RESPONSE OF VARIOUS MARINE ANIMALS TO OCEAN ACIDIFICATION AND WARMING

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Most of the ocean acidification research conducted to date has focused solely on the biological impacts of declining seawater pH. Few studies have investigated the interactive effects of ocean acidification and temperature. This summary examines what has been learned in several such studies of various marine organisms that challenge the alarming and negative projections of the IPCC on the matter.

Starting with some of the smallest of marine animals, calanoid copepods are a type of zooplankton that feeds on phytoplankton and are themselves the food of higher trophic levels. In a study of the long-term effects of both high CO_2 levels and temperatures on Arctic calanoid copepods, Hildebrandt *et al*. (2014)[1] "incubated late copepodites and females of two dominant Arctic species, *Calanus glacialis* and *Calanus hyperboreus*, at 0°C and at 390 and 3000 µatm pCO_2 for several months in fall/winter 2010," while in an attempt "to detect synergistic effects," they say that in 2011 "*C. hyperboreus* females were kept at different pCO_2 and temperatures (0, 5, 10°C)." The three German researchers indicate that their experiments, which were conducted over several months with repeated measurements, including several aspects of the animals' ecology and physiology, demonstrated that the sub-adult and adult life stages of the Arctic *Calanus* species they studied "were robust to pCO_2 even above future levels of ocean acidification," with the "only synergistic effects of pCO_2 and temperature on body mass of *C. hyperboreus* females found at 5°C." And in light of what they observed in the laboratory, Hildebrandt *et al*. conclude that Arctic calanoid copepods "can tolerate pCO_2predicted for a future ocean." But they caution that in combination with increasing temperatures they could *possibly* experience some form of negative repercussion, but one that would not be fatal.

Thiyagarajan and Ko (2012)[2] conducted a number of laboratory studies designed to see how the larval growth stage of the Portuguese oyster responds to various "climate change stressors," as they describe them, by investigating the effects of low pH (7.9, 7.6, 7.4) at ambient salinity (34 ppt) and low salinity (27 ppt), while "the combined effect of pH (8.1, 7.6), salinity (24 and 34 ppt) and temperature (24°C and 30°C) was examined using factorial experimental design." In describing their findings, the two researchers say, "surprisingly, the early growth phase from hatching to 5-day-old veliger stage showed high tolerance to pH 7.9 and pH 7.6 at both 34 ppt and 27 ppt," while they report "larval shell area was significantly smaller at pH 7.4 only in low-salinity." Then, in the 3-factor experiment, they observed "shell area was affected by salinity and the interaction between salinity and temperature but not by other combinations." And they discovered "larvae produced the largest shell at the elevated temperature in low-salinity,

[1] http://www.co2science.org/articles/V17/N30/B3.php.
[2] http://www.co2science.org/articles/V16/N16/C3.php.

regardless of pH." In light of these several positive findings, Thiyagarajan and Ko conclude "the growth of the Portuguese oyster larvae appears to be robust to near-future pH level (>7.6) when combined with projected elevated temperature and low-salinity in the coastal aquaculture zones of [the] South China Sea."

Pansch *et al*. (2012)[3] write that to date, "most studies have focused on ocean acidification (OA) effects in fully marine environments, while little attention has been devoted to more variable coastal ecosystems, such as the Western Baltic Sea." And since they indicate "natural spatial and temporal variability of environmental conditions such as salinity, temperature or CO_2 impose more complex stresses upon organisms inhabiting these habitats, species [living there] can be expected to be more tolerant to OA (or warming) than fully marine taxa."

The growth of the Portuguese oyster larvae appears to be robust to near-future pH level (>7.6) when combined with projected elevated temperature and low-salinity in the coastal aquaculture zones of [the] South China Sea.

In exploring this hypothesis, Pansch *et al*. acquired data on the variability of temperature and pH within the inner Kiel Fjord of Schleswig-Holstein, Germany, as well as on "the responses of the barnacle *Amphibalanus improvisus* from this habitat to simulated warming and OA during its early development." This was accomplished by exposing *A. improvises* nauplii (the first larval stage of many crustaceans) and cyprids (the second larval stage of barnacles) to different temperatures (12, 20 and 27°C) and CO_2 (nominally 400, 1,250, and 3,250 ppm) treatments for eight and four weeks, respectively," while "survival, larval duration and settlement success were monitored."

With respect to their findings, first of all, the four researchers found a prolongation of the nauplius phase that they acknowledge could "lead to a mismatch of the larvae with their phytoplankton prey." However, they note the predicted increase in seawater temperature would likely "accelerate nauplii development and, thus, may buffer OA effects," and they say such results have actually been observed "in sea urchin larvae and oysters, where higher temperatures mitigated negative effects of OA," citing the work of Brennand *et al*. (2010) and Waldbusser *et al*. (2011). In their study, on the other hand, they found things were just the opposite, indicating "warming negatively impacted cyprid survival," but "OA counteracted these negative effects."

"It should also be stressed," as they continue, "that only the most severe OA level applied herein (3,250 ppm CO_2) had occasional effects, whereas the OA conditions as predicted by the end of this century (1,250 ppm CO_2) in most cases did not affect *A. improvisus* larvae." In addition, and "interestingly," they report "the major release of larvae and thus, development, settlement and first intense calcification in *A. improvisus* occurs during early summer when pH is lowest." And they add "*A. improvisus* is also found in stands of the brown

[3] http://www.co2science.org/articles/V15/N44/EDIT.php.

macroalga *Fucus* spp. where 2,500 ppm CO_2 (pH 7.4) can be measured," and they write that "another barnacle species, *Chthamalus stellatus*, was shown to survive and grow at extremely low mean pH of 6.6 in the vicinity of volcanic CO_2 vents in Ischia, Italy (Hall-Spencer *et al*., 2008)."

In summing things up, Pansch *et al*. write "given their present wide tolerance and the possibility to adapt to shifting environmental conditions over many generations, barnacles (*A. improvisus*) from the Western Baltic Sea might be able to overcome OA as predicted by the end of this century." And, "supporting this," they note Parker *et al*. (2011) have shown "selectively bred lines of the estuarine oyster *Saccostrea glomerata* to be more resilient to OA than wild populations."

In a similar study published one year later, Pansch *et al*. (2013)[4] also collected juvenile barnacles (*Amphibalanus improvisus*) from Kiel Fjord in the western Baltic Sea after which they were distributed to different temperature and pH treatment combinations in a laboratory setting: seawater of two temperatures (20 and 24°C) and three ocean acidification levels (mean pCO_2 values of 700, 1,000, and 2,140 µatm). There they were fed a mix of two marine diatoms every other day until day 24, after which they were additionally fed with specified amounts of brine shrimp until the end of the experiment on day 62. The four German scientists observed "reduced growth rates as well as weakening of barnacle shells only under very high pCO_2 (>1930 µatm)." However, they state "even under these highly acidified conditions, and corroborating other recent investigations on barnacles (e.g., McDonald *et al*., 2009; Findlay *et al*., 2010a,b), these impacts were subtle and sub-lethal." And "furthermore," as they continue, "ocean warming as expected to occur in the future (IPCC, 2007) has the potential to mitigate the negative effects of ocean acidification (Brennand *et al*., 2010; Waldbusser, 2011; present study)."In light of the findings of Pansch *et al*., as well as those of the other researchers they cite, it would appear juvenile barnacles of the species they studied are already equipped to meet the challenges of a significantly warmed and acidified ocean should such challenges occur.

Introducing their work, Landes and Zimmer (2012)[5] state "both ocean warming and acidification have been demonstrated to affect the growth, performance and reproductive success of calcifying invertebrates." However, they say "relatively little is known regarding how such environmental change may affect interspecific interactions." In a study designed to explore this real-world situation, Landes and Zimmer separately treated green crabs (*Carcinus maenas*, the predators) and periwinkles (*Littorina littorea*, their prey) under conditions that mimicked either ambient conditions (control) or warming and acidification (both separately and in combination), for a period of five months, after which the predators, their prey, and the predator-prey interaction were assessed for CO_2- and warming-induced changes in response to the environmental perturbations they imposed on them.

Results indicated "acidification negatively affected the closer-muscle length of the crusher chela and correspondingly the claw-strength increment in *C. maenas*," while "the effects of warming

[4] http://www.co2science.org/articles/V16/N51/B3.php.
[5] http://www.co2science.org/articles/V15/N35/B1.php.

and/or acidification on *L. littorea* were less consistent but indicated weaker shells in response to acidification." And as might have been expected on the basis of these individual species responses to ocean acidification and warming (weaker claw strength in the predator, but weaker shells in the prey), Landes and Zimmer say "on the community level," they "found no evidence that predator-prey interactions will change in the future."

Introducing their work, Chan *et al*. (2013)[6] write "the majority of marine benthic invertebrates protect themselves from predators by producing calcareous tubes or shells that have remarkable mechanical strength," but they note "an elevation of CO_2 or a decrease in pH in the environment can reduce intracellular pH at the site of calcification and thus interfere with the animal's ability to accrete $CaCO_3$," which "may result in the animal producing severely damaged and mechanically weak tubes." In light of these concerns, Chan *et al*. investigated how the interaction of environmental drivers affects the production of calcareous tubes by the serpulid tubeworm, *Hydroides elegans*, in a factorial manipulative experiment where they analyzed the effects of pH (8.1 and 7.8), salinity (34 and 27‰), and temperature (23 and 29°C) on the biomineral composition, ultrastructure and mechanical properties of the tubeworm's tubes.

The five researchers report, "at an elevated temperature of 29°C, the tube calcite/aragonite ratio and Mg/Ca ratio were both increased, the Sr/Ca ratio was decreased, and the amorphous $CaCO_3$ content was reduced." And "notably," as they emphasize, at elevated temperature with decreased pH and reduced salinity, "the constructed tubes had a more compact ultrastructure with enhanced hardness and elasticity compared to decreased pH at ambient temperature." As for what these findings suggest about the future, Chan *et al*. conclude their "results from the analyses of tube mineralogy, ultrastructure and mechanical properties showed that predicted coastal warming may not hinder *H. elegans* ability to build normal tubes even in the face of projected near-future decreases in pH or salinity."

The Norway lobster (*Nephrops norvegicus*) is a decapod crustacean found on the continental shelf and slope throughout the northeastern Atlantic Ocean and the Mediterranean Sea. Styf *et al*. (2013)[7] exposed berried Norway lobsters (females carrying fertilized eggs on the undersides of their abdomens) to four months of "the combination of six ecologically relevant temperatures (5-18°C) and reduced pH (by 0.4 units)," during which time they studied embryonic development of the species "by quantifying proxies for development rate and fitness including: % yolk consumption, mean heart rate, rate of oxygen consumption, and oxidative stress." The three Swedish scientists report several important findings: (1) "the rate of yolk consumption per day, as a measure of embryonic development rate, significantly increased with temperature," (2) lower pH "had no effect on development rate," (3) "pH had no effect on heart rate," (4) "there was no interaction between pH and temperature," (5) "there was no significant effect of temperature on oxidative stress when analyzed independent of embryonic age," (6) "there was a significantly higher level of oxidative stress in the control embryos compared with the embryos developed in low pH," and (7) they "observed no mortality nor abnormalities." Thus, the three researchers conclude "this species would benefit from global warming and be able to withstand the predicted decrease in ocean pH in the next century

[6] http://www.co2science.org/articles/V17/N6/B3.php.
[7] http://www.co2science.org/articles/V17/N11/B3.php.

during their earliest life stages," which is a significant expression optimism for a species considered the most important crustacean in all Europe (Nofima, 2012).

[Winans and Purcell (2010)][8] tested the ability of jellyfish to respond to changes in water temperature and pH during the early life stages. For their analysis, polyps produced by medusae collected from the moon jellyfish (*Aurelia labiata*) in Dyes Inlet, Washington (USA) were arbitrarily assigned (18 each) to one of six treatments comprised of all combinations of two water temperatures (9 and 15°C) and three pH levels (7.2, 7.5 and 7.9), where they were allowed to develop under controlled conditions for 122 days. Results indicated "polyp survival was 100% after 122 days in seawater in all six temperature and pH combinations;" and because few polyps strobilated at 9°C and "temperature effects on budding were consistent with published results," they say they "did not analyze data from those three treatments further." At 15°C, there were also no significant effects of pH on the numbers of ephyrae or buds produced per polyp or on the numbers of statoliths per statocyst." However, they state "statolith size was significantly smaller in ephyrae released from polyps reared at low pH."

Given such findings, Winans and Purcell conclude "*A. labiata* polyps are quite tolerant of low pH, surviving and reproducing asexually even at the lowest tested pH." Nevertheless, the authors note "the effects of small statoliths on ephyra fitness are unknown," which means that the phenomenon *could* bode poorly for Earth's jellyfish. On the other hand, they acknowledge that many organisms "may be able to acclimate or adapt to slowly changing pH conditions." And in this context they report in Puget Sound "pH fluctuates from 7.2 to 9.6 in 2.4-meter deep water over the span of a couple of days," stating "with such large pH fluctuations due to plant photosynthesis during the day and respiration at night, many organisms may be exposed to low pH conditions routinely." And, obviously, they are also successfully dealing with those low pH conditions routinely, as are an enormous amount of other marine organisms.

The Norway lobster … "would benefit from global warming and be able to withstand the predicted decrease in ocean pH in the next century during their earliest life stages," which is a significant expression optimism for a species considered the most important crustacean in all Europe.

That the findings of Winans and Purcell should not be considered as evidence of future jellyfish blooms is made clear by the study of [Condon *et al*. (2013)][9]. Writing as background for their work, Condon *et al*. note there is "concern about the deterioration of the world's oceans," and that one line of evidence for this concern is "an increasing incidence of jellyfish blooms." However, they say this "perception," as they describe it, is "largely based on reports of increases in a few disparate regions (Condon *et al*., 2012)," as well as on "an analysis of media reports and perceptions of scientific experts and fishers (Brotz *et al*., 2012)." In revisiting this

[8] http://www.co2science.org/articles/V13/N30/B1.php.
[9] http://www.co2science.org/articles/V16/N30/B1.php.

important subject, Condon *et al*. (2013) set out to analyze "all available long-term datasets on changes in jellyfish abundance across multiple coastal stations, using linear and logistic mixed models and effect-size analysis," in order "to test the null hypothesis that jellyfish population sizes and the occurrence of blooms have not significantly increased in the world's oceans."

The ultimate result of the several analyses of the 22 researchers-who hail from Argentina, Australia, Canada, Japan, Norway, Peru, Slovenia, Spain, the United Kingdom and the United States-was "there is no robust evidence for a global increase in jellyfish." Although they acknowledge "there has been a small linear increase in jellyfish since the 1970s," they say "this trend was unsubstantiated by effect-size analysis that showed no difference in the proportion of increasing vs. decreasing jellyfish populations over all time periods examined." Instead, they report "the strongest non-random trend indicated jellyfish populations undergo larger, worldwide oscillations with an approximate 20-year periodicity, including a rising phase during the 1990s that contributed to the perception of a global increase in jellyfish abundance." Thus, the results of Condon *et al*.'s study do not support the view that the global abundance of jellyfish is increasing as a result of "the deterioration of the world's oceans." What they do imply, as the international research team concludes, is the continuance of normal "recurrent phases of rise and fall in jellyfish populations that society should be prepared to face."

Vehmaa *et al*. (2012)[10] state "maternal effects are defined as cross-generation phenotypic plasticity, implying the capability of a mother to adjust the phenotype of her offspring [in] response to environmental cues that her offspring will encounter, in a manner that enhances offspring fitness (Parker and Begon, 1986; Lacey, 1998)," stating as an example "Sydney rock oyster larvae are larger and develop faster in higher CO_2 conditions, if the adults also have been incubated in high CO_2 conditions (Parker *et al*., 2012)."

As their contribution to the subject, Vehmaa *et al*. "tested the reproductive response of *Acartia* sp. calanoid copepods and the importance of maternal effects in determining the offspring quality in a changing environment according to a 2100 climate scenario of a pH decline by 0.4 unit and a temperature elevation of 3°C." This was accomplished by monitoring the egg production of copepods incubated in four different pH and temperature conditions for five consecutive days, and on days 1, 3 and 5 dividing the eggs and allowing them to hatch in either the same or in different conditions than those in which they were produced.

Discussing their findings, the three Finnish researchers report "higher production temperature induced a positive maternal effect resulting in faster hatching and indicating that the mothers can invest more in their eggs, and therefore produce better quality eggs." In addition, they further note, in this regard, that the similar studies of Karell *et al*. (2008) and Jonasdottir *et al*. (2009) showed how "the egg quality in terms of maternal immunological or nutritional provisioning improved," and they suggest this phenomenon may explain "the declining effect of pH difference on egg hatching." Taken together, Vehmaa *et al*. conclude these several observations demonstrate that maternal effects "are an important mechanism in the face of environmental change."

[10] http://www.co2science.org/articles/V16/N20/B3.php.

The several studies highlighted above suggest that rising sea temperatures and a lowering of the pH of the ocean's surface waters will prove less of a problem to many marine animals than the IPCC projects. In fact, for many species, it may well prove to be a *non*-problem.

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