Selective feeding of *Arctodiaptomus salinus* (Copepoda, Calanoida) on co-occurring sibling rotifer species

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SUMMARY

1. Using two- and three-dimensional video recordings, we examined the steps involved in predation that lead to the differential vulnerability of three sympatric rotifer sibling species (*Brachionus plicatilis*, *B. ibericus* and *B. rotundiformis*) to a co-occurring, predatory, calanoid copepod (*Arctodiaptomus salinus*).
2. *Brachionus rotundiformis*, the smallest prey tested, was the most vulnerable with the highest encounter rate, probability of attack, capture and ingestion, and the lowest handling time.
3. Comparison of our results with those of a previous study shows that *A. salinus* is a more efficient predator than a co-occurring cyclopoid copepod (*Diacyclops bicuspidatus odessanus*) feeding on these same rotifer species. However, despite its higher capture rates, *A. salinus* seems to be less selective than *D. b. odessanus* based on attack distances and prey handling times.
4. The differential vulnerability to both calanoid and cyclopoid copepod predation can help explain the coexistence and seasonal succession of these co-occurring rotifer species.

Keywords: calanoid, cryptic species, prey selectivity, video recording, zooplankton

Introduction

Predator–prey interactions are a major force structuring zooplankton communities, with selective feeding and prey defence strategies the main components of this interaction (Lynch, 1979; Greene, 1983; Brandl, 1998). Many studies have demonstrated the strength and selective nature of copepod predation on natural assemblages of rotifers (Williamson, 1987; Conde-Porcuna & Declerck, 1998; Ciros-Pérez *et al.*, 2004). In contrast to visual vertebrate predators, predatory copepods detect their prey by mechano- and/or chemoreception (Moore, Fields & Yen, 1999; Bundy & Vanderploeg, 2002) located primarily on their first and second antennae (Strickler, 1975; Williamson, 1991). Once detected, copepods raptorially capture prey with their mouthparts and grasp them with the maxillae and maxillipeds (Williamson, 1991). In contrast to cyclopoid copepods, there is a strong interaction between feeding and swimming behaviour in calanoid copepods because the cephalic appendages and maxillipeds are utilised for both behaviours (Greene, 1988; Williamson, 1991). The current created by their feeding appendages, besides serving for propulsion, provides information about prey location by transporting chemical cues or fluid disturbances created by the prey. After detection, calanoid copepods are able to direct their attack and actively capture prey by coordinated movements of the mouthparts (Williamson & Butler, 1986; Bundy & Vanderploeg, 2002). Post-encounter events in calanoid predation have been studied mostly in tethered copepods and/or using non-motile and inert particles as prey (Vanderploeg & Paffenhöfer, 1985; Bundy & Vanderploeg, 2002). However, few studies have dissected the components of prey–predator interac-

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tions between calanoid copepods and rotifers using Holling's (1966) model.

A variety of morphological features and behavioural mechanisms protect rotifers against copepod predators. For example, the presence of permanent or inducible spines makes prey more difficult to capture, manipulate and ingest, and the mucus sheaths reduce copepod attack and capture success (Stemberger & Gilbert, 1987). Escape responses reduce the probability of capture (Gilbert & Kirk, 1988) and other behavioural features such as swimming speed and predictability of movement influence prey detection and selection (Gómez, Cecchine & Snell, 1997; Lapesa *et al.*, 2002). Besides these traits, rotifer body size relative to that of the predator can affect the probability of detection and capture, the escape probability after capture and handling time. Any protection conferred by a stiff lorica and spines may be reduced or lost if predator body size is large in relation to prey body size (Stemberger & Gilbert, 1984).

The *Brachionus plicatilis* rotifer species complex is composed of at least fourteen sibling species (Suatoni, 2003). Three of these have been named, based upon morphological traits, as *B. plicatilis* (Müller), *Brachionus rotundiformis* (Tschugunoff) and *Brachionus ibericus* (Ciros-Pérez, Gómez & Serra, 2001b). They differ in size and have minor differences in shape, primarily in three pairs of spines located in an antero-dorsal position. *Brachionus plicatilis* is the biggest species, followed by *B. ibericus* and by *B. rotundiformis*. Although they do have preferences for different ecological conditions and show different seasonal distributions, they also have long periods of co-occurrence in several ponds of the Mediterranean coast of Spain (Gómez, Temprano & Serra, 1995; Ortells, Gómez & Serra, 2003). Laboratory studies have proposed mechanisms by which coexistence among *B. plicatilis*, *B. rotundiformis* and *B. ibericus* is possible. Firstly, they strongly compete for algae, but differential use of resources and variance in food availability could promote coexistence (Ciros-Pérez, Carmona & Serra, 2001a). Secondly, their differential vulnerability to cyclopoid copepod predation can extend coexistence (Ciros-Pérez *et al.*, 2004) and probably plays a significant role in their seasonal succession. In recognition of the important role of copepod predation in seasonal succession and coexistence of sibling species, Lapesa *et al.* (2002) studied the behavioural mechanisms by which cyclopoid copepod predation differentially affects *B. plicatilis*, *B. rotundiformis* and *B. ibericus*.

The aim of this paper is to extend predation studies on rotifer sibling species to naturally co-occurring calanoid copepods. These copepods have been found in sympatry with the three rotifer sibling species in several inland and coastal ponds of Spain (S. Lapesa, unpublished observations). Using two- and three-dimensional video recordings we describe the components of the predatory interaction according to the Holling (1966) model, including attack distances and angles of attack. We also compare our results for calanoids with those obtained by Lapesa *et al.* (2002) for a cyclopoid copepod and the same rotifer prey.

Methods

Calanoid copepod predators were adult females of *Arctodiaptomus salinus* (Daday) and prey were rotifers of three sibling species, *B. plicatilis* (strain L1), *B. ibericus* (strain SM2) and *B. rotundiformis* (strain SS2). Rotifers were originally isolated from Poza Sur of Prat de Cabanes-Torreblanca Marsh located 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). The length of the dorsal-external spine, which is the largest one, was 12–26 μm for *B. plicatilis*, 12–21 μm for *B. ibericus* and 15–22 μm for *B. rotundiformis* (Ciros-Pérez *et al.*, 2001b). Copepod females were isolated from El Salobrejo (Albacete Province), an inland salt pond in southeast Spain, 150 km from the Mediterranean coast. The average body length (excluding the caudal setae) of an adult copepod female was 1.5 mm. Stock cultures of copepods and rotifers were maintained in artificial sea water at 12 g L^{-1} salinity of Instant Ocean® seasalts (Aquarium Systems, Mentor, OH, U.S.A.), fertilised with f/2 modified medium (Guillard & Ryther, 1962) at 20 °C and constant illumination of 0.45 W m^{-2}. Stock cultures of rotifers were fed with *Tetraselmis suecica* Kylin (Butch) originally from the algae collection of the Instituto de Ciencias Marinas in Cádiz (Andalucía, Spain). Copepod cultures were maintained on a mixed diet of the three species of rotifer used in the experiment.

Three different video recording experiments were carried out to measure the five different components of predation: *encounter* – entrainment of the prey in

the copepod feeding current; *attack* – copepod reaction so that the feeding appendages are reoriented towards the prey; *capture* – prey held by the mouthparts of the predator for more than one second; *ingestion* – disappearance of the prey within the feeding chamber of the copepod; and *handling time* – time span from the capture onset to the end of the prey ingestion. Ingestion was considered to end when the copepod resumes swimming in a cruising motion. *Attack distance* is defined as the distance between copepod and prey when the copepod first orients towards the prey. *Angle of attack* is the angle between the anterior-posterior body axis and a line joining the midpoint of the rotifer body and the copepod rostrum.

Experiments were performed separately for each rotifer species in the presence of the copepod. Experimental temperature was maintained at 20 °C and the filming vessel was covered by transparent plastic film to minimise turbulences.

Rotifers were transferred to the filming vessels by filtering them from the stock cultures using 35 μm Nytex mesh and washing with sea water. *Arctodiaptomus salinus* adult females were starved for 16–18 h before experiments and then were transferred to the vessels using a Pasteur pipette. Predator density was 0.5 female mL^{-1}, and rotifer density was 20 rotifers mL^{-1}.

First experiment

From this experiment we estimated the encounter rate and the percentage of attack after encounter. Four replicates were carried out for each prey–predator combination. The animals were recorded in a squared glass vessel (49 mm length × 49 mm width × 52 mm height) containing 75 mL of artificial seawater. The encounter rate for each replicate was calculated as: [(number of encounters/volume recorded)/density of rotifers]/observation time.

Filming was carried out using a Schlieren optical pathway with a HeNe laser (633 mm) (Newport, Irvine, CA, U.S.A.) as a light source (Strickler, 1985; Yen & Fields, 1992). 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 Corporation, Newbury Park, CA, U.S.A.). A cube of 3.3 mL of medium in the experimental tank was filmed for analysis. Images and time code (Comprehensive Video Supply Corporation; Horita,

Mission Viejo, CA, U.S.A.) were recorded on a Panasonic AG-1960 video recorder (Matsushita, Secaucus, NJ, U.S.A.). To increased temporal resolution, individual video frames (33 ms) were split and analysed field by field (16.7 ms). The experimental vessel was recorded for 2 h.

Second experiment

From this experiment we estimated the percentage of capture after attack, the percentage of ingestion after attack and the handling time. Four replicates were carried out for each prey–predator combination. The animals were recorded in a squared glass vessel (11 mm length × 11 mm width × 38 mm height) containing 4 mL of artificial seawater. Filming was carried out as in the first experiment.

Third experiment

A three-dimensional recording using two cameras was made to estimate the copepod's angle and distance of attack. Three replicates were carried out for each prey–predator combination. The animals were recorded in a squared glass vessel (49 mm length × 49 mm width × 52 mm height) containing 60 mL of artificial seawater.

Two HeNe laser light paths intersecting at a 90° angle at the experimental vessel were focused onto two perpendicular mounted video cameras, one of them equipped with a 100-mm macro-zoom and the other equipped with a 55-mm macro zoom Vivitar lens. The two cameras provided orthogonal views representing the *x-y* and the *z-y* planes.

A cube of 3.3 mL of medium in the center of the experimental tank was filmed for analysis. The images were recorded on two Panasonic AG-1960 video recorders (Matsushita, Secaucus, NJ, U.S.A.) synchronised with a Comprehensive Video Supply Corporation time code generator (Horita, Mission Viejo, CA, U.S.A.).

In addition to the angle of attack defined before, we obtained two additional angles of attack for each copepod-rotifer pair, the angle of attack from the dorsal view of the copepod and the angle of attack from the lateral view of the copepod. We used only those attacks where the antero-posterior plane was in the focal plane of one camera and the sagital plane of the copepod was in the focal plane of the other camera.

The x, y data and the z, y data recorded in the space coordinate system were transformed into the copepod coordinate system as explained in Lapesa *et al.* (2002). Those observations where the differences in the y coordinate were >10% were not used (only two cases).

To compute attack distance and angles of attack, the coordinates of the rotifer in the copepod coordinate system were used (see Lapesa *et al.*, 2002). Distance of attack was computed as $d = (x^2 + y^2 + z^2)^{1/2}$, where x, y and z are the rotifer coordinates in the copepod coordinate system. Angles of attack were computed as $\Phi_{dorsal} = \arctan(x/y)$, $\Phi_{lateral} = \arctan(z/y)$ and $\Phi_R = \arccos(y/d)$. Φ_R is the angle of attack; that is, the angle between the antero-posterior copepod axis and the line joining the midpoint of the rotifer body and the copepod rostrum.

Statistical data analysis of the three experiments was performed using SPSS (release 11.5. SPSS Inc., Chicago, IL, U.S.A.) and R. v. 1.7.1 statistical software (R. Development Core Team 2003, Ihaka & Gentleman, 1996).

Results

Arctodiaptomus salinus swam in a 'cruise and sink' mode *sensu* Greene (1988). The cruising motion resulted from the continuous oscillation of the feeding appendages. The current created by this motion was also used to capture prey. This swimming behaviour was modified when a predation event occurred. Previous to the attack, the copepod either slowly reoriented itself or made a reorientation jump. With this behaviour the feeding appendages of the copepod became closer to the prey so that the prey was positioned inside a more central area of the feeding appendages, where it was more difficult to escape. The successful capture of the prey was usually accompanied by a smooth stroke of the caudal region of the copepod. After capturing the prey, the copepod sank, usually to the bottom of the experimental vessel, to ingest the prey. After ingestion the copepod restarted the cruising motion.

Tables 1 and 2 show the estimates for the predation cycle parameters and the handling time. We per-

Prey species	n	Total number of encounters	Encounter rate ± SE (min^{-1})	E → AT
Brachionus plicatilis	4	96	0.0031 ± 0.0006	53%*
Brachionus ibericus	4	79	0.0025 ± 0.0005	49%
Brachionus rotundiformis	4	147	0.0047 ± 0.0009	70%
Statistical significance (probability)			0.120[†]	0.002[‡]

Table 1 Predation by adult females of the calanoid copepod *Arctodiaptomus salinus* on three rotifer sibling species: *Brachionus plicatilis*, *B. ibericus* and *B. rotundiformis* (first experiment)

*Heterogeneous replicates.
[†]ANOVA.
[‡]Fisher's exact test (prey species with homogeneous replicates).
Predator density = 0.5 female mL^{-1}; prey density = 20 rotifers mL^{-1}; total experimental volume = 75 mL; n: number of replicates; E → AT: percentage of encounters resulting in attack.

Prey species	n	Total number of attacks	AT → CP	CP → I	Handling time, (s ± SE)
Brachionus plicatilis	4	95	47%	44%	16 ± 2
Brachionus ibericus	4	91	80%*	60%	21 ± 2
Brachionus rotundiformis	4	110	66%*	82%	11 ± 1
Statistical significance (probability)				<0.000[†]	0.448[‡]

Table 2 Predation by adult females of the calanoid copepod *Arctodiaptomus salinus* on three rotifer sibling species: *Brachionus plicatilis*, *B. ibericus* and *B. rotundiformis* (second experiment)

*Heterogeneous replicates.
[†]Fisher's exact test (generalised for 2 × 3 independent tables).
[‡]Two-level nested ANOVA. Effects: prey species (fixed), replicate (random), event (random, error).
Predator density = 0.5 female mL^{-1}; prey density = 20 rotifers mL^{-1}; total experimental volume = 4 mL; n: number of replicates; AT → CP: percentage of attacks resulting in capture; CP → I: percentage of captures resulting in ingestion.

formed a test of homogeneity for the replicates within species on a parameter-by-parameter basis because several events in a replicate could be dependent if the same copepod was involved. Homogeneity was used as a criterion for the lack of an individual copepod effect. Tests for prey-species differences were restricted to homogeneous replicates. The differences in the percentage of attack after encounter and in the percentage of ingestion after capture were statistically significant ($P < 0.01$). The differences in the percentage of attack after encounter compared *B. rotundiformis* and *B. ibericus* (Table 1). The smallest species, *B. rotundiformis*, experienced the highest percentage of attack after encounter. Percentage of ingestion after capture also showed a negative relationship with prey size (Table 2). The percentage of capture after attack was higher in the two smaller species, *B. rotundiformis* and *B. ibericus*, with *B. ibericus* being the most vulnerable. However, those differences were not statistically tested because the two species showed heterogeneous replicates (Table 2). No significant differences were found for encounter rate (Table 1) or handling time (Table 2) among rotifer species.

Prey location prior to attack by *A. salinus* in shown in Fig. 1. Prey were attacked within an ovoid volume centred forward to the paired first antennules of *A. salinus*. The dimension of this attack volume fell along the *x*-axis approximately 1 mm lateral to the rostrum in each direction. The distance of attack is very similar among the rotifer species. *B. plicatilis*, the largest prey, and *B. rotundiformis*, the smallest prey, had a very similar attack distance of 1.65 ± 0.19 mm and 1.63 ± 0.20 mm respectively, while *B. ibericus* showed the lowest attack distance of 1.31 ± 0.15 mm; however, these differences were not significant ($F = 0.701$, $P = 0.502$; one-way ANOVA). Fig. 2 shows the frequency distribution of the attack distance of *A. salinus* on all three rotifer species. The distances ranged from 0.44 to 4.59 mm, but the highest proportions (>70%) of the attacks occurred in the interval 0.5–2.0 mm.

The average angle between the antero-posterior copepod axis and the line joining the midpoint of the rotifer body and the copepod rostrum (Φ_R) was 40.94 ± 5.83° for *B. plicatilis*, 33.04 ± 4.16° for *B. ibericus* and 32.24 ± 4.42° for *B. rotundiformis*. However, the differences among prey were not significant statistically ($F = 0.933$, $P = 0.401$; one-way ANOVA). Fig. 3 shows the frequency distribution of Φ_R for the three
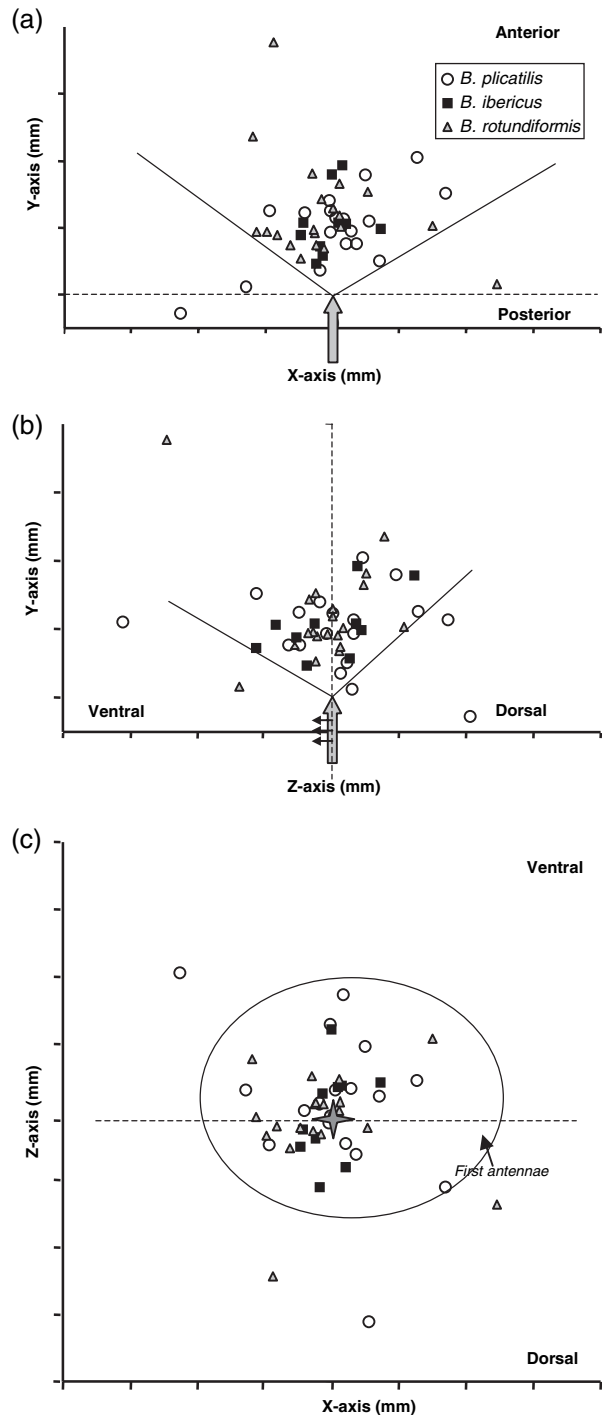

Fig. 1 Rotifer position prior to the attack of *Arctodiaptomus salinus* plotted in three two-dimensional planes. Each point distinguishes different rotifer prey individuals with different symbols for the three species. (a) Dorsal view of the copepod. (b) Lateral view of the copepod. The thick arrows show the orientation of the copepod head. The thin arrows show the orientation of the ventral part of the copepod. (c) Anterior view of the copepod with dashed line representing first antennules and the star representing the copepod head.
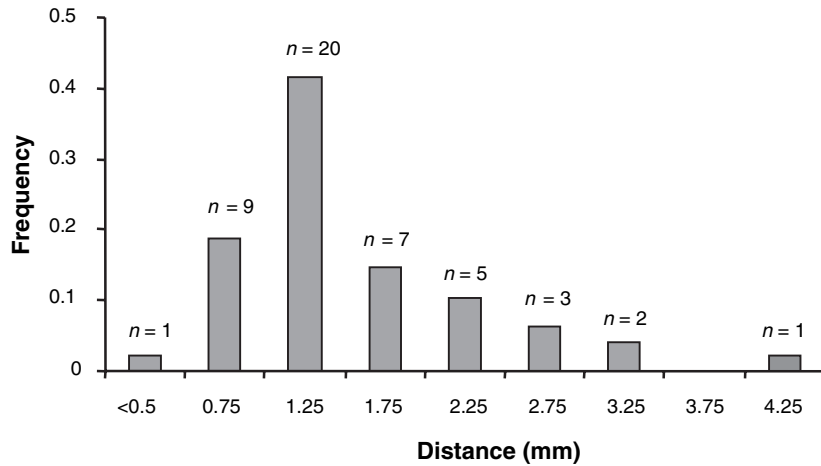
Fig. 2 Frequency distribution of the attack distance performed by *Arctodiaptomus salinus*. The mid-point of each 0.5-mm interval is shown in the *x*-axis. The data include *Brachionus plicatilis*, *B. rotundiformis* and *B. ibericus*. On the top of each bar the number of attack events is indicated.
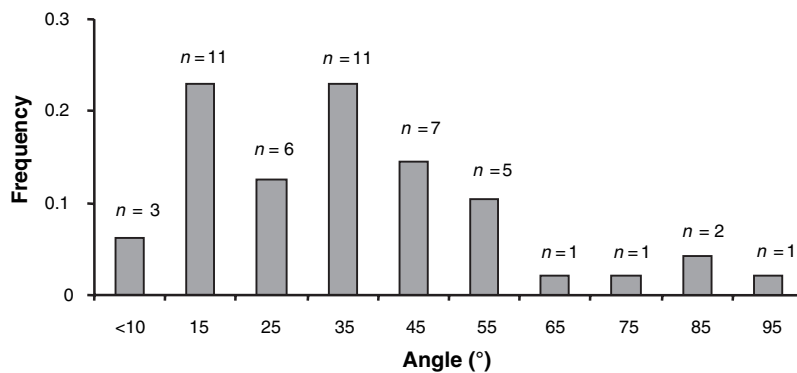

Fig. 3 Frequency distribution of the angle of attack (Φ_R) displayed by *Arctodiaptomus salinus*. The mid-point of each 10° interval is shown in the *x*-axis. The data include *Brachionus plicatilis*, *B. rotundiformis* and *B. ibericus*. On the top of each bar the number of attack events is indicated.

rotifer species. Most of the attacks occurred with Φ_R between 10° and 50°. Both the angle between the prey and the antero-posterior plane of the copepod (Fig. 1a) and between the prey and the dorso-ventral plane of the copepod (Fig. 1b) were frequently lower than ±10°. The average angle between the prey and the antero-posterior plane of the copepod was 8.66 ± 8.71° for *B. plicatilis*, −4.94 ± 6.23° for *B. ibericus* and −7.83 ± 7.44° for *B. rotundiformis*. The average angle between the prey and the dorso-ventral plane of the copepod was from −0.66 ± 9.54° for *B. plicatilis*, −6.57 ± 10.22° for *B. ibericus* and −3.52 ± 6.39° for *B. rotundiformis*. No significant differences among prey were found in the dorsal ($F = 1.303$, $P = 0.282$; one-way ANOVA) or lateral angle of attack ($F = 0.100$, $P = 0.905$; one-way ANOVA).

Discussion

Arctodiaptomus salinus has been commonly described as an herbivorous copepod with a typical suspension-feeding swimming mode (Tolomeyev, 2002). However, although copepodite stages may feed on phytoplankton (Temerova, Tolomeyev & Degermendzhy, 2002) our results show that adult stages can consume small zooplankters. Its predatory behaviour, far from being a passive intake of food through the current created by the feeding appendages, includes active, prey-oriented movements, with predation efficiency dependent on the rotifer prey species. As *A. salinus* has been found frequently associated with sibling species of the *Brachionus* complex in lakes and ponds of Spain (S. Lapesa, unpublished observation), it has the potential to be an important predator of these rotifer species in natural communities.

Arctodiaptomus salinus shows a 'cruise and sink' swimming behaviour. This is an intermediate behaviour between a predominantly stationary suspension-feeding pattern and a continuously cruising raptorial predation pattern, and it is exhibited by many omnivorous calanoids (Greene, 1988). During the 'cruise and sink' swimming behaviour, the

cruising mode is interrupted by pauses in appendage activity. The frequency and duration of such pauses appear to be related to food level, but the nature of this relationship seems to vary among species (Buskey, 1984). When *A. salinus* detected a rotifer, it reoriented itself in order to bring the feeding appendages closer to the prey. This reorientation could be made when the rotifer is close to the feeding currents of the copepod or could be accompanied by a jump, suggesting that *A. salinus* can locate prey from a distance. This reorientation jump is a common behaviour among carnivorous and omnivorous calanoids (Williamson, 1987; Doall *et al.*, 2002) and has been observed even when capturing inert particles (Bundy & Vanderploeg, 2002). Several studies suggest that the feeding current provides information to the copepod about the location of distant prey mainly by two mechanisms. Firstly, it transports chemical cues from the prey to its sensory receptors (Moore *et al.*, 1999), and secondly, it mechanically stimulates the antennae to detect water disturbances (Bundy & Vanderploeg, 2002).

Most of the *A. salinus* attacks occurred within an angle <50°, supporting the idea that successful attacks occurred mainly in the high velocity portion of the feeding current. More than 70% of *A. salinus* attacks occurred at a distance between 0.5 and 2.0 mm. Doall *et al.* (2002) reported average attack distance close to that interval (i.e. 1.5 mm) for another calanoid copepod (*Euchaeta rimana* Bradford) feeding on small copepods, whereas Williamson (1987) found a much lower attack distance (<0.5 mm) for the calanoid *Diaptomus pallidus* Herrick feeding on rotifers. We found that a successful rotifer capture by *A. salinus* was usually accompanied by a smooth stroke of the caudal part of the copepod, and this behaviour seems to be very important to catch the prey judging from the capture difficulties observed in tethered individual *A. salinus* (S. Lapesa, personal observation).

During ingestion, *A. salinus* stopped swimming and sank. *Arctodiaptomus salinus* seems not to be able to handle a prey while swimming, probably because of the use of the same thoracic appendages in both swimming and feeding behaviour in calanoid copepods (Greene, 1988; Williamson, 1991). The handling time was relatively long for the three rotifer species, averaging from 11 to 21 s when compared with <4 s for the calanoid copepod *D. pallidus* preying on several soft-bodied and hard loricae rotifer species

(Williamson, 1987). Williamson found the longest handling time for *Keratella cochlearis* Gosse (12 s) and argued that this species with a hard lorica was most difficult to ingest after capture. Thus, the hard lorica of *Brachionus* could result in lower predation efficiency by increasing the handling time and consequently reducing the available searching time. A hard lorica can also work as an individual prey defence, as rotifers rejected after 5 s in the grasp of the copepod still continued swimming (S. Lapesa, personal observation).

Apart from the protection of the lorica, the species of the *B. plicatilis* complex do not show markedly different morphological or escape defences that could influence rotifer vulnerability to copepod predation (Stemberger & Gilbert, 1987). However, body size, the most noticeable difference among the three rotifer prey studied here, seems to have a protective effect. Our results suggest that the smaller species is more frequently attacked (*B. rotundiformis versus B. ibericus*), and captured (*B. ibericus versus B. plicatilis*). Ingestion is also less likely to be completed if the prey is larger (*B. rotundiformis versus B. plicatilis*).

By contrast, our results regarding encounter rates and attack distance do not support an effect of prey size on prey detection. This is in disagreement with the hypothesis that, if calanoid copepods are able to use mechanoreception on the antennae to detect fluid disturbances, a positive relationship between prey size and prey detection is expected, because of the greater disturbance created by bigger prey (Kerfoot, 1977; Williamson, 1983). We speculate that other behavioural traits, such as differences in swimming patterns, could affect prey detection (Lapesa *et al.*, 2002). Although we found that the smallest species required lower handling times than the two largest species, there was no clear correlation between prey size and handling time, as the biggest species (*B. plicatilis*) showed lower handling time than the intermediate species (*B. ibericus*). These results contrast with data reported for *Acantocyclops robustus* Sars by Roche (1990) and for *Diacyclops bicuspidatus odessanus* Schmankevitch by Ciros-Pérez *et al.* (2004).

Lapesa *et al.* (2002) studied the predation cycle of *D. b. odessanus* with the same rotifer species studied here. *D. b. odessanus* is a 0.78 mm long cyclopoid and *A. salinus* is a 1.5 mm long calanoid, both inhabiting brackish ponds in eastern Spain and coexisting with *Brachionus* species. This allows us to compare, in a

similar context, predation by these two copepods, although any generalisation from this comparison to calanoid versus cyclopids predators needs to be made with caution.

Diacyclops bicuspidatus odessanus showed much lower capture rates than *A. salinus*. The latter copepod captured prey in a narrower frontal angle window around its body axis. It is known that the prey-copepod angle may be critical in calanoid copepod predation, as the fluid velocity of the feeding current is maximal at low angles, and the probability of a successful attack increases (Bundy & Vanderploeg, 2002). By contrast, *A. salinus* showed longer attack distances than *D. b. odessanus*. Interestingly, *B. rotundiformis*, the smallest and most vulnerable rotifer species, elicited *D. b. odessanus* attacks from much greater distance than *B. ibericus* and *B. plicatilis* (Lapesa *et al.*, 2002), a difference not observed for *A. salinus*.

Prey body size has an important effect on predation susceptibility to both copepods, larger prey being associated with low attack and capture rates, which resulted in selective predation by both *D. b. odessanus* and *A. salinus* on *B. rotundiformis*, the smaller and more vulnerable of the species tested. Nevertheless, *A. salinus*, the most efficient predator, seems to be less selective, based on attack distance and handling time (Lapesa *et al.*, 2002; Ciros-Pérez *et al.*, 2004). We hypothesise that the larger size of *A. salinus* is the cause of both higher efficiency and reduced selectivity. Although less selected, *B. plicatilis*, the largest prey, does seem to be preyed on by *A. salinus*. The body length ratio between predator and prey is 6.1, a value very similar to the ratio for *D. b. odessanus* and *B. rotundiformis*, the smallest rotifer (ratio: 6.6). Both behavioural and population dynamics experiments have shown that *D. b. odessanus* is an efficient predator on *B. rotundiformis* (Lapesa *et al.*, 2002; S. Lapesa, unpublished observation).

Studies reporting the existence of sibling species in zooplankton communities have increased during recent years (Hebert, 1998; Ortells *et al.*, 2003). The common sympatric occurrence of similar species raises the issue of what factors mediate coexistence. A series of experimental studies have been carried out in order to gain insights into the mechanisms allowing *Brachionus* sibling species to coexist. These studies have shown that a cyclopoid copepod, *D. b. odessanus*, has the potential to affect rotifer population dynamics and to promote coexistence (Lapesa *et al.*, 2002; Ciros-Pérez *et al.*, 2004). This study has shown that *A. salinus*, not previously considered a zooplankton predator, is also an efficient and selective predator on *Brachionus* sibling species, but leaves open the question of the effects of this calanoid copepod on *Brachionus* population dynamics.

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