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Notes

Measurement of *Diporeia* respiration rate for Lake Superior

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ABSTRACT

The freshwater amphipod *Diporeia* is a dominant macroinvertebrate species in Lake Superior's benthic community and an important prey item for many fish. A capacity to predict growth and production rates of *Diporeia* using a bioenergetics model requires information on physiological processes of the species. The objective of this study is to quantify oxygen consumption of Lake Superior *Diporeia* and to determine if respiration rate changes with body length. *Diporeia* were collected from Lake Superior and kept over natural sediment maintained at 4 °C. Dissolved oxygen levels for groups of immature (2 mm), juvenile (4 mm), and adult (6 mm) *Diporeia* in 20 ml microcosms were measured using a polarographic microelectrode. Mass-specific respiration rates for Lake Superior *Diporeia* ranged from 32.0 to 44.7 mg O_2 g DW^{-1} day^{-1}. A significant relationship between body length and mass-specific respiration rate ($p > 0.1$) was not found. The estimate of *Diporeia* respiration presented here is significantly higher ($p < 0.05$) than previous findings from populations in Lakes Michigan and Ontario. This study provides new data on respiration rates of Lake Superior *Diporeia* and compares findings to studies for other connecting Great Lakes.

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Introduction

Members of the genus *Diporeia* spp., previously known as *Pontoporeia* (Bousfield, 1989), have historically been the most prominent macroinvertebrate of the benthic communities of the Laurentian Great Lakes (Cook, 1975; Stimpson, 1870; Winnell and White, 1984). This amphipod (herein referred to as *Diporeia)* is a major component in the diets of numerous commercial and sport fish species (Nalepa et al., 2006; Rennie et al., 2009; Scharold et al., 2004). From C and N stable isotope signatures *Diporeia* are suggested to feed on organic matter, bacteria and/or settling primary producers in aquatic systems (Guiguer and Barton, 2002). *Diporeia* are also an effective energy source for other organisms due to their high lipid content (Gardner et al., 1985; Kainz et al., 2010), indicating that they can be a key link between primary production and higher trophic level consumers.

Ecological monitoring of lake systems includes an analysis of production using: production = consumption − (respiration + waste). Sensitivity analyses of bioenergetics models have shown that consumption and respiration rates have the greatest influences on model predictions (Kitchell et al., 1977; Rice and Cochran, 1984). Kitchell et al. (1977) found that excretion parameters within a bioenergetics model for fish had moderate sensitivity on simulated growth rates. Data on respiration for benthic invertebrates in the Great Lakes is limited. This lack of information is often due to methodological challenges associated with measuring physiological functions non-invasively (Mills, 2007). Studies examining *Diporeia* respiration have used the Winkler titration method for dissolved oxygen (DO) in water (Johannsson et al., 1985; Quigley et al., 2002). While this is a widely used method for measuring DO concentrations in wet chemistry (Sahoo et al., 2010), it cannot be used to continuously monitor animal respiration throughout the duration of an experiment due to sample extraction. Alternatively, polarographic microelectrodes have previously been used to monitor respiration of various living organisms (e.g. soil microbes, larval fish, aquatic invertebrates, etc.) and can measure DO concentration in water on a continuous scale with a response time less than 1 s. Johnson and Brinkhurst (1971) examined respiration rates of Lake Ontario *Diporeia* using a polarographic microelectrode (YSI model 54) which had a probable error rate of 4.8%. At the time of their study, the electrode required that water be constantly stirred to avoid oxygen consumption effects from the cathode. Modern sensors are able to measure oxygen concentrations with a precision of about 0.1 μM, or 0.05%, and without mixing the water surrounding the sensor. Previous work by Landrum and Stubblefield (1991) and Quigley et al. (2002) suggest that body sizes of *Diporeia* are inversely related to their mass-specific respiration rate. The objective of the present study was to quantify oxygen consumption of Lake Superior *Diporeia* and to determine if respiration rate changes with body length. These findings will be used to develop a bioenergetics model for predicting Lake Superior ecosystem responses to climate change. Lake Superior *Diporeia* are hypothesized to have respiration

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rates similar to those found in populations from Lakes Michigan and Ontario and to have increased mass-specific respiration rates with decreasing body length.

Production of *Diporeia* in Lake Superior has been of interest due to population declines experienced in Lakes Erie, Huron, Michigan, and Ontario (Barbiero et al., 2011; Lozano et al., 2001, 2003; Nalepa et al., 1998, 2006). It has been suggested that the occurrence of these declines is correlated with the introduction of non-native species, particularly zebra and quagga mussels (*Dreissena polymorpha* and *Dreissena bugensis*) (Landrum et al., 2000; Nalepa et al., 2006; Vanderploeg et al., 2002). *Diporeia* populations have yet to deviate from historical levels in Lake Superior (Auer and Kahn, 2004; Auer et al., 2013; Barbiero et al., 2011; Cook and Johnson, 1974; Kraft, 1979), the only Laurentian Great Lake that has not been subjected to widespread invasion by mussels. Understanding the causes of subtle changes in *Diporeia* physiology (e.g. respiration rate) could have a significant utility in understanding their population dynamics.

Reduced dissolved oxygen conditions are believed to have detrimental effects on amphipod fitness (Johansson, 1997). Chapelle and Peck (2004) found that sizes of various species of amphipods increase with increasing oxygen availability. Additionally the rate at which *Diporeia* assimilate contaminants present in the environment such as heavy metals was shown to be linked with oxygen uptake (Landrum and Stubblefield, 1991). Consequently, examination of *Diporeia* respiration will further our understanding of factors that drive population abundances of these organisms.

Materials and methods

Animal collection and maintenance

During October 2012, samples were collected aboard the Michigan Technological University R/V *Agassiz* from 70 m in Lake Superior located 5 km offshore on the western coast of the Keweenaw Peninsula, Michigan, USA. Sediment with live *Diporeia* was collected using a PONAR grab (area = 0.046 m^2) and placed into plastic bins with lake water from the collection sites, then transported back to the laboratory where they were stored in constant darkness at 4 °C. Fresh lake water was added to *Diporeia* cultures every 2 weeks.

Microelectrode calibration

Diporeia respiration was estimated using an OX50 Unisense microsensor (Unisense A/S, Aarhus, Denmark) to measure oxygen partial pressure (pA) during laboratory experiments. Data acquisition was performed automatically using SensorTrace PRO 3.0.1 (Microsoft Excel format, Unisense A/S). A Clark-type polarographic microelectrode sensor allowed oxygen to diffuse through a thin silicone membrane to a polarized cathode (Oxygen Sensor Manual, Unisense A/S). This cathode reduced oxygen and the reduction current was measured and reported by the Unisense Microsensor Multimeter in millivolts (mV). Because these microsensors respond linearly to changes in oxygen levels, it was assumed that two points would be sufficient for calibrating the sensor to report the correct oxygen concentration. Calibration was performed by placing the sensor into an anoxic solution of ≈2 g sodium ascorbate dissolved in 100 ml of 0.1 M NaOH, and when the signal had stabilized, the mV output was set as 0 mg O_2 L^{-1}. The sensor was then rinsed and placed into filtered lake water that was aerated through vigorous bubbling, allowed to stabilize, and the signal was set as our value for full saturation. Each experiment was performed using the same electrode.

Control trials using filtered lake water maintained at 4 °C consistently showed an exponential decline of observed DO within the first hour with concentrations asymptotically approaching a constant value thereafter (Fig. 1). Elevated initial values were likely related to oxygen contained within the electrolyte solution (Gundersen et al., 1998). To accommodate this, data collection was delayed for 1.25 h after sealing the experimental system (see below). Additionally, a slow, but consistent decline in oxygen concentrations (0.02 mg L^{-1} h^{-1}, n = 7) was observed in control trials likely due to oxygen consumption by the electrode (Marsh and Manahan, 1999). The results of trials with animals were corrected for this background consumption, which was small in comparison to consumption through respiration (0.1–1 mg L^{-1} h^{-1}).

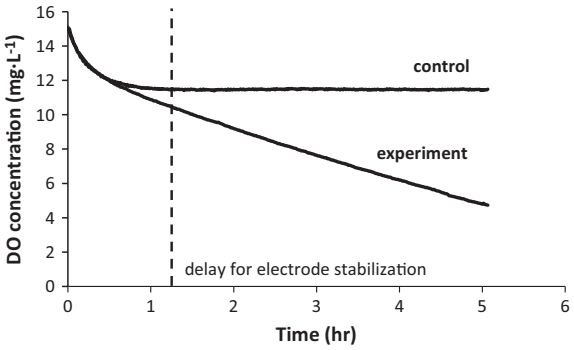

Fig. 1. Observed dissolved oxygen (DO) concentrations over time during a control trial (i.e. no test animals in microcosm) and an experimental trial using an OX50 Unisense microsensor in 20 ml of filtered lake water.

Oxygen uptake experiments

Respiration rates of Lake Superior *Diporeia* were obtained from an analysis of microcosm DO concentrations in a series of experiments during October–December 2012. *Diporeia* were gently sieved from laboratory cultures and individuals for each trial were selected based on body length. A total of 13 trials were conducted for three length classes: individuals of approximately 2 mm were termed immatures (n = 4), those of approximately 4 mm were termed juveniles (n = 5), and individuals of approximately 6 mm were termed adults (n = 4). The experimental animal density in each trial (8–22 individuals per vial) was chosen based on the DO detection limits of the electrode. The number of individuals used was typically 10 per vial for trials with juveniles and with adults. Additional animals were used for trials with immatures (19–22 individuals) in order to measure changes in DO concentrations more accurately. Amphipods were placed into vials filled with 20 ml of fully-oxygenated filtered lake water (0.7-μm GF/F filters). The microelectrode was then sealed to the vial with no air between the water and cap. It was assumed that the absence of sediment would not alter *Diporeia* respiration based on previous findings (Quigley et al., 2002). Dissolved oxygen content of the system was tracked for 5 h in the dark at 4 °C (Fig. 1). This duration was chosen in order to eliminate the possibility of decreased oxygen availability associated with bottle effects. Starting O_2 concentrations for each of the trials varied slightly, yet final O_2 was never below 20% of the initial concentration for any trial. Extending the time of each experiment would also have required a decrease in the frequency of readings due to the software data storage. Though previous work has shown that *Diporeia* have elevated respiration rates after being introduced to a new environment (Quigley et al., 2002), no initial increase in respiration rate was observed in this study when monitored for 24 h. In preliminary trials, O_2 depletion rates stayed constant for the initial 9 h and then began to fluctuate. We speculate that this fluctuation was due to bottle effect (i.e. insufficient oxygen supply); so experiment durations were limited to 5 h.

Immediately after each experiment *Diporeia* were photographed using a QImaging MicroPublisher 5.0 RTV camera (QImaging, Surrey, BC) and body lengths were determined using the image processing program Image-Pro Plus 7.0. The length of each animal was measured from the tip of the rostrum to the tip of the telson following the gut line. Animals were then grouped together, dried at 60 °C for 24 h, and weighed to the nearest 0.001 mg. Mass-specific respirations rates (i.e. mg O_2 g

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