Opinion

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_2, seawater chemistry, and marine life

Anthropogenic emissions of carbon dioxide (CO_2) since the beginning of the industrial revolution (ca. 1780) have caused atmospheric CO_2 to increase at an unprecedented rate and have resulted in a corresponding increase in dissolved CO_2 in the global ocean [1]. This addition of CO_2 has altered the carbonate chemistry of seawater, increasing hydrogen ion (H^+) and bicarbonate ion (HCO_3^-) concentrations, and reducing the concentration of carbonate ions (CO_3^{2-}) (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 ($CaCO_3$) for calcifying marine species.

Calcification involves the concentration of $CaCO_3$ 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_2 to seawater alters the concentrations of hydrogen (H^+), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}) 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_2 over the past 200 years has already changed the concentration of dissolved ions in seawater (30% increase in H^+, 5.6% increase in HCO_3^-, and a 17.8% decrease in CO_3^{2-} [11]), OA may alter the metabolic efficiency of marine organisms that possess poor ionoregulatory mechanisms [1].

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Keywords: ocean acidification; hosts; parasites; bioindicators; calcification; pH; CO_2; carbonate chemistry.

1471-4922/$ – see front matter © 2012 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.pt.2012.06.007 Trends in Parasitology, September 2012, Vol. 28, No. 9

Box 1. Fundamentals of ocean acidification

Carbon dioxide (CO_2) in the atmosphere is in equilibrium with CO_2 dissolved in the oceans. When CO_2 is added to the atmosphere, the concentration of CO_2 in seawater also increases. Once absorbed by the oceans, CO_2 undergoes several interrelated chemical reactions, which alter the speciation of dissolved carbon and cause a decrease in oceanic pH:

$$CO_2 + H_2O \leftrightarrow H_2CO_3 \qquad [I]$$

$$H_2CO_3 + H_2O \leftrightarrow HCO_3^- + H^+ \qquad [II]$$

$$HCO_3^- + H_2O \leftrightarrow CO_3^{2-} + H^+ \qquad [III]$$

CO_2 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_2, or one-third of anthropogenically produced CO_2, has been absorbed by the global ocean over the past 200 years [11].

Over the past 400 000 years, atmospheric CO_2 has varied between 200 ppm and 280 ppm. Since the industrial revolution began in the late 18th century, atmospheric CO_2 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_2 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].

Box 2. Fundamentals of calcification

Calcification is the process through which calcifying organisms cause the precipitation of calcium carbonate ($CaCO_3$) from seawater and synthesise it into biomineral structures such as shells. The formation of $CaCO_3$ in seawater is described by the following equation:

$$Ca^{2+} + 2HCO_3^- \leftrightarrow CaCO_3 + CO_2 + H_2O \qquad [IV]$$

Calcifying marine organisms predominantly use two polymorphs of $CaCO_3$: coccolithophores and foraminifera use calcite, pteropods and corals use aragonite, and molluscs use either or both [67]. The ability of calcifiers to synthesise $CaCO_3$ 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_{solute}). Omega values greater than one indicate supersaturation and less than one undersaturation, e.g., $\Omega_a > 1$ indicates the supersaturation of aragonite in solution. In undersaturated conditions (Ω_a or $\Omega_c < 1$), the biosynthesis of aragonite or calcite cannot occur, and $CaCO_3$ 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 $CaCO_3$ structures dissolve, that is, where Ω_a or $\Omega_c \leq 1$, is known as the saturation horizon. The addition of CO_2 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_2, and hypoxic zones typically have high CO_2 levels due to microbial respiration.

Calcification (Box 2) is the process through which calcifying organisms, such as molluscs, crustaceans, corals, echinoderms, and many species of plankton, synthesise $CaCO_3$ structures from dissolved calcium (Ca^{2+}) and CO_3^{2-} ions in seawater [12]. Predicted decreases in CO_3^{2-} 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^{2+} and CO_3^{2-} in extracellular compartments prior to biomineralisation [12]. A decrease in ambient levels of CO_3^{2-} 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 $CaCO_3$ will reveal interspecific differences in the efficiency of Ca^{2+} and CO_3^{2-} 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 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

[29–32]. Accordingly, it is likely that changing oceanic pH will have an effect on marine parasite survival or infectivity, especially for species that produce free-living developmental stages (reviewed in [33]). In addition, infection-induced host mortality rates can be exacerbated by changing abiotic conditions which increase host stress, potentially resulting in synergistic interactions between infection and one or more abiotic factor (e.g., temperature [34], anoxia [35], and anthropogenic stressors [36]). As it has been demonstrated that host species such as molluscs and crustaceans are vulnerable to stressors associated with OA [4], it is not unrealistic to assume that parasitic infection of these species could cause increased pathogenicity if the parasites are less affected than the hosts. Conversely, if parasites prove less tolerant of reduced pH than their hosts, pathogenicity could be decreased, modifying an important regulatory factor of host populations.

Ultimately, the interaction of the stress responses of hosts and parasites, in the context of OA, could potentially alter community parameters that can affect ecosystem stability, e.g., species-specific mortality rates, population density, fecundity (in the case of castrating parasites), competition, and predator–prey relationships. Changes to any of these parameters could destabilise trophic interactions and affect marine community biodiversity and ecosystem function [34,37], particularly if species which play a keystone or ecosystem engineer role exhibit a low tolerance to the abiotic stressors associated with OA.

Parasites as bioindicators

The use of host–parasite interactions as an effective bioindicator of anthropogenic perturbation of community biodiversity and ecosystem structure has been frequently encouraged since 1997 [38–41]. Parasites are a ubiquitous component of all ecosystems and, due to their complex life cycles, experience a wide range of environments which represent most biological niches possibly affected by abiotic stressors, for example, the internal compartments of host species (endoparasites), the microenvironment surrounding the host's tegument (ectoparasites), and exposure to ambient conditions during indirect transmission between hosts. Parasite species often possess very different developmental stages which may exhibit a range of tolerances to changing abiotic conditions. Although ecotoxicologists have not reached a consensus on the effects of pollutants on parasites [42], there exists a wealth of empirical data regarding the direct and indirect effects of a wide range of anthropogenic stressors on many parasitic taxa which may contribute to their use as bioindicators. Direct effects include: (i) altered parasite survival (trematodes [43], monogeneans [44]); (ii) reduced transmission success (trematodes [45]); and (iii) altered host susceptibility to infection (acanthocephalans [46], trematodes, and ciliates [47]). Indirect effects include modified host species interactions (gastropod–trematode [48]), which can result from increased host tolerance to toxicants due to parasitic infection (bivalve–trematode [49]; gastropod–trematode [50]; crustacean–isopod and teleost–nematode [51]).

Preliminary data regarding the direct effects of anthropogenic disturbance also indicate that abiotic stressors have the greatest impact on free-living larval stages of the parasitic life cycle, such as trematode cercariae and miracidiae [33]. Similarly, current research shows that the larval forms of fish, molluscs, echinoderms, and crustaceans are vulnerable to stressors associated with OA [21–23]. As free-living parasitic larvae and the larvae of other marine organisms share many morphological and physiological characteristics [52], it is possible that the free-living larval stages of parasites will prove vulnerable to stressors associated with OA and will be an effective bioindicator of OA disturbance. Standard procedures have been established for the experimental exposure of marine larvae to simulated OA conditions [53]. These protocols could be applied to miracidiae and cercariae to establish baseline data on survival, longevity, and infectivity.

Parasite diversity and abundance can also provide data on the presence or absence of host species, as parasites rely on the presence of one or more particular hosts to complete their life cycles [9]. For instance, trematode parasites require a mollusc as their first intermediate host, and OA-induced reductions in the local abundance of these calcifiers would reduce infections in subsequent hosts in the life cycle and endanger the local persistence of trematode species. Consequently, a decrease in parasitic diversity may reflect changes in the availability of one or more host species. This approach would obviously be limited to parasites whose life cycles are fully described. Such observational evidence, in combination with experimental data regarding host species tolerance to abiotic factors, could identify host species that are vulnerable to stressors associated with OA.

Concluding remarks

Despite the abundance of evidence which suggests that the overall effects of OA will be negative, a significant number of marine organisms either benefit from, or are unaffected by, the associated changes to seawater chemistry [1]. For example, some pteropod species which naturally migrate through oxygen minimum zones are unaffected by elevated CO_2 levels [54], whereas certain coccolithophore species increase calcification rates under simulated OA conditions [55]. These positive or neutral responses may be the result of a bias towards short-term experiments which do not test the long-term consequences of OA or demonstrate actual species-specific or life history stage-specific tolerance to an acidified environment. In either case, the data aptly illustrate our lack of a comprehensive understanding of the effects of OA at a basic, organismal level. The study of host–parasite interactions in the context of OA will not only help rectify this knowledge gap but will also begin to elucidate the impacts of an acidified environment on community and ecosystem processes, such as trophic dynamics and biodiversity.

One of the most complex and well-studied ecosystems affected by OA is the intertidal zone, which includes some of the most biologically productive marine habitats, for example, upwelling areas, kelp forests, mangroves, and estuaries; these habitats possess rich parasite faunas that are known to regulate invertebrate populations and affect biodiversity [6]. These systems may serve as a useful and easily accessible starting point for an investigation of OA effects on host–parasite interactions. The intertidal zone also experiences extreme natural variation in many abiotic parameters, such as temperature and salinity, which can interact synergistically with pH (temperature [56] and salinity [57]). Therefore, intertidal organisms may have preadaptations to these abiotic factors, or be living at or close to their tolerance limit. Consequently, a study of hosts and parasites from the intertidal zone could reveal a rich cross-section of marine species that will benefit from, be unaffected by, or be negatively affected by OA.

Coastal ecosystems are also commonly exposed to a range of anthropogenic stressors: global warming, eutrophication, hypoxia, and petroleum contamination; these could synergistically interact with the effects of OA. Recent publications have stressed the importance of multifactor experiments which combine the effects of OA with other environmental variables [58]. Given the increasing availability of data regarding the tolerance of parasites to a range of abiotic factors [26,59–61], the identification of host–parasite pairs for use in the study of interactions between OA and anthropogenic stressors should be straightforward. In this context, the use of host–parasite associations as indicators of community and ecosystem change caused by OA becomes even more relevant. Viewed simplistically, OA is one of many abiotic perturbations imposed on marine ecosystems as a result of human activity. Multiple stressors caused by these perturbations have the potential to interact synergistically and push marine systems past their ecological tipping points. Therefore, the responses of host and parasite species to multiple stressors, including OA, could function as bioindicators of OA-mediated change and interactions between OA and pre-existing anthropogenic stressors.

Our recommendations to incorporate parasitology into the study of OA and employ host–parasite interactions as bioindicators of OA disturbance are: (i) host–parasite pairs must be used in long-term CO_2 perturbation experiments, which simulate current and future seawater conditions; (ii) specific host–parasite pairs that have demonstrated low tolerances to other anthropogenic stressors should be assessed as bioindicators of OA disturbance, for example, *Littorina littorea* (mollusc) and *Cryptocotyle lingua* (trematode) (heavy metal contamination [62]); and (iii) data generated by the use of host–parasite associations as bioindicators of OA disturbance should be incorporated into a holistic view of how the global oceans are affected by human activity.

Acknowledgements

We wish to thank A. Studer and H. Randhawa for their constructive comments on an earlier draft of this article. This research was funded by the University of Otago, New Zealand.

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