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Motility and size of rotifers as risk factors for being consumed by the passive protistan predator *Actinosphaerium* sp.

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Abstract Predation is a well-known factor that structures rotifer communities. However, the role of protists as predators is relatively understudied. Here, we investigated predatory behavior of *Actinosphaerium* sp., a freshwater heliozoan, on seven rotifer species. Predators and prey were collected from a local playa; except for *Brachionus calyciflorus* that served as a naive prey control. Prey included large species (≥ 175 µm mean length: *Asplanchna sieboldii*, *B. calyciflorus*, *Platyias quadricornis,* and *Lacinularia flosculosa*) and small species (< 175 µm: *Cephalodella gibba, Euchlanis dilatata,* and *Lepadella patella*). Four experiments were conducted. (1) Single prey items of varying size and motility. Larger prey types were ~ 1.7 to 3.0 times more likely to be ingested than small prey. No *L. flosculosa* were ingested, contrary to field observations. No correlation was found between swimming speed and predation risk. (2) Preference tests. *Asplanchna sieboldii* and *B. calyciflorus* were favored prey. (3) Growth rate of *Actinosphaerium* on mixed diets, with and without *Asplanchna*. Highest population growth of *Actinosphaerium* was observed in presence of *A. sieboldii*. (4) Prey defenses. Susceptibility of spined versus unspined *B. calyciflorus* resulted in no significant difference in predation risk. Thus, size and being mobile (compared to sessility) are the primary risk factors influencing rotifer predation vulnerability.

Keywords Heliozoan · Predation · Prey preference · Swimming speed

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Introduction

Rotifers play an important role as primary consumers in freshwater systems (Wallace et al., 2006, 2015), so understanding how their communities are structured is key to interpreting ecological and evolutionary processes affecting them. Predation is a well-known factor that structures rotifer communities (Lynch, 1979; Williamson, 1983; Li et al., 2022). Rotifers are consumed by an array of freshwater predators including larval fishes (Stenson, 1982; Zhang et al., 2022), aquatic insects (Moore & Gilbert, 1987; Walsh, 1995; Hampton et al., 2000; Hampton & Gilbert, 2001), hydra (Walsh, 1995), cyclopoid copepods (Williamson, 1983), predatory rotifers (Gilbert, 1967, 2017,

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2019), and some protists (Bell et al., 2006; Weithoff & Bell, 2022). However, they are not defenseless.

Defensive mechanisms exhibited by freshwater protists and invertebrates are varied and widespread across the phylogenetic spectrum [e.g., ciliates (Buonanno et al., 2013, 2017, 2020), cladocerans (Stenson, 1987; Herzog et al., 2016), copepods (Almeda et al., 2017; Buskey et al., 2017), insects and mites (Kerfoot et al., 1980; Kerfoot, 1982; Hershey & Dodson 1987), and gastrotrichs (Balsamo et al., 2020)]. In Rotifera (*sensu stricto*) defensive mechanisms include behavioral, morphological, and chemical strategies (Stemberger, 1985; Wallace et al., 2015). Behavioral defenses include diel vertical migration (DVM) (Williamson & Magnien, 1982), changes in swimming velocity (Williamson, 1987; Gilbert & Kirk, 1988; Parysek & Pietrzak, 2020) and turning angles (Obertegger et al., 2018), passive sinking (Stemberger & Gilbert, 1987a), and facultative sessility (Gilbert, 2019). But swimming behavior can be modified depending on whether the individual possesses another defense mechanism. For example, Parry et al. (2022) found that *Brachionus calyciflorus* Pallas, 1766, which lack defensive spines increased their swimming speed in presence of the rotiferan predator *Asplanchna brightwellii* Gosse, 1850, but spined (defended) individuals did not. Behavioral defenses also can be associated with specific structures. For example, *Polyarthra* species make rapid saltatory movements by rapidly moving their paddles, flexing them anteriorly from the resting position alongside the body. In *Polyarthra vulgaris* Carlin, 1943 these jumps can move the animal 15 body lengths within ~ 60 ms^{-1}. Saltation movements also are produced by the movement of arms in *Hexarthra*. In *Scaridium* an elongated foot and toes appear to enable similar escape movements (H. Segers, pers. commun.). In contrast, *Filinia terminalis* (Plate, 1886) possesses long spines that flex, but these function act as foils to deter predation by the predatory copepod *Skistodiaptomus* (*Diaptomus) pallidus* (Herrick, 1879). On the other hand, Yin et al., (2017) showed that lorica thickness increased in the offspring of amictic females of two species of *Brachionus* (*Brachionus angularis* Gosse, 1851 and *B. calyciflorus*) when the adult females were exposed to a kairomone produced by *A. brightwellii* (Gosse, 1850).

Another method of avoiding predation is by increasing size. In the colonial rotifer, *Conochilus hippocrepis* (Schrank, 1803), overall colony size is important in deterring predation by the copepod *Parabroteas sarsi* (Daday, 1901), which can consume entire small colonies (Diéguez & Balseiro, 1998). Larger colonies of the sessile rotifer *Sinantherina socialis* (Linnaeus, 1758) are also better at avoiding the predatory snail *Physa* sp. and the amphipod *Hyallela azteca* (Saussure, 1858) than are solitary animals (Garcia, 2004). On the other hand, the larger size achieved by coloniality should increase the risk of predation (Wallace et al., 2015). Species in the genus *Sinantherina* may be avoiding this size pitfall in two ways: (1) *Sinantherina spinosa* (Thorpe, 1893) possess short spines on their anteroventral surface that may irritate the buccal cavity of small-mouthed fishes (Wallace et al., 2015); (2) *Sinantherina socialis* has been shown to be unpalatable to certain small mouthed fishes and the nymphs of dragonflies and damselflies (Felix et al., 1995; Walsh et al., 2006). Rotifers also may have better survival by avoiding sympatric predators spatially or temporally: spatially by DVM (noted above); temporally by differences in seasonal growth (Feike & Heerkloss, 2009) or by initiating mixis (diapause) at low population levels (Gilbert & Diéguez, 2010).

Other mechanisms that aid in evading predation include spines located at the anterior and/or posterior end of the animal; these interfere with a predator's ability to manipulate the prey. Permanent spines are found in species of *Kellicottia* (Havens, 1990), *Keratella* (Stemberger, 1985; Williamson, 1987; Green, 2007; Gilbert, 2009; Zhang et al., 2017), and *Plationus* (Sarma et al., 2011). Some genera possess species with spines that are induced embryologically when a specific predator's kairomone is present at sufficient levels. This phenomenon is seen in certain species of *Brachionus* (Gilbert, 2017, 2018), *Keratella* (Garza-Mouriño et al., 2005; Gilbert, 2011), *Lecane* (Soto & Sarma, 2009), and perhaps *Notommata* (Koste 1981). In a similar fashion male *Asplanchna sieboldii* (Leydig, 1854) are protected from cannibalistic females by development of lateral, body wall outgrowths induced by their diet (Gilbert, 1977).

While much is known about consumption of rotifers by predaceous zooplankters and other aquatic invertebrates and how they can reduce predation risk (Table 1), comparatively little is known about the role of protists as predators on rotifers or the factors that influence their prey selectivity. Actinophryid

Table 1 Examples of rotifers that possess features that may reduce their vulnerability to predation by tactical and visual predators: see also (Walsh et al., 2006; Wallace & Smith, 2009; Wallace et al., 2015)

Features	Species	Selected references
Tactile predators		
Concealment (gelatinous sheaths & tubes)	Several species including *Collotheca* spp., *Floscularia* spp., *Ptygura* spp., *Stephanoceros* spp.	Wallace (1980, 1987)
Rapid jumps (hydrofoil saltation)	*Hexarthra* spp.; *Polyarthra* spp.	Gilbert (1985), Williamson (1987)
Spines increasing individual size	*Brachionus calyciflorus*; *Brachionus bidentatus*; *Brachinous sericus; Keratella cochlearis*; *Keratella slacki; Keratella testudo*	Gilbert (1966, 1967), Pourriot (1974), Gilbert and Stemberger (1984), Stemberger and Gilbert (1984, 1987b)
Spines acting as foils	*Filinia* spp.	Williamson (1987), Hochberg and Ablak Gurbuz (2007)
Swimming speed increased	*Keratella cochlearis*	Williamson (1987)
Swimming stoped	*Keratella* spp.	Stemberger and Gilbert (1987a)
Visual predators		
Chemical deterrence (warts)	*Ascomorpha ecaudis; Sinantherina* spp. including *semibullata* & *socialis*	Felix et al. (1995), Williamson (1983), Walsh et al. (2006), Hochberg et al. (2015)
Colony size contractions	*Sinantherina semibullata*	Gunter and Knight (1978), Kossova (1979)
Colony size enlargement	*Conochilus hippocrepis*; *Conochilus unicornis; Sinantherina socialis*	Gilbert (1980b), Wallace (1987), Diéguez and Balseiro (1998),
Diel vertical migration	*Conochilus causayae; Polyarthra remata*	Gilbert and Burns (2000)
Irritating spines	*Sinantherina spinosa*	Wallace (1987)

heliozoans are common passive predators of microorganisms, including rotifers, in freshwater systems (Mikrjukov & Patterson, 2001; Weithoff & Bell, 2022). Previous studies indicate that heliozoans can feed on varied prey having a wide range of sizes and that the consumption of their prey varies among species (Bell et al., 2006; Weithoff & Bell, 2022). For instance, Bell et al. (2006) found that although *Actinophrys sol* (Müller, 1773) ingested a variety of prey, they showed positive population growth only under certain diets, including those with rotifers present. Weithoff and Bell (2022) noted higher consumption of *Elosa worrallii* Lord, 1891 than *Cephalodella* sp., although the mechanism leading to increased predation risk was not clear.

Here we investigated predatory behavior of *Actinosphaerium* sp. on seven rotifer species to test the hypothesis that motility and prey size influence predator selection behavior. Observations of *Actinosphaerium* sp. (hereafter *Actinosphaerium*) consuming a variety of prey in field samples led to four types of laboratory experiments: (1) Feeding trials: Single prey type trials were conducted to see which of six naturally co-occurring rotifer species and one naïve species can be consumed by *Actinosphaerium*; (2) Preference tests: Ingestion of combinations of six prey types were compared; (3) Population growth: *Actinosphaerium* fed with mixed prey diets with and without *A. sieboldii* were monitored to determine whether presence of a predatory rotifer influenced their population growth; and (4) Prey defenses: *B. calyciflorus* with and without were tested to determine whether spines altered predation susceptibility.

Methods

Collection

Brachionus calyciflorus was obtained from Florida Aquafarms (http://floridaaquafarms.com/), the remaining rotifer species and the predator were collected from two sites at Hueco Tanks State Park & Historic Site, El Paso, TX, USA. The predator, *Actinosphaerium*, and the prey species—*Asplanchna sieboldii, Platyias quadricornis* (Ehrenberg, 1832),

and *Lacinularia flosculosa* (Müller, 1773)—were collected from Laguna Prieta (GPS coordinates: 31.9247, − 106.0471), while *Cephalodella gibba* (Ehrenberg, 1830), *Euchlanis dilatata* Ehrenberg, 1830 and *Lepadella patella* (Müller, 1773) were isolated from Behind Ranch House playa (GPS coordinates: 31.9241, − 106.0417).

Laboratory observations

Field collected samples were placed in large Petri dishes within the first 12 h after collection and observed under a dissecting microscope every 1–2 days for approximately 2 weeks. Predatory events were documented by taking photomicrographs.

Culture techniques

Cultures of all species were maintained at room temperature, except for *B. calyciflorus* which was cultured at 25°C, in modified MBL media (Stemberger 1981) under a 16:8 L:D cycle. *Asplanchna sieboldii* was fed with *B. calyciflorus* and *Chlamydomonas reinhardtii* Dangeard, 1888 (UTEX Culture Collection for Algae at UT-Austin strain 90); while the remainder of the rotifers were fed a mixture of *Chlorella vulgaris* (UTEX strain 30) and *C. reinhardtii*. *Actinosphaerium* were fed with ciliates found in the original field sample and a mixture of the rotifers used as prey in this study. All *Actinosphaerium* sp. used in the experiments were isolated without food for 48 h prior to experimentation and ranged in maximum length from 513 to 976 µm.

Swimming speed and size

Swimming speeds were obtained from the literature (Table 2). Sizes of rotifer species used in this study (Table 2) were determined by using a SPOT© digital camera and Spot 5.6 software©, attached to a Zeiss Axioscope©. To determine the influence of swimming speed on predation risk, rotifer species were placed into three groups: sessile (~0 mm/s), slow (< 400 mm/s) and fast (≥ 400 mm/s). To see effect of prey size on the number of captures by *Actinosphaerium*, prey items were grouped into two sizes categories based on their maximum length (excluding foot, toes, and spines): small (< 175 µm) and large (≥ 175 µm). Shapiro–Wilk test, ANOVA, and a Tukey post-hoc test were conducted for both swimming speed and size.

Feeding trials

Except for *L. flosculosa*, experimental treatments consisted of 20 prey items of a single species offered to an *Actinosphaerium* for 40 min. Experiments were conducted in ambient light at 25°C in 1 ml of MBL using 24-well plates with 4 replicates per treatment. Due to the difficulty of separating the colonies without harming the individual animals, treatments for *L. flosculosa* consisted of single colonies comprised of 10–21 animals ($n = 10$). ANOVA and a Tukey post-hoc test were done to compare captures by the predator.

Table 2 Length and swimming speed of rotifer prey and *Actinosphaerium* sp. used in this study

Species	Mean length (µm)	Swimming speed (mm/s)	Source
Asplanchna sieboldii	548	0.95	Salt (1987)
Brachionus calyciflorus	201	0.37	Rico-Martinez and Snell (1997)
Cephalodella gibba	160	0.174	Santos-Medrano et al. (2001)
Euchlanis dilatata	150	0.98	Rico-Martinez and Snell (1997)
Lepadella patella	77	0.262	Santos-Medrano et al. (2001)
Platyias quadricornis	176	0.529	Santos-Medrano et al. (2001)
Lacinularia flosculosa	316	Sessile	–
Actinosphaerium sp.	682	N/A	–

Values shown were used for statistical analysis and represent the average length of individuals used in the experimental populations and the values found in the literature for their swimming speed. Length measurements do not include foot, spines, or axopods

N/A not applicable

Preference tests

All prey rotifer species were used in the choice trials except for *L. flosculosa* since it was not consumed in the single species feeding trials. Five rotifers of each species were simultaneously offered to a single predator under the same conditions as the feeding trials and observed for 40 min. Each treatment was replicated four times. Ivlev's electivity index (1) was calculated to determine predator preferences among the prey items (Jacobs, 1974).

$$E = (r - p)/(r + p), \quad (1)$$

where E is the electivity index, r is the fraction food type eaten, and p is the fraction of the food type available in the experiment. Additionally, a Chi-Squared and Fisher's exact test were conducted to analyze capture frequencies of the prey in preference trials.

Population growth

Following the preference test, treatments were incubated at 25°C with 16:8 L:D cycle. *Actinosphaerium* were counted at 24, 48 and 72 h. Treatments consisted of two mixed diets offered to a single *Actinosphaerium* at a single time: (1) 5 rotifers of each species except *L. flosculosa* and *A. sieboldii* and (2) 5 rotifers of each species including *A. sieboldii*. Treatments were incubated at 25°C under a 16:8 L:D cycle in modified MBL. *Actinosphaerium* were counted at 24, 48, and 72 h. Means of the diet treatments were compared using an unpaired *T*-test.

Prey defenses

Diapausing eggs from the commercial stock of *B. calyciflorus* were hatched and incubated in MBL at 25°C under a 16:8 L:D cycle following the manufacture's protocol. After 72 h, cultures were separated into two containers of 1 l and place at room temperature (~20°C). After 2 days, approximately 200 ml of *A. sieboldii* culture media filtrate along with 20 *A. sieboldii* were added to one of the cultures to induce spine formation in *B. calyciflorus*. Later, a single species feeding trial was carried out as described above for the prey consisting of *B. calyciflorus* with and without spines. Finally, a preference test was conducted as described above except that prey consisted of 10 spined and 10 un-spined *B. calyciflorus* per treatment ($n=4$). Means of the two prey groups were compared using an unpaired *T*-test.

Analyses

All statistical analyses were done using RStudio version 4.1.3 (R_Core_Team, 2022).

Results

Observations

In field samples that were transferred into large Petri dishes to facilitate observation, *Actinosphaerium* were observed to consume diverse prey such as midge larvae, sessile colonial ciliates, and several rotifer species including the sessile colonial species *L. flosculosa* (Fig. 1).

Swimming speed and size

In single-prey trials, predation risk varied among the three motility categories (ANOVA, $F=5.9$, $P=0.007$) with increased risk for motile prey (fast and slow) as compared to sessile prey (Tukey's multiple comparison, $P<0.05$). However, there was no significant difference in risk between the two motile categories (slow and fast) (Fig. 2). No *L. flosculosa* (sessile) were consume even after 72 h of exposure to *Actinosphaerium*. These results show that although the ability to move is a risk factor for rotifers, speed is not. Additionally, in single-prey trials, larger prey were captured twice as often as small prey (ANOVA, $F=11.4$, $P=0.002$) (Fig. 3).

Feeding trials

The naïve prey *B. calyciflorus* was the most consumed prey (ANOVA, $F=24.7$, $P<0.001$, Tukey, $P<0.05$), while *Lacinularia flosculosa* was not consumed at all (Fig. 4). In fact, 95% of *Actinosphaerium* produced cysts (#/individual, mean ± SD: 9.6 ± 3.5) in the *Lacinularia* treatment, which is a known response to starvation in heliozoans (Smith, 1903; Bell et al., 2006). For the rest of the prey, although the consumption rate was variable, it was not statistically significant. Of prey consumed, *B. calyciflorus* was ingested from 15.2 to 56.5% more frequently than the other prey species. Under our experimental conditions, naïve preys are

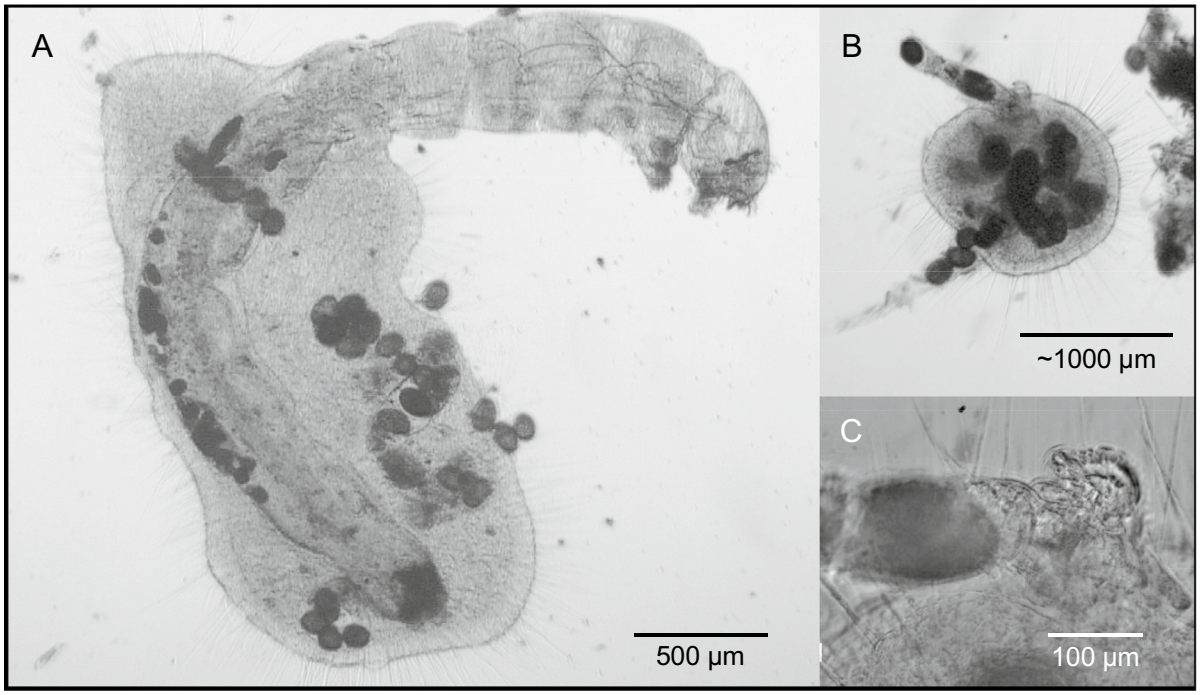

Fig. 1 *Actinosphaerium* as a predator: **A** an unknown number of merged heliozoans engulfing multiple prey including *Lacinularia flosculosa* and a midge larva; **B** an individual protist ingesting multiple *Lacinularia flosculosa* (with diapausing eggs); **C** an individual heliozoan consuming a *Lacinularia* adult

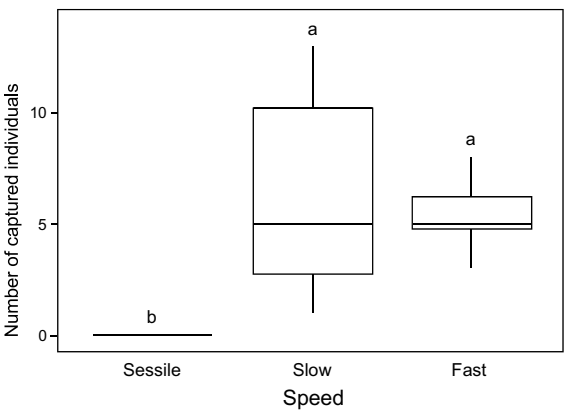

Fig. 2 Predation by the heliozoan predator *Actinosphaerium* on rotifers with different swimming speeds (i.e., sessile, slow, fast). Duration of the experiments was 40 min per trial. Whiskers delimit the range of values from the minimum to the maximum; boxes enclose the interquartile range from 25 to 75%; the horizontal line represents the mean; statistical differences are represented by different letters

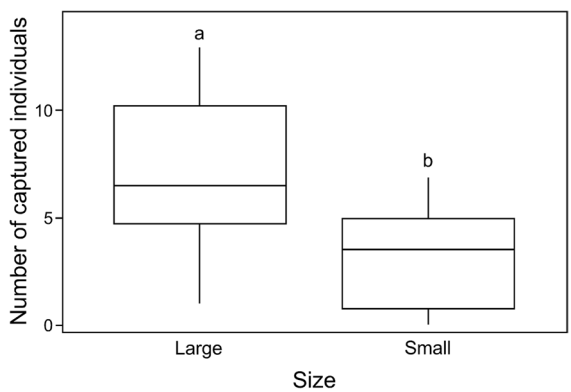

Fig. 3 Predation trials the heliozoan predator *Actinosphaerium* on single rotifer prey species grouped by size. Duration of the experiments was 40 min per trial. Large ≥ 175 µm, Small ≤ 175 µm. Whiskers delimit the range of values from the minimum to the maximum; boxes enclose the interquartile range from 25 to 75%; the horizontal line represents the mean; statistical differences are represented by different letters

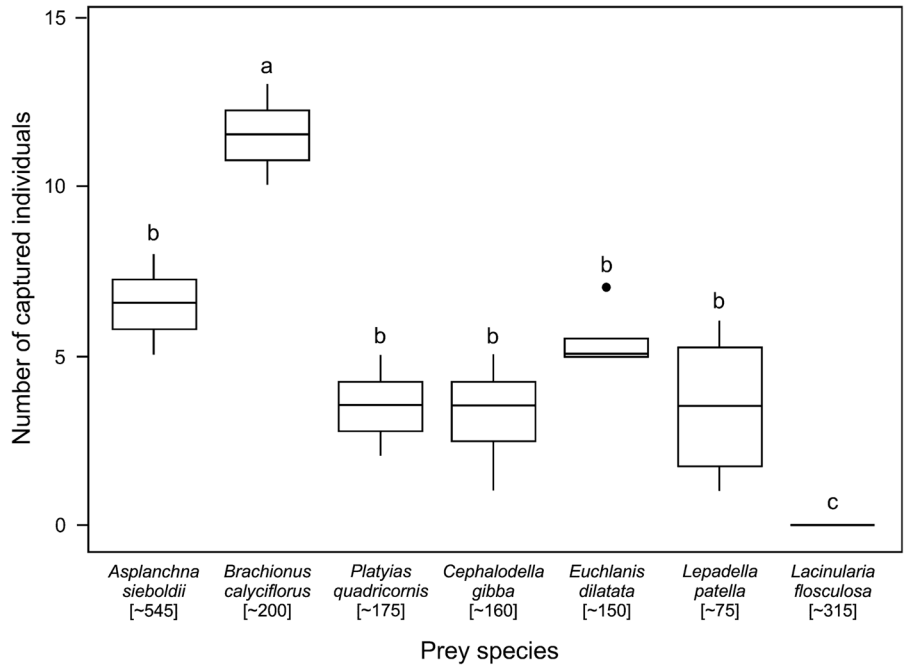

Fig. 4 Predation by the heliozoan predator *Actinosphaerium* on single rotifer species. Prey with the same letters indicate that the mean number of prey captures are not significant. Duration of the experiments was 40 min per trial. Whiskers delimit the range of values from the minimum to the maximum; boxes enclose the inter-quartile range from 25 to 75%; the horizontal line represents the mean; while statistical differences are represented by different letters. Values in brackets are approximate mean lengths

more susceptible to predation by *Actinosphaerium* than naturally co-occurring prey species.

Preference tests

Statistical analysis was done by the size-grouping categories previously described. Large and small prey were captured at significantly different frequencies ($\chi^2 = 8.4$, $P = 0.004$); larger prey species were captured 13 times more frequently than small species (Fisher's Exact test, Odds Ratio = 13.0, $P = 0.004$). Consistent with the feeding trials, these preference test results show that size influences *Actinosphaerium* prey selection. Ivlev's electivity index showed *A. sieboldii* (0.33) and *B. calyciflorus* (0.33) as favored prey items. Low or negative values were found for *C. gibba* (0.20), *P. quadricornis* (− 0.33), *E. dilatata* (− 1.00), and *L. patella* (− 1.00) (Fig. 5). Values in brackets are approximate mean lengths (μm).

Population growth

The population growth of *Actinosphaerium* on mixed prey diets with and without *A. sieboldii* showed that highest population growth occurred in the presence of *A. sieboldii*. Population growth was higher when the protist was fed with *A. sieboldii* than without at each time point (*T*-test, $t = 6.1$ (24 h), 6.6 (48 h), and 6.8 (72 h), all $P \leq 0.05$) (Fig. 6). After 3 days, no rotifers remained in any of the treatments.

Prey defenses

There was no significance difference in the frequency of capture of *B. calyciflorus* individuals with and without spines ($\chi^2 = 0.48$, $P = 0.488$), that is, although the capture of spined specimens was 1.5 times higher than that of specimens without spines, the differences were not statistically significant (Fisher's Exact Test, Odds Ratio = 1.5, $P = 0.488$). This indicates that the spines are not efficient defenses for this predator.

Discussion

Our research demonstrates that the freshwater heliozoan *Actinosphaerium* is an effective predator on many rotifer species with which it co-occurs in temporary desert playas. In field observations, *Actinosphaerium* with partially ingested and digested rotifers were observed frequently during the summer growing season. In samples from field collections, we observed large numbers of the sessile rotifer *L. flosculosa* being consumed by the heliozoan and we saw the resting

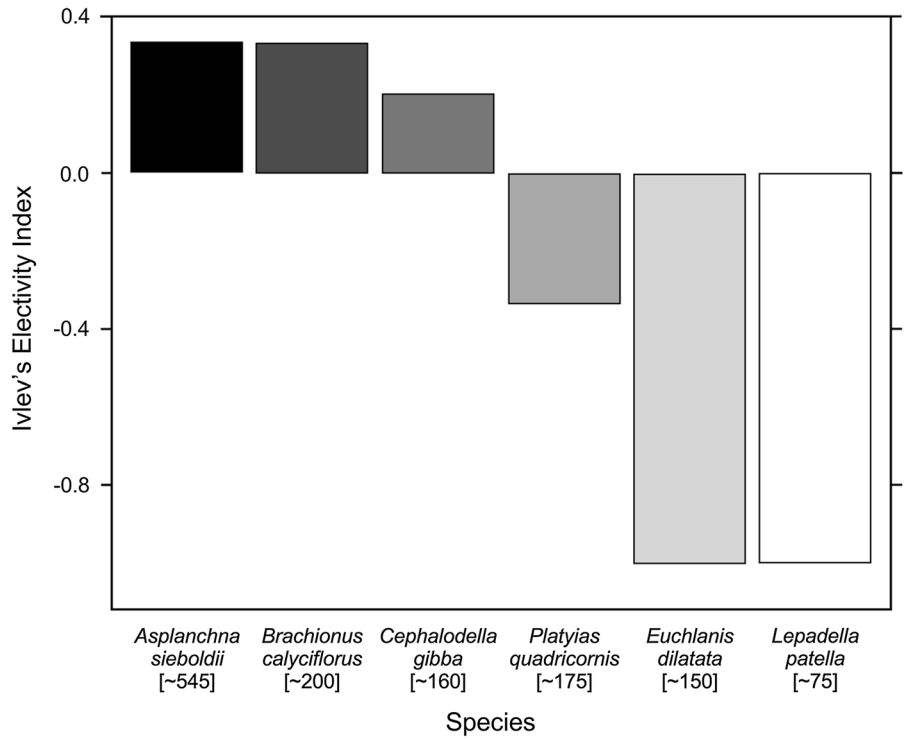

Fig. 5 Ivlev's electivity index for *Actinosphaerium* fed rotifer species of variable sizes as prey. Duration of the experiments was 40 min per trial. See the text for additional information. Values in brackets are approximate mean lengths (μm)

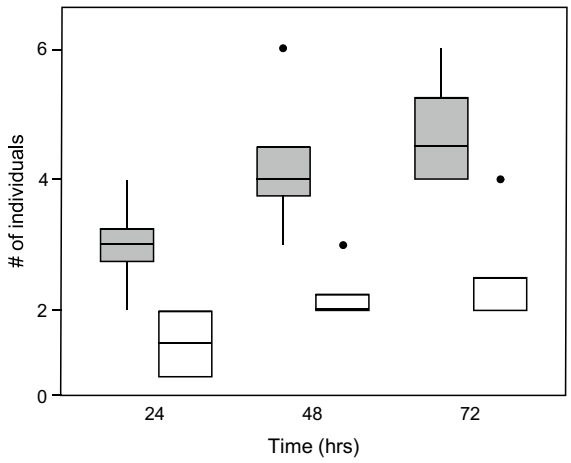

Fig. 6 *Actinosphaerium* population growth under two diets. Shaded boxes, with the presence of the predatory rotifer *Asplanchna sieboldii.* Duration of the experiments was 72 h per trial. Open boxes, without *A. sieboldii*. Whiskers delimit the range of values from the minimum to the maximum; boxes enclose the interquartile range from 25 to 75%; the horizontal line represents the mean

eggs of this species within the heliozoans. However, in laboratory feeding trials, no *L. flosculosa* were ingested; this may be an artifact of our experimental protocol. In the field, heliozoans may come into contact with sessile colonies due to wind, animal, or other natural disturbances that mix the water column producing currents. However, in laboratory conditions we found that predation risk was greater for motile prey. As noted above, with sessile prey the predator often produced cysts as a survival strategy. Although swimming speed was not correlated with increased predation (see next), this result was likely due to increased probably of predator–prey interactions.

Swimming speed and size

Two factors that determine prey vulnerability are their motility and size. Examples illustrating the importance of these factors include the following. Jara and Perotti (2010) reported a reduction of activity in three species of anuran tadpoles in response to presence of aquatic insect predators; they also noted a relationship between prey size and predation susceptibility. In their study of oyster-eating snails, Pusack et al. (2018) reported that predatory drills prefer to eat medium-sized oysters (50–75 mm). Sarma and Nandini (2007) found that rotifer size affects vulnerability to predation in rotifer-rotifer interactions, while (Parry et al.,

2022) observed swimming speed changes of spineless *B. calyciflorus* in the presence of *A. brightwellii.* Similarly, Santos-Medrano et al. (2017) found that rotifer and non-rotifer prey selection by *A. brightwellii* is influenced by the size, biomass, and swimming speed of their prey. These predators are all active in seeking their prey. Heliozoans are passive predators so we assumed that increased prey swimming speeds and/or specific swimming behaviors would lead to increased encounters between heliozoans and their prey. However, in our study we found no significant differences in consumption rate for rotifers with swimming speed ranging from 0.98 to 0.17 mm s^{-1}.

Predation trials and preference tests

In single prey exposure trials, we expected a higher consumption of small prey since they comprise lower biomasses than larger prey. However, we found that larger prey items were captured more often in both single and multiple-prey exposure trials. It is possible that *Actinosphaerium* did not reached its feeding saturation point, even with a prey density of 20 individuals ml^{-1}, and that large prey were easier to capture due to the larger surface area that can come into contact with the axopods. Aside from the *B. calyciflorus* population used in this study, which rarely co-occurs with the predator in our collection site, *Asplanchna sieboldii* was the preferred prey. That preference could be important because predation on *Asplanchna* may potentially have an indirect control of herbivores in an ecosystem (Snyder & Wise, 2001). That is, predilection of *Actinosphaerium* for *A. sieboldii* might cause a trophic cascade: reduction in the population of *Asplanchna* would release its control of herbivorous rotifers, which would then lead to a reduction in the algae population. On the other hand, given that sexuality and cannibalism induction in *Asplanchn*a can be affected by diet and population density (Gilbert & Thompson, 1968; Gilbert & Litton, 1978; Gilbert, 2017), another possibility is that this type of intraguild predation has the opposite effect: it could keep the *Asplanchna* population stable and thereby controlling the population levels of grazing rotifers. This has been seen in other studies where intraguild predation allows *Asplanchna* populations to persist (Gilbert & Confer, 1986; Gilbert, 2017). In either case, predation on *Asplanchna* would influence algae populations, which would then have implications for community structure, as well as water clarity and oxygenation (Järvenpää & Lindström, 2004; Morgan et al., 2006). For instance, Weithoff and Bell (2022) showed that interactions between heliozoan predators and rotifer/ciliate prey had different outcomes on community structure as algal concentrations varied.

Population growth

We also found that heliozoan growth was greatest when the predatory rotifer *Asplanchna* was present. These results show that the predation strategy of *Actinosphaerium* follows the principles of Optimal Foraging Theory, which states: (1) that the energetic profitability of the prey determines the selectivity of the predator and (2) the contribution of an individual to the next generation depends on its foraging strategy (MacArthur & Pianka, 1966; Pyke, 1984; Kumar et al., 2022). This is consistent for two reasons. (1) Assuming a larger prey size tends to a higher biomass, the passive predation of *Actinosphaerium* selecting large and mobile prey implies a higher biomass consumption with minimum energy expenditure. (2) Results of the population growth experiment showed that heliozoans fed *Asplanchna* produced more offspring.

The greater population growth of the heliozoan in the presence of *Asplanchna* may be explained by a greater amount of biomass in the treatment. However, a reduction in the growth of *Actinosphaerium* would also have been expected due to competition exerted by *Asplanchna*. Given that the prey species used in this experiment have different biomasses, equitable distribution among the treatments represented a challenge; however, future research could control the number of rotifers per treatment, for example, by adding one extra individual per species in the treatment without *Asplanchna* to equalize the total number of rotifers. In this study we maintained the same number of individuals per species (except *A. sieboldii*) in both treatments, thus the biomass of the prey species remains controlled, making the *Asplanchna* effect easier to visualize, but certainly the model is not exempt from improvements.

Prey defenses

Coloniality and morphological adaptations seem to be inefficient methods used by rotifers to evade predation by heliozoans. *Brachionus calyciflorus* spines were not an effective defensive strategy against predation

by *Actinosphaerium*. Likewise, previous reports (Kulmer et al., 2020) and our field observations provided evidence of the consumption of colonial protozoans and rotifers. In addition, Chin et al. (2022) found that *Amoeba proteus* (Pallas, 1766) was able to consume colonial choanoflagellates more efficiently than single individuals by changing its behavior. On the other hand, the method by which heliozoans capture prey seems to be largely mediated by chemicals (Sakaguchi et al., 2001). Thus, defense strategies could be chemical rather than morphological. Actynophrids possess at least two types of extrusomes (Mikrjukov & Patterson, 2001) that secrete glycoprotein-binding substances involved in chemical prey recognition (Sakaguchi et al., 2001; Bhadra et al., 2017) and immobilization (Esteban & Fenchel, 2020). Furthermore, glycoprotein classes of pheromones on the surface of rotifers varies among species (Snell & Morris, 1993; Snell et al., 1995; Snell & Rico-Martinez, 1996; Jezkova et al., 2022), which could modify predation susceptibility as has been reported in other predator–prey interactions (White et al., 2022). For these reasons, chemical defense mechanisms should be a topic for future research.

Predation pressure favors the appearance of defensive strategies (Gilbert, 1980a; Riessen & Gilbert, 2018; Alvarado-Flores et al., 2022). Both intraguild and generalist predation can dampen trophic cascades (Snyder & Wise, 2001). The top-down regulation of the predator to its prey is stronger in specialist predators than in generalists (Lou & Nie, 2022), although the effect of generalists is more marked when they inhabit a low-diversity community (Strong, 1992; Snyder & Wise, 2001). Therefore, although the susceptibility of rotifer prey was different in this study, given that *Actinosphaerium* sp. is a generalist predator, perhaps the predation pressure exerted is not strong enough to induce the evolution of defense mechanisms in its prey.

Conclusions

Rotifers fall prey to a variety of predators, and because of their small size they are components in both the classic food web and the microbial loop (Wallace et al., 2015). Yet they are not without their defenses, which include (1) small size, (2) escape movements, both slow (small increases in swimming speed), swift ones (jumps), and diel migrations, (3) physical foils, and (4) unpalatability (Wallace et al., 2006, 2015). However, many rotifers appear to have no defense against being engulfed whole by (1) protists (Wallace et al., 2015), (2) Cnidaria (*Hydra*) (Walsh, 1995), (3) micrometazoans (i.e., rotifers (Gilbert, 1980b) and copepods (Green & Shiel, 1992)), (4) insects (Walsh, 1995; Hampton & Gilbert, 2001), and (5) vertebrates (Lair et al., 1996; Snell et al., 2018). Of these predators, we know relatively little about the dynamics of interactions with protists. Here we have shown that there are two important risk factors for predation by *Actinosphaerium*: (1) prey size and (2) prey movement in relationship to the predator. Movement could be either by the prey's own movement or that initiated by water currents. Another factor that might influence prey susceptibility include habitat complexity such as that found in the littoral zone (Walsh, 1995; Meksuwan et al., 2014). Most studies to date have focused on planktonic predator–prey interactions or laboratory studies in the absence of vegetation. *Actinosphaerium* fed efficiently on colonies in glass dishes containing plants with abundant *L. flosculosa* colonies.

Our observations indicate that *Actinosphaerium* can consume a varied diet, with its prey including insect larvae, ciliates, and rotifers, but prefer larger, mobile prey (> 175 µm). These results are consistent with Optimal Foraging Theory, which makes heliozoan/rotifer predator–prey interactions a suitable model for future research on intraguild predation and Optimal Foraging Theory. However, some limitations of this research should be considered. For example, the volume of the experimental vessel and the static experimental conditions are very different from natural settings. Both factors may have contributed to the discrepancy between predation on *L. flosculosa* in field samples and in our experiments. Finally, if we are to understand the importance of actynophryds within the microbial loop in aquatic systems and their influence of community structure, additional research is needed on a wider variety of prey types.

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Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no conflicts of interest/competing interests. The sponsors had no role in the design, execution, interpretation, or writing of the study.

Ethical approval Heliozoans and rotifers from Hueco Tanks State Park and Historic Site were collected under permit 07-21 issued to E.J. Walsh.

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