

Response of the invertebrate predator *Bythotrephes* to a climate-linked increase in the duration of a refuge from fish predation

Marina Manca^{a,*} and William R. DeMott^{b,1}

^aNational Research Council, Institute of Ecosystem Study, Verbania, Italy

^bDepartment of Biology, Indiana–Purdue University, Fort Wayne, Indiana

Abstract

Climate warming can affect ecological food chains directly by increasing the rates of physiological processes and indirectly by changing habitat use and altering predator–prey interactions. In Lake Maggiore, Italy, a greater than 10-fold increase in the mean annual population density of *Bythotrephes longimanus* (Cladocera Onychopoda) was recorded between 1987 and 1993, when high values of the North Atlantic Oscillation winter index indicate warmer winter and spring temperatures across Europe. *Bythotrephes* remained abundant and further increased during the following 10 yr, as water temperature continued to increase. We analyzed changes in water temperature, timing of thermal stratification, and hypolimnion depth to test whether changes in the duration and thickness of a warm, low-light, deep-water refuge from fish predation can account for increases in the invertebrate predator's abundance and seasonal duration. Using a 21-yr data set, we found that the sharpest increase in *Bythotrephes* abundance coincided with a shift from late August to May in its first appearance in the water column. The appearance of the planktonic population was, in turn, linked with earlier thermal stratification and earlier establishment of the predation refuge. The duration and thickness of the refuge increased as a result of earlier warming and deeper mixing, factors affected by climate rather than decreased water clarity. *Daphnia hyalina galeata*, the dominant grazer and a prey of *Bythotrephes*, decreased sharply as *Bythotrephes* increased. This study provides an example of how climate warming can indirectly affect the population density and phenology of a key invertebrate predator and, hence, the functioning of the pelagic food web.

The global mean surface air temperature rose 0.5°C in the 20th century (Houghton et al. 1995; IPCC 2008). Using correlation analysis, ecologists have sought linkages between climate warming and phenomena such as earlier breeding of amphibians and birds, upward movement of alpine floras, northward shift in the range of butterflies, and changes in plant community composition (Walther et al. 2002). In both terrestrial and aquatic environments in Europe, advances in phenology (seasonal timing) have been correlated with the North Atlantic Oscillation (NAO) winter index (Walther et al. 2002), which is associated with warmer winter and spring temperatures. In lakes across Europe, higher NAO values are correlated with earlier thermal stratification, earlier peaks in zooplankton abundance, and an earlier clear water phase caused by *Daphnia* grazing (Straile 2000, 2002). In this example, the earlier peak in *Daphnia* abundance is due to the direct effect of increased spring water temperatures on *Daphnia*'s growth and development. A rise in ambient temperature is also predicted to result in a eutrophication-like pattern, with increased density and biomass of plankton, as a result of enhanced rates of physiological and direct ecological processes (Schindler 2001; Visconti et al. 2008).

Climate warming can also have indirect effects on populations and food webs by altering habitat structure in ways that change predator–prey interactions (Schmitz et

al. 2003). In pelagic systems, thermal stratification provides habitat structure that can influence both spatial overlap between predators and prey and the effectiveness of visual predators in locating prey. For example, the development of a warm epilimnion separated from a deeper, dark and cooler hypolimnion can favor the establishment of a low-light, oxygenated water layer in which large-bodied zooplankton prey can find a refuge from predation by fish (Wright and Shapiro 1990; Tessier and Woodruff 2002).

As a result of its large body size and conspicuousness, *Bythotrephes*, the spiny water flea, is a strongly preferred prey of planktivorous fish (de Bernardi et al. 1987; Coulas et al. 1998). Like other cladocerans, *Bythotrephes* produces resting eggs, which aid in dispersal and allow the population to survive unfavorable conditions. *Bythotrephes* typically overwinters as resting eggs and recruits to the plankton during spring or summer (Yurista 1997). The invasion of *Bythotrephes* into the North American Great Lakes and surrounding region during 1980s stimulated renewed interest in factors determining the voracious predator's abundance, colonization success, and effects on prey communities (Lehman and Cáceres 1993; Yan et al. 2002). In a key 5-yr study, Yan et al. (2001) found that between-year variation in *Bythotrephes* abundance in Harp Lake, Ontario, Canada, was correlated with the thickness of a low-light, warm-water refuge from planktivorous fish. In further support of the predation refuge hypothesis, a study of 53 lakes in northern Minnesota and adjacent Ontario found that *Bythotrephes* invasion success was linked to the presence of a deep-water, low-light refuge (Branstrator et al. 2006). Manca and Ruggiu (1998) showed that a greater than 10-fold increase in *Bythotrephes* in Lake

* Corresponding author: m.manca@ise.cnr.it

¹ Present address: Department of Aquatic Food Webs, Centre for Limnology, Netherlands Institute for Ecology, Nieuwersluis, The Netherlands

Maggiore between 1987 and 1993 resulted in a sharp decline in *Daphnia hyalina galeata*, a key prey and the dominant grazer in the lake. Manca et al. (2007a) further documented that the increase in *Bythotrephes* abundance was associated with a shift from August–September to April–May in its first appearance in the water column.

Similar to other lakes worldwide, Lake Maggiore has been influenced by climate warming (Ambrosetti and Barbanti 1999). We hypothesized that changes in water temperature and the thermal stratification regime have driven the changes in *Bythotrephes* phenology and abundance. Warming is expected to influence the phenology of *Bythotrephes* population growth directly by increasing physiological rates and indirectly by influencing vulnerability to fish predation. Here we use a 21-yr data set to examine links between climate change and *Bythotrephes* success. We sought to test whether changes in water temperature and thermal stratification regime and their effects on the availability of a predation refuge can account for the dramatic changes in the phenology and abundance of *Bythotrephes*.

Methods

Study site—Lake Maggiore is a large (212.5-km²), deep (maximum depth 371 m, mean depth 171 m) subalpine lake (194 m above sea level) with a long (54-km), narrow (mean breadth, 2.94-km) basin in a mountain valley on the border between Italy and Switzerland. Compared to lakes in the Great Lakes region of the United States and Canada, Lake Maggiore experiences warmer winters and cooler summers. The lake does not freeze and never mixed completely (i.e., down to the bottom) during the 21 yr of this study. Incomplete mixing results in a ‘climate memory’ (temperature anomalies marking maximal mixing depths) in the deep hypolimnetic waters (Ambrosetti and Barbanti 1999). In comparison to lakes experiencing continental climates, reduced seasonality makes the timing of the onset of thermal stratification more sensitive to climate warming. Partial protection from wind also means a greater role for air temperature in influencing thermal stratification. Phosphorus loading in Lake Maggiore peaked in 1979 and then declined in response to a phosphorus abatement program (de Bernardi et al. 1990). Total phosphorus in spring declined from about 22 to 10 $\mu\text{g L}^{-1}$ during our 21-yr study (Visconti et al. 2008).

Sampling and data analysis—The same sampling and data collection protocols were followed over the course of our 21-yr study. Zooplankton samples were collected with a Clarke–Bumpus plankton sampler (126- μm nylon net) from a boat moving at a low, constant speed (0.6 m s⁻¹). Samples were collected at least monthly all year and fortnightly or weekly in spring and summer at a central station corresponding to the maximum depth of the lake (see Manca et al. [2000] for a map of the lake, including the sampling station). The plankton sampler was pulled in a sinusoidal trajectory between the surface and a depth of 50 m to integrate horizontal and depth variation and to provide a sufficient sample for detecting zooplankton

species with low abundance (filtration of at least 1000 liters of lake water). The samples were preserved in pure ethanol and counted entirely for *Bythotrephes* density. Samples collected in 1992–1993 with a 20-liter Schindler–Patalas trap at 2-m intervals within the upper 50 m verified that in all seasons *Bythotrephes* is mainly distributed above the hypolimnion during the day. This agrees with the finding that 98% of the *Bythotrephes* in Harp Lake, Ontario, were located above the hypolimnion during the day (Hall and Yan 1997).

On each sampling date we measured the Secchi Disk water transparency (m), from which the euphotic zone depth was calculated ($1.6 \times$ Secchi depth; Ruggiu et al. 1998). We also quantified the thermal stratification on each sampling date from the water temperature vertical profiles measured at 1-m intervals using a thermistor thermometer. We identified the top of the hypolimnion as the depth at which the decline of temperature with depth fell to $<1^\circ\text{C m}^{-1}$ (Yan and Pawson 1998) or became lower than the maximum vertical gradient measured at each sampling date. We applied the method proposed by Yan and Pawson (1998) to estimate the availability of a refuge from visual predation for *Bythotrephes*. In this method, the thickness of the refuge layer is the difference between the depth of the top hypolimnion and the bottom of the euphotic layer. Positive values indicate a dark layer in which *Bythotrephes* may find a refuge from visual predation during the daytime. In contrast, negative values, resulting from light penetration in the hypolimnion, indicate high vulnerability to visual fish predation. Our estimates of the duration of thermal stratification and the predation refuge do not include periods of deep mixing during late fall, winter, and early spring, when the lake lacked a thermocline. We estimated the onset and duration (d) of the refuge together with the appearance and duration of *Bythotrephes* planktonic population, recording the date of first appearance in plankton, the time period (days) in which it was detected in the zooplankton samples (abundance $> 1 \text{ ind m}^{-3}$), as well as the population density. Mean annual population density (ind m^{-3}) was calculated for the upper 50 m using samples collected during all 12 months of the year. We tested the statistical significance of correlations (Pearson’s r) between *Bythotrephes* mean annual density and phenology and climate- and trophic-related parameters (water temperature, thermal stratification, euphotic zone thickness, and the occurrence and thickness of the predation refuge).

Mean annual values of the NAO station-based winter index were obtained from the Climate Analysis Section, National Center for Atmospheric Research (Boulder, Colorado; <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>). Data on the annual commercial catch of nonpiscivorous fish for 1983–1995 were taken from Grimaldi (1997).

Results

Mean water temperature in the upper 20 m increased from about 11°C to 14°C during the 21-yr study (Fig. 1A). The increased temperature in the upper 20 m was due to both warming of the epilimnion and deeper mixing, leading to a thicker epilimnion and a deepening of the upper

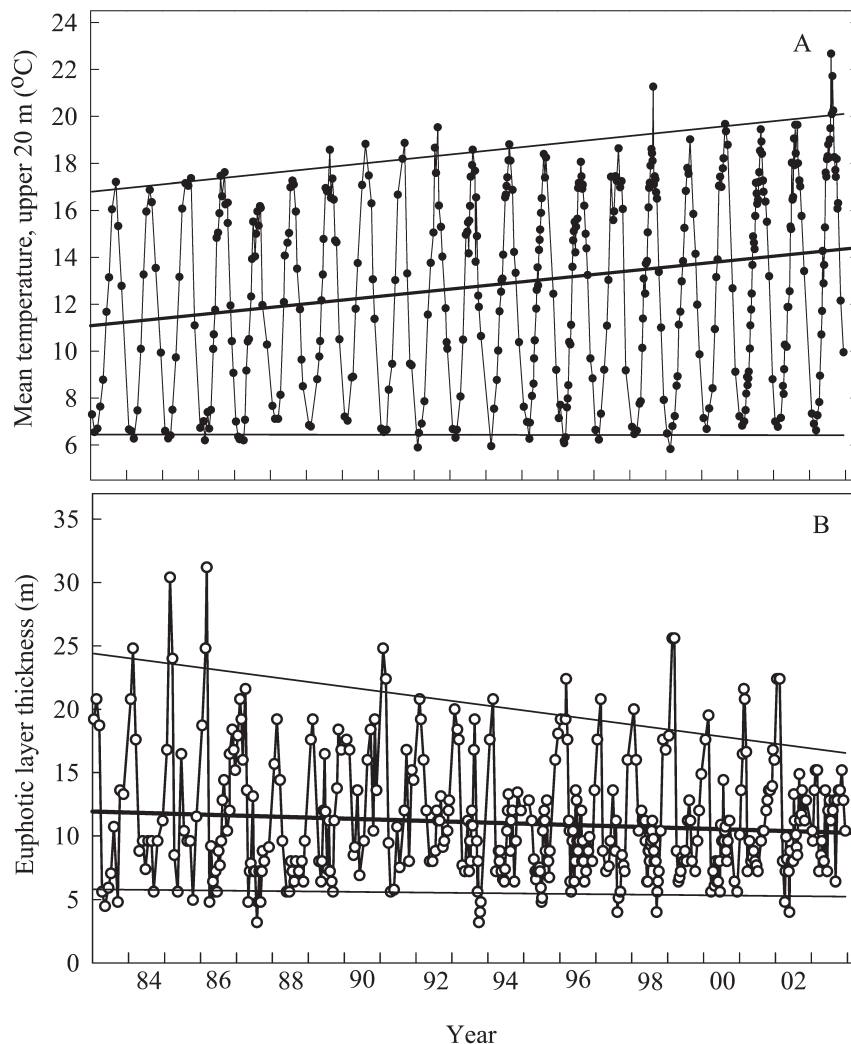


Fig. 1. Seasonal and between-year changes in (A) mean temperature of the upper 20 m and (B) thickness of the euphotic layer. The upper and lower trend lines in each panel are linear regressions of the annual minimal and maximal values, whereas the center lines are regressions using all dates.

boundary of the hypolimnion. The winter minimum temperature was highest during 1988–1990 and showed no trend over time ($r = 0.02$). The first 6 yr included the six coolest maximal temperatures, while the last 6 yr included the five warmest maximal temperatures. Thus, there was a linear trend of warming maximal temperatures of the upper 20 m over the study period ($r = 0.75$, $n = 21$, $p < 0.001$). Temperatures for 2003 were exceptionally high; it was the warmest year in the region for the last two centuries (Visconti et al. 2008). The coldest winter minimum temperature occurred during 1999, which was the year during the study when the water column mixed most deeply.

The thickness of the euphotic layer showed a decreasing trend during the study period (Fig. 1B). This was mainly due to a decrease in water clarity during the period of greatest clarity and deep water mixing in winter (maximal values vs. year; $r = -0.56$, $p < 0.001$).

Between 1986 and 1993 *Bythotrephes* exhibited a greater than 10-fold increase in mean annual abundance.

This increase in abundance was sharpest between 1987 and 1990, during a period when exceptionally high NAO winter index values indicate warm winter and spring conditions (Fig. 2A). The three highest values in the 140+-yr history of the NAO winter index occurred during 1989 (5.08), 1990 (3.96), and 1995 (3.96). The commercial catch of nonpiscivorous fish (predominately planktivorous coregonids) increased during the period of sharpest increase in *Bythotrephes* mean annual abundance and then declined after *Bythotrephes* became abundant (Fig. 2A).

The increase in *Bythotrephes* mean annual density was accompanied by marked changes in population phenology, which were associated with earlier appearance and greater duration of the predation refuge. From 1983 to 1987 the predatory cladoceran was first detected in the open water between mid-August and late September, whereas by the early 1990s it first appeared in plankton samples as early as mid-April (Fig. 2B). During 1983–1985 the predation

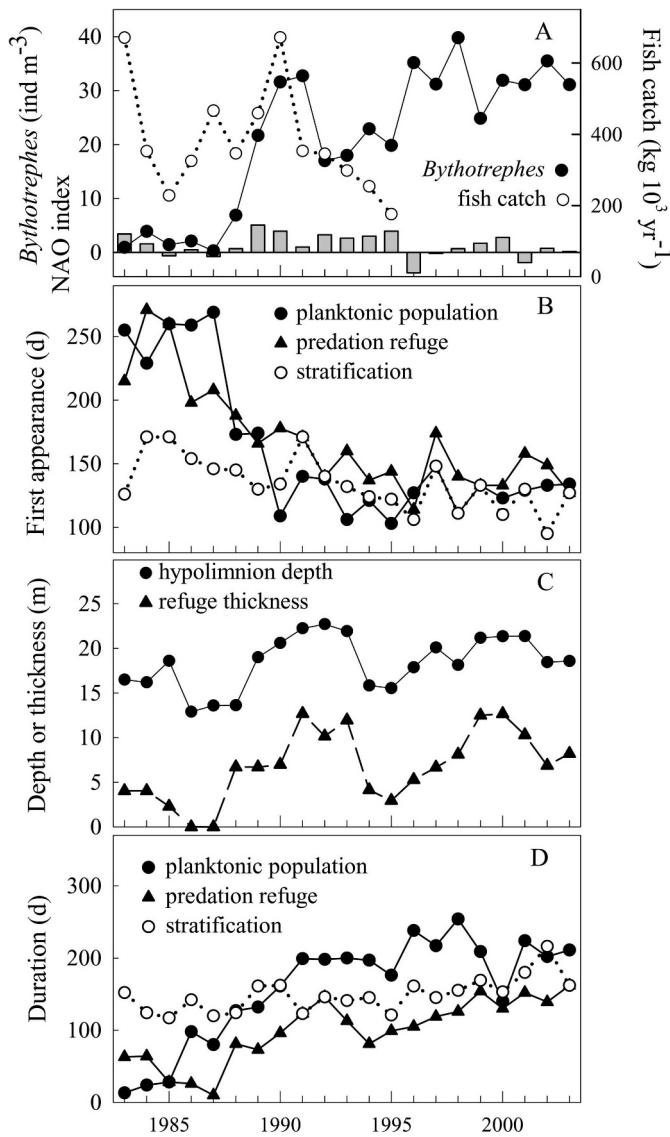


Fig. 2. Changes between years in (A) mean annual *Bythotrephes* abundance, commercial catch of nonpiscivorous fish, and the NAO winter index (bars); (B) the first appearance of the planktonic population, the predation refuge, and thermal stratification; (C) the depth of the top of the hypolimnion and predation refuge thickness; and (D) the duration of planktonic population, the predation refuge, and thermal stratification.

refuge first became available in August or September, whereas in 1992, the predation refuge first appeared in mid-May (Fig. 2B). Interestingly, in 1986 and 1987, at the start of the rapid advance in phenology, the first appearance of the planktonic population lagged behind the first appearance of the predation refuge by about 2 months, whereas after 1989, the planktonic population appeared before or coincident with the predation refuge (Fig. 2B).

The earlier appearance of the predation refuge was associated with an earlier onset of thermal stratification and a deeper hypolimnion. In 1984–1985 the lake stratified in late June, whereas in 1989 and 1990, the lake stratified during the second week of May (Fig. 2B). The earliest

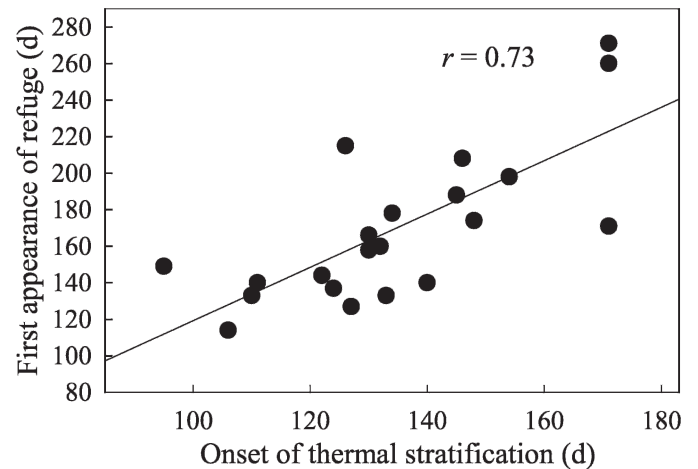


Fig. 3. Relationship between the onset of thermal stratification and the first appearance of the predation refuge. Annual values are fit to a linear regression.

stratification occurred during the first week of April 2002 (Fig. 2B). During 1986–1988 the depth of the top of the hypolimnion ranged from 12.9 to 13.6 m, but by 1990 it surpassed 20 m (Fig. 2C). An increase in the mean epilimnetic temperature of only about 1°C during this period of rapid population change is trivial in comparison to the effects of climate on the timing of stratification and the depth of the hypolimnion. For example, 1986 and 1987 gave the coolest maximal temperatures (Fig. 1A) because a shallow hypolimnion led to the inclusion of >6 m of cold hypolimnetic waters in the upper 20 m.

An increase in refuge thickness can result from lower light penetration (decrease in the euphotic layer depth) and/or a deeper upper boundary of the hypolimnion. An analysis of partial correlation coefficients based on the dates for which the refuge was present (i.e., positive values of the difference between top of the hypolimnion and the euphotic layer depths) indicated that only hypolimnion depth was statistically significant in determining refuge thickness ($\beta = 0.83 (\pm 0.040)$; $t(184) = 20.648$; $p < 0.0001$).

The duration of the planktonic population increased gradually during the study period, with minimal values of 13–28 d in 1983–1985 and maximal values of 217–254 d from 1996 to 1998 (Fig. 2D). The duration of the predation refuge showed a similar pattern, with minima of 10–63 d from 1983 to 1987 and maxima of 153–170 d from 1997 to 2003 (Fig. 2D). Over the study period the onset of stratification shifted about 6 weeks earlier, and the total duration increased by about 7 weeks. The *Bythotrephes* mean annual abundance peaked in 1996–1998 (Fig. 2A) during a period of maximal duration of the planktonic population and the predation refuge (Fig. 2D).

Scatter plots and correlations help confirm the links between climate change, the onset and duration of the predation refuge, and population abundance and duration. First, the appearance of the predation refuge is correlated with the onset of thermal stratification, a factor related to climate (Fig. 3; $r = 0.73$, $n = 21$, $p < 0.001$). Second, both the seasonal duration of the planktonic population

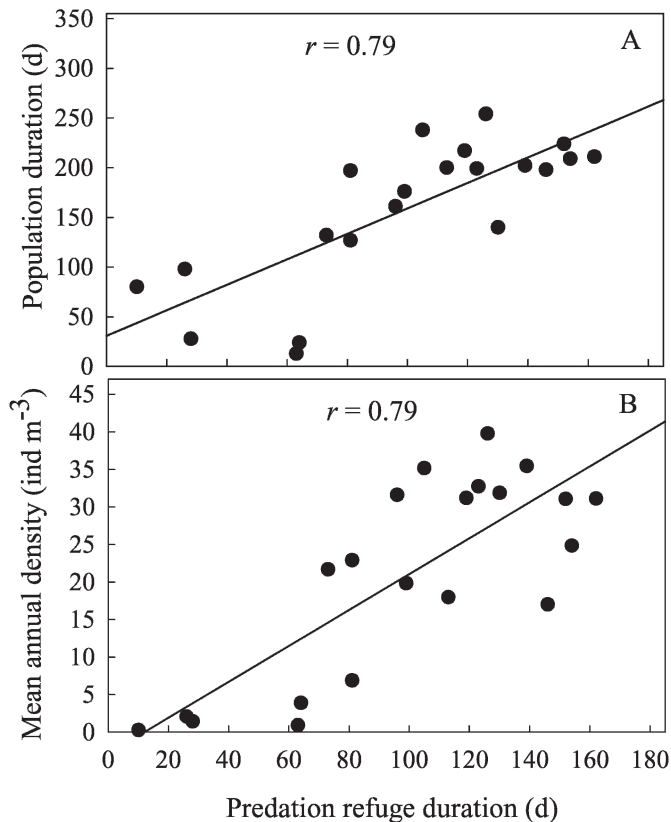


Fig. 4. Relationship between the duration of the predation refuge and (A) the duration of the planktonic population and (B) mean annual *Bythotrephes* abundance. Annual values are fit to linear regressions.

(Fig. 4A; $r = 0.79$, $p < 0.001$) and its mean annual abundance (Fig. 4B; $r = 0.79$, $p < 0.001$) are strongly correlated with the duration of the predation refuge.

Discussion

Our main finding is that the more than order-of-magnitude increase in the mean annual abundance of *Bythotrephes* is tightly linked to earlier establishment and longer duration of a warm-water, low-light refuge from fish predation. Changes in the refuge, in turn, are directly linked to climate warming that lead to earlier stratification and a deeper hypolimnion. The role of this recent climate warming on stratification timing and duration has been documented in lakes throughout Europe (Blenckner et al. 2007) and in North American (Winder and Schindler 2004). In comparison to lakes in these studies, our results show that the effects of climate warming on stratification timing and duration have been especially strong in Lake Maggiore. An increase in refuge thickness can result from lower light penetration (decrease in the euphotic layer depth) and/or a deeper upper boundary of the hypolimnion. Our results show that variation in the thickness of the predation refuge was determined primarily by changes in the depth of the hypolimnion.

Lakes across the United Kingdom and continental Europe experienced similar winter and spring warming

during the strong NAO index years in the 1980s and 1990s (Straile 2002; Blenckner et al. 2007). The increase in summer temperatures in the subalpine European lakes during the same period may be better correlated with subtropical Atlantic indices, as has been shown for Lake Geneva (Molinero et al. 2007). Among the large subalpine lakes, only Lake Maggiore appears to have experienced a marked increase in the abundance and seasonal duration of *Bythotrephes*. Like Lake Maggiore, Lake Constance showed earlier warming and earlier stratification during spring during the strong NAO years in the late 1980s–1990s (Straile 2000). However, *Bythotrephes* in Lake Constance generally recruited to the plankton in May and June in studies spanning 1920 to 1995 (Straile and Geller 1998). Interestingly, climate warming coincided with a decline in the abundance of *Bythotrephes* in Lake Geneva, which was tentatively attributed to a decline in *Daphnia* abundance (Molinero et al. 2007). These authors did not consider the possible effects of a change in the availability of a predation refuge. The dramatic and apparently unique changes in *Bythotrephes* phenology and abundance in Lake Maggiore during the study period may reflect the particular mixing characteristics of the lake that resulted in a dramatic increase in the availability of the predation refuge.

Three lines of evidence indicate that the direct effects of warming on *Bythotrephes* physiology were minor in influencing the cladoceran's phenology, compared to the indirect effects mediated by the seasonal changes in the predation refuge. Using long-term data from 28 lakes in central Europe, Straile (2002) found that climate warming advanced the timing of *Daphnia* population growth, on the average, by about 2 weeks. Since *Daphnia* and *Bythotrephes* have similar life histories and development rates, this indicates that the direct effects of warmer temperatures on population growth can account for only a small part of the more than 3-month advance in *Bythotrephes* appearance observed in Lake Maggiore. Second, since *Bythotrephes* has long recruited to the plankton in May and June in the more-northern Lake Constance (Straile and Geller 1998), the first appearance of the cladoceran in Lake Maggiore in August or September in the early part of our study cannot be caused by cooler temperature alone. Finally, the direct effects of temperature warming are expected to be gradual and proportionate to temperature change. However, as expected for an indirect effect of warming, *Bythotrephes* showed an abrupt increase in abundance and seasonal duration in Lake Maggiore, with most of the increase occurring from 1987 to 1990.

Changes in the predation refuge are expected to influence primarily the species that are more vulnerable to visual predation. As shown by de Bernardi et al. (1987), *Bythotrephes* is by far the most preferred prey of the coregonids, the most important zooplanktivorous fish of Lake Maggiore. The finding that *Bythotrephes* was strongly affected by changes in refuge availability is therefore consistent with this interpretation of our results. Moreover, the sharpest increase in *Bythotrephes* occurred when the pelagic fish stock, indicated by the commercial catch, was also increasing. Thus, a decrease in fish abundance can be ruled out as a potential cause for the invertebrate

predator's increase in abundance. Our results indicate that an increase in the availability of a predation refuge can be more important for *Bythotrephes* success than changes in fish stock. Comparisons between lakes of varying depths indicate a similar importance of a deep-water refuge from fish predation for large *Daphnia* (Tessier and Woodruff 2002). The fish catch declined after *Bythotrephes* became abundant. This decline may have been due to overfishing, declining lake productivity, or, perhaps, to the sharp decline in *Daphnia* coupled with low availability of *Bythotrephes*.

Our results complement and support studies showing that the ability of *Bythotrephes* to invade North American lakes is closely tied to the presence of a deep-water refuge from planktivorous fish (Branstrator et al. 2006). Studies of Harp Lake, Ontario, have also documented up to 10-fold between-year changes in *Bythotrephes* abundance that were correlated to changes in the thickness and seasonal occurrence of a deep-water refuge from a coregonid fish. However, as might be expected for a small lake, there were no between-year trends in *Bythotrephes* abundance, as the availability of the refuge apparently responded to local changes in weather and lake productivity rather than to longer-term regional changes in climate.

Sporadic historical studies document the occurrence of *Bythotrephes* in Lake Maggiore in low abundance since at least 1949 (Manca et al. 2007b). Despite wide variation in fish abundance during those early years (de Bernardi et al. 1987), *Bythotrephes* did not become abundant until the period of climate warming analyzed in this study.

The effect of *Bythotrephes*' sharp increase in abundance on zooplankton prey in Lake Maggiore is comparable to that documented in North American lakes in which invading *Bythotrephes* established high abundance (Yan et al. 2001, 2002). The most obvious effect of the *Bythotrephes* increase in Lake Maggiore was a concomitant and drastic decline in the dominant zooplankton grazer *Daphnia hyalina galeata* (Manca and Ruggiu 1998; Manca et al. 2000). *Daphnia* population density dropped down to very low values (mean annual value dropped from 2000 ind m⁻³ in the early 1980s to <100 ind m⁻³ in 1996). Its replacement by large, spherical *Conochilus* colonies was not sufficient to offset the decline in *Daphnia* grazing (Manca et al. 2000). Spring and summer phytoplankton density increased, and despite declines in total phosphorus, water transparency did not increase. *Daphnia* should have also benefited from a deep-water refuge from fish predation. The fact that *Daphnia* declined sharply is best explained by the increase in *Bythotrephes* and spatial overlap between the two species.

Our study points to the importance of long-term monitoring and empirical approaches (Pace 2001) in understanding the direct and indirect effects of climate warming on natural communities. Much of the evidence for impacts of climate warming on natural systems has come from documenting earlier breeding and range expansion (Walther et al. 2002). These direct effects are usually proportionate to the temperature change and might, therefore, be readily predicted if we can predict the rate of temperature change. However, as pointed out by Schmitz et

al. (2003), climate changes that alter predator-prey interactions can cause disproportionate effects that cascade through the food chain. Their examples include loss of snow cover, which is expected to reduce moose vulnerability to wolf predation while increasing snowshoe hare vulnerability to lynx predation. In both of these examples, changes in herbivore abundance are expected to cascade to the primary producer level. Our study provides an example in which decreased vulnerability of an invertebrate predator to fish predation apparently produced abrupt changes in the food chain that cascaded to the primary producers. Such indirect effects are difficult to predict but are likely to be very important for understanding the effects of climate warming on ecological systems.

References

- AMBROSETTI, W., AND L. BARBANTI. 1999. Deep water warming in lakes: An indicator of climatic change. *J. Limnol.* **58**: 1-9.
- BLENCKNER, T., AND OTHERS. 2007. Large-scale climatic signatures in lakes across Europe: A meta-analysis. *Glob. Change Biol.* **13**: 1314-1326.
- BRANSTRATOR, D. K., M. E. BROWN, L. J. SHANNON, M. THABES, AND K. HEIMGARTNER. 2006. Range expansion of *Bythotrephes longimanus* in North America: Evaluating habitat characteristics in the spread of an exotic zooplankton. *Biol. Invasions* **8**: 1367-1379.
- COULAS, R. A., H. J. MACISAAC, AND W. DUNLOP. 1998. Selective predation on an introduced zooplankton (*Bythotrephes cederstroemi*) by lake herring (*Coregonus artedii*) in Harp Lake, Ontario. *Freshw. Biol.* **40**: 343-355.
- DE BERNARDI, R., G. GIUSSANI, AND M. MANCA. 1987. Cladocera: Predators and prey. *Hydrobiologia* **145**: 225-243.
- , G. GIUSSANI, M. MANCA, AND D. RUGGIU. 1990. Trophic status and the pelagic system in Lago Maggiore. *Hydrobiologia* **191**: 1-8.
- GRIMALDI, E. 1997. Progressive decline in fish productivity from Lago Maggiore as recorded by fish catch data (1991-1995), p. 61-73 [in Italian]. In A. Calderoni [ed.]. Report of the Swiss Italian Commission for Professional Fish Catch in Lake Maggiore Waters. Swiss-Italian Commission for the protection of Lake Maggiore waters.
- HALL, R. I., AND N. D. YAN. 1997. Comparing annual population growth estimates of the exotic invader *Bythotrephes* using sediment and plankton records. *Limnol. Oceanogr.* **42**: 112-120.
- HOUGHTON, J. T., L. G. MERIA FILHO, B. CALLENDER AND N. HARRIS [EDS.]. 1995. The science of climate change. Cambridge Univ. Press.
- INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2008. Technical paper on climate change and water [Internet]. Available from <http://www.ipcc.ch/meetings/session28/doc13.pdf>. Accessed 12 January 2009.
- LEHMAN, J. T., AND C. E. CÁCERES. 1993. Food-web responses to species invasion by a predatory invertebrate: *Bythotrephes* in Lake Michigan. *Limnol. Oceanogr.* **38**: 879-891.
- MANCA, M. M., M. PORTOGALLO, AND M. E. BROWN. 2007a. Shifts in phenology of *Bythotrephes longimanus* and its modern success in Lake Maggiore as a result of changes in climate and trophy. *J. Plankton Res.* **29**: 515-525.
- , C. RAMONI, AND P. COMOLI. 2000. The decline of *Daphnia hyalina galeata* in Lago Maggiore: A comparison of the population dynamics before and after oligotrophication. *Aquat. Sci.* **62**: 142-153.

- , AND D. RUGGIU. 1998. Consequences of pelagic food web changes during a long-term lake oligotrophication process. *Limnol. Oceanogr.* **43**: 1368–1373.
- , B. TORRETTA, P. COMOLI, S. L. AMSINCK, AND E. JEPPESEN. 2007b. Major changes in trophic dynamics in large, deep sub-alpine Lake Maggiore from the 1940s to 2002: A high resolution comparative palaeo-neolimnological study. *Freshw. Biol.* **52**: 2256–2269.
- MOLINERO, J. C., O. ANNEVILLE, S. SOUISSI, L. LAINÉ, AND D. GERDEAUX. 2007. Decadal changes in water temperature and ecological time series in Lake Geneva, Europe—relationship to subtropical Atlantic climate variability. *Clim. Res.* **34**: 15–23.
- PACE, M. L. 2001. Prediction and the aquatic sciences. *Can. J. Fish. Aquat. Sci.* **58**: 63–72.
- RUGGIU, D., G. MORABITO, P. PANZANI, AND A. PUGNETTI. 1998. Trends and relations among basic phytoplankton characteristics in the course of the long-term oligotrophication of Lago Maggiore (Italy). *Hydrobiologia* **369–370**: 243–257.
- SCHINDLER, D. W. 2001. The cumulative effects of climate warming and other human stresses on Canadian freshwaters in the new millennium. *Can. J. Fish. Aquat. Sci.* **58**: 18–29.
- SCHMITZ, O. J., E. POST, C. E. BURNS, AND K. M. JOHNSTON. 2003. Ecosystem responses to global climate change: Moving beyond color mapping. *BioScience* **53**: 1199–1205.
- STRAILE, D. 2000. Meteorological forcing of plankton dynamics in a large and deep continental European lake. *Oecologia* **122**: 44–50.
- . 2002. North Atlantic Oscillation synchronizes food-web interactions in central European lakes. *Proc. R. Soc. Lond. B* **269**: 391–395.
- , AND W. GELLER. 1998. Crustacean zooplankton in Lake Constance from 1920 to 1995: Response to eutrophication and re-oligotrophication. *Adv. Limnol.* **53**: 255–274.
- TESSIER, A. J., AND P. WOODRUFF. 2002. Cryptic trophic cascade along a gradient of lake size. *Ecology* **83**: 1263–1270.
- VISCONTI, A., M. MANCA, AND R. DEBERNARDI. 2008. Eutrophication-like response to climate warming: An analysis of Lago Maggiore (N. Italy) zooplankton in contrasting years. *J. Limnol.* **67**: 87–92.
- WALTHER, G.-R., AND OTHERS. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–395.
- WINDER, M., AND D. E. SCHINDLER. 2004. Climatic effects on the phenology of lake processes. *Glob. Change Biol.* **10**: 1844–1856.
- WRIGHT, D., AND J. SHAPIRO. 1990. Refuge availability: A key to understanding the summer disappearance of *Daphnia*. *Freshw. Biol.* **24**: 43–62.
- YAN, N. D., A. BLUKACZ, W. G. SPRULES, P. K. KINDY, D. HACKETT, R. E. GIRARD, AND B. J. CLARK. 2001. Changes in zooplankton and the phenology of the spiny water flea, *Bythotrephes*, following its invasion of Harp Lake, Canada. *Can. J. Fish. Aquat. Sci.* **58**: 2341–2350.
- , R. GIRARD, AND S. BOUDREAU. 2002. An introduced invertebrate predator (*Bythotrephes*) reduces zooplankton species richness. *Ecol. Lett.* **5**: 481–485.
- , AND T. W. PAWSON. 1998. Seasonal variation in the size and abundance of the invading *Bythotrephes* in Harp Lake, Canada. *Hydrobiologia* **361**: 157–168.
- YURISTA, P. 1997. *Bythotrephes cederstroemi* diapausing egg distribution and abundance in Lake Michigan and the environmental cues for breaking diapause. *J. Gt. Lakes Res.* **23**: 202–209.

Associate editors: John P. Smol and Warwick F. Vincent

Received: 07 October 2008
 Accepted: 16 February 2009
 Amended: 23 March 2009