by the following equation:



Calcifying marine organisms predominantly use two polymorphs of CaCO<sub>3</sub>: coccolithophores and foraminifera use calcite, pteropods and corals use aragonite, and molluscs use either or both [67]. The ability of calcifiers to synthesise CaCO<sub>3</sub> structures depends upon the concentration, or saturation state, of the mineral in the surrounding seawater. Saturation states indicate whether a solvent is supersaturated or undersaturated with respect to a specific solute, and are represented by the symbol omega (Ω<sub>solute</sub>). Omega values greater than one indicate supersaturation and less than one undersaturation, e.g., Ω<sub>a</sub> > 1 indicates the supersaturation of aragonite in solution. In undersaturated conditions (Ω<sub>a</sub> or Ω<sub>c</sub> < 1), the biosynthesis of aragonite or calcite cannot occur, and CaCO<sub>3</sub> structures begin to dissolve; some research also indicates that calcification rates are affected when omega values are greater than one [68]. The depth below which CaCO<sub>3</sub> structures dissolve, that is, where Ω<sub>a</sub> or Ω<sub>c</sub> ≤ 1, is known as the saturation horizon. The addition of CO<sub>2</sub> to the atmosphere ultimately causes the saturation horizon to become shallower; since ca. 1780, it has become shallower by between 30 and 200 m [69].

Predictive models have suggested that the surface oceans at high latitudes and in hypoxic areas will be the first marine environments affected by the shallowing of saturation horizons, for example, the subarctic Pacific and tropical Indian Ocean [13,68,69]. The colder seawater temperatures found at high latitudes increase the solubility of CO<sub>2</sub>, and hypoxic zones typically have high CO<sub>2</sub> levels due to microbial respiration.

responses to OA stress: (i) calcifying phytoplankton and macroalgal species, as well as corals and molluscs, have demonstrated reduced calcification rates [14,16–18]; (ii) mollusc species have weaker calcified structures [19,20]; (iii) mollusc and echinoderm species have exhibited altered metabolic rates [3]; and (iv) the larvae of molluscs, echinoderms, crustaceans, and teleost fish have demonstrated a suite of reactions to OA stress which include reduced growth and survival, delayed development, and behavioural modification (echinoderms and molluscs [21], fish [22], molluscs and crustaceans [23]). Other, less frequently, described effects of OA include impaired immune response (bivalves [24]) and a reduced accumulation of essential trace elements (cephalopods [25]).

Despite this increase in research into the effects of OA, very few papers have considered a parasitic species in the context of OA (but see trematodes [26]). To date, no investigation has examined the combined effects of OA on host–parasite interactions, i.e., pH and calcification stress on host species with pH stress on parasitic species, and/or subsequent alterations to community biodiversity or ecosystem structure.

**Ecological role of parasites**

Undoubtedly, pH is an important regulatory factor in parasite physiology and population dynamics, as demonstrated by research into the effects of pH on parasites in culture [27], in the internal environment of the host [28], and, perhaps most importantly, in freshwater habitats

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