PRIMARY RESEARCH PAPER

Pelagic flatworm predation on daphniids in a subtropical reservoir: different effects on *Daphnia galeata* and on *Ceriodaphnia quadrangula*

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Abstract Following a reduction in fish populations in 2004–2005, a new, single annual pulse of pelagic flatworms was observed in early summer during 2006–2009 in Liuxihe, a freshwater reservoir in South China. As soon as these worms appear, *Daphnia galeata* retreats into dormancy, one month earlier (July) in the presence of flatworms than previously observed (August) with fish, while the population of the related *Ceriodaphnia quadrangula* tends to increase. We show, through in situ lake sampling, in large enclosures and by laboratory observations, that *Ceriodaphnia,* although perhaps competitively inferior in its ability to acquire algal food, has a higher tolerance to flatworm toxins. As a result, *Ceriodaphnia* manages to coexist with and proliferate in the presence of the flatworm. Observations in the laboratory suggest that flatworm population autoregulates by being sensitive to their own toxins and that *Ceriodaphnia*, even if prey to the worms, likely incurs more benefit than cost from their presence.

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Introduction

Typhloplanid flatworms, mainly *Mesostoma* and related genera, are widespread in the limnetic plankton of tropical and sub-tropical water bodies (Kolasa, 2001). In the temperate zone and in the arctic, they are more often sighted from the benthos-littoral (Maly et al., 1980; Schwartz & Hebert, 1986) and from temporary pools (De Roeck et al., 2005). They have been sighted from lakes in Africa (Rwanda), Sumatra, and the European Mediterranean region (Hutchinson, 1967; Dumont et al., 1973, Blaustein, 1990; Blaustein & Dumont, 1990; Caramujo & Boavida, 2000), in South America (Rocha et al., 1990), and also in South China. Not only are they present; they often are dominant, especially in open tropical waters (Rocha et al., 1990). They are carnivores that feed on a variety of small invertebrates, that include crustaceans, rotifers (Nandini et al., submitted), but also chironomids (Blaustein, 1990), and even larvae of bivalved mollusks (Delp, 2002). They stand out by their unique way of prey catching, frequently using toxins to sedate prey prior to consumption (Dumont & Carels, 1987;

Dumont & Schorreels, 1990). Almost all zooplankton groups, but especially cladocerans suffer from flatworm toxins, and these toxins may be persistent in the environment, at least for a while (Nandini et al., 2010). It is therefore regrettable that so little is known about the temporal and quantitative effects of flatworms on the dynamics of their prey—the mesocosm studies by Beisner et al. (1996, 1997) on temperature-mediated effects of *Mesostoma* on *Daphnia pulex* being a notable exception. However, it is still unclear whether all prey species react to the worm predator in the same manner, and whether there exist interspecific differences, as most information is based on observations on *Daphnia* and *Moina*.

In this investigation, we study the zooplankton of a subtropical reservoir in South China. We test the predation effects of planktonic typhoplanid flatworms on the dynamics of the two prey, the daphniid cladocerans, *Daphnia galeata* and *Ceriodaphnia quadrangula*, using field sampling, enclosure manipulation, and laboratory observations.

Materials and methods

This study was carried out at Liuxihe Reservoir (23°45′N, 113°46′E), a ca. 50-year-old impoundment in Guangdong Province, South China. It has a mean depth of 21 m, a maximum depth of 73 m, a volume of 325,000,000 m^3, a surface area of 15.25 km^2, and is thermally stratified all year round. The annual average precipitation is 2098 mm, and the climate has a rainy summer from April to September (flood season) and a dry winter from October to March (dry season). The natural crustacean zooplankton of the reservoir includes about eight cladoceran species, with the daphniids, *Daphnia galeata* and *Ceriodaphnia quadrangula,* being the largest and most abundant species. Invertebrate predators include *Chaoborus* larvae, and the large cladoceran *Leptodora richardi*. Fish predation used to be important, as 2 t of larvae (weight ca. 20 g per specimen) of pelagic fish (mainly *Aristichtys nobilis, Hypophthalmichthys nobilis,* and *H. molitrix*) were stocked at yearly intervals. Yearly stocking was necessary, because there was no natural reproduction of the fish in the reservoir. Stocking was stopped in 2003 and 2004, and a private company removed most fish from the lake in 2004–2005, with a peak removal of ca. 160 t in 2004 (Fig. 1). After the collapse of the pelagic fish population in 2004, the contract of the private company was terminated, and re-stocking by the local administration resumed, but at a much lower level: ca. 200 kg per year, about equaling removal by local fishermen and anglers (ca. 12 t per year).

Almost immediately after the manipulation (2005), a pelagic flatworm was spotted in the pelagic zone, particularly in early monsoon (May). The flatworm may have been present in the years prior to 2005 but at undetectable abundances, such that it was not recorded by Lin et al. (2003). It is ca. 2-mm-long, dark gray in color, and has a characteristically pointed head. Fixation and identification of such animals is difficult, but few live specimens submitted to the University of Hasselt, Belgium, led to the suggestion that it belongs to the genus *Rhynchomesostoma* of the family Typhloplanidae (Tom Artois, Hasselt, personal communication). We investigated

Fig. 1 Fish stocking to and removal from Liuxi He reservoir between 2001 and 2009. Raw data provided by the Liuxi He Reservoir Fishery group
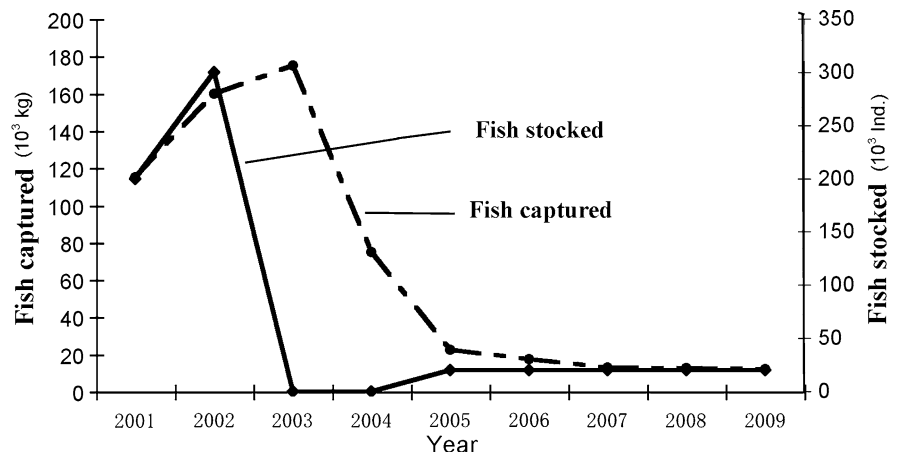
the temporal incidence of the worm and other zooplankton, sampling near the dam monthly from January 2001 till December 2005 and from May 2006 till August 2009, pumping water into a 5-l Van Dorn sampler, at 2-m intervals from 0.5 to 20 m. A single compound sample therefore represented 55–60 l in all. The water was filtered through a 50-μm mesh plankton net, and samples were preserved in 4% formalin added with sugar.

Phytoplankton was collected with the Van Dorn sampler at the same depths as zooplankton, conserved with formalin, and allowed to sediment in the lab for several weeks before the algal sediment was removed and counted under an inverted microscope. Numbers were converted to biomass using the method of Hillebrand et al. (1999). The period considered for phytoplankton was from May 2007 to December 2008.

A number of environmental variables were recorded together with the biological samples. Here, we only consider water temperature, recorded using an YSI model 85 instrument, at 1-m intervals. The average temperature over the top 20 m was calculated.

Furthermore, we used two replicate enclosures (encoded C2 and C3) to document the relationship between the flatworm and its potential prey in greater detail starting in late May 2009. Each enclosure was 4 m in length, 4 m in width, and 6 m in depth, and had a volume of ca. 85 m^3.

Enclosure C2 at the start of the manipulation was already rich in flatworms (density ca. 0.5 ind/l). They had abundant growth in the course of May 2009 by wiping out a rich population of *Daphnia galeata* inside this enclosure (*Daphnia* was the dominant zooplankton species before the flatworm invasion). On May 31, we first pumped 1/3 of the water in this enclosure to the lake, another one third to C3, and restored the full volume by pumping lake water (with natural zooplankton) at a rate of 10 m^3 per hour, to both enclosures. At the end, both enclosures contained the same volume of water, with flatworms from C2 (28.3 m^3) and the rest from the reservoir (56.7 m^3). Zooplankton observations were carried out from May 31 to August 9, 2009. Zooplankton in the enclosures was sampled every two days in the beginning and at 4 or 5 days intervals later.

In the laboratory, we maintained a stock culture of flatworms in plastic buckets of ca. 30-l volume, feeding them with mixed zooplankton at 3–4-day intervals and examining them visually daily. This culture was used as a source of worms that were transferred to Petri dishes and given *Daphnia* and *Ceriodaphnia* as prey. The predation acts were observed visually and recorded. We also set up cultures of *Daphnia* and *Ceriodaphnia* in 500-ml Erlenmeyer flasks, feeding them *Chlorella*, and examined the effect of adding water from the flatworm culture in a qualitative manner. About 50 ml of paper-filtered culture water of flatworms were added at intervals, and the effect thereof on survival and reproduction was evaluated qualitatively.

Statistics

The nature of the correlation between the two cladocerans and between each cladoceran and its worm predator was explored by calculating pairwise correlation coefficients. Because of non-normality of the cladoceran abundances in the reservoir, a logarithmic transformation of the biological variables was applied.

Results

Dynamics in the reservoir

Flatworms appeared during one period each year, sharply delimited in time, with peak abundances of 0.2–0.4 ind/l. They first appeared around May, and disappeared by the end of August (Fig. 2).

Daphnia galeata typically occurred only at times when flatworms were absent but at higher abundances than in the "fish period" (see Lin et al., 2003). It also avoided the hottest months of summer: a regression of abundance against temperature during 2001–2004 (the period before the appearance of the flatworms) showed a strong negative correlation ($r = -0.82$, $P < 0.001$), with no individuals surviving an average temperature of 25°C (Fig. 3). However, during 2006–2009, with flatworms present, this correlation collapsed and was only marginally significant ($r = -0.25$, $P = 0.075$, $n = 35$). The full disappearance of *Daphnia* also came on average one month earlier under the "flatworm predation regime" (Fig. 4A) than under the previous "fish predation regime" (Fig. 4B). In addition, there was a time gap between the yearly disappearance of the flatworms and the reappearance of *Daphnia*, while the disappearance of
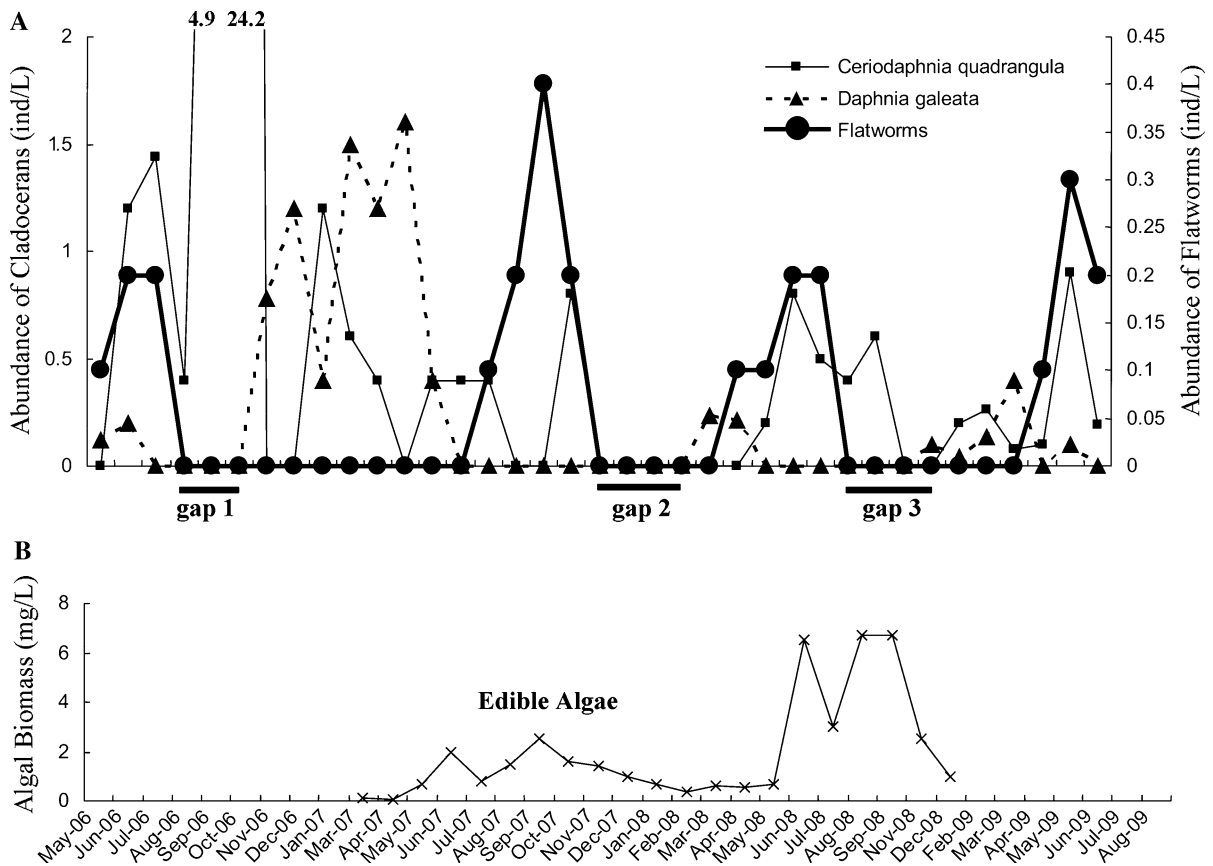
Fig. 2 **A** Phenology of *Daphnia galeata*, *Ceriodaphnia quadrangula,* and *Rhynchomesostoma* sp. in the top 20 m of the pelagic plankton of Liuxihe Reservoir. Note that the single annual peak of flatworms starts during a *Daphnia* phase, and is separated by a time gap from the next *Daphnia* peak. **B** Biomass of edible algae (2–30 μm in size) in 2007–2008, depleted during winter and during *Daphnia* peaks, but not during *Ceriodaphnia* peaks

Daphnia always overlapped with the first appearance of the flatworms (Fig. 2A). During 2001–2004, *Daphnia* predictably disappeared from the plankton around August, during 2006–2009 its yearly demise had shifted to July (Fig. 4). During 2006–2007 there was an unusually strong *Daphnia* development in the cooler parts of the year, starting in November 2006 and lasting until June 2007.

Ceriodaphnia quadrangula had a greater co-occurrence with flatworms than with *Daphnia*. Their correlation was significantly negative ($r = -0.3$, $n = 36$, $P = 0.03$), suggesting that one of the partners exploits the other (Fig. 2A). In contrast, flatworms and *Ceriodaphnia* were statistically unrelated ($r = -0.003$), whereas the correlation between *Daphnia* and *Ceriodaphnia* ($r = -0.15$, $n = 36$, $P = 0.18$) was negative, but statistically not significant, although the peaks of both species tended to

alternate with each other. Of the three species, *Ceriodaphnia* is the one that maintained a population in the pelagic zone for the longest duration.

Edible phytoplankton (2–30 μm) in 2007–2008 (Fig. 2B): after a depletion in March–April 2007, there was a pronounced summer peak that was followed by a second winter depression in 2007–2008 and a very strong peak in summer and autumn of 2008. Edible algae negatively correlated with *Daphnia* $r = -0.34$, $P = 0.07$, $n = 20$), at the limit of significance, and positively correlated to *Ceriodaphnia* ($r = 0.46$, $P = 0.02$, $n = 20$).

Dynamics in the enclosures

In both enclosures, flatworms were present from the very beginning (May), but only lasted until mid-July, a shorter period than in the reservoir (Fig. 5). On the
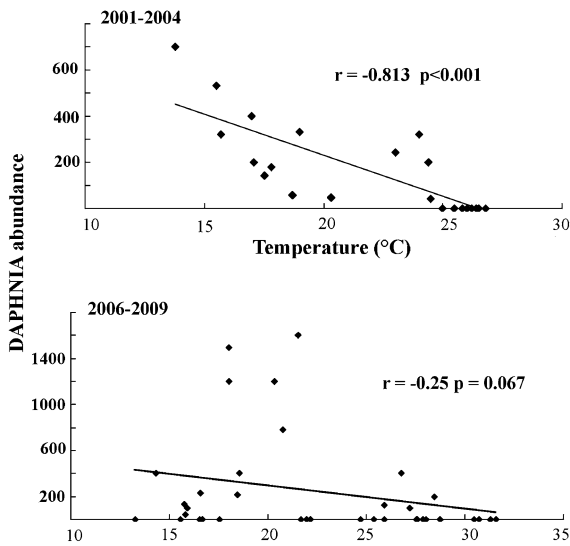
Fig. 3 Relationship between *Daphnia* and water temperature (top 20 m, averaged) in two study periods, 2001–2004 (fish) and 2006–2009 (flatworms). With fish present, *Daphnia* correlated strongly negatively with temperature under a continuous but tolerable predation pressure. With flatworms, under a time-focused but intolerable predation pressure, the correlation disappeared: *Daphnia* reached higher abundances before flatworm development, but collapsed at a temperature that was still favorable to it
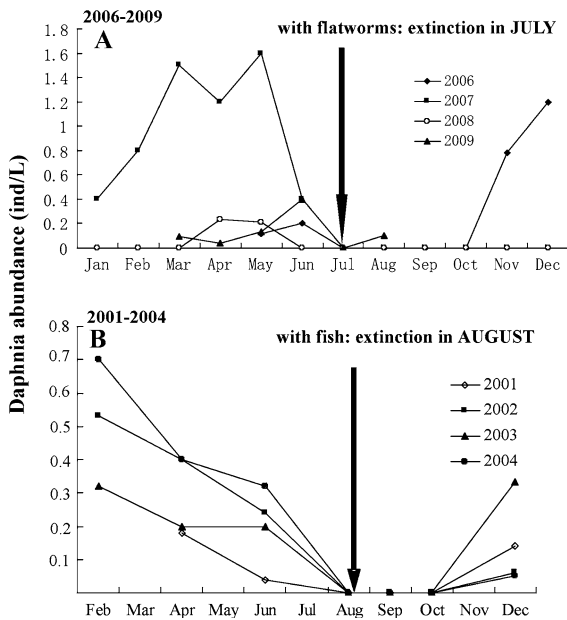

Fig. 4 Time of extinction (retreat into diapause) of the active population of *Daphnia* in Liuxihe: **A** with flatworms as the main predator (July), **B** with fish as the main predator (August)
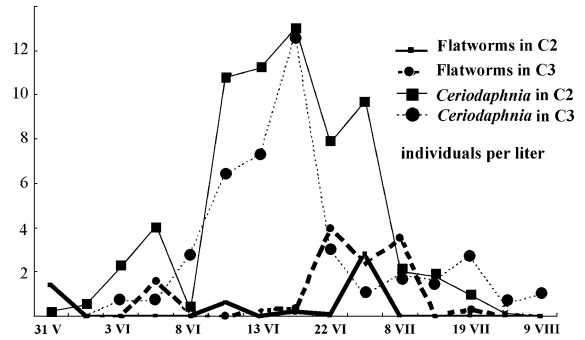

Fig. 5 Dynamics of *Daphnia* and *Ceriodaphnia* in two large enclosures during May–August 2009. Note that the toxic level in the enclosures was too high for *Daphnia* even at the beginning of the observations. *Ceriodaphnia* and the flatworms, in contrast, reached higher abundances than in the lake, with *Ceriodaphnia* only collapsing at concentrations of flatworms over 2 ind/L

other hand, their abundance was up to ten times higher than in the lake, reaching up to 3–4 per liter. *Daphnia* was absent, except in C2 until the first week of June. *Ceriodaphnia*, in contrast, had high densities during most of the observation period, peaking in June–July, and at abundances similar or somewhat higher than in the reservoir. Ephippium formation and males were observed as soon as abundance was ca. 2 ind/l. The brief appearance of *Daphnia* in C2 related negatively to *Ceriodaphnia* ($r = -0.90$, $P = 0.04$, $n = 4$), and somewhat less with flatworms ($r = -0.56$, $P = 0.2$, $n = 4$); in both enclosures, *Ceriodaphnia* was again unrelated to flatworms (C2: $r = 0.28$, $P = 0.15$, $n = 15$; C3: $r = -0.17$, $P = 0.29$, $n = 13$).

Cultures

Attempts to maintain permanent cultures of flatworms were initially not successful: as soon as abundances reached 1–2 ind/l, the animals stopped growing. Instead of more or less passively "hanging" in the water column, they started swimming around relentlessly and stopped feeding. After few days, the culture would die out. Better results were obtained if the culture medium was refreshed as soon as densities reached 2–3 per liter, which happened after 3–4 days when worms were fed with zooplankton ad libitum.

Daphnia and *Ceriodaphnia* cultures were maintained in triplo in about 500 ml of reservoir water in Erlenmeyer flasks; to these, up to 100 ml of water from a flatworm culture was added. The *Daphnia*

died within 12 h, whereas those in control bottles survived. The *Ceriodaphnia* survived and increased in abundance in both worm-conditioned and worm-free water, even if more worm water was added after few days. There was no obvious difference between *Ceriodaphnia* cultures to which worm water had been added, and those that had received only filtered reservoir water.

Microscopic observations

Occasionally, predation of flatworms on *Daphnia* and *Ceriodaphnia* was observed in a shallow petri-dish under a dissecting microscope: worms always attacked their prey from the dorsal side, striking at it once or several times. After a strike, *Daphnia* usually became motionless, but the heart kept beating and the limbs continued moving. *Ceriodaphnia* was attacked in the same way, but remained motionless for shorter period and escaped more frequently. Apart from that, both cladocerans were attacked and consumed equally well. Worms approached them as soon as they had become motionless and consumption proceeded by pumping the content of the prey body from the dorsal side. On average, consumption took not more than ca. 2 min, depending on prey size. In the case of big *Daphnia*, some worms were seen to penetrate the valves and consumed the prey from within.

Discussion

Like many snakes, free-living typhloplanid flatworms are poisonous carnivores. However, beyond this general statement, their ecology has long been neglected. The *Rhynchomesostoma* of Luixihe reservoir is rather a large and easily visible thermophilic animal that swims slowly and therefore faces a double problem: avoiding being eaten by carnivores larger than itself, and catching evasive prey. The flatworms' toxins do not seem to protect it against vertebrate predators: prior to the removal of fish from the lake, flatworms were not seen in the pelagic zone. It is therefore likely that before the elimination of fish, they were consumed along with other zooplankton, and were either much rarer than today or absent. Even during 2006–2009, they avoided the upper water layers: vertical sampling showed that they

aggregated at 8 m, about twice Secchi depth, and were seldom found at the surface in daytime.

To catch prey, flatworms have developed a technique, consisting of secreting mucus and simultaneously releasing toxins to the environment, which work by slowing down or at least sedating their prey to facilitate capture. Because reproduction in typhoplanids is mainly by parthenogenesis, and a large number of eggs may develop simultaneously, flatworms encountering a favorable feeding environment will typically develop exponentially. They can rapidly evolve from numbers so small as to go unnoticed to a hyper-abundance. In our enclosures, they initially found a plethora of food and deployed a rapid and short life history, usually emerging in late spring and disappearing in mid-summer. This disappearance of the flatworms was preceded by a short phase of dormant egg production. At first sight, this suggests that the worms die out after exhausting their prey. Indeed, when *Daphnia* got depleted, the worms rapidly collapsed in their turn. However, it is unlikely that this was the result of hunger alone, because their disappearance from the enclosures happened extremely rapidly, in a matter of one or two days, and preceded their demise from the reservoir by at least one month. Moreover, the elimination of *Daphnia*, at least in the semi-natural environment of the enclosures, was not only by consumption but by a poisoning of the prey, resembling a case of wasteful killing. Our laboratory cultures, especially the problems in keeping a flatworm culture healthy at higher worm concentrations, furthermore suggest that they may be susceptible to their own toxin if this becomes too concentrated.

Daphnia and *Ceriodaphnia* are both filter-feeders that collect particles down to a fraction of a micrometer in size (see Dumont & Negrea, 2002 for a discussion and additional references). The larger *Daphnia* is expected to have access to a wide range of food sizes but with an overlap with *Ceriodaphnia*. If the degree of conflict is dependent on the relative importance of the contested size fraction, then *Daphnia* should exert a more severe competitive influence on *Ceriodaphnia* than vice versa (Danie & Scott, 1982). In Liuxihe Reservoir, *Daphnia* builds a population in late autumn, and becomes abundant in winter and spring, but only as long as predators are absent. Until 2004, these predators were predominantly fish, and *Daphnia* retreated in dormancy by the

end of July (males and ephippial females seen), when *Daphnia* also reached the limit of its thermal tolerance. Under these conditions, *Ceriodaphnia* was a marginal species in the lake.

With the invasion of flatworms and their unique and destructive way of preying, the balance of competition was tipped. We hypothesize, based on our lab and enclosure observations, that it is *Daphnia*'s extraordinary sensitivity to flatworm toxin that led to its disappearance one month earlier than with fish as the dominant predator. *Ceriodaphnia,* which is clearly less sensitive to toxin than *Daphnia* (see also below), became a more dominant element of the plankton, at least during periods with flatworms prevalent. Although flatworms were visually confirmed to consume *Ceriodaphnia,* both the worm and the cladoceran coexisted. Further evidence that *Daphnia galeata* is sensitive to flatworm toxins also results from the fact that it does not re-appear immediately after the disappearance of the flatworms from the plankton (Fig. 2). This suggests that the toxins are persistent for a while, as noted in *Mesostoma lingua* (Dumont & Carels, 1987), and that *Daphnia* cannot recolonize before they have naturally degraded.

In the enclosures, the abundance of *Ceriodaphnia* increased up to 14 ind/l, while in the plankton, except for one brief peak in late summer 2006, they almost never reached higher than 0.4 ind/l (Fig. 5). Together with the qualitative indications from the cultures, we therefore conclude from this finding that *Ceriodaphnia* is not only capable of coexisting with a predator like *Rhynchomesostoma*, but obtains a net benefit from its presence.

The nature of that benefit, that appears worm-density dependent, is currently hypothetical and in need of further testing. We note that the competitively superior *Daphnia* is capable of limiting edible algal biomass in the reservoir (both are negatively correlated, i.e., *Daphnia* depletes algal biomass), while *Ceriodaphnia* is not (both are positively correlated, i.e., in spite of *Ceriodaphnia* grazing, algal stocks continue to be high). Possibly, *Ceriodaphnia quadrangula* is more specialized in its food requirements than we currently assume, but little study has been done on this species, compared to the numerous studies that deal with *Daphnia* (see Dumont & Negrea, 2002, for an overview). One distinct possibility is that *Ceriodaphnia* is selective

within the size range of 2–30 μm studied here, and possibly has a preference for smaller, bacterium-sized food items (cf. Pourriot, 1965). Planktonic blooms of bacteria require a large source of organic carbon as observed for blooms that have occurred in the Caspian basin after its invasion by the ctenophore *Mnemiopsis leidyi* (Shiganova et al., 2004). The source of organic matter in that case was mucus, released by the ctenophore. Flatworms, while swimming, not only release toxin but mucus as well, and we hypothesize that its breakdown by bacteria may be the resource utilized by *Ceriodaphnia*.

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