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Predation on and by pelagic Turbellaria in some lakes in Brazil

Odete Rocha[1], Takako Matsumura-Tundisi[1], José Galizia Tundisi[2] & Claudia Padovesi Fonseca[3]
[1]*Federal University of São Carlos – Laboratory of Limnology*; [2]*University of São Paulo – Canter of Water Resource and Applied Ecology*; [3]*Post-graduate student – University of São Paulo*

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Abstract

Planktonic Turbellaria are of common occurrence in both natural and man-made lakes in Brazil. Experiments were performed in 1987 and 1989 to determine which zooplankton species are consumed by predatory *Mesostoma* sp. from three natural lakes in the Rio Doce Valley. Experiments were also performed in 1989 with a yet unidentified flatworm from Barra Bonita reservoir. Both predators consumed *Daphnia* and *Ceriodaphnia* at a high rate: 4 individuals per day in the case of *Mesostoma* sp., a large species and 1.5 ind day^{-1} in the case of the smaller species from Barra Bonita reservoir. Consumption of copepod nauplii, copepodids and adults was much lower, and Ostracoda were not consumed at all. Experiments on food selectivity showed a clear preference by the flatworms for cladocerans.

In the lakes studied, flatworms are heavily preyed upon by larvae of *Chaoborus* and by *Mesocyclops* species.

Turbellaria densities in the natural lakes were around 300 individuals per cubic meter, whereas in Barra Bonita reservoir, 1000 individuals per cubic meter was a mean value in a fifteen days study.

Introduction

Besides food limitation, predation by either vertebrate or invertebrate predators has a decisive effect in structuring zooplankton communities (Macan, 1977; Lane, 1979; Anderson, 1980). A variety of invertebrate predators can be found in most water bodies, and their particular effects and interactions have attracted the attention of many planktonologists in recent years. Most studies have emphasized microcrustaceans, rotifers or midge larvae, due to their importance in terms of numerical density and biomass, and perhaps because of their conspicuousness. In many plankton studies, and at least in those performed in tropical fresh waters, the occurrence, distribution, abundance and predator-prey interactions of planktonic Turbellaria have been neglected. One reason for this is that flatworms do not often form a substantial component of the zooplankton community, and thus do not appear in samples of small volume. Another reason is the difficulty of their identification in preserved samples.

There are few studies which have quantified planktonic Turbellaria predation. Maly *et al.* (1980) examined the effect of the flatworm *Mesostoma ehrenbergi* on zooplankton inhabiting small high altitude ponds in western Colorado. They found that flatworm predation had an important effect on a *Daphnia middendorffiana* population. For the same flatworm species, Schwartz & Hebert (1982) determined predation rates on pond populations, and found it to be a voracious predator, eating more than 10 prey per day. It preferred *Daphnia pulex*, *Daphnia laevis* and *Simocephalus vetulus*. Collins & Washino (1979, 1980) examined the effect of predation of two microturbellarians, *Mesostoma lingua* and *Rhynchomesostoma rostratum*, on the abundance of mosquito larvae in California rice fields. They observed that flatworms preferred soft bodied oligochaetes and mosquito larvae, but also consumed microcrustaceans and other aquatic insects. They suggested that *M. lingua* is an important natural predator of *Culex tarsalis* and could be used in mosquito control. Similar findings from a field study in experimental rice plots are presented by Blaustein & Dumont (this volume).

In all works dealing with predation, *Mesostoma* were considered as benthic animals, crawling along surfaces of substrates. However, Dumont *et al.* (1973) found a pelagic rhabdocoelid in Dayat Ifrah, a Moroccon Atlas lake, and cite three other records of truly planktonic rhabdocoelids, two of which deal with tropical lakes.

In the Rio Doce Valley lakes, Brasil, our attention became focused on a pelagic *Mesostoma* when, during an investigation on *Chaoborus* emergence by Fukuhara (1989), a large number of flatworms were captured by the insect emergence trap. We here present some results on predation experiments with two different species of pelagic flatworms as well as some information on their natural densities, vertical migration, and vertical distribution.

Material and methods

Mesostoma sp was collected in lake D. Helvecio using a *Chaoborus* larvae trap. Animals migrating to the surface during the night were captured and removed early in each morning. In the laboratory, they were maintained in filtered lake water and fed *Ceriodaphnia* and *Daphnia* neonates.

The flatworm from Barra Bonita reservoir was sampled by vertical and horizontal net hauls in the open water.

Predation experiments were carried out in 250 ml beakers filled with 200 ml of lake or reservoir water. Predator density was 3–5 flatworms and prey density was 30–50. Only one type of prey was offered at each time. Before each experiment, flatworms were starved for 24 hours and maintained at the experimental temperature. All experiments were run at 24 $\pm$ 2 °C and under reduced light. Experiments lasted 4–6 days and prey were replaced daily. After 24 hours, predators were counted and transferred to another experimental flask with the initial prey concentration. The remaining prey were killed and counted. *Mesostoma* offspring produced were removed and counted. Empty carapaces were checked for attack marks.

Feeding experiments were also performed with the well known invertebrate predators *Mesocyclops longisetus* and *Chaoborus* larvae. A food preference experiment was done by offering multispecific prey assemblages. All experiments lasted 6 days and replacement of prey species was carried out each day in equal numbers to those killed, in order to maintain a constant number of prey per day.

Zooplankton samples from previous studies (Matsumura-Tundisi, 1985; Matsumura-Tundisi *et al.*, 1989) were analysed in order to determine natural flatworm densities, as well as their vertical distribution and diurnal migration in the Rio Doce Valley lakes. Samples were taken on one day between 10:00 and 11:00 hs. Data from Barra Bonita reservoir were obtained by a 15 days daily sampling study carried out during March 1988. In both places, lake and reservoir zooplankton was sampled at different depths by pumping 200–400 litres of water, filtered through a net of 68 μm mesh size. All samples were preserved in 4% formaldehyde.

Results

Experimental feeding rates of flatworms on different zooplankton species

Experiments performed with *Mesostoma* sp (size range: 3-4 mm) and various zooplankton prey show that this flatworm consumes *Daphnia laevis* (mean size: 0.8 mm) and *Ceriodaphnia silvestris* (mean size: 0.4 mm) at high rates, 3.75 (SE: 1.49) and 4.44 (SE: 1.25) prey ind^{-1} day^{-1} respectively (Table 1). It can consume nauplii (0.25 mm) and adults of *Argyrodiaptomus furcatus* (1.2 mm), but here a large variation among replicates and different days of the experiment occurred (Table 2).

In experiments with the omnivorous cyclopoid *Thermocyclops minutus* and with the ostracod *Physiocypria* sp., *Mesostoma* sp was found capable of consuming these prey, but with an extremely large variation between replicates (Table 3).

Another set of feeding experiments were carried out with a relatively abundant pelagic flatworm from Barra Bonita reservoir. This – yet unidentified – flatworm is smaller than *Mesostoma* sp from lake D. Helvecio (size range 1.5 to 2.5 mm) and has a distinct shape.

The results of the experiments are presented in Tables 4 and 5. They are similar to those obtained for *Mesostoma* sp., except that the rates are much lower. The daily prey consumption by a flatworm was 1.70 ± 0.41 for *Ceriodaphnia silvestris* and 1.41 ± 0.68 for *Daphnia laevis* neonates. The Barra Bonita flatworm showed a comparatively higher rate of predation on nauplii and adults of

Table 1. Number of organisms consumed by *Mysostoma* sp. from lake D. Helvecio on consecutive days, feeding upon two species of cladocerans, predation rates are expressed in prey ind.$^{-1}$ day^{-1} (mean values).

Prey	Consecutive days	Replicates			
		1	2	3	4
Ceriodaphnia silvestris	1	12	20	15	10
	2	16	16	14	11
	3	19	19	17	12
	4	14	8	6	14
	5	8	8	12	16
	6	14	14	14	10
	Predation rate: 4.44				
Daphnia laevis	1	15	10	18	16
	2	9	6	11	12
	3	11	8	13	17
	4	13	3	17	10
	5	16	0	14	13
	6	14	0	10	14
	Predation rate: 3.91				

Table 2. Number of organisms consumed by *Mesostoma* sp. from lake D. Helvecio fed on nauplii and adult of *Argyrodiaptomus furcatus* on consecutive days. Predation rates are expressed in prey ind.$^{-1}$ day^{-1} (mean values).

Prey	Consecutive days	Replicates			
		1	2	3	4
Adult	1	1	2	1	0
	2	0	3	1	1
	3	1	0	2	4
	4	1	0	0	2
	5	2	1	0	1
	6	0	0	0	1
	Predation rate: 0.33				
Nauplii	1	7	2	0	3
	2	1	5	11	1
	3	5	4	1	0
	4	5	3	1	5
	Predation rate: 1.06				

Table 3. Number of *Thermocyclops minutus* (Cyclopoida) and *Physiocypria* sp. (Ostracoda) consumed by *Mes ostoma* sp. from lake D. Helvecio on consecutive days. Predation rates are expressed in prey ind.$^{-1}$ day^{-1}.

Prey	Consecutive days	Replicates			
		1	2	3	4
Thermocyclops minutus	1	0	0	0	–
	2	1	0	0	–
	3	2	1	0	–
	4	4	0	0	–
	Predation rate: 0.22				
Physiocypria sp.	1	0	1	0	0
	2	0	0	0	0
	3	0	0	0	0
	4	0	0	0	0
	Predation rate: –				

Table 4. Number of *Ceriodaphnia silvestris* and *Daphnia laevis* (neonates) consumed by the flatworm from Barra Bonita reservoir on consecutive days. Predation rates are expressed in prey ind.$^{-1}$ day^{-1}.

Prey	Consecutive days	Replicates			
		1	2	3	4
Ceriodaphnia silvestris	1	6	9	12	12
	2	6	7	7	8
	3	9	7	7	10
	4	7	8	9	12
	Predation rate: 1.70				
Daphnia laevis	1	8	9	9	4
	2	6	6	11	3
	3	13	4	6	3
	4	14	4	5	6
	Predation rate: 1.41				

Table 5. Number of nauplii and adults of *Notodiaptomus iheringi* consumed by the flatworm from Barra Bonita reservoir on consecutive days. Predation rates are expressed as prey ind.$^{-1}$ day^{-1}.

Prey	Consecutive days	Replicates			
		1	2	3	4
Adults	1	0	2	3	3
	2	0	2	4	2
	3	2	5	4	4
	4	0	2	4	1
	Predation rate: 0.46				
Nauplii	1	11	9	13	16
	2	4	8	10	0
	3	4	1	13	0
	4	6	12	10	7
	Predation rate: 1.56				

Notodiaptomus iheringi than the D. Helvecio flatworm.

Results from the food preference experiments (Table 6) reveal a preference of *Mesostoma* for the cladocerans *Daphnia* and *Ceriodaphnia*. *Daphnia laevis* neonates were consumed at a slightly higher rate than *Ceriodaphnia silvestris*, a result somewhat different from that obtained in the one prey species experiments. In general the results obtained from monospecific prey experiments were validated by the results from the multispecific ones: cladocerans are eaten at higher rates than copepods, and ostracods are very rarely eaten.

Mesocyclops longisetus and Chaoborus larvae as predators of Mesostoma sp.

It was observed that the flatworms were themselves preyed upon by *Mesocyclops* and *Chaoborus*. The results presented in Tables 7 and 8 reveal that both species can heavily prey upon flatworms, and that *Chaoborus* larvae are espe-

Table 6. Feeding preferences of *Mes os toma* sp. fed with a multispecies prey assemblage. Numbers represent total numbers of individuals of each species consumed.

Species	Trial 1 n°. ind (%)	Trial 2 n°. ind (%)	Trial 3 n°. ind (%)	Trial 4 n°. ind (%)	Mean (percentage)
Daphnia laevis (neonate)	27 (90)	21 (70)	29 (90)	19 (63)	80
Ceriodaphnia silvestris	19 (63)	17 (57)	21 (70)	16 (53)	61
Argyrodiaptomus furcatus (nauplii)	08 (27)	04 (13)	10 (33)	05 (17)	20
Argyrodiaptomus furcatus	02 (07)	07 (23)	06 (20)	09 (30)	20
Physiocypria sp.	00 (00)	01 (03)	01 (03)	00 (00)	02
Thermocyclops minutus	01 (03)	06 (20)	02 (07)	03 (10)	10

Table 7. Predation of *Mesocyclops longis etus* on *Mes os toma* sp. – Number of organisms consumed on consecutive days; mean value of predation rate is expressed as prey ind.$^{-1}$ day^{-1}.

Consecutive days	Replicates 1	2	3	4
1	4	2	4	7
2	5	5	3	1
3	4	6	4	1
4	4	5	5	2
	Predation rate: 1.29			

Table 8. Predation of *Ch aob orus* larvae (instar IV) on *Mes os toma* sp. Mean value of predation rate is expressed as prey ind.$^{-1}$ day^{-1}.

Replicates	Exposure time in hours 05h	12h	24h	Total consumed
1	10	6	9	25
2	12	6	4	22
3	18	1	11	30
	Predation rate: 8.55			

cially voracious, consuming up to 10 flatworms per individual per day.

Analysis of natural flatworm populations in different lakes

Figure 1 shows the vertical distribution of different components of the zooplankton community, including Turbellaria, during the circulation period (July, 1983). The depth distribution is shown as a percentage of the total for each population. The pattern of distribution of *Mesostoma* is similar to that displayed by rotifers, cladocerans and copepods, showing a peak of density between 2.0 and 5.0 m depth. In Fig. 2, the vertical distribution of *Mesostoma* is compared with that of other groups during lake

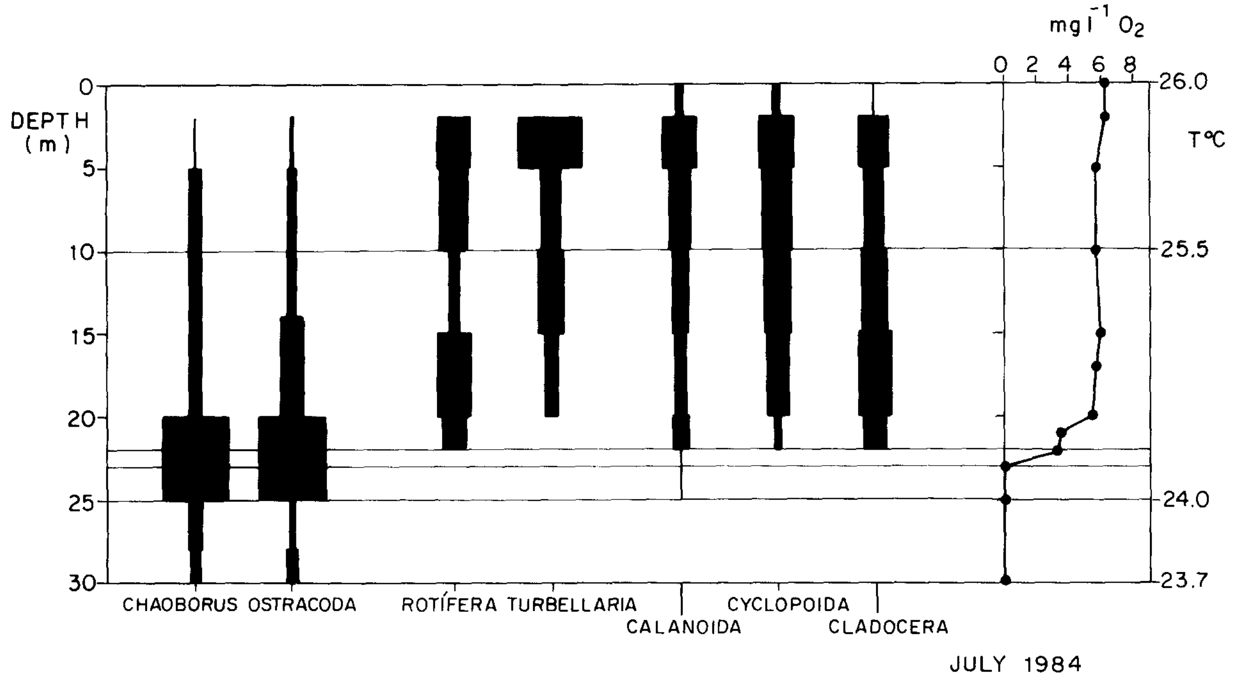

Fig. 1. Vertical distribution of zooplankton groups in lake D. Helvecio during circulation in terms of relative abundance. Isotherms and the profile of oxygen concentration are presented together.

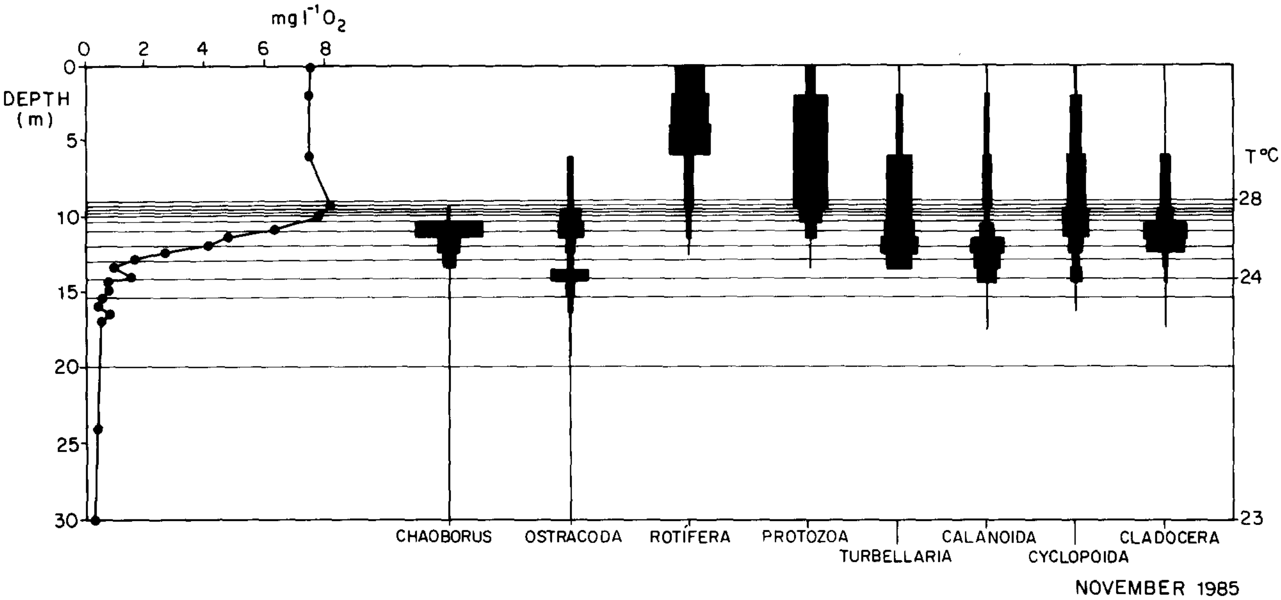

Fig. 2. Vertical distribution of zooplankton groups in lake D. Helvecio during stratification in terms of relative abundance. Isotherms and the profile of oxygen concentration are presented together.

stratification (November, 1985). The distribution of flatworms is again similar to that of cladocerans and copepods, with highest abundance in the metalimnion.

Mesostoma sp. densities recorded in vertical profiles taken at lake D. Helvecio, lake Jacaré and Barra Bonita reservoir in different years are shown in Table 9.

In Fig. 3, mean densities of flatworms for the whole water column are plotted with those for the other zooplankton groups. Despite a relatively low abundance, flatworms were a true component

Table 9. Flatworm densities in lakes: D. Helvecio, Jacaré and Barra Bonita reservoir on different sampling dates (number of individuals per cubic meter).

Depth (m)	D. Helvecio		Jacaré		Barra Bonita reservoir	
	26/07/1983	29/11/1985	11/10/1981	29/06/1983	10/03/1989	12/03/1989
0.0	0	0	40	0	2200	4167
2.0	487	60	10	13	3600	2200
5.0	150	0	8	–	2665	1450
6.0	–	300	0	38	1200	2333
9.5	–	300	0	0	2000	–
10.0	142	0	–	0	–	–
10.5	–	350	–	0	–	–
11.5	–	600	–	–	–	–
12.5	–	300	–	–	–	–
15.0	78	0	–	–	1900	2080
20.0	0	0	–	–	–	–
25.0	0	0	–	–	–	–
29.0	0	0	–	–	–	–

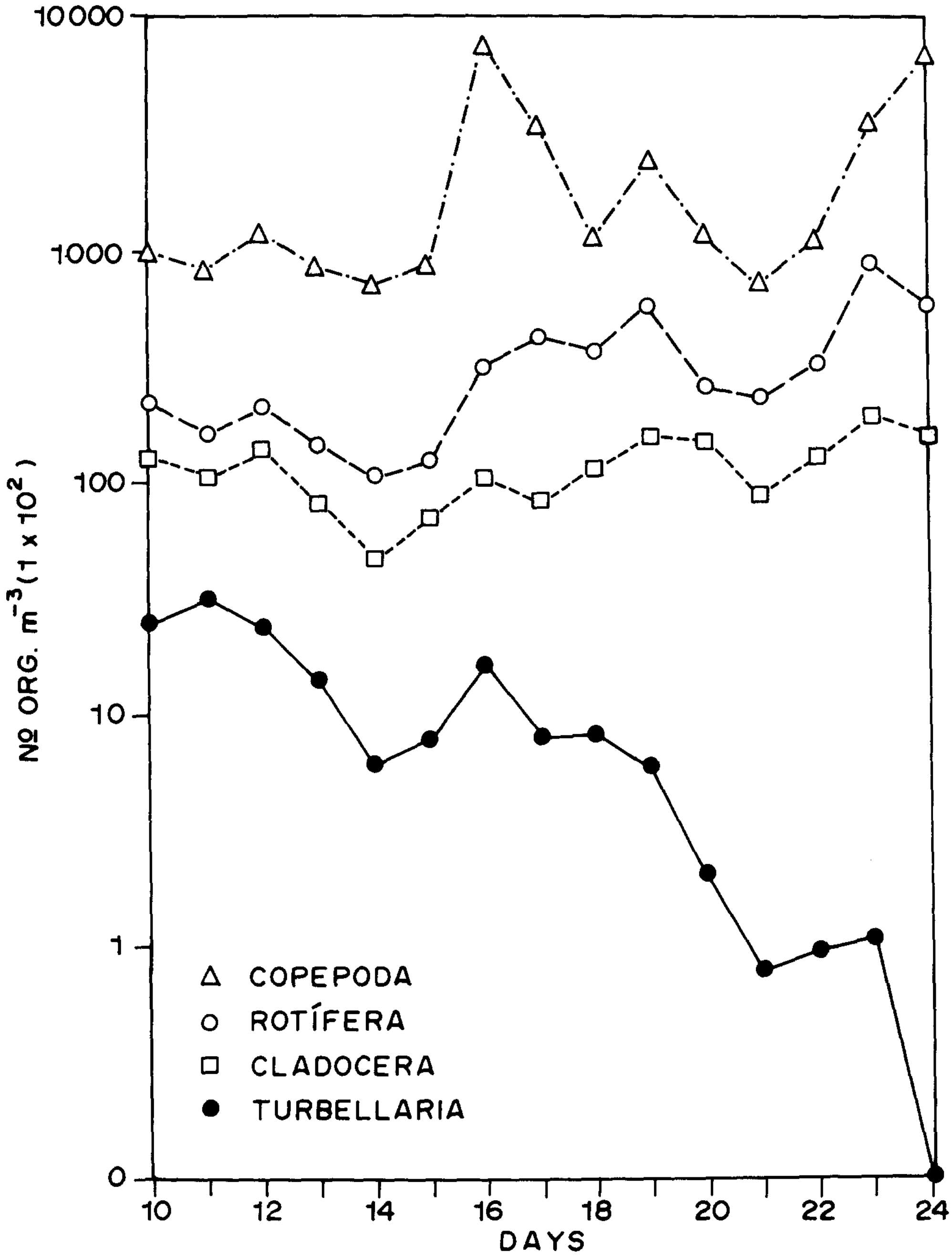

Fig. 3. Daily changes in the density of zooplanktonic organisms (mean values for the water column) in Barra Bonita reservoir, including Turbellaria. Copepod numbers include the nauplii stage.

of the pelagic zooplankton during a 15-days daily sampling carried out in Barra Bonita reservoir in March, 1988. Comparing the flatworms' vertical distribution with that of other zooplankton components on the days when flatworm densities were highest (Fig. 4), a similar pattern emerges for all groups.

Figure 5 shows the diurnal vertical movements of *Mesostoma* sp. in lake D. Helvecio. During daylight hours, flatworms occupied the layer

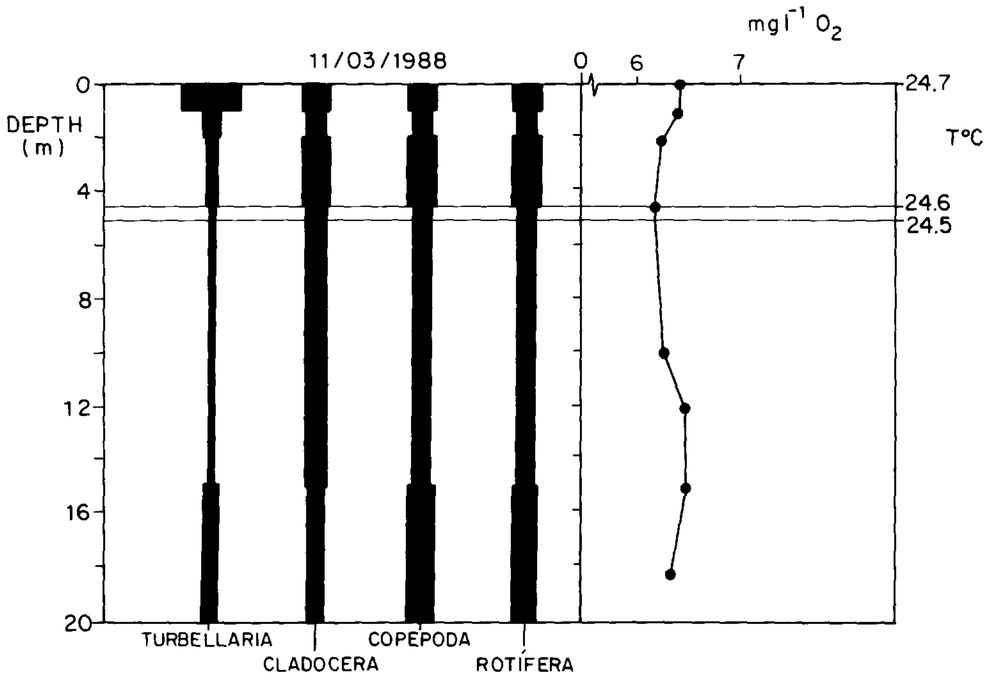

Fig. 4. Percentage depth distribution for the main component groups of zooplankton in Barra Bonita reservoir. Isotherms are drawn for every 0.1 °C and oxygen profile is shown.

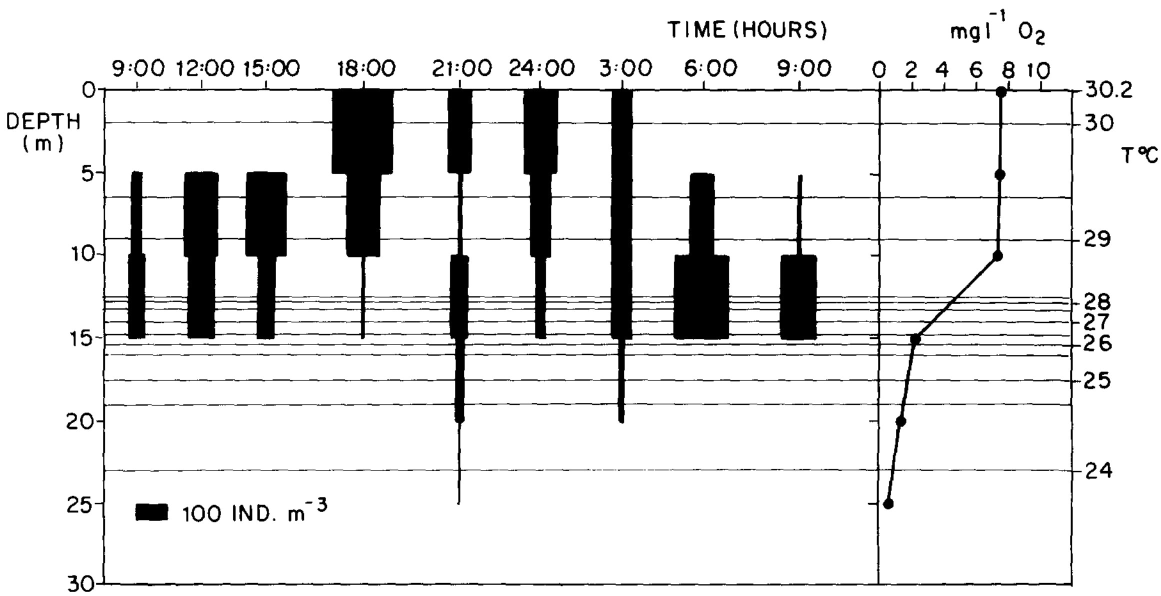

Fig. 5. Vertical migration of *Mesostoma* sp. in lake D. Helvecio (March, 1978). Isotherms and oxygen profile are shown together.

between 5 and 15 m depth. They moved to the surface at sunset, remaining in the upper layer throughout the night, and descended again at dusk. As shown by the isotherms, the lower limit of their vertical distribution coincides with the thermocline. The profile of dissolved oxygen plotted with the mean values for the 24 hours of sampling shows that their lower limit corresponds to around 2.0 mg l^{-1}.

Discussion

Data on experimental feeding rates for planktonic Turbellaria are not yet extensive; nevertheless, some preliminary generalizations may be made. The results obtained in this study corroborate the general finding that planktonic flatworms prey preferentially on cladocerans. Among the five items tested, high rates of consumption were found only for the cladocerans.

Predation rates of flatworms on copepods were low, similarly to what we observed by Maly *et al.* (1980). Such low consumption is probably not even enough to meet the flatworms' minimum nutritional requirements. According to Dumont & Schorreels (1990), *Mesostoma lingua* requires a ration of 1.63 *Daphnia magna* per day at 25 °C to be well fed. Taking into account the smaller size of predators and prey in the present study, a consumption requirement of at least two *Daphnia* per day and something similar in the case of copepods can be inferred.

Regarding flatworm food preferences, it is not clear yet whether this is determined by the size, escape behaviour, or other characteristics of the prey. Schwartz & Hebert (1982) detected a size-dependent predation for *Mesostoma ehrenbergii* when fed cladocerans of different sizes. The low feeding rates on *Thermocyclops minutus* found in the present study, despite having similar sizes of readily consumed cladocerans such as *Daphnia laevis* neonates, suggest additional factors. These could be related to the prey specificity of flatworms toxins (Dumont & Carels, 1987), or to exoskeleton thickness (Schwartz & Hebert, 1986).

Escape behaviour seems less effective for the prey in the case of flatworms whose modes of feeding include injecting a paralising neurotoxin into the prey, and mucus trapping (Schwartz & Hebert, 1982; Dumont & Carels, 1987). The extremely short time of the attack, taking only milliseconds (Dumont, personal communication), makes prey escape unlikely.

During trial experiments, it was observed that large *Daphnia laevis* (mean size 1.6 mm), chydorids, and the colonial rotifer *Synantherina* sp. were often captured by the mucus web but were not consumed. They proved to be undamaged when released.

Morphological prey characteristics seem to be important also. Observations made on two species of Ostracoda gave different results regarding *Mesostoma's* ability to prey upon them. When a flatworm and an ostracod belonging to the genus *Physiocypria* were kept together in an excavated glass-slide, *Mesostoma* could eat *Physiocypria* by introducing its eversible pharynx between the valves and sucking out the whole body content.

Observations performed with another (unidentified) species of ostracod gave different results, however. This species had a spiny carapace and a narrow gap between valves, unlike the *Physiocypria*. Despite trying for a long time, the flatworm did not succeed in introducing its everted pharynx between the valves. It does appear, therefore, that morphological differences among related species can make a great difference in vulnerability to flatworm predation.

It would be expected that being mid- to large-sized, non transparent, soft-bodied and slow-moving, flatworms would themselves be vulnerable prey to planktonic invertebrates and small fishes.

The present study confirms that planktonic flatworms are indeed not free from predation. *Chaoborus* larvae and *Mesocyclops longisetus* preyed extensively on them. The impact of such predation on flatworm populations was not quantified in this study; however, several studies regarding other prey species have shown that *Chaoborus* larvae and *Mesocyclops* can have an important influence on prey populations (Karabin, 1978; Pastorok, 1978; Hanazato, 1990). It can therefore be expected that *Mesocyclops longisetus* and *Chaoborus* larvae exert a significant control on flatworm populations. Fukuhara (personal communication) observed a decline in the number of flatworms captured by the insect emergence trap at the time when *Chaoborus* instar IV was most abundant.

Population densities of pelagic Turbellaria are generally low, when compared with other zooplankton groups. In Rio Doce Valley lakes, numbers were never higher than 600 ind m^{-3}. In Barra Bonita reservoir, a peak of 8500 ind m^{-3} was found in the surface waters during a fifteen days daily study, but at their maximum, flatworms accounted for only 3% of the total zooplankton density. Dumont *et al.* (1973) recorded a maximum density of 1600 ind m^{-3} of *Mesostoma* sp. in the surface waters of Dayat Ifrah, a small Moroccon lake. The highest density reported by Maly *et al.* (1980) was 2644 ind m^{-2} in small ponds in Colorado.

It appears that planktonic flatworms are not food limited in ponds, lakes or reservoirs where they occur, since their prey are always present in high numbers. Also, they have relatively high reproductive potential. A fecundity of 10–20 eggs each 10 days has been observed for *Mesostoma ehrenbergi* (Beauchamp, 1923 apud Marcus, 1943). Therefore, their low numbers are probably determined by predation pressure. Flatworms could well be excluded from small ponds and lakes where combined vertebrate and invertebrate predation is severe. This might be the reason for the absence of *Mesostoma ehrenbergi* from ponds with *Ambystoma tigrinum* present, as reported by Maly *et al.* (1980).

The occurrence of pelagic flatworms in lakes and reservoirs in Brazil is not a rare phenomenon. Up to now planktonic flatworms have been recorded in lakes D. Helvecio, Anibal, Jacaré, Águas Claras and Baixa Verde in the Rio Doce lake system. Adequate sampling (large volumes) and carefull examination will certainly increase this distribution to most of the c. 100 perennial lakes of this basin. Pelagic *Mesostoma* has long been recorded in South-east Brazil (Marcus, 1943). According to this author, flatworms are frequently found in ponds near São Paulo city and in low-speed segments of the Tietê and Pinheiros rivers. Flatworms are also present in large man-made lakes such as the one at Barra Bonita, the subject of the present study.

Analysis of flatworm vertical distributions has demonstrated that these organisms preferentially occupy the well oxygenated layers of lakes during periods of stratification. They seem to have a more restricted vertical distribution than cladocerans and copepods, their potential prey. Whether this is the result of a lower tolerance to oxygen depletion should be investigated in future experiments.

Analysis of vertical migration of *Mesostoma* sp. from lake D. Helvecio has shown that field populations perform nocturnal vertical migration with a similar pattern to such cladocerans as *Bosmina hagmani* and *Diaphanosoma brachyurum*, and Calanoid copepods (Matsumura-Tundisi *et al.*, 1984). The population which is mainly situated in the layers between 5 and 15 m, moves upwards just before sunset, concentrating in the surface waters. The descent starts some hours before sunrise. At 3 : 00 hr they were already moving downwards. It is quite clear that the thermocline is setting a barrier to downward movement.

Considering their low numbers compared to those of their prey, it is not clear whether we can expect a direct control of cladoceran or copepod numbers by flatworm predation pressure.

However, as suggested by Macan (1977), indirect as well as combined effects of vertebrate and invertebrate predation are probably cooperating in shaping community structure. In such a context, small changes introduced by an uncommon predator such as a flatworm might produce a large effect by shifting a delicately balanced equilibrium.

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