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Factors affecting the vertical distribution of the zooplankton assemblage in Lake Michigan: The role of the invasive predator *Bythotrephes longimanus*

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ABSTRACT

We analyze six years of survey data in Lake Michigan, which spanned large ranges in the abundance of the invasive predatory cladoceran *Bythotrephes*, to quantify the effect of this predator on the daytime vertical distribution of the nine most common species and life stages of Lake Michigan zooplankton. We found that *Bythotrephes* abundance and hypolimnion depth explained almost 50% of the variation in the vertical distribution of many zooplankton. *Bythotrephes* abundance was associated with significant and large (approximately 5–11 m) depth increases in cladocerans *Daphnia* and *Bosmina*, adult and copepodite stages of cyclopoid copepods, and adult diaptomid copepods *Leptodiaptomus minutus*, and *Leptodiaptomus ashlandi*; but did not significantly affect the depth of copepod nauplii, diaptomid copepodites, and adult *Leptodiaptomus sicilis*. Whereas other environmental factors, such as light attenuation coefficient, epilimnion and hypolimnion temperature, and sampling date significantly influenced the depth of various species and life stages, the inclusion of such environmental factors into linear models did not significantly lower the predicted influence of *Bythotrephes*. These results suggest that *Bythotrephes* abundance has a significant and large influence on the vertical distribution of a large component of the zooplankton assemblage in Lake Michigan. We argue that this pattern is driven by a *Bythotrephes*-induced anti-predator response in zooplankton prey. Such effects could lead to widespread growth costs to the zooplankton assemblage due to the colder water temperatures experienced at greater depths, which could in turn affect the rapidly changing Lake Michigan food web.

Introduction

The vertical distribution of zooplankton in the world's lakes and oceans has critical economic and ecological importance. Zooplankton are resources for larval and young of year stages of many commercially and ecologically important fishes (Cushing, 1972; Horwood et al., 2000) and zooplankton vertical distribution may affect zooplankton growth rate (and hence abundance) and dictate their positional overlap and hence availability to fish. The vertical migrations of zooplankton also affect transport and cycling of carbon and nutrients (Steinberg et al., 2000), and so environmentally induced changes in their distribution may influence energy transfer and ecosystem functioning.

Predators are generally thought to play a central role in the vertical distribution of some zooplankton (Hays, 2003b; Lampert, 1989; Zaret and Suffern, 1976). Visually-orienting planktivores can exert strong predation pressure, which zooplankton avoid by migrating downward where it is darker (e.g., Aksnes and Giske, 1993). Based on this predation pressure, and because predation pressure may vary, many zooplankton have been shown to modify their daytime vertical position in response to changes in the abundance of fish which are visually-oriented (Bollens and Frost, 1991; Lass and Spaak, 2003; Van Gool and Ringelberg, 1998).

Bythotrephes longimanus is an invasive predatory cladoceran in the Great Lakes with the potential to strongly affect zooplankton vertical distribution. A visual predator, *Bythotrephes* can reach high densities in the epi- and metalimnion (Bourdeau et al., 2011; Pangle et al., 2007), representing a risk to zooplankton in the upper lake strata. A behavioral shift to occupy deeper, darker water below areas of high predation risk by *Bythotrephes* could therefore be adaptive for Lake Michigan zooplankton. Such adaptive avoidance responses to invertebrate predators have been documented in zooplankton groups (cladocerans and copepods) similar to those found in Lake Michigan (Neill, 1990; Nesbitt et al., 1996).

Previous research suggests that *Bythotrephes* may be affecting the vertical position of zooplankton in Lake Michigan. Laboratory studies indicate that the cladoceran *Daphnia mendotae*, and the copepods *Diacyclops thomasi* and *Leptodiaptomus minutus* respond to waterborne chemical cues from *Bythotrephes* by moving deeper in experimental water columns (Bourdeau et al., 2011; Pangle and Peacor, 2006,). Further, field surveys in the Great Lakes indicate positive associations between *Bythotrephes* abundance and the depths of *D. mendotae*,

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Daphnia retrocurva, *Bosmina longirostris* (Lehman and Cáceres, 1993; Pangle et al., 2007) and the adult stages of cyclopoid and diaptomid copepods (Bourdeau et al., 2011).

Whereas these previous lab and field patterns suggest that *Bythotrephes* is affecting zooplankton distribution in the field, potential confounding environmental influences on zooplankton depth in the field have not yet been considered. Further, previous studies have not quantified how deep zooplankton move in response to changes in *Bythotrephes* abundance — especially when considering the influence of other potentially correlated factors, such as light, temperature, and food resources. Quantifying the effect of *Bythotrephes* abundance within the context of other environmental influences in the field is important for two main reasons: (1) factors other than predator abundance can influence zooplankton vertical position, and (2) the effects of predators on zooplankton vertical distribution can be complex and indirect and cannot easily be extrapolated from laboratory studies. For example, zooplankton daytime distribution may be influenced by a number of factors other than just predator abundance; including water temperature (Cooke et al., 2008), water transparency (e.g., Dodson, 1990), and vertical gradients of food (e.g., Leibold, 1990) and light (e.g., Van Gool and Ringelberg, 1998). Moreover, variables such as predator abundance, light, and temperature, which are often studied in isolation in the laboratory, are correlated in the field and may co-vary seasonally. Further, whereas laboratory studies can be instructive by e.g., showing that zooplankton can sense predator kairomones and that they can respond by migrating (e.g. downwards), the magnitude of the response in the field cannot be determined.

The effect *Bythotrephes* has on the vertical position of zooplankton under prevailing environmental conditions in the field is important because it could influence the effect of *Bythotrephes* on zooplankton abundance, which has been suggested to be large in the Great Lakes and other ecosystems it has invaded (Bunnell et al., 2011; Strecker et al., 2011; Vanderploeg et al., 2012). Several mechanisms may be involved. First, costs associated with *Bythotrephes*-induced vertical shifts could reduce zooplankton growth rates. One particular cost to vertical avoidance behavior is a significant reduction in growth rate due to low temperatures (Dawidowicz and Loose, 1992; Loose and Dawidowicz, 1994). Such costs could be particularly large in the summer when large lakes are thermally stratified. For example, we have proposed *Bythotrephes* negatively affects Lake Michigan *D. mendotae* populations through the induction of greater downward vertical migration into cool suboptimal feeding habitats during the day (Pangle et al., 2007). In laboratory experiments, we found that *D. mendotae* incurred a 36% reduction in somatic growth rate in the presence of *Bythotrephes* kairomones by migrating to lower positions in experimental columns with a thermal gradient (Pangle and Peacor, 2006). We have predicted similar reductions in *D. mendotae's* population growth rate in the field due to an observed correlation between deeper depths of *Daphnia* and *Bythotrephes* density (Pangle et al., 2007). Second, induced changes in zooplankton vertical distribution can affect the availability of these prey to both *Bythotrephes* and larval and young-of-the-year fish. Lastly, among-species and life stage differences in the magnitude of vertical responses and associated costs could shift the balance of competitive interactions within the zooplankton assemblage.

Here we combine six years of field survey data to quantify the relative importance and magnitude of the effect of *Bythotrephes* abundance on the daytime vertical distribution of the nine most common species and life stages of the Lake Michigan crustacean zooplankton assemblage. Previous laboratory studies have shown that several species respond to waterborne chemical cues (kairomones) from *Bythotrephes* in laboratory experiments (Bourdeau et al., 2011; Pangle and Peacor, 2006) and correlations between zooplankton depth and *Bythotrephes* abundance have been documented over shorter-term studies (Bourdeau et al., 2011; Pangle et al., 2007). Our goal here is to more thoroughly explore the effect of *Bythotrephes* on zooplankton vertical distribution in Lake Michigan with a larger data set and with a more comprehensive statistical analyses in order to both consider the influence of other (potentially confounding) environmental factors, and to estimate the magnitude of the effect (rather than simply testing whether it exists). We discuss the implications of our findings in the context of non-consumptive effects in the rapidly changing Lake Michigan food web.

Methods

General overview

We conducted field surveys in which we sampled the daytime vertical distribution of the most abundant species and life stages of crustacean zooplankton (9 groups total), the abundance of their potential predator, the planktivorous cladoceran *B. longimanus*, and several relevant limnological variables (e.g., light, temperature, and food) over a range of dates and locations in Lake Michigan.

We used three complimentary statistical approaches to examine if *Bythotrephes* abundance and other factors affected zooplankton vertical position. First, our principal approach was to use formal model selection and averaging of multiple linear regression (MLR) models within the context of other environmental factors that could affect zooplankton vertical distribution. Second, because zooplankton depth may be explained by several factors that may be correlated among one another, and because such correlations among explanatory variables may compromise the ability to reliably estimate their effects in MLR, we employed partial least squares regression (PLSR), which is particularly well suited to analyzing data with a sample size that is small relative to a large number of related explanatory variables. Third, we analyzed the effect of *Bythotrephes* abundance on the vertical distribution of each zooplankton group using ordinary least squares (OLS) regression. This third test was performed to better understand how environmental factors influenced the statistical significance and the magnitude of the estimate of the *Bythotrephes* effect. That is, we compared the statistical significance and the magnitude of the *Bythotrephes* abundance effect on zooplankton depth from multimodel averaging of MLR models to that obtained from the OLS regression, in which *Bythotrephes* abundance was the sole predictor variable.

Lastly, we used results from the MLR analysis to estimate the magnitude of the effect of *Bythotrephes* abundance on the vertical position of zooplankton.

Field surveys

We sampled the daytime vertical distribution of zooplankton at several offshore locations and a range of dates that spanned different *Bythotrephes* abundances. There were 25 total sampling events (i.e., a single stratified vertical distribution sample), which spanned six different years (2004–06, 2009–11) and three established offshore sampling locations (identified as M45, M60, M110) in Lake Michigan off of Muskegon, MI (see Table 1 for sampling date and location details). Each sampling event consisted of collecting lake water with a 40-meter hose connected to a diaphragm pump. The water was filtered through a 64-μm-mesh zooplankton net on the deck of a research vessel. We used two stratified pump sampling procedures: (1) collecting one cubic meter of lake water from each of five different depths ranging from 4 m to 40 m corresponding with the centers of the epilimnion, metalimnion, hypolimnion, and the transitions between them, or (2) collecting one cubic meter of lake water from ten equally spaced depth intervals by gradually moving the pump hose from 40 m depth to the surface. All sampling events were carried out at midday between 1100 and 1400 to ensure that variation in time of day that we sampled would not affect our estimates of zooplankton depth. Each depth sample was preserved in either buffered sugar–formalin solution (2004–06) or 95% ethanol (2009–11).