

Predatory interactions between a cyclopoid copepod and three sibling rotifer species

S. LAPESA,* T. W. SNELL,† D. M. FIELDS† and M. SERRA*

*Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, València, Spain

†School of Biology, Georgia Institute of Technology, Atlanta, GA, U.S.A.

SUMMARY

1. Cyclopoid copepod predation on rotifers affects the dynamics and structure of zooplankton communities. We address the differential vulnerability of three sympatric rotifer sibling species belonging to the *Brachionus plicatilis* species complex. These co-occur with their cyclopoid predator, *Diacyclops bicuspidatus odessanus*.
2. Using video recording and tracking, we analysed the steps in predation including attack distance, attack angle, and rotifer species swimming in the presence and absence of the predator. Our results show the greater vulnerability of *B. rotundiformis* (the smallest species) to *D. b. odessanus* predation, which is associated with a high percentage of attacks after contact. *Brachionus plicatilis* (the biggest species) is the less vulnerable prey, with low percentage of attacks after contact and captures after attacks. *Brachionus ibericus*, the intermediate sized species, had also intermediate vulnerability.
3. The differential vulnerability provides insight into the coexistence and seasonal succession of these competing rotifer species. Our results show that the competitive superiority of *B. rotundiformis* may be balanced by its greater vulnerability to copepod predation.

Keywords: *Brachionus*, *Diacyclops*, predation vulnerability, size-dependent predation, tracking

Introduction

Invertebrate predation has major effects on the dynamics and structure of zooplankton communities, particularly in habitats where vertebrate predators are scarce or absent (Kerfoot, 1977; Herwig & Schindler, 1996; Wissel & Benndorf, 1998; McNaught *et al.*, 1999). Predator feeding strategies and prey defences are main components of predatory interactions (Kerfoot, Kellong & Strickler, 1980; Williamson & Gilbert, 1980; Havel, 1987; Sih, 1987; Brandl, 1998). Behavioural studies of predatory copepods (Kerfoot, 1978; Williamson & Gilbert, 1980; Williamson, 1980, 1987; Brandl, 1998; Caparroy, Thygesen & Visser, 2000) have shown that the morphological and behavioural characteristics of copepods and their prey have a large

effect on the outcome of individual feeding processes and thus on zooplankton community structure.

Although some rotifers are predators (e.g. *Asplanchna*) and feed on other rotifer species (Gilbert, 1980a), they typically are generalist suspension feeders (Rothhaupt, 1990a,b) that form an important part of the diet of cyclopoid and calanoid copepods (e.g. Gilbert & Williamson, 1978; Williamson, 1983b, 1987; Roche, 1987; Stemberger & Gilbert, 1987). A variety of morphological features protect rotifers against copepod predators (Stemberger & Gilbert, 1987). Permanent or inducible spines are present in species of *Keratella*, *Notholca* and *Brachionus*, which make them more difficult to capture, manipulate and ingest, whilst mucus sheaths reduce copepod attack and capture success in the rotifers *Ascomorpha* and *Conochiloides*. Besides these traits, body size relative to that of the predator can affect rotifer probability of detection and capture, escape probability after capture, and handling time. Any protection conferred by

Correspondence: S. Lapesa, Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, A.O. 2085, València 46071, Spain. E-mail: sara.lapesa@uv.es

a stiff lorica and spines may be reduced or lost if predator body size is relatively large in relation to prey body size (Stemberger & Gilbert, 1984; Gilbert & Williamson, 1978).

Cyclopoid copepods detect prey by mechanoreception and manipulate captured prey before ingestion. Prey body size affects: (1) the magnitude of the fluid mechanical disturbance created, which in turn affects prey detection distance and attack probability by cyclopoid copepods (Kerfoot, 1977; Gilbert & Williamson, 1978; Jamieson, 1980); (2) prey capture efficiency and (3) predator handling time. All three characteristics affect the probability of the prey being attacked and ingested (Brandl & Fernando, 1978; Roche, 1987, 1990). Some recent studies have stressed the need for behavioural approaches to better understand the factors regulating selective consumption in cyclopoid copepods (e.g. Kerfoot *et al.*, 1980; Williamson, 1983a; Stemberger, 1985; Brandl, 1998). These studies have reported a great variety of escape and evasive responses among rotifers. Some features such as rotifer swimming speed (Gómez, Cecchine & Snell, 1997) and predictability of movement (Gilbert, 1985) influence prey vulnerability and predator selection in conjunction with other animal characteristics such as body size (Kerfoot, 1977; Gilbert & Williamson, 1978; Stemberger, 1985; Williamson, 1987).

The *Brachionus plicatilis* species complex is composed of at least three sibling rotifer species commonly found in Eastern Spain (Gómez, Temprano & Serra, 1995; Gómez, Carvalho & Lunt, 2000; Ortells *et al.*, 2000). The sibling species, now named *B. plicatilis* (Müller), *B. rotundiformis* (Tschugunoff) and *B. ibericus* (Ciros-Pérez, Gómez & Serra, 2001b), do not produce hybrids where they co-occur. The species have only slight differences in size and shape, the latter including their three pairs of spines located in an antero-dorsal position. Although spine differences are not very noticeable, *B. rotundiformis* has more acute spines (Ciros-Pérez *et al.*, 2001b). These species strongly compete for algae (Ciros-Pérez, Carmona & Serra, 2001a). Laboratory experiments have shown that coexistence based on differential use of resources (algae) and variance in food availability is possible (Ciros-Pérez *et al.*, 2001a). However, in a wide range of conditions, competitive exclusion was also observed. The three species show markedly different ecological preferences in relation to temperature and salinity. Despite having different seasonal distributions, they

were found to have long periods of co-occurrence in several ponds on the Mediterranean coast of Spain (Gómez, 1996; Ortells *et al.*, 2000). In these habitats, several species of cyclopoid and calanoid copepods are also present during a part of the annual cycle. There is evidence of differential vulnerability to cyclopoid predation (J. Ciros-Pérez & S. Lapesa, unpublished data), suggesting *B. rotundiformis* is the most vulnerable prey. Competition experiments and these observations suggest that differential predation may play an important role in seasonal succession and coexistence of the sibling species.

In this paper we examine the differential vulnerability to a cyclopoid predator of the three sibling species. Using video recording and tracking, we describe the sequence of copepod predation and attack distances. We also describe rotifer differences in swimming behaviour, and discuss the implications for susceptibility to predators.

Methods

Experimental animals were adult females of the predatory cyclopoid copepod *Diacyclops bicuspidatus odessanus* (Schmankevitch) and rotifers were *B. plicatilis* (strain L1), *B. ibericus* (strain SM2) or *B. rotundiformis* (strain SS2). Rotifers were originally isolated from Poza Sur of Torreblanca Marsh (Prat de Cabanes-Torreblanca) on the Mediterranean coast of Spain (see Gómez *et al.*, 1995). The average length of the adult lorica was 240 µm for *B. plicatilis*, 160 µm for *B. ibericus* and 120 µm for *B. rotundiformis* (Gómez *et al.*, 1995). Copepod females were isolated from Charca Sur of El Hondo de Elche, a pond 5 km inland from the Mediterranean coast and 225 km south of Torreblanca Marsh. The average body length (excluding the caudal setae) of an adult copepod female was 780 µm. Stock cultures of copepods and rotifers were grown in artificial sea water using Instant Ocean® seasalts (Aquarium Systems, Mentor, OH, USA) and fertilised with f/2 modified medium (Guillard & Ryther, 1962) at 20 °C, 12 g L⁻¹ salinity, and constant fluorescent illumination of 3000 lux. Stock cultures of rotifers were fed with *Tetraselmis suecica* Kylin (Butch) while copepod cultures were maintained on a mixed culture of the three species of rotifer used in the experiments.

Two different kinds of recording were carried out. The first consisted of videotaping the experimental

animals to estimate parameters of the predation. The second was computer tracking to analyse rotifer swimming behaviour and the predator effect on it. Pre-experimental conditions were the same in both experiments.

Predation parameters

Experiments were performed separately for the three rotifer species in the presence of copepods. Two to six replicates were carried out for each feeding trial.

All predation events (contact, avoidance, attack and capture), as defined below, were counted from two dimensional videotaping.

Contact: Any physical contact between prey and predator.

Avoidance: Physical contact that results in a direction change of the copepod increasing the distance between prey and predator.

Attack: Physical contact produced by any leaping or pouncing movement of the predator towards the prey; physical contact accompanied by grasping movements of the mouthparts.

Capture: Prey held by the mouthparts of the predator.

(Note that some contacts may result in no response; that is, neither avoidance nor attack).

The animals were recorded in a rectangular glass vessel (5.0 cm length \times 2.5 cm width \times 7.0 cm height) containing 30 mL of 12 g L⁻¹ salinity artificial sea water, maintained at 20 °C. The vessel was covered by a transparent plastic film to minimise disturbances. Rotifers were transferred into the filming vessel by filtering them from the stock cultures using 35 µm Nytex mesh (Sefar-Maissa S.A., Barcelona, Spain) and washing with clean sea water. *Diacyclops b. odessanus* females (instar C5 or adults) were starved for 16–18 h before experiments and then were transferred to the vessel using a Pasteur pipette (Corning Costar Corporation, Cambridge, MA, USA). Predator density was 1 female mL⁻¹, and rotifer density ranged from 9 to 17 rotifers mL⁻¹. Filming was carried out using a Schlieren optical pathway with a HeNe laser (633 nm) (Newport, Irvine, CA, USA) as a light source (Strickler, 1985; Yen & Fields, 1992; Fields & Yen, 1993). The 1 mm laser beam was expanded to 20 mm and then projected onto a video camera (Pulnix TM – 745 Pulnix, Sunnyvale, CA, U.S.A.) equipped with a 100-mm macro-zoom Vivitar lens (Vivitar Corpora-

tion, Newbury Park, CA, USA). A cube of approximately 1.3 mL of fluid in the experimental tank was filmed for analysis using a magnification of 10 \times . Images were recorded on a Panasonic AG-1960 video recorder (Matsushita, Secaucus, NJ, USA) synchronised with a Comprehensive Video Supply Corporation time code generator (Horita, Mission Viejo, CA, U.S.A.). To increase temporal resolution, individual video frames (33 ms) were split and analysed field by field (16.7 ms). The experimental vessel was recorded from 2 to 6 h.

Most captures were observed directly. However, a few times copepod mouthparts were hidden by its body and captures were inferred by a postattack prey disappearance. Rotifer density was estimated from the videotapes by counting the number of rotifers on the screen and calculating the recorded volume. The contact rate for each replicate was calculated as follows: [(number of contacts/volume recorded)/density of rotifers]/observation time.

From the video tapes used in the analysis of predation, we estimated attack distance and angle of attack using a computerised system. We selected events where a clear attack sequence could be observed (i.e. a stationary copepod leaping towards the prey) with the prey and the predator in the same focal plane. In these cases, the video frame preceding the pouncing movement was captured on a Macintosh computer (Apple, Cupertino, CA, USA) using an NIH Image (U.S. National Institutes of Health, available at <http://rsb.info.nih.gov/nih-image>).

In order to compute the attack distance and attack angles, the *x*, *y* data recorded in the space coordinate system were transformed into the copepod coordinate system (Fig. 1). The angle of attack is defined as the angle between the antero-posterior body axis and a line joining the rotifer and the copepod rostrum.

From the values of the copepod coordinate system, attack distance, *d*, was computed as $d = [(x'_R)^2 + (y'_R)^2]^{1/2}$, and angle of attack was computed as $\phi = \arcsin(x'_R/d)$.

The time spent in the attack pouncing movement (*T_p*) was also measured by direct observation using the time code generator.

Rotifer swimming behaviour

Swimming velocities, net displacements and path sinuosity were measured for the three rotifer species

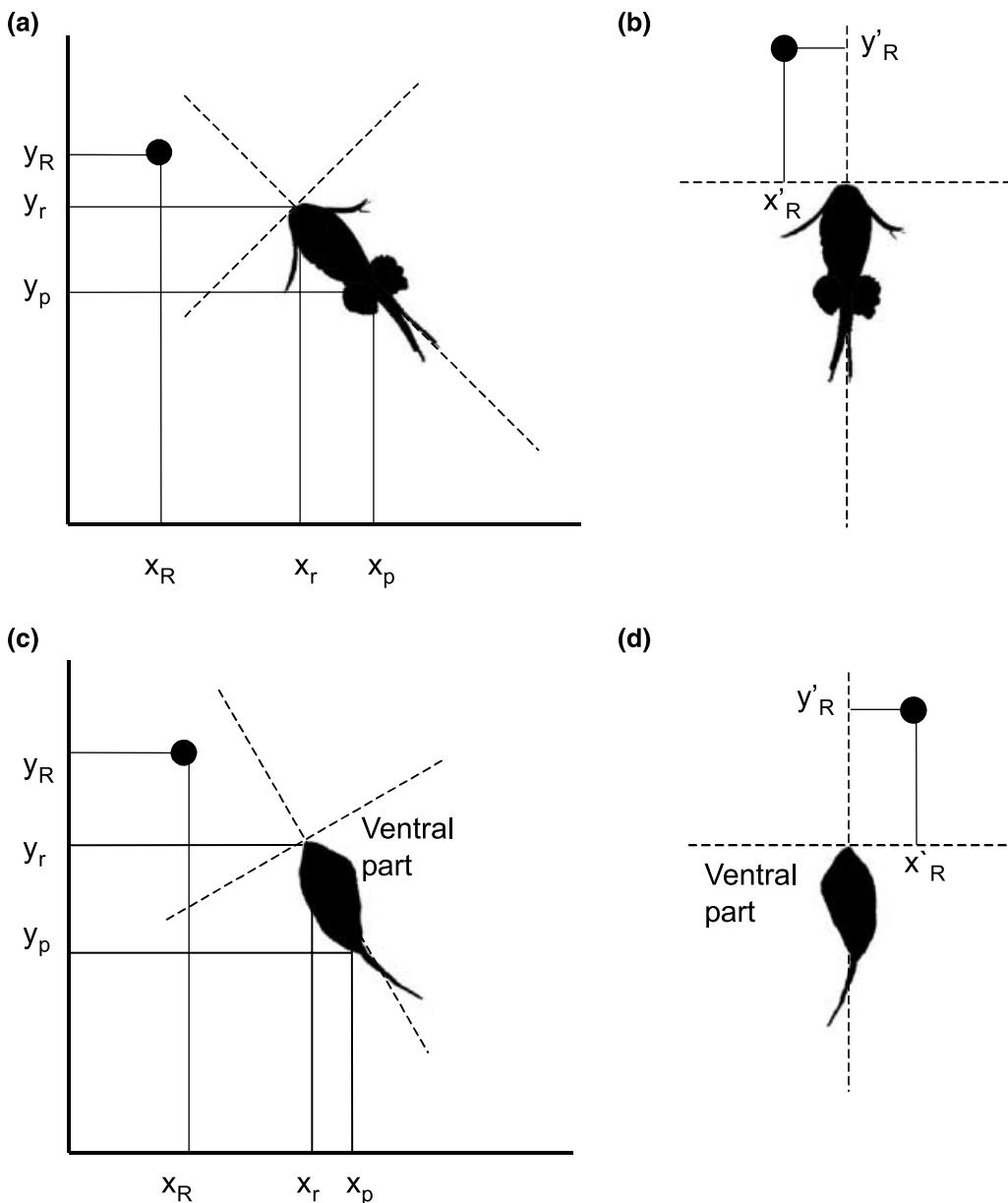


Fig. 1 Transformation of the data from the space coordinate system into the copepod coordinate system. Copepod is represented as a silhouette in dorsal view (a and b) or lateral view (c and d) and rotifer is represented as a solid circle. (a) and (c) shows animal position in the space coordinate system. The (x_R, y_R) are the coordinates of central point of the rotifer body. (x_r, y_r) are the coordinates of copepod rostrum, and (x_p, y_p) are the coordinates of the end of copepod prosome. (b) and (d) shows the rotifer position (x'_R, y'_R) in the copepod coordinate system, which was computed as follows: $x'_R = K [(x_R - x_r) \cos \alpha - (y_R - y_r) \sin \alpha]$, $y'_R = (x_R - x_r) \sin \alpha + (y_R - y_r) \cos \alpha$, where $\alpha = \text{arc tangent} [(x_p - x_r)/(y_p - y_r)] + Z$. Z accounts for the position head-up or head-down of the copepod and was 0 if $y_r > y_p$ and $+180^\circ$ if $y_r < y_p$ ($y_r = y_p$ was not needed). K accounts for the lateral position of the copepod (right or left orientation of the ventral part) and was -1 if the ventral part of the copepod was at right and 1 in any other case. If a dorsal view was registered K is not needed ($K = 1$).

in the presence and absence of *D. b. odessanus* females (C5-adult). Experiments were performed in cell culture flasks of 200 mL. Density of predators, if present, was 1 female mL^{-1} and rotifer density ranged from 9 to

16 rotifers mL^{-1} . The volume of experimental medium was 200 mL. Two replicates for each of the six experimental combinations (three rotifer species \times predator presence versus predator absence) were performed.

Experimental cultures were illuminated by a white light of 100 W–110 V, with a red filter placed between the experimental culture and the light source. A Pulnix TM 745 black/white video camera (Hitachi America, Ltd., San Jose, CA, U.S.A.) was connected to a Macintosh computer and focused on the experimental flask. The rotifer movements were followed using the ImageTracker 1.61 L subprogram of NIH Image (D. B. Dusenberry 1999, unpublished). This program can simultaneously track up to 20 rotifers which appear as dots, detected because of their brightness and motion. The program output is the time course of x , y coordinates, which are recorded every 0.5 s.

From 8 to 20 video sequences of 175 s were recorded per replicate. From these data, parameters of swimming behaviour were measured in 30 rotifers per replicate over 20 s. Gross displacement was computed as the summation of the 20-s linear distance between the position of each consecutive 0.5-s step. Net displacement was computed as the linear distance between the first (0 s) and the last (20 s) position. From the gross displacement, swimming velocity was computed as mm s^{-1} and as body length per second. Path sinuosity was calculated as: 1 – (net displacement/gross displacement).

Results

The three rotifer species showed very similar swimming behaviour, moving helicoidally almost continuously and rarely attaching to surfaces with their foot. Although the rotifers did not show a noticeable escape response when they physically contacted a copepod, in some cases they would stop swimming or with-

draw into the lorica after contact. In contrast, the copepod typically exhibited an attack or avoidance response with or without physical contact.

Diacyclops b. odessanus showed three well differentiated swimming modes: (1) hop and sink motion, as described by Strickler (1975); (2) continuous motion, with the copepod moving faster than in mode 1 with outstretched antennae either in dorsal or ventral position, and (3) looping motion, where the copepod moved as in mode 1, but in circles to the left or right. This latter behaviour was frequently associated with prey contacts.

The copepod pouncing movement towards their prey lasted from about 17–30 ms ($n = 23$; note that the minimum time resolved by the recording set-up was about 17 ms). The times spent attacking each rotifer prey species were not statistically different (one-way ANOVA; $F = 0.502$; d.f.: 2, 20; $P = 0.613$). During copepod attacks, *D. b. odessanus* often changed the orientation of its body while placing its mouthparts to contact the prey. *Diacyclops b. odessanus* was able to hold the prey with its mouthparts while swimming.

Several parameters characterising copepod predation on the three rotifer species are shown in Table 1. Only the differences in the percentage of attacks after contact were statistically significant ($P = 0.05$). *Brachionus rotundiformis*, the smallest prey, had the highest percentage of attacks after contact, *B. plicatilis*, the largest prey, had the lowest percentage, and *B. ibericus*, the intermediate size prey, had an intermediate percentage. Percentage of attacks resulting in captures were nearly significant ($P = 0.1$), with *B. plicatilis* showing the lowest percentage. No significant differences among rotifer

Table 1 Predation by females (C5-adult) of the cyclopoid copepod *D. bodessanu*s on three rotifer sibling species *B. plicatilis*, *B. ibericus* and *B. rotundiformis*. Predator density = 1 female mL^{-1} , n: number of cultures replicates, C → AV: contacts resulting in avoidance responses, C → A: contacts resulting in attacks, A → CP: attacks resulting in captures

Prey species	n	Total observation time (min)	Rotifer densities, ($\text{mL}^{-1} \pm \text{S.E.}$)	Total number of contacts	Contact rate, ($\text{min}^{-1} \pm \text{S.E.}$)	C → A	C → A	A → CP
<i>B. plicatilis</i>	6	860	12.6 ± 8.6	41	0.0051 ± 0.0018	12.2%	43.9%	11.1%
<i>B. ibericus</i>	3	165	16.1 ± 7.4	27	0.0029 ± 0.0006	22.2%	59.2%	37.5%
<i>B. rotundiformis</i>	2	620	9.5 ± 0.8	57	0.0064 ± 0.0002	12.3%	68.4%	28.2%
Statistical analysis								
Probability					0.60 ^a	0.15 ^b	0.05 ^b	0.10 ^b

^aANOVA, ^bChi-square. The following independence test were performed: prey species × (contacts resulting in avoidance responses versus contacts resulting in no response), prey species × (contacts resulting in attacks versus contacts not resulting in attacks) and prey species × (attacks resulting in captures versus attack not resulting in captures).

species were found for predator contact rate or avoidance percentage.

Prey location just prior to the pouncing behaviour of *D. b. odessanus* is shown in Fig. 2 for cases where the copepod was in dorsal or lateral view. Note that these two data sets are independent observations. The distance to the prey before copepod pouncing ranged from 0.3 to 1.6 mm. Both *B. plicatilis* and *B. ibericus* had very similar mean attack distances (average distances 0.53 and 0.70 mm, respectively), but *B. rotundiformis* elicited predator pouncing from a greater distance (average distance 1.11 mm). These differences were marginally statistically significant ($P = 0.07$). The pouncing angle between the antero-posterior copepod body axis and the prey ranged from -54° to 68° (dorsal view) and from -15° to 77° (lateral view). The average value for the dorsal view (5.2°) did not differ significantly from 0. However, the average value for the lateral view (17.2°) showed a possible dorsal bias ($P = 0.12$), which may have reached significance with a larger sample size. No significant differences among prey were found for the angle formed with the copepod prior to pouncing behaviour.

Rotifer swimming speed in the presence and absence of the copepod is shown in Fig. 3. Relative swimming speed (body lengths s^{-1}) of *B. rotundiformis* was faster than the other two species. However, *B. plicatilis* was the fastest species when absolute swimming speed ($mm s^{-1}$) is considered. Swimming speed was significantly different among species (Table 2), with *B. plicatilis* swimming 24% faster than

B. rotundiformis. The three species showed a reduction in their absolute and relative swimming speed in presence of the predator, but this reduction was not statistically significant (Table 2).

Figure 4 shows the net distance covered in 20 s by the three rotifer species in the presence and absence of the predator. The differences among species were statistically significant (Table 2). *Branchionus plicatilis* showed the largest net displacement in the absence of the predator, followed by *B. rotundiformis* and *B. ibericus* (the same ranking as for absolute swimming speed). Reduction of rotifer net displacement in the presence of the copepod was species-dependent (effect of copepod, $P = 0.02$; interaction, $P = 0.08$). *Brachionus rotundiformis* showed a very slight reduction and had the highest net displacement when the copepod was present.

The differences among species in path sinuosity were statistically significant (Table 2). *Brachionus ibericus* showed the highest swimming sinuosity both in the presence and absence of *D. b. odessanus* (Fig. 5). The presence of the predator modified prey path sinuosity in a species-dependent manner. Both *B. plicatilis* and *B. ibericus* increased their swimming sinuosity in the presence of the predator, whereas *B. rotundiformis* showed a reduction.

Discussion

For a predator, successful hunting produces an increase in fitness through higher reproduction rates and probability of offspring survival, whereas for a

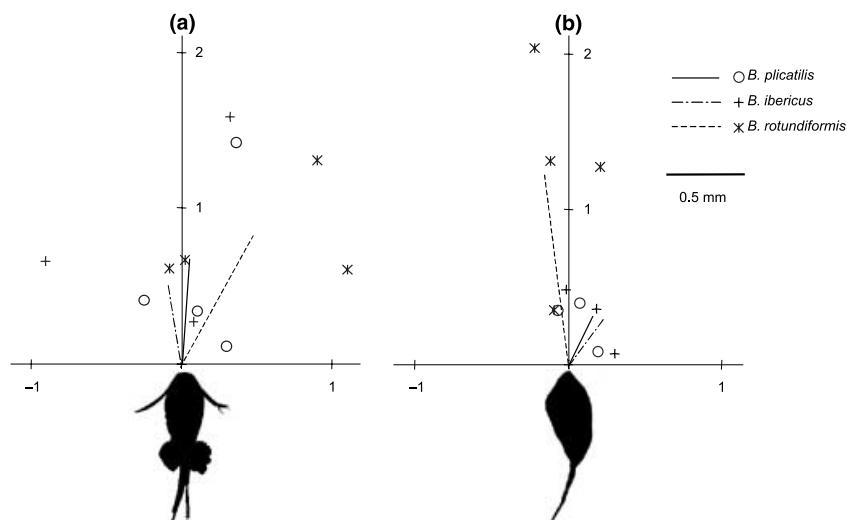


Fig. 2 Rotifer position before being attacked by *D. b. odessanus* (a) dorsal view of the copepod (silhouette); (b) lateral view of the copepod (silhouette). Each line represents the average attack distance and angle of attack for a rotifer species.

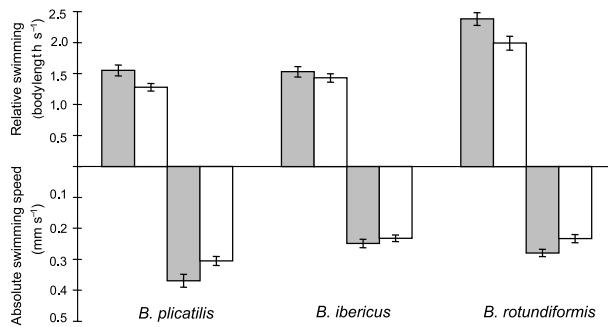


Fig. 3 Swimming speed of the three rotifer species in body-length s^{-1} (upper) and $mm\ s^{-1}$ (lower). The dark bar is rotifer swimming speed in the absence of the copepod *D. b. odessanus* and the open bar is rotifer swimming speed in the presence of the copepod. Thin bars represent standard error.

prey it represents decreased fitness through mortality. With such strong selective pressures, predators have evolved tactics to effectively capture and ingest prey, and prey have evolved countermeasures for protection against predation. Selective feeding is an important mechanism by which planktonic communities are structured by predation, and an understanding of mechanisms is important for interpreting the dynamics of predator–prey interactions.

In contrast to vertebrate predators, predatory copepods do not use visual orientation to capture prey. They detect their prey by mechano- and/or chemoreception (i.e. Williamson, 1991; Wong, 1995; Rabette, Thouvenot & Lair, 1998; Moore, Fields & Yen, 1999). Cyclopoid copepods use mechanoreceptors on their first and second antennae (Strickler, 1975; Kerfoot, 1977; Kerfoot, 1978; Williamson, 1991; Rabette *et al.*, 1998) to detect fluid disturbances created by moving objects. Thus, faster, bigger and more active rotifers may be more easily detected by cyclopoid copepods because of the greater noise that they create (Kerfoot, 1977; Gilbert & Williamson, 1978; Williamson,

1983a; Preston, Cecchine & Snell, 1999). Our results on pouncing attacks support the notion that *D. b. odessanus* is able to detect prey at distance. As Williamson & Gilbert (1980) reported when working on a different cyclopoid–rotifer system, attacks seem to be frequently initiated several body lengths from the prey. In our observations, when a remote response occurred, it was from a greater average distance than reported by Williamson & Gilbert (1980) (< 0.5 versus 0.5–1.1 mm). However, in contrast to previous findings, our results do not support the hypothesis that bigger prey are detectable at a larger distance, as we found the opposite pattern. On the other hand, the helical swimming path showed by the three rotifer species is similar to that described for other *Brachionus* species and is typical of non-sessile rotifers (Starkweather, 1987). This behaviour relies on simple cilia (Clément, 1987), and is regarded as inefficient metabolically (Epp & Lewis, 1984), with metabolic costs increasing with body size (Sleigh & Blake, 1977).

The hop and sink motion observed in *D. b. odessanus* is similar to that described by Strickler (1975) for other *Diacyclops*. The flexible body and swimming legs of *D. b. odessanus* allow it great momentary acceleration and speed (Kerfoot *et al.*, 1980), the metabolic relative cost of the swimming strokes being very low because of the presence of resilin in the cuticle (around 0.069% of total energetic budget; see Alcaraz & Strickler, 1988). The observed looping motion is probably because of the copepod searching across the wall of the vessel or may be induced by the loss of a captured prey (Kerfoot, 1978; Brandl, 1998). Our observation of this motion associated with prey contact supports the idea that it is a searching behaviour (Kerfoot, 1978; Williamson, 1980, 1981; Brandl, 1998). *Diacyclops b. odessanus* can be classified as a cruising predator, specialised in attacking slow-moving prey (Gerritsen & Strickler, 1977; Gerritsen, 1980). It is much more

Table 2 ANOVA results for rotifer swimming behaviour parameters. Effects are: rotifer species, fixed; predator presence, fixed; replicate, random

Source	d.f.	Absolute swimming speed		Relative swimming speed		Net displacement		Path sinuosity	
		F	P	F	P	F	P	F	P
Rotifer species	2,6	4.97	0.05	9.46	0.01	9.68	0.01	9.42	0.01
Predator presence	1,6	2.49	0.16	2.52	0.16	10.58	0.02	2.29	0.18
Interaction	2,6	0.26	0.78	0.28	0.77	9.92	0.08	5.85	0.04
Replicate	6,348	5.54	0.00	5.40	0.00	1.20	0.30	1.09	0.37

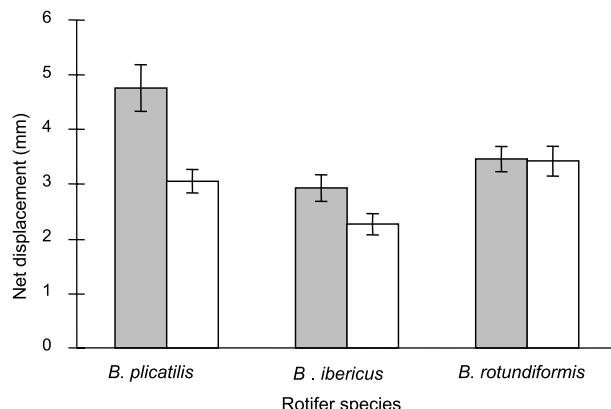


Fig. 4 Net displacement of the three rotifer species in mm. The dark bar is rotifer net displacement in the absence of the copepod *D. b. odessanus* and the open bar is rotifer net displacement in the presence of the copepod. Thin bars represent standard error.

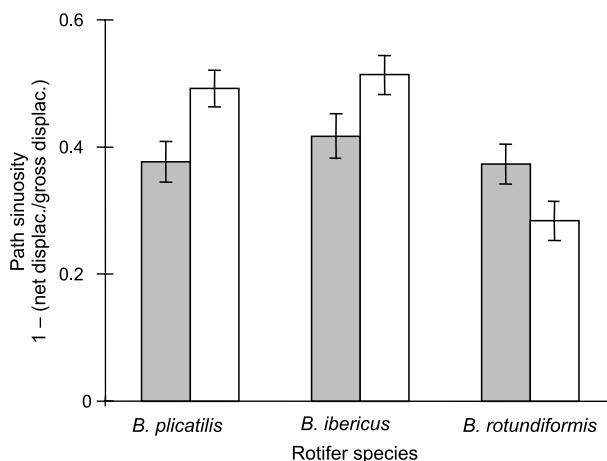


Fig. 5 Path sinuosity 1 – (net displacement/gross displacement) of the three rotifer species. The dark bar is rotifer path sinuosity in the absence of the copepod *D. b. odessanus* and the open bar is rotifer path sinuosity in the presence of the predator. Thin bars represent standard error.

efficient at capturing rotifers like *Brachionus* than other invertebrate prey. *Diacyclops b. odessanus* has been found frequently associated with sibling species of the *Brachionus* complex in ponds on the Mediterranean Spanish coast. Therefore, it is probably an important predator of these rotifer species.

In contrast to several other rotifer species, species of the *B. plicatilis* complex do not have marked morphological or escape defences (Green & Lan, 1974; Lewis, 1977; Williamson, 1987; Kirk & Gilbert, 1988). Thus,

their protection relies on a combination of other strategies, including swimming speed and swimming pattern. For example, a reaction after copepod contact that could be considered a passive defence similar to the dead-man sinking response (Stemberger & Gilbert, 1987; Wallace & Snell, 1991), was observed occasionally in the three rotifer species. In this behaviour, rotifers stop swimming, thus decreasing the vibrations which may be detected by the copepod. The corona retraction that often accompanies this behaviour makes the spines more prominent and increases rotifer stiffness, making it more difficult to be grasped by the predator. This passive defense has been observed in other rotifer species vulnerable to copepod predation such as *Keratella* (Stemberger, 1985; Roche, 1987), *Asplanchna* (Williamson, 1983a; Roche, 1987), *Synchaeta* and *Notholca* (Roche, 1987), as well as in some small cladocerans like *Bosmina* (Williamson, 1983a; Brandl, 1998). We speculate that this kind of response could explain the low percentage of attack after contact. However copepod satiation, favoured by high experimental prey densities, could also explain this low percentage of attack after contact as well as the low contact rates if satiation changes swimming patterns of copepods. On the other hand, capture percentage after attack is also low. We found an association between capture failure and size. Therefore, low capture proportions could be the result of low predator efficiency to catch the size range of the studied rotifer species.

Besides detection distance, the swimming speed of both prey and predator positively affected encounter rate (Gerritsen & Strickler, 1977; Gerritsen, 1980; Rothschild & Osborn, 1988). *Brachionus* species seem to detect and adapt their swimming behaviour to the presence of the predator; significantly decreasing their net displacement. It has been reported that rotifers are able to detect the presence of predators in their habitat and to develop morphological defences (Gilbert, 1980b; Gilbert & Stemberger, 1984). Thus, it is possible they could also modify their behaviour. However, the small change in swimming rotifer behaviour, if promoting predation avoidance, is puzzling, given the high mortality risk caused by predators. A possible explanation is that predation risk detection would be ineffective. Alternatively, when modifying swimming behaviour, rotifers should trade off predation risk and filtration rate, hence decreasing swimming speed would also decrease food intake. *Brachionus*

rotundiformis is an exception with no change in net displacement in the presence of the predator.

In many studies of selective predation by cyclopoids, it has been argued that prey body size may be an important component of prey selection when only similar size prey species are available (Kerfoot *et al.*, 1980; Williamson, 1983a; Stemberger, 1985). In our study, we compared species that differed in traits other than size (e.g. prey swimming sinuosity) which we propose are important to prey detection. However, the morphological similarity among these rotifers and their differences in size allow for a good assessment of the effects of body size on predation susceptibility according to the Holling model for ingestion (Holling, 1966). Our results show that the smaller the species, the higher the probability that a contact would result in attack (Table 1). The probability of the larger species being captured after an attack was also much lower (< 50%) than the other two species. This may be the result of the ratio of prey–predator body size, which has an important influence on the probability of capturing prey and on predator handling ability. A higher proportion of attacks after contacting smaller prey may be either because of a better recognition as an edible particle or recognition as more easily handled prey.

Finally, our observations suggest that contact is sometimes uncoupled from detection and thus is not equivalent to encounter. First, some contacts were not followed by any observed change in copepod behaviour. Secondly, some rotifer prey were detected at a distance, so an encounter occurred prior to contact. These observations also complicate the interpretation of the events distinguished in a predation cycle, as contacts (if they are real encounters) might be required for a copepod attack, or alternatively they might be the result of an attack decision if detection occurred at distance. Therefore, some caution is needed when attack–contact ratio is interpreted as an *a priori* conditional probability.

Sibling species in zooplankton communities have been recognised as a common phenomenon (Serra, Galiana & Gómez, 1997; Hebert, 1998; Ortells *et al.*, 2000). Their co-occurrence in sympatry is not rare, and poses the problem of what factors mediate coexistence. Differential predation on superior competitors might have an important role in maintaining species diversity. It is now known that *B. rotundiformis* is a better competitor in a wide range of trophic conditions

(Ciros-Pérez *et al.*, 2001a) and that its vulnerability to predation promotes its coexistence with *B. plicatilis* and *B. ibericus* (Ciros-Pérez, 2001). Our study provides some insight into the behavioural mechanisms involved in coexistence and thus in the maintenance of species diversity in rotifer assemblages.

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