EFFECTS OF OCEAN ACIDIFICATION ON MARINE COCCOLITHOPHORES

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Coccolithophores are single-celled algae and protists that are found throughout the surface euphotic zones of the world's oceans. They contain chlorophyll, conduct photosynthesis and possess special plates or scales known as coccoliths, which they create via the process of calcification. This summary briefly reviews the results of several studies investigating how coccolithophores may be affected by ocean acidification in a CO_2-enriched world of the future. As indicated below, the findings of these several works challenge the alarmist view of ocean acidification espoused by the IPCC and others. Instead of experiencing great harm in response to future declines in oceanic pH predicted for the future, coccolithophores will likely adapt and possible even *thrive* under such changes.

Introducing this complex subject of global change research, over a decade ago Riebesell (2004)[1] wrote that a doubling of present-day atmospheric CO_2 concentrations "is predicted to cause a 20-40% reduction in biogenic calcification of the predominant calcifying organisms, the corals, coccolithophorids, and foraminifera." On the other hand, he noted that "a moderate increase in CO_2 facilitates photosynthetic carbon fixation of some phytoplankton groups," including "the coccolithophorids *Emiliania huxleyi* and *Gephyrocapsa oceanica*." And in what constituted a major challenge to the model-based claim that atmospheric CO_2 enrichment will harm such marine organisms, Riebesell went on to suggest that "CO_2-sensitive taxa, such as the calcifying coccolithophorids, should therefore benefit more from the present increase in atmospheric CO_2 compared to the non-calcifying diatoms."

One year later, in a test of this hypothesis Leonardos and Geider (2005)[2] grew a non-calcifying strain (PML 92A) of the marine coccolithophorid *Emiliania huxleyi* (Lohmann) Hay & Mohler in chemostats-cyclostats that were aerated with air of either 360 or 2000 ppm CO_2 under both high- and low-light conditions in seawater either *replete with* or *deficient in* nitrogen and/or phosphorus, while measuring a suite of physical and biochemical properties of the coccolithophorid populations and the media in which they lived. This experiment revealed that "increased atmospheric CO_2 concentration enhances CO_2 fixation into organic matter," but "only under certain conditions, namely high light [HL] and nutrient limitation." Under N-limited conditions, for example, they found that particulate organic carbon (POC) "was greatest under HL and elevated CO_2 (by up to 46% relative to HL and ambient CO_2)." And their work also revealed that "the increase in POC was a consequence of both an increase in cell density and an increase in the cell organic carbon content."

The two UK researchers thus stated that "enhanced CO_2 uptake by phytoplankton such as *E. huxleyi*, in response to elevated atmospheric CO_2, could increase carbon storage in the nitrogen-limited regions of the oceans and thus act as a negative feedback on rising atmospheric CO_2 levels." In fact, they calculated that if the results they obtained for *E. huxleyi* were indicative of the effects of CO_2 on primary production in other N-limited phytoplankton, then changes of the magnitude they measured in *E. huxleyi* due to increased CO_2 could increase export production of

[1] http://www.co2science.org/articles/V8/N6/EDIT.php
[2] http://www.co2science.org/articles/V9/N21/B3.php

the oligotrophic ocean by an amount equivalent to the estimated post-industrial increase in the terrestrial carbon sink.

As for corroborating evidence, Leonardos and Geider said their findings were "consistent with the response of primary productivity to manipulation of aqueous phase CO_2 in the oligotrophic North Atlantic (Hein and Sand-Jensen, 1996)," where increases in primary productivity "of up to 100% were observed, although the average increase was 15% to 19%." In addition, they noted that stimulation of carbon fixation by elevated CO_2 had already been documented for nutrient-limited lake phytoplankton (Urabe *et al*., 2003)."

Shortly thereafter, working with two previously untested coccolithophores -- *Calcidiscus leptoporus* and *Coccolithus pelagicus* -- which they described as two of the most productive marine calcifying species, Langer *et al.* (2006)[3] conducted batch-culture experiments in which they observed (1) a deterioration of coccolith production above as well as below present-day CO_2 concentrations in *C. leptoporus*, and (2) a lack of a CO_2 sensitivity of calcification in *C. pelagicus* over an atmospheric CO_2 concentration range of 98-915 ppm, both of which observations, in their words, "refute the notion of a linear relationship of calcification with the carbonate ion concentration and carbonate saturation state," as proposed early-on by various scientists.

But what about the apparent *negative* finding in the case of *C. leptoporus*, where Langer *et al*. observed that at both higher and lower CO_2 concentrations than those of today, the proportion of coccoliths showing incomplete growth and malformation notably increased?

To determine if such was also the case in the *real world*, the seven scientists studied coccolith morphologies in six sediment cores extracted along a range of latitudes in the Atlantic Ocean. As they described it, this work indicated that changes in coccolith morphology similar to those "occurring in response to the abrupt CO_2 perturbations applied in our experimental treatments are not mirrored in the sedimentary record," which finding indicates, as they suggested, that "in the natural environment *C. leptoporus* has adjusted to the 80 ppm CO_2 and 180 ppm CO_2 difference between present, preindustrial and glacial times, respectively."

> **"Genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean."**

In further discussing these observations, the team of researchers from Germany and the United Kingdom said that "it is reasonable to assume that *C. leptoporus* has adapted its calcification mechanism to the change in carbonate chemistry having occurred since the last glacial maximum," suggesting as a possible explanation for this phenomenon that "the population is genetically diverse, containing strains with diverse physiological and genetic traits, as already demonstrated for *E. huxleyi* (Brand, 1981, 1982, 1984; Conte *et al*., 1998; Medlin *et al*., 1996; Paasche, 2002; Stolte *et al*., 2000)." And they also stated that this adaptive ability "is not likely to be confined to *C. leptoporus* but can be assumed to play a role in other

[3] http://www.co2science.org/articles/V10/N4/EDIT.php

coccolithophore species as well," which led them to conclude that such populations "may be able to evolve so that the optimal CO_2 level for calcification of the species tracks the environmental value." With respect to the future, therefore, Langer *et al*. ended their paper on an extremely positive note, stating that "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean."

> "In the real ocean the larger coccolithophore species increase their calcification in response to anthropogenic CO_2 release."

Working with the same sediment core, Halloran *et al*. (2008)[4] analyzed the size distribution of $CaCO_3$ particles in the less-than-10-µm sediment fraction over the past quarter-century. This work revealed, as they described it, a history of "changing particle volume since the late 20th century consistent with an increase in the mass of coccoliths produced by the larger coccolithophore species," leading them to conclude that "in the real ocean the larger coccolithophore species increase their calcification in response to anthropogenic CO_2 release." In addition, the four researchers stated that this positive calcification response "could be attributed to an alleviation of CO_2 limitation in species that partly rely on the diffusive supply of dissolved carbon dioxide for photosynthesis, as demonstrated by a rise in photosynthetic efficiency with increasing carbon dioxide in cultures of *E. huxleyi* (Rost *et al*., 2003)."

Shortly thereafter, Stoll (2009)[5] addressed the speculative claims of scientists promoting the view that "ocean acidification in response to excess carbon dioxide in the atmosphere could become a problem for marine organisms, especially those that make skeletons or shells out of calcium carbonate," including the coccolithophorids that are, by volume, the most important shell producers. However, she had a much more *optimistic* view of the subject, thanks in large part to the concomitant research findings of Langer *et al*. (2009).

The latter scientists -- hailing from France, Germany, Spain and the Netherlands -- grew four different strains of the coccolithophore *Emiliania huxleyi* in dilute batch cultures of seawater with carbonate chemistries characteristic of those expected to prevail beneath an atmosphere with CO_2 concentrations ranging from approximately 200 to 1200 ppm, while they measured particulate organic carbon content, particulate inorganic carbon content, and organic and inorganic carbon production. By these means, they found that the four strains "did not show a uniform response to carbonate chemistry changes in any of the analyzed parameters and none of the four strains displayed a response pattern previously described for this species." In light of these findings, therefore, plus other aspects of their earlier studies (Langer *et al*. 2006, 2007) and the diverse findings of still others (all of whom had used different strains of the species), the five scientists concluded that "the sensitivity of different strains of *E. huxleyi* to acidification differs substantially" and "likely has a genetic basis."

[4] http://www.co2science.org/articles/V12/N13/B1.php
[5] http://www.co2science.org/articles/V13/N11/EDIT.php

Stoll agreed with this assessment, stating that Langer *et al*. argued convincingly in this regard; and she added that the work of those who foresaw disastrous consequences typically "precludes the kind of natural selection and adaptation that might occur over decades and centuries in the ocean." And in further discussing the subject, Langer *et al*. (2009) said that "shifts in dominance between species and/or between clones within a species might therefore be expected," as the air's CO_2 content continues to rise; but they indicated that far too often "the possibility of adaptation is not taken into account."

This ought not be, for the great genetic diversity that exists, both among and within species, in the words of Stoll, "is good insurance in a changing ocean." Indeed, it can be interpreted as evidence that Earth's coccolithophorids are *well prepared* for whatever the future may thrust at them in this regard; for as Langer *et al*. (2006) more boldly and explicitly stated, "genetic diversity, both between and within species, may allow calcifying organisms to prevail in a high CO_2 ocean," which does, in fact, appear to be the consensus of most studies that have moved from the initial state of *theoretical speculation* to the intermediate crucible of *laboratory experimentation* to the final field work of *real-world observation*.

Two years later, Beaufort *et al*. (2011)[6] wrote that "culture experiments investigating the physiological response of coccolithophore calcification to increased CO_2 have yielded contradictory results between and even within species," citing the studies of Riebesell *et al*. (2000), Langer *et al*. (2006), Iglesias-Rodriguez *et al*. (2008) and Langer *et al*. (2009). And to further explore the subject and assess the influence of the environment on coccolithophore calcification, they investigated 180 surface-water and 555 sediment-core samples encompassing a wide spectrum of present and past oceanic conditions, some stretching back in time as much as 40,000 years. And what did they find?

The thirteen researchers reported that "significant overall correlations of coccolith mass with pH and pCO_2 were recorded, but with notable regional variations, indicating that these parameters are not solely responsible for the observed trend." They also reported that some cultured strains of coccolithophores "are capable of maintaining calcification (degree and/or rate) over certain carbonate-chemistry ranges, a phenomenon that could contribute to localized within-sample deviations from the broad trend linking coccolith mass to carbonate chemistry." In fact, they indicated that *changes in the relative abundance of taxa* were "predominantly responsible for the decrease in coccolith mass with ocean acidification that was seen in modern samples."

Also adding to the complexity of the situation, Beaufort *et al*. noted that "in Patagonian-shelf and Chilean upwelling waters with low CO_3^{2-}, in which the overall trend would predict low coccolith mass," they detected "an unexpectedly highly calcified *Emiliania huxleyi* morphotype," and they indicated that "the relative abundance of this morphotype increased with decreasing pH along the Pacific transect towards Chile." In addition -- and noting that "because coccolith morphotype is thought to be subject to genetic regulation (Langer *et al*., 2009)" -- they stated that "this highly calcified *E. huxleyi* morphotype may be a genetic entity with an adaptation enabling it to calcify heavily in the relatively acidic upwelling waters."

The international team of scientists thus concluded that "the presence of highly calcified *E. huxleyi* in CO_2-rich modern waters demonstrates that prediction of future responses is unlikely to be straightforward," and that "such complexity could account for the lack of an obvious overall

[6] http://www.co2science.org/articles/V14/N42/B3.php

direction in the response of coccolithophore calcification over a potentially analogous ocean acidification event about 55 million years ago at the Palaeocene-Eocene Thermal Maximum," citing the study of Gibbs *et al*. (2006). And these several observations would seem to suggest that rising atmospheric CO_2 concentrations will very likely *not* bring a halt, or even a significant reduction, to coccolithophore calcification in either the decades or centuries to come.

Two years later, Fiorini *et al*. (2011)[7] measured the growth rates of three coccolithophores (*Emiliania huxleyi*, *Calcidiscus leptoporus* and *Syracosphaera pulchra*) in laboratory batch cultures in both their haploid and diploid life stages, while they were growing in filtered seawater maintained in equilibrium with air containing either 400 or 760 ppm CO_2. This work revealed that for all three species, "the growth rate was consistently higher at elevated pCO_2," but that "the response of other processes varied among species." Calcification rates of *C. leptoporus* and *S. pulchra*, for example, did not change at elevated pCO_2, whereas this important process was increased in the case of *E. huxleyi*. And they also found that these CO_2-induced impacts were most pronounced in the haploid stage.

In a very simple and straightforward conclusion to their study, Fiorini *et al*. thus stated that these effects "must be taken into account when predicting the fate of coccolithophores in the future ocean." And when they are taken into account, it should be added, the devastating future that is generally portrayed to the public on this issue disappears from view. Rather, in the words of the European scientists, "the phenotypic and physiological differences of the two life stages allow each species to use two different niches to exploit a wider range of ecological conditions (Cros *et al*., 2000), to limit the competition in the utilization of resources (food, light) inside the species and to rapidly escape negative selection pressures exerted on one stage such as grazing, parasitic attack, viral infections (Frada *et al*., 2008), or abrupt environmental changes (Noel *et al*., 2004)." And in this way, as they continued, "the survival of a species is ensured by one life stage when the environmental conditions do not favor the development of the other life stage (Houdan *et al*., 2005)."

Shortly thereafter, Lohbeck *et al*. (2012)[8] noted that our present understanding of the sensitivity of marine life to ocean acidification has been based primarily on short-term experiments that often depict negative effects. However, they went on to say that phytoplanktonic species with short generation times "may be able to respond to environmental alterations through adaptive evolution." And with this tantalizing possibility in mind, they studied, as they described it, "the ability of the world's single most important calcifying organism, the coccolithophore *Emiliania huxleyi*, to evolve in response to ocean acidification in two 500-generation selection experiments."

Working with freshly isolated genotypes from Bergen, Norway, the three German researchers grew them in batch cultures over some 500 asexual generations at three different atmospheric CO_2 concentrations -- ambient (400 ppm), medium (1100 ppm) and high (2200 ppm) -- where the medium CO_2 treatment was chosen to represent the atmospheric CO_2 level projected for the beginning of the next century. This they did in a multi-clone experiment designed to provide *existing genetic variation* that they said "would be readily available to genotypic selection," as well as in a single-clone experiment that was initiated with one "haphazardly chosen genotype," where evolutionary adaptation would obviously require *new mutations*.

[7] http://www.co2science.org/articles/V15/N12/B3.php
[8] http://www.co2science.org/articles/V15/N28/EDIT.php

Compared with populations kept at ambient CO_2 partial pressure, Lohbeck *et al*. found that those selected at increased CO_2 levels "exhibited higher growth rates, in both the single- and multi-clone experiment, when tested under ocean acidification conditions." Calcification rates, on the other hand, were somewhat lower under CO_2-enriched conditions in *all* cultures; but the research team found that they were "up to 50% higher in adapted [medium and high CO_2] compared with non-adapted cultures." And when all was said and done, they thus concluded that "contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change."

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In other ruminations on their findings, the marine biologists indicated that what they called the *swift adaptation processes* they observed may "have the potential to affect food-web dynamics and biogeochemical cycles on timescales of a few years, thus surpassing predicted rates of ongoing global change including ocean acidification." And they also noted, in this regard, that "a recent study reports surprisingly high coccolith mass in an *E. huxleyi* population off Chile in high-CO_2 waters (Beaufort *et al*., 2011)," which observation was said by them to be indicative of "across-population variation in calcification, in line with findings of rapid microevolution identified here."

In light of these several observations, Lohbeck *et al*. went on to suggest that "contemporary evolution could help to maintain the functionality of microbial processes at the base of marine food webs in the face of global change." And in writing about this development in a *News & Views* item in the same issue of *Nature Geoscience*, Collins (2012) also highlighted the fact that "marine microbes, with their large population sizes and fast division rates, are certainly going to evolve over a timeframe of decades," and that "we can expect that future coccolithophore populations will be shaped by a combination of species succession and adaptive evolution," both of which phenomena bode well, indeed, for the future of Earth's marine biosphere.

In a related contemporary publication, McCarthy *et al*. (2012)[9] wrote that *diatoms* are a type of algae, most of which are unicellular, that serve as primary producers in various marine food chains; and, therefore, they felt it was critically important to know how they may respond to continued increases in the air's CO_2 content, especially since they are responsible for about 40% of current marine primary productivity (Field *et al*., 1998). Likewise, it is also important to know how other

[9] http://www.co2science.org/articles/V15/N43/EDIT.php

unicellular algae, such as coccolithophores, will respond to rising CO_2 concentrations, since they are globally-distributed phytoplankton that are major marine calcifiers, the calcium carbonate scales of which sink to the bottom of the sea upon their deaths, where the carbon they contain is sequestered far away from the atmosphere. And so it was that McCarthy *et al*. (2012) decided to examine *both* of these groups of microalgae within the context of CO_2-induced ocean acidification, which has often been claimed will ultimately spell the ruin of both marine food production and marine carbon storage.

In describing their approach to analyzing this potential problem, the team of four Canadian researchers said they grew the coccolithophore *Emiliania huxleyi* and two strains of the diatom *Thalassiosira pseudonana* under low light in turbidostat photobioreactors bubbled with air containing either 390 ppm or 750 ppm CO_2, finding that "increased CO_2 led to increased growth rates in all three strains" and that "CO_2 thus had a fertilization effect on all species, enhancing growth rates 20%-40%." They also reported that "total cellular protein did not change between ambient and 750 ppm CO2 treatments," but that "cellular RUBISCO content showed a 2- to 3-fold increase with [elevated] CO_2 in both E. huxleyi and in the coastal diatom strain."

In commenting on their observations, McCarthy *et al*. noted that the CO_2 fertilization effect on the growth rates of *T. pseudonana* and *E. huxleyi* provides these species with increased competitive ability. And they thus concluded that their results suggest "there could be a net increase in capacity for primary productivity at 750 ppm CO_2, at least with regard to small diatoms and coccolithophores in coastal environments," where the two types of phytoplankton provide the bulk of current marine primary productivity.

In another contemporary study, Smith *et al*. (2012)[10] wrote that "laboratory studies are unrealistic in many respects and, because of their typically short timescales, preclude the possibility of evolutionary adaptation to the imposed change, a key uncertainty in OA [ocean acidification] research," citing Gattuso and Buddemeier (2000), Langer *et al*. (2006) and Ridgwell *et al*. (2009). And, therefore, they felt that it was *vital* "to complement laboratory experiments with observational studies of coccolithophores living in the natural habitats to which they are evolutionarily adapted."

Focusing on two morphotypes (over-calcified and normal) of the world's most abundant coccolithophore species (*Emiliania huxleyi*), Smith *et al*. assessed their numbers, along with seawater carbonate chemistry and other environmental variables, at monthly intervals between September 2008 and August 2009 along a 1,000-km route, including over deep oceanic waters in the Bay of Biscay. And this work revealed that there was a pronounced seasonality in the morphotypes of *E. huxleyi*. "Surprisingly," as they described it, "the over-calcified morphotype was found to dominate the *E. huxleyi* population in winter," in spite of the fact that seawater pH and $CaCO_3$ saturation were *lowest* in winter, while the heavily-calcified form of *E. huxleyi* dominated *dramatically*, shifting from less than 10% of the total *E. huxleyi* population in summer to more than 90% of the population in winter.

In discussing their findings, Smith *et al*. acknowledged that they "do not suggest that the changing carbonate chemistry was necessarily responsible for this shift in morphotypes." However, they stated that "if it was not, then the alternative is that carbonate chemistry is not the sole and overriding control over coccolithophore calcification," which should, in their words, "seriously

[10] http://www.co2science.org/articles/V15/N45/C3.php

call into question" the contention of some that "ocean acidification will lead to a replacement of heavily-calcified coccolithophores by lightly-calcified ones."

Next to weigh in on the subject was Jin *et al*. (2013)[11] who wrote that "as a key group of oceanic primary producers, [coccolithophores] play a crucial role in the global carbon cycle, not only in terms of photosynthesis but also by producing calcium carbonate in the form of extracellular plates." In addition, they noted they are "important in the sulfur cycle in terms of dimethyl-sulphide (DMS) production (Malin and Erst, 1997)," which leads to enhanced cloud formation and the reflectance back to space of increased amounts of incoming solar radiation, which phenomenon tends to cool the planet.

The three researchers also noted that the particulate inorganic carbon (PIC) that is produced by coccolithophores in the surface ocean sinks to the deep-sea, which phenomenon, known as the *carbonate pump*, "is a critical part of the global carbon cycle and has a major feedback effect on global climate (Hutchins, 2011)." And in light of these several positive phenomena, Jin *et al*. decided to conduct a laboratory experiment where they grew the coccolithophore *Gephyrocapsa oceanica* for approximately 670 generations in water in equilibrium with both ambient and CO_2-enriched (1000 ppm) air, the latter of which treatments reduced the water's pH to a value of 7.8. And what did they learn?

Very briefly, Jin *et al*. found that "high CO_2-selected cells showed increases in photosynthetic carbon fixation, growth rate, cellular particulate organic carbon (POC) or nitrogen (PON) production, and a decrease in the C:N elemental ratio, indicating a greater up-regulation of PON than of POC production under ocean acidification." And they noted that these findings were "in good agreement with a recent study in which *E. huxleyi* positively adapted to increased CO_2 levels," citing Lohbeck *et al*. (2012). Given such findings, Jin *et al*. thus concluded that their data suggest that "the coccolithophorid could adapt to ocean acidification with enhanced assimilations of carbon and nitrogen," becoming even *more* productive than it is now.

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Berger *et al*. (2014)[12] investigated the effects of oceanic pH on the coccolith family Noelaerhabdaceae, which family constitutes the majority of the coccolith assemblage inhabiting the North Atlantic Ocean. In analyzing average coccolith weights obtained from three Holocene sediment cores extracted along a north-south North Atlantic transect, the four-member research

[11] http://www.co2science.org/articles/V16/N45/B2.php
[12] http://www.co2science.org/articles/V17/N29/B3.php

team documented the occurrence of "weight changes during the Holocene of the same amplitude as previously reported for the CO_2 increase of the last glacial to interglacial change, but with opposing trends in different regions." And in this regard, they suggested that "differences in nutrient or productivity settings between the sites are likely influencing the response of Noelaerhabdaceae coccolith weight," or that weight increases could be due to "an abundance shift to heavily calcifying morphotypes, such as the increase of an over-calcified type of *E. huxleyi*, even during times of decreasing carbonate ion concentration." As for the significance of these findings, Berger *et al*. wrote that "the high natural variability of coccolith weight during the Holocene raises the question as to whether future changes in the carbonate system of the oceans will have a positive or negative effect on coccolithophore calcification," which is a valid point to be made in the debate over the impacts of ocean acidification.

In another more recent experiment, Fukuda *et al*. (2014)[13] exposed *Emiliania huxleyi* coccolithophores to acidified seawater in which the little creatures were maintained in the laboratory by two different means: (1) adding hydrochloric acid (HCL) directly to the seawater to obtain pH treatments of 8.2-8.4, 7.6-7.8 and 7.1-7.3, or (2) bubbling CO_2-enriched air of 406, 816 and 1192 ppm into the seawater to establish pH treatments of 8.0-8.3, 7.6-7.9 and 7.5-7.7. Under such conditions, Fukuda *et al*. reported that both "cell growth and cellular calcification of *E. huxleyi* were strongly damaged by acidification by HCl, but not by acidification by CO_2 enrichment." In fact, they stated their study "clearly showed that the coccolithophore, *E. huxleyi*, has an ability to respond positively to acidification with CO_2 enrichment." And they therefore concluded the report of their work by stating it "suggests that physiological activities of *E. huxleyi* cells will not be seriously damaged by ocean acidification at least up to 1200 ppm CO_2 in the atmosphere."

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In one final study, Lohbeck *et al*. (2014)[14] introduced their work by writing that "evolutionary adaptations in key phytoplankton species have only recently come into the focus of marine ecology and biogeochemistry." But they say "such processes are of high relevance for a comprehensive understanding of how global change will affect marine ecosystem functioning and

[13] http://www.co2science.org/articles/V17/nov/a24.php
[14] http://www.co2science.org/articles/V17/N38/B2.php

biogeochemical cycles," referencing, in this regard, the studies of Lohbeck *et al*. (2012), Reusch and Boyd (2013) and Sunday *et al*. (2014).

Hoping to add knowledge to this topic, in a laboratory study, Lohbeck *et al*. determined the expression levels of ten candidate genes putatively relevant to pH regulation, carbon transport, calcification and photosynthesis in *E. huxleyi* populations that were *short-term* exposed to ocean acidification conditions *subsequent* to acclimation (a physiological response) and *after* 500 generations of high CO_2 adaptation (an adaptive response).

According to the three researchers, "in the adaptive response, putative pH regulation and carbon transport genes were up-regulated, matching partial restoration of growth and calcification in high CO_2-adapted populations." Quoting Lohbeck *et al*., it would appear that "adaptive evolution may thus have the potential to partially restore cellular pH regulatory capacity and thereby mitigate adverse effects of ocean acidification." And who knows what *additional* benefits *another* 500 generations of adaptive evolution might provide?

In conclusion, and based on the experimental findings and real-world observations discussed above, it is quite clear that the Earth's coccolithophores are well equipped to deal with whatever degree of ocean acidification may yet be experienced by the world's great water bodies. Additional material supporting this conclusion can be found in our Subject Index section Simultaneous Ocean Acidification and Warming (Effects on Marine Plants: Coccolithophores)[15].

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[15] http://www.co2science.org/subject/o/acidwarmcocco.php

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