



International news

Special issue: Influence of Environmental Variability on Climate Change Impacts in Marine Ecosystems

This Topic calls for studies addressing whether environmental variability acts as a buffer or amplifier of the effects of climate change on marine ecosystems.

Marine environments, particularly coastal and shallow-water habitats, often experience strong fluctuations of biotic and abiotic drivers at temporal scales of hours to weeks. These can arise from biological activity, irradiance variation, tides, weather-driven changes in water level, waves, temperature, and up- or downwelling events. These natural short-term (hours to weeks) fluctuations can amplify (adding stress to the system), or buffer (enabling recovery) environmentally-induced stress, and thereby can strongly modulate the impacts of climate change on organism physiology and ecosystem resilience.

Results obtained from the many studies that have tested the effects of constant environmental conditions can be of limited relevance to the real world where fluctuations are common. Of the >1500 articles that have tested the biological effects of (constant levels of) ocean acidification <25 have investigated the effects of pH fluctuations, highlighting the need for more detailed assessments. The few available studies on the effects of pH or thermal variability demonstrate widely varying responses that differ from those in constant conditions. Recently, theoretical frameworks have been used to predict the effects of fluctuations from (e.g.) thermal performance curves established under constant experimental treatments, as well as how variation in thermal environments alters organismal thermal preferences. These predictions have rarely been tested against empirical observations, and the mechanisms underlying responses are unclear.

Here, we call for the latest experimental and theoretical research investigating the effects of fluctuating environmental drivers on marine organisms and ecosystems. Preferably, drivers shall be applied along a species' performance gradient, i.e. from optimal to moderate and stressful environmental conditions (e.g. outside a species thermal (etc.) optimum). Focal drivers should be environmental parameters with ecosystem-wide impacts such as temperature, pH, salinity, or oxygen and/or biological drivers such as food availability and/or quality; this list, however, is not exclusive. Investigations of the interplay of multiple fluctuating environmental drivers are welcome and timely. Further, experiments testing whether performance curves are adaptive in the short- (via phenotypic plasticity) or the long-run (by evolution) would be highly valuable.

This Topic is clearly different from purely observational approaches looking e.g. into the impacts of extreme events such as marine heatwaves on marine communities, and topics focussing on purely behavioral mechanisms in response to environmental heterogeneity.

This Topic stresses the need to integrate variability into eco-physiological approaches focusing on functional traits, for understanding ecological and evolutionary changes driven by a changing ocean.

<https://www.frontiersin.org/research-topics/12912/influence-of-environmental-variability-on-climate-change-impacts-in-marine-ecosystems>

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A review and meta-analysis of potential impacts of ocean acidification on marine calcifiers from the southern Ocean. Understanding the vulnerability of marine calcifiers to ocean acidification is a critical issue, especially in the Southern Ocean (SO), which is likely to be the one of the first, and most severely affected regions. Since the industrial revolution, ~30% of anthropogenic CO₂ has been absorbed by the global oceans. Average surface seawater pH levels have already decreased by 0.1 and are projected to decline by ~0.3 by the year 2100. This process, known as ocean acidification (OA), is shallowing the saturation horizon, which is the depth below which calcium carbonate (CaCO₃) dissolves, likely increasing the vulnerability of many resident marine calcifiers to dissolution. The negative impact of OA may be seen first in species depositing more soluble CaCO₃ mineral phases such as aragonite and high-Mg calcite (HMC). Ocean warming could further exacerbate the effects of OA in these particular species. Here we combine a review and a quantitative meta-analysis to provide an overview of the current state of knowledge about skeletal mineralogy of major taxonomic groups of SO marine calcifiers and to make projections about how OA might affect a broad range of SO taxa. We consider a species' geographic range, skeletal mineralogy, biological traits, and potential strategies to overcome OA. The meta-analysis of studies investigating the effects of the OA on a range of biological responses such as shell state, development and growth rate illustrates that the response variation is largely dependent on mineralogical composition. Species-specific responses due to mineralogical composition indicate that taxa with calcitic, aragonitic, and HMC skeletons, could be at greater risk to expected future carbonate chemistry alterations, and low-Mg calcite (LMC) species could be mostly resilient to these changes. Environmental and biological control on the calcification process and/or Mg content in calcite, biological traits, and physiological processes are also expected to influence species-specific responses. Figuerola B., Hancock A. M., Bax N., Cummings V. J., Downey R., Griffiths H. J., Smith J. & Stark J. S., 2021. A review and meta-analysis of potential impacts of ocean acidification on marine calcifiers from the southern Ocean. *Frontiers in Marine Science* 8: 584445. doi: 10.3389/fmars.2021.584445. [Article](#).

Magnitude and predictability of pH fluctuations shape plastic responses to ocean acidification. Phenotypic plasticity is expected to facilitate the persistence of natural populations as global change progresses. The attributes of fluctuating environments that favor the evolution of plasticity have received extensive theoretical investigation, yet empirical validation of these findings is still in its infancy. Here, we combine high-resolution environmental data with a laboratory-based experiment to explore the influence of habitat pH fluctuation dynamics on the plasticity of gene expression in two populations of the Mediterranean mussel, *Mytilus galloprovincialis*. We linked differences in the magnitude and predictability of pH fluctuations in two habitats to population-specific gene expression profiles in ambient and stressful pH treatments. Our results demonstrate population-based differentiation in gene expression plasticity, whereby mussels native to a habitat exhibiting a large magnitude of pH fluctuations with low predictability display reduced phenotypic plasticity between experimentally imposed pH treatments. This work validates recent theoretical findings on evolution in fluctuating environments, suggesting that the predictability of fluctuating selection pressures may play a predominant role in shaping the phenotypic variation observed across natural populations.

Bitter M., Kapsenberg L., Silliman K., Gattuso J.-P., & Pfister C. A., in press. Magnitude and predictability of pH fluctuations shape plastic responses to ocean acidification. *The American Naturalist*. [Article](#).

Futureproofing the green-lipped mussel aquaculture industry against ocean acidification. Two mitigation strategies – waste shell and aeration – were tested in field experiments to see how effective they are at mitigating acidification around mussel farms. This report outlines the results and recommendations from this research.

- The inner Firth of Thames currently experiences the lowest seasonal pH of the sites monitored, with a daily minimum of 7.84 (7.79–7.96) in autumn, with short-term (15-minute) pH minima as low as 7.2. Time-series data in the inner and outer Firth of Thames, and also on a mussel farm in the western Firth, show episodic declines in carbonate saturation to the critical carbonate saturation state $\Omega_{AR} = 1.0$ at which solid aragonite (the form of carbonate in mussel shells) will start to dissolve. Consequently, mussels in the Firth of Thames experience episodic corrosive conditions.
- The mean pH in the Marlborough Sounds region is projected to decrease by 0.15–0.4 by 2100 depending on future emission scenario. The corresponding decline of 0.5–1.25 in the saturation state of aragonite (Ω_{AR}), results in the critical threshold of $\Omega_{AR} = 1$ being reached by 2100 under the worst-case scenario. These projections are based only on future CO₂ emission scenarios and do not consider other coastal sources of acidity in coastal waters which may also alter in the future.
- At night pH within the boundary layer on a mussel dropper line may be up to 0.1 lower than the surrounding water due to respiration in the absence of photosynthesis. Consequently, mussels experience a more corrosive environment at night on dropper lines relative to the surrounding water.
- To raise pH from the present-day minimum to present-day mean in a one-hectare mussel farm would require instantaneous addition of 0.6 tonnes of dissolved carbonate. However, dilution by currents is high, and so to maintain this supply of dissolved carbonate would require 3.5–36 tonnes/day, depending on mussel farm location and current regime.
- Screening tests using mild acid to assess the factors influencing dissolution of waste shell identified shell particle size as a primary factor, with powdered shell dissolving faster than whole, fragmented, or crushed shell. Older shells

dissolved more readily than fresh shell, and highest dissolution rates were obtained after waste shell had been submerged in coastal water or buried in sediment for one month.

- Laboratory tests using coastal seawater confirmed the threshold for mussel shell dissolution at a $\Omega\text{AR} = 1.1$, slightly higher than the accepted ΩAR value of 1.0. This ΩAR value is already experienced episodically on mussel farms in the Firth of Thames.
- In dissolution tests, waste shell maintained on dropper lines showed an average mass loss of 0.012%/day (range 0.002–6%), which is lower than reported dissolution rates at the sediment surface. Maintenance of waste shell on dropper lines also had negligible measurable effect on pH.
- To raise pH from the present-day minima to present-day mean within the boundary layer ($\sim 10\text{m}^3$) of a dropper line would require dissolved carbonate addition of 8.5–85 kg/day at current speeds of 0.01–0.1 m/s. If this were delivered by waste shell the slow dissolution rate would necessitate loading of 0.9–3.6 tonnes waste shell/m dropper line at the lowest current speeds, which is not practical.
- The impact of waste shell addition on growth and survival of spat could not be tested on dropper lines due to low spat availability for seeding. Instead, juvenile mussels were tested in laboratory experiments under present-day pH and future pH projected for the year 2050. The presence of waste shell had no effect on juvenile mussel growth (shell length or width), or their overall physical or physiological condition over a 5-week experimental timescale.
- Although deposition of waste shell on the seafloor may be practical an excessive amount of waste shell ($>11,000$ tonnes) is required to significantly raise pH and carbonate availability on a one-hectare mussel farm. The waste shell would need to be at least 1.5 km upstream of the farm to ensure vertical mixing and availability of the resulting dissolved carbonate to mussels on the upper dropper lines.
- Aeration tests in a coastal seawater pond determined the efficiency of different tubing and flow rates, with the results extrapolated to a mussel farm. This technique has potential to raise pH and carbonate availability, but its effectiveness is also reduced by dilution. For example, aeration of 50% of the volume of a one-hectare mussel farm would raise dissolved carbonate levels by less than 5%. The associated air delivery requirement would be high and incur significant capital and power generation costs.
- Location of aeration needs to be assessed as a pilot test on a mussel farm identified that near-surface aeration (4 m depth) within the farm resulted in re-suspension of particulate matter and a reduction in pH and dissolved oxygen. Within the scope of this study the application of waste shell has minimal potential for ameliorating ocean acidification within mussel farms. Alternative applications of waste shell, such as incorporation within the matrix of dropper lines and calcination to produce lime may represent more effective ways of using waste shell. CO_2 removal by aeration has limited potential for raising pH over a mussel farm, although further studies could investigate the potential of microscale aeration within dropper lines, and other potential “bio-buffering” options such as macroalgae beds upstream of mussel farms.

Law C. S., Barr N., Gall M., Cummings V., Currie K., Murdoch J., Halliday J., Frost E., Stevens C., Plew D., Vance J. and Zeldis J., 2020. Futureproofing the green-lipped mussel aquaculture industry against ocean acidification. *National Science Challenges, Sustainable Seas*. [Report](#).

Gene expression patterns of red sea urchins (*Mesocentrotus franciscanus*) exposed to different combinations of temperature and $p\text{CO}_2$ during early development

The red sea urchin *Mesocentrotus franciscanus* is an ecologically important kelp forest herbivore and an economically valuable wild fishery species. To examine how *M. franciscanus* responds to its environment on a molecular level, differences in gene expression patterns were observed in embryos raised under combinations of two temperatures (13 °C or 17 °C) and two $p\text{CO}_2$ levels (475 μatm or 1050 μatm). These combinations mimic various present-day conditions measured during and between upwelling events in the highly dynamic California Current System with the exception of the 17 °C and 1050 μatm combination, which does not currently occur. However, as ocean warming and acidification continues, warmer temperatures and higher $p\text{CO}_2$ conditions are expected to increase in frequency and to occur simultaneously. The transcriptomic responses of the embryos were assessed at two developmental stages (gastrula and prism) in light of previously described plasticity in body size and thermotolerance under these temperature and $p\text{CO}_2$ treatments.

Although transcriptomic patterns primarily varied by developmental stage, there were pronounced differences in gene expression as a result of the treatment conditions. Temperature and $p\text{CO}_2$ treatments led to the differential expression of genes related to the cellular stress response, transmembrane transport, metabolic processes, and the regulation of gene expression. At each developmental stage, temperature contributed significantly to the observed variance in gene expression, which was also correlated to the phenotypic attributes of the embryos. On the other hand, the transcriptomic response to $p\text{CO}_2$ was relatively muted, particularly at the prism stage.

M. franciscanus exhibited transcriptomic plasticity under different temperatures, indicating their capacity for a molecular-level response that may facilitate red sea urchins facing ocean warming as climate change continues. In contrast, the lack of a robust transcriptomic response, in combination with observations of decreased body size, under elevated $p\text{CO}_2$ levels suggest that this species may be negatively affected by ocean acidification. High present-day $p\text{CO}_2$ conditions that occur due to coastal upwelling may already be influencing populations of *M. franciscanus*. Wong J. M. & Hofmann G. E., 2021. Gene expression patterns of red sea urchins (*Mesocentrotus franciscanus*) exposed to different combinations of temperature and $p\text{CO}_2$ during early development. *BMC Genomics* 22: 32. doi: 10.1186/s12864-020-07327-x. [Article](#).

seacarb is a **seacarb** extension written in R, which enables to use seacarb (Gattuso et al., 2019) for deep-time carbonate system calculations or for culturing studies carried out in seawater with modified $[\text{Mg}^{2+}]$ and $[\text{Ca}^{2+}]$. For

this, the functions *carb*, *K0*, *K1*, *K2*, *Ks*, *Kw*, *Kb*, *Kspa*, and *Kspc* were modified to account for the effect of seawater [Mg²⁺] and [Ca²⁺] on the dissociation constants of carbonic and boric acid. In addition to the modified functions, seacarb contains *MyAMI* that are tabulated parameters defining the temperature and salinity dependencies of the conditional equilibrium constants for [Mg²⁺] and [Ca²⁺] in the range 1–60 mM (from Hain et al., 2015, 2018), as well as a function for bilinear interpolation

Markus Raitzsch, Mathis Hain, Michael Henehan & Jean-Pierre Gattuso. *Zenodo*, 11 January 2021. [More information](#).

Ocean acidification locks algal communities in a species-poor early successional stage Long-term exposure to CO₂-enriched waters can considerably alter marine biological community development, often resulting in simplified systems dominated by turf algae that possess reduced biodiversity and low ecological complexity. Current understanding of the underlying processes by which ocean acidification alters biological community development and stability remains limited, making the management of such shifts problematic. Here, we deployed recruitment tiles in reference (pH_T 8.137 ± 0.056 SD) and CO₂-enriched conditions (pH_T 7.788 ± 0.105 SD) at a volcanic CO₂ seep in Japan to assess the underlying processes and patterns of algal community development. We assessed (i) algal community succession in two different seasons (Cooler months: January–July, and warmer months: July–January), (ii) the effects of initial community composition on subsequent community succession (by reciprocally transplanting preestablished communities for a further 6 months), and (iii) the community production of resulting communities, to assess how their functioning was altered (following 12 months recruitment). Settlement tiles became dominated by turf algae under CO₂-enrichment and had lower biomass, diversity and complexity, a pattern consistent across seasons. This locked the community in a species-poor early successional stage. In terms of community functioning, the elevated pCO₂ community had greater net community production, but this did not result in increased algal community cover, biomass, biodiversity or structural complexity. Taken together, this shows that both new and established communities become simplified by rising CO₂ levels. Our transplant of preestablished communities from enriched CO₂ to reference conditions demonstrated their high resilience, since they became indistinguishable from communities maintained entirely in reference conditions. This shows that meaningful reductions in pCO₂ can enable the recovery of algal communities. By understanding the ecological processes responsible for driving shifts in community composition, we can better assess how communities are likely to be altered by ocean acidification.

Harvey B. P., Kon K., Agostini S., Wada S. & Hall-Spencer J. M., in press. Ocean acidification locks algal communities in a species-poor early successional stage. *Global Change Biology*. doi: 10.1111/gcb.15455. [Article](#) (subscription required)

Impacts of acclimation in warm-low pH conditions on the physiology of the sea urchin *Heliocidaris erythrogramma* and carryover effects for juvenile offspring. Ocean warming (OW) and acidification (OA) affects nearly all aspects of marine organism physiology and it is important to consider both stressors when predicting responses to climate change. We investigated the effects of long-term exposure to OW and OA on the physiology of adults of the sea urchin, *Heliocidaris erythrogramma*, a species resident in the southeast Australia warming hotspot. The urchins were slowly introduced to stressor conditions in the laboratory over a 7-week adjustment period to three temperature (ambient, +2°C, +3°C) and two pH (ambient: pH_T 8.0; –0.4 units: pH_T 7.6) treatments. They were then maintained in a natural pattern of seasonal temperature and photoperiod change, and fixed pH, for 22 weeks. Survival was monitored through week 22 and metabolic rate was measured at 4 and 12 weeks of acclimation, feeding rate and ammonia excretion rate at 12 weeks and assimilation efficiency at 13 weeks. Acclimation to +3°C was deleterious regardless of pH. Mortality from week 6 indicated that recent marine heatwaves are likely to have been deleterious to this species. Acclimation to +2°C did not affect survival. Increased temperature decreased feeding and increased excretion rates, with no effect of acidification. While metabolic rate increased additively with temperature and low pH at week 4, there was no difference between treatments at week 12, indicating physiological acclimation in surviving urchins to stressful conditions. Regardless of treatment, *H. erythrogramma* had a net positive energy budget indicating that the responses were not due to energy limitation. To test for the effect of parental acclimation on offspring responses, the offspring of acclimated urchins were reared to the juvenile stage in OW and OA conditions. Parental acclimation to warming, but not acidification altered juvenile physiology with an increase in metabolic rate. Our results show that incorporation of gradual seasonal environmental change in long-term acclimation can influence outcomes, an important consideration in predicting the consequences of changing climate for marine species.

Hariato J., Aldridge J., Torres Gabarda S. A., Grainger R. J. & Byrne M., 2021. Impacts of acclimation in warm-low pH conditions on the physiology of the sea urchin *Heliocidaris erythrogramma* and carryover effects for juvenile offspring. *Frontiers in Marine Science* 7: 1197. doi: 10.3389/fmars.2020.588938. [Article](#).

Effect of environmental history on the habitat-forming kelp *Macrocystis pyrifera* responses to ocean acidification and warming: a physiological and molecular approach. The capacity of marine organisms to adapt and/or acclimate to climate change might differ among distinct populations, depending on their local environmental history and phenotypic plasticity. Kelp forests create some of the most productive habitats in the world, but globally, many populations have been negatively impacted by multiple anthropogenic stressors. Here, we compare the physiological and molecular responses to ocean acidification (OA) and warming (OW) of two populations of the giant kelp *Macrocystis pyrifera* from distinct upwelling conditions (weak vs strong). Using laboratory mesocosm experiments, we found that juvenile *Macrocystis* sporophyte responses to OW and OA did not differ among populations: elevated temperature reduced growth while OA had no effect on growth and photosynthesis. However, we observed higher growth rates and NO₃⁻ assimilation, and enhanced expression of metabolic-genes involved in the NO₃⁻ and CO₂ assimilation in individuals from the strong upwelling site. Our results suggest that

despite no inter-population differences in response to OA and OW, intrinsic differences among populations might be related to their natural variability in CO₂, NO₃⁻ and seawater temperatures driven by coastal upwelling. Further work including additional populations and fluctuating climate change conditions rather than static values are needed to precisely determine how natural variability in environmental conditions might influence a species' response to climate change.

Fernández P. A., Navarro J. M., Camus C., Torres R. & Buschmann A. H., 2021. Effect of environmental history on the habitat-forming kelp *Macrocystis pyrifera* responses to ocean acidification and warming: a physiological and molecular approach. *Scientific Reports* 11: 2510. doi: 10.1038/s41598-021-82094-7. [Article](#).

Connecting to the oceans: supporting ocean literacy and public engagement Improved public understanding of the ocean and the importance of sustainable ocean use, or ocean literacy, is essential for achieving global commitments to sustainable development by 2030 and beyond. However, growing human populations (particularly in mega-cities), urbanisation and socio-economic disparity threaten opportunities for people to engage and connect directly with ocean environments. Thus, a major challenge in engaging the whole of society in achieving ocean sustainability by 2030 is to develop strategies to improve societal connections to the ocean. The concept of ocean literacy reflects public understanding of the ocean, but is also an indication of connections to, and attitudes and behaviours towards, the ocean. Improving and progressing global ocean literacy has potential to catalyse the behaviour changes necessary for achieving a sustainable future. As part of the Future Seas project (<https://futureseas2030.org/>), this paper aims to synthesise knowledge and perspectives on ocean literacy from a range of disciplines, including but not exclusive to marine biology, socio-ecology, philosophy, technology, psychology, oceanography and human health. Using examples from the literature, we outline the potential for positive change towards a sustainable future based on knowledge that already exists. We focus on four drivers that can influence and improve ocean literacy and societal connections to the ocean: (1) education, (2) cultural connections, (3) technological developments, and (4) knowledge exchange and science-policy interconnections. We explore how each driver plays a role in improving perceptions of the ocean to engender more widespread societal support for effective ocean management and conservation. In doing so, we develop an ocean literacy toolkit, a practical resource for enhancing ocean connections across a broad range of contexts worldwide.

Kelly, R., Evans, K., Alexander, K. et al. Connecting to the oceans: supporting ocean literacy and public engagement. *Rev Fish Biol Fisheries* (2021). <https://doi.org/10.1007/s11160-020-09625-9>