EFFECTS OF OCEAN ACIDIFICATION AND WARMING ON CORALS (LABORATORY STUDIES)
Most of the ocean acidification research conducted to date has focused solely on the biological impacts of declining seawater pH. Fewer studies have investigated the interactive effects of ocean acidification and temperature. This summary examines what has been learned in several of such studies for coral reefs, as reported in various laboratory-based studies on the topic. Contrary to what is widely assumed and reported, the studies reviewed here collectively reveal that many corals will remain unaffected by rising temperatures and atmospheric CO$_2$ concentrations. Furthermore, in contrast to projections, some will likely experience growth and performance benefits.

In a paper published in *Nature Climate Change*, McCulloch et al. (2012)\(^1\) describe how biogenic calcification occurs within an extracellular calcifying fluid located in the semi-isolated space between a coral’s skeleton and its calcicoblastic ectoderm, where during active calcification the pH of the calcifying fluid (pH$_{cf}$) is often increased relative to ambient seawater pH. At a typical seawater pH of ~8.1, for example, they state that the pH of aragonitic corals shows a species-dependent range of 8.4 to 8.7, representing a systematic increase in pH$_{cf}$ relative to ambient seawater (ΔpH) of ~0.3-0.6 units. In fact, they report that *in situ* measurements of pH within the calcifying medium of live coral polyps using microelectrodes (Al-Horani *et al.*, 2003; Ries, 2011a) and pH-sensitive dyes (Venn *et al.*, 2011) have registered enhanced pH$_{cf}$ values between 0.6 and 1.2 (and sometimes up to 2) pH units above seawater during the day, when both net production and calcification are highest.

Using a model of pH regulation combined with abiotic calcification, McCulloch *et al.* (2012) additionally show that “the enhanced kinetics of calcification owing to higher temperatures has the potential to counter the effects of ocean acidification,” adding that “the extra energy required to up-regulate pH is minor, only <1\% of that generated by photosynthesis,” which highlights the importance of maintaining the zooxanthellae-coral symbiosis for sustaining calcification. And they further note, in this regard, that their model predicts “a ~15\% increase in calcification rates from the Last Glacial Maximum to the late Holocene,” which increase they describe as being “consistent with the expansion of tropical habitats that occurred during this time despite $P_{CO_2}$ increasing.”

Projecting into the future with their experimentally-verified model, the four researchers assess the response of coral reefs to both global warming, with mean tropical sea surface temperatures ~2°C higher, and with $P_{CO_2}$ increasing from present-day levels to ~1,000 ppm by the year 2100.” And for this scenario, they report that their model predicts “either unchanged or only minimal effects on calcification rates.” Thus, from a strictly chemical and kinetic perspective, their model indicates that “ocean acidification combined with rising ocean temperatures should have only

\(^1\) [http://www.co2science.org/articles/V15/N50/EDIT.php](http://www.co2science.org/articles/V15/N50/EDIT.php)
minimal effects on coral calcification,” which they describe as “a direct outcome” of corals’ ability to up-regulate pH at the site of calcification.

Rodolfo-Metalpa et al. (2010)² collected three live colonies of the Mediterranean zooxanthellate coral Cladocora caespitosa in the Bay of Villefranche (Ligurian Sea, France) at about 25 meters depth in July 2006 plus three other colonies in February 2007. The colonies were then divided into fragments and carefully removed single polyps that they attached to PVC plates and randomly assigned to aquariums that were continuously supplied with unfiltered seawater and maintained at ambient or elevated water temperature (T or T + 3°C) in equilibrium with air of ambient or elevated CO₂ concentration (400 or 700 ppm), subjecting them to “(1) mid-term perturbations (1 month) in summer and winter conditions of irradiance and temperature, and (2) a long-term perturbation (1 year), mimicking the seasonal changes in temperature and irradiance.”

Results indicated that “an increase in CO₂, in the range predicted for 2100, does not reduce [the coral’s] calcification rate,” and that “an increase in CO₂, alone or in combination with elevated temperature, had no significant effect on photosynthesis, photosynthetic efficiency and calcification.” However, they report that a 3°C rise in temperature in winter resulted in a 72% increase in gross photosynthesis, as well as a significant increase in daytime calcification rate.

In light of their several significant findings, Rodolfo-Metalpa et al. conclude that “the conventional belief that calcification rates will be affected by ocean acidification may not be widespread in temperate corals.” In this regard, for example, they note that Ries et al. (2009) have reported that the calcification rate of the temperate coral Oculina arbuscula is also unaffected by an increase in atmospheric CO₂ concentration of up to 840 ppm, and that a large decrease in calcification was only found at a CO₂ concentration in excess of 2200 ppm. In addition, they write that “some marine invertebrates may be able to calcify in the face of ocean acidification or, contrary to what is generally expected, may increase their calcification rates as reported on the ophiourid brittlestar Amphiura filiformis (Wood et al., 2008), the seastar Pisaster ochraceus (Gooding et al., 2009) exposed to lower pH (7.8-7.3), the Caribbean coral Madracis mirabilis at pH 7.6 (Jury et al., 2010), and shown for coralline red algae, calcareous green algae, temperate urchins, limpets, crabs, lobsters and shrimp (Ries et al., 2009).” Likewise, they write that there are many cases where “rates of photosynthesis are either not affected (e.g. Langdon et al., 2003; Reynaud et al., 2003; Schneider and Erez, 2006; Marubini et al., 2008) or slightly increased (e.g. Langdon and Atkinson, 2005) at the level of CO₂ expected in 2100.”

² http://www.co2science.org/articles/V13/N21/C2.php
In a study designed to explore what controls calcification in corals, Sandeman (2012) suspended, by means of a torsion microbalance (as per Kesling and Crafts, 1962), small pieces of coral that he carefully removed from the edges of thin plates of Agaricia agaricites corals and lowered into gently-stirred temperature-controlled seawater, after which he used the microbalance to measure coral net calcification rates over a range of seawater temperature and pH. Results of the experiment indicated that calcification rates of live A. agaricites coral increased by 15-17.7% per °C as seawater temperature rose from 27 to 29.5°C, and in his experiments in which the pH of the seawater was reduced from an average of 8.2 to 7.6, he observed that calcification in living corals increased significantly. On the other hand, similar experiments conducted with small portions of dead coral skeleton revealed that “when the average pH was reduced from 8.2 to 7.5, calcification rate decreased.” More specifically, he determined that the difference between calcification rates in going from seawater of pH 8.2 to seawater of pH 7.8 ranged from +30% for coral with no dead areas to -21.5% for coral with 30% dead exposed surface area.

Commenting on the analysis, the Trent University researcher from Peterborough, Ontario (Canada) says his findings suggest that lower seawater pH due to atmospheric CO₂ enrichment and increased temperature (but short of reaching the bleaching level) “will both enhance active biotic calcification.” And he therefore states that the wide range of results between his and other scientists’ studies of calcification rate and carbon dioxide “may be explainable in terms of the ratio of ‘live’ to ‘dead’ areas of coral,” as is also suggested by the work of Rodolfo-Metalpa et al. (2011) and Ries (2011b), all of which information leads him to conclude that coral species that typically have smaller areas of exposed dead surface “may have a better chance of survival as pH levels drop.”

Introducing their work, Schoepf et al. (2013) write that "since scleractinian corals are calcifying organisms that already live close to their upper thermal tolerance limits, both ocean warming and acidification severely threaten their survival and role as reef ecosystem engineers." Yet they further state that "no studies to date have measured energy reserve pools (i.e., lipid, protein, and carbohydrate) together with calcification under ocean acidification conditions under different temperature scenarios," which omissions inspired them to conduct an experiment that actually did what was needed to be done in this regard.

Specifically, Schoepf et al. studied the single and interactive effects of pCO₂ (382, 607 and 741 ppm) and temperature (26.5 and 29.0°C) on coral calcification, energy reserves (i.e., lipid, protein, and carbohydrate), chlorophyll a and endosymbiont concentrations in four species of Pacific coral having different growth morphologies (Acropora millepora, Pocillopora damicornis, Montipora monasteriata and Turbinaria reniformis). In doing so, the thirteen researchers discovered that coral energy reserves were largely not metabolized "in order to sustain calcification under elevated pCO₂ and temperature," in harmony with the fact that "maintenance of energy reserves has been shown to be associated with higher resistance to coral bleaching and to promote recovery from bleaching (Rodrigues and Grottoli, 2007; Anthony et al., 2009)." In fact, they report that lipid concentrations actually increased under ocean acidification conditions in both A. millepora and P. damicornis, and that they "were fully maintained in M. monasteriata and T. reniformis," while protein, carbohydrate and tissue biomass were also "overall maintained under ocean acidification conditions in all species." And,

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3 http://www.co2science.org/articles/V15/N31/B2.php
4 http://www.co2science.org/articles/V17/N1/B2.php
therefore, they found that "only one of the four corals species studied [Acropora millepora] decreased calcification in response to average ocean acidification levels expected by the second half of this century (741 ppm), even when combined with elevated temperature (+2.5°C)."

As a result of their several findings, Schoepf et al. concluded that "some corals could be more resistant to combined ocean acidification and warming expected by the end of this century than previously thought," such that "the immediate effects of rising seawater temperature and ocean acidification may be tolerable for some species," possibly because the increased availability of CO$_2$(aq) under ocean acidification conditions may enhance algal productivity, especially in Symbiodinium phylotypes with less efficient carbon-concentrating mechanisms that rely to a greater extent on the passive, diffusive uptake of CO$_2$(aq) and its fertilization effect, citing in this regard the work of Herfort et al. (2008) and Brading et al. (2011).

In a study published in the journal Marine Ecology Progress Series, Chua et al. (2013)$^5$ purposed to test "whether temperature might act in combination with OA to produce a measurable ecological effect on fertilization, development, larval survivorship or metamorphosis of two broadcast spawning species, Acropora millepora and A. tenuis, from the Great Barrier Reef. More specifically, the four researchers studied the effects of four different treatments: control, high temperature (+2°C), high partial pressure of CO$_2$ (pCO$_2$, 700 µatm), and a combination of both high temperature and high pCO$_2$, corresponding to the current levels of these parameters and the values projected for them by the end of this century in the IPCC's A2 scenario. And what did they thereby learn?

Chua et al. say they "found no consistent effect of elevated pCO$_2$ on fertilization, development, survivorship or metamorphosis, neither alone nor in combination with temperature," contrasting with the results found by Schoepf et al. (2013) for A. millepora discussed earlier. As for warming, they also say that it "had no consistent effect on fertilization, survivorship or metamorphosis." However, they observed that the two degrees of warming actually increased rates of development, providing encouraging news concerning the future of these organisms.

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$^5$ http://www.co2science.org/articles/V17/nov/a21.php
Determined to discover "whether elevated pCO\textsubscript{2} predicted for the year 2100 (85.1 Pa) affects bleaching in the coral \textit{Seriatopora caliendrum} either independently or interactively with high temperature," Wall \textit{et al.} (2014)\textsuperscript{6} collected specimens of the species from Nanwan Bay, Taiwan, and subjected them to combinations of temperature (27.7 vs. 30.5°C) and pCO\textsubscript{2} (45.1 vs. 85.1 Pa) for 14 days," while assessing all pertinent biological responses of the coral. In discussing their findings, the three researchers report that "high temperature reduced values of all dependent variables (i.e., bleaching occurred), but high pCO\textsubscript{2} did not affect \textit{Symbiodinium} photophysiology or productivity, and did not cause bleaching," either "individually, or interactively with high temperature." Given such findings, Wall \textit{et al.} concluded that "the present results clearly support a null effect for high pCO\textsubscript{2}." Or as they state in the final sentence of their paper's abstract, "short-term exposure to 81.5 Pa pCO\textsubscript{2}, alone and in combination with elevated temperature, does not cause or affect coral bleaching."

Introducing their recent work, Levas \textit{et al.} (2015)\textsuperscript{7} write that "research to date has largely neglected the individual and combined effects of OA and seawater temperature on coral-mediated organic carbon (OC) fluxes," noting that this void of knowledge "is of particular concern as dissolved and particulate OC (DOC and POC, respectively) represent large pools of fixed OC on coral reefs."

In an attempt to reduce this knowledge void, the sixteen scientists assessed coral-mediated POC and DOC, as well as total OC (TOC = DOC + POC), plus the relative contributions of each of them to coral metabolic demand for two species of coral, \textit{Acropora millepora} and \textit{Turbinaria reniformis}, at two different levels of pCO\textsubscript{2} (382 and 741 µatm) and seawater temperatures (26.5 and 31.0°C). And what did they thereby learn? Levas \textit{et al.} report that "independent of temperature, DOC fluxes decreased significantly with increases in pCO\textsubscript{2} in both species, resulting in more DOC being retained by the corals and only representing between 19 and 6% of TOC fluxes for \textit{A. millepora} and \textit{T. reniformis}," while at the same time POC fluxes were unaffected by elevated temperature and/or pCO\textsubscript{2}. And, thus, they were able to conclude that "these findings add to a growing body of evidence that certain species of coral may be less at risk to the impacts of OA and temperature than previously thought."

In one final study, Towle \textit{et al.} (2015)\textsuperscript{8} examined "the ability of coral heterotrophy to mitigate reductions in growth due to climate change stress in the critically endangered Caribbean coral \textit{Acropora cervicornis} via changes in feeding rate." This they did in a laboratory study where the

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  \item Such results "show for the first time that a threatened coral species can buffer ocean-acidification-reduced calcification by increasing feeding rates."
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\textsuperscript{6} http://www.co2science.org/articles/V17/N19/C3.php
\textsuperscript{7} http://www.co2science.org/articles/V18/jun/a10.php
\textsuperscript{8} http://www.co2science.org/articles/V18/aug/a2.php
corals in question "were either fed or unfed and exposed to elevated temperature (30°C), enriched pCO₂ (800 ppm) or both (30°C/800 ppm) as compared to a control (26°C/390 ppm) for 8 weeks."

This experiment revealed, as the three researchers describe it, that the "fed corals were able to maintain ambient growth rates at both elevated temperature and elevated CO₂, while unfed corals experienced significant decreases in growth with respect to fed conspecifics." In light of these findings, therefore, the three researchers write that their results "show for the first time that a threatened coral species can buffer ocean-acidification-reduced calcification by increasing feeding rates." And they thus conclude with the good-to-hear news that "a critically endangered species with access to food sources other than photosynthate may be able to maintain growth physiology under climate change stress."

Although, much remains to be learned on this subject, it is clear that many corals will not succumb to the presumed negative impacts of rising temperatures and ocean acidification. And when adaptive and evolutionary responses are considered, it may be that few, if any, corals will actually suffer harm from increases in these two phenomena. In fact, many coral species could well benefit from the warmer ocean temperatures and higher atmospheric CO₂ concentrations predicted for the years and decades ahead.

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