

Ocean Acidification in Pacific Northwest coastal waters: what do we know?

Prepared by Jan Newton and Terrie Klinger, University of Washington¹

Our growing understanding of the causes and consequences of ocean acidification in local marine waters has been reported in the peer-reviewed scientific literature and summarized in the [Scientific Summary of the Washington State Blue Ribbon Panel on Ocean Acidification](#) (hereafter, Scientific Summary) released in 2012. The purpose of this short communication is to clearly and succinctly present the current scientific understanding of ocean acidification in the Pacific Northwest based on evidence from the peer-reviewed scientific literature.

The scientific evidence for ocean acidification in the Pacific Northwest is compelling. This evidence consists of numerous scientific papers, published over a period of many years, representing contributions from multiple scientists at multiple institutions. The scientific evidence comes from investigations of the natural and anthropogenic², biogeochemistry Pacific Northwest waters, organismal sensitivity to relevant biogeochemical conditions, physiological mechanisms that determine sensitivity, and successful adaptation of culture practices in hatcheries.

Six things we know about ocean acidification in Pacific Northwest coastal waters:

1. Rising atmospheric CO₂ changes ocean chemistry and negatively impacts shelled organisms.

The concentration of CO₂ in the atmosphere has increased due to human activities, primarily combustion of fossil fuels and deforestation³. The addition of carbon dioxide to seawater increases the concentration of hydrogen ions (H⁺), reducing both the pH and the dissolved carbonate ion concentration. This is the phenomenon known as ocean acidification (OA)⁴. Even though seawater remains a basic solution, it becomes acidified by the addition of CO₂⁵. It is well established that Pacific Northwest marine waters, like the global oceans, undergo the highly predictable chemical reactions that reduce both the pH and the concentration of carbonate ions⁶.

The concentration of carbonate ions is important because these ions, along with dissolved calcium, are the building blocks of shells and skeletons of many marine organisms. Both aragonite and calcite are common biominerals of calcium carbonate produced by shellfish and other calcifying marine organisms. Aragonite is produced by the larvae of many Pacific Northwest shellfish (e.g., clams, mussels, oysters) and is the form more sensitive to increasing CO₂.

The stability of minerals such as calcium carbonate is defined by a term called the saturation state⁷ or omega (Ω). Because calcium is abundant, the saturation state of calcium carbonate minerals is mainly controlled by the carbonate ions in seawater. When the carbonate ion concentration is high, $\Omega_{\text{aragonite}}$ is high and mineral formation is favored ($\Omega_{\text{aragonite}} > 1$); when the carbonate ion concentration is low, Ω is low and mineral formation is not favored ($\Omega_{\text{aragonite}} < 1$). When the $\Omega_{\text{aragonite}}$ is below the value of 1.0, the water is termed “corrosive” because dissolution of pure aragonite and unprotected aragonite shells will begin to occur⁸.

The global increase in atmospheric CO₂ from human activity is large enough to reduce seawater $\Omega_{\text{aragonite}}$ by biologically significant amounts⁹. The global increase in atmospheric CO₂ since the pre-industrial era has caused a decline in the pH of surface seawater by about 0.1¹⁰. Simultaneously, the calcium carbonate saturation state has decreased by 20%¹¹. Research over the past two decades has underscored the importance of calcium carbonate saturation state to understanding the effects of ocean acidification on

calcifying organisms¹². For many shell-forming organisms it is the aragonite saturation state, not pH, that has been shown to be most critical to survival and growth¹³.

Declining calcium carbonate saturation state makes it more difficult for calcifying organisms (oysters, clams, mussels, crabs, corals, etc.) to produce or maintain their calcium carbonate shells or skeletons¹⁴.

2. Pacific Northwest shellfish are sensitive to reduced calcium carbonate-saturation state within the current range of conditions.

Shellfish in Pacific Northwest marine waters are particularly vulnerable to ocean acidification-driven effects. Pacific Northwest waters are colder and fresher than the global average ocean¹⁵, which means CO₂ gas dissolves more effectively in these waters. Consequently, the pre-industrial $\Omega_{\text{aragonite}}$ was already lower here than in the average ocean, with a pre-industrial of ~ 2.5 , compared to the open ocean average value of ~ 3.6 ¹⁶.

Starting from pre-industrial values of $\Omega_{\text{aragonite}} \sim 2.5$ in Pacific Northwest waters, modern-day surface waters in contact with increased atmospheric CO₂ have experienced a decrease in the aragonite saturation state of about 0.5 units. Because water from upwelling was last in contact with the surface ~ 30 -50 years ago, the anthropogenic signal is weaker in those source waters. Mixtures of these two sources, however, results in a reduction in $\Omega_{\text{aragonite}}$ due to anthropogenic CO₂ off the Pacific Northwest outer coast of ~ 0.25 -0.5¹⁷.

Even weakly supersaturated conditions can be harmful: significant losses in oyster production have been observed at aragonite saturation states below 2.0¹⁸. This is due to negative effects on the energy budget of developing larvae that must produce shell at a rate several-thousand times higher than the chemical rates of aragonite formation¹⁹.

The decrease in calcium carbonate saturation state from ocean acidification is important to Pacific Northwest shellfish living in saturation conditions that are naturally close to harmful thresholds.

3. Natural and anthropogenic contributions are additive.

As reported in the Scientific Summary²⁰, “Washington State is particularly vulnerable to pH decline because regional drivers can combine with the global atmospheric CO₂ contribution to exacerbate the acidification process.” Several factors, both natural and anthropogenic, drive low- $\Omega_{\text{aragonite}}$ events in the Pacific Northwest. As addressed in the Scientific Summary and the many scientific papers referenced therein, the primary drivers of low $\Omega_{\text{aragonite}}$ in Washington’s marine waters are global atmospheric CO₂, upwelling²¹, respiration/hypoxia²², watershed inputs²³, and non-CO₂ acidic gases. The effects of these multiple drivers are additive.

The current contribution of atmospheric CO₂ from human activity in local waters increases the likelihood that conditions for shell formation will be unfavorable. Because this contribution reduces $\Omega_{\text{aragonite}}$ on the order of 0.25-0.5 units, it can and sometimes does cause thresholds harmful to calcifying organisms to be crossed. A recent paper²⁴, describes how conditions in the coastal ocean have affected saturation state in Netarts Bay, Oregon. This paper established a direct correlation between saturation state and larval production in a shellfish hatchery there, finding that net larval growth became negative below $\Omega = 1.7$. Other observations have shown that corrosive waters with $\Omega_{\text{aragonite}} < 1$ now reach the surface near shore, and found that the contribution from anthropogenic CO₂ was necessary to cross this threshold²⁵.

Freshwater input and human-derived factors causing low $\Omega_{\text{aragonite}}$ are minimal in Netarts Bay, but in other Pacific Northwest bays and estuaries, freshwater, nutrients and organic material can also contribute to reductions in $\Omega_{\text{aragonite}}$ ²⁶. This is because the $\Omega_{\text{aragonite}}$ of some rivers is low and, in areas with high human and natural loads of carbon and nitrogen, CO₂ derived from respiration can be substantial²⁷. Although the details vary between locations²⁷, it remains the case that the anthropogenic CO₂ effect is always to further reduce $\Omega_{\text{aragonite}}$ below conditions resulting from natural variability alone.

Anthropogenic additions of CO₂ significantly contribute to conditions that cause $\Omega_{\text{aragonite}}$ in surface waters to reach levels that are detrimental (e.g. $\Omega_{\text{aragonite}} < 1.7$) or even corrosive ($\Omega_{\text{aragonite}} < 1.0$), creating conditions that are unfavorable or harmful for some local organisms.

4. Anthropogenic contributions to ocean acidification are detectable and have increased the frequency, intensity, and duration of harmful conditions.

The relative magnitude of anthropogenic and non-anthropogenic contributions to rising CO₂ in waters of the Pacific Northwest can be determined and have been reported in the scientific literature²⁹. These studies reported that, of the total increase in CO₂ from the pre-industrial in subsurface waters of Hood Canal, 24-49% was attributable to anthropogenic CO₂³⁰, and that an average decline in aragonite saturation state ranges from 0.2³¹ to 0.5³¹ units in shelf waters of the Pacific Northwest. While anthropogenic CO₂ is the largest single source of acidifying pollution to the Pacific Northwest waters³², it does not currently dominate local variability at daily to seasonal timescales. However, it does add an amount of CO₂ that can significantly worsen already-low $\Omega_{\text{aragonite}}$ conditions for shelled organisms. This contribution essentially ‘makes a bad day worse.’

For the continental shelf of Oregon, “Pre-industrial $\Omega_{\text{aragonite}}$ was rarely undersaturated whereas contemporary surface values occasionally drop as low as 0.66. At the shelf break, contemporary $\Omega_{\text{aragonite}}$ is undersaturated ~30% of the time, whereas pre-industrial undersaturation occurred only ~10% of the time. These changes in $\Omega_{\text{aragonite}}$ from pre-industrial levels are consistent with the findings of the modeled simulations of Hauri et al. (2013), which also concluded that contemporary $\Omega_{\text{aragonite}}$ observations in the California Current System have already shifted substantially from the pre-industrial range.”³⁴ This effect is projected to grow with time, at current CO₂ emission rates³⁵.

As the total amount of CO₂ in the atmosphere and ocean grows, the frequency, intensity, and duration of adverse conditions increases³⁶. Thus, despite well-known natural variability in pH and aragonite saturation state, marine organisms now are exposed to adverse conditions more often than in the past, and these conditions are likely to be more extreme, causing more harm³⁷. Vulnerable organisms such as pteropods and vulnerable life stages such as oyster larvae can suffer mortality or abnormal development following even brief exposures to harmful conditions³⁸, and the negative biological consequences of even brief exposure can persist even after environmental conditions improve³⁹.

Significant effects of rising anthropogenic atmospheric CO₂ are detectable in Pacific Northwest waters now, and these effects will continue to grow as CO₂ continues to increase.

5. Small changes in the environment can cause large responses among living organisms.

While most marine organisms can tolerate a range of environmental conditions, at some point their tolerance fails. For example, fish die when dissolved oxygen reaches critically low levels, and intertidal organisms can die on hot sunny days when temperatures reach critically high levels. Thus, *even small changes in the environment can cause an abrupt biological response when the limits of tolerance are approached or passed*. This general rule holds for exposure to low pH and $\Omega_{\text{aragonite}}$. For example, the shells of free-swimming pteropods begin to dissolve when the aragonite saturation state is ~1.0⁴⁰. For Pacific oysters growing in the Pacific Northwest, the negative impacts begin when $\Omega_{\text{aragonite}}$ drops below 2.0, with net larval growth occurring only when $\Omega_{\text{aragonite}} > 1.7$ ⁴¹. With respect to low pH and aragonite saturation state, the events that drive the observed negative biological effects⁴² are happening now in waters of the Pacific Northwest and are significantly exacerbated by anthropogenic CO₂. These events will become more frequent and increasingly harmful to shell-forming organisms as levels of CO₂ in the environment grow.

Small changes in the environment can cause an abrupt biological response when the limits of tolerance are approached or passed.

6. Local species are affected.

Pacific oysters in aquaculture facilities in Washington and Oregon have shown clear negative responses to low $\Omega_{\text{aragonite}}$ ⁴³. Significantly, these negative responses are ameliorated when CO₂ concentrations in hatchery water are artificially reduced. Pacific oysters are not native to the Pacific Northwest, but they have been grown in aquaculture and in the natural environment here for a century and are naturalized in Washington waters. Studies of the Olympia oyster, which is native to Washington, that were performed in northern California (where the species also is native) showed that survival and growth of larvae and juveniles decreased with exposure to low pH and $\Omega_{\text{aragonite}}$ in both the laboratory and field⁴⁴. Other species native to the Pacific Northwest—for example, red urchins, northern abalone, turban snails—in laboratory settings have shown negative responses when exposed to levels of low pH and high CO₂ that are known to occur in local waters⁴⁵. The larval stages of calcifying invertebrates appear to be highly sensitive to low pH and pCO₂, but negative effects have been observed in multiple life history phases, from gamete fertilization through adults⁴⁶. Moreover, research indicates that combining two or more stressors—for example, high temperature and low pH or $\Omega_{\text{aragonite}}$ —can cause more harm than either stressor alone⁴⁷. Consequently, when considering the effects of increasing CO₂ on local marine life, we need also consider other stresses imposed on those organisms to make accurate predictions of potential harm.

The larval stages of calcifying invertebrates appear to be highly sensitive to low aragonite saturation state.

References

1. This presentation benefited from input and review from Richard Feely, NOAA, Burke Hales, OSU, Steve Emerson, UW, George Waldbusser, OSU, Jennifer Ruesink, UW, and Jim Murray, UW
2. Anthropogenic is defined as originating from human activity
3. IPCC (Intergovernmental Panel on Climate Change), Core Writing Team, R. K. Pachauri and A. Reisinger (Eds.). 2007. [Climate Change 2007: Synthesis Report](#). Contributions of Working Groups I, II, and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.
4. The phenomenon is called “ocean acidification” because of how acidity is defined in basic chemistry. Acidity refers to the concentration of H⁺ ions in solution (Millero, 1996; Emerson and Hedges, 2008; see below for full references); thus, as the concentration of H⁺ ions increases, so does the acidity of the solution. The chemistry of ocean acidification follows established and accepted thermodynamic relationships (Doney et al., 2009; Feely et al., 2009; Waldbusser and Salisbury, 2013; see below for full references). For the complete chemical reactions of ocean acidification, see Dickson, A.G., C.L Sabine, and J.R. Christian (Eds.)(2007): Guide to Best Practices for Ocean CO₂ measurements. PICES Special Publication, 191 pp.
Doney, S. C., V. J. Fabry, R. A. Feely, and J. A. Kleypas. 2009. Ocean acidification: The other CO₂ problem. [Annual Review of Marine Science](#), 1: 169–192.
Feely, R. A., S. C. Doney, and S. R. Cooley. 2009. Ocean acidification: Present conditions and future changes in a high-CO₂ world. [Oceanography](#), 22(4): 36–47.
[Emerson, S. and J. I.](#) Hedges. 2008. Chemical Oceanography and the Global Carbon Cycle, Cambridge University Press, Cambridge U.K. 453 p.
Millero, F.J. 1996. Thermodynamics of the carbon dioxide system in the oceans. *Geochimica et Cosmochimica Acta*, 59(4): 661-677.

Waldbusser, G. G., and J. E. Salisbury. 2013. Ocean acidification in the coastal zone from an organism's perspective: multiple system parameters, frequency domains, and habitats. [The Annual Review of Marine Science, 6: 11.1-11.27.](#)

5. Seawater is basic (pH>7) and remains so at today's concentrations of carbon dioxide (CO₂). Like a freezing day can warm to 40 degrees F, but still not be warm, seawater in the alkaline (or basic) range can acidify without becoming acidic.

6. Hales, B., T. Takahashi, and L. Bandstra. 2005. Atmospheric CO₂ uptake by a coastal upwelling system. [Global Biogeochemical Cycles, 19: 1-11.](#)

Feely, R. A., C. L. Sabine, J. M. Hernandez-Ayon, D. Ianson, and B. Hales. 2008. Evidence for upwelling of corrosive "acidified" water onto the continental shelf. [Science, 320: 1490-1492.](#)

Feely, R. A., S. R. Alin, J. Newton, C. L. Sabine, M. Warner, A. Devol, C. Krembs, and C. Maloy. 2010. The combined effects of ocean acidification, mixing, and respiration on pH and carbonate saturation in an urbanized estuary. [Estuarine, Coastal and Shelf Science, 88: 442-449.](#)

Harris, K. E., M. D. DeGrandpre, and B. Hales. 2013 (and references therein). Aragonite saturation state dynamics in a coastal upwelling zone. [Geophysical Research Letters, 40: 1-6.](#)

7. The tendency for calcium carbonate to remain as a solid and not to dissolve is represented by its "saturation state," represented as $\Omega = [\text{Ca}^{2+}][\text{CO}_3^{2-}]/K_{\text{sp}}$; where Ω is a measure of the stability of CaCO₃ in seawater and is defined as the product of the concentrations of calcium ions (Ca²⁺) and CO₃²⁻ divided by the stoichiometric solubility product (K_{sp}).

8. Feely et al., 2008

9. Barton, A., B. Hales, G. G. Waldbusser, C. Langdon, and R. A. Feely. 2012. The Pacific oyster, *Crassostrea gigas*, shows negative correlation to naturally elevated carbon dioxide levels: Implications for near-term ocean acidification effects. [Limnology and Oceanography, 57\(3\): 698-710.](#)

Waldbusser, G. G., E. L. Brunner, B. A. Haley, B. Hales, C. J. Langdon, and F. G. Prahl. 2013. A developmental and energetic basis linking larval oyster shell formation to acidification sensitivity. [Geophysical Research Letters, 40: 1-6.](#)

10. This amount equates to an increase in acidity of ~30% because pH is measured a logarithmic scale: pH = -log (H⁺).

Royal Society. 2005. Ocean acidification due to increasing atmospheric carbon dioxide. London: The Royal Society, 223 pp.

11. Royal Society, 2005

12. Fabry, V. J., B. A. Seibel, R. A. Feely, and J. C. Orr. 2008. Impacts of ocean acidification on marine fauna and ecosystem processes. [ICES Journal of Marine Science, 65\(3\): 414-432.](#)

Doney et al., 2009 and references therein

13. Barton et al., 2012

Waldbusser et al., 2013

14. Barton et al., 2012

Hettinger, A., E. Sanford, T. M. Hill, E. A. Lenz, A. D. Russell, and B. Gaylord. 2013. Larval carry-over effects from ocean acidification persist in the natural environment. [Global Change Biology, 19: 3317-3326.](#)

Waldbusser and Salisbury, 2013

15. Feely et al., 2008

Feely et al., 2009

16. Open ocean average surface water temperature and salinity are close to 20 °C and 35, respectively, while Pacific Northwest surface waters are closer to 10 °C and 32. For a pre-industrial atmospheric CO₂ of 280 ppm, open ocean surface waters would have $\Omega_{\text{aragonite}} = \sim 3.6$, while local waters would have $\Omega_{\text{aragonite}} \sim 2.5$ (calculations from CO₂calc).

17. Feely et al., 2008

Harris, K. E., M. D. DeGrandpre, and B. Hales. 2013. Aragonite saturation state dynamics in a coastal upwelling zone. *Geophysical Research Letters*, 40: 1-6.

18. Barton et al., 2012

19. Waldbusser et al., 2013

20. Washington State Blue Ribbon Panel on Ocean Acidification. 2012. [Scientific Summary of Ocean Acidification in Washington State Marine Waters](#). NOAA OAR Special Report.

21. Upwelling, causing CO₂-rich waters to shoal to the surface (Feely et al., 2008; Harris et al., 2013) is a very important factor in this region with consequences for local organisms. This seasonal phenomenon occurs along the entire coast of the Pacific Northwest, typically in late spring to summer months. While there are differences in the intensity and duration of upwelling conditions in any given year, upwelling consistently occurs off our coast and its effects can be strong on the scale of days to weeks. It is this daily to weekly time-scale of exposure that is relevant to calcifying organisms. Due to upwelling and other processes described in Feely et al., 2008; Feely et al., 2010 and Harris et al., 2013, waters in the Pacific Northwest naturally show low values of $\Omega_{\text{aragonite}}$ (Barton et al., 2012, Waldbusser and Salisbury, 2013). Upwelling effects reach inland waters including Puget Sound and Hood Canal (Feely et al., 2010).

22. Respiration is a biological source of CO₂ and can be a large contributor in productive subsurface coastal waters such as those in the Pacific Northwest. Shallow estuaries have benthic production and respiration signals that can be strong (Waldbusser and Salisbury, 2013; Scientific Summary of Ocean Acidification, 2012).

23. In some regions watershed effects can be substantial in areas where riverine inputs are significant. Rivers can have naturally low pH and can carry a load of organic material or nutrients that increases respiration (Scientific Summary of Ocean Acidification, 2012).

24. Barton et al., 2012

25. Feely et al., 2008

Harris et al., 2013

26. Scientific Summary of Ocean Acidification, 2012

27. Scientific Summary of Ocean Acidification, 2012

28. Published summaries of datasets from diverse national and global locations have shown substantial differences in the variation of pH or CO₂ concentration of marine waters (Hoffmann et al 2011 (see below for full reference); Waldbusser and Salisbury, 2013). What is equally clear in Washington coastal waters is that ocean acidification differs between locations in ways that reflect local drivers. Data collected at regional scales reveal substantial spatial and temporal variability (Scientific Summary on Ocean Acidification, 2012). Over time, we see seasonal and daily variations in pH and aragonite saturation state, hence a single value does not and cannot describe the ocean acidification status of a system. Diurnal changes in production and respiration, tidal intrusions interacting with river plumes, and seasonality in phytoplankton growth and respiration processes all contribute to the ocean acidification signal, and all vary over different scales of time and space.

- Hofmann, G. E., J.E. Smith, K.S. Johnson, U. Send, L.A. Levin, F. Micheli, A. Pavtan, N.N. Price, B. Peterson, Y. Takeshita, P.G. Matson, E.D. Crook, K.L. Kroeker, M.C. Gambi, E.B. Rivest, C.A. Frieder, P.C. Yu, and T.R. Martz. 2011. High-frequency dynamics of ocean pH: a multi-ecosystem comparison. [PLoS ONE, 6\(12\): e28983](#).
29. Feely et al., 2008
Feely et al., 2010
Harris et al., 2013
30. Feely et al., 2010
31. Feely et al., 2008
32. Harris et al., 2013
33. Scientific Summary on Ocean Acidification, 2012
34. Harris et al., 2013
35. Gruber, N., C. Hauri, Z. Lachkar, D. Loher, T. L. Frölicher, and G.-K. Plattner. 2012. Rapid progression of ocean acidification in the California Current System. [Science, 337\(6091\): 220–223](#).
- Hauri, C. (a), N. Gruber, M. Vogt, S. C. Doney, R. A. Feely, Z. Lachkar, A. Leinweber, A. M. P. McDonnell, M. Munnich, and G.-K. Plattner. 2013. Spatiotemporal variability and long-term trends of ocean acidification in the California Current System. [Biogeosciences, 10: 193-216](#).
36. Hauri et al., 2013 (a)
- Hauri, C. (b), N. Gruber, A. M. P. McDonnell, and M. Vogt. 2013. The intensity, duration, and severity of low aragonite saturation state events on the California continental shelf. [Geophysical Research Letters, 40: 3424-3428](#).
- Harris et al., 2013
37. Waldbusser and Salisbury, 2013 and references therein
38. Bednarsek, N., G.A. Tarling, D.C.E. Bakker, S. Fielding, E.M. Jones, H.J. Venables, P Ward, A. Kuzirian, B. Leze, R.A. Feely, and E.J. Murphy. 2012. Extensive dissolution of live pteropods in the Southern Ocean. [Nature Geoscience 5: 881-885](#).
- Hettinger et al., 2013
39. Hettinger et al., 2013
- Hettinger, A., E. Sanford, T.M. Hill, A. D. Russell, K. N. S. Sato, J. Hoey, M. Forsch, H. N. Page, and B. Gaylord. *In press*. Persistent carry-over effects of planktonic exposure to ocean acidification in the Olympia oyster. Ecological Society of America.
40. Bednarsek et al., 2012
41. Barton et al., 2012
42. Waldbusser and Salisbury, 2013
43. Barton et al., 2012
- Waldbusser et al., 2013
44. Hettinger et al. 2013
- Hettinger et al. *in press*

45. Nienhuis, S., A. R. Palmer, and C. D. Harley. 2010. Elevated CO₂ affects shell dissolution rate but not calcification rate in a marine snail. [Proceedings of the Royal Society B—Biological Sciences, 277\(1693\): 2553–2558.](#)

Crim, R. N., J. M. Sunday, and C. D. G. Harley. 2011. Elevated seawater CO₂ concentrations impair larval development and reduce larval survival in endangered northern abalone (*Haliotis kamtschatkana*). [Journal of Experimental Marine Biology and Ecology, 400\(1–2\): 272–277.](#)

Reuter, K. E., K. E. Lotterhos, R. N. Crim, C. A. Thompson, and C. D. G. Harley. 2011. Elevated pCO₂ increases sperm limitation and risk of polyspermy in the Red Sea urchin *Strongylocentrotus franciscanus*. [Global Change Biology, 17\(1\): 163–171.](#)

46. Kroeker, K. J., R. L. Kordas, R. N. Crim, and G. G. Singh. 2010. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. [Ecology Letters, 13\(11\): 1419–1434.](#)

47. O'Donnell, M. J., L. M. Hammond, and G. E. Hofmann. 2009. Predicted impact of ocean acidification on a marine invertebrate: elevated CO₂ alters response to thermal stress in sea urchin larvae. [Marine Biology, 156: 439–446.](#)