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*Editorial*

# Impact of Ocean Acidification on Marine Organisms—Unifying Principles and New Paradigms

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**Abstract:** This special issue combines original research with seminal reviews of the biological impact of ocean acidification. The ten contributions cover a wide range of topics from chemical and biological responses to increased $CO_2$ and decreased pH to socio-economical sensitivities and adaptation options. Overall, this special issue also highlights the key knowledge gaps and future challenges. These include the need to develop research strategy and experiments that factor in evolution, incorporate natural variability in physical conditions (e.g., pH, temperature, oxygen, food quality and quantity) and ecological interactions. The research presented in this special issue demonstrates the need to study more habitats (e.g., coastal, deep sea) and prioritize species of ecological or economic significance.

**Keywords:** ocean acidification; pH; carbon dioxide; future research

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## 1. Introduction

Ocean acidification—the decrease in seawater pH caused by uptake of anthropogenic carbon dioxide from the atmosphere—has emerged as an issue of great concern since it is believed to pose a major threat to marine ecosystems, their sustainability and the services they provide society. Rates of anthropogenic $CO_2$ emissions, and the sea surface warming and acidification this causes, are accelerating. This special issue of the journal *Water* brings together a series of papers that assess the kinds of marine organisms and ecosystem services that will suffer ("losers") or benefit ("winners") from the increase in $CO_2$ levels. It turns out that the impact of ocean acidification is highly species and population specific, and that in laboratory studies the effects very much depend on life-history stages and the processes studied. An additional complication is that ocean acidification is not acting alone, so our contributors also consider how rapid rates of falling pH and carbonate saturation will affect oceans in the real world, where other changes, such as increased temperature, overfishing, eutrophication and pollutants modify our seas. This also highlights the important (and often overlooked) fact that impacts will vary according to geographical region, latitude, *etc*.

The topic of ocean acidification has expanded almost exponentially in the past 10 or more years and more recently has been moving forward as a hypothesis-driven research field with formerly established paradigms (e.g., ocean acidification will negatively impact calcifiers) now being revisited. For example, some of the taxa predicted to be heavily impacted by acidification appear to be surprisingly resilient to low pH/high $pCO_2$ yet the chronic corrosive effects of acidified seawater on calcareous habitats is emerging as a major concerns since when carbonate reefs dissolve the protection they provide to coasts, and the habitats they provide for commercially important species is lost.

There is a growing awareness that to project the impact of ocean acidification on marine ecosystems it is important to understand how it will interact with other stressors to modify the evolutionary rules shaping marine ecosystems.

## 2. Contributions

### *2.1. The Modulating Role of Evolution and the Need for Long Term Studies*

Pauline Ross and colleagues at the University of Western Sydney and the Port Stephens Fisheries Centre in Australia produced a review of the effects of ocean acidification on the early life-history stages of invertebrates including fertilisation, larval development and the implications for dispersal and settlement of populations [1]. They concluded that although fertilisation appears robust to near future predictions of ocean acidification, larval development is much more vulnerable across major invertebrate groups such as molluscs and echinoderms. They drew together evidence showing that the impacts of ocean acidification can be particularly severe for organisms which start to calcify in their larval and/or juvenile stages. Ross *et al.* [1] highlighted important gaps in the literature such as the need for more studies investigating the interactive effects of acidification and warming, and the need for long-term multigenerational experiments to determine whether vulnerable species have the capacity to adapt to elevations in atmospheric $CO_2$ over the next century.

Ben Harvey from the University of Aberystwyth in Wales teamed up with 17 other researchers from institutes in Brazil, Germany, Italy, Norway, Spain, the UK and the USA at a course on "Marine

Evolution under Climate Change" held at the Sven Lovén Centre for Marine Sciences—Kristineberg. They review the potential evolutionary strategies available to marine organisms under climate change at different levels of biological organisation, since most studies do not consider the role that adaptive evolution will play in modulating biological responses to climate change [2]. Their review compares investigations that show both individual species and ecological processes exhibit diverse responses climate change. This body of work has typically been focused at specific biological levels (e.g., cellular, population, community) and often lacks a consideration of interactions among levels. These researchers highlight the point that since all levels of biological organisation are sensitive to global climate change, there is a need to elucidate how hierarchical interactions will influence species fitness. Harvey *et al.* [2] conclude that in order to establish the role of acclimatisation and adaptation in community and population responses to global change collaborations are needed to integrate research at genetic, cellular, community and ecosystems levels.

Juancho Movilla from the Institut de Ciències del Mar in Barcelona conducted a study concerning the resistance of two Mediterranean cold-water coral species to long term exposure to low pH with co-workers in the same institute and with researchers at the Spanish Centro Oceanográfico de Baleares and the Institució Catalana de Recerca i Estudis Avançats [3]. Few studies have been carried out on the vulnerability of deep-sea organisms to ocean acidification yet this is an important topic since deep-water ecosystems are expected to be among the first to be exposed to waters that are corrosive to calcium carbonate. Movilla *et al.* [3] investigated the effects of decreased pH on calcification of *Madrepora oculata* and *Lophelia pertusa*, which are widely distributed in the Mediterranean. Surprisingly, they found no significant effects of acidification on skeletal growth rate, microdensity and porosity in either species after 6 months incubation in aquaria. However, they caution that newly settled *L. pertusa* may have higher energy demands, and so reductions in calcification might occur during long-term exposure to acidified conditions.

### 2.2. The Importance to Capture Environmental Complexity

As part of his PhD, Christopher Jury worked with colleagues at the University of Hawaii, including Marlin Atkinson, who is now sadly deceased, on a modelling study that concerns the capacity of coastal waters to buffer reductions in pH [4]. They produced a model of a coastal tropical coral reef that incorporates the fact that as the buffer capacity of seawater decreases, daily variations in chemistry increase. This daily variation in carbonate chemistry is affected by ecosystem feedbacks that exacerbate the effects of ocean acidification at night. They found that an increase in offshore $pCO_2$ and temperature (to 900 μatm and +3 °C) can be expected to increase daily pH variation by a factor of 2.5 and increase $pCO_2$ variation by a factor of 4.6. This paper highlights the importance of considering changes not only in average carbonate chemistry but also the changes in coastal carbonate chemistry that occur diurnally—since this diurnal variation can affect organisms and ecosystems.

Ocean acidification is not occurring in isolation and two research articles highlight the potential interactions with other relevant global drivers: temperature and oxygen.

In a globally collaborative project Mikko Vihtakari, based jointly at the Arctic University of Norway and the Fram Centre in Tromsø, worked with research scientists at the University Centre on Svalbard, the University of Gothenburg, the Mediterranean Institute for Advanced Studies in Spain and the University of Western Australia to assess the effects of ocean acidification with and without warming on sperm activity and early life stages of the mussel *Mytilus galloprovincialis* [5]. This study is highly relevant to the aquaculture industry since these mussels are grown commercially both in the Mediterranean and in the Atlantic. Shellfish hatcheries in the NE Pacific have found that oyster larvae are especially vulnerable to ocean acidification, and Vihtakari *et al.* [5] investigated the effects of low (380 ppm) and high levels of $pCO_2$ (1000 ppm) on *M. galloprovincialis* sperm and late trochophore/early D-veliger stages. They found that high $pCO_2$ had a negative effect on the percentage of motile sperm and sperm swimming speed, possibly indicating reduced fertilization capacity. Their experiments on larvae showed that an increase in temperature from *ca.* 17 °C to 20 °C had more effect on larval stages than differences in $pCO_2$. The larvae reared in warmer seawater had an increased energy demand, were smaller and had reduced survival rates. The authors advise that increasing surface seawater temperatures can be expected to have more of an adverse impact on early larval stages of *M. galloprovincialis* than ocean acidification.

Michael Navarro worked with colleagues at Scripps Institution of Oceanography and the University of Southern California to test in the laboratory whether or not squid statolith geochemistry reflects environmental pH and $[O_2]$ [6]. They used levels of pH and $[O_2]$ found at squid spawning grounds on the continental shelf off California where ocean acidification, deoxygenation and intensified upwelling lower the pH and $[O_2]$. Embryo exposure to high and low pH and $[O_2]$ both alone and together during development over four weeks only moderately affected elemental concentrations of the statoliths, with uranium proving to be an important element driving these differences. Uranium:Ca was eight-times higher in statoliths exposed to low $pH_T$ (7.57–7.58) and low $[O_2]$ (79–82 $\mu mol \cdot kg^{-1}$) than those exposed to higher ambient $pH_T$ (7.92–7.94) and $[O_2]$ (241–243 $\mu mol \cdot kg^{-1}$). They found that statoliths of squid embryos developing inside capsules have the potential to reflect environmental pH and $[O_2]$, but that these "signals" are generated in concert with the physiological effects of the capsules and embryos themselves which complicates their use as proxies for oceanographic conditions.

Biotic environmental drivers can also play a critical role in modulating the response to ocean acidification. These include food quality and quantity. Cathryn Wynn-Edwards, at the Institute for Marine and Antarctic Studies, University of Tasmania, draws attention to the fact that increased seawater $pCO_2$ has the potential to alter phytoplankton biochemistry, which in turn may negatively affect the nutritional quality of phytoplankton as food for grazers. To address this issue Wynn-Edwards *et al.* [7] developed an inexpensive phytoplankton culture system for ocean acidification experiments that reduces the time required to maintain cultures in exponential growth for extended periods of time. This system was used to investigate the nutritional quality of southern ocean phytoplankton in response to elevated $pCO_2$ with colleagues at the University, at CSIRO Division of Marine and Atmospheric Research and at the Australian Antarctic Division [8]. They maintained continuous cultures of Antarctic phytoplankton and subjected them to a range of $pCO_2$ from ambient to 993 µatm and measured responses in terms of cell size, carbohydrates and fatty acids. The C:N ratio was unaffected by $CO_2$ concentration in the three species, while carbohydrate content decreased in *Pyramimonas gelidicola*, but increased in *Phaeocystis antarctica*. They found a significant reduction in the content of nutritionally important polyunsaturated fatty acids in *Pyramimonas gelidicola* cultures under high $CO_2$ treatment, while cellular levels of the polyunsaturated fatty acid 20:5ω3, EPA, in *Gymnodinium* sp. increased. The authors argue that these changes in fatty acid profile could affect the nutritional quality of phytoplankton food for grazers as the Southern Ocean continues to acidify, but acknowledge the difficulties in extrapolating from laboratory-based experiments on individual species to natural communities.

### *2.3. Potential Socio-Economic Consequences and What Can We Do?*

Nathalie Hilmi and colleagues at the Centre Scientifique de Monaco spearheaded an interdisciplinary collaboration between researchers with social, economic and environmental science backgrounds based at institutes in Australia, France, Germany, Iceland, the USA, the UK and Sweden. They examined the potential effects of ocean acidification on fisheries around the Mediterranean Sea basin by examining the sensitivities at the chemical, biological, and macro-economic levels [9]. They found that limited information available on impacts of ocean acidification on harvested (industrial, recreational, and artisanal fishing) and cultured species (aquaculture) is a major research gap. However, it appears that non-developed nations around the Mediterranean, particularly those for which fisheries are increasing, and rely heavily on artisanal fleets, are most greatly exposed to socioeconomic consequences from ocean acidification.

Another PhD candidate, Giulia Ghedini, and her supervisors at the University of Adelaide addressed the pressing issue of how best to manage local stressors in coastal systems to reduce the ecological effects of ocean acidification and warming [10]. Their review highlights the fact that local stressors (e.g., eutrophication and overfishing) can be controlled more rapidly through local management whereas the global stressors of ocean warming and acidification require reductions in carbon emissions that require international agreements and management applications that take considerable time to develop. An important conclusion of their assessment is that managers may "buy time" by acting on issues that can be governed locally (e.g., reducing nutrient input) and are known to synergize with global stressors (e.g., rising $CO_2$ levels). Such local actions may disrupt interactions with the more slowly changing global stressors that can only be reduced over longer time scales.

## 3. Discussion

We are now forewarned that that daily variations in seawater chemistry may increase on tropical coral reefs because ocean acidification causes a marked reduction in the buffering capacity of seawater on the reefs at night [4], but at least by acting on local stressors (e.g., eutrophication and overfishing) managers may be able to "buy time" as we grapple with international agreements on reducing $CO_2$ emissions [10]. The finding that simulated ocean acidification had no significant effects on the growth and skeletal structure of the adult stages of two widespread cold-water corals [3], but can be particularly severe for organisms which start to calcify in their larval and/or juvenile stages [1] and there may also be indirect effects through loss of food quality since rising $CO_2$ levels affect the biochemistry of phytoplankton [7,8] highlights the fact that there is likely to be significant variations in species' responses. The otoliths of squid embryos are affected by the combined effects of acidification and lowered oxygen, although conditions within the brood capsule also affect their geochemistry. In the commercially important mussel *Mytilus galloprovincialis*, increasing surface seawater temperature is expected to have more of an adverse impact on larval stages than ocean acidification [5]. Hilmi *et al.* [9] call for the urgent need for this type of work on the impacts of ocean acidification on harvested (industrial, recreational, and artisanal fishing) and cultured species (aquaculture) so that we can assess the socioeconomic consequences of ocean acidification, whilst Harvey *et al.* [2] call for integrated research from the genetic to the ecosystems level to establish the role of acclimatisation and adaptation in community and population responses to global change.

Given the scale of the problems associated with rapidly rising $CO_2$ levels it is encouraging to see the level of collaboration that has gone into the manuscripts within this issue, cutting across traditional research fields in the biological sciences and reaching out to other disciplines.

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## Conflicts of Interest

The authors declare no conflict of interest.

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