EFFECTS OF OCEAN ACIDIFICATION ON FISH

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As the air's CO_2 content rises in response to ever-increasing anthropogenic CO_2 emissions, and as more and more carbon dioxide therefore dissolves in the surface waters of the world's oceans, theoretical reasoning suggests the pH values of the planet's oceanic waters should be gradually dropping. The IPCC and others postulate that this chain of events, commonly referred to as *ocean acidification*, will cause great harm -- and possibly death -- to marine life in the decades and centuries to come. However, as ever more pertinent evidence accumulates, a much more optimistic viewpoint is emerging. This summary examines the topic of the potential impacts of ocean acidification on fish.

The IPCC and others postulate that ocean acidification, will cause great harm -- and possibly death -- to marine life in the decades and centuries to come. However, as ever more pertinent evidence accumulates, a much more optimistic viewpoint is emerging.

In an early review of the subject, Ishimatsu *et al.* (2005)[1] write that fish "constitute a major protein source in many countries," adding that the "potential reduction of fish resources by high-CO_2 conditions due to the diffusion of atmospheric CO_2 into the surface waters ... can be considered as another potential threat to the future world population." And in response to this self-expressed concern, they conducted a survey of the scientific literature with respect to the potential negative consequences of atmospheric CO_2 enrichment for the health of marine fish that could arise from continued anthropogenic CO_2 emissions.

Focusing on the possible threat of hypercapnia-a condition that is characterized by an excessive amount of CO_2 in the blood that typically results in acidosis, which is a serious and sometimes fatal condition characterized in humans by headache, nausea and visual disturbances-they say their survey revealed "hypercapnia acutely affects vital physiological functions such as respiration, circulation, and metabolism, and changes in these functions are likely to reduce growth rate and population size through reproduction failure." Although this potential threat sounds dire, it represents an egregious flight of the imagination in terms of what could realistically be expected to happen *anytime* to fish in Earth's future. Ishimatsu *et al*. report, for example, "predicted future CO_2 concentrations in the atmosphere are lower than the known lethal concentrations for fish," noting "the expected peak value is about 1.4 torr [just under 1850 ppm CO_2] around the year 2300 according to Caldeira and Wickett (2003)."

[1] http://www.co2science.org/articles/V8/N42/B3.php.

With respect to just how far below the lethal CO_2 concentration for fish 1.4 torr is, in the case of short-term exposures on the order of a few days, Ishimatsu *et al*. cite a number of studies that yield median lethal concentrations ranging from 37 to 50 torr, which values are 26 and 36 times greater than the maximum CO_2 concentration expected some 300 years from now!

In the case of long-term exposures, the results are even more comforting. To cite just a few examples, Ishimatsu *et al*. report Fivelstad *et al*. (1999) observed only 5 and 8% mortality at the end of 62 days of exposure to CO_2concentrations of 5 and 9 torr, respectively, for freshwater Atlantic salmon smolts, while mere 1 and 5% mortalities were found for seawater postsmolts of the same species at 12 and 20 torr after 43 days (Fivelstad *et al*., 1998). In addition, they say Smart *et al*. (1979) found little difference in mortality for freshwater rainbow trout reared for 275 days at 4 to 17 torr, and that no mortality occurred by the tenth week of exposure of juvenile spotted wolf fish to 20 torr (Foss *et al*., 2003).

Fish embryos and larvae, however, are often more vulnerable to environmental stresses than are adult fish. Yet even here, Ishimatsu *et al*. report the 24-hour median lethal concentration of CO_2 on both eggs and larvae of several marine fish studied by Kikkawa *et al*. (2003) "ranged widely from 10 torr to 70 torr among species," with the smaller of these two values being over seven times greater than the CO_2 concentration expected 300 years from now.

With respect to growth, Ishimatsu *et al*.'s review reveals reductions of 24 to 48%; but, again, the CO_2 concentrations needed to induce those growth reductions ranged from 17 to 20 torr, or 12 to 14 times more than the CO_2concentration expected 300 years from now. Consequently, the scientific literature review of Ishimatsu *et al*. suggests Earth's fish-both freshwater and marine-will most likely *never* experience any ill effects due to elevated atmospheric CO_2 concentrations caused by the burning of fossil fuels.

With respect to Earth's 30,000 species of teleost fish, which include virtually all of the world's important sport and commercial fishes, Melzner *et al*. (2009)[2] state several of them have also been shown to be able to "fully compensate extra cellular fluid pH," as well as "maintain oxygen consumption rates and growth performance under ocean acidification conditions (e.g. Larsen *et al*., 1997; Foss *et al*., 2003; Fivelstad *et al*., 1998, 2003; Deigweiher *et al*., 2008)," but they add there have been no studies of these phenomena that have lasted for more than a few days. Therefore, to rectify this situation, they maintained a group of Atlantic Cod (*Gadus morhua*) for four months in a re-circulating aquaculture system of 15 cubic meters volume at an atmospheric CO_2 partial pressure of 0.3 kPa (~3,000 ppm) and another group for twelve months at a CO_2 partial pressure of 0.6 kPa (~6,000 ppm), after which the fishes' swimming metabolism was investigated in a swim-tunnel respirometer, and tissue samples of their gills were taken for various chemical analyses, including gill Na^+/K^+-ATPase capacity, which serves as a general indicator for ion regulatory effort.

The six German scientists report "motor activity in adult Atlantic Cod is not compromised by long-term exposure to water pCO_2 levels of 0.3-0.6 kPa," which are "scenarios exceeding the 0.2 kPa value predicted for surface ocean waters around the year 2300 (Calderia and Wickett,

2 http://www.co2science.org/articles/V12/N35/C2.php.

2003)." And in light of what they learned, Melzner *et al*. conclude "adults of active fish species with a high ion regulatory capacity [which is employed to eliminate metabolic CO_2] are well equipped to cope with prospected scenarios of global climate change," even those far beyond what could likely be produced by the burning of all fossil fuels in the crust of the Earth.

Checkley *et al*. (2009)[3] report on their work with fish otoliths, i.e., bony structures consisting of aragonite-protein bilayers that are used by fish to sense orientation and acceleration. Noting that atmospheric CO_2 enrichment had been calculated to decrease the saturation state of carbonate minerals such as aragonite in the world's oceans, the six scientists "hypothesized that otoliths in eggs and larvae reared in seawater with elevated CO_2 would grow more slowly than they do in seawater with normal CO_2," and to test this hypothesis, they "grew eggs and pre-feeding larvae of white sea bass (*Atractoscion nobilis*) under a range of CO_2 concentrations [380, 993 and 2558 ppm] and measured the size of their sagittal otoliths."

These experiments indicated-and "contrary to expectations," in the words of Checkley *et al*.- "the otoliths of fish grown in seawater with high CO_2, and hence lower pH and aragonite saturation, were significantly larger than those of fish grown under simulations of present-day conditions." More specifically, they found "for 7- to 8-day-old fish grown under 993 and 2558 ppm CO_2, the areas of the otoliths were 7 to 9% and 15 to17% larger, respectively, than those of control fish grown under 380 ppm CO_2." With respect to how these gains were realized, the marine researchers went on to state young fish are "able to control the concentration of ions (H^+ and Ca^{2+}) ... in the endolymph surrounding the otolith," where "with constant pH, elevated CO_2 increases CO_3^{2-} concentration and thus the aragonite saturation state, accelerating formation of otolith aragonite."

Munday *et al*. (2009)[4] preface their study on the early life stages of fish by noting "there is concern that continued increases in atmospheric CO_2 over the next century could have significant impacts on a wide range of marine species, not just those with calcified skeletons." In the case of fish, however, which "control their tissue pH by bicarbonate buffering and the exchange of ions, mostly across the gills," they write "small changes in internal or external pH can readily be compensated (Heisler, 1989; Claiborne *et al*., 2002)." Fish embryos and young larvae, on the other hand, are possibly "more sensitive to pH changes than are juveniles and adults," and "significant effects of ocean acidification are most likely to be detected in these early life stages," which possibility they thus go on to explore.

Working with a 70,000-liter recirculating seawater system at James Cook University's experimental marine aquarium facility, Munday *et al*. grew wild-caught pairs of the orange clownfish (*Amphiprion percula*) in 70-liter tanks containing seawater simulating a range of ocean acidification scenarios for the next 50-100 years-390 (current day), 550, 750 and 1030 ppm atmospheric CO_2-while documenting various aspects of egg, embryo and larval development. In doing so, the four researchers-all from the School of Marine and Tropical Biology of Australia's James Cook University-determined "CO_2 acidification had no detectable effect on embryonic duration, egg survival and size at hatching," and that it actually "tended to

3 http://www.co2science.org/articles/V12/N46/EDIT.php.
4 http://www.co2science.org/articles/V12/N49/B2.php.

increase the growth rate of larvae." Eleven days after hatching, for example, they observed "larvae from some parental pairs were 15 to 18 per cent longer and 47 to 52 per cent heavier in acidified water compared to controls," further noting that there was a "positive relationship between length and swimming speed," and "large size is usually considered to be advantageous for larvae and newly settled juveniles."

In discussing their findings within the context of current concerns over potential effects of the ongoing rise in the air's CO_2 content on marine fish, Munday *et al*. say "the most common prediction is that ocean acidification could [negatively] affect individual performance (e.g. development, growth, survival, swimming ability)," especially during the early life history of the fish. However, they write "contrary to expectations," their findings indicate "CO_2-induced acidification up to the maximum values likely to be experienced over the next 100 years had no noticeable effect on embryonic duration, egg survivorship and size at hatching for A. percula, and tended to have a positive effect on the length and weight of larvae." As for adult fish, they state "most shallow-water fish tested to date appear to compensate fully their acid-base balance within several days of exposure to mild hypercapnia," citing the observations of Michaelidis *et al*. (2007) and Ishimatsu *et al*. (2008).

Introducing their work, Frommel *et al*. (2010)[5] say "elevated CO_2 concentrations can disturb the acid-base regulation, blood circulation, and respiration, as well as the nervous system of marine organisms, leading to long term effects such as reduced growth rates and reproduction," especially in fish, because the majority of them, as they describe it, "are external fertilizers, and sperm are activated by seawater as they are expelled into the open ocean during a spawning event," citing the work of Westin and Nissling (1991). To explore this subject further, Frommel *et al*. collected sperm from ripe adult male cod fish (*Gadus morhua*, that they had caught during an August cruise through their spawning grounds in the Baltic Sea's Bornholm Basin), which they exposed to seawater that had been brought into equilibrium (by bubbling) with air of either 380 or 1400 ppm CO_2 (leading to seawater pH values of 8.080 and 7.558, respectively), during which exposure period sperm swimming behavior was recorded using a digital camera.

Data showed that "the eggs and early larval stages of Baltic cod seem to be robust to even higher levels of OA (3,200 µatm), indicating an adaptational response to CO_2."

In describing their findings the scientists report, "we found no significant effect of decreased pH on sperm speed, rate of change of direction or percent motility for the population of cod analyzed." In light of their careful and meticulous observations, Frommel *et al*. conclude "future ocean acidification will probably not pose a problem for sperm behavior, and hence fertilization success, of Baltic cod."

[5] http://www.co2science.org/articles/V14/N13/B3.php.

Still studying Baltic cod, three years later Frommel *et al*. (2013)[6] investigated the effects of ocean acidification on a number of egg and larval properties of *G. morhua* "over the range of CO_2 concentrations predicted in future scenarios for the Baltic Sea (from current values of 380 µatm up to 3,200 µatm CO_2 water)," both "with and without the combination of increasing temperature." The four German scientists report "no effect on hatching, survival, development, and otolith size was found at any stage in the development of Baltic cod," where "in situ levels of $pCO_2$are already at levels of 1,100 µatm with a pH of 7.2." In fact, they say their data showed that "the eggs and early larval stages of Baltic cod seem to be robust to even higher levels of OA (3,200 µatm), indicating an adaptational response to CO_2." Thus, in the concluding sentence of their revealing paper, Frommel *et al*. suggest that "since the Baltic Sea is naturally high in pCO_2, its fish stocks may be adapted to conditions predicted in ocean acidification scenarios for centuries to come."

Franke and Clemmesen (2011)[7] also investigated the potential impacts of ocean acidification on the early life stages of fish. Focusing on Atlantic herring (*Clupea harengus* L.), the pair of researchers conducted a study in which eggs of the fish were fertilized and incubated in artificially acidified seawater corresponding to atmospheric CO_2 concentrations of 1260, 1859, 2626, 2903 and 4635 ppm and compared to a control treatment of 480 ppm CO_2 until the main hatch of the herring larvae occurred, after which they say "the development of the embryos was monitored daily and newly hatched larvae were sampled to analyze their morphometrics." In doing so they report elevated CO_2 "neither affected the embryogenesis nor the hatch rate," and they say "the results showed no linear relationship between CO_2 and total length, dry weight, yolk sac area and otolith area of the newly hatched larvae." Given such findings, Franke and Clemmesen conclude "herring eggs can cope at current temperature conditions with an increase in CO_2," even one "exceeding future predictions of CO_2-driven ocean acidification."

Bignami *et al*. (2013a)[8] introduce their work by writing "there is a critical need to understand the effects of acidification on the vulnerable larval stages of marine fishes, as there is a potential for large ecological and economic impacts on fish populations and the human economies that rely on them." And, therefore, they set out to study "the larvae of*Rachycentron canadum* (cobia), a large, highly mobile, pelagic-spawning, widely distributed species with a life history and fishery value contrasting other species studied to date." More specifically, Bignami *et al*. raised larval cobia through the first three weeks of ontogeny under conditions of predicted future ocean acidification to determine effects on somatic growth, development, swimming ability, swimming activity, and the formation of otoliths, which are structures of the inner ear that are used as gravity, balance, movement and directional indicators that have a secondary function in sound detection in higher marine vertebrates.

Based on their analysis, the three U.S. researchers report "cobia exhibited resistance to treatment effects on growth, development, swimming ability, and swimming activity at 800 and 2100 µatm pCO_2," while also finding "these scenarios resulted in a significant increase in otolith size (up to 25% larger area)." As a result of these observations, Bignami *et al*. conclude, "this study demonstrates that cobia is unlikely to experience a strong negative impact from CO_2-

[6] http://www.co2science.org/articles/V16/N52/B3.php.
[7] http://www.co2science.org/articles/V15/N32/B1.php.
[8] http://www.co2science.org/articles/V16/N35/B3.php.

induced acidification predicted to occur within the next several centuries," which consequence they speculate "may be due to the naturally variable environmental conditions this species currently encounters throughout ontogeny in coastal environments," which they further suggest "may lead to an increased acclimatization ability even during long-term exposure to stressors."

Writing as background for their work, Munday *et al*. (2011a)[9] state "in general, marine fish appear to be relatively tolerant to mild increases in ambient CO_2, presumably because well-developed mechanisms for acid-base regulation allow them to compensate for cellular acidosis caused by exposure to elevated pCO_2 (Portner *et al*., 2005; Ishimatsu *et al*., 2008; Melzner *et al*., 2009)." However, due to the fact "fish otoliths (earbones) are composed of aragonite," they say there is a concern they "could be susceptible to the declining carbonate ion concentrations associated with ocean acidification," which could well be imagined to be quite serious, due to the fact "fish ears detect sound, body orientation and acceleration from the position of the otoliths in the inner ear and movement of the otoliths over sensory hair cells (Helfman *et al*., 1997; Popper and Lu, 2000)."

In further exploring this intriguing subject, Munday *et al*. reared larvae of the marine clown fish *Amphiprion percula*throughout their entire larval phase at three different ocean acidification levels-ambient or control conditions (CO_2 ~ 390 ppm, pH ~ 8.15) and higher CO_2/lower pH conditions (CO_2 ~ 1050 ppm, pH ~ 7.8; CO_2 ~ 1721 ppm, pH ~ 7.6) representative of conditions predicted to prevail in AD 2100 and AD 2200-2300, respectively-in order to determine if the elevated CO_2/reduced pH conditions would alter otolith size, shape, symmetry (between left and right otoliths) or chemistry compared to current conditions. Under such conditions, the four researchers report "there was no effect of the intermediate treatment on otolith size, shape, symmetry between left and right otoliths, or otolith elemental chemistry, compared with controls." In the more extreme treatment the story was much the same, except that otolith area and maximum length were slightly larger than controls, while "no other traits were significantly affected." Munday*et al*. thus state their data suggest the larval clown fish is "capable of regulating endolymphic fluid chemistry even in waters with pH values significantly lower than open ocean values," and they conclude "the larval clown fish is robust to levels of ocean chemistry change that may occur over the next 50-100 years," which conclusion is about the same as that reached by Munday *et al*. (2011b), who they say "detected no effects of ~850 ppm CO_2 on size, shape or symmetry of otoliths on juvenile spiny damselfish, a species without a larval phase."

Miller *et al*. (2013)[10] assessed the impact of ocean acidification on the breeding success of cinnamon anemone fish. For their experiment, they employed three 8,000-L recirculating aquarium systems, each set to a different CO_2 and corresponding pH level. The treatments consisted of a current-day Control CO_2 (430 µatm), a mid-century Moderate CO_2 (584 µatm) and an end-of-century High CO_2 (1032 µatm).

9 http://www.co2science.org/articles/V14/N35/B2.php.
10 http://www.co2science.org/articles/V16/N51/B1.php.

Eighteen pairs of cinnamon anemone fish (*Amphiprion melanopus*) collected from Australia's Great Barrier Reef were placed into each of these three aquariums after all individuals had been weighed and measured for length. At the start of the experiment, pairs of fish were placed into individual 45-L tubs with continuous water flow at winter non-breeding temperatures and ambient pCO_2 values, which were gradually adjusted over a two-week period to the desired levels. Then, temperature was increased by 0.5°C per week, until the average summer breeding temperature was reached, after which the pairs of fish remained in these conditions for a 9-month period that included the summer breeding season, during which period various assessments of breeding success were made.

The four Australian researchers report that "unexpectedly, increased CO_2 dramatically stimulated breeding activity." Over twice as many pairs of the fish bred in the Moderate and High CO_2 treatments (67% and 55%) compared to the Control treatment (27%). Furthermore, "pairs in the High CO_2 group produced double the number of clutches per pair and 67% more eggs per clutch compared to the Moderate and Control groups." As a result, the researchers determined "reproductive output in the High group was 82% higher than that in the Control group and 50% higher than that in the Moderate group." And they make a point of noting, "despite the increase in reproductive activity, there was no difference in adult body condition among the three treatment groups," and "there was no significant difference in hatchling length between the treatment groups." In light of such findings, Miller *et al*. conclude "this study provides the first evidence of the potential effects of ocean acidification on key reproductive attributes of marine fishes and, contrary to expectations, demonstrates an initially stimulatory effect in response to increased pCO_2."

This study provides the first evidence of the potential effects of ocean acidification on key reproductive attributes of marine fishes and, contrary to expectations, demonstrates an initially stimulatory effect in response to increased pCO_2.

In prefacing their investigation of ocean acidification on otoliths of cobia, Bignami *et al*. (2013b)[11] write "the days- to month-long pelagic larval period is an ecologically vital ontogenetic phase in marine fishes because it constitutes the primary mode of dispersal in many species (Cowen and Sponaugle, 2009) and represents the life stage most susceptible to mortality (Houde, 1997)," and they thus go on to say "during this phase, the sensory abilities of larval fishes are important determinants of survival (Montgomery *et al*., 2006) and ultimately influence the persistence of viable populations." Against this backdrop the five researchers, as they describe it, "used new 3D microcomputed tomography to conduct in situ analysis of the impact of ocean acidification on otolith (ear stone) size and density of larval cobia (*Rachycentron canadum*), a large, economically important pantropical fish species that shares many life history traits with a diversity of high-value, tropical pelagic fishes."

[11] http://www.co2science.org/articles/V16/N36/B2.php.

According to the researchers, at an atmospheric partial pressure of 2100 ppm CO_2 there was a significant increase in otolith size (up to 49% greater volume and 58% greater relative mass), as well as a 6% increase in otolith density, while the estimated relative mass of larval cobia otoliths in an end-of-century 800 ppm CO_2 treatment was 14% greater. Equipped with these experimental observations, Bignami *et al*. go on to demonstrate "these changes could affect auditory sensitivity including a ~50% increase in hearing range at 2100 ppm CO_2." And they say "this is a potentially optimistic result, indicating some resistance to acidification and suggesting that under near-future scenarios these impacts may be most relevant in habitats already experiencing high pCO_2 levels."

In another relevant study, Hurst *et al*. (2013)[12] examined the direct effects of projected levels of ocean acidification on the eggs and larvae of walleye pollock in a series of laboratory experiments that focused on determining the effects of elevated CO_2 levels on size-at-hatch and early larval growth rates, where treatments were selected to reflect ambient conditions and conditions predicted to occur in high latitude seas in the next century (a 400-600 ppm increase), as well as a significantly higher CO_2 treatment (~1200 ppm). In describing their findings, the three U.S. researchers say "ocean acidification did not appear to negatively affect size or condition of early larval walleye pollock." In fact, they note there was "a trend toward larger body sizes among fish reared at elevated CO_2 levels," while adding that this trend toward faster growth rates among larvae reared at elevated CO_2 levels has also been observed in experiments with orange clownfish (Munday *et al*., 2009), as well as in the study of juvenile walleye pollock conducted by Hurst *et al*. (2012). Such findings, in the words of the authors, suggest "the growth dynamics of early life stages of walleye pollock are resilient to projected levels of ocean acidification."

High CO_2 did not have any effect on metabolic rate or aerobic performance. And they say that contrary to expectations, "fish diversity and community structure differed little between CO_2 seeps and nearby control reefs."

Munday *et al*. (2014)[13] write in introducing their work that "there is growing concern that rising CO_2 levels and ocean acidification will have profound impacts on marine biodiversity and the function of marine ecosystems," citing Wittmann and Portner (2013). However, they note that "most evidence for negative effects of ocean acidification comes from short-term laboratory experiments on single species," and that "there is increasing evidence that some species can adjust to high CO_2 levels over the longer term," citing Form and Riebesell (2012), Miller *et al*. (2012), Parker *et al*. (2012) and Dupont *et al*. (2013). In further exploring the subject, Munday *et al*. took advantage of naturally acidified seawater in the vicinity of Papua New Guinea, which is located near cool volcanic seeps that

[12] http://www.co2science.org/articles/V16/N45/B1.php.
[13] http://www.co2science.org/articles/V17/oct/a2.php.

raise the acidity of the nearby seawater to levels similar to projections for the coming century, in order to test for the effects of continuous exposure to elevated CO_2 on reef fish behavior and metabolism in their natural habitat, and to examine the potential consequences for reef fish communities.

The five scientists determined that high CO_2 did not have *any effect* on metabolic rate or aerobic performance. And they say that *contrary to expectations*, "fish diversity and community structure differed little between CO_2 seeps and nearby control reefs." In light of these welcome findings, Munday *et al*. conclude that "recruitment of juvenile fish from outside the seeps, along with fewer predators within the seeps, is currently sufficient to offset any negative effects of high CO_2 within the seeps."

Additional optimism with respect to the future health and well-being of fish facing ocean acidification comes from recent research focusing on adaptation.

Writing as background for their work, Allan *et al*. (2014)[14] state that although many scientists have studied the potential impacts of rising temperatures and declining seawater pH on marine organisms, "the potential for adaptation or acclimation over climate change relevant timescales remains largely unresolved (Kelly and Hofmann, 2013)." Yet they note "the environmental conditions experienced by parents may affect their [offspring's] physiological condition and provide the opportunity for non-genetic effects to be transferred to their offspring (Marshall and Morgan, 2011; Bonduriansky *et al*., 2012)." In exploring this possibility for what they describe as transgenerational acclimation, Allan*et al*. studied the ability of juvenile cinnamon anemone fish (*Amphiprion melanopus*) to adjust their escape responses from predators across generations of exposure to elevated CO_2.

To accomplish their design, the researchers examined "the acute (within-generation) effects of increased CO_2 on juvenile escape performance," testing "whether such effects were mediated by exposure of parents to increased CO_2." Seven variables were utilized to assess the escape response, which was initiated by a simulated predatory disturbance that included the sudden release of an object into the tank. Four of the variables examined related to motion-response distance (total distance traveled in response to the simulated disturbance), mean response speed (as measured by the average duration of the first two flips of a fish's tail), maximum speed (recorded at any time during the response), and response duration (total elapsed time from the start of the simulated disturbance until the fish came to rest). The other three variables assessed fish responsiveness (the percent of fish that responded to the simulated disturbance with a sudden acceleration of movement), directionality (whether the escape response was directed toward or away from the simulated disturbance), and response latency (the time elapsed between the initial disturbance and initial fish movement).

All testing was conducted in an environmentally-controlled aquarium facility at James Cook University, Townsville, Australia. Three treatment groups were used to study the difference between acute exposure to CO_2 and parental (transgenerational) effects of CO_2 on juvenile reef fish - (i) juveniles from parents reared in control CO_2 (400 µatm) hatched into control CO_2 levels

14 http://www.co2science.org/articles/V17/N33/C3.php.

(400 µatm), (ii) juveniles from parents acclimated to high CO_2 (1087 µatm) hatched into high CO_2 (1087 µatm), and (iii) juveniles from parents reared in control CO_2 (400 µatm) hatched into high CO_2(1087 µatm) - where juvenile fish escape performance was analyzed at the end of the pelagic larval phase (10-11 days posthatching).

Acute exposure to high CO_2 levels of juveniles from parents reared in control CO_2 had a statistically significant negative effect on each of the four variables pertaining to motion (response distance, mean response speed, maximum speed, response duration). However, the response of juveniles whose parents had been acclimated to high CO_2 was not statistically different from the response of juveniles reared under control conditions, indicating that the parental effects of transgenerational acclimation reduced the negative effects of elevated CO_2 exposure.

A similar situation was observed with respect to fish responsiveness and directionality. Juveniles that descended from parents reared under control CO_2 conditions responded negatively under acute exposure to high CO_2, while juveniles that descended from parents who were previously acclimated to high CO_2 exhibited escape responses that were not statistically different from control conditions. Response latency remained unaffected by CO_2 treatment.

In discussing the significance of their findings, Allan *et al*. note that "transgenerational acclimation can help to overcome behavioral impairment observed in fishes exposed to high CO_2," adding that "as CO_2 levels rise over coming decades, both parental and offspring generations will experience similar elevated CO_2 levels; thus our results indicate that this parental exposure will help to reduce some of the negative effects of high CO_2 on behavior."

Introducing their work, Murray *et al*. (2014)[15] write that "contemporary coastal organisms already experience a wide range of pH and CO_2 conditions, most of which are not predicted to occur in the open ocean for hundreds of years - if ever," citing Cai *et al*. (2011) and Melzner *et al*. (2012). And, therefore, they consider coastal waters to be natural laboratories for studying *transgenerational plasticity* or TGP, a phenomenon that they describe as "the ability of the parental environment prior to fertilization to influence offspring reaction norms without requiring changes in DNA sequence (Salinas and Munch, 2012)," which adaptive transformation, in their words, is "often attributed to epigenetic inheritance and found in such diverse taxa as plants, insects, marine invertebrates, and vertebrates, including humans," citing the studies of Jablonka and Raz (2009) and Salinas *et al*. (2013). Against this backdrop, Murray *et al*. used what they called "a novel experimental approach that combined bi-weekly sampling of a wild, spawning fish population (Atlantic silverside *Menidia menidia*) with standardized offspring CO_2 exposure experiments and parallel pH monitoring of a coastal ecosystem," by which means they "assessed whether offspring produced at different times of the spawning season (April to July) would be similarly susceptible to elevated (~1100 µatm, pH=7.77) and high CO_2levels (~2300 µatm, pH=7.47)."

With respect to their findings, the four U.S. scientists report that "early in the season (April), high CO_2 levels significantly reduced fish survival by 54% (2012) and 33% (2013) and reduced 1

[15] http://www.co2science.org/articles/V17/N35/B2.php.

to 10 day post-hatch growth by 17% relative to ambient conditions." However, they found "offspring from parents collected later in the season became increasingly CO_2-tolerant until, by mid-May, offspring survival was equally high at all CO_2 levels." As a result, Murray *et al*. conclude their study "suggests that transgenerational acclimation to increasing CO_2 levels is not just a laboratory phenomenon but likely comprises a common adaptive strategy in marine fish and other organisms coping with the biologically driven, natural pH and CO_2 variability in coastal habitats."

Unfortunately, only a few studies have incorporated the concept of transgenerational acclimation when studying the response of marine life to rising temperatures and CO_2. Given the findings of Allan *et al*. and Murray *et al*., however, more researchers would be wise to incorporate it into their experimental design; for in so doing, they will likely come closer to the true response of marine life to future climate and seawater pH conditions. And that response is looking to be more and more encouraging for fish.

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