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Evaluating the importance of abiotic and biotic drivers on *Bythotrephes* biomass in Lakes Superior and Michigan

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ABSTRACT

The ability of planktivorous fishes to exert top-down control on *Bythotrephes* potentially has far-reaching impacts on aquatic food-webs, given previously described effects of *Bythotrephes* on zooplankton communities. We estimated consumption of *Bythotrephes* by planktivorous and benthivorous fishes, using bioenergetics and daily ration models at nearshore (18 m), intermediate (46 m), and offshore (110 m) depths along one western Lake Superior transect (April, and September–November) and two northern Lake Michigan transects (April, July, and September). In Lake Superior, consumption (primarily by cisco *Coregonus artedi*) exceeded *Bythotrephes* production at all offshore sites in September–November (up to 396% of production consumed) and at the intermediate site in November (842%) with no evidence of consumption nearshore. By comparing *Bythotrephes* biomass following months of excessive consumption, we conservatively concluded that top-down control was evident only at the offshore site during September–October. In Lake Michigan, consumption by fishes (primarily alewife *Alosa pseudoharengus*) exceeded production at nearshore sites (up to 178%), but not in deeper sites (<15%). Evidence for top-down control in the nearshore was not supported, however, as *Bythotrephes* never subsequently declined. Using generalized additive models, temperature, and not fish consumption nor zooplankton prey density, best explained variability in *Bythotrephes* biomass. The non-linear pattern revealed *Bythotrephes* to increase with temperature up to 16 °C, and then decline between 16 and 23 °C. We discuss how temperature likely has direct negative impacts on *Bythotrephes* when temperatures near 23 °C, but speculate that predation also contributes to declining biomass when temperatures exceed 16 °C.

Introduction

Aquatic invasive species have dramatically altered the dynamics of many food webs throughout the world (Strayer, 2010). Yet understanding how they influence interactions between trophic levels can be especially difficult given the complexity within systems (Vitousek et al., 1997). The Laurentian Great Lakes underwent a number of biological invasions that systematically restructured their food-webs (Mills et al., 1993; Ricciardi and MacIsaac, 2000). The spiny water flea *Bythotrephes longimanus* (hereafter *Bythotrephes*) is a predatory cladoceran that was introduced via ballast water (Sprules et al., 1990). It quickly established itself in the Great Lakes (Bur et al., 1986), as well as inland lakes (Yan et al., 1992) via anthropogenic and biotic routes. Following its invasion, numerous cladoceran and cyclopoid copepod species markedly declined in abundance or became extremely rare (Yan and Pawson, 1997). *Bythotrephes* influences the planktivorous fish community as both a competitor for zooplankton and as a prey item itself. Consumption models have revealed that *Bythotrephes* can consume more zooplankton than the entire planktivorous fish community (Hoffman et al., 2001; Bunnell et al., 2011), especially reducing densities of species that are easier to capture (see Vanderploeg et al., 1993). As prey, its long spine and large compound eye make it a conspicuous zooplankter, most often consumed by larger juvenile and adult fish species (Barnhisel and Harvey, 1995; Jarnagin et al., 2014).

Given the multiple negative impacts of *Bythotrephes* on zooplankton and planktivorous fishes, a pivotal research goal is to determine the circumstances under which fish predation can control or limit *Bythotrephes* production. The word “control” is often used in ecological literature, and its definition widely varies. Carpenter et al. (1985) suggested that consumers control prey when they alter species composition, biomass, or productivity, whereas others have used more strict definitions such as declines in prey production (Dettmers and Stein, 1992) or consumption reaching some large percentage of the prey's production or standing stock (Rudstam et al., 1994a; Eckmann et al., 2002). We defined control as occurring when 1) the biomass consumed

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of a given prey species exceeds its production and 2) the biomass of the prey species subsequently declines. Evidence for the first criterion was demonstrated by alewife *Alosa pseudoharengus* consuming *Bythotrephes* in the nearshore environment (10-m depth) of Lake Michigan (Pothoven et al., 2007). Possible explanations for control in shallow habitat include relatively high fish densities or lack of deepwater refuges from planktivory (Pothoven et al., 2001; 2003). Extending this logic to deepwater habitats, there could be less top-down control of *Bythotrephes* in deeper waters because it can migrate into the metalimnion to minimize predation (Young and Yan, 2008).

Aside from top-down control by fish, other factors likely influence *Bythotrephes* distribution and abundance. Biotic factors, such as the availability of its preferred prey items, should increase *Bythotrephes* production, and ultimately its density. Likewise, competition from other predatory zooplankton also could lead to decreases in *Bythotrephes* abundance (Vanderploeg et al., 2002). Abiotic drivers such as epilimnetic water temperature could also affect production because *Bythotrephes* can consume more prey and grow faster at higher temperatures (Yurista and Schulz, 1995; Yurista et al., 2010). However, at temperatures above 23 °C, respiratory enzymes become inactive preventing oxygen consumption (Yurista, 1999) and mortality occurs within 1–2 days at 28 to 32 °C (Kim and Yan, 2010). Exploring the potential influence of several of these factors (e.g., temperature, planktivore consumption, prey availability) can aid in determining which lakes will continue to be inundated with this invader as well as which lakes are candidates for range expansion.

Herein, we sought to determine the key drivers of *Bythotrephes* dynamics. Specifically, we evaluated which fish species consumed more *Bythotrephes* than were produced, whether our criteria for control was met, and which biotic and abiotic factors best explained variability in *Bythotrephes* biomass. We addressed these questions in three near to offshore transects (one in Lake Superior and two in Lake Michigan) using field sampling, laboratory analyses, and modeling.

Methods

Sampling design

Three sites were sampled along transects at nearshore (18 m), intermediate (46 m), and offshore (110 m) depths (Fig. 1). Lake Superior samples were taken offshore of Stockton Island (46.92°, −90.52°; 46.94°, −90.51°; and 46.92°, −90.48°) in the Apostle Islands National Lakeshore in 2011. Lake Michigan samples were taken in the northern basin offshore of Frankfort, MI (44.52°, −86.26°; 44.48°, −86.30°; and 44.48°, −86.33°) and Sturgeon Bay, WI (44.75°, −87.28°; 44.73°, −87.26°; and 44.69°, −87.15°) in 2010. Lake Superior fish and zooplankton were sampled in April, September, October, and November. Lake Michigan fish were sampled in April, July, and September, whereas zooplankton was sampled monthly from April to October.

Zooplankton sampling and processing

Zooplankton samples were collected identically in each lake to estimate density and biomass of *Bythotrephes*, as well as other zooplankton. At each depth, whole-water column samples were collected (1 m above lake bottom) during the day using a set of replicate tows with a 153-μm mesh, 0.5-m diameter net, retrieved at a speed of 0.5 m/s. We used an antacid bath to narcotize zooplankton for measurement and biomass determination prior to fixation in 5% sucrose formalin. Laboratory enumeration and measurements followed zooplankton processing protocols (U.S. Environmental Protection Agency, 2003) as described in Bunnell et al. (2012). The first 20 individuals in each taxon and life-stage were measured under a dissecting microscope. Measurements were applied to length–weight regressions (Table 1) to estimate biomass by dry weight.

Bythotrephes production estimates

We used regression equations to estimate *Bythotrephes* production from biomass and temperature. Each individual *Bythotrephes* was classified to instar (number of paired barbs on spine), and for each instar that occurred, up to twenty individuals were measured from the proximal end of its spine to the base of the kink of the spine or where spinules were located in sexually-produced individuals to obtain weight from length (Garton and Berg, 1990). A Seabird electronic bathythermograph (BT, CTD; SeaBird, Inc., Bellevue, WA, U.S.A.) was used at collection sites to estimate the vertical temperature profile. Because *Bythotrephes* typically occupy the epilimnion (Lehman and Cáceres, 1993), we calculated the mean epilimnetic temperature, or mean temperature of the top 20 m when not stratified. In cases where in situ temperature profiles were not available ($n = 9$), we predicted epilimnetic temperature using surface temperatures from Great Lakes Coastal Forecasting System (Schwab and Bedford, 1999) (epilimnetic $= 1.45 + 0.89 \cdot$ (surface); $n = 33$; $R^2 = 0.68$). We estimated production using: $P/B_{\text{daily}} = 10^{(\alpha + \beta \cdot T)}$ where P = production (g/m^2/day), B = biomass (g), and T = epilimnetic temperature (°C), $\alpha = -1.725$ and $\beta = 0.044$ (Shuter and Ing, 1997). Although these coefficients were developed for herbivorous cladocerans, the predicted production estimate was not different from egg-ratio production estimates (Foster and Sprules, 2009). All production estimates were calculated on an areal basis (g/m^2/day) to facilitate comparisons with consumption of *Bythotrephes* by fish.

Post-hoc analysis for day and night *Bythotrephes* collections sampled within 12 h of one another revealed that day samples yielded estimates lower than night samples (Keeler unpubl. data). Samples pooled from both Lake Huron in 2012 ($n = 9$) and Lake Superior in 2011 ($n = 7$) revealed estimated biomasses (mean ± SD) from night samples to be 2.06 ± 0.90 times greater than those estimated from day samples (paired t-test, $t_{16} = -4.97$; $p < 0.001$). Because we wanted to ensure we included the highest possible biomass estimate for *Bythotrephes* which, in turn, would force the most rigorous evaluation of top-down control, we multiplied our daytime estimates of *Bythotrephes* biomass by 2.06.

Fish sampling

Fish were collected at the same sites and depths using bottom trawl and midwater trawl gear. We used a "Yankee-style" bottom trawl with a 12-m headrope. Fish were sorted by species, and weighed in aggregate (nearest g). Up to 50 fish per species were measured for total length (TL; nearest mm), and up to 40 fish per species were immediately frozen for diet analysis. Densities (#/ha) were estimated using area swept by the trawl, which was a function of time-on-the-bottom, vessel speed, and width of net. Bottom trawl collections were used to estimate densities of benthic fish species including deepwater sculpin *Myoxocephalus thompsonii*, slimy sculpin *Cottus cognatus*, and round goby *Neogobius melanostomus*.

We also conducted nighttime stepped-oblique midwater trawls using Netmind sensors (Northstar Technical, Inc., St. John's, Newfoundland, Canada) to estimate fishing depth with an echosounder to acoustically estimate pelagic fish density in every 5 m of water column (excluding 1 m above bottom and below vessel hull). Acoustics data were collected with BioSonics (Seattle, WA, U.S.A.) DT-X split beam echosounder version 4.0 with 38 and 120 kHz transducers following guidelines for Lake Michigan (Warner et al., 2008; Parker-Stetter et al., 2009; and Warner et al., 2009) and Lake Superior (Rudstam et al., 2009). Acoustic densities were apportioned to species using a combination of midwater trawl species and size composition data and in situ target strength (TS) information derived from analysis in Echoview © 4.6 following the Lake Michigan (Warner et al., 2008; 2009) and Lake Superior (Yule et al., 2007; Myers et al., 2009) approaches. Mean mass of fish <40 m below the surface was obtained

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