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How does Body Size Affect Zooplankton Feeding in a Low Oxygen Environment?

By Jacob Mikullitz
Anthropogenic climate change is likely to affect natural systems in the coming decades. Whereas climate change acting on its own will be impactful enough, the interaction between it and other disturbances could also be significant. Coupling stressors together often affect a system greater than either one would individually, but this is highly dependent on the two occurring close enough together in space and time (Buma 2015; Molinos and Donohue 2010). As a uniquely global disturbance, climate change will affect systems over the entire Earth, meaning all disturbances will be interacting with climate change to some degree. Generally, disturbance interactions result in one disturbance lowering a system’s resistance to the other, allowing for a greater effect, or through affecting the likelihood that the second effect occurs (Buma 2015).

One of these climate-change-influenced threats that has come to light in the last few decades is algal blooms. Algal blooms can lead to anoxic “dead zones” that kill aquatic life. Climate change is already known to exacerbate these blooms through higher temperatures that better facilitate algal growth, but another way is its effect on the grazers that would naturally control blooms (Ficke, Myrick, and Hansen 2007; Kankaala et al. 2002). Zooplankton grazers feed less effectively at higher temperatures, meaning that feeding rates will decrease as algal growth rates increase (West and Post 2016). Zooplankton will also face another major factor besides just increased temperature: lower dissolved oxygen (DO) content due to higher water temperatures. At the same time, the metabolic rates of aquatic organisms increase with water temperature, meaning organisms require more oxygen when it is less available (Ficke, Myrick, and Hansen 2007). Whereas most organisms can survive at reduced DO levels as low as 5 mg/l, increased temperatures can drive DO content below the 2-3 mg/l hypoxic threshold where long-term survival becomes more difficult (Ficke, Myrick, and Hansen 2007).
Adding to this complication is that it matters whether larger or smaller zooplankton are performing better at feeding, as larger zooplankton have been shown to be more important in reducing algal numbers (Brooks and Dodson 1965; Scharf 2007; Holm, Ganf, and Shapiro 1983). At normal temperatures, large grazer species typically outcompete smaller species due to their improved ability to collect food, as their larger filtering apparatus let them take in more food (Brooks and Dodson 1965). However smaller zooplankton often outperform larger ones at higher temperatures, likely due to the ability of small zooplankton to feed faster (West and Post 2016). These two observations are consistent with two of the three “rules” investigated by Kingsolver and Huey in 2008: that hotter is smaller, meaning that adults typically develop to be smaller in hotter conditions, and larger is better, meaning that generally larger body size equates to better fitness. Although strong support exists for a smaller body size under high temperatures, less evidence supports that a larger body size performs better at low oxygen levels. However, some researchers suggest that oxygen restraints are in fact what leads to the “hotter is smaller” prediction (Sentis, Binzer, and Boukai 2017). In general, it appears that the main argument for larger individuals performing better is that they more effectively gather food; however, studies with other organisms in low oxygen environments indicate that the ability to feed on larger prey is essentially useless in low oxygen environments as the increase in energy is not worth the greater time required (Shin et al. 2005). In comparison, smaller organisms would do better because their total respiration is lower, and therefore easier to maintain even under low oxygen conditions (Simic 2010). In this study I predict that smaller grazing zooplankton will outperform larger species in feeding on algae at low DO levels due to their lower metabolic needs.

**Methods**
Zooplankton specimens were gathered from Swan Lake and Mirror Lake on the University of Connecticut campus using a tow net. Two samples were taken from each water body. After collection the samples were examined for cladocerans, each of which was identified to species or genus using a light microscope and sorted into separate vials. Identifications were based on the University of New Hampshire Center for Freshwater Biology’s Image-based Key to the Zooplankton of North America (Haney et al. 2015). Only two cladoceran taxa were abundant enough to use in experiment: *Chydorus sphaericus* (*C. sphaericus*) and *Eurycercus spp*. Five random individuals from each of these groups were measured lengthwise to provide information about the body size for these two taxa.

Next the different experimental groups were created. For each species, five individuals were placed in one of three oxygen treatments: normal oxygen (approximately 9.5 mg/l $O_2$), medium oxygen (approximately 4.5 mg/l $O_2$) and low oxygen (approximately 2.5 mg/l $O_2$). These different treatments were created by bubbling nitrogen through containers of 350 ml of filtered water from the Fenton River. This was done by bubbling nitrogen gas in the water using a diffusion stone for different amount of times depending on the treatment (Butler et al. 1994). No bubbling was needed for the normal oxygen treatment, ten seconds of bubbling was used for the medium oxygen treatment, and thirty seconds of bubbling was used for the low oxygen treatment. Four replicates were created for each treatment. The temperature and oxygen content of each container was measured using a dissolved oxygen meter. Following this, 600 microliters of *Scenedesmus* algae solution with a concentration of fifty million cells per milliliter was added to each container, bringing the concentration of algae in each container to approximately 85,714 algae cells per milliliter of water. The experimental groups were then placed in an incubator set to $20^\circ$ C.
Every two hours following the start of the experiment the concentration of algae cells in each experimental group was measured using a hemocytometer reading of a ten-microliter sample. Three hemocytometer measurements were taken per experimental group per two-hour time step, and results averaged. The water in each container was mixed prior to taking samples to ensure that the number of cells in homogenous in all parts of the container. Oxygen content and temperature were also measured again at these two-hour marks using the oxygen meter. Measurements were repeated every two hours until the oxygen level of the low oxygen treatments returned to its approximate pre-treatment levels, which in this instance was approximately six hours or after three sets of measurements were taken.

Results

*Eurycercus spp.* are significantly larger on average than other *C. sphaericus*, with an average length of 0.52 micrometers as compared to an average length of 0.2 micrometers (Figure 1). This size difference fulfills the requirement that two species of significantly different size are being compared.

The average starting oxygen levels for the different treatments depending on amount of time that nitrogen bubbling was done were found to be 9.46 mg/l for no bubbling, 4.51 mg/l for ten second of bubbling, and 2.52 mg/l for thirty second of bubbling. Again these differences are significant enough to create three distinct oxygen concentrations that do not overlap. Unaltered oxygen concentrations stayed consistently around 9.2 mg/l throughout the length of the experiment (Figure 2). In treatments with oxygen levels that were lowered, the rate of return to normal oxygen levels was 0.60 mg/l per hour for the treatment brought down to around 4.51 mg/l and 1.05 mg/l per hour for the treatment brought down to around 2.52 mg/l (Figure 2). Therefore, the rate of return depends on how low the oxygen concentration is brought down, with the
average rate of change of around 0.83 mg/l per hour. This rate of change was not significantly faster or slower for any specific species, so even with oxygen levels that change they changed consistently and the different treatments can still be compared.

The change in algae concentration significantly differed between the two differently-sized zooplankton species depending on the oxygen treatment used. With no changes to oxygen *Eurycercus spp.* surpassed *C. sphaericus* in feeding on algae until the sixth hour measurement, at which point *Eurycercus spp.* feeding slowed and *C. sphaericus* ended with a lower concentration (Figure 3). At medium reduced oxygen levels *C. sphaericus* surpassed *Eurycercus spp.* by a significant margin until the 4 hour mark, when again there was a switch and *Eurycercus spp.* ended with a larger concentration (Figure 4). The lowest oxygen levels showed the least amount of change over time, with the *C. sphaericus* and *Eurycercus spp.* showing essentially the exact same rate of change over the length of the experiment, with the *Eurycercus spp.* consistently outcompeting (Figure 5).

An ANOVA analysis of the interaction between zooplankton species and oxygen concentration returned a p-value of 0.06139 and F-value of 3.0670. This suggests a marginally significant interaction between zooplankton treatment, and therefore zooplankton size, and oxygen concentration that affects feeding rate, but not as was expected. When the total change in algae concentration for the different sized cladocerans is graphed along the oxygen concentration gradient, there is no significant change in algae concentration for the small cladocerans depending on the oxygen concentration, but there is for the large cladocerans. Large cladocerans will feed more than small cladocerans at low oxygen levels, but are outfed at higher oxygen concentrations, with the change from one to the other occurring at a concentration of around 6.5 mg/l (Figure 6).
Discussion

The oxygen levels tested well represent both current and future conditions that will likely occur in Connecticut. The current average DO content in Connecticut lakes and ponds is approximately 10.19 mg/l, which is comparable to the unaltered oxygen level of 9.46 mg/l used in the experiment (Healy and Kulp 1995). The medium altered concentration of 4.51 mg/l can be compared to the 5 mg/l threshold that is thought to be the lower threshold for many aquatic species. The low altered concentration of 2.52 mg/l can then be compared to the 2-3 mg/l concentration that is thought to be the low estimate for future water dissolved oxygen concentrations due to the warming effect of global warming (Ficke, Myrick, and Hansen 2007).

Originally, I predicted that smaller zooplankton would outcompete their larger counterparts in a low oxygen scenario due to their lower metabolic needs (Kingsolver and Huey 2008). The data gathered in this experiment seems to support the opposite idea that larger zooplankton will be more successful in a low oxygen scenario, with the lower the oxygen the greater the larger zooplankton perform. Strangely this difference is not due to small zooplankton performing worse, as their feeding did not differ significantly depending on the oxygen level, but instead because the larger zooplankton fed more at lower oxygen levels (Figure 6). The greater effectiveness larger zooplankton have as filter feeders therefore appears to be more than the lower metabolic needs that small zooplankton have.

The original prediction for this study, that low oxygen would favor smaller body sizes, was conceived as a mechanism to explain the results observed by West and Post in 2016, where smaller zooplankton showed a greater feeding rate at high temperatures despite showing a lower one at low-to-normal temperatures. However, the actual results of this study may help explain the results of another study which found that zooplankton raised in heated lakes were generally
larger than those from unheated lakes (Dziuba, Cerbin, and Wejnerowski 2015). This finding is of particular interest as it serves as an exception to the “hotter is smaller” rule that zooplankton generally follow but based on what has been found in my study low oxygen could be a potential mechanism that allows zooplankton to ignore this rule (Kingsolver and Huey 2008). This fits because the heated lakes studied were generally isolated from other bodies of water, and would be more vulnerable to a lowered oxygen concentration than other water bodies with greater connectivity (Dziuba, Cerbin, and Wejnerowski 2015).

The experimental groups in this experiment were fed a greater concentration of cells than is usually provided to a zooplankton stock, approximately an extra ten thousand algal cells per milliliter of water (Nadeau personal communication). This excess concentration of food was meant to better replicate the eutrophic conditions where the role of zooplankton as grazers would be of particular importance, and it may also explain why the larger individuals ultimately showed a greater feeding rate. In past experiments comparing feeding rate to body size under different dissolved oxygen concentrations, which typically found smaller body sizes performed better in low oxygen conditions, food was generally limited. As a result, the metabolic costs to obtain food were higher making the more efficient use of oxygen by smaller organisms more important than the greater potential feeding rate of larger organisms (Gophen 1976; Shin et al. 2005).

However, in a food saturated environment, as was found in this experiment and would be found in a eutrophic water body, obtaining food requires less energy overall, allowing the larger organism’s greater feeding rate to take precedence.

The results of this study were relatively limited by the equipment and specimens available, and further experimenting on this topic should aim to reduce the blanks in information this has caused. Future studies should include a larger spectrum of specimen sizes to ensure that
the differences observed are consistent with even larger and smaller zooplankton. Future studies should also find a way to test over a longer period of time at reduced oxygen levels, as it is possible that the differences observed do not hold constant over a longer period of time. Also important would be expanding the study beyond feeding to compare survival of different sized zooplankton in reduced oxygen environments. Whereas this study focuses on the role of zooplankton as algae grazers, which makes feeding the key difference, if the zooplankton cannot survive for an extended period of time in a reduced oxygen concentration their grazing ability is not relevant. The interaction between temperature and oxygen on determining size should also be more closely examined in future studies, as recent studies have suggested they impact one another more significantly than once thought (Walcynzska A and Sobczyk L 2017).

Based on the results of this study, it appears that the reduced DO concentration in water due to climate change may actually help to combat the rising threat of algal blooms (Brooks and Dodson 1965; Scharf 2007). Larger zooplankton grazers that are more effective at combating these blooms will have higher fitness in future low oxygen environments.

Conclusion

The generally accepted rule of zooplankton is that smaller organisms show greater fitness when it is hotter. In an aquatic environment, however, ambient temperature is not an independent factor, but also determines the amount of dissolved oxygen available. This study suggests that when these two qualities, temperature and dissolved oxygen concentration, are separated they exert contrasting forces, with a high temperature favoring a small body size but a low oxygen concentration favoring a large body size. Loss of dissolved oxygen may therefore serve as a mediating effect on the predicted shrink in average zooplankton body size that would occur as water temperatures rise under the influence of climate change. Preserving larger zooplankton in
turn would help reduce the effect of algal blooms that are also expected to become more of a problem due to the effects of climate change. The interaction between reduced water DO concentrations and algal blooms therefore serves as another example of the odd mix of both positive and negative effects that climate change will have on natural systems.

References


Figures and Tables
Figure 1.

Figure 2.
Figure 3.

Figure 4.
Figure 5.

Figure 6.
Analysis of Variance Table

Response: log10(Algae)

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Table 1. Results of ANOVA analysis of interaction between oxygen concentration and algae concentration.