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Feeding of *Boeckella gracilipes* (Copepoda, Calanoida) on ciliates and phytoflagellates in an ultraoligotrophic Andean lake

ESTEBAN G. BALSEIRO, BEATRIZ E. MODENUTTI AND CLAUDIA P. QUEIMALIÑOS

LABORATORIO DE LIMNOLOGÍA, CENTRO REGIONAL UNIVERSITARIO BARILOCHE, UNIVERSIDAD NACIONAL DEL COMAHUE, UNIDAD POSTAL UNIVERSIDAD, 8400 BARILOCHE, ARGENTINA

The calanoid copepod, Boeckella gracilipes, is the dominant crustacean zooplankton in South Andean deep ultra-oligotrophic lakes. Combining field and experimental data we explored the feeding of the copepod and its access to the mixotrophic ciliate, Ophrydium naumanni, in Lake Moreno Oeste (Patagonia, Argentina). Phytoplankton was dominated by nanoflagellates throughout the water column. Ophrydium naumanni, which accumulates much of the chlorophyll a, as do copepodites and adults of B. gracilipes, has a deep distribution during the day, with maximal abundances around 30 m depth. Mouth-part morphology analysis of B. gracilipes indicated that the copepod has an omnivorous diet. Laboratory experiments showed that B. gracilipes could access O. naumanni only when it is offered as a single food item. However, when natural phytoplankton and ciliate assemblages (including O.naumanni) are offered, B. gracilipes did not eat Ophrydium and preyed on the oligotrich, Strombidium viride, and phytoflagellates like Chrysochromulina parva. The range of ingested sizes was broad (3.9–33 μm of equivalent spherical diameter) but all selected particles were motile ones with distinctive movements, which would enhance the copepod particle detection.

INTRODUCTION

In Andean lakes a distinctive assemblage of large mixotrophic ciliates (>80 μm), dominated by the peritrich *Ophrydium naumanni* Pejler and the heterotrich *Stentor araucanus* Foissner & Wölfl, has been previously reported (Wölfl, 1995; Modenutti, 1997; Queimaliños *et al.*, 1999; Modenutti *et al.*, 2000). These two species have been found only in large, deep ultra-oligotrophic lakes (area >5 km^2, Z_{max} ≈100 m), where they develop large populations. In previous studies of Lake Moreno Oeste (Queimaliños *et al.*, 1999; Modenutti *et al.*, 2000), *O. naumanni* dominated the ciliate assemblage, showing a marked vertical distribution pattern during the early summer months. The symbiotic *Chlorella* of this ciliate caused a deep chlorophyll maximum at 30 m depth, contributing up to 90% of the total photosynthetic biomass (Queimaliños *et al.*, 1999). In spite of the great importance of this source of energy for the planktonic food web, direct predation on *Ophrydium* cells, which would cause *Chlorella* mortality, has not been observed.

Freshwater calanoid copepods (*Epischura* and *Diaptomus*) can efficiently remove several species of ciliate oligotrichs (Burns and Gilbert, 1993). Therefore, by feeding selectively at high rates, calanoids may suppress populations of some ciliates and thereby influence microzooplankton community structure (Burns and Gilbert, 1993). Recently, top-down effects that extended to the level of flagellates and bacteria have been studied in two species of *Boeckella*, *B. hamata* and *B. dilatata*, in New Zealand lakes (Burns and Schallenberg, 1996, 1998). These results revealed a stronger grazing pressure on protozoa exerted by copepods than by cladocerans (Burns and Schallenberg, 1998).

In Araucanian lakes of Argentina and Chile, *Boeckella gracilipes* Daday is the most important zooplankton in terms of frequency of occurrence and density (Zúñiga, 1988; Bayly, 1995; Modenutti *et al.*, 1998). Therefore, we expect that this copepod would graze on *O. naumanni* in Andean lakes.

In the present study we analyse vertical copepod distribution in relation to phytoplankton and ciliates in the water column of Lake Moreno Oeste. Through laboratory experiments and studying mouth-part morphology

we test the access of *B. gracilipes* to *O. naumanni*. In addition, we used grazing experiments to evaluate the ability of the copepod to graze efficiently on phytoflagellates and other ciliates in natural densities.

METHOD

Study area

Lake Moreno Oeste (41°5′S; 71°33′W; 758 m above sea level) is included in the Nahuel Huapi National Park (Patagonia, Argentina). Lake Moreno Oeste is a warm, monomictic, ultra-oligotrophic, deep lake, with a particularly high transparency (summer Secchi depth: 20 m). It has a surface area of 6 km^2 and a maximum depth of 90 m. The lake remains thermally stratified from late November through to April (spring/summer months). During the period of direct stratification the lake develops a marked thermocline at around 30 m depth, and temperatures range from 11°C to 18°C in the epilimnion, while the hypolimnion remains at 7°C. The mixed period occurs during the late autumn and winter months and the temperature is 7°C throughout the water column. Dissolved oxygen concentration remains at saturation levels all along the water column. In Lake Moreno Oeste during thermal stratification, the vertical distribution of oxygen describes an orthograde curve, typical of an unproductive lake. Dissolved organic carbon (DOC) and phosphorus [total (TP) and total dissolved (TDP)] concentrations are very low (DOC 0.6 mg l^{-1}, TP 3.46 μg l^{-1} and TDP 1.81 μg l^{-1}) and no remarkable shifts were noted along the water column (Queimaliños *et al.*, 1999; Modenutti *et al.*, 2000). Epilimnetic chlorophyll *a* concentration was always less than 0.6 μg l^{-1}, while in the metalimnion it increased up to 1.5 μg l^{-1} producing a deep chlorophyll maximum at 30 m depth, as was reported in a previous study (Queimaliños *et al.*, 1999).

Field study

The study was conducted in a central sampling point located at the deepest part of the basin (z = 70 m). Between November 1998 and April 1999, the lake was sampled nine times. All samplings were carried out 1 h before astronomic noon. Temperature and light [Photosynthetically Active Radiation (PAR), 400–700 nm] profiles were measured from 0 to 60 m with a PUV 500B submersible radiometer (Biospherical Instruments). Concurrently, water samples were taken from 0 to 52 m at 4 m intervals. The samples were obtained with a 12 l Schindler-Patalas trap and this volume was distributed between different sampling bottles in order to determine nutrients, DOC, bacteria, phytoplankton and ciliate concentrations. Zooplankton samples were also obtained with the Schindler-Patalas trap and filtered through a plankton net of 55 μm mesh size.

Samples for phytoplankton and ciliates were fixed with acid Lugol solution and were quantified with an inverted microscope using 50 ml Utermöhl chambers. Phytoplankton enumeration was performed following Utermöhl's technique at 400×. The distinction between nanoplankton and net phytoplankton was considered to be 20 μm greatest axial linear dimension (GALD). Ciliate quantification was carried out by scanning the entire chamber surface at 200×. Ciliate species identification was based on works in the literature (Pejler, 1962; Foissner *et al.*, 1991, 1992, 1994, 1995; Foissner and Wölfl, 1994).

At least 30 cells of each phytoplankton and ciliate species were measured and cell biovolume was calculated by approximation to appropriate geometric figures. The equivalent spherical diameter (ESD) was estimated as the diameter of a sphere of equal volume.

Boeckella gracilipes copepodite stages and adults were counted under a stereomicroscope in a 5 ml Bogorov chamber. Mouth-parts (mandibles, first and second maxillae and maxillipeds) were dissected under a stereomicroscope and mounted in polyvinyl alcohol–lactophenol on glass microscope slides. The mouth-parts were observed under a direct microscope Olympus BX50 at 400×, and images were digitalized using the Image Pro Plus Program (Media Cybernetics). Mouthparts were measured using the same computer program. Following Green and Shiel (Green and Shiel, 1999) the Edge Index was applied.

$$\text{Edge Index} = \sum\{[(w_i/W) \times (h_i/H) \times 10^4]/\mathcal{N}\}$$

where W is the total length of the cutting edge; H is the height of the ventral tooth; h_i is the depth of the ith intercusp depression; and w_i is the distance between peaks of adjacent cusps.

An index value lower than 500 indicates a herbivore feeding mode, a value between 500 and 1000 indicates an omnivore and values higher than 1000 indicate a carnivorous feeding mode (Green and Shiel, 1999).

Experimental study

A series of laboratory experiments were performed during the sampling season. The experiments consisted of the incubation of *O. naumanni* in Moreno Oeste lake water, filtered through GF/C filters, with (Treatments) and without (Controls) the presence of adults of *B. gracilipes*. The water used in the experiments was freshly collected from 20 m depth on the same day as experimentation. The experiments lasted between 24 and 72 h and they were conducted in a growth chamber at 14°C in a 14 : 10 light : dark photoperiod; light intensity inside the chamber

was 39.0 μE m^{-2} s^{-1}. These conditions closely resembled the summer epilimnion of Lake Moreno Oeste at 20 m depth (Queimaliños *et al.*, 1999). The experiments were run in 10 ml test tubes or in 50 ml Erlenmeyer flasks that were rotated on a turntable at 2 r.p.m. Before starting the experiments all vessels and test tubes were carefully cleaned and sterilized (121°C, 1 atm., 20 min). The specimens used in the experiments were collected from 20 m depth from Lake Moreno Oeste the day before the experiment and maintained under the experimental conditions (light and temperature). Individuals were transferred to experimental vessels and counted with a sterilized pipette under a stereomicroscope. The experimental design (Table I) consisted of one treatment and one control with five replicates each. Each experiment was started with 10, 50, or 100 individuals of *O. naumanni* per replicate, and treatment consisted of the addition of one or two adult females of *B. gracilipes* (Table I).

Results of the experiments were expressed as growth rates (r) such that:

$$r = (\ln N_t - \ln N_0)/t$$

where N_0 is the number of individuals at the beginning of the experiment; N_t is the number of individuals at the end of the experiment and t is the period of experimentation. Experimental results were compared through t-tests.

In addition, a series of feeding experiments were carried out monthly during the summer (December 20–21, 1999; January 7–8, 2000; February 22–23, 2000 and March 8–9, 2000). The specimens and water used in these experiments were also collected at 20 m depth from Lake Moreno Oeste. We used 150 ml glass-stoppered Erlenmeyer flasks filled with lake water filtered through a 120 μm sieve. At the beginning of the experiment five replicates were fixed with acid Lugol solution in order to assess the initial cell concentration. Treatments consisted of the addition of six adults of *Boeckella* (field density was increased fourfold), while final controls were flasks without copepods. Both treatments and final controls were run in five replicates and they were maintained for 24 h in a growth chamber at 16°C and a 14 : 10 light : dark photoperiod. The light intensity inside the chamber was 39.0 μE m^{-2} s^{-1}. At the end of the exposure the water was fixed with acid Lugol solution. Phytoplankton and ciliate enumerations were carried out as previously described.

Table I: Experimental design of the incubation experiments of Ophrydium naumanni with (Treatment) or without (Control) the addition of Boeckella gracilipes adults

Experiment	Volume (ml)	*Ophrydium* number	*Boeckella* number	Exposure time (h)
a	10	10	1	24
b	10	10	1	24
c	10	50	1	24
d	50	50	1	48
e	50	50	1	72
f	50	100	2	48

To assess the clearance rates (CR), the Gauld formula (Gauld, 1951) was applied:

$$\mathrm{CR} = V(\ln C_c - \ln C_t)/(t \times N)$$

where V is the volume of the flasks in ml, t is the time in hours during which the animals fed, N is the number of the animals, C_c is the control cell concentration and C_t is the treatment cell concentration.

RESULTS

During the sampling period phytoplankton was scarce, since total cell abundance was, on average, less than 1000 cells ml^{-1}, reaching a maximum of 1500 cells ml^{-1} (Figure 1). Nanoplankton contribution to total cell abundance was always higher than 95% (Figure 1). This fraction was dominated by nanoflagellates such as the prymnesiophyceans *Chrysochromulina parva* Lackey and *Chrysochromulina* sp., the cryptophycean *Rhodomonas lacustris* (Pascher & Ruttner) Javornicky and the chrysophycean *Ochromonas ovalis* Dofl. In addition, the dinoflagellate *Gymnodinium* aff. *varians* Maskell was present in all samples, but at low densities; while *Peridinium* sp. was recorded from December to April. Net phytoplankton cell abundance always remained below 25 cells ml^{-1} (Figure 1). This fraction mainly consisted of dinoflagellates, with *Gymnodinium paradoxum* Schilling as dominant, and the chrysophyceans *Dinobryon divergens* Imhof and *D. sertularia* Ehr.

The ciliate assemblage in Lake Moreno Oeste was characterized by the presence of two species of large (>80 μm) mixotrophic ciliates, the peritrich *Ophrydium naumanni* and the heterotrich *Stentor araucanus*. *Ophrydium naumanni* was the dominant species throughout almost all the study period (Figure 2), showing an increase in cell density at or below 30 m depth, near the limit of the euphotic zone and just below the upper limit of the metalimnion. In addition, the ciliate assemblage also contained medium-sized ciliates (<50 μm) such as oligotrichs [*Strombidium viride* Stein and *Strobilidium* spp. and *Pelagohalteria viridis* (Fromentel)] and prostomate and mesodiniid holotrichs [*Balanion planctonicum* (Foissner, Oleksiv and

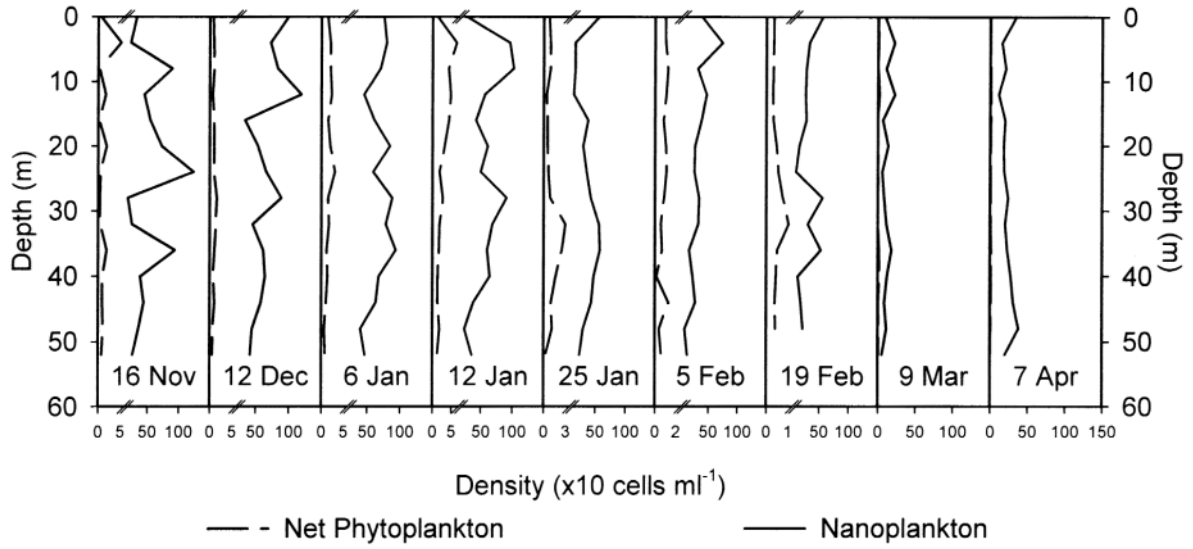

Fig. 1. Phytoplankton distribution along the water column (November 1998 to April 1999). Note breaks in scale.

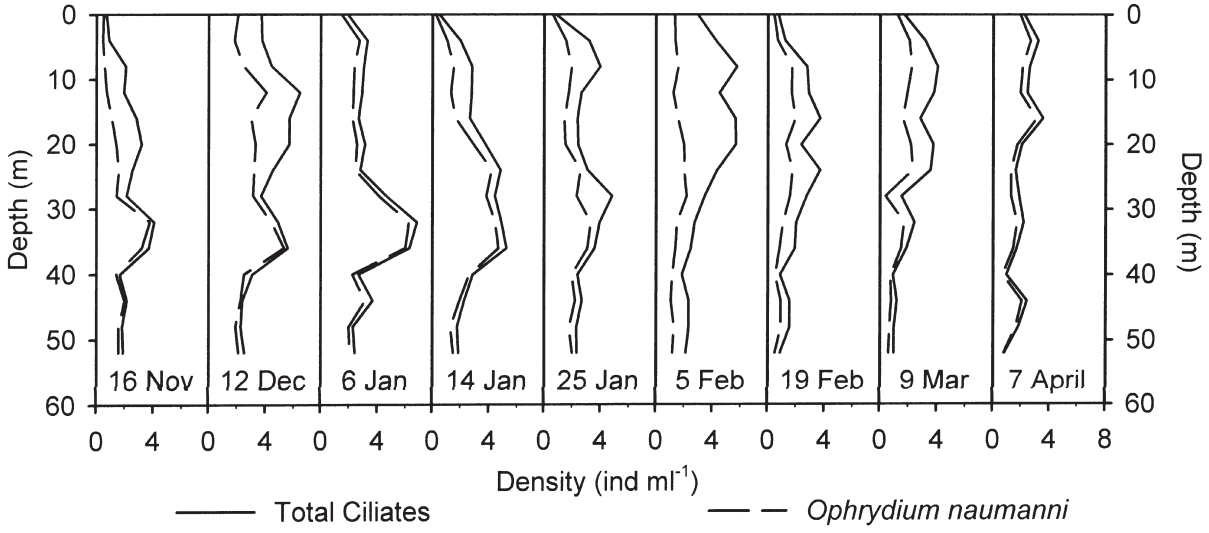

Fig. 2. Total ciliates and *Ophrydium naumanni* distribution along the water column (November 1998 to April 1999).

Müller), *Urotricha* spp. and *Askenasia* sp.]. These smaller ciliates were more abundant at the upper levels of the epilimnion (Figure 2).

Boeckella gracilipes copepodites and adults were present throughout the sampling period with maximum densities in late spring (November/December) and late summer (March/April) (Figure 3). Vertical distribution at midday showed a marked preference for the levels around 30 m depth and no remarkable differences were observed between the distribution of copepodites and adults (Figure 3).

The mouth-part morphology of *B. gracilipes* showed a number of features reported in other *Boeckella* species from Australia, New Zealand and Antarctica (Evans, 1970; Heywood, 1970; Weller, 1977; Green and Shiel, 1999). The edge index varied around 750 (mean ± S.E. 784 ± 34) and this value is within the omnivorous range.

In the experiments where *O. naumanni* was offered to *B. gracilipes* as a single food item we obtained variable results. Some experiments showed no significant differences in ciliate growth rates with and without the exposure to *Boeckella* (Figure 4 b, e and f), whereas in others, significant

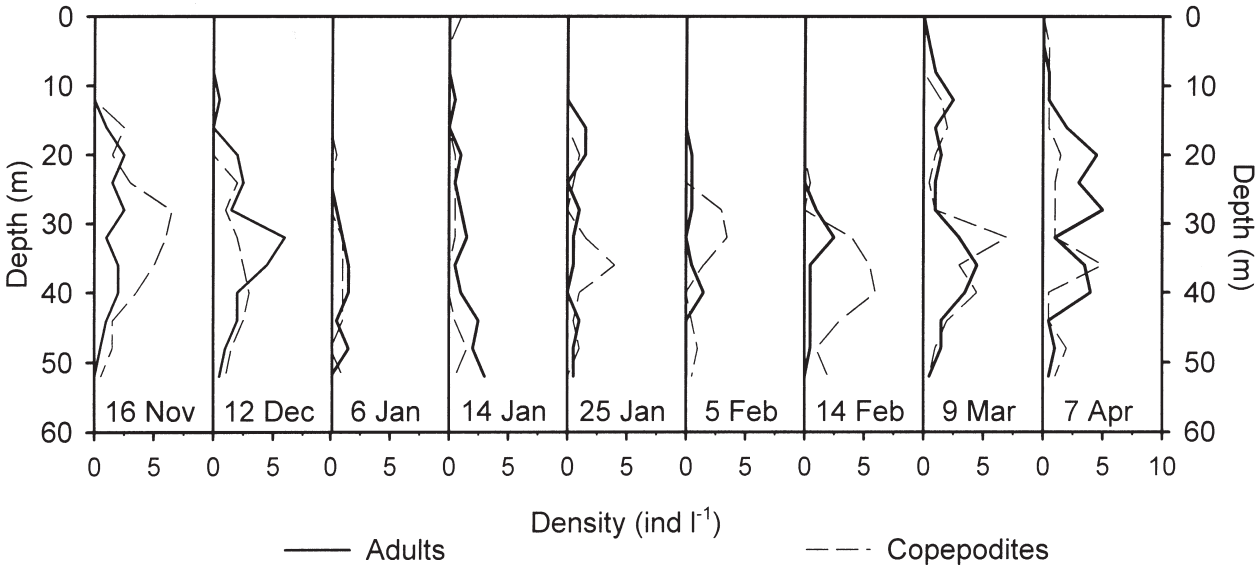

Fig. 3. *Boeckella gracilipes* copepodites and adults distribution along the water column (November 1998 to April 1999).

differences were obtained ($P < 0.05$, Figure 4 a, c and d). In all treatments with copepods, *O. naumanni* showed negative growth rates. This result was enhanced when experiments were carried out in 10 ml test tubes (Table I, Figure 4 a, b and c). These results do not prove that *B. gracilipes* eats *O. naumanni* substantially, but they indicate that the copepod can eat them when they are offered as the single food item.

The second set of experiments was performed to measure clearance rates of *B. gracilipes* on natural planktonic assemblages, including *O. naumanni*. In all these experiments a clearance rate on *O. naumanni* of 0 ml individual^{-1} h^{-1} was obtained, indicating that this particular ciliate was not eaten by the copepod. *Stentor araucanus*, the other large ciliate that is widespread in Araucanian lakes was not eaten either.

In addition, in these experiments we measured the clearance rate of *B. gracilipes* on other phytoplankton and zooplankton species. In four consecutive months the copepod cleared almost the same species from the natural plankton assemblages (Figure 5). Among them, the ciliate oligotrich *Strombidium viride* and the nanoflagellates

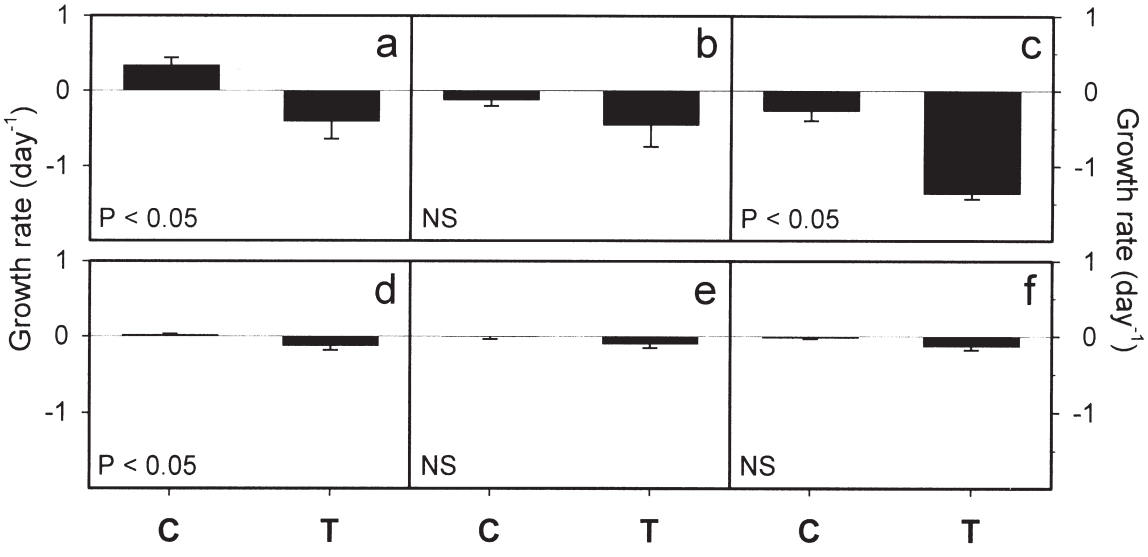

Fig. 4. Growth rates of *Ophrydium naumanni* during the incubation experiments. Experimental design as in Table I. References: C = Controls (without *Boeckella gracilipes*); T = Treatments (with *Boeckella gracilipes*); NS = non significant.

Chrysochromulina parva and *Rhodomonas lacustris* were cleared at the highest rates. A maximum clearance rate of 1.87 ml individual^{-1} h^{-1} was obtained for *S. viride* in December, whereas for flagellates the highest value was of 1.47 ml indivual^{-1} h^{-1} for *C. parva* in February (Figure 5). The size spectrum of the consumed items was broad, ranging from 3.9 to 33 μm ESD (Table II). Only flagellated algal species were cleared, since diatoms [*Rhizosolenia eriensis* Smith, *Aulacoseira granulata* (Ehr.) Simonsen, *Synedra ulna* (Nit.) Ehr.] were not consumed. Within ciliates, oligotrichs were the most consumed item. These observations indicate that size is not the only factor in the food selection by *B. gracilipes*.

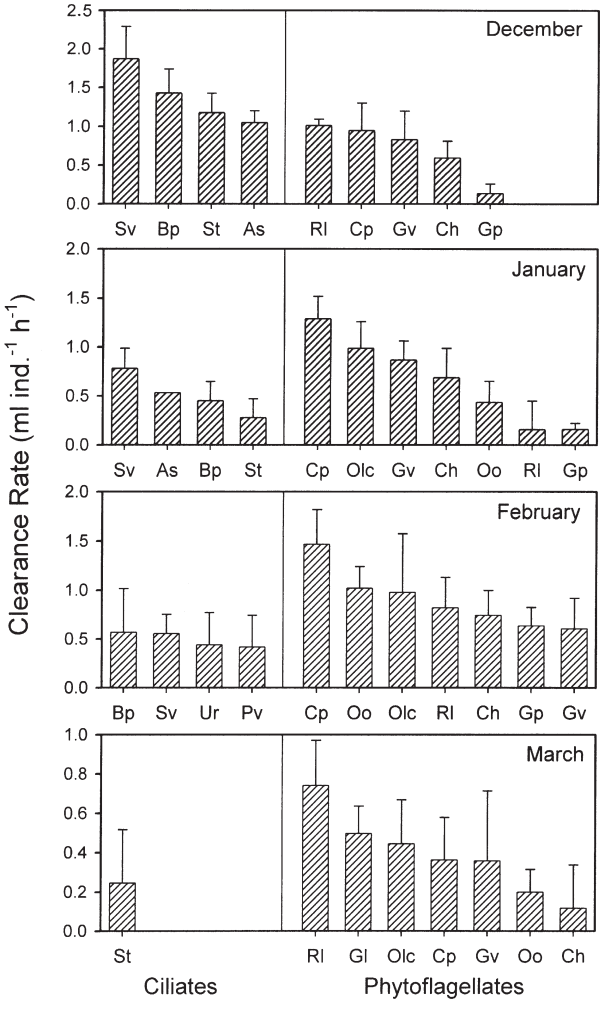

Fig. 5. Clearance rates of *Boeckella gracilipes* on phytoflagellate and ciliate species. References: Ciliates: Sv, *Strombidium viride*; Pv, *Pelagohalteria viridis*; St, *Strobilidium* sp.; Ur, *Urotricha* sp.; As, *Askenasia* sp.; Bp, *Balanion planctonicum*. Phytoflagellates: Cp, *Chrysochromulina parva*; Ch, *Chrysochromulina* sp.; Rl, *Rhodomonas lacustris*; Oo, *Ochromonas ovalis*; Olc, *Ochromonas*-like cells; Gv, *Gymnodinium* aff. *varians*; Gp, *G.paradoxum*; Gl, *Glenodinium* sp.

DISCUSSION

Calanoids are fundamentally omnivorous with varying tendencies to herbivory or carnivory (Williamson and Butler, 1986; Vanderploeg, 1994). In some *Boeckella* species, it has been demonstrated that they consume animals (rotifers and crustaceans) in addition to algae (Modenutti, 1993; Green and Shiel, 1999; Green *et al.*, 1999). In contrast, in Lake Titicaca, *B. titicacae* (= *B. gracilipes* Bayly, 1995) grazed selectively on small seston (<10 μm) (Haney and Trout, 1985). The results obtained for *B. gracilipes* in Lake Moreno Oeste indicated that the mouth-part morphology corresponds to the omnivore feeding type. Our feeding experiments also show that *B. gracilipes* consumes oligotrich ciliates at comparable rates to those of nanoflagellates (Figure 5). Similar results were obtained for *B. dilatata* and *B. hamata* in two New Zealand lakes of different trophic levels (Burns and Schallenberg, 1996, 1998). In these lakes, oligotrichs comprised a high percentage (83 and 87%) of total ciliates, and most of these were large (>20 μm); through experiments it was shown that there was a clear decrease in ciliate abundances when *Boeckella* was present. Burns and Gilbert (Burns and Gilbert, 1993) indicated that oligotrichs were efficiently removed by adult copepods of *Epischura lacustris*, *Diaptomus minutus* and *D. pygmaeus*.

In contrast, Lake Moreno Oeste was dominated by the very large peritrich *O. naumanni* that was not substantially eaten by *B. gracilipes* (Figures 4 and 5). The results obtained in our feeding experiments indicated that *Boeckella* ate particles up to 33 μm ESD (Table II). As *O. naumanni* has an ESD of 53 μm (Table II), this size should be an effective refuge against predation by *B. gracilipes*. In addition to solitary individuals, *O. naumanni* occurs in small colonies with 5–20 individuals in a jelly (Modenutti, 1988); this feature can increase the refuge since the total size of the colony is considerably greater than one individual (threefold).

Behavioural differences among ciliates, and the presence of other ciliate species, contributed to differences in ciliate susceptibility to predation and suggested reasons why removal is not only related to size (Burns and Gilbert, 1993). The results obtained in our incubation and feeding experiments would also indicate that factors other than size could influence *B. gracilipes* selectivity. In some incubation experiments, when *O. naumanni* was offered as a single food item, *B. gracilipes* could access it (Figure 4). In these experiments only solitary individuals were provided, which might have increased the access of the copepod to this large ciliate. In addition the reduced volume of the experiments carried out in test tubes (Figure 4 a, b and c) might have increased the effect of *B. gracilipes* on *O. naumanni* mortality. In those experiments, carried out in larger volumes, the negative rates of increase of *O. naumanni*

Table II: Size features of ciliate and phytoflagellate species consumed and not consumed by B. gracilipes

	Biovolume (μm^3)	ESD (μm)
Ciliates		
Consumed		
Strombidium viride Stein	15,552.87	30.96
Strobilidium humile Penard	2160.78	16.03
Pelagohalteria viridis (Fromentel)	18,934.22	33.06
Strobilidium sp.	6924.59	23.64
Urotricha sp.	8215.85	25.03
Askenasia sp.	5970.30	22.50
Balanion planctonicum (Foissner, Oleksiv & Müller)	1082.37	12.73
Not consumed		
Ophrydium naumanni Pejler	79,168.13(*)	53.27(*)
Stentor araucanus Foissner and Wölfl	1,067,303.74	126.79
Strobilidium lacustris Foissner, Skogstad & Pratt	63,648.89	49.53
Phytoflagellates		
Consumed		
Chrysochromulina parva Lackey	27.39	3.74
Chrysochromulina sp.	169.03	6.86
Rhodomonas lacustris (Pascher & Ruttner) Javornicky	113.50	6.01
Ochromonas ovalis Dofl.	43.10	4.35
Ochromonas-like cells	77.80	5.29
Gymnodinium aff. *varians* Maskell	371.10	8.92
G. paradoxum Schilling	18,227.77	32.65
Peridinium sp.	2155.30	16.03
Not consumed		
Gymnodinium helveticum Penard	6462.35	23.11
G. uberrimum (Allman) Kofoid and Swezy	42,439.82	43.28
Dinobryon divergens Imhof	49.49(*)	4.56(*)
D. sertularia Ehr.	81.63(*)	5.38(*)

(*)Species that form colonies, dimensions of individuals are indicated; ESD = Equivalent Spherical Diameter.

exposed to the copepod were much lower (Figure 4 d, e and f). However, no differences were obtained between experiments carried out in 50 ml flasks with one and two copepods (20 individuals l^{-1} and 40 individuals l^{-1}, respectively), indicating low effect of interference between copepods at these densities.

However, when the offer of *O. naumanni* included solitary and small colonies together with phytoflagellates and other ciliate species, *B. gracilipes* did not remove the large ciliate (clearance rate = 0 ml individual^{-1} h^{-1}). In these cases the copepod clearly preferred oligotrichs and nanoflagellates. The higher clearance rate on *Strombidium viride* and *Chrysochromulina parva* (Figure 5) cannot be related only to size, which is similar to that of other ciliate or algal species. *Strombidium viride* has a distinctive swimming pattern. First, it shakes in one place; then suddenly, with short movements, swims rapidly to another place where it restarts the activity, describing a random trajectory (personal observation). Considering that selective feeding by copepods involves detection and active capture, and that mechanoreception is the primary mechanism for remote detection of large particles (DeMott and Watson, 1991), the swimming pattern of *S. viride* might explain the higher consumption of this species. On the other hand, the swimming behaviour of *O. naumanni* is extremely slow and is restricted to contractions of the zooid (personal observation). Consequently, the absence of fast movements in this species would reduce detection by the

copepod, which would only be possible in experimental conditions run in a small volume (Table I and Figure 4, Experiments a, b and c).

The successful detection of smaller cells such as *C. parva* can be related to its motility, which is an important factor in algal detection (DeMott and Watson, 1991). The fast rotating movement of *C. parva* with its undulating flagella (Parke *et al.*, 1962) may improve the detection. All of the algae consumed by *B. gracilipes* have flagella (Table II). However, the presence of flagella did not itself explain the observed selection, since the colonies of *Dinobryon* were never eaten. *Dinobryon* individuals inside a lorica are aggregated in colonies forming large arborescent structures that may be inaccessible to *B. gracilipes*.

It is clear that in this lake *B. gracilipes* does not eat *O. naumanni*. Considering that *O. naumanni* contains a large proportion of the chlorophyll *a* of the lake (Queimaliños *et al.*, 1999), it seems that *B. gracilipes* does not have access to an important fraction of the productive biomass. On the other hand, *O. naumanni* has rather low growth rates (Queimaliños *et al.*, 1999), and probably the absence of strong predation on it also contributes to the success of *O. naumanni* in Araucanian lakes. If a widespread copepod like *B. gracilipes* were able to access *O. naumanni*, it would probably not be able to compensate for losses by predation with its low reproductive rates. Primary production within the symbiotic algae of *O. naumanni* appears not to be available via copepods to higher levels of the food web.

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