ORIGINAL ARTICLE

A long-term study on crustacean plankton of a shallow tropical lake: the role of invertebrate predation

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ABSTRACT

The primary factor that governs the size and species composition of zooplankton is still a controversial issue and temperature is considered the main factor responsible for latitudinal differences. In waters with a narrow temperature range, such as in the tropics, predation may be a more important factor. Nearly three decades of intermittent studies of the crustacean plankton in a shallow tropical lake revealed that the main event that led to their restructuring was the appearance of a second predator, the water mite Krendowskia *sp. The new predator and larvae of the dipteran* Chaoborus brasiliensis *Theobald exerted a combined, although asymmetrical effect on microcrustaceans. The period when the mite was detected was followed by the restructuring of the crustacean plankton community. Predation by these two invertebrates emerged as the factor responsible for community changes, involving an increased contribution of copepods and decreases in the relative abundance of smaller cladoceran species. In the short term, the mite caused a decrease in species richness and the annual mean instantaneous composition of cladocerans, a predominance of large-sized species (*Daphnia ambigua *Scourfield and* Daphnia gessneri *Herbst) and the virtual disappearance of small species (*e.g.,* Bosmina tubicen *Brehm). The long-term impact resulted in increased species richness and the dominance of large and medium-sized cladocerans, such as D. gessneri and Ceriodaphnia richardi *Sars. The larger body size of three cladocerans, the two* Daphnia *species and B. tubicen, in the long term, may be a response to the dominant predator,* Chaoborus. *The seasonal variation in the predator abundance, mainly* Chaoborus *larvae, allowed the prey to recover during the cool season. The copepods* Tropocyclops prasinus meridionalis *(Fischer) and* Thermocyclops decipiens *Kiefer were less affected by predation than the cladocerans; their contribution to the crustacean plankton increased 12-28% after the mite appeared. The top-down effect on crustacean plankton did not affect the phytoplankton, which remained dominated by chlorophyceans and the nanoplankton fraction before and after the zooplankton community restructuring.*

Key words: Copepods; cladocerans; chaoborid; water mite; species and size composition.

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INTRODUCTION

Long-term studies are essential for understanding ecological processes such as the influence of stressors and are basic for modeling, but are few in number because of their inherent difficulties, including costs (Jackson and Füreder, 2006; Maberly and Elliott, 2012). In particular, long-term studies of zooplankton can reveal the influence of past factors, including management decisions (Hambright, 2008). Some causes of changes in the zooplankton that are perceptible over a longer period include alterations of abiotic factors or predator invasion (Yan *et al.*, 2008).

The factors that affect the diversity and size of zooplankton species are intriguing issues, but still subject to controversy. From the classic paper by Brooks and Dodson (1965) to recent studies, several factors have been contemplated, and temperature has emerged as the preponderant factor for explaining latitudinal differences in zooplankton body size (Gillooly and Dodson, 2000). Gillooly and Dodson compared more than 1100 lakes lo-

cated between 81°N and 77°S latitude, and found that the size variation of cladoceran species was related to latitude, with smaller sizes in the tropics and the Arctic and a greater difference between the tropics and the temperate zone. According to these authors, the highest mean sizes were observed between 6°C and 8°C, declining at higher or lower temperatures. Havens *et al.* (2015), comparing 122 lakes located from 6° to 74°N and from 19° to 21°S, showed a relationship between size (as weight) of cladocerans and cyclopoid copepods and temperature. In contrast, Iglesias *et al.* (2011) suggested that predation by fish is the major factor explaining the smaller size of zooplankton in warm lakes. Hart and Bychek (2011), in their extensive review of the many factors that could potentially influence zooplankton size, addressed extrinsic factors such as temperature, food and predation, amongst others, besides intrinsic ones. The authors concluded, however, that although a general pattern may occur, different results can arise from distinct ecosystems.

Although in these ample compilations on size of microcrustaceans in lakes at different latitudes, temperature has emerged as the most important factor concerning physiological aspects, its influence has been revealed mainly on a macro scale. However, on a smaller scale within a narrower temperature range, such as in the tropics, other factors influence the composition and size structure of zooplankton communities.

Predation affects the size structure of the zooplankton community and the sizes of individual species, with direct and indirect effects on the community (reviews by Zaret, 1980; Kerfoot and Sih, 1987). The relationships between predators and zooplankton composition were summarized in a conceptual model, showing the strength of the different predatory actions (Lampert and Sommer, 2007, Fig. 6.33, p. 180). The species' sizes in a zooplankton community subjected to different predatory forces could be predicted, depending on the interaction between visual and non-visual predators in the ecosystem. Thus, the larger species would be visually preyed on and the small- and medium-sized ones would be preyed on by invertebrates, which are oriented by tactile stimuli. However, it is not always easy to distinguish clear patterns and zooplankton communities are generally composed of medium-sized species (Hart and Bychek, 2011). Furthermore, visual predation is not always determinant in controlling zooplankton, since tactile predation can play the main role (Blumenshine and Hambright, 2003). In some temperate lakes and ponds, the main controlling agent of zooplankton may be primary productivity (Finlay *et al.*, 2007) or temperature and pH (Steiner, 2004), rather than predation. Saunders *et al*. (1999), in their conceptual model of the influence of factors on planktonic herbivores (Fig. 10), highlighted food, temperature, and predation as major forces in lakes. However, the authors showed that the predation pressure differs in lakes at different latitudes, with a longer action period in tropical and subtropical lakes. Therefore, the predation pressure in warm lakes is stronger than in their temperate counterparts.

Planktivorous fish commonly occur in the limnetic zone of temperate lakes, particularly in eutrophic systems (Jeppesen *et al*., 2003). In contrast, omnivory predominates in tropical and subtropical lakes (Lazzaro, 1997; Jeppesen *et al*., 2007; González-Bergonzoni *et al*., 2012), except in some high-altitude tropical lakes in Ethiopia (Vijverberg *et al*., 2014). In addition, young and small-sized fish species that could potentially exploit zooplankton are mostly associated with the littoral zone in warm lakes (Fernando, 1994; Arcifa and Northcote, 1997; Meschiatti and Arcifa, 2002; Agostinho *et al*., 2003; Teixeira-de Mello *et al*., 2009), and are, therefore, segregated from the limnetic zooplankton. Predatory invertebrates can exert greater pressure on zooplankton if they are not strongly controlled by fish (Lampert and Sommer, 2007; Pinto-Coelho *et al*., 2008). However, when other factors, such as turbidity and dissolved oxygen, reduce the spatial

overlap between fish and *Chaoborus*, prey consumption by the dipteran larvae can exceed that of fish, becoming the major predatory force even when planktivores are abundant (Liljendahl-Nurminen *et al*., 2003).

Lake Monte Alegre is no exception, amongst warm lowland lakes, to the pattern of relatively low predation pressure on zooplankton exerted by visual predators. The only planktivore is represented by adults of the exotic cichlid *Tilapia rendalli* Boulenger, which are pump filter-feeders that consume mostly phytoplankton (Arcifa and Meschiatti, 1993, 1996). Larvae of the dipteran *Chaoborus brasiliensis* Theobald were earlier identified as the main predators in this lake (Arcifa *et al*., 1992), but in 1998-99 another invertebrate predator of zooplankton was detected, the water mite *Krendowskia* sp. (Cassano *et al*., 2002).

We investigated the species composition and size structure of zooplankton in Lake Monte Alegre, in intermittent studies during nearly three decades, addressing several issues: I. whether observed long-term changes in species composition and size of crustacean plankton were related to the detection of a new invertebrate predator, a water mite; II. predation by invertebrates is the main factor structuring the community; III. predation pressure varies seasonally, inducing higher prey abundance in the cool season, when predators are less abundant; IV. predation pressure is stronger on cladocerans than on copepods; V. the effects of the restructured microcrustacean community on the phytoplankton composition.

METHODS

Study area

Lake Monte Alegre (21°10'04"S, 47°51'28"W) is a small, shallow, eutrophic reservoir located in southeastern Brazil. It belongs to the warm discontinuous polymictic type (area: 7 ha; Z_{max}: 5 m; mean depth: 2.9 m; altitude 500 m asl). The reservoir was closed in 1942, by damming Laureano Creek in the Pardo River basin. In the warm season its stratification is relatively stable, leading to oxygen depletion near the bottom in the deepest part of the limnetic zone (Arcifa *et al*., 1990). Although Monte Alegre is a reservoir, it functions similarly to a natural shallow lake, due to certain features such as lack of manipulation of the dam and the outlet at the surface, and the relatively long retention time (*ca*. 45 days) for its dimensions. The regional climate is tropical, with a dry winter - Köppen Aw (Alvares *et al*., 2013) and a defined cool-dry season (May-September) and a warm-wet one (October-April) (Nimer, 1989).

In 1998-99, the fish fauna of the lake consisted of 9 species, mainly small- and medium-sized cichlids and characiforms, most of them inhabitants of the littoral zone and macrophytes (Meschiatti and Arcifa, 2002). The main food item of the fish fauna, in 1988-89 and 1998-99, was aquatic insects, with zooplankton representing a minor dietary item (Arcifa and Meschiatti, 1993; Meschiatti and

Arcifa, 2002). The planktivorous fish *T. rendalli* is diurnal, limnetic, not abundant, and did not cause a decrease in plankton abundance in mesocosm experiments (Silva *et al.*, 2014).

Larvae of *C. brasiliensis* (max length ~6 mm) are omnivores, III and IV instars feeding mostly on microcrustaceans and dinoflagellates (Arcifa, 2000; Castilho-Noll and Arcifa, 2007a). The larvae are more abundant in the benthos of the limnetic zone than in the littoral zone (Cleto-Filho and Arcifa, 2006), as well as in the water column of the limnetic zone. The water mite *Krendowskia* sp. (max length ~1.1 mm) is also a limnetic dweller (Arcifa *et al.*, 2013), but its densities are lower than those of *Chaoborus* larvae.

Sampling

Zooplankton and invertebrate predators were sampled in the periods 1985-86, 1988-89, 1998-99, 2001-02, 2006-07, and 2011-12. The sampling frequency was weekly (1985-86, 2011-12), biweekly (1988-89, 1998-99, 2006-07) and monthly (2001-02).

The organisms were always collected in the deepest area of the lake (5 m), which is the best site for planktonic organisms and representative of this small lake. They were collected vertically in the water column, with a 70 μm-mesh net, in the first two periods (1985-88, 1988-89, 2 replicates of 271 L each) and with a pump (Jabsco, model 34600-0000), delivering 30 L min⁻¹, in the remaining periods (1 sample of 120 L in 1998-99; 1 sample of 150 L in 2006-07; 2 replicates in 2001-02 and 3 in 2011-2012, filtering 150 L each). The invertebrate predators were not counted in all periods, but their occurrence was always recorded. At least three sub-samples taken with Stempel pipettes were counted on a gridded chamber under a stereomicroscope. Samples with low densities, larvae of *C. brasiliensis*, and the mite *Krendowskia* sp. were counted completely. Whenever possible, 30 of the standard size (largest adult individuals) of the most abundant cladoceran species were measured in samples in some of the study periods.

At the same station, phytoplankton samples were taken biweekly in the euphotic zone in 1988-89, and weekly in 2011 (April through June). Sedimented samples were counted under a Zeiss inverted microscope, according to Utermöhl (1958), in random fields (Uehlinger, 1964). Temperature, electrical conductivity (at 25°C), pH, dissolved oxygen (DO) and chlorophyll-*a* were measured in all periods. In the first two periods, the temperature was measured with a thermometer attached to a Ruttner bottle; the electrical conductivity and pH with the Metrohm E 382 and Orion (model 301) probes, respectively; and DO by the Winkler method. From 1998 onwards, Yellow Springs Inc. probes were used, models 95 (DO and temperature), 60 (pH) and 30 (conductivity). Chlorophyll-*a* was analysed by the method of Jeffrey and Humphrey

(1975), except in 1998-99, when the method of Lorenzen (1967) was used. The analyses of Total Nitrogen (TN) and Total Phosphorus (TP) followed the methodology of APHA (1995) and were performed for unfiltered water samples collected in 2011-12.

The data base of this study originates from articles covering the periods 1985-86 and 1988-99 (Arcifa *et al.*, 1992, 1998), and unpublished data from theses in the other periods. This data set was re-analysed to provide a long-term overview.

One-way ANOVA (*Post-hoc* Tukey test) was used for evaluating differences in mean densities of copepods and chaoborid larvae in the different periods. The differences for cladocerans were assessed by the Kruskal-Wallis test. Mann-Whitney (Statistica, StatSoft) was applied to test differences in mean densities of prey and predators between seasons and the size of cladocerans in the different periods. The Multi-Response Permutation Procedure (MRPP) was used to test the significance of the Detrended Correspondence Analysis (DCA). The factors used in the DCA were the annual mean density for each species in each period.

RESULTS

Abiotic features, including pH, electrical conductivity and DO were conservative during the nearly three decades of study. Their values in the surface layers, throughout the year, were 6-8 (pH), 50-80 μS cm⁻¹ (conductivity) and 80-120% oxygen saturation (DO). Concentrations of TN and TP, ranging from 229-961 μg L⁻¹ and 22-643 μg L⁻¹, respectively, were obtained in the surface layers, in 2011-12. Mean concentrations of chlorophyll-*a* showed interannual variations, with lower levels in 1998-99 and 2006-07 (Tab. 1). However, the lower concentrations in 1998-99, compared to most periods, may also be related to the method used (Lorenzen, 1967), which only considers active chlorophyll-*a*. The minimum temperatures in the cool season and the maximum temperatures in the warm season varied little across periods (Tab. 1).

Nine species of planktonic cladocerans and two cyclopoid copepods occurred in the course of the study period (Tab. 2). The 1998-99 period proved to be critical for the planktonic crustacean community and hereafter is termed the *key period*. This period was marked by the de-

Tab. 1. Annual mean concentrations (± SE) of chlorophyll-*a* and minimum and maximum temperatures during the study periods.

Period	Chlorophyll-*a* (μg L⁻¹)	Temperature (°C)
1985-86	22.91±1.38	18-31
1988-89	18.11±0.70	18-29
1998-99	9.07±0.90	20-31
2001-02	15.01±2.33	20-29
2006-07	8.82±0.62	19.5-29
2011-12	21.37±1.66	19-30

tection of the mite *Krendowskia* sp., which was virtually absent from the samples in previous periods. Ordering the periods and species revealed a clear and significant grouping (A=0.1163, P=0.03), and the key period (1998-99) was essential in separating a previous phase (1985-86 and 1988-89) from a later one (2001-02, 2006-07, and 2011-12) after the mite detection (Fig. 1). We do not know exactly when the mite appeared, since a decade elapsed between the previous sampling period (1988-89) and its appearance in significant numbers in 1998-99. However, based on the clear differences between the two groups of periods, before and after the mite was detected, we presume that it appeared or increased at some time close to the key period.

Some cladoceran species, such as *Daphnia gessneri* Herbst and *Bosmina tubicen* Brehm, underwent a significant increase in mean maximum size from the first to the last study period (Tab. 2). In two periods (1998-99 and 2011-12) the mean size of *Daphnia ambigua* Scourfield was larger than 1 mm, exceeding that of 1985-86. In nu-
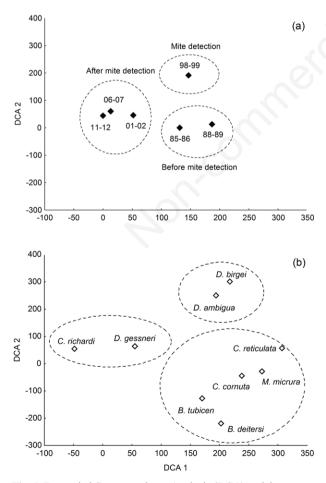
merical terms, copepods always dominated in relation to cladocerans, contributing ca. 67% before the key period, and 77-95% afterwards (Fig. 2). The number of cladoceran species, 5 to 7, was reduced to 3 in the key period (Fig. 3). The mean annual instantaneous composition of cladocerans was 4-5 species, and decreased to 2.4 in the key period.

Given their higher species richness, cladocerans were more appropriate for comparing the periods than were the copepods. Starting from 9 species in 1985-86, the species richness subsequently declined, with the virtual disappearance of *Bosminopsis deitersi* Brehm, *Ceriodaphnia reticulata* (Jurine) and *Moina minuta* Hansen (Fig. 4). *D. gessneri* was a constant species that contributed substantially to the cladoceran composition. *Ceriodaphnia richardi* Sars, on the other hand, was detected from 2001-02 onwards and continued to increase, reaching its highest value in the last period. The most remarkable event was the disappearance of the class of small-sized cladocerans and a clear dominance of the largest species in the key period (Fig. 5). The contribution of the small-sized class declined from 47% before the key period to 0.3-16% afterwards. The contribution of the medium- and large-sized classes increased after the key period, except in the last period (2011-12), when a medium-sized species dominated.

Annual mean densities of cladocerans varied amongst periods (Kruskal-Wallis test, H=34.6, P=0.000); one period (2006-07) showed a significantly higher mean density (70 ind L^{-1}). Cladocerans showed a trend towards a higher mean density in the cool season than in the warm one, with significant differences in the periods 1985-86 (P=0.001), 2001-02 (P=0.01) and 2011-12 (P=0.001) (Fig. 6a). Annual mean densities of copepods did not change significantly before and during the key period (1985-86, 1988-89, 1998-98), but showed a highly significant increase after the key period (2001 through 2012) (One-way ANOVA, F=221.05, P<0.001). Mean density of copepods showed no clear seasonal trend except in
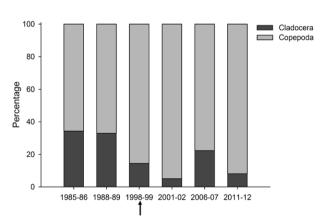

Fig. 1. Detrended Correspondence Analysis (DCA) and the groupings of periods (a) and species of cladocerans in the periods (b).

Fig. 2. Relative abundance of groups of microcrustaceans in the different periods. Arrow indicates the key period (1998-99).

2006-07, when the density increased in the cool season (P=0.001) (Fig. 6b).

The mean densities of *Chaoborus* larvae fluctuated significantly amongst periods (One-way ANOVA, F=365.5, P<0.001). There were no significant differences amongst the 1985-86, 1998-99 and 2006-07 periods, but densities were significantly higher in 2001-02 (2.3 ind L^{-1}) and 2011-12 (0.8 ind L^{-1}). A trend towards greater abundance of chaoborid larvae in the warm season was significant for three periods (1985-86, P=0.006; 2001-02, P=0.05; 2011-12, P=0.05) (Fig. 7). The same tendency was not found for mites, except in 2011-12 (P=0.001).
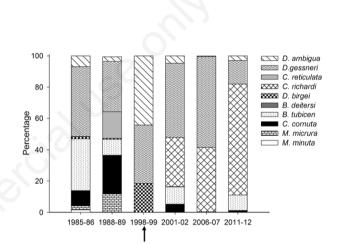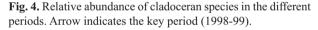
The phytoplankton was dominated by chlorophyceans before and after the key period, with cyanobacteria contributing 18 and 9.6%, respectively in 1988-89 and 2011 (Fig. 8). The phytoplankton fractions fluctuated, including seasonally, but on average the nanoplankton (≤ 20 µm) predominated overall.

DISCUSSION

The data showed no evidence of relationships between the changes in the structure of the microcrustacean community and the temperature and food in Lake Monte Alegre, in the long-term. In experiments, a lower temperature influenced several life-table parameters of three species

Fig. 3. Species richness of cladocerans and the mean annual instantaneous composition of species in the different periods. Arrow indicates the key period (1998-99).

Fig. 4. Relative abundance of cladoceran species in the different periods. Arrow indicates the key period (1998-99).

Tab. 2. Species and maximum length of microcrustaceans.

	Size±SD (mm) 1985-86	Size±SD (mm) 2011-12
Cladocera		
Large species		
Daphnia ambigua Scourfield	0.86±0.05	1.03±0.02
Daphnia gessneri Herbst	1.07±0.07	1.22±0.01**
Medium-sized species		
Ceriodaphnia reticulata (Jurine)	0.70±0.04	Absent
Ceriodaphnia richardi Sars	Absent	0.70±0.00
Diaphanosoma birgei Kořínek	0.61±0.02	Absent
Small species		
Bosminopsis deitersi Richard	0.32±0.05	Absent
Bosmina tubicen Brehm	0.41±0.06	0.58±0.02*
Ceriodaphnia cornuta Sars	0.46±0.03	0.49±0.01
Moina micrura Kurz	0.48±0.04	Absent
Moina minuta Hansen	0.45±0.04	Absent
Copepoda		
Thermocyclops decipiens Kiefer	0.74±0.03	No data
Tropocyclops prasinus meridionalis (Fischer)	0.49±0.07	No data

*Significant difference in length: *P=0.01; **P<0.001.*

of cladocerans from the lake, *D. ambigua*, *D. gessneri* and *M. micrura*, which showed significantly lower population growth rates at 19°C (winter temperature) than at 27°C (mean summer temperature) (Bunioto and Arcifa, 2007). However, although temperature could occasionally cause a decline in densities of cladocerans during the cool season, it is an unlikely explanation for the observed long-term changes, since the lowest winter temperatures were similar amongst the periods. Although in this lake food quantity and quality can be limiting during the cool season (Ferrão-Filho *et al*., 2003, 2005), there was no indication of a long-term influence on the microcrustaceans. Finlay *et al*. (2007), studying several temperate lakes, concluded that zooplankton were controlled mainly by primary productivity (bottom-up) and not by predators (top-down). However, the seasonal increase in food availability in Lake Monte Alegre, with higher primary productivity of the phytoplankton (1998-99; Feresin *et al*., 2010) or biomass (2011-12; Ferreira, 2013) in the warm season, did not result in corresponding increases of herbivorous microcrustaceans, particularly cladocerans (Fig. 6a).

The detection of the mite in the lake was the most striking event over 27 years, and its presence apparently changed both the species composition and the size and abundance of some microcrustacean species. Although members of its genus are considered benthic (Fernández and Fossati-Gaschignard, 2011), in this lake *Krendowskia* sp. was collected from both the bottom sediments and in the water column of the limnetic zone. The mite performed nocturnal vertical migration in 2001-02, when most individuals disappeared from the water column during the day. Therefore, in addition to the direct effect of predation by mites on the community restructuring, an indirect effect cannot be ruled out, which is the change in the migratory behaviour of *Chaoborus*, one of their prey (Cassano *et al*.,
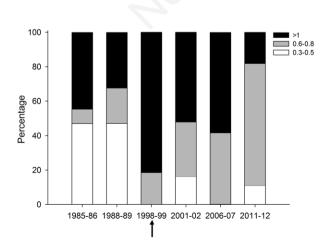
2002). The instar IV of *Chaoborus*, which migrated to the bottom sediments during the day, before the appearance of the mite (Arcifa, 1997), occupied the water column more after the key period, probably as a strategy to decrease overlap with mites at the bottom. This change in behaviour may have resulted in increased predation pressure by chaoborids on microcrustaceans, on a diel cycle.

Several studies have demonstrated the influence of mites on zooplankton species, depending on their density. Half of the mortality of *Bosmina* could be related to mite densities of 200-300 ind m^{-3} (Balseiro, 1992). Death rates of *Daphnia* and densities of mites were correlated, when the mites reached 400 ind m^{-3} (Matveev *et al*., 1989). In the key period in Lake Monte Alegre, the mites reached maximum densities of 312 ind m^{-3}, and in the summer of 1999, aggregates of 1800-2000 ind m^{-3} were recorded at night (Perticarrari, 2000).

Independently of species and their sizes, water mites prefer small- and medium-sized cladocerans, as reported by Gliwicz and Biesiadka (1975) and Riessen (1982); most of the species studied are larger than *Krendowskia*
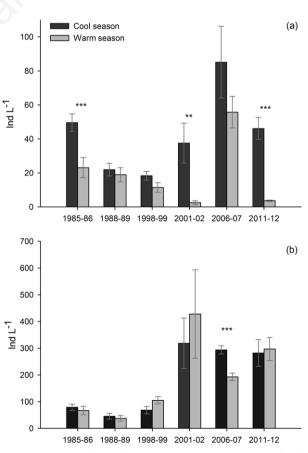

Fig. 5. Relative composition of size classes (mm) of cladoceran species in the different periods. Arrow indicates the key period (1998-99).

Fig. 6. Mean densities of cladocerans (a) and copepods (b) in the cool and warm seasons, in the different periods. Significant differences between seasons: **P=0.01; ***P=0.001.

sp. Adults of the mite *Piona constricta* (Wolcott) showed the following ranked prey preference: *Bosmina > Daphnia, Ceriodaphnia > Chydorus > Diaphanosoma, Diaptomus > Mesocyclops* (Riessen, 1982), *i.e.*, a small cladoceran species was the favourite prey. Riessen (1982) found that the ingestion time of *P. constricta* is proportional to prey size, from 3-5 min for *Bosmina* and young *Ceriodaphnia* to 35-40 min for the large *Daphnia pulex* Leydig. *B. tubicen* is the preferred prey of *Chaoborus* larvae in Lake Monte Alegre (Arcifa, 2000; Castilho-Noll and Arcifa, 2007a), and is possibly also preyed upon by mites. Its virtual disappearance from the limnetic zone in the key period was attributed to the pressure of the two invertebrate predators (Cassano *et al.*, 2002). *D. gessneri* was preyed upon in laboratory experiments (Cassano *et al.*, 2002), but in mesocosm experiments there was no evidence of a negative effect of the mite on its population dynamics (Castilho-Noll and Arcifa, 2007b), which may have contributed to its persistence in the lake. The presence of multiple predators can increase or decrease the impact on their prey (review by Sih *et al.*, 1998). The mite *Piona carnea* (Koch) exerted a negative effect on *D. pulex*, which depended on the system productivity and the mite density (Stegen and Black, 2011); however, predation by the mite and by *Chaoborus americanus* (Johannsen) had no combined effect, decreasing the risk for prey in their joint action. This conclusion is not supported by our results regarding the cladocerans in Lake Monte Alegre, where pressure by both predators decreased cladoceran abundance and species richness.

The increased contribution of copepods to the crustacean community after the key period is an indication that this group is subject to a lower negative impact of predation by invertebrates. Copepods are also resistant to predation by fish (Jeppesen *et al.*, 2001) and were preyed on by *Chaoborus flavicans* (Meigen) when cladocerans were scarce (Jäger *et al.*, 2011). In Lake Monte Alegre, *Chaoborus* consumed proportionally more copepods after the decline of the favourite prey *Bosmina tubicen* (Perticarrari *et al.*, 2004). Researchers studying Lake Monte Alegre have suggested that copepods are less sensitive to the effects of predation by invertebrates due to reproductive traits, such as greater fertility and more rapid development of eggs (Castilho-Noll and Arcifa, 2007b), and behavioural, such as reverse vertical migration (Perticarrari *et al.*, 2004; Minto *et al.*, 2010). The population dynamics of copepods was not affected by *Chaoborus* larvae in mesocosms (Castilho-Noll and Arcifa, 2007b), and they are not preyed on by the mite (Cassano *et al.*, 2002). Marine copepods detect predators by mechanoreception, and their myelinated nerves allow rapid conduction of impulses and consequent rapid escape movements (Buskey *et al.*, 2012). Some copepods, such as *Cyclops scutifer* Sars, can escape a predator at a speed of 50 cm s^{-1} (Strickler, 1975), an incredible velocity compared to cladocerans. They seem to detect chemical cues from predators,

amongst other skills to decrease predation risk (Heuschele and Selander, 2014). Sensitivity to kairomones released by *Chaoborus* was suggested to explain the reverse migration of copepods, from Lake Monte Alegre, in experiments (Minto *et al.*, 2010). This reverse-migration behaviour appeared after *Chaoborus* began to predate more intensely on copepods (Perticarrari *et al.*, 2004). Cladocerans from the lake, however, are more susceptible than copepods to predation by invertebrates (Cassano *et al.*, 2002, Castilho-Noll and Arcifa, 2007a,b). Apparently, *D. gessneri* is less sensitive to kairomones than copepods, and its diel vertical migration was related to physical contact with *Chaoborus* (Minto *et al.*, 2010). The small species *B. tubicen*, which comprised 53-56% of the diet of *Chaoborus* instars III and IV in the first period (1985-1986; Arcifa, 2000), disappeared from their diet in the key period (Castilho-Noll and Arcifa, 2007a), when it was also absent in the limnetic samples.

According to pioneer studies (Brooks and Dodson, 1965), small-sized zooplankton would dominate when
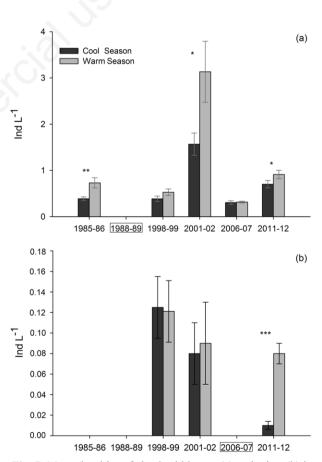

Fig. 7. Mean densities of chaoborid larvae (a) and mites (b) in the cool and warm seasons, in the different periods. Periods inside rectangles indicate that predators were present but were not counted. Significant differences between seasons: $^*P=0.05$; $^{**}P=0.006$; $^{***}P=0.001$.

planktivorous fish are abundant, and large-sized plankton when invertebrate predators predominate (Dodson, 1974), as summarized by Lampert and Sommer (2007; in Fig. 6.33). The decline in the contribution of smaller cladoceran species during and after the key period in Lake Monte Alegre reflects the greater influence of both invertebrate predators. Selective predation on smaller species or juveniles of larger species, related to the limitation imposed by the mouth size of *Chaoborus* larvae (Moore and Gilbert, 1987; Arcifa, 2000), influences the size composition of the community.

Not only can the size structure of the community respond to predation, but also the size structure within a population. The selection of larger phenotypes in some cladoceran populations can be a response to predation. Kerfoot (1974) reported that in a temperate lake, specimens of *Bosmina longirostris* (O. F. Müller) were larger in winter, when predation by fish decreased and the abundance of invertebrate predators (cyclopoids and chaoborids) increased. *Bosmina* can respond to changes in predation pressure by invertebrate predators with increasing size and change of some carapace structures, as reported in a review of paleolimnological studies (Korosi *et al.*, 2013). In Lake Monte Alegre in 2011-12, the size of *B. tubicen* and *D. ambigua* was significantly larger in the warm season compared to the cool one, when *Chaoborus* larvae were more abundant (Souza, 2015). Carter *et al.* (2008) observed a smaller body size of *D. ambigua* exposed to kairomones from a mite species, indicating that the response to predators can vary according to their type and selectivity. Life-table parameters of various *Daphnia* species changed when the cladocerans were exposed to kairomones of different predators, such as *Chaoborus*, *Notonecta* and fish (review by Riessen, 1999); the size at first reproduction was slightly larger under the influence of *Chaoborus* kairomones, whereas it decreased when in contact with kairomones of the other two predators. *Daphnia pulex* can reach a larger size when exposed to kairomones of *Chaoborus*, by controlling the growth rate (Beckerman *et al.*, 2010). Assuming that chaoborids induce an increase in the body size of prey and sucking predators (mites, notonectids) induce a decrease, the increase in body length of three cladoceran species in Lake Monte Alegre after the mite was detected could be a response to the most dominant predator, *Chaoborus*. A larger body size would be adaptive for the prey population to escape from at least one of the chaoborid instars. The increased body size of the small *B. tubicen* possibly prevented juveniles from being preyed on by the second instar of *Chaoborus*, which selects only immature individuals (Arcifa, 2000). Chaoborid larvae select only small juveniles of large species, such as *Daphnia* (Castilho-Noll and Arcifa, 2007a); although mites are able to prey on large specimens (Cassano *et al.*, 2002), they seem to prefer small prey. We can hypothesise that even a small reduction in predation on *Daphnia*

species due to a larger body size would be advantageous to the populations.

The trend towards greater abundance of *Chaoborus* in the warm season, and the presence of the mite, indicate that predation by both invertebrates is a key factor for the lower abundance of cladocerans in that season. The lack of a clear seasonal variation in copepod density through five periods is consistent with the smaller negative predator effects on them than on cladocerans. An increase in the abundance of *Chaoborus* larvae due to the introduction of piscivorous fish, which has caused changes in the fish fauna in Brazilian lakes, has driven the disappearance of cladocerans and the dominance of copepods in the lakes most heavily stocked by chaoborid larvae (Pinto-Coelho *et al.*, 2008), giving support to our conclusion.

Predation by two limnetic invertebrates emerged in this study as a major force in structuring the plankton community in Lake Monte Alegre, on a macro scale, in the course of almost three decades. The impact of increased predation, detected in the key period, led to a predominance of large-sized cladocerans and the
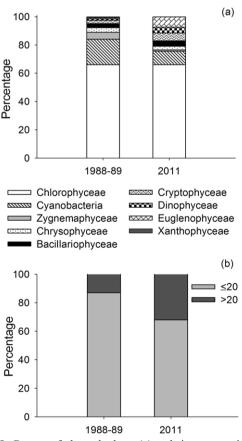

Fig. 8. Groups of phytoplankton (a) and size composition (b) in periods before and after the key period. Nanoplankton (≤20 μm) and microplankton (>20 μm). Source: Silva, 1995 (*and unpublished data*).

disappearance of small species. A new structuring of species dominance, with a preponderance of copepods and a medium-sized *r*-strategist cladoceran (*C. richardi*), which is competitively superior to a larger species (*D. gessneri*) (Ferreira, 2013), was apparent in the last two periods. The success or recovery of some populations after the key period may be related to the ability to occupy also the littoral zone of the lake, where *Chaoborus* and mites are less abundant, as observed for *B. tubicen* (Arcifa *et al*., 2013; Souza, 2015). We presume that these areas are not permanent habitats, but serve to maintain a minimum population density and enable the reoccupation of the limnetic zone when conditions are more favourable, as we are observing for *B. tubicen*.

An invading species can affect the zooplankton community structure. An example is the predacious cladoceran *Bythotrephes*, which initially caused a decrease in the zooplankton diversity, but a long-term restructuring of the community eventually led to increased diversity (Kelly *et al*., 2013). Comparing Canadian and Norwegian lakes, the authors concluded that changes in species interactions, development of anti-predator strategies, and adaptation to the presence of predators have contributed to the increase of remnant populations, some decades after the *Bythotrephes* invasion. In Lake Monte Alegre, after a decade, a new structuring of the microcrustaceans' community has established the dominance of species that are less sensitive to predatory effects, *i.e.*, that are less impacted by predation or have anti-predator strategies and higher reproductive rates.

The coincidence between low chlorophyll-*a* concentrations and the highest densities of cladocerans, comparing all periods, ca. 58% composed of a large-sized species, in 2006-07, suggests the control of phytoplankton by zooplankton. The restructuring of the microcrustacean community could theoretically be reflected in the phytoplankton through a top-down effect. Increased copepod dominance together with the predominance of large- and medium-sized cladocerans might lead to changes in the phytoplankton composition. The most abundant species of cyclopoid copepod, *T. prasinus meridionalis*, was successfully reared in the laboratory from nauplii to adult on a diet of seston <20 µm and cultured green algae *Scenedesmus spinosus* and *Ankistrodesmus falcatus* (Minto, 2009), suggesting that herbivory is its predominant habit. However, comparison of the phytoplankton biomass and composition in different periods, before and after the key period, indicates that the top-down effect on zooplankton does not cascade to the phytoplankton in the long-term.

CONCLUSIONS AND FINAL REMARKS

On a macro scale, over almost three decades of intermittent studies, predation by invertebrates was the predominant factor influencing the species composition and size structure of planktonic microcrustaceans in Lake Monte Alegre. The appearance of a second predator initially increased the pressure on the smaller cladoceran species, leading to the dominance of large- and medium-sized species in the long term. Before the mite appeared, predation by instars III and IV of *Chaoborus*, with mean densities of about 0.5 ind L^{-1} and a lower spatial overlap with prey, due also to the diurnal migration of the larvae to the sediment, allowed populations of smaller species to persist. The mite increased the predation pressure on microcrustaceans, especially on smaller species; its predation on *Chaoborus* has induced changes in the diel vertical migration of instar IV, increasing the impact of this instar on its prey.

The mite is usually not abundant, and its erratic and uncoordinated movements are not well adapted to planktonic life, in Lake Monte Alegre. *Krendowskia* sp. differs from other mite species that are more adapted to open waters, such as *Piona limnetica* Biesiadka (Gliwicz and Biesiadka, 1975). Even so, there was a combined effect of both predators, although the effect of mite predation is lower than that of the chaoborid larvae, as the prey responses seem to be more related to *Chaoborus* than to the impact of the mite.

Lampert and Sommer (2007) outlined the possible changes in the structure of the zooplankton community in response to predation. The situation in Lake Monte Alegre could be identified with their Fig. 6.33a, due to the absence of vertebrate visual predators and the presence of two invertebrate predators in the limnetic zone. Our long-term study showed that there was a period (key period) similar to the diagram of Fig. 6.33a, with a predominance of larger cladoceran species. Higher predation pressure from both predators clearly impacted the smaller species, leading to their virtual extinction in the limnetic zone. After a longer period, however, the community structure departed from the diagram of Lampert and Sommer, due to the increasing dominance of a medium-sized species.

This change in the microcrustacean composition, after the initial impact of a new predator, agrees with the observations of Kelly *et al*. (2013) and Yan *et al*. (2008), amongst other examples. Similarly to the Canadian lakes that they studied, a short-term impact, following the detection of the mite in Lake Monte Alegre, resulted in a marked decrease in species richness. In the long term, however, the species richness increased, as in the Norwegian lakes. This difference between the short- and long-term composition and size of the community indicates that a new equilibrium was reached after a longer period of coexistence with the new predator in the lake.

The difficulty of predicting the impact of a predator in the long term resides in the dynamic nature of zooplankton communities, which can adapt to the new conditions and the new predator, including species replacement. In addition, other factors in the ecosystem may influence the species differently, with opposing ef-

fects, for example, predation inducing a smaller size range and competition tending to expand the size range (Quintana *et al*., 2015). To date, about 12 years after the greatest impact of the new predator (key period), we observe an increasing contribution of a medium-sized, *r*-strategist and competitively superior species (Ferreira, 2013), which can also inhabit the littoral zone of the lake where *Chaoborus* and mites are almost absent (Souza, 2015). At the same time, there has been a partial recovery of small-sized populations, such as *Bosmina*, and an increase in species richness, which is comparable to the pre-mite period. Successful behavioural strategies to reduce predation may have been selected, *i.e.*, reducing the spatial overlap with the predominant predator (Souza, 2015), as well as increasing body size, which is apparently advantageous for decreasing *Chaoborus* predation. The ability of some species, such as *B. tubicen*, *D. birgei* and *C. richardi*, to occupy the littoral zone and also the uppermost layer of the water column, seems to provide protection against both invertebrate predators. In addition to prey strategies, the seasonal variation in predation pressure, with lower abundance of the predators, particularly *Chaoborus*, in the cool season, also provides a seasonal refuge for prey. The spatial refuge is also enlarged in the cool season when the entire water column is available, since dissolved oxygen is not limiting below 3-3.5 m as in the warm season. A thicker oxygenated layer allows more space for evading predators using certain strategies such as diel vertical migration (Perticarrari *et al*., 2003, 2004).

The classic trophic chain of many temperate lakes (piscivorous fish – planktivorous fish – zooplankton, planktivorous invertebrates – phytoplankton) (Carpenter *et al*., 1985) does not apply to Lake Monte Alegre or to most warm lakes. The main reason is that visual predators occur mainly in the littoral zone (Fernando, 1994; Arcifa and Northcote, 1997; Meschiatti and Arcifa, 2002; Agostinho *et al*., 2003; Teixeira-de Mello *et al*., 2009) and are omnivores (Lazzaro, 1997; Jeppesen *et al*., 2007; González-Bergonzoni *et al*., 2012), with some exceptions. Predation on invertebrate predators, namely *Chaoborus* larvae, is exerted by omnivorous rather than planktivorous fish, whereas mites are rarely preyed on by fish in the lake (Meschiatti and Arcifa, 2002). The trophic structure in the lake departs in some aspects from the conceptual model presented by Carpenter *et al*. (1985; Fig. 2) and can be roughly outlined as follows: piscivorous fish – omnivorous fish – invertebrate predators – zooplankton – phytoplankton. The control exerted by crustacean plankton on phytoplankton seems to be less efficient in this lake than in temperate systems, where the classic trophic chain and larger herbivorous microcrustaceans are established.

We can conclude that the structure of the crustacean community is better understood in long-term studies, although these are not always feasible. The value of this study is the large data set with support from several individual studies, and the possibility to extrapolate the findings to other lakes with similar basic characteristics, without the need of further local long-term studies.

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