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Population dynamics of *Chaoborus flavicans* and *Daphnia* spp.: effects on a zooplankton community in a volcanic eutrophic lake with naturally high metal concentrations (L. Monticchio Grande, Southern Italy)

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ABSTRACT

The response of Daphnia *populations to invertebrate predators involves morphological or behavioural changes. Few studies suggest that contaminant aqueous metals, like Cu or Ni at environmentally relevant concentrations, interfere with invertebrate chemical communication systems, such as that which operates between* Daphnia *and* Chaoborus*. The objective of our study was to determine if this interference could be also observed in lakes naturally rich in dissolved metals, such as volcanic lake (Lago Grande di Monticchio). This study aimed to assess if natural dissolved metals (e.g., Fe, Mn and Sr) could impair the ability of* Daphnia pulex *and* D. galeata × hyalina × cucullata *'complex' populations to respond to* Chaoborus *kairomones by producing morphological defenses against potential predation, and to understand how* Chaoborus *predation might affect zooplankton community composition and overall zooplankton density. The predator impact did not result in: i) any morphological changes; ii) any apparent shift in body size pattern of the prey population; iii) any shift in life history traits.* Chaoborus *accounted for high mortality rates in Cladocera and strongly reduced the chance of individuals to reach maturity. Moreover, highly significant negative correlations between abundance of dominant taxa of zooplankton and* C. flavicans *were found. The last larval instars of* C. flavicans *seem to reduce the number of crustaceans, particularly cladocerans and copepod adults and could play an important role in structuring zooplankton communities. Our results suggest that metal inhibition of defence strategies induction probably occurs along the signal transduction pathway in Lake Grande di Monticchio. Impairment of chemosensory response to predatory chemical cues may have widespread ecological consequences in aquatic systems.* Chaoborus *predation effects can greatly affect both zooplankton biomass and community composition, impact interactions at lower trophic levels and generate an ecological cascade leading to a rapid eutrophication.*

Key words: predator-prey system, zooplankton, metal inhibition, volcanic lake

1. INTRODUCTION

Predation is one of the most important factors controlling the structure and dynamics of natural ecosystems (Wellborn *et al*. 1996; Van de Meutter *et al*. 2005). Invertebrate predators, such as *Chaoborus* (Diptera) larvae, play a major role in structuring zooplankton communities in lakes by directly limiting prey populations (Hanazato & Yasuno 1989; Hanazato 1990) and altering the dynamics, size and structure of prey populations (Neill 1981; Mumm 1997; Riccardi *et al*. 2002). The '*Chaoborus–Daphnia* / predator–prey' system is very well studied. *Daphnia* are known to respond to the presence of predators by changing their life history, morphology and behaviour (reviewed in Tollrian & Dodson 1999). The induction of an antipredator defence in *Daphnia* is thought to be mediated by the presence of predatory cues: kairomones, which are thought to be a low molecular weight, nonolefinic hydroxyl-carboxylic acid (Tollrian & von Elert 1994). In the presence of *Chaoborus* kairomones, cladocerans reproduce later at a larger size, and they produce larger but fewer daphniids (Jeyasingh & Weider 2005). As suggested by Lynch (1980), there is a trade-off between energy allocated for somatic growth and energy allocated for reproduction. Moreover, kairomones of invertebrate predators are known to induce elongation of tail spines, enlarged helmet crests or the development of neck teeth in *Daphnia* spp. (Parejko 1991; Spitze 1992; Black 1993; Repka *et al.* 1995) as a defence mechanism that makes the handling of prey more difficult (Caramujo & Boavida 2000) and/or increases the prey's escape ability (Mort 1986; Swift 1992).

Morphological adaptations may prevent local extinction of *Daphnia* by *Chaoborus*. Induction of such morphological adaptations requires *Daphnia* to be able to detect the kairomones. Several studies have shown that metals can affect chemoreception in fish (Hansen *et al.* 1999; Beyers & Farmer 2001). Hunter & Pyle (2004) demonstrated experimentally that *Chaoborus* kairomones neck tooth induction in *Daphnia pulex* was reduced in the presence of the dissolved metals Cu and Ni at environmentally relevant concentrations, whereas no significant effects were observed on body length or brood size.

This study aimed to assess the '*Chaoborus*–zooplankton / predator–prey' system in populations inhabiting a lake naturally rich in dissolved metals, and to understand how *Chaoborus* predation might affect zooplankton community composition and overall zoo-

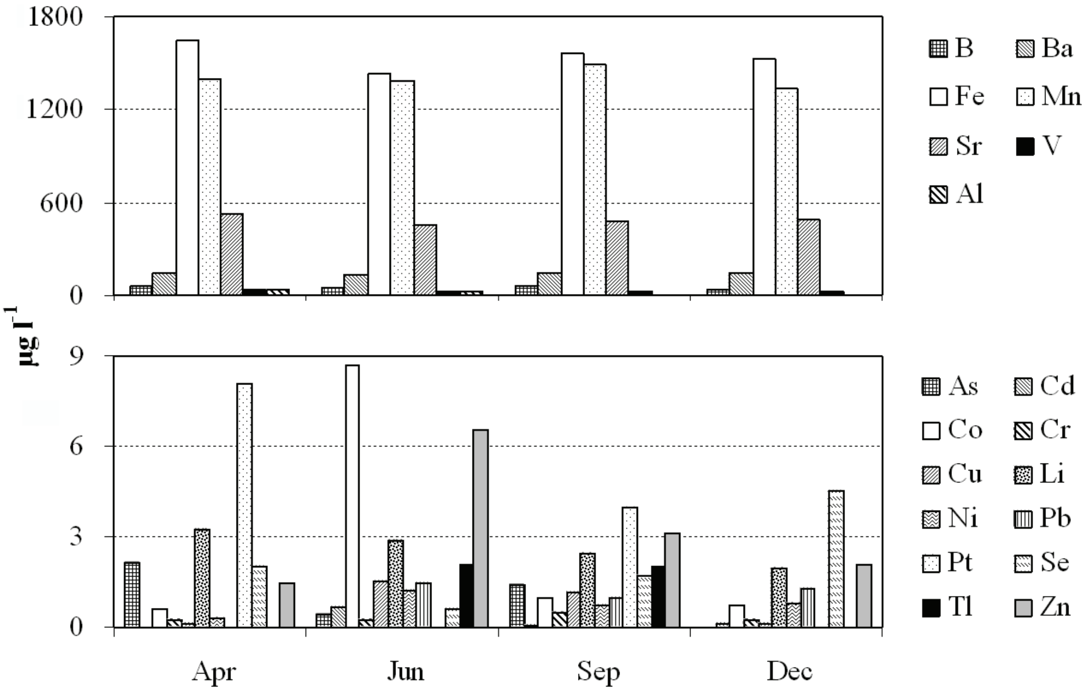

Fig. 1. Seasonal changes in mean concentrations of dissolved metals in the water column of MG Lake in 2005.

plankton density. We hypothesized that natural dissolved metals could impair the ability of some zooplanktonic taxa to respond to *Chaoborus* kairomones, and may therefore lead to the failure of individuals to produce life history and morphological changes as a defence against potential predation. In particular, we estimated the effects of dissolved metals on the *Chaoborus-Daphnia* system, one of the best-known examples of inducible defences and an important trophic link in pelagic food webs (Boeing *et al.* 2005). To this end we analysed the population dynamic of *Chaoborus flavicans* and the size structure and morphology traits of *Daphnia pulex* and *D. galeata* × *hyalina* × *cucullata* 'complex' and in a volcanic lake naturally rich in dissolved metals (Lake Grande di Monticchio).

1.1. Study site

Lake Grande di Monticchio (hereafter referred to as MG Lake) is the larger of two adjacent maar lakes, lakes of Monticchio (650 m a.s.l., 40°55'N, 15°35'E), within a caldera on the western slopes of the Mount Vulture in the Basilicata region of southern Italy. Despite the name Lago Grande (Large Lake), it is a small (0.41 km^2) and relatively deep lake (maximum depth = 36.3 m; mean depth = 8.5 m). It has a small drainage area (3.9 km^2) and its most important water sources are represented by internal springs, precipitation, runoff and water coming from Lago Piccolo di Monticchio (Small Lake), a small oligotrophic basin connected to Lago Grande by a short stream (length: 216 m, flow: 50 L s^{-1}).

MG Lake is a meromictic lake, characterised by high concentrations of ions in deeper layers (the monimolimnion). Among the consequences of stable stratification of lake waters is that the monimolimnion (from -20 to 38 m) becomes depleted of oxygen (less than 1 mg L^{-1}). However, MG Lake has two separate areas differing in morphometry. A large area is relatively shallow (maximum depth 12 m) and rich with macroscopic submersed vegetation, and the water is mixed completely twice a year. The oxygen concentration remains fairly high for a few months, but stratification forms, during summer, an oxygen profile representing a clinograde, with a chemocline occurring at a depth of 5 m.

Chemical data show a situation between eutrophic and hypereutrophic conditions, with a total P concentration frequently exceeding 60 µg $L^{-1}$and a Secchi disk depth in summer of about 70 cm. The pH profile decreases from the surface to the bottom, ranging from 9.1 to 5.9. This pH gradient exists because volcanic spring waters are rich in CO_2 and SO_2 escapes from the residual volcanic activity. The concentration of dissolved metals in the water is very high and is due to emissions of mineral water from submerged springs, resulting in elevated concentrations of iron, manganese and strontium (Fig. 1).

The most common aquatic plants in the lake are *Typha latifolia*, *Phragmites* spp., *Ceratophyllum* spp. and *Nymphaea alba*. The fish assemblage is dominated by cyprinids, with tench (*Tinca tinca*), common carp (*Cyprinus carpio*), rudd (*Scardinius erythrophthalmus*) perch (*Perca fluviatilis*) representing the major fish species in MG Lake. Larvae of *Chaoborus flavicans*

(Meigen) are found in the lake. This species is widely distributed in the holarctic region, has four larvae instars, and is usually univoltine. It inhabits eutrophic lakes and is adapted to coexist with dense fish populations, which has usually been explained by its ability to avoid predation by vertical migrations (McQueen *et al.* 1999; Gliwicz *et al.* 2006). Some studies also suggest that the ability to disperse horizontally when faced with food shortage, and the flexible utilization of benthic and limnetic habitats, may facilitate the maintenance of large populations (Liljendahl-Nurminen *et al.* 2002).

2. METHODS

Zooplankton and *Chaoborus* larval samples were taken monthly in 2005 using Wisconsin nets (40 cm in diameter, 200 and 60 µm mesh) hauled vertically from a 10-m depth to the surface. The use of this type of net and mesh sizes efficiently captures zooplankton like Rotifera, Cladocera and Copepoda, including copepodites and nauplii, and occasional plankton organisms such as dipteran larvae. Each sample was obtained by pooling three replicate hauls collected in correspondence at the deepest point. The volume of water filtered was determined indirectly, assuming that the net filters the whole volume of the water column. Zooplankton and *Chaoborus* larvae were preserved for analysis in a 4% buffered sucrose-formalin solution. In the laboratory, identification and counts of adult crustaceans and rotifers were made mostly to the species level, while nauplii and copepodite stages (C1-C5) were categorized to different suborders (Cyclopoida and Calanoida). Taxon identification was performed with reference to Ruttner-Kolisko (1974), Margaritora (1983), Dahms & Fernando (1993), Nogrady *et al.* (1993) and Dussart & Defaye (1995).

Measurements of total length (length from the anterior end of the carapace to the end of the tailspine), mean length (length from the anterior end of the carapace to the base of the tailspine) and height were performed only on individuals of the *Daphnia galeata* × *hyalina* × *cucullata* 'complex' using a PC provided with image analysis software. Pictures of adult females were taken using a digital camera (Olympus Camedia C-7070) installed on a microscope (Wild Leitz GMBH). The number of individuals analysed varied among samples (from 20 to 100) and depended on the density of the population. Sizes at maturity for individuals of the *Daphnia* 'complex' were determined according by Caramujo *et al.* 1997.

The number of *Chaoborus* larvae and relative abundance of each developmental stage were estimated microscopically for the whole sample. The head capsule length of all larvae for each instar was measured using a PC, similar to the system used for *Daphnia* individuals. The mouth width was estimated as approximately half of the head capsule length (Mumm & Sell 1995).

Spearman's rank correlation coefficient was calculated to measure the correlation between *Chaoborus* abundance and more representative taxa of zooplankton density and the correlation between male proportions with changes in *Chaoborus* densities. Spearman's analysis was also applied to detect a possible effect of size-selective predation on the *Daphnia* 'complex'. Body length, total length and height of more than 80 individuals per sampling date were measured and the analysis was performed using mean total length, mean length, mean height (and their standard deviation).

Performing many tests on the same set of data may have resulted in an increased risk of type I statistical error, i.e., the rejection of the null hypothesis due to mere chance. To solve this problem Bonferroni correction is usually applied, but a strict application of this method strongly reduces the power of statistical test. A new approach that avoids such problem is to adopt False Discovery Rate (FDR) correction (Benjamini & Hochberg 1995; Garcia 2003; Verhoeven *et al.* 2005). However, in the absence of a general consensus for how to apply correction methods in multiple tests (see Nakagawa 2004), we decided to adopt the following approach. We will present uncorrected *P*-values and, for simplicity, will report values lower than 0.05 as significant. However, we will also apply FDR correction and report the tests that were significant according to this procedure. In the discussion, we will warn the reader that some of the statistical tests reported as significant may reflect type I statistical errors.

3. RESULTS

3.1. Zooplankton dynamics

In the zooplankton assemblage of MG Lake we found 15 taxa of Rotifera, 6 taxa of Cladocera and 1 taxon belonging to the Copepoda. The maximum density of zooplankton was recorded in February (146581 ind m^{-3}) and a progressive decrease was observed during spring and summer, with values subsequently declining to reach a minimum in July (12941 ind m^{-3}), followed by a small increase in autumn (76775 ind m^{-3}). The community was always dominated by Rotifera in terms of abundance: 43% in February; 95% in July, and 85% in December. Copepoda relative abundance varied considerably, ranging from 35% in February to 3% in June, whereas the Cladocera showed a great density percentage (25%) from February to May that decreased during June (1%). *Polyarthra* was the dominant genus in the lake from April to August, while *Keratella cochlearis* was the dominant species in autumn and winter. Other taxa such as *Keratella quadrata*, *Brachionus* spp., *Tricocherca* spp. and *Synchaeta* spp. showed exiguous and sporadic populations (Fig. 2a). In the lake, Copepoda were only represented by *Cyclops lacustris*. Cyclopoids showed a conspicuous density in February (52038 ind m^{-3}) when the over-wintered adults were prevalent. From May to October, the copepod commu-

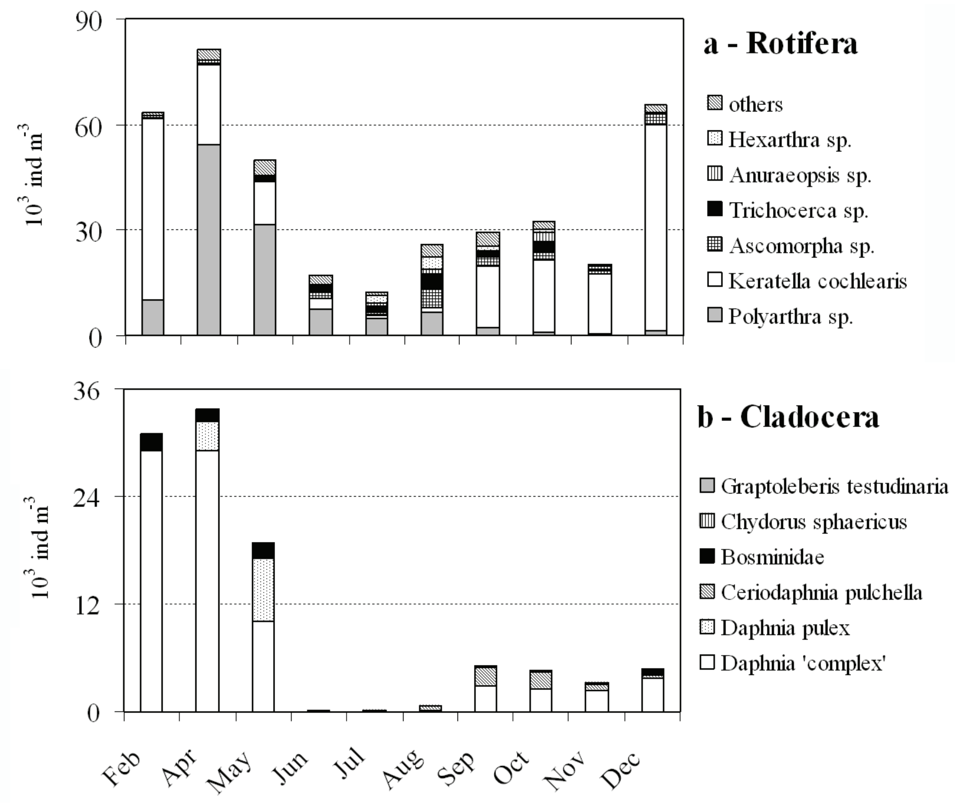

Fig. 2. Population dynamics of Rotifera (**a**) and Cladocera (**b**). Others: *Brachionus urceolaris*, *Ploesoma* sp., *Filinia longiseta*, *Lecane luna*, *Synchaeta* sp., *Euchlanis dilatata*, *Monommata longiseta*, *Keratella quadrata* and *Asplanchna priodonta*.

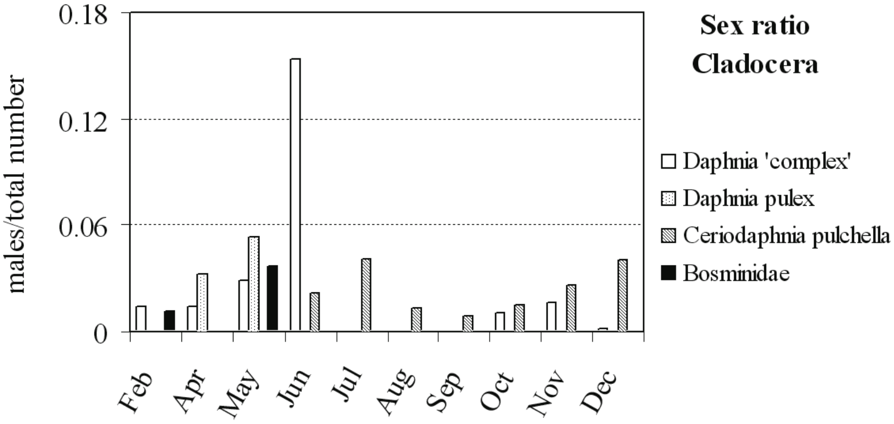

Fig. 3. Seasonal variation in sex ratio (male number *vs* total number) of dominant taxa of Cladocera.

nity was dominated in abundance by nauplii and copepodites (ranging from 60 to 80%). Cladocerans had their maximum development in April, and thereafter nearly all of the cladoceran species decreased dramatically. In September, only the small species *Ceriodaphnia pulchella* and members of the *Daphnia* 'complex' showed a slight increase in abundance. A peak of Bosminidae and *Daphnia pulex* was observed during late-winter and spring, but *D. pulex* declined after June and did not recover. Among the Cladocera, members of the *Daphnia galeata* x *hyalina* x *cucullata* 'species complex' (reviewed in Schwenk & Spaak 1997) dominated the community (Fig. 2b).

Cladoceran reproduction in MG Lake involved cyclical parthenogenesis, and the parthenogenetic phase always coexisted with an amphigonic phase. Males and ephippial females of nearly all taxa occurred in the lake (Fig. 3). The production of diapausing eggs occurred earlier in the year in *Daphnia* spp. and Bosminidae (from February). Males of *C. pulchella*, a warm stenotherm species, occurred from June to December.

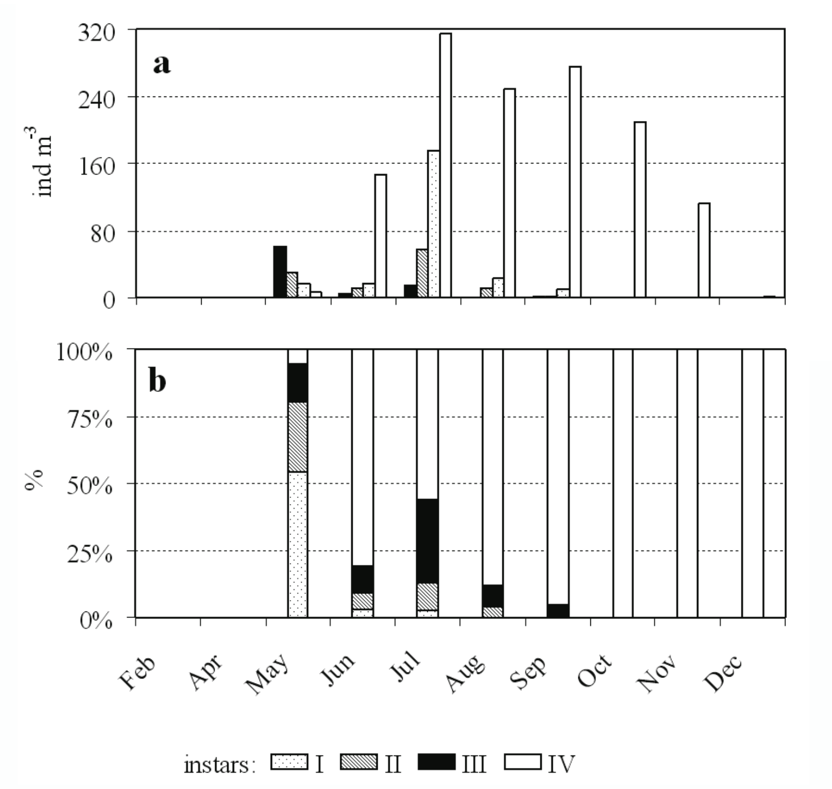

Fig. 4. Seasonal variation in the density (**a**) and in the percentage (**b**) of the larval instars (I, II, III, IV) of *Chaoborus flavicans* from February to December 2005.

3.2. Chaoborus flavicans *larval dynamics*

Chaoborus flavicans larvae were not encountered in plankton samples in early spring. They first appeared in the water column in May, sharply increased in summer, and were still present in December. Higher fractions (about 60% of total instar larvae) of first instar larvae in the lake during May suggest that this may have been caused by stronger recruitment through *Chaoborus* eggs laid on the water surface (Fig. 4). The abundance of later instars (III and IV) sharply increased from June (80% of all instars) to October when only 4th instar larvae were present. The abundance (± S.D.) of larvae in the lake from May to July ranged from 113.6 ± 4.5 to 570 ± 124 ind m^{-3} and decreased in September, probably due to pupation and adult emergence but also likely due to predation by planktivorous fish (unfortunately, no data is available about ichthyofauna in MG Lake). The average mouth width of IV instar larvae varied from 363 to 628 µm (mean 580 µm ± S.D. 39.3).

3.3. Relationships between zooplankton and C. flavicans

Spearman's rank correlation analysis was used to estimate the relationships between metazooplankton and its possible predator. Nine out of the 36 correlation tests, performed for separate larval instars of *Chaoborus* (I, II, III and IV), were significant at the $P < 0.05$ level (Tab. 1). All significant correlations between the abundance of more representative taxa of zooplankton and *C. flavicans* were negative and interested both small (e.g., Bosminidae) and large (e.g., *D. pulex*) cladocerans, adult copepods and rotifer species. Eight of the nine tests that showed a significant correlations involved III and IV larval instars of *C. flavicans*. Four tests of Spearman's correlation, including *Daphnia* 'complex', Bosminidae and *K. cochlearis*, were still significant after False Discovery Rate (FDR) correction (Tab. 1).

Tab. 1. Spearman's rank correlation analysis between the abundance of more representative taxa of zooplankton and their predator. Analysis was performed for separate larval instars of *Chaoborus* (I, II, III and IV). Values in bold are significant, those that are still significant after FDR correction are underlined. Superscript letters indicate the significance level: ^{a}: $P \leq 0.001$; ^{b}: $0.001 < P \leq 0.005$; ^{c}: $0.005 < P \leq 0.01$; ^{d}: $0.01 < P < 0.05$.

	Chaoborus flavicans (larvae instars)			
	I	II	III	IV
Daphnia 'complex'	-0.307	-0.545	**-0.679^{d}**	**-0.802^{b}**
Daphnia pulex	0.277	0.069	-0.095	**-0.657^{d}**
Ceriodaphnia pulchella	-0.228	-0.144	-0.033	0.646
Bosminidae	-0.205	-0.506	**-0.679^{d}**	**-0.821^{b}**
Cyclops lacustris -adults	-0.533	-0.506	-0.511	**-0.754^{c}**
Cyclops lacustris - nauplii	-0.092	-0.127	-0.208	-0.208
Keratella cochlearis	-0.601	**-0.856^{b}**	**-0.899^{a}**	**-0.717^{d}**
Polyarthra sp.	0.204	0.285	0.213	-0.432
Trichocerca sp.	0.300	0.597	0.679	0.790

The carapace height of *Daphnia* 'complex' adult females ranged from 360 to 650 µm (mean 518 µm ± S.D. 130) and total length ranged from 870 to 1300 µm (mean 1003 µm ± S.D. 160). The carapace height of *Daphnia pulex* ranged from 455 to 1243 µm (mean 980 µm ± S.D. 233) and total length ranged from 1310 to 2120 µm (mean 1561 µm ± S.D. 220). Adults of both *Daphnia* taxa were above the size range for *Chaoborus* predation (see Results: *Chaoborus* larval dynamics). However, *D. pulex* individuals were bigger than those of the *Daphnia* 'complex' and could therefore be expected to be less vulnerable at a given developmental stage (Sell 2006).

No *Daphnia* spp. collected during the presence of *C. flavicans* in the water column showed a helmet, neck teeth, or other morphological changes.

Spearman's correlation analysis was also applied to detect a possible effect of size-selective predation on the *Daphnia* 'complex'. The correlation was calculated to measure the intensity of the association between chaoborid density and body length, total length and height. No significant correlations were found between dimensions of adult females and abundance of *Chaoborus* (Tab. 2, see also Fig. 5).

Tab. 2. Spearman's correlation coefficients correlating morphological metrics of adult females of *Daphnia* 'complex' with densities of III and IV larval instars of *C. flavicans*. No significant correlations were found. Analysis was performed on more than 80 individuals per sample (see Methods). Mean total length: length from the anterior end of the carapace to the end of the tailspine; mean length: length from the anterior end of the carapace to the base of the tailspine; S.D. standard deviation.

	Chaoborus flavicans (larvae instars)	
Daphnia 'complex'	III	IV
mean length	0.327	-0.455
mean total length	0.764	0.084
mean height	0.096	-0.711
S.D. of mean length	0.546	-0.024
S.D. of mean total length	0.327	0.132
S.D. of mean height	0.627	0.263

Spearman's rank correlation analysis was used to estimate the relationships between cladocerans males and *Chaoborus*. Two out of the 16 correlation tests, performed for separate larval instars of *Chaoborus* (I, II, III and IV), were significant at the P <0.05 level (Tab. 3). Significant correlations were negative and involved *Daphnia* 'complex' males and III and IV larval instars of *C. flavicans*, one test was still significant after False Discovery Rate (FDR) correction (Tab. 3).

4. DISCUSSION AND CONCLUSIONS

The zooplankton features of MG Lake are typical of eutrophic lakes. An ecosystem generally becomes poor at high trophic levels (Kira 1993) with few species and a low structural complexity. A small number of taxa, few dominant species, and a high share of rotifers in the zooplankton are characteristic of MG Lake. Among the copepods, juveniles (nauplii and copepodites) dominate. In eutrophic water bodies, the life time of dominant species is short and young individuals prevail, while the adults are strongly decimated by predators (Ponyi & Zankai 1982; Nicholls & Tudorancea 2001). Metazooplankters inhabit mainly the epilimnion and metalimnion, where they find suitable living conditions. The anoxic hypolimnion does not qualify as a habitat for many zooplankters. This unsuitable zone expands during the process of eutrophication. The main factors controlling the abundance of chaoborid larvae seem to be stratification and the degree of the hypolimnetic oxygen deficit; the highest biomass of these dipterans is often found in eutrophic conditions, in which oxygen depletion is most common (Sæther 1997; Liljendahl-Nurminen *et al.* 2002). Co-occurrence of chaoborids with fish is confined to species that conduct diel vertical migrations, like *C. flavicans* (von Ende 1978; Sutor *et al.* 2001). The abundance of *Chaoborus* larvae in MG Lake is low when compared to the data of other studies (Mumm 1997). Since all samples were taken at a fixed depth (10 m) and time (*circa* 10:00 a.m.), the abundance of invertebrate predators may have been underestimated in some cases. Nevertheless, a theoretical model developed by Riessen (1992) predicts that *Chaoborus* densities >0.5 ind L^{-1} can have a significant impact on *Daphnia* populations, and several studies have shown that *Chaoborus* at moderate density causes a reduction in the density of zooplankton communities (e.g., Vanni 1988; Hanazato & Yasuno 1989; Riccardi *et al.* 2002). *Chaoborus* can be more selective only if prey are abundant, choosing organisms that are easier to ingest based on size, shape or nutritive value (Pastorok 1981), but when food was scarce, as in MG lake, prey were attacked indiscriminately (Pastorok 1981; Riessen 1992).

Tab. 3. Spearman's rank correlation analysis between the abundance of cladocerans males and larval instars of *Chaoborus* (I, II, III and IV). Values in bold are significant, those that are still significant after FDR correction are underlined. Superscript letters indicate the significance level: ^{a}: $P \leq 0.001$; ^{d}: $0.01 < P < 0.05$.

	Chaoborus flavicans (larvae instars)			
	I	II	III	IV
Daphnia 'complex'	-0.305	-0.560	**-0.702**^{d}	**-0.889**^{a}
Daphnia pulex	0.307	0.148	-0.055	-0.456
Ceriodaphnia pulchella	-0.302	-0.264	-0.171	0.537
Bosminidae	0.307	0.148	-0.055	-0.456

Correlation analyses indicated that the strong decrease in zooplankton abundance in June and July was likely due to an increased mortality by predation. Highly significant negative correlations between abundance of dominant taxa of zooplankton and *C. flavicans* were found. The third and fourth larval instars of *C. flavicans* seem to significantly reduce the number of

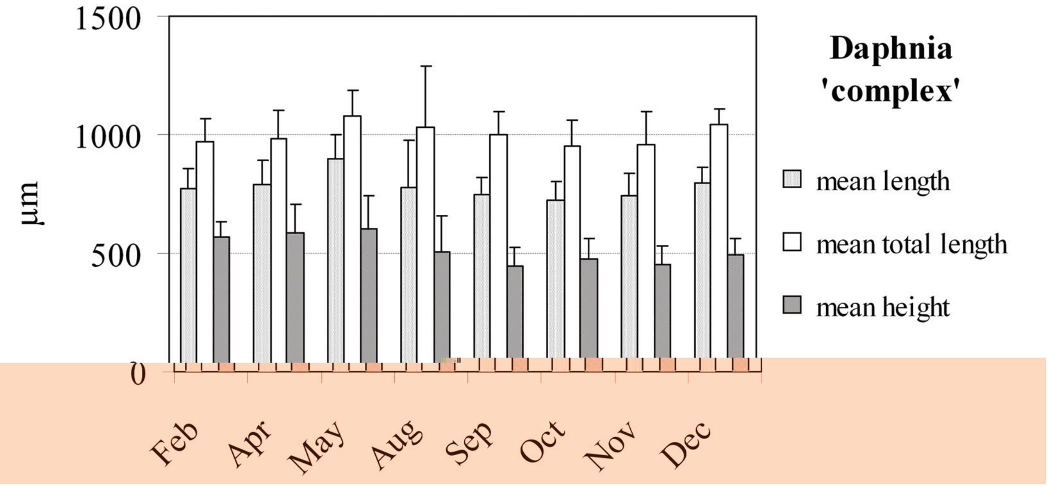

Fig. 5. Seasonal variation of morphological metrics of adult females of *Daphnia* 'complex' (mean value + S.D.). Analysis was performed on more than 80 individuals per date (see Methods). Total length: length from the anterior end of the carapace to the end of the tailspine; length: length from the anterior end of the carapace to the base of the tailspine.

crustaceans, particularly cladocerans and copepod adults and could play an important role in structuring zooplankton communities.We are therefore confident that the results were not biased. It must be emphasized that we ran several statistical tests and we consequently increased the risk of incurring type I statistical errors. Statistical tests may thus have led to erroneous rejection of the null hypothesis by pure chance in some cases. However, five correlation remained significant also after correcting the results of False Discovery Rate (FDR) procedure.

The hypothesis of a significant *Chaoborus* impact on zooplankton seems to be corroborated by the low density of adults in the populations; in fact, the maximum peak in egg and juvenile production observed in May seems not to have resulted in an increase in the number of adults. The presence of *Chaoborus* strongly reduces the chances of individuals reaching maturity (Sell 2000, 2006). A slight increase of the total population density should have been observed in August due to the absence of a high predation rate.

Evolution towards larger body size is expected to occur in *Daphnia* populations exposed to chaoborid predation (Black & Dodson 1990; Stibor 1992). The *Daphnia* 'complex' of MG Lake don't show an increase in adult body size that is clearly related to size-selective predation (Fig. 5). Similarly, the high predation pressure did not result in morphological changes (e.g., neck teeth and tail spines).

Populations of cyclically parthenogenetic taxa reproduce asexually until unfavourable conditions arise (e.g., Gyllström & Hansson 2004). Under unfavourable conditions, males are produced parthenogenetically and then sexual females produce haploid eggs that are fertilized by these males, resulting in 'resting eggs' that are able to withstand extreme situations and that hatch upon the resumption of favourable conditions. The switch to sexual reproduction appears to be related to a deterioration in the environment due to over-crowding, reduced food, a change in temperature and photoperiod (Stross 1971; Korpelainen 1992; Spaak 1995; Deng 1996; Innes & Singleton 2000), or to predation (Nielsen *et al*. 2000; Cousyn *et al*. 2001).

If resting-egg production is the result of long-term adaptation to intense predation by *Chaoborus*, it is expected that males appear with an increase of dipteran density, while no significant positive correlations were found between male proportions and abundance of *Chaoborus* (Tab. 3). Since parthenogenic and amphigonic reproductions coexist throughout the year in MG Lake, another stressor factor probably exists and affects the populations over multiple years.

Overall, it seems that despite the apparent impact of *Chaoborus* on zooplankton in MG Lake no anti-predator strategies are developed. This failure to respond to changes in predation pressure might be related to an incapacity of prey to reliably detect chemical signals distributed by predators. Hunter & Pyle (2004) demonstrated that the chemical communication system between *Chaoborus* spp. and *D. pulex* was impaired by environmentally relevant concentrations of metals (Cu and Ni). The molecular mechanism that underlies chemoreception in invertebrates has been investigated only in *Caenorhabditis elegans* and *Drosophila melanogaster* and is not well understood in other invertebrate species (Krieger & Breer 1999). Metals may interfere with some process along the signal transduction pathway from kairomone reception to the production of morphological change, and elevated concentrations of Cu and Ni may alter the chemistry of kairomones or out-compete kairomone molecules at kairomone receptor sites (Hunter & Pyle 2004). At present, the mechanism of metal impairment of chemosensory function in *Chaoborus*-*Daphnia* predator-prey system remains unknown and warrants further investigation (Hunter & Pyle 2004), and involves a system in which emissions of mineral water from submerged springs result in elevated metal concentrations.

The concentration of dissolved metals in MG Lake is very high: mean concentrations of iron and manganese exceed 1200 µg L^{-1} and those of strontium reach 500 µg L^{-1} (see Fig. 1). We are not aware of any studies detailing any adverse effects of these dissolved metals on prey-predator systems; however, an influence cannot be excluded and their presence may interfere with the chemical communication system between *Chaoborus* and cladocerans. Larvae of *C. flavicans* seemed to top-down control the densities of zooplankton in MG Lake. Zooplankton organisms apparently fail to evolve effective strategies to minimise the risk of predation in this metal naturally rich lake, possibily because of an interference of metals with the chemical communication system of prey organisms. Zooplankton population declines could lead to a variation of the overall grazing rate, and to an increase in the abundance of phytoplankton which are typically grazed by zooplankton. This sort of top-down ecosystem disturbance could impact interactions at lower trophic levels and contribute to eutrophication (Sutor *et al*. 2001; Thorp & Covich 1991).

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