Trait-Mediated Effects of Invasive Predatory Cladocerans

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Sponsor: Great Lakes Fishery Commission

Overview

Two invasive predatory cercopagid cladocerans, *Cercopagis pengoi* and *Bythotrephes longimanus*, are recognized as potential "disruptive" factors in Great Lakes food webs. Cercopagids may, for example, divert energy away from the early life history stages of fishes, and thus limit the recruitment potential of fishes (Fig. 3). Potential mechanisms that cause these effects include:

1. The direct reduction of zooplankton abundance ("lethal" or "density" effects)
2. The indirect modification of the zooplankton prey phenotype ("nonlethal" or "traits-mediated" effects)

Implications of density effects on fish recruitment are obvious, less obvious are nonlethal (trait-mediated) effects; cercopagid-induced changes in diel vertical distribution and activity of zooplankton could:

1. Reduce growth rate and thus density of zooplankton
2. Shift zooplankton to areas where they are less (or more) vulnerable to fish

It is becoming increasingly recognized that such nonlethal effects can contribute substantially to the net effects of predators in aquatic systems. In fact behavioral responses of zooplankton are well studied, but the effects on species fitness and interactions are not. To fully understand and model the impacts of invasive predatory species on Great Lakes food webs (including on fish), we must understand how they modify the behavior, habitat use, and growth rate of their prey. We therefore are examining the disruptive effects of cercopagids through trait-mediated effects on their zooplankton prey with laboratory experiments and field surveys. Our recent research is indicating that indeed, the effect of *Bythotrephes*-induced changes in zooplankton behavior is as important, if not more important, than the lethal effects through predation. This has implications to Great Lakes fish recruitment, and this study will further build tools and approaches to examine the influence of trait-mediated interactions between other species (including future invasives) in the Great Lakes. This work is supported by a grant from the Great Lakes Fisheries Commission.

2006 Accomplishments

2006 Lake Michigan Field Sampling

Field sampling was conducted to obtain information regarding zooplankton, fish, and phytoplankton density and vertical distribution during day and night periods, as well as vertical profiles of abiotic factors. Sampling occurred during 8 day-night cruises in June, July, August, and September at the M45 site.

Fish data was collected using two methods.

- **Method 1** entailed determining fish vertical distribution and abundance acoustically using a split-beam ecosounder. This instrument also provided the body lengths of each target. Acoustic measurements was taken both during midday and midnight.
- **Method 2** entails collecting fish with 300-micron Tucker trawl during midnight. We lowered the trawl to depths where fish are observed acoustically and then fished the trawl for 6, 10-minute intervals at a speed of 2 nauts.

Trawling helped match the size distribution of netted fish with those acquired using acoustics, thereby identifying fish species. In addition, we plan to evaluate gut content of netted fish to determine characteristics of fish planktivory.

Zooplankton data was also collected using two methods.

- **Method 1** entailed pumping zooplankton from 10, continuous 4-m tall sections of the water column, spanning 1 to 40 m below the surface. Starting at bottom section, water was pumped from a 40-m depth into a 64-micron plankton net for 2.5 minutes, and then the suction hose was lifted to a 39-m depth, and pumping was repeated, and then again for 38 and 37-m depths. In total, pumping for each 4-m section lasted for 10 minutes and comprise about 1000 L. At the end of each sampling interval, the net was rinsed off, captured zooplankton were preserved, and the next 4-m interval was started. We

conducted this sampling during both midday and midnight to determine changes in the vertical distribution of zooplankton species.

- **Method 2** entailed towing a 64-micron, 0.5 m diameter plankton net from 40-m depth to the surface. Two replicate tows were conducted during the midnight sampling period.

Physical data were collected during midday and midnight using a Seabird CTD profiler. This instrument obtained vertical profiles of temperature, light intensity, and chlorophyll. In addition, Secchi depth and ambient sunlight intensity were also measured during midday.

2006 Laboratory Experiments

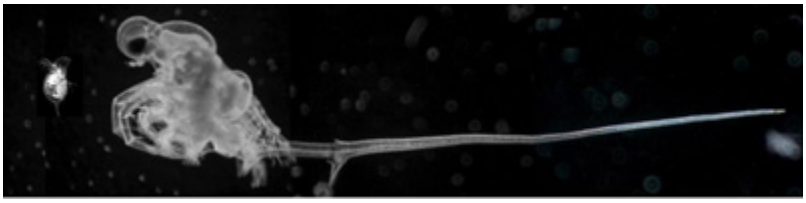
Predation Experiments

Last summer, we conducted a series of *Bythotrephes* predation experiments that focused on the consumption of *Daphnia* mendotae. This summer we conducted experiments that focused on the consumption of other prey species that might also be important to *Bythotrephes*. Our first experiment used a prey assemblage that *Bythotrephes* encounter offshore in near-surface regions of the water column during the daytime. Our second experiment used a prey assemblage from the near-shore region. In both experiments, *Bythotrephes* significantly reduced copepod nauplii and Bosmina longirostris, but consumption of these prey items was at a lesser rate than those rates observed for *Bythotrephes* consuming *Daphnia*. Our results help provide a better understanding of *Bythotrephes* predation in different mixtures of prey types.

In Lake Michigan, *Daphnia* mendotae migrate downward when faced with *Bythotrephes* predation risk. This migration may affect competition between D. mendotae and other herbivorous zooplankton, which remain in near-surface regions during the day. Therefore, predators of *Daphnia* may have an indirect positive affect other herbivorous zooplankton. We conducted an experiment to evaluate the importance of *Bythotrephes*-mediated indirect interactions between *Daphnia* and near-surface zooplankton. Over a 6-day period, we incubated a natural assemblage of near-surface zooplankton in 1-L bottles that were filled with lake water. To the bottles, we also added different densities of *Daphnia* mendotae. At the end of the experiment, we evaluated *Daphnia* 's effect on its competitors' survival, development, egg production, and somatic growth. Data from this experiment are in the process of being analyzed. Growth bioassay experiments We conducted two growth bioassay experiments, one in July and one in August, to evaluate food resource conditions at different depth and to determine if a food resource gradient would influence tradeoffs associated with prey vertical migration. Because

food resource conditions may change within a year and from year to year, it was necessary to conduct these experiments this year to compare results with similar experiments conducted last year. Results of this year's experiments showed that growth differences due to food resources effects are minor compared to water temperature effects, which was similar to the results of the previous experiments thus supporting the generality of our findings.

Competition Experiment



Bythotrephes chasing Daphnia

Column Experiments

In previous column experiments conducted by us and other researchers, the response of *Daphnia* to predator kairomones has been dependent on light conditions. In the past, we have modified light conditions by changing the intensity of overhead lighting; however, this methodology can limit experiment design. We conducted experiments this summer that tested a second approach to modify light conditions, one in which dye is used to intensify light attenuation. Data from this experiment are in the process of being analyzed.

Resting Egg Study

We began research to examine *Bythotrephes* nonlethal effects in an evolutionary context. We plan to do this by evaluating the response of *Daphnia* hatched from resting eggs that were deposited before and after *Bythotrephes* invasion. This summer we have collected sediment cores, isolated resting eggs for the sediment and hatched them out in the lab. We now plan to use column experiments to determine at what time in history do *Daphnia* respond to *Bythotrephes*' predation risk. Results of this research could shed light into changes in nonlethal effects on Great Lakes zooplankton over the last two decades and further our understanding of the nonlethal effects of invasive species in general.

Accomplishments

Laboratory Studies

Emphasis was placed on developing the "organ" experimental set up. This system incorporates a flow-through design using a peristaltic pump, in which resource and predator cue can be added at a constant rate, and which allows us to run experimental over several-day periods. This is important, because we can determine the long-term effects of induced changes on individual and population growth rate of zooplankton. Further, we improved our control of a temperature gradient across the experimental cylinders.

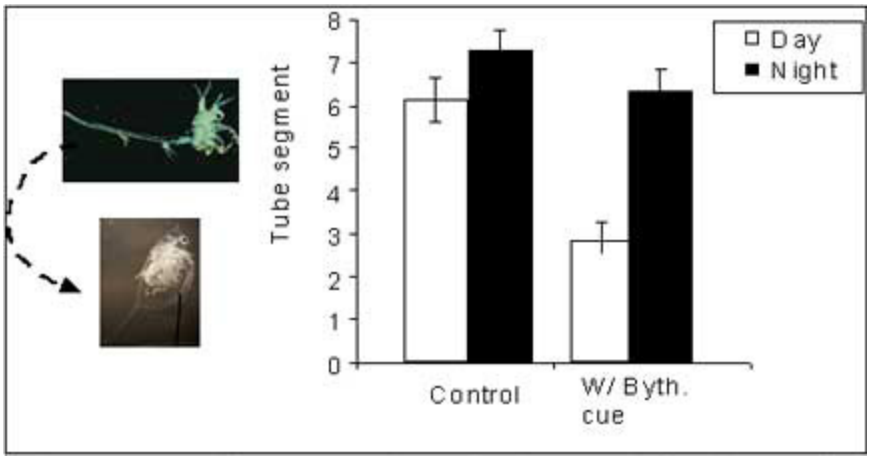


Figure 1*: Day and night mean vertical position (+/- SE bars) of Daphnia mendotae to karimones of Bythotrephes*

We conducted several laboratory experiments designed to examine anti-predator tactics in zooplankton induced by invasive predatory cladocerans (IPC). We focused specifically on non-lethal interactions between *Bythotrephes longimanus* and *Daphnia* mendotae because it is an important food resource to both *Bythotrephes* and native fishes, and it is a model organism to study predator-induced tactics. Results of the experiment indicate that D. mendotae in fact do respond to the presence of *Bythotrephes* by modifying their behavior. In particular, D. mendotae responded to *Bythotrephes* kairomone (extruded chemicals) by significantly lowering their vertical position into cooler thermal conditions (Figure 1). This induced behavior resulted in a 40% reduction of individual growth rate.

Another experiment strengthens the assertion that *Bythotrephes* cue levels are strong enough in the field to elicit responses from zooplankton. We found that water collected from a site with high *Bythotrephes* density elicited a very strong response, while water collected from a site with low *Bythotrephes* did not. (Fig. 2).

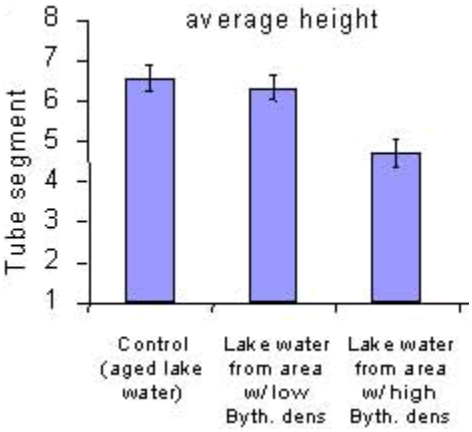


Figure 2*: Vertical height of Daphnia mendotae in cylinders with aged lake water, and lake water from areas with low and high density of Bythotrephes.*

These results suggest that *Bythotrephes* could have serious consequences to *Daphnia* population density and dynamics through induced (trait mediated) effects. In addition, *Bythotrephes* -induced responses like those observed in our experiment may reduce the availability of this resource to native Great Lakes fishes.

Results

1. Diacyclops thomasi responded to fish kairomone by lowering their vertical position in the day, not at night.
2. Diacyclops thomasi responded to *Bythotrephes* in a similar manner to that of fish, but did not respond to *Mysis* .
3. *Daphnia* mendotae responded to fish kairomone by lowering their vertical position in the day and night.
4. *Daphnia* mendotae respond differently to *Mysis* and *Bythotrephes*.

Field Survey Work

Another component of our research involves field work in off shore Muskegon starting from June to October 2004, in coordination with other research projects (i.e., Vanderploeg and Picklova invasive predator cladoceran project). A number of vessel excursions were made to accomplished several goals. First, we tested the use of a diaphragm-pump sampler for determining vertical distribution of zooplankton, including IPC. This sampling technique was compared to the use of plankton nets and proved to be an adequate means of collecting zooplankton. This tool is important because it allows us to follow the vertical movements of both invertebrate predators and prey. The diaphragm-pump sampler was also found to be less destructive on zooplankton specimens than typical net sampling. This will allows better estimates of zooplankton life-history characteristics as well as overall productivity. Second, we collected live organisms for use in the laboratory experiments above. Currently, there is no protocol for culturing *Bythotrephes* in a laboratory environment, so this was key to our successful completion of the anti-predator tactics studies. Third, we completed surveys that followed the vertical distribution of zooplankton at near- and offshore sites (i.e., m15, m45, and m110). The surveys provided information about how the zooplankton density and vertical distribution change spatially, seasonally, inter-annually, and with respect to IPC densities. In addition to these day trips, we collaborated with other GLERL researchers on the diel sampling cruise conducted over two, 4-d periods in August. We used the diaphragm-pump sampler to provide important information of the day and night vertical distribution of zooplankton.

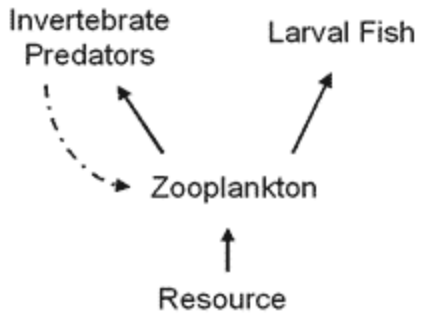


Figure 3*: Invertebrate predators may indirectly affect larval fish through density effects (predation, straight arrows) on zooplankton or inducing changes in zooplankton phenotype (trait changes, dashed arrow) such as changed vertical habitat migration or activity that affects growth rate and vulnerability*.

Awards/Recognitions

Invited to participate in a working group at the highly regarded National Center for Ecological Analysis and Synthesis (NCEAS, in Santa Barbara, CA). Participants are examining the role of species interactions on species abundances and dynamics, and ecosystem properties such as stability and carbon flow.

Winner of "Best Student Presentation" given to paper presented in 2005: Pangle, K. L., and Peacor, S. D and Vanderploeg, H.A. Anti-predator behavior elicited by a nonnative invertebrate predator: Lake Michigan *Daphnia* and *Bythotrephes*.48th Conference of the International Association for Great Lakes Research, Ann Arbor, MI, May 2005.

Products

Publications

Pangle, K.L., S.D. Peacor and O. Johannsson. 2006. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. *Ecology.* In Press.

Pangle, K.L. and S.D. Peacor. 2006. Nonlethal effect of the invasive predator *Bythotrephes longimanus* on *Daphnia* mendotae. *Freshwater Biology* 51: 1070-1078.

Peacor, S., K. Pangle, and H. A. Vanderploeg. 2005. Behavioral response of Lake Michigan *Daphnia* galeata mendotae to *Mysis* relicta. *Journal of Great Lakes Research* 31:144-154.

2006 Presentations

Peacor, S .D. Nonlethal effect of an invasive invertebrate predator, *Bythotrephes, on zooplankton population growth rate in the Great Lakes*. Bowling Green State University, Dept. of Biological Sciences. Bowling Green, OH. Dec. 2006.

Peacor, S. D. *Context dependence of trait-mediated indirect interactions and implications for scaling up to long-term predictions*. 90th Annual Meeting of the Ecological Society of America.

Organized oral session *“When does fear matter? A road map to the implications of trait-mediated effects to ecology”.* Memphis, TN. Aug. 2006.

Pangle, K. L., and Peacor, S. D., Johannsson, O. R., *Nonlethal effect of an invasive predator, Bythotrephes, on the population growth rate of zooplankton prey in Lakes Michigan and Erie*. 90th Annual Meeting of the Ecological Society of America. Memphis, TN. Aug. 2006.

Pangle, K. L., and Peacor, S. D and Vanderploeg, H.A. *Non-lethal effects of the invasive invertebrate predator, Bythotrephes, on Lake Michigan zooplankton*. 49th Conference of the International Association for Great Lakes Research, Windsor, ON, May 2006.