Invasions and re-emergences: an analysis of the success of *Bythotrephes* in Lago Maggiore (Italy)

Marina MANCA

CNR Institute of Ecosystem Studies, Largo Tonolli 50, I - 28922 Verbania, Italy
e-mail: m.manca@ise.cnr.it

ABSTRACT

Bythotrephes *was first seen in North America in 1982 (single individual, Lake Ontario) and noticed elsewhere in the Laurentian Great Lakes in abundance in 1985. Starting from 1987 it sharply increased in the open-water zooplankton of Lago Maggiore, reaching values never recorded in the past 40 years. Despite being native, the species' impact on Lago Maggiore was somewhat comparable to that observed in invaded North American lakes. The re-emergence led to an overall increase in invertebrate predation which became permanent five years after* Bythotrephes' *establishment, causing direct and indirect effects on the food web. Changes included a sharp decrease in the large filter-feeder* Daphnia*, whose mortality rate increased, and consequently an increase in phytoplankton cell density; an increase in abundance and size of colonial rotifers with a decline in* Leptodora *abundance, and an overall decrease in zooplankton biomass were also observed. The increase of* Bythotrephes *in Lago Maggiore, however, was related to a shift in population phenology, which resulted in seasonal growth starting earlier and lasting longer.* Daphnia *phenology changed only later, suggesting that the impact was consequent to a temporary decoupling between* Bythotrephes *and its preferred prey. The shift in density and phenology became permanent. Over the long-term, however, potential competitors and prey were able to recover, reaching levels of abundance comparable to those recorded before the* Bythotrephes' *re-emergence. Such a response is likely attributable to behavioural adaptation mechanisms resulting in temporal and spatial displacement of potential competitors, predators and prey.*

Key words: Bythotrephes*, re-emergence; zooplanktivorous fish; population phenology*

1. INTRODUCTION

Bythotrephes longimanus (Leydig), the palearctic predator which has invaded more than 200 lakes in North America, is indigenous to European subalpine lakes (Ishreyet 1938; Hovius *et al.* 2007). Originally reported from Lake Constance, it was first recorded not as zooplankton, but as part of the stomach content of *Coregonus wartmanni*, the zooplanktivore most commonly fished commercially (in Sars 1861). In his original description, reflected in the name he attributed to this large cladoceran, Leydig (1860) emphasized a behavioural attribute of the species - a preference for the deep epilimnion - and its most important anatomical feature, a long tail spine, from which the common name "spiny water flea" derives.

These historical data are also reflected in the research performed on *Bythotrephes* in Lago Maggiore. Before the establishment in the late seventies of the International Commission for the Protection of Lago Maggiore waters, which prompted a long-term monitoring program of the Lago Maggiore pelagic community, including zooplankton, studies dealing with *Bythotrephes* largely focused on its role in the diet of zooplanktivorous fish, mainly whitefish species (Giussani 1974). Not only was *Bythotrephes* found to compose more than 80% of whitefish stomach content in late summer and fall (expressed as relative abundance,

therefore presumably much more when expressed as contribution to total biomass), it also appeared to be more detectable earlier in the season and for a longer time in the fish stomaches than in zooplankton samples taken in open-water. This pattern suggests that the *Bythotrephes* population was subject to strong pressure from zooplanktivores.

The effects of fish predation pressure were clear when the body size of the prey in fish stomachs was compared with its body size in open water; though it was less clear when it came to explaining changes in *Bythotrephes* abundance in the water column, which were overlooked given the very low levels and the short growth period of the planktonic population (Giussani 1974). In fish stomachs, *Bythotrephes* body length was significantly higher (between 1775 and 1900 μm, from late summer to fall) than in open water, where it ranged between 1650 and 1820 μm during the same period (Giussani, ibidem).

The marginal role of *Bythotrephes* in studies on Lago Maggiore zooplankton was further emphasized after a monitoring program was set up following the eutrophication of the lake (de Bernardi *et al.* 2000). The enrichment in algal nutrients led to *Leptodora kindtii* (Focke), the predatory Cladocera which coexisted with *Bythotrephes*, becoming by far the most prevalent predatory cladoceran in the lake (e.g., Manca *et al.* 1992). Its impact on the abundance and population dynamics of *Daphnia*, the most efficient filter-feeder in

the pelagia of the lake, became the main focus of the research activity on Lago Maggiore zooplankton (de Bernardi *et al*. 1990).

It was only with its unexpected, sharp increase in abundance during re-oligotrophication that *B. longimanus* began to be regarded as a non-negligible component of Lago Maggiore's zooplankton population as well as of the whitefish diet (Manca *et al*. 2008). Its increase was so successful that it is justifiable to describe it as a re-emergence. A re-emergence may have an impact comparable to that of an invasion; it differs, however, because the invasion process lacks of an evolutionary history and a co-adaptation between the predator and the prey. The latter is also likely characterized by a low genetic variability. Because of its invasive nature, and the huge effort made to study all the possible implications of its invasion, most of our present knowledge on *Bythotrephes* as a predatory zooplankter comes from studies on invaded sites. These studies made a major contribution to understanding the impact of the species' increase on the Lago Maggiore pelagic environment.

In this paper, I will review evidence of the direct and indirect effects of the increase of *Bythotrephes* in Lago Maggiore, discussing the most striking changes in zooplankton and phytoplankton observed along with its success. I shall present historical data from the early 20th Century, following which I will focus mainly on the period of *Bythotrephes* increase (1983-1995) for which data on the commercial fish catch are also available. The impact of its re-emergence in Lago Maggiore will be compared with the pattern observed in invaded lakes elsewhere, also in view of an identification of mechanisms responsible for its recent success.

2. MATERIALS AND METHODS

Zooplankton data from the early 20th Century were taken from Baldi *et al*. (1953; in Manca *et al*. 1992). I used only data from samples collected at the same station (Ghiffa), where the lake reaches its maximum depth (370 m), and which has historically been used as representative of the pelagic planktonic community (de Bernardi 1974). All samples were collected with a Clarke-Bumpus plankton sampler, fitted with a 76 μm nylon net, towed down to 50 m depth and up to surface, from a boat moving at a low, constant cruise speed (0.6 m s^{-1}), to allow for the filtration of at least 1000 L of lake water on a sinusoidal trajectory. The integrated samples were representative of the pelagic crustacean zooplankton, during the day in major part distributed within the upper 50 m depth (de Bernardi *et al.* 1988). The sampling frequency was the same from the 1980s onward: at least monthly, and fortnightly or weekly in spring and summer (Manca & Ruggiu 1998).

Samples were preserved in pure (99% volume) ethanol and counted. For some years of the period, *Daphnia* clutch size was recorded, and body length (from the apex of the head to the base of the carapace spine)

measured on 200 individuals, or, when fewer, on the total number of individuals in the sample. The minimum size at maturity (MSP), taken as the minimum body length of ovigerous females, and the maximum size (MS) were also estimated in each sample. *Bythotrephes* body and tail spine lengths were measured for some years (1988, 1992-93, 1996-97, 2001; Manca & Comoli 1988; Manca *et al*. 2000; Manca *et al*. 2008; data not shown), and the clutch size of ovigerous females estimated after extruding embryos from the mother's brood pouch, to allow them to be counted and measured (1983-1988 and 1992). *Per capita* mortality and death rates of *Daphnia* and *Bythotrephes* were calculated from Paloheimo's equation (Paloheimo 1974), using mean water temperature of the sampled layer to estimate the developmental time of embryos (Manca *et al*. 2000; Yurista 1992).

The Statsoft program Statistica version 6 was used to analyze the data. We tested the statistical significance of correlations (Pearson's *r*) between *Bythotrephes* mean annual density and population phenology and abundance and biomass of potential prey and competitors.

2.1. Study lake

Lago Maggiore is the second largest (212.5 km^2) and deepest (maximum depth 370 m, mean depth 171 m) subalpine lake in Italy (194 m a.s.l.). Oligotrophic by nature, the lake became mesotrophic in the 1970s. Its slow recovery from eutrophication, due to the gradual implementation of sewage treatment plants and the reduction of the phosphorus content in detergents in the 1980s, has been documented in a long series of papers and technical reports (e.g., de Bernardi *et al*. 1990; Manca *et al*. 2007). During re-oligotrophication, total phosphorus (TP) and reactive phosphorus (RP) concentrations (measured at the winter mixing) decreased from 38 and 28 μg L^{-1}, respectively to *ca* 20 and 13 μg L^{-1} in the late 1980s, approaching values of 10 and 6 μg L^{-1} in the mid 1990s (Fig. 1A). Since 1995 TP averages 10 μg L^{-1}. Chlorophyll-*a* concentration (mean annual value) also decreased, more sharply in the first half of the 1990s, from *ca* 5 mg m^{-3} to *ca* 3 mg m^{-3} (Manca & Ruggiu 1998).

2. RESULTS AND DISCUSSION

Although Lago Maggiore used to be defined as a "Copepod lake", it was Cladocera that actually typified its trophic evolution (de Bernardi *et al*. 1990). With data available from the middle of the 20th Century on, we can trace the change from the original cladoceran community of the pre-eutrophication years and the community established during the mesotrophic phase, and compare both of them with the community established when the lake returned to oligotrophy (Fig. 1B). In the middle of the 20th Century, the mean annual abundance of *Bythotrephes* was fully comparable to that of *Leptodora*. The latter became far more prevalent, along with the large
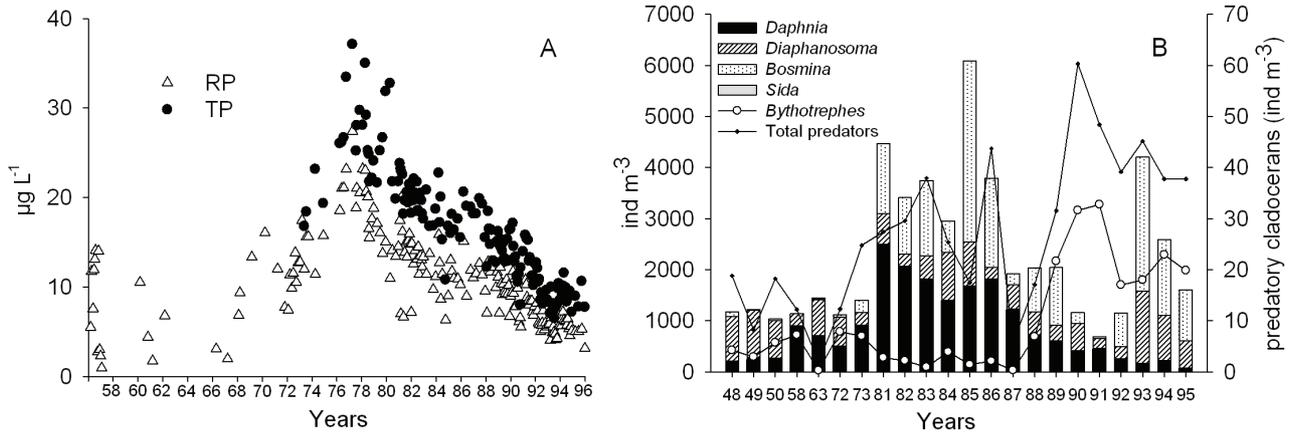
Fig. 1. (**A**) Long-term changes in total (TP) and reactive (RP) phosphorus concentrations and (**B**) long-term changes in Cladocera abundance and taxa composition. in Lago Maggiore.
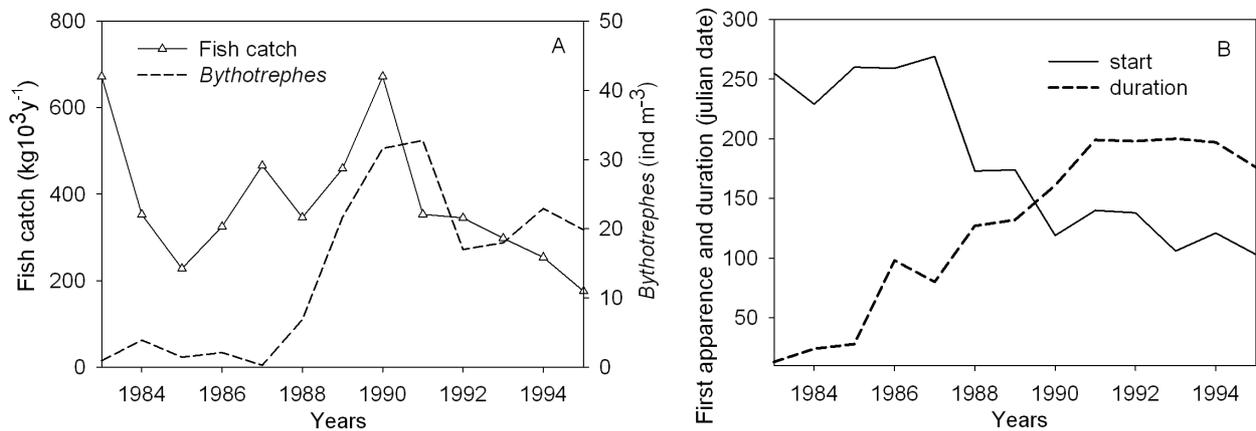

Fig. 2. Changes in mean annual *Bythotrephes* population density and commercial catch of non-piscivorous fish (data from Grimaldi 1997) (**A**); time at growing start and of duration of *Bythotrephes* planktonic population (**B**).

filter feeder *Daphnia*, during mesotrophy (1970s-mid 1980s).

The one-order-of magnitude increase in abundance of *Bythotrephes* from 1988 to 1990, during the re-oligotrophication of the lake, led to a substantial change in the Cladocera community, which became permanent, and resulted in an increase in abundance of invertebrate predators to levels never reached before. *Leptodora* population density was low in 1987-1988 (Manca *et al*. 1992); however, its decrease was not such as to counterbalance the increase of *Bythotrephes*. A temporary low density of the potential competitor *Leptodora* might be regarded as a favourable condition for the successful increase of *Bythotrephes*. The success of an invader (i.e. the "when" of a successful invasion) is often associated with the decrease of a potential competitor - a "temporary condition of advantage", which might favour invasion, in the same way as happened with the spread of *Daphnia* hybrids in European lakes (Hoekstra & Spaak1995). A similar mechanism was found to explain the recent successful invasion of Lago Maggiore by *Eudiaptomus gracilis*, which has supplanted the native *Mixodiaptomus laciniatus* (Visconti & Manca 2010).

Unlike what has been observed in some invaded lakes (Foster & Sprules 2009), however, *Bythotrephes* population density is not inversely correlated at a statistically significant level with that of *Leptodora* in Lago Maggiore.

The *Bythotrephes* increase occurred when the pelagic fish stock was not decreasing [data on commercial fish catch from Grimaldi (1997); Fig. 2A]. The result is also consistent with previous studies, and with data from invaded lakes; according to the latter, among-year variations in *Bythotrephes* level of population density could not be predicted at a reasonable level of statistical significance from changes in zooplanktivorous fish stock (Yan & Pawson 1998; Yan *et al*. 2001). Instead, in Lago Maggiore, whitefish (data from commercial fishing catch) seem to have increased between 1988 and1990, reaching a level quite similar to that recorded in 1983 (Fig. 2A). Such an increase might have been favoured by an increased growth rate consequent to higher availability over the year of their preferred, large-sized food item. The sharp decrease in fish commercial catch in 1991, and the gradual decline in the following years, might be partly attributable to the
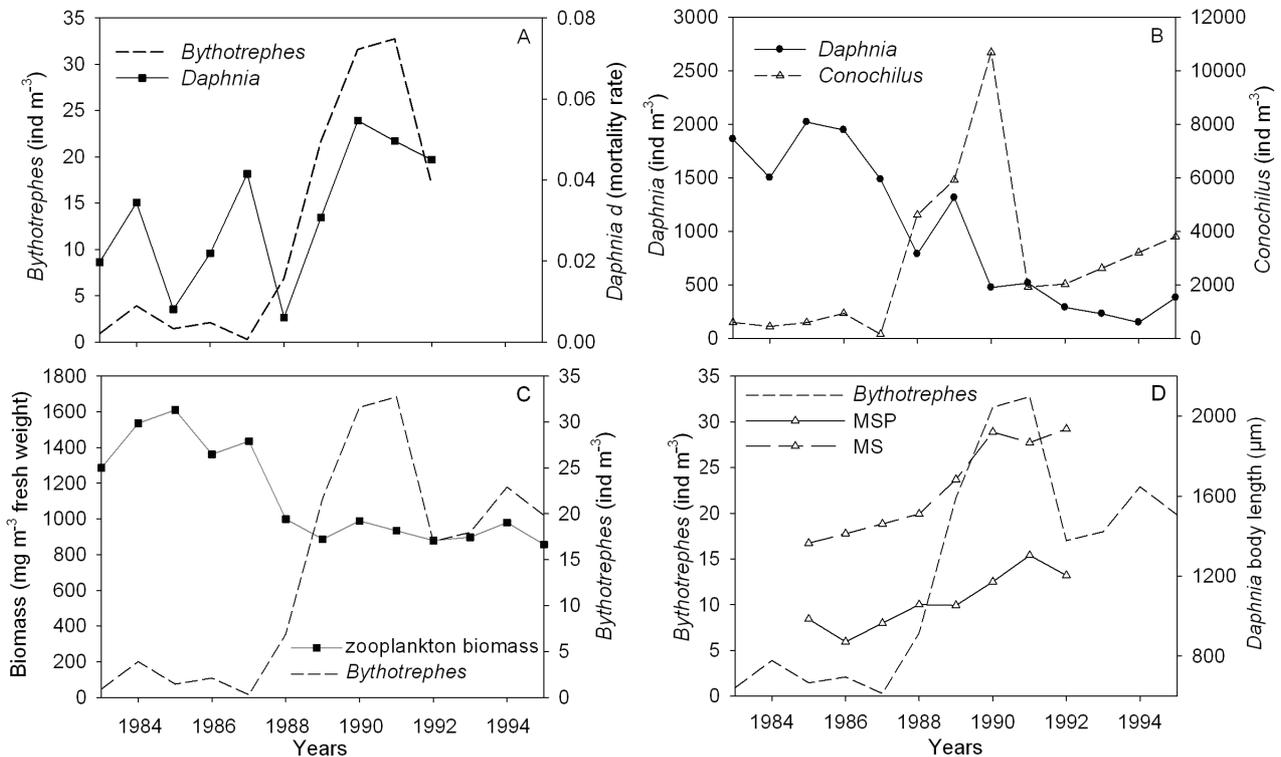
Fig. 3. (**A**) *Bythotrephes* population density and *Daphnia per capita* mortality rate; (**B**) *Daphnia* and *Conochilus* population densities (1983-1995) (from Manca & Sonvico 1996); C) *Bythotrephes* abundance and zooplankton biomass; **D**) *Daphnia* body size (length; for explanation of MSP and MS see methods) and *Bythotrephes* abundance. All panels refer to the period 1983-1995.

oligotrophication process because of the delayed response of zooplanktivores compared to planktonic organisms, as a consequence of their longer generation times. Studies on *Bythotrephes*-invaded lakes, however, also suggest that an overall increase in predatory cladocerans might result in an increase in competition with young fish for herbivorous zooplankton (Dimitru *et al*. 2001). The increase in growth efficiency of the young fish resulting from their consumption of larger prey might not be sufficient to offset the negative effect of the increased competition with invertebrate predators (Foster & Sprules 2009).

The increase in abundance of *Bythotrephes* in Lago Maggiore was related to major changes in phenology, with an earlier start, and a longer persistence, of the population in the water column (Fig. 2B). Time at start was correlated with mean and maximum year population densities, as well as with the time at which the density peak was reached (Yan & Pawson 1998; Manca & DeMott 2009).

During the increase, the mean annual *per capita* mortality rate of the *Bythotrephes* population decreased (data not available for all the years). It was on average 0.23 in 1983-1986, declined to 0.17 in 1987-1988 and then to 0.10 in 1992. The *per capita* mean annual birth rate increased from 0.17 to 0.24 between 1985 and 1987, before the increase in abundance, decreasing to 0.20 and 0.08 in 1988 and 1992, respectively.

The *Bythotrephes* increase was accompanied by a decrease in the *Daphnia* population density (Fig. 3A). The mean annual abundance of the predator and its preferred prey were negatively correlated at a high level of significance (Spearman r = -0.76; n = 13; p <0.01). This result is consistent with published reports on the effects of invasive *Bythotrephes* on the open water Cladocera community in North America lakes (Lehman 1988; Pangle *et al*. 2007). In Lago Maggiore, however, the impact on *Daphnia* was related to an initial change in phenology of *Bythotrephes*, a change which was not initially observed for the prey. *Daphnia* peak timing remained quite stable, around Julian day 200, in 1983-1990, but decreased by about two months only as of 1991 (Visconti *et al*. 2008). The earlier start of seasonal growth and peak density of *Bythotrephes* exposed *Daphnia* to early predation, most probably also on ovigerous females, which are usually abundant before the population density peak. Before the *Bythotrephes* re-emergence, *Daphnia* had been able to cope with a strong predation pressure by *Leptodora*, mainly directed towards young (de Bernardi 1974), which caused a sharp decline in population density in late July-August. This decline, however, was linked to an increase in the birth rate of the prey (a "stabilizing effect" following a release in intraspecific competition; Polishchuck 1995). *Daphnia* may have been initially unable to buffer the impact of an earlier predation by voracious *Bythotre-*
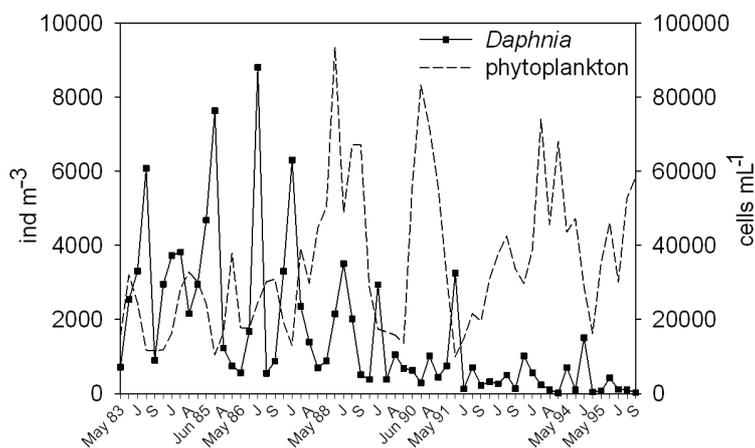
Fig. 4. Changes in *Daphnia* abundance (May-September) with phytoplankton cell numbers over the period 1983-1995 (from Manca & Ruggiu 1998).

phes, which could also prey on ovigerous females (Manca *et al*. 2000; Manca *et al*. 2008). In Lago Maggiore, the strong selection by *Bythotrephes* on *Daphnia* throughout the year is also confirmed by the strong, positive correlation between the carbon isotopic signatures of the two ($r = 0.89$; n = 18; $p <0.001$; Visconti & Manca 2011). Only in winter does the *Bythotrephes* signature suggest that they feed mainly on cyclopoid copepods. Over the time period considered in this paper, however, the population density and biomass of copepods was not affected by the *Bythotrephes* increase.

The mean annual *per capita* mortality rate of *Daphnia* increased by two to three times in 1988-1990 (Fig. 3A) compared to previous years. The birth rate also increased, from 0.04 (in 1988) to 0.06 in 1991. It ranged between 0.02 and 0.03 in 1983-1987. During the changes in *Daphnia* and *Bythotrephes* population densities, the ratio between the two decreased sharply, from 103 *Daphnia/Bythotrephes* in 1983-1988 to 10 in 1989-1993, decreasing further to reach a minimum of 10^{-2} in 1996.

During the *Daphnia* decline and the *Bythotrephes* increase (1988-1990), the colonial rotifer *Conochilus unicornis-hippocrepis* (gr. *sensu* Ruttner-Kolisko 1974) became dominant in Lago Maggiore open-water zooplankton, reaching levels of abundance never recorded before (Fig. 3B). Both the number of colonies×L^{-1} and the number of individuals × colony^{-1} increased, with an overall density increment of an order of magnitude compared to the years before the increase of *Bythotrephes* (Manca *et al*. 2000). As in the case of invaded lakes, *Conochilus* growth might have been favoured by the decrease in its main predator, *Leptodora* (Hovius *et al*. 2007), suggesting an indirect effect of the *Bythotrephes* increase. Throughout the season, *Conochilus* appeared to be able to replace *Daphnia* as the main particle filter feeder in the pelagia, with its maximum population density coupled to a spring increase in water

transparency (Manca & Sonvico 1996). The decline in *Leptodora* was only temporary, however; over the long-term, the species was able to recover, reaching since the 2000s, levels of abundance comparable to those recorded before the *Bythotrephes* increase. The recovery might have also been favoured by differences in the seasonal dynamics, with *Leptodora* increasing in abundance when *Bythotrephes* is at a low density. Such a recovery led to an overall increase in invertebrate predation (Manca *et al*. 2000), never recorded before.

The abundance of small zooplanktonic cladocerans, i.e. *Bosmina* (mainly of the species *Eubosmina longispina*) and *Diaphanosoma brachyurum*, was generally lower in 1988-1990 than in the previous years when the lake was mesotrophic. They became dominant in 1991-1995, when the mean annual *Daphnia* population density was approaching its absolute minimum (in 1996; Manca *et al*. 2000; Fig. 1B). A similar pattern was observed as a secondary effect of the *Bythotrephes* invasion (Dimitru *et al*. 2001), although the response was delayed in the case of Lago Maggiore.

Mean annual total zooplankton biomass decreased with the *Bythotrephes* increase, with a high and statistically significant negative correlation between the two ($r = 0.79$; $p = 0.001$; n = 13) (Fig. 3C).

During its decline in density, *Daphnia* body size increased (mean annual data, not measured for all years), to reach values comparable to, or slightly higher than, pre-mesotrophic values. Both the minimum size of primiparae (MSP) and the maximum size (MS) increased, particularly in 1988-1990 (Fig. 3D).

The decrease in abundance of the large filter feeder *Daphnia* resulted in a >twofold increase in phytoplankton cell numbers (Fig. 4; from Manca & Ruggiu 1998), which may be seen as resulting from a release in grazing pressure. Phytoplankton numbers and *Daphnia* density were negatively correlated at a high level of significance ($r = -0.35$; n = 61; $p <0.01$). The cascading effect, however, was only evident when phytoplankton cell num-

bers were used; it was not seen when phytoplankton biovolume and chlorophyll-*a* data were tested (Manca & Ruggiu 1998), as has been found in invaded lakes. A return to small celled phytoplankton might also be associated with oligotrophication: this does not seem the case, however, as the total biomass of phytoplankton did not decline at the same time.

4. CONCLUSIONS

The successful increase of *Bythotrephes* in the open water zooplankton of Lago Maggiore shares some of the direct and indirect effects observed from its invasion of North American sites. These include a decrease in the population density of *Daphnia* species, an increase in colonial rotifers and phytoplankton cell numbers, and a subsequent increase in the contribution of small cladocerans to total abundance (Yan *et al*. 2001). The increase was also accompanied by an overall decrease in herbivorous zooplankton biomass (Boudreau & Yan 2003).

As in invaded lakes, the re-emergence of *Bythotrephes* and the overall increase of invertebrate predators in Lago Maggiore might be interpreted as increasing competition with young fish for herbivorous zooplankton (Dimitru *et al*. 2001). The young fish might not be compensated by the increased growth resulting from an increase in prey size. In Lago Maggiore, however, the potential increase in availability of a larger prey (*Bythotrephes*) was consequent not only to a higher abundance, but also to an earlier and longer growing season of its open water population.

While the mean annual *per capita* birth rate of *Bythotrephes* increased before the increase in abundance, the *per capita* mortality rate tended to decrease during the increase in abundance, suggesting that the hypothesis of an enhanced open water refuge was reliable. Population phenology change is also in agreement with the fact that *Bythotrephes* success is favoured when invasion occurs in May-July (Drake *et al*. 2006).

It was also of key importance for the impact on *Daphnia*, exposing the latter to an earlier (as early as spring and early summer) and stronger (because of the persistence of *Leptodora*) invertebrate predation than before. Considering all the factors, the temporary decoupling between *Bythotrephes* and its preferred prey observed in Lago Maggiore might be similar to the *Daphnia*-phytoplankton decoupling consequent to climate warming (Straile 2000).

Despite the *Bythotrephes* shift and the permanent increase in invertebrate predation, however, *Daphnia* was able to increase again since the 2000s, reaching levels comparable to those observed before the *Bythotrephes* re-emergence (i.e. before 1988). Behavioural adaption mechanisms, including changes in vertical distribution might be responsible for the recovery of the system.

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