

Influence of spatial heterogeneity on predation by the flatworm *Mesostoma ehrenbergii* (Focke) on calanoid and cyclopoid copepods

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Through laboratory experiments, we analysed the influence of spatial heterogeneity on predation by Mesostoma ehrenbergii on the calanoid Boeckella gracilis and the cyclopoid Acanthocyclops robustus in four horizontal and two vertical spatial arrangements. This spatial heterogeneity simulated that of Juncaceae stems, a major macrophyte in the natural environment of these zooplankton. Our results indicated that M. ehrenbergii preyed differently on these copepod species. The rate of predation of M. ehrenbergii on A. robustus females reached saturation in all the treatments with and without horizontal spatial heterogeneity, but lower predation rates were observed in the medium heterogeneity treatment. Predation rates of Mesostoma on B. gracilis increased with the increase in prey abundance in the treatment without heterogeneity, while predation rates reached saturation in the treatments with horizontal spatial heterogeneity. Mesostoma ehrenbergii consumed males and females of B. gracilis in each of the arrangements tested. In natural habitats, interaction between extent of macrophyte development and intensity of predation by M. ehrenbergii on copepods species may be expected. We suggest that the structural complexity given by macrophytes in Patagonian fishless habitats provide a bottleneck for M. ehrenbergii predation.

INTRODUCTION

Spatial heterogeneity plays an important role in nature (Dutilleul, 1993). In particular, it may influence the impact of predation, since heterogeneous habitats may provide a better chance to escape from predation by increasing the availability of hiding places and/or decreasing predator foraging manoeuvres (Crowder and Cooper, 1982; Hixon and Menge, 1991). Therefore, predation success could be higher in homogeneous habitats, where prey may be more easily detectable and susceptible to attacks by predators (Gilinsky, 1984). Encounter is the central process in governing direct or indirect interactions between prey and predators. In particular, it can be assumed that spatial heterogeneity influences the probability and frequency in which prey and predator encounter each other. This probability is

also affected by the prey and predators swimming behaviour (Gerritsen, 1980; Riessen *et al.*, 1984). Depending on the nature of predation (visual or tactile, size selectivity preferences), different behavioural strategies have evolved in prey organisms to minimize encounter rates. Predators often avoid attacking prey that are clearly difficult to capture, handle or digest and prey often restrict their activity to microhabitats where predators are less effective, i.e. use of refuges (Kerfoot and Sih, 1987). Macrophyte stands have been demonstrated to provide refuges for zooplankton under visual predation (Schriver *et al.*, 1995; Phillips *et al.*, 1996). Submerged macrophytes may be considered ecosystem engineers as they influence resource availability by modifying, maintaining and/or creating new habitats that are subsequently used by other organisms (Jones *et al.*, 1994,

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1997). In this sense, spatial heterogeneity generated by macrophytes may modulate predation pressure.

The flatworm *M. ehrenbergii* (Focke) is a predator, highly adapted to live among submerged vegetation (Schwartz and Hebert, 1982; Blaustein and Dumont, 1990), but it also swims in the water column of small shallow lakes (Brugni, 1993). This turbellaria is a voracious predator of zooplankton in freshwater fishless ecosystems (Maly *et al.*, 1980; Schwartz and Hebert, 1982; Blaustein and Dumont, 1990; Beisner *et al.*, 1997; Brendonck *et al.*, 2002) and is a common inhabitant of Patagonian wetlands (Brugni, 1993). Within these habitats, *M. ehrenbergii* adults and juveniles were observed not only in the littoral but also in the open waters (Brugni, 1993). *Mesostoma ehrenbergii* is a tactile predator with external digestion that displays a plastic feeding behaviour, which depends upon the type and size of prey involved (Wrona and Koopowitz, 1998). It detects disturbances in the water caused by prey with its mechanoreceptors (MacIsaac and Hutchinson, 1985; Wrona and Koopowitz, 1998). *Mesostoma ehrenbergii* can act as a sit and wait predator, and also actively search for prey, in both cases, capture is associated with a mucus-trapping tactic (Bauchhenss, 1971; Pennak, 1978; Schwartz and Hebert, 1982; Trochine *et al.*, 2005). *Mesostoma ehrenbergii*'s preference for cladocerans over copepods has been observed in many systems (Maly *et al.*, 1980; Schwartz and Hebert, 1986; Rocha *et al.*, 1990). However, zooplankton in Patagonian shallow fishless freshwater environments is dominated by copepods (Modenutti and Balseiro, 1994; Diéguez and Balseiro, 1998). Particularly, during early spring calanoids and cyclopoids are the only zooplankters that coexist with *Mesostoma* in fishless ponds (Trochine, personal observation) suggesting that copepods are an important part of the flatworm diet. Our previous study on *M. ehrenbergii* predation indicates that this species eats copepods readily; the secretion of mucus threads allows *Mesostoma* to immobilize this 'evasive' prey (Trochine *et al.*, 2005). In Patagonian shallow lakes, aquatic vegetation is generally irregularly distributed; this spatial heterogeneity may affect the predator-prey encounter due to the different type of predation strategies exhibited by *M. ehrenbergii*. The swimming and feeding behaviour of the copepod prey under different environmental heterogeneity may also affect *M. ehrenbergii* predation rates. The outcome of predator-prey interactions may therefore be modulated by the different spatial structures provided by macrophytes (Heck and Crowder, 1991; Warfe and Barmuta, 2004). We hypothesized that the coexistence of the cyclopoid *Acanthocyclops robustus* (Sars) and the calanoid *Boeckella gracilis* (Daday) and their predator *M. ehrenbergii*, in Patagonian

shallow lakes, may be influenced by habitat heterogeneity originated by macrophytes. In the present study, we examine experimentally the ability of *M. ehrenbergii* to consume these two prey under variable spatial heterogeneity.

METHOD

Study site

Laguna Ñirihuau (41°07' S, 71°27' W, 750 m a.s.l) is a temporary fishless pond, located in north Patagonia, Argentina, in the steppes near Nahuel Huapi lake. Annual rainfall in the area is 800 mm. The hydroperiod of the pond extends from May to December. Maximum water levels are registered in late autumn and winter, when the maximum depth reaches ~70 cm. Water temperature ranges from 24°C in December to 0°C in July and August (winter) when it may freeze solid. The bottom is covered with macrophytes dominated by two Juncaceae: *Juncus pallescens* (Lam) and *Juncus arcticus* (Willd). The cyclopoid copepod *A. robustus* and the calanoid copepod *B. gracilis* are common zooplankters that co-occur with *M. ehrenbergii* in the pond.

Experimental containers design

Horizontal spatial heterogeneity due to the distribution of stems of Juncaceae in natural environment was previously assessed through photograph analyses. This analysis was carried out in a 20-cm spatial scale. Photographs of 60 squares of 20 cm side were processed with an image analysis system (Image ProPlus; Media Cybernetics); and spatial heterogeneity was assessed numerically following Johnson and Zimmer (Johnson and Zimmer, 1985) (see *Calculations*). To simulate spatial heterogeneity for our experiments, different numbers of cylindrical wooden sticks (four, six and nine; 40 mm length × 3 mm diameter) were placed in 200-mL vessels in different vertical arrangements. Each spatial arrangement simulated a particular spatial heterogeneity that was also assessed numerically following Johnson and Zimmer (Johnson and Zimmer, 1985) (see *Calculations*). The arrangement with nine sticks provided the low spatial heterogeneity ($I = 1.15$), four sticks stood for medium spatial heterogeneity ($I = 1.27$) while six sticks represented the high spatial heterogeneity ($I = 1.41$). Containers without wooden sticks were also used; these vessels represented the no spatial heterogeneity arrangement (NH). Therefore, the treatments run to test influence of horizontal spatial heterogeneity on *M. ehrenbergii* predation were NH, low, medium and high.

An additional experiment was carried out to investigate how predation rate varied with vertical spatial heterogeneity. A disc of 1-cm-plastic mesh size that covered

the inner section of the 200-mL container was placed at 2 cm from the bottom.

Experimental design

Adults of *M. ehrenbergii*, *A. robustus* and *B. gracilis* were collected in Ñirihuau pond using a hand net (200-µm size pore). A series of laboratory experiments were conducted in order to test how predation rate varied in relation to three different factors: spatial heterogeneity (HET), prey abundance (ABU) and prey species (SPECIES). Details of the treatments were slightly different between prey types. For the experiments run with *A. robustus*, we used an experimental design with four different spatial arrangements (NH, low, medium and high) and three prey abundances with five replicates for each treatment (Table I). In the NH treatment, two additional abundances (10 and 40) were also tested (Table I). For *B. gracilis*, a full factorial design was carried out with two prey conditions (COND: females and males) in four spatial arrangements (NH, low, medium and high) and five prey abundances (Table I). Each treatment was replicated five times.

All trials were conducted in 175 mL of filtered pond water (55-µm mesh size). The copepods were identified, separated and counted using a stereomicroscope (×12). After placing the prey, four adult *M. ehrenbergii* (~8mm in length) were added to each container. Ovigerous and non-ovigerous females were used in similar proportions. *Mesostoma* were starved for 24 h prior to the experiments. The experiments were run for 24 h in a temperature-light controlled incubator at 10°C and a light : dark cycle of 10:14 h. After running the experiment, all live copepods were sorted and counted.

In the additional experiment with vertical spatial heterogeneity, a factorial design was carried out with eight treatments and three replicates each: vessels without

spatial heterogeneity (NHV) and with vertical spatial heterogeneity and two prey species in two abundances (10 and 40 prey). The experiment was run under the conditions described for the horizontal heterogeneity. The temperature and light regime were the same as described above.

Calculations

Predation rates per day (*PR*) were calculated as

$$PR = \frac{NiP}{Npr \times t}$$

where *NiP*, number ingested prey, *Npr*, number predators per container and *t*, time (days).

To quantify the heterogeneity of experimental vessels and *Juncaceae* in natural environment, photographs were processed with the image analysis system (Image ProPlus). The Analysis of Point Patterns was applied following Johnson and Zimmer (Johnson and Zimmer, 1985):

$$I = (n + 1) \frac{\sum_{i=1}^n (d_i^2)^2}{\left(\sum_{i=1}^n d_i^2\right)^2}$$

where *d_i*, the nearest neighbour distance, *n*, the number of cylindrical sticks per container and *Juncaceae* stems in the 20 × 20 cm squares as per the photographed natural habitat.

The expected value of the index is 1.0 for random pattern. A larger variance term would reflect proportionately more short and long distances; thus ratios larger than 1.0 indicate clumping, while smaller ratios indicate regular or uniform patterns.

Table I: Experimental design of Mesostoma ehrenbergii predation experiments under variable horizontal heterogeneity

	<i>Acanthocyclops robustus</i>				<i>Boeckella gracilis</i>							
	Females				Females				Males			
	NH	L	M	H	NH	L	M	H	NH	L	M	H
Abundance	5	5	5	5	5	5	5	5	5	5	5	5
	10	–	–	–	10	10	10	10	10	10	10	10
	20	20	20	20	20	20	20	20	20	20	20	20
	40	–	–	–	40	40	40	40	40	40	40	40
	80	80	80	80	80	80	80	80	80	80	80	80

NH, no heterogeneity; L, low spatial heterogeneity (*I* =1.15); M, medium spatial heterogeneity (*I* =1.27) and H, high spatial heterogeneity (*I* =1.41).

Copepod biomass was estimated from length-weight regression following Dumont *et al.* (Dumont *et al.*, 1975).

Statistical analysis

Data were analysed separately for the two copepod species by two-way and three-way analysis of variance, with HET and ABU as treatment variables in the case of *A. robustus* and HET, ABU and COND in the case of *B. gracilis*. A three-way analysis of variance (ANOVA) was applied to test the influence vertical heterogeneity on the predation rate of *M. ehrenbergii* on *B. gracilis* and *A. robustus* copepods, SPECIES, HET and ABU were used as treatment variables. Data was transformed (ln) when needed to meet ANOVA requirements.

RESULTS

Calculations of Juncaceae species spatial distribution in the natural environments showed clumping patterns, spatial heterogeneity values ranged between $I = 1.21$ and $I = 2$. These clumping arrangements are in the same order as those of our experimental design.

The functional response obtained for the rates of predation of *M. ehrenbergii* on both copepod species differed greatly (Fig. 1). Predation rates of *M. ehrenbergii* on *A. robustus* females increased curvilinearly with prey abundance reaching saturation level at ~ 7 prey per day. Contrarily, predation rates on *B. gracilis* females increased with prey abundance without reaching saturation level. *Acanthocyclops robustus* females are larger than *B. gracilis* females (1.67 mm and 1.48 mm, respectively), however, a correction of predation rate by biomass did not change the observed trends.

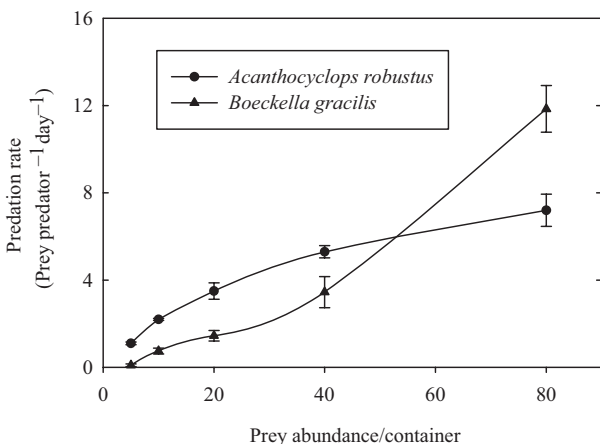


Fig. 1. Predation rates obtained for *Mesostoma ehrenbergii* on *Acanthocyclops robustus* females and *Boeckella gracilis* females in the arrangement without heterogeneity (NH) at the abundances tested.

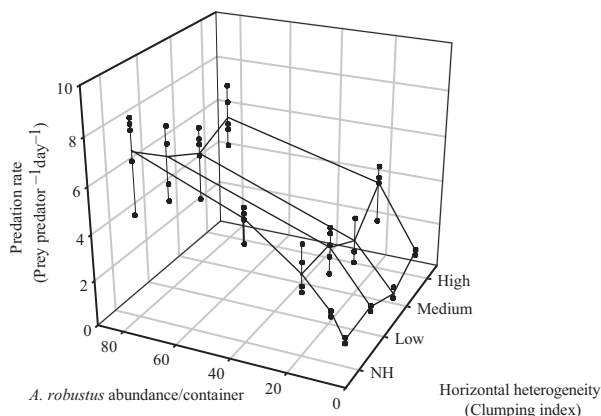


Fig. 2. Predation rates obtained for *Mesostoma ehrenbergii* on *Acanthocyclops robustus* females in the different spatial arrangements (NH and low, medium and high horizontal heterogeneity) at the tested abundances.

The influence of spatial heterogeneity on *M. ehrenbergii* predation pressure on *A. robustus* revealed that spatial heterogeneity might not have a monotonous effect on its predation rates (Fig. 2). The lower predation rates were obtained in the medium heterogeneity treatment at all the abundances tested (Fig. 2) ($P < 0.001$ ANOVA and Tukey's *post hoc* test).

Females and males of *B. gracilis* were equally eaten in the tested spatial arrangements (Fig. 3, Table II). A positive interaction for HET and ABU was found (Table II). *Mesostoma ehrenbergii* ate fewer females and males of *B. gracilis* in the NH treatment in the lower abundance (five prey) and showed the highest predation rates in the higher abundance tested (80 prey) also in the NH treatment ($P < 0.001$ ANOVA and Tukey's *post hoc* test). In the other abundances tested (10, 20 and 40 prey), the higher attack rates were obtained for the high heterogeneity treatment (Fig. 3), the rates of predation obtained in this system differed from the rates obtained in the other spatial arrangements ($P < 0.001$ ANOVA and Tukey's *post hoc* test). Low and medium heterogeneity treatments showed the most similar predation rates (Fig. 3). The inclusion of spatial heterogeneity (low, medium and high) seemed to have modulated *M. ehrenbergii* predation pressure, since rates of predation of *Mesostoma* on females and males of *B. gracilis* reached saturation level in all the treatments with spatial heterogeneity (Fig. 3). The highest abundances tested in our experiments might replicate natural aggregations of *B. gracilis*, since calculation of dispersion ($\sigma^2/\mu = 268.12$, $n = 10$) indicates high clumping of individuals in nature (Trochine, unpublished data).

The experiment that tested the influence of vertical heterogeneity on *M. ehrenbergii* predation rate showed that *M. ehrenbergii* preyed differently on *B. gracilis* and *A. robustus* (Fig. 4). Predation rates on both copepod

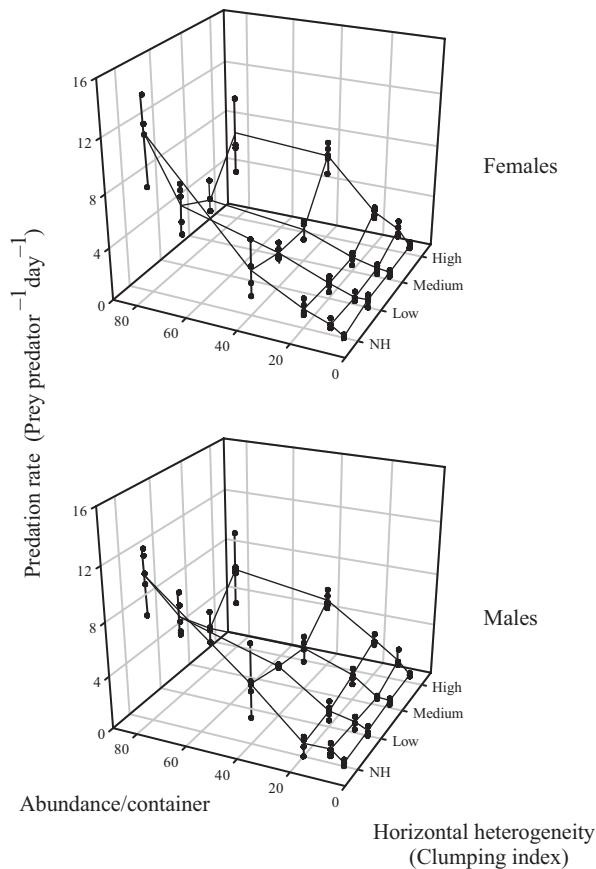


Fig. 3. Predation rates obtained for *Mesostoma ehrenbergii* on females and males of *Boeckella gracilis* in the different spatial arrangements (NH and low, medium and high horizontal heterogeneity) at the abundances tested.

species were higher in the trials run under vertical heterogeneity and in the highest abundance tested ($P = 0.029$ and $P < 0.001$ ANOVA and Tukey's *post hoc* test) (Table II; Fig. 4). However, *Mesostoma* ate more *A. robustus* than *B. gracilis* in both treatments ($P = 0.003$ ANOVA and Tukey's *post hoc* test).

DISCUSSION

Our present study indicated that *M. ehrenbergii* predation pressure was highly influenced by spatial heterogeneity. In natural habitats, interactions between macrophyte development and intensity of predation by *M. ehrenbergii* on copepods species may be expected. The role of submerged macrophytes in shaping the interactions between fish and its prey have shown that increased structural complexity typically leads to a decrease in the foraging ability of the predator concerned (Diehl, 1988; Bean and Winfield, 1995; Tatrai and Herzig, 1995). Thus, in the presence of visual predators, prey may switch habitat preference, perhaps abandoning the

profitable open water zone for the relative safety of structured habitats (Gliwicz and Jachner, 1992; Lauridsen and Lodge, 1996). However, Gonzalez Sagrario and Balseiro (Gonzalez Sagrario and Balseiro, 2003) showed that macroinvertebrate predators might exert a higher predation pressure on zooplankton in the vegetated zone. Regarding turbellarian predators, those studies that have attempted to assess the importance of prey refuges have yielded contrasting results. Pickavance (Pickavance, 1971) found that the presence of cover for prey (mud, leaves or pebbles) had little or no effect on the capture efficiency of the planarian *Dugesia tigrina* (Girard). In contrast, De Silva (De Silva, 1976) observed higher predation rates by *Dendrocoelum lacteum* (Mueller) in experiments with prey cover. Adams (Adams, 1980) found that the effect of cover (scrubbed stones) was species dependant: when prey shelter was provided, *Bdellocephala punctata* (Pallas) predation on *Asellus* increased, but predation on *Chironomus* decreased. MacIsaac and Hutchinson (MacIsaac and Hutchinson, 1985) demonstrated that vegetation (algae and moss) may significantly increase the predation success of *Mesostoma lingua*. These authors indicated that habitat complexity typical of vegetated littoral zones of arctic ponds may not necessarily promote prey survival. They demonstrated that *Daphnia* were consistently captured and eaten at a higher rate when pond vegetation was present, but they indicated that pond vegetation had no influence on either copepods or chironomids survival.

Previous studies on *M. ehrenbergii* predation have shown that cladocerans were its preferred prey and, in comparison, copepods were less consumed by this flatworm (Maly *et al.*, 1980; Schwartz and Hebert, 1986; Rocha *et al.*, 1990). However, our results indicated that the two copepods, *B. gracilis* and *A. robustus*, were important food items for *M. ehrenbergii*. The examination of dead prey showed that >95% were empty, indicating that the flatworm not only killed the copepods but actually fed on them. These contrasting results suggest a strong effect of habitat in the type of prey attacked by *Mesostoma*. Maly *et al.* (Maly *et al.*, 1980) indicated that surface to volume ratio of the lake may also influence the rates of predation of *M. ehrenbergii*. Predation effect would be more pronounced in shallow habitats where pelagic prey items are in proximity to the predator (Schwartz and Hebert, 1986; Blaustein and Dumont, 1990).

Our experiments showed that *M. ehrenbergii* preyed differently on the cyclopoid copepod *A. robustus* and the calanoid copepod *B. gracilis*. Among copepods, motion behaviour includes diverse small-scale (millimetre-centimetre) swimming patterns (Tiselius and Jonsson, 1990; Bundy and Paffenhöfer, 1996) and is a characteristic feature that may reveal important aspects of

Table II: Summary (probability values) of the statistical results of the experiments

Source	Horizontal heterogeneity		Vertical heterogeneity (<i>Acanthocyclops robustus</i> and <i>Boeckella gracilis</i> females ^b)
	<i>Acanthocyclops robustus</i> females	<i>Boeckella gracilis</i> females and males ^a	
COND ^a /SP ^b	–	0.121 ^c	0.003 ^d
HET	<0.001 ^d	<0.001 ^d	0.029 ^d
ABU	<0.001 ^d	<0.001 ^d	<0.001 ^d
HET × ABU	0.383 ^c	<0.001 ^d	0.130 ^c
COND ^a /SP ^b × HET	–	0.126 ^c	0.532 ^c
COND ^a /SP ^b × ABU	–	0.684 ^c	0.639 ^c
COND ^a /SP ^b × HET × ABU	–	0.118 ^c	0.875 ^c

Two-way analysis of variance (ANOVA) of *Mesostoma ehrenbergii* predation rates on *Acanthocyclops robustus* females on each spatial arrangement (HET:NH and low, medium and high horizontal heterogeneity) at the abundances tested. Three-way ANOVA of *Mesostoma ehrenbergii* predation rates on each prey condition (COND: females and males) of *Boeckella gracilis* on each spatial arrangement (HET:NH and low, medium and high horizontal heterogeneity) at the tested abundances and three-way ANOVA of *M. ehrenbergii* attack rates on each prey species (SP: *B. gracilis* and *A. robustus*) on the different spatial arrangements (NHV and vertical heterogeneity) at the tested abundances.

^aComparing *Boeckella gracilis* females and males (COND).

^bComparing *Acanthocyclops robustus* and *Boeckella gracilis* females (SP).

^cNot significant.

^dSignificant.

animal–environment interactions (Mazzocchi and Paffenhöfer, 1999). Calanoid copepods generally swim along a smooth path; usually propelled by the rapid stroking on their second antennae, while cyclopoid copepods move in a ‘hop-and-sink’ manner (Kerfoot *et al.*, 1980). Different motion features probably create different hydrodynamic signals for the predator’s mechanoreceptors, that interacting with habitat com-

plexity might result in a differential ability for prey detection.

Our results showed that the predation rates of *M. ehrenbergii* on *A. robustus* females reached saturation in all the treatments with and without spatial heterogeneity. However, the lower rates obtained in the medium heterogeneity treatment indicated that this system represents a macrophyte distribution that might favour prey escape or prevent prey detection. The influence of spatial heterogeneity was also evident in the rates of predation of *Mesostoma* on females and males of *B. gracilis*, since significant differences were obtained between treatments (Fig. 3). On the homogeneous system, predation rates kept increasing with the increase in prey abundance while rates reached saturation in all the heterogeneous treatments. Thus, heterogeneous environments seemed to be advantageous for these copepods prey. The inclusion of spatial heterogeneity may have modulated *M. ehrenbergii* predation pressure. The foraging efficiency of *Mesostoma* interacted with habitat complexity, and this interaction was clearly species dependent. The spatial arrangements that we used simulated spatial heterogeneities that are effectively found in Patagonian shallow lakes. Moreover, the calanoid copepod *B. gracilis* is also commonly found in dense aggregations in these environments.

Clumping in planktonic copepods has been suggested as an adaptive advantage including protection from predators and enhancing mating opportunities (Folt, 1987; Buskey *et al.*, 1996). In this case, clumping of *B. gracilis* associated with macrophytes stands may enhance their

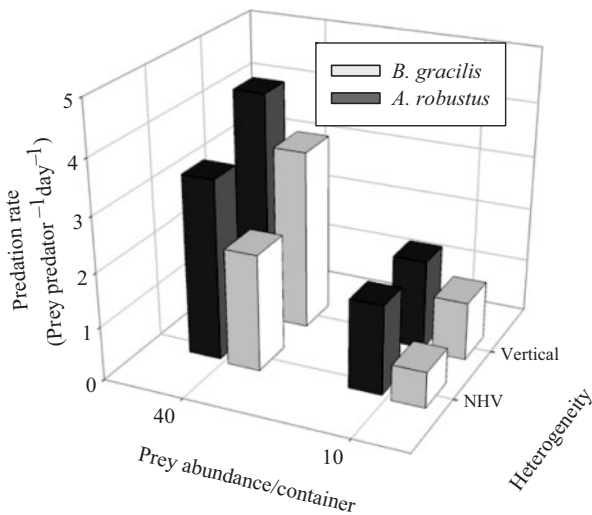


Fig. 4. Predation rates on each prey species (*Boeckella gracilis* and *Acanthocyclops robustus*) on the different spatial arrangements (NHV and vertical heterogeneity) at the abundances tested.

survival. It is possible to speculate that copepods actually prefer open waters, and that *Mesostoma's* presence would drive them to the vegetated area as predation rates decrease in heterogeneous systems. In such case, a different copepod distribution between vegetated areas and open water should be observed in the presence or absence of *M. ehrenbergii* in the pond. However, previous studies have shown that *B. gracilis* did not modify its habitat preference or its sex ratio when *M. ehrenbergii* was absent or present (Trochine *et al.*, 2005). Thus, it is unlikely that *Mesostoma* may modify the habitat selection of these two copepods.

We have shown that *M. ehrenbergii* feed differentially on two commonly available species of copepod prey of Patagonian wetlands. This predator–prey interaction may be of particular importance in these Patagonian shallow fishless lakes. *Acanthocyclops robustus* and *B. gracilis* are inhabitants of open waters and littoral zones, therefore, encounter *Mesostoma* frequently in the natural environments. Community composition may thus be affected by the presence or absence of *M. ehrenbergii*. In particular, *A. robustus* and *B. gracilis* enhance their survival when associated with macrophyte stands. However, the response of the predator to an increased prey number differed between prey. *Mesostoma ehrenbergii* proportionally ate more *A. robustus* at low abundances, while in the highest prey abundance tested *B. gracilis* was more consumed. In natural environments, *B. gracilis* is generally present in higher abundances than *A. robustus*. Thus, the differences in predation pressure might be part of *M. ehrenbergii* adaptive response to enhance encounter probability with its prey, and the structural complexity given by macrophytes in Patagonian fishless habitats would provide a bottleneck for this particular predator.

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