Workshop on "*Impacts of Ocean Acidification on Zooplankton*"

by M. Brady Olson and So Kawaguchi

During the 5th International Zooplankton Production Symposium in Pucón, Chile, the authors of this article co-convened a workshop entitled "*Impacts of ocean acidification on zooplankton*". This workshop, to our knowledge, provided the first opportunity to discuss the biological effects of ocean acidification (OA) that was exclusive to zooplankton ecologists. The workshop agenda was to include, and specifically extend, the conversation on the effects of OA beyond direct acute effects on calcifying zooplankton. In particular, we solicited contributions that documented how OA sub-acutely and sub-lethally affects zooplankton biology, ecology and physiology. We were thrilled by the international participation in our workshop, having 9 oral and 4 poster presentations by scientists and students from 6 countries. Although the study of the OA effects on zooplankton is still in its infancy, this did not deter, and likely contributed to, active participation and interest from a packed audience. Workshop presentations included talks and posters ranging from field and laboratory experiments to time-series analysis showing effects of OA on the biology and ecology of microzooplankton, copepods, euphausiids, invertebrate larvae and pteropods. Although this level of taxonomic diversity and experimental scope was encouraging, it also helped to illuminate the general conclusion of the workshop: we currently, and perhaps indefinitely, are unable to make generalizations regarding the effects of OA on zooplankton. Validation of the above statement, we hope, can be found in the summation of workshop presentations below.

Brad A. Seibel (University of Rhode Island, USA), the invited speaker for this workshop, opened with an insightful talk reminding us that through synergy with hypoxic and anoxic waters, ecologists have been interested in, and have been studying the effects of, high $p\text{CO}_2$ conditions on ocean biota for decades. He provided evidence to show that isolating both the short- and long-term biotic responses to OA is challenging, and will remain so due to organismal plasticity, acclimation and adaptation, and multiple stressors acting in synergy with rising $p\text{CO}_2$. He suggested that, as a scientific discipline, our perceived understanding of the biological effects of OA is ahead of the information provided by empirical data, given the disproportionate number of reviews compared to research manuscripts. Further, he showed that much of the small yet growing body of work documenting effects of OA on zooplankton shows no discernable effect at relevant $p\text{CO}_2$ concentrations (IPCC IS92a CO_2 scenario), and that other environmental stressors synergistic with high $p\text{CO}_2$ (*e.g.*, hypoxia/anoxia) may be equally, if not more, stressful to marine organisms and worthy of our scientific attention.

Many of the talks and poster presentations showed no discernable direct effect of OA on zooplankton. M. Brady Olson (Western Washington University, USA) *et al*. demonstrated that ingestion and growth rates of micro-zooplankton acclimated to a range of $p\text{CO}_2$ concentrations (up to 1000 $p\text{CO}_2$) did not differ from ambient controls when fed phytoplankton prey grown under ambient $p\text{CO}_2$. When microzooplankton, in turn, were fed phytoplankton acclimated to elevated $p\text{CO}_2$, preliminary results indicated that microzooplankton ingestion and growth rates differed from ambient $p\text{CO}_2$ controls, presumably from phyto-plankton physiological or biochemical alterations in response to elevated $p\text{CO}_2$. This indirect effect of OA, precipitated through changes in prey state, was also seen by Cathryn Wynn-Edwards (University of Tasmania, Australia) *et al*., whose poster showed that although mortality rates of Antarctic krill were unaffected, intermolt periods, growth rates, and vitality were reduced when feeding on diatoms grown at 950 ppm CO_2. In a mesocosm experiment, Barbara Niehoff (Alfred Wegener Institute for Polar and Marine Research, Germany) *et al*. presented data indicating that no quantified metric of holo- and meroplanktonic zooplankton biology (*e.g.*, egg production, development) or ecology (*e.g.*, total abundance, species composition, sediment trappings)

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differed across eight pCO_2 treatments ranging from 180 to 1350 ppm CO_2. A poster by Kristian McConville (Plymouth Marine Laboratory, UK) *et al*. showed that even at pH 7.7 copepod feeding rate, egg production and hatching success was unaffected compared to controls. Leah Feinberg (Oregon State University, USA) *et al*. demonstrated that for *Euphausia pacifica*, egg hatching success and larval development were dependent on maternal effects rather than reduced pH, even at pH 7.2.

Other presentations showed that, indeed, increased pCO_2 appears to affect aspects of zooplankton biology. So Kawaguchi (Australian Antarctic Division, Australia) *et al*. established that while Antarctic krill larvae develop normally at pCO_2 380 and 1000 µatm, between 1000 and 2000 µatm embryo development is nearly totally halted, and James Robinson (University of Tasmania, Australia) *et al*. discovered that Antarctic krill recruitment may also suffer from elevated pCO_2. Steve Doo (Northeastern University, USA) presented a paper by Byrne *et al*. demonstrating decreased development and size in sea urchin larvae above 1000 ppm pCO_2, and Jörg Dutz (National Institute of Aquatic Resources, Denmark) *et al*. found that in addition to prey strain variability, reduced pH may play a role in hatching success of copepod eggs. Two time-series presentations showed changes in pteropod abundance, biomass, and species composition [Galbraith and Mackas (Institute of Ocean Sciences, Canada)] and shell porosity [Roger (University of Western Australia, Australia) *et al*.] across the Pacific continental shelf and in Australian tropical waters, respectively. For both studies, the degree to which these changes can be attributed to OA remains uncertain.

Following the conclusion of the formal oral presentations, we were left with twenty minutes to moderate a short, yet lively discussion. Considering the content of Seibel's talk, we began the discussion by asking the audience to what degree we should be concerned about OA and its effects on zooplankton. Have we, as a research discipline, raised the red flag too soon? That is, is OA really a threat to zooplankton that supersedes other climate stressors, and is it worthy of discipline-wide research focus? Not surprisingly, the audience was largely non-committal. Further discussion revealed several reasons for the participants' ambivalence:

- Many of the presentations in this workshop showed no discernable individual or community zooplankton response to elevated pCO_2 or decreased pH at IPCC IS92a CO_2 scenarios. Additionally, due to environmental variability (*e.g*., upwelling), diapause at depth, and ontogenetic development during ascent from great depths, many zooplankton (including larval stages) already experience pH levels well below what is predicted for surface waters in year 2100. It is difficult to comprehend a zooplankton response in these already 'corrosive' environments arising from comparatively subtle, long-term shifts in pH.
- When effects from OA were demonstrated, they occurred near, or above, the extreme pCO_2 concentrations predicted by IS92a CO_2 scenarios. It was argued that these findings cannot be dismissed as ecologically unrealistic because model projections show that depths where some zooplankton life histories occur may experience pCO_2 as high as 1400 µatm by year 2100.
- In most studies the metric used to quantify effects from OA are acute (*e.g*., mortality, morphology, embryological development, egg hatching success, alterations in community composition). By looking at obvious, discernable biological variables we may be missing subtle responses that, over time, magnify into alterations in individuals and populations that, in turn, may affect ecosystem function. It was recognized that as a research community we should focus future experiments on testing variables that will expand our knowledge of the effects of OA to less conspicuous, but equally important, changes to zooplankton biology.
- Experimental designs and pCO_2 treatment concentrations used for incubations lack formal rigor across the research community. This approach can lead to uncertainty in assigning ecological relevance of empirical findings, and handicaps our ability to characterize the impacts that OA may have on future zooplankton populations and ecosystems. Further, despite recognition that isolating single mechanisms governing biological change (*i.e*., elevated pCO_2) is important, few studies incorporate obvious variables that will change in concert with increasing pCO_2, and which may enhance or moderate the effects of elevated pCO_2 alone.
- Generating active discussion was the need to, and relevancy of, incorporating diel and seasonal variability of pCO_2 concentration into experimental designs. This is especially true for zooplankton ecologists working in temperate upwelling environments where infusion of cold, nutrient-rich water already low in pH and high in pCO_2 is chemically altered over short time scales by high phytoplankton productivity. This chemical alteration results in diel pH oscillations significantly greater than the range predicted to occur over the next century. Additionally, zooplankton ecologists working with organisms whose ontogenetic development and recruitment to surface waters begins at great depths with already low pH conditions face the pragmatic challenge of designing cross-generational experiments at wide-ranging pCO_2 concentrations.

The final point of discussion emphasized that when considering the degree to which OA may alter zooplankton biology, physiology and ecology, we need to consider how any zooplankton responses will affect adjacent trophic levels, and *vice versa*. For example, how might changes from OA to zooplankton ingestion rates, assimilation efficiencies, egesta stoichiometry, and production alter the ecology of microbial and higher-order individuals and communities? Further, how might these 'second order effects' alter basin-scale elemental cycling?