

# When prey mating increases predation risk: the relationship between the flatworm *Mesostoma ehrenbergii* and the copepod *Boeckella gracilis*

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With 4 figures and 4 tables

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**Abstract:** The zooplanktivorous flatworm *Mesostoma ehrenbergii* and the calanoid copepod *Boeckella gracilis* were observed to coexist in Patagonian fishless ponds. In laboratory experiments, we studied the vulnerability of *B. gracilis* to *M. ehrenbergii* predation, testing the attack rates on copulating pairs and single adults in different abundances. We also determined *B. gracilis* dimorphism, sex ratio and copulating pair ratio on two occasions in a temporary pond, with and without *M. ehrenbergii*. Our results indicated that *B. gracilis* exhibited a male-skewed sex ratio irrespective of the presence of the predator. A marked dimorphism characterized this copepod species (females are about 40 % larger than males) and a large proportion of adults were observed participating in copulating pairs that lasted for days. *M. ehrenbergii* ate similar quantities of single males and females of *B. gracilis* but significantly more copulating pairs. The use of mucus threads allowed *Mesostoma* to ingest both members of the pairs instead of only one in most attacks. Larger prey may create more turbulence in the water while swimming, so the hydrodynamic signals produced by pairs should be greater than those produced by single individuals, making them more vulnerable. Besides, the attack rates obtained in the different prey abundances showed that encounter rate is the factor that determines *M. ehrenbergii* predation. We suggest that *B. gracilis* prolonged mating duration (days) is dangerous because it increases predation risk.

**Key words:** *Mesostoma ehrenbergii*, *Boeckella gracilis*, copulating pairs, predation, sexual size dimorphism, sex ratio.

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## Introduction

Predation is a major force governing zooplankton population dynamics and community structure (ZARET 1980). Predators can directly affect relative and absolute prey abundances and species diversity, and indirectly affect morphology and behavior of prey (SIH 1987). In particular, invertebrate predators detect and locate their prey by means of tactile information rather than vision; their prey size preference drops at a certain point as larger prey became too difficult to capture and ingest (GLIWICZ & PIJANOWSKA 1989). However, prey selection is also affected by prey morphology, carapace integrity and swimming behavior: including swimming speed, pattern and escape response (LI & LI 1979, MACISSAC & HUTCHINSON 1985, WILLIAMSON 1986, ROCHE 1990, HELLSTEN et al. 1999, BALSEIRO 1992, GILBERT & BURNS 1999, CHANG & HANAZATO 2003).

Sexes of dimorphic species may be also subject to different levels of predation pressure or interespecific competition, resulting in altered population dynamics (BLAIS & MALY 1993). Several studies have shown that mating can involve increased danger (WARD 1986, WING 1988, SIH et al. 1990, RONKAINEN & YLÖNEN 1994) and searching for partners increases the probability of encounters with predators (MAGNHAGEN 1991). Pairs in copulation are larger, more visible and probably slower moving with a weaker ability to escape (WARD 1986, ARNQVIST 1989). In addition, sex-specific differences in relation to predation risk have been indicated for copepods (HAIRSTON et al. 1983, SVENSSON 1992, 1997). Pairs in copulation and females of *Cyclops vicinus* (ULJANIN) have been shown to be more vulnerable than males to *Chaoborus* predation (MAIER et al. 2000).

The flatworm *Mesostoma ehrenbergii* (FOCKE) is a voracious predator of zooplankton in freshwater fishless ecosystems (MALY et al. 1980, SCHWARTZ & HEBERT 1982, BEISNER et al. 1997, BRENDONCK et al. 2002). This species is a common inhabitant of temporary Patagonian wetlands (BRUGNI 1993). *M. ehrenbergii* is a tactile predator with external digestion that displays a plastic feeding behavior, which depends upon the type and size of prey involved (WRONA & KOPOWITZ 1998). These features determine the likelihood that *M. ehrenbergii* can handle prey [e.g. use of mucus trapping] or the prey's escape and evasion tactics. As the feeding of *M. ehrenbergii* includes mucus trapping and external digestion, prey size does not depend upon the size of the predator's mouthparts as observed for copepods and insect predators (SCOTT & MURDOCH 1983, SWIFT 1992, BALSEIRO & VEGA 1994). This situation should allow *Mesostoma* to feed on a broader size range of prey. In Patagonian temporary ponds *M. ehrenbergii* co-occurs with calanoid copepods of the genus *Boeckella*. Female calanoid copepods are larger than males (BAYLY 1978, MALY & MALY 1999). In particular, some *Boeckella* species can differ

greatly between sexes (BAYLY 1978, 1992). During previous surveys in fishless ponds, we observed that a large proportion of *Boeckella gracilis* (DADAY) adult females and adult males were attached as pairs in copulation. In these ponds *M. ehrenbergii* is the most abundant invertebrate predator (TROCHINE pers. obs.).

The present study aimed to examine experimentally the predatory effect of *M. ehrenbergii* on *B. gracilis*, testing predation rates on pairs and single individuals. During swimming, the prey creates hydrodynamic signals which might be sensed by the predator (KERFOOT 1978). Larger individuals might create more turbulence in the water while swimming, increasing prey encounter rate with the predator. We hypothesized that individuals in pairs should be more vulnerable than single individuals to *M. ehrenbergii* predation. Thus, copulating pairs should be more susceptible to *Mesostoma* predation than single individuals, and females more vulnerable than males. In addition, we postulate that females in pairs may be eaten at a higher rate than males in pairs. If the male of a copulating pair is captured first the female may not detach and hence may not escape from *M. ehrenbergii* predation, but if the female is captured, then the male would be able to release the female and escape.

## Material and methods

### 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 approximately 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 vegetation dominated by Cyperaceae and Juncaceae and species that colonize flooded soils such as *Gunnera magellanica* (LAM) and *Potentilla anserina* (LINÉE) are present.

### Swimming, mating and feeding observations

Direct observations of the swimming behavior of copulating pairs of *Boeckella gracilis* were made under a stereomicroscope (6×). Couples were placed in 5 cm diameter Petri dishes with 10 ml of filtered pond water (55-µm mesh size).

To determine mating duration of *B. gracilis*, females were combined with males in small (< 100 ml) vessels. Generally, copulation started within a few minutes. After pairing was observed the vessels were placed in a temperature-light controlled incubator, at 10 °C and a light : dark cycle of 10 : 14 h. Mating was monitored for several days. In total, 63 matings were monitored, observation on the status of the pairs were made every 4 hours.

For feeding observations, adults of *Mesostoma ehrenbergii* were starved for 24 h and placed with single adults or copulating pairs of *B. gracilis* in the same conditions used to study the swimming behavior. We performed 30 observations and in each case five males, five females or five copulating pairs were exposed to one *M. ehrenbergii*. *Mesostoma*'s feeding behavior was observed under a stereomicroscope (12 $\times$ ). Swimming and feeding activity sequence were recorded using an image analyzer (Image Pro, Media Cybernetics).

### ***Boeckella gracilis* sex ratio, copulating pair ratio and sexual size dimorphism**

*B. gracilis* sex ratio and copulating pair ratio were determined in the pond twice, in July and November, when *M. ehrenbergii* were absent and present, respectively. On both occasions, we obtained five zooplankton samples using a 5-L Schindler-Patalas plankton sampler. This volume was filtered with a 55- $\mu\text{m}$  pore size plankton net and copepods in copulating pairs were immediately counted in the field using a stereomicroscope (6 $\times$ ). This procedure was used because copepod pairs detached after preservation but not after the filtering procedure. After counting all pairs the samples were preserved in 4% formalin solution. In the laboratory, *B. gracilis* females and males were identified and counted under a stereomicroscope (12 $\times$ ) in 5 ml Bogorov chambers. In addition, prosome and total lengths (with furcal rami and without setae) of 40 individuals of *B. gracilis* adults (females and males) were measured using an ocular grid at 50 $\times$  magnification (nearest 0.02 mm). Sexual size dimorphism was calculated as the ratio between female and male prosome length.

### **Attack rates of *M. ehrenbergii* on *B. gracilis* females, males and copulating pairs**

We conducted a series of experiments in order to test how attack rate varied with prey abundance and prey condition (female, males and copulating pairs). Adults of *M. ehrenbergii* and *B. gracilis* were collected from Ñirihuau pond using a hand net (200- $\mu\text{m}$  size pore). The trials were conducted in 200 ml vessels filled with 175 ml of filtered pond water (55- $\mu\text{m}$  mesh size). The copepods were identified, separated and counted using a stereomicroscope (12 $\times$ ). Four prey abundances (5, 10, 20 and 40) in each condition (females, males and copulating pairs) were tested. We used egg-bearing females and adult females without eggs in similar proportions. An additional prey abundance of 80 individuals was tested for single females and males. After placing the prey, four adult *M. ehrenbergii* (~ 8 mm in length) were added to each container. *Mesostoma* were starved for 24 h prior to the experiments. Each treatment was replicated five times. The experiments were run for 24 h in a temperature-light controlled incubator at 10 $^{\circ}\text{C}$  and a light:dark cycle of 10:14 h. After running the experiment, all live copepods were sorted and counted. In addition, in the treatments run with copulating pairs, differential survivorship of the live copepods (females, males and pairs) was assessed to compare the effect of *M. ehrenbergii* predation on one, or both, members of copulating pairs.

## Calculations

Attack rates per day (*AR*) were calculated as:

$$AR = \frac{NaP}{Npr * t}$$

where *NaP* = number attacked prey, *Npr* = number predators per container, *t* = time (days). In the case of single *B. gracilis* (females or males) the attacked individuals were the ingested individuals. However, the attack on *B. gracilis* copulating pairs implied the end of the mating procedure either by the ingestion of one or both members of the pair. Thus, the number of attacked copulating pairs was measured as the result of subtracting the number of live pairs after the experiment to initial pair number.

## Statistical analysis

A factorial analysis (Two-way ANOVA), followed by Tukey's *post hoc* test was applied to test differences in predator attacks to copulating pairs and single individuals (females or males), whether predators ate more females than males within copulating pair treatment, and in both cases whether attack rates change among the tested abundances. Normality and homoscedasticity were tested and transformation (ln) was applied when needed. To test whether predation on females and males within copulating pair treatment varied among the replicates a Heterogeneity Chi-squared test (SOKAL & ROHLF 1981) was calculated. A t-test or an U-test (Mann Whitney), dependent on whether data were normally distributed or not, served to test for differences in total and prosome length between females and males and a Chi-square test was applied to calculate differences in sex ratio (SigmaStat 2.03 and Jump 5.0.1).

## Results

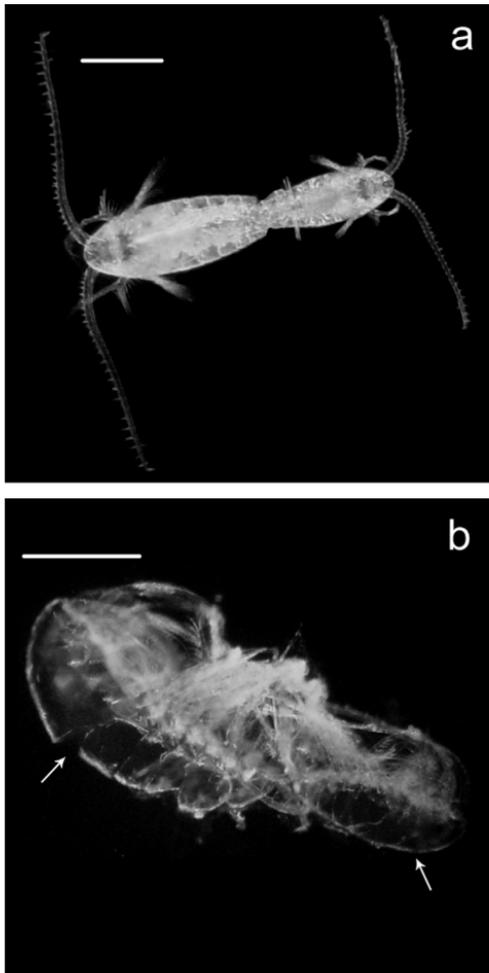
### Swimming, mating and feeding observations

Males held onto female genital segments with their modified and very robust fifth leg. The female swam while the male hung passively with its first antennae perpendicular to the body axis so the couple moved in the direction of the female longitudinal axis (Fig. 1 a). Both ovigerous and non ovigerous females were observed participating in copulating pairs. The mating procedure lasted  $117.2 \pm 13.52$  h (mean  $\pm$  S. E.).

The feeding behavior sequence described by WRONA & KOPOWITZ (1998) was confirmed in the capture and consumption of *B. gracilis* individuals by *M. ehrenbergii*. The discrete actions involving prey recognition and arousal, prey capture (strike, adhesion, lunge, mounting and prey immobilization), feeding (positioning, pharynx attachment, penetration, extraction and ingestion) and post-extraction activities (prey relinquishment or initiation of further bouts of feeding) were all observed. However, *Mesostoma* penetrates the body integu-

ment of *B. gracilis* dorsally behind the cephalothorax only once, and ingests all the body contents.

When attacking copulating pairs of *B. gracilis*, *M. ehrenbergii* captures only one individual and displays a similar behavior to that observed for one prey alone. However, in this case the secretion of mucus threads over the body of the prey that is being handled generally prevents the other member of the couple from releasing itself. When *Mesostoma* finishes eating its first prey it detaches and reattaches to the live individual in the couple reinitiating the ingestion activity. Thus, the capture of one individual generally results in the death



**Fig. 1.** *Boeckella gracilis* copulating pairs. **a)** Live *B. gracilis* copulating pair in ventral view, scale bar 500  $\mu\text{m}$ . **b)** Empty exoskeletons of *B. gracilis* copulating pair after *Mesostoma ehrenbergii* attack, arrows indicate points of *M. ehrenbergii* pharynx penetration, scale bar 250  $\mu\text{m}$ .

**Table 1.** Summary of total length (Mean  $\pm$  S.E.), prosome length (Mean  $\pm$  S.E.) and sexual size dimorphism of *Boeckella gracilis* in Ñirihuau pond.

	<i>n</i>	Total length (mm)		Prosome length (mm)		Dimorphism (female/male)
		Females	Males	Females	Males	
July ( <i>M. ehrenbergii</i> absent)	40	1.48 $\pm$ 0.008	1.03 $\pm$ 0.005	1.08 $\pm$ 0.006	0.73 $\pm$ 0.004	1.48
Nov ( <i>M. ehrenbergii</i> present)	40	1.38 $\pm$ 0.005	0.98 $\pm$ 0.005	1.00 $\pm$ 0.004	0.69 $\pm$ 0.004	1.45

**Table 2.** *Boeckella gracilis* sex ratio and singles to pairs ratio for males and females in Ñirihuau pond.

<i>B. gracilis</i>	<i>n</i>	Sex ratio (male/female)	Males (singles/pairs)	Females (singles/pairs)
July ( <i>M. ehrenbergii</i> absent)	601	2.71*	2.28	0.21
Nov ( <i>M. ehrenbergii</i> present)	5553	3.15*	3.49	0.42

\* Significant differences Chi-squared =  $P < 0.001$ .

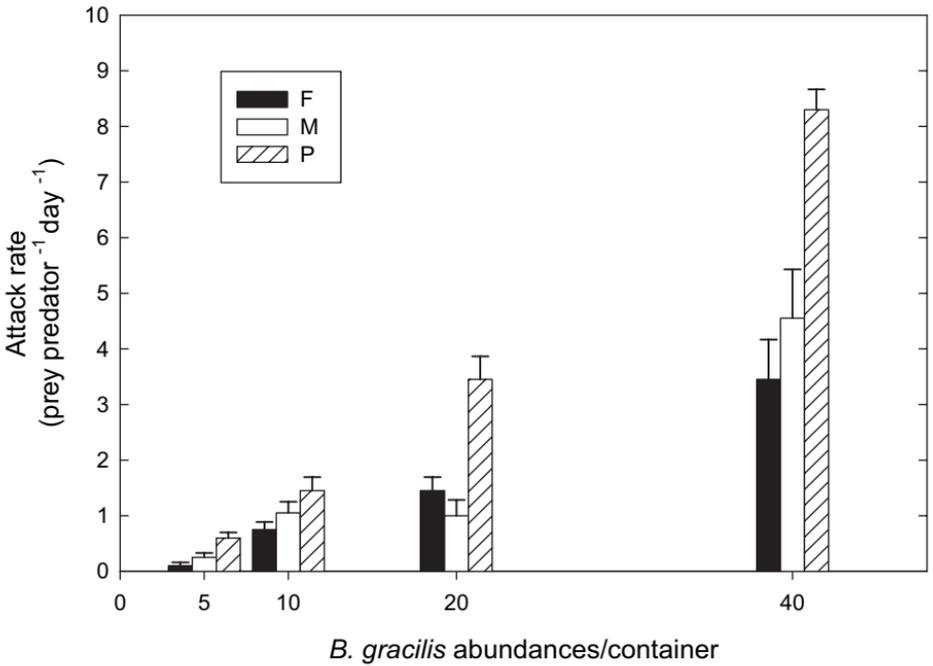
of both members of the copulating pair (Fig. 1 b). Our direct observations indicated that copulating *B. gracilis* are not likely to separate from each other when exposed to *M. ehrenbergii* in the same container.

### ***Boeckella gracilis* total length, sexual size dimorphism, sex ratio and copulating pair ratio**

*B. gracilis* copulating pairs are considerably larger than single females or males. The total length of a pair in copulation is the result of adding the female and male prosome length plus a small fraction of the female urosome (Fig. 1 a). *B. gracilis* females were about 40 % larger than males in Ñirihuau pond in July and November (*t*-tests on total length,  $P < 0.001$ ; prosome length,  $P < 0.001$ ) (Table 1). On both sampling occasions sex ratios were highly skewed in favor of males. The ratios of singles to pairs for males and females showed that most females in the pond were participating in copulation while most males remained as singles (Table 2).

### **Attack rates of *M. ehrenbergii* on *B. gracilis* females, males and copulating pairs**

The rates of attack of *M. ehrenbergii* on *B. gracilis* females, males and copulating pairs increased with prey abundance (Fig. 2). However, the experiments

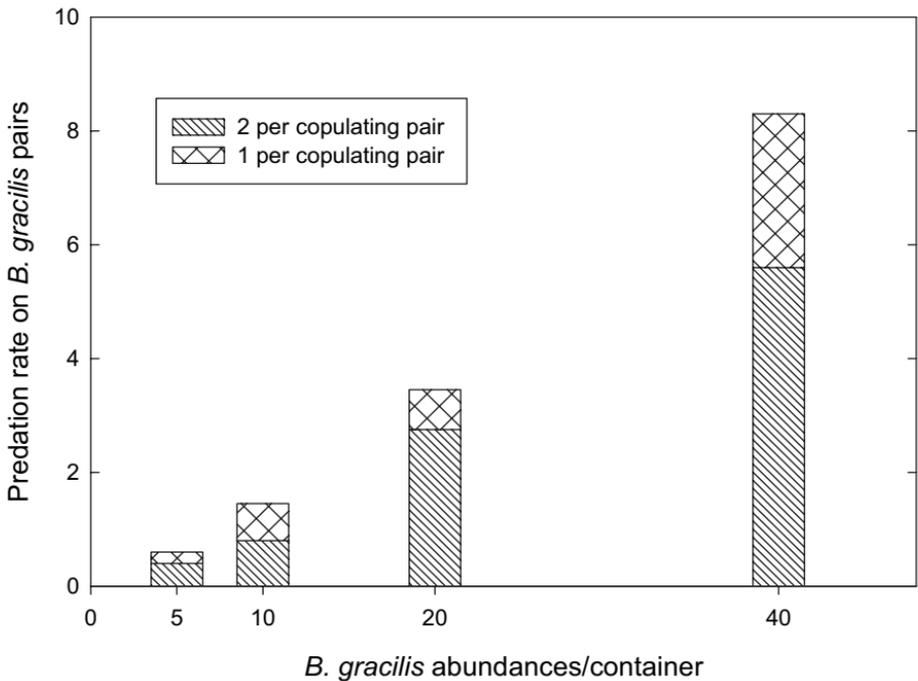


**Fig. 2.** Attack rates obtained for *Mesostoma ehrenbergii* on females (F), males (M) and copulating pairs (P) of *Boeckella gracilis* at the abundances tested. (Error bar = 1 standard error).

**Table 3.** Results of two-way ANOVA of *Mesostoma ehrenbergii* attack rates on each prey condition [adult females, adult males and copulating pairs of *Boeckella gracilis*] for the different abundances tested.

	DF	SS	MS	F	P
Condition	2	3.236	1.618	27.567	<0.001
Abundance	3	18.358	6.119	104.251	<0.001
Interaction	6	0.899	0.150	2.551	0.032
Residual	48	2.817	0.059		
Total	59	25.310	0.429		

showed that *M. ehrenbergii* preyed differentially on single or pairs of *B. gracilis*. *Mesostoma* attacked similar quantities of female and male individuals but significantly more copulating pairs ( $P < 0.001$  ANOVA and Tukey's *post hoc* test) (Table 3, Fig. 2). The analysis of the interaction indicated that the probability of encountering copulating pairs, and thus their vulnerability to *M. ehrenbergii* predation, increased in the highest abundances tested (20 and 40 *B. gracilis* copulating pairs per container,  $P < 0.001$  ANOVA and Tukey's *post hoc* test).



**Fig. 3.** Predation rates obtained for *Mesostoma ehrenbergii* on one member or both members of *Boeckella gracilis* copulating pairs at the abundances tested.

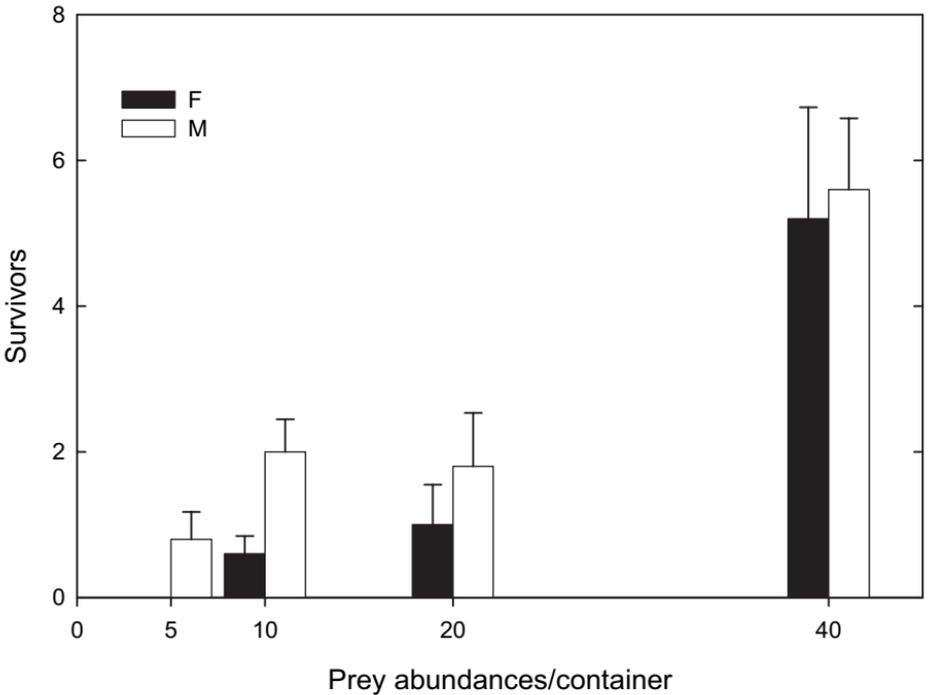
**Table 4.** Results of two-way ANOVA of prey [adult females and adult males of *Boeckella gracilis*] survivorship within the copulating pair treatment in the tested abundances.

	DF	SS	MS	F	P
Sex	1	7.225	7.225	2.546	0.120 <i>ns</i>
Abundance	3	149.075	49.692	17.512	<0.001
Interaction	3	1.275	0.425	0.150	0.929 <i>ns</i>
Residual	32	90.800	2.838		
Total	39	248.375	6.369		

*ns*: not significant.

The attack rates of *M. ehrenbergii* on 80 single females and 80 single males of *B. gracilis* (11.85 ind. d<sup>-1</sup> and 10.85 ind. d<sup>-1</sup>, respectively) indicated that predation kept increasing with the increase in prey abundance.

When *M. ehrenbergii* attacked a copulating pair both members of the couple were ingested, in most cases, at all the abundances tested (Fig. 3). There were no significant differences ( $P > 0.05$ ) between *M. ehrenbergii* predation on males and females within pairs (Fig. 4, Table 4). The heterogeneity Chi-



**Fig. 4.** *Boeckella gracilis* survivors [females (F) and males (M)] within copulating pair treatment at the tested abundances. (Error bar = 1 standard error).

squared test ( $P > 0.05$ ) showed that there were no differences between female and male survivors among the replicates of each abundance.

## Discussion

Our experiments indicate that *Mesostoma ehrenbergii* ate more copulating pairs of *Boeckella gracilis* than single females or males. These results support our initial hypothesis. A tactile predator such as *M. ehrenbergii* uses mechanoreceptors to sense prey (WRONA & KOPOWITZ 1998), therefore prey movement is necessary for a successful prey encounter and localization. Pairs in copulation are considerably larger than single individuals. As a consequence, the hydrodynamic signals produced by pairs should be greater than those produced by single individuals, making them a more vulnerable prey for *M. ehrenbergii*. Although we did not measure swimming velocities of females, males and copulating pairs, we observed that pairs are very active and do not seem to be less active than single individuals. A weak escape response of *B. gracilis* pairs could be also responsible for their higher mortalities; MAIER et al. (2000) suggested that females of *Cyclops vicinus* in copulating pairs are

probably handicapped when escaping because they are carrying the males. Our observations of the swimming of *B. gracilis* pairs behavior support this idea.

MAIER et al. (2000) found that egg-bearing females were detected significantly earlier than adult females without eggs. Since we used egg-carrying and non ovigerous females combined in a similar proportion, this potential difference was not tested.

Encounter rate determines *M. ehrenbergii* predation on *B. gracilis*, rather than handling time within the prey abundances that we tested. As prey abundance increased *M. ehrenbergii* ate more prey; in the highest prey abundances tested, copulating pairs were detected at a higher rate than single individuals. Thus, the mechanical stimuli created by more copulating pairs of *B. gracilis* increased their encounter probability with *M. ehrenbergii*. Neither the predator nor the prey tended to remain near the bottom or sides of the container and both were observed actively swimming in the water column. Therefore, the experimental container did not affect the encounter rate.

*M. ehrenbergii* displays external digestion. Thus it does not ingest the copulating pair as one food item, but ingests each individual in a copulating pair in a separate event, unlike predators such as *Chaoborus* which ingests a pair in a single event which depends upon its mouth diameter (MAIER et al. 2000). When *M. ehrenbergii* captured one member of a couple, the other member was generally eaten too. The use of mucus threads allowed *M. ehrenbergii* to ingest two individuals instead of only one in most attacks on copulating pairs. Contrary to our expectation, both sexes in copulating pair were equally eaten, though the number of male survivors was slightly higher at all the abundances tested. A small proportion of males were probably able to escape when *Mesostoma* captured the females first.

Most females (71%) in the natural population were part of a copulating pair (Table 2); thus *B. gracilis*' reproductive rate needs to be high to compensate for the high risk associated with its prolonged mating process. It is unusual that a freshwater copepod such as *B. gracilis* remains as pairs in amplexus for such extremely long periods of time (days). *B. gracilis* did not decrease the mating duration when *M. ehrenbergii* was present in the same container; this was also observed by MAIER et al. (2000) for pairs of *C. vicinus* in the presence of *Chaoborus*.

Short mating duration has been reported for *Eudiaptomus gracilis* (BERGER & MAIER 2001) and *Diaptomus leptopus* (GRAD & MALY 1992) as a strategy to reduce the predation risk associated with frequent matings. However, in diaptomid copepods every clutch produced requires a separate insemination (WATRAS & HANEY 1980), unlike centropagid copepods, where one insemination by a male may result in the production of more than one clutch of eggs (JAMIESON & BURNS 1988, MALY 1991).

The high dimorphism in *B. gracilis* (Table 1) could be related to its copulation duration since GRAD & MALY (1988) found that copulation duration had a positive correlation with sex size ratio. At a large sex size ratio, a small male may require more time to place the spermatophore properly. Besides, MAIER (1996) showed that sex ratio affected mating duration. *C. vicinus* mating lasted longer when sex ratio was male biased. The mate guarding phase (spermatophore transfer until separation) was twice as long as in female biased trials (MAIER 1996). There was a marked male-biased sex ratio for *B. gracilis* in the pond (Table 2). The duration of mating in other species of copepods has not exceeded 77 min. (JACOBY & YOUNGBLUTH 1983, GRAD & MALY 1992, MAIER 1992, 1996), except in *Eurytemora* that can remain paired for several days (GAULD 1957). Therefore, dimorphism and sex ratio could be two of many reasons for prolonged copulation in *B. gracilis*.

Unexpectedly, *B. gracilis* mortality was independent of sex. As *B. gracilis* females are larger than males we expected them to be more susceptible to *Mesostoma* detection. Swimming behavior, escape ability and morphology have been reported to contribute to the sex-specific mortality (BLAIS & MALY 1993, SVENSSON 1997). Directional components of prey swimming seem to be important for the success of predator strikes. *Eudiaptomus gracilis* females were more vulnerable to *Chaoborus* predation because strikes against males were less efficient. Analysis of the attack events indicated that swimming angle of prey in relation to *Chaoborus* larvae affected the probability of being captured (SVENSSON 1997). In addition, male copepods were reported to be inferior to females in escaping predators (GERRITSEN 1978, SVENSSON 1992). The absence of differences in body morphology, such as spines and appendages, between *B. gracilis* female and male may make them equally susceptible prey to *M. ehrenbergii*. So, features such as swimming behavior, escape ability and morphology may act in compensatory ways to make both sexes of *B. gracilis* equally susceptible to *M. ehrenbergii* predation.

In summary, our results show that factor(s) other than *M. ehrenbergii* predation must be responsible for the observed male-biased sex ratio of *B. gracilis* in Ñirihuau pond (Table 2). Sex ratio was skewed in favor of males on both sampling occasions (with and without *M. ehrenbergii* present) and the rate of attack of *M. ehrenbergii* in our experiments showed that female and male *B. gracilis* were equally susceptible to predation as single individuals or pairs.

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