

Effect of zooplankton type and abundance on prey consumption by the fairy shrimp, *Streptocephalus proboscideus* (Anostraca: Crustacea)

A. Jawahar Ali, S. S. S. Sarma, G. Murugan & H. J. Dumont

Laboratory of Animal Ecology, University of Ghent, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium

Received 9 February 1995, revised and accepted 10 May 1995

Key words: fairy shrimp, zooplankton, prey size, prey density, electivity index, filtration rate.

Abstract

Laboratory cultured *Streptocephalus proboscideus* (three sizes (mm), viz. 8.44 ± 0.95 (virgin), 14.18 ± 1.49 (adult I) and 19.24 ± 1.52 (adult II)) were offered (separately for males and females) field collected zooplankton (12 prey types) at three levels of abundance (1.0 ml^{-1} , 2.0 ml^{-1} and 4.1 ind. ml^{-1}) in 30-minute feeding experiments. Gut contents, analyzed for abundance and diversity of prey type, showed that predator size, sex and their interaction had strong effects on prey consumption. Regardless of their size, and of prey density, *S. proboscideus* females consumed 25–90% more prey than males. Their filtration rates (adult II) were higher ($125 \text{ ml ind.}^{-1} \text{ h.}^{-1}$) than those of males ($30 \text{ ml ind.}^{-1} \text{ h.}^{-1}$) too. Rotifers had the highest numerical percentage in the gut, regardless of predator size or sex. Cladocerans were only consumed by adults I and II. Adult II females consumed $28.5\text{--}43.3 \mu\text{g}$ zooplankton dry weight $\text{ind.}^{-1} \text{ h.}^{-1}$. Size distribution of *B. longirostris* in the field and in the gut were closely similar. This study confirms *S. proboscideus* as a non-selective filter feeder. Since it did not eat jumping rotifers, copepod nauplii and copepodites, it may contribute to structuring its prey communities, because good escapers will be enriched in the medium, while poor escapers will be depleted.

Introduction

Predation is a major structuring force of plankton communities. Numerous studies have shown that many vertebrate predators (fish) feed visually, and selectively consume the largest and most conspicuous zooplankton prey (Zaret, 1980; Kerkfoot & Sih, 1987).

Non-visual invertebrate predators, cannot usually handle large prey, and therefore depend on smaller organisms. Experimental studies have largely focused on predators such as the midge-larva *Chaoborus* (Lynch, 1979), copepods, mysids, mites, and flatworms (Hall *et al.*, 1976; Sih *et al.*, 1985; Dumont *et al.*, 1990), but rarely on anostracans.

Freshwater anostracans (fairy shrimps) are often confined to environments which dry out periodically. Such habitats predominantly occur under (semi-) arid and temperate climates (Hartland-Rowe, 1972; Belk & Cole, 1975; Wiggins *et al.*, 1980; W. D. Williams, 1985; D. D. Williams, 1987).

Information on the feeding of anostracans tends to suggest a non-selective, detritic and phytoplanktic

diet (Cannon & Leak, 1933; Cannon, 1935; Reeve, 1963a, b; Brendonck, 1993a, b). Some large species, such as *Branchinecta gigas*, have long been known to be raptorial feeders (Fryer, 1966; White *et al.*, 1969; Fryer, 1983), but field observations have revealed the presence of zooplankton in the gut of smaller species as well (Bernice, 1971). Recent studies have confirmed that several small anostracans readily feed on tiny invertebrates like protozoans, nematodes (Mertens *et al.*, 1990), rotifers (Dumont *et al.*, 1994; Dierckens *et al.*, in press) and larval crustaceans (Brown & Carpelan, 1971). These studies were based on direct observations of feeding behaviour under laboratory conditions or on gut content analysis on field-collected specimens.

Zooplankton such as cladocerans (*Daphnia*, *Moina*), copepods (*Metacyclops*, *Metadiaptomus*), and rotifers (*Asplanchna*, *Brachionus*, *Keratella*) (Bernice, 1971; W. D. Williams, 1985; D. D. Williams, 1987) commonly occur in temporary pools. Their co-occurrence with anostracans sometimes show an

inverse relation (Mertens *et al.*, 1990), suggesting a predatory interaction.

Since anostracans are considered non-selective, prey characteristics such as evasiveness and size can be expected to act as constraints (Mertens *et al.*, 1990). Of course, predator size and sex will also influence prey availability. Although different types of planktonic prey have been seen in the gut of field-collected anostracans (Bernice, 1971), they have never been rigorously analyzed with reference to the above prey characteristics. Therefore, the objective of the present study was to examine effects of prey size, type, and abundance on feeding of a fairy shrimp, *S. proboscideus*, as a function of its size and sex.

Materials and methods

S. proboscideus, obtained from resting eggs collected from rainpools in Khartoum, Sudan, has been mass-cultured in our laboratory for over 5 years. Three sizes (mean \pm S.D.) of both sexes (virgin, 8.44 ± 0.95 mm; adult I, 14.18 ± 1.49 mm; and adult II, 19.24 ± 1.52 mm) were isolated, acclimated and starved for 4 hours. Their length was measured under a stereomicroscope fitted with camera lucida, and calibrated using a curvimeter. For prey items, we used zooplankton from a pond near the University Campus (Citadel Park). Zooplankton was collected by filtering a known quantity of pond water through 20 and 500 μm mesh. Phytoplankton and detritus were removed by the lower mesh and large organisms (e.g. insect larvae) by the larger mesh. The size range of zooplankton offered was thus between 20 and 500 μm . Few copepodites of 750 μm length were noticed in the filtered medium.

We used starved animals, because we had evidence (e.g. the occurrence of cannibalism and other indications, see 'discussion') that starvation may actually be common in natural conditions too. In order to standardize the relationship between feeding rates of previously starved animals and feeding time, we carried out a feeding trial using a single rotifer prey, *Anuraeopsis fissa* (Gosse), for feeding durations ranging from 7 to 360 min. at an optimal density of 320 ind. ml^{-1} , kept constant through out the experiment, following Dumont *et al.* (1994). Feeding rates were found to decrease hyperbolically with time (Fig. 1), and approached an asymptote of ~ 250 prey min^{-1} , which is roughly half the amount consumed per minute after the first 30 minutes. For further reasons justifying the use of starved animals fed 30 min., see discussion.

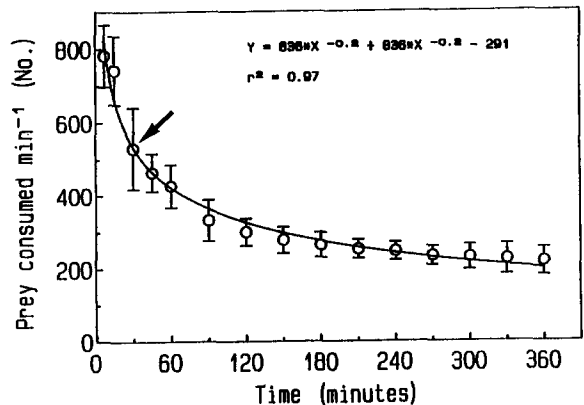


Fig. 1. Prey (*Anuraeopsis fissa*) consumption of *S. proboscideus* as function of time (ranging from 7 to 360 minutes) at a constant prey density of 320 ml^{-1} . Shown are mean \pm S.D. (4 replicates) of number of prey consumed per minute).

We used three prey concentrations (1) undiluted pond zooplankton (filtered to remove phytoplankton, detritus and large insect larvae), (2) plankton concentrated twice, and (3) concentrated four times (designated as low, medium and high prey densities, respectively). Twenty litres of pond water were centrifuged at 4000 rpm and the supernatant (free from phyto and zooplankton) was used as a medium. The prey composition was estimated from 100 ml sub-samples. We used 200 ml-capacity plastic beakers as test vessels. Prey types, size and density are shown in Table 1.

Into each of 54 test vessels (3 predator sizes \times 2 sexes \times 3 prey concentrations \times 3 replicates) containing 100 ml pond water with known density and composition of zooplankton, we introduced 2 predators of known stage and sex and allowed them to feed for 30 minutes. The experiments were conducted at 25 ± 1 $^{\circ}\text{C}$ under diffuse illumination. After the experiment, both predator and prey were preserved in 4% formalin.

The intestine of each predator was carefully dissected out and gut contents were examined under a stereomicroscope. Data on prey composition, density and size were recorded.

For measuring size structure of prey populations, we considered only *B. longirostris*, the most abundant crustacean in our zooplankton. We did not determine the size of rotifers, because, unlike cladocerans, they show little somatic growth after maturity (King, 1967; Sarma, 1989).

Table 1. Zooplankton type, density (No. ml⁻¹) and mean size (length μm) offered as prey at low concentration to *S. proboscideus*.

Prey type	Density (ml ⁻¹)	Size (μm)
Cladocera		
Unidentified cladocerans	0.037	450
<i>Daphnia</i> sp.	0.010	400
<i>Bosmina longirostris</i>	0.097	350
Copepoda		
Copepodites	0.015	750
Copepod nauplii	0.152	300
Rotifera		
<i>Brachionus calyciflorus</i>	0.005	225
<i>Keratella quadrata</i>	0.010	210
<i>Epiphanes macrourus</i>	0.025	150
<i>Polyarthra vulgaris</i>	0.025	120
<i>Pompholyx sulcata</i>	0.163	105
<i>Keratella cochlearis</i>	0.530	105
<i>Brachionus angularis</i>	0.008	105

We classified the *B. longirostris* in 100 ml sub-samples in 4 classes viz., 201–275 μm , 276–350 μm , 351–425 μm , 426–500 μm , and expressed each as a percentage.

Prey selection by the fairy shrimp was measured using the electivity index (ϵ_i) of Chesson (1983).

$$\epsilon_i = \frac{m\alpha_i - 1}{(m - 2)\alpha_i + 1},$$

where m is the number of prey types available and α_i , the positive numbers ranging from 0 to 1 calculated according to the following formula (Mainly *et al.*, 1972; Chesson, 1983):

$$\alpha_i = \frac{\ln[(n_{i0} - r_i)/n_{i0}]}{\sum_{j=1}^m \ln[(n_{j0} - r_j)/n_{j0}]},$$

where n_{i0} is the number of prey items of prey type i present at the beginning of the experiment and r_i is the number of items of prey type i in the predator's diet. The electivity index ϵ_i can take any value between -1 and +1, irrespective of prey density.

The biomass (dry weight) of the crustacean prey types was determined from Dumont *et al.* (1975) and Bottrell *et al.* (1976). For the estimation of rotifer biomass, we followed Ruttner-Kolisko (1977).

The filtration rate (F) was calculated using Peters' (1984) formula:

$$F = \frac{V(k - f)}{N},$$

where:

V = test volume;

N = Number of predators;

k (growth coefficient) = $\frac{\ln C_{bt} - \ln C_{bo}}{t}$;

C_{bt} = prey concentration at time t ;

C_{bo} = initial concentration in control;

t = experimental period;

f (feeding coefficient) = $\frac{\ln C_t - \ln C_o}{t}$;

C_t = prey concentration at time t ;

C_o = initial prey concentration.

Since feeding experiments were conducted for only 30 min., with phytoplankton and detritus removed, no increase in prey concentration could be occur. Hence, $k = 0$.

Data on prey density as a function of predator size, sex and different prey concentrations were analyzed by Analysis of Variance.

Results

The composition, density and size of zooplankton prey offered to *S. proboscideus* are presented in Table 1. Numerically, *K. cochlearis* constituted about 50% of the total zooplankton. In terms of size, cyclopoid copepodites were the largest prey (750 μm).

Results of a three-way ANOVA indicated that predator stage, sex, and their interaction had a significant effect on prey consumption. This trend remained unaffected, whether quantity of prey consumed was expressed as numbers or as dry weight (Table 2a, b).

Regardless of predator size and prey concentration, *S. proboscideus* females consumed significantly more prey than males (Fig. 2). Among prey types consumed, rotifers constituted a much higher numerical percentage, regardless of predator sex or stage. Cladocerans were seldom found in virgin predators (Fig. 2).

Data on zooplankton dry weight (DW) consumed by three sizes of *S. proboscideus* under different prey concentrations, are given in Table 3. Adult II females consumed 28.5–43.3 $\mu\text{g DW ind.}^{-1} \text{ h.}^{-1}$ depending on prey concentration, but males consumed only 9.9 to 20.9 $\mu\text{g DW ind.}^{-1} \text{ h.}^{-1}$. Virgin females consumed zooplankton (mainly rotifers) at a rate of 0.01 to 0.69

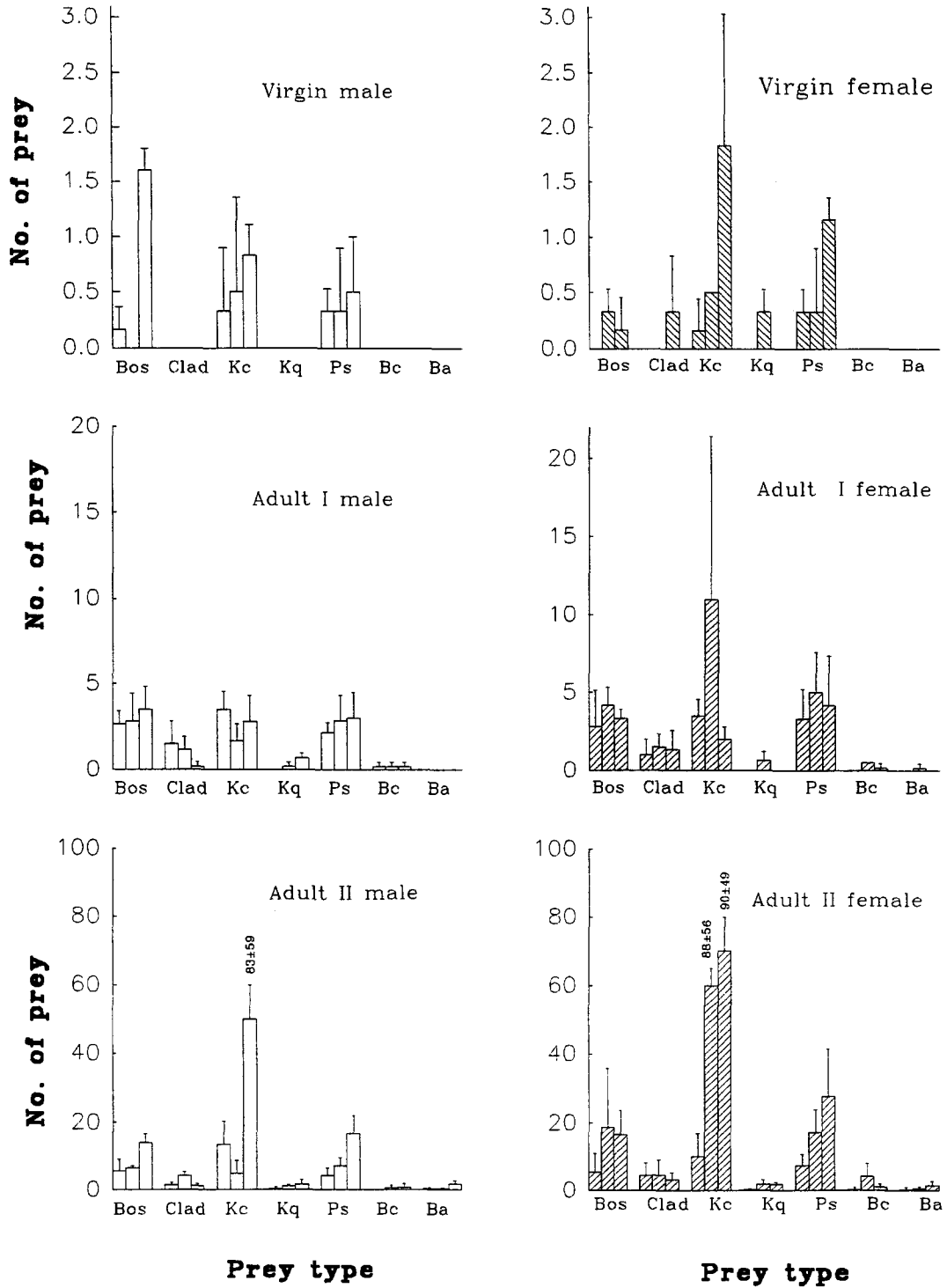


Fig. 2. Abundance of zooplankton in the gut contents of *S. proboscideus*. Bos, Clad, Kc, Kq, Ps, Bc, Ba represent prey types *B. longirostris*, other Cladocerans, *K. cochlearis*, *K. quadrata*, *P. sulcata*, *B. calyciflorus* and *B. angularis*, respectively. Each prey species was offered in three concentrations represented by three bars. First, second and third bars represent prey concentrations low, medium and high respectively. (Note the difference in scale in Y axis.)

Table 2a. Zooplankton consumption (total number of animals) by *S. proboscideus* in relation to predators size and sex as function of prey concentration. Three-way ANOVA.

Variable	Source of variation	df	SS	MS	F
Consumption (total number)	Stage	2	67336.9	33668.4	35.2***
	Sex	1	19627.2	19627.2	20.5***
	Conc.	2	191.9	95.9	0.1 ^{ns}
Interactions	Stage*sex	2	31020.7	15510.4	16.2***
	Stage*conc.	4	269.4	67.3	0.1 ^{ns}
	Sex*conc.	2	343.3	171.6	0.2 ^{ns}
	Stage*sex* conc.	4	421.7	105.4	0.1 ^{ns}
	Error	36	34449.8	956.9	--

*** = $p < 0.001$; ns = non-significant ($p > 0.05$)

Table 2b. Zooplankton consumption (dry weight) by *S. proboscideus* in relation to predators size and sex as function of prey concentration. Three-way ANOVA.

Variable	Source of variation	df	SS	MS	F
Consumption (dry weight)	Stage	2	1662.84	831.42	38.4***
	Sex	1	200.75	200.75	9.3**
	Conc.	2	21.87	10.94	0.5 ^{ns}
Interactions	Stage*sex	2	264.34	132.17	6.1**
	Stage*conc.	4	18.79	4.69	0.2 ^{ns}
	Sex*conc.	2	47.74	23.87	1.1 ^{ns}
	Stage*sex* conc.	4	44.03	11.01	0.5 ^{ns}
	Error	36	779.79	21.66	--

*** = $p < 0.001$; ** = $p < 0.01$; ns = non-significant ($p > 0.05$)

$\mu\text{g DW ind.}^{-1} \text{ h.}^{-1}$, while the similarly sized males consumed 0.01 to 0.04 $\mu\text{g DW ind.}^{-1} \text{ h.}^{-1}$. The adult I class showed intermediate consumption rates.

Chesson's electivity index increased with predator size. Maximum positive index values were observed in adult II (Fig. 3).

No naupliar and copepodite stages of copepods, or *Daphnia*, were observed in the anostracan gut. Similarly, the rotifer species *Polyarthra* and *Epiphanes* were

Table 3. Zooplankton consumption ($\mu\text{g ind.}^{-1} \text{ h.}^{-1}$) by *S. proboscideus* in relation to predators size and sex as function of prey concentration. Values shown are mean \pm S.D. based on three replicates.

Predator stage	Prey conc. ($\times 1.037$) (no. ml ⁻¹)	Prey consumption ($\mu\text{g ind.}^{-1} \text{ h.}^{-1}$)	
		Male	Female
Virgin	1	0.04 \pm 0.06 (0.0048)	0.01 \pm 0.12 (0.0012)
	2	0.01 \pm 0.01 (0.0012)	0.14 \pm 0.08 (0.016)
	4	0.01 \pm 0.02 (0.0012)	0.69 \pm 0.98 (0.079)
Adult I	1	6.50 \pm 3.83 (0.447)	13.00 \pm 6.58 (0.940)
	2	7.35 \pm 6.09 (0.506)	7.54 \pm 7.43 (0.546)
	4	8.54 \pm 6.65 (0.587)	9.94 \pm 1.98 (0.179)
Adult II	1	11.70 \pm 8.20 (0.625)	43.30 \pm 31.00 (2.194)
	2	9.90 \pm 0.79 (0.529)	28.50 \pm 2.32 (1.444)
	4	20.90 \pm 5.55 (1.16)	38.80 \pm 16.40 (1.966)

(Values in parantheses represent prey consumption per unit length of the predator)

not recorded in the predator's gut, although they were offered in the medium.

Most individuals of *B. longirostris* were in the size range of 276–350 μm ; few ($< 10\%$) were larger than 425 μm (Fig. 4). Similarly, the size distribution of *B. longirostris* in the guts contained a consistently higher percentage of individuals in the range of 276–350 μm (Fig. 4). Of the four size classes offered, the smallest three (201–275, 276–350, 351–425 μm) were present in the gut of adult I and adult II anostracans, while the fourth (426–500 μm) was only found in adult II females and at the highest prey concentration. There was a significant correlation ($r = 0.45$; $n = 96$) between predator size and the maximum sized prey in the gut (Fig. 5).

With increasing body size, predators also widened their prey spectrum. Thus, out of 12 zooplankton types offered, virgins consumed a maximum of 3 prey types, while adult II consumed 7 prey types. There was again a significant difference between males and females

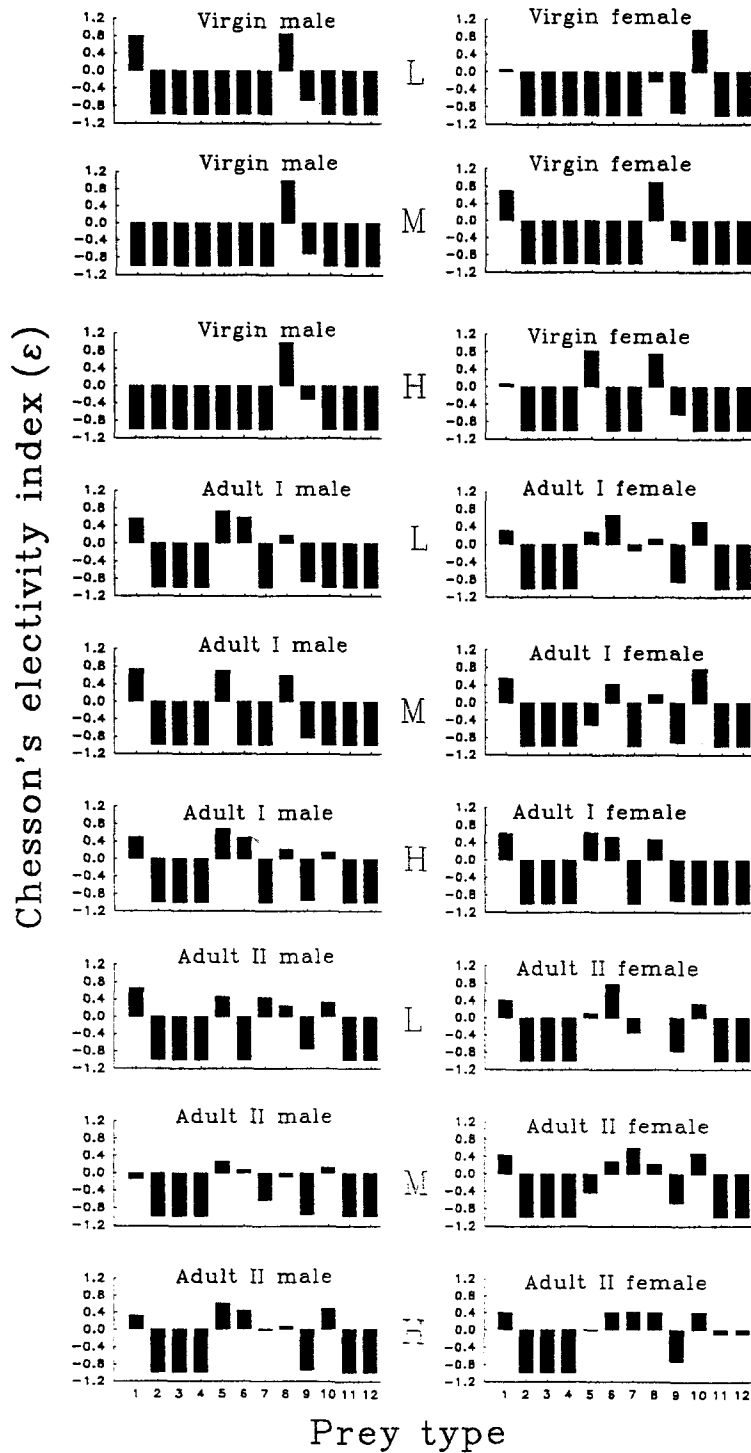


Fig. 3. Chesson's electivity index values for prey selection by differentially sized (virgin, adult I, adult II) *S. proboscideus* at low (L), medium (M) and high (H) prey density. Prey type no. 1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11 and 12 on the X axis represent *B. longirostris*, *Daphnia*, Copepodites, Copepod nauplii, other cladocerans, *B. calyciflorus*, *B. angularis*, *P. sulcata*, *K. cochlearis*, *K. quadrata*, *E. macrourus* and *P. vulgaris*, respectively.

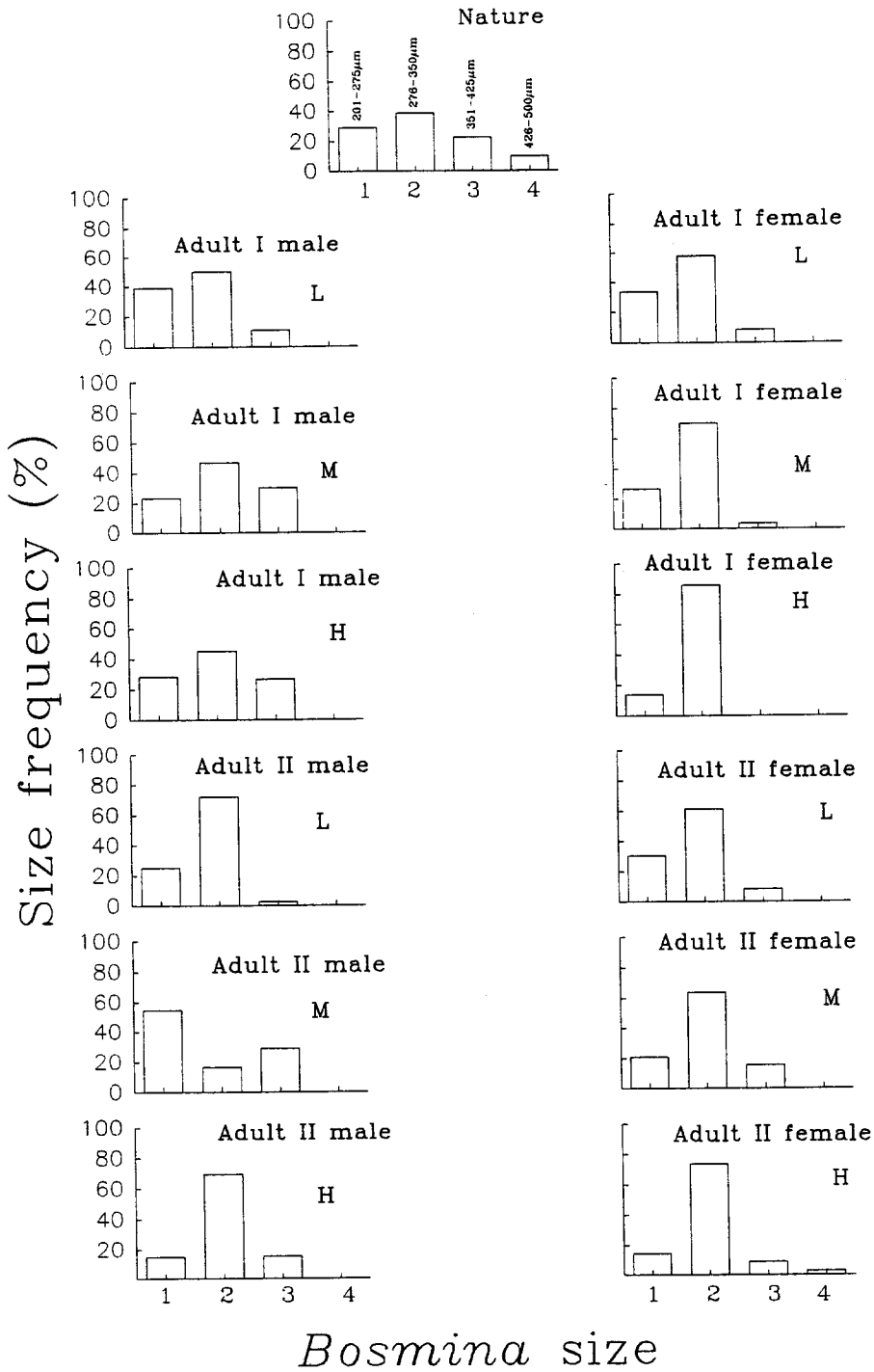


Fig. 4. Size distribution of *B. longirostris* in the gut of *S. proboscideus*. Sizes 1, 2, 3 and 4 (in X axis) represent the range of (μm) 201-275, 276-350, 351-425 and 426-500, respectively. *B. longirostris* were rarely found in the gut of virgins, and hence not included here.

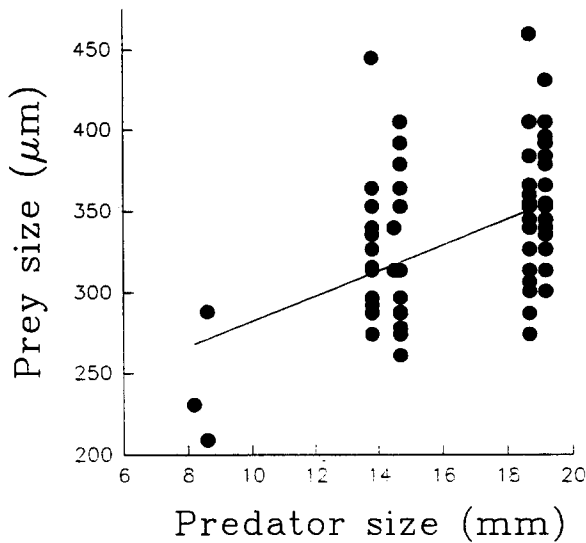


Fig. 5. Relation between predator length (μm) and maximum prey size recorded from the gut of *S. proboscideus*. Predator's length measurements include both male and female individuals. For each prey concentration and for each replicate, size of 3 largest prey from the gut were recorded. A combined regression line was drawn since the slope for males and females was almost same.

with respect to this characteristic ($p < 0.001$; Tables 4 and 5).

Filtration values (calculated in terms of prey number) were significantly influenced by stage ($p < 0.001$), sex ($p < 0.01$), and stage*sex related interaction ($p < 0.01$) (Fig. 6 and Table 6). In general, higher filtration rates were recorded at lower prey concentrations, while larger adults filtered more than smaller ones. At any particular size class of the predators, females filtered significantly more than males (up to $125 \text{ ml}^{-1} \text{ ind.}^{-1} \text{ h.}^{-1}$ for females and $30 \text{ ml ind.}^{-1} \text{ h.}^{-1}$ for males).

Discussion

The experimental data so far available on the feeding habits of fairy shrimps suggested a phytoplanktivorous/detrivorous diet, although gut contents of field-collected *Streptocephalus* include animal prey, e.g. ciliates, rotifers and crustaceans (Bernice, 1971). However, like other aquatic invertebrate predators, *Streptocephalus* might have size-related feeding modes (Pastorok, 1981; Stream, 1994). This is confirmed by our results: early stages of *Streptocephalus* handle small-

Table 4. Zooplankton diversity (number of prey types) in the gut of *S. proboscideus* in relation to predators size and sex as function of prey concentration. Values shown are mean \pm S.D. based on three replicates.

Predator stage	Prey conc. (x 1.037) (No. ml ⁻¹)	Prey diversity in the gut	
		Predator sex	
		Male	Female
Virgin	1	1.3 \pm 0.6	3.0 \pm 1.7
	2	1.0 \pm 1.0	2.0 \pm 1.0
	4	0.7 \pm 1.2	2.0 \pm 1.0
Adult I	1	4.3 \pm 0.6	6.0 \pm 1.0
	2	3.7 \pm 0.6	4.7 \pm 1.2
	4	4.7 \pm 0.6	4.0 \pm 1.0
Adult II	1	5.0 \pm 1.0	6.7 \pm 0.6
	2	5.0 \pm 1.0	6.0 \pm 1.0
	4	6.0 \pm 1.0	7.0 \pm 0

Table 5. Zooplankton diversity in the gut of *S. proboscideus* in relation to predators size and sex as function of prey concentration. Three-way ANOVA.

Variable	Source of variation	df	SS	MS	F
Prey diversity	Stage	2	171.44	85.72	94.5***
	Sex	1	15.57	15.57	17.2***
	Conc.	2	4.00	2.00	2.2 ^{ns}
Interactions	Stage*sex	2	1.15	0.57	0.6 ^{ns}
	Stage*conc.	4	4.89	1.22	1.3 ^{ns}
	Sex*conc.	2	2.82	1.41	1.6 ^{ns}
	Stage*sex*conc.	4	2.30	0.57	0.6 ^{ns}
	Error	36	32.67	0.91	--

*** = $p < 0.001$; ns = non-significant ($p > 0.05$)

er organisms, probably including bacteria and phytoplankton, while advanced stages feed increasingly on zooplankton.

Published information using monospecific small zooplankton (rotifers) as prey have revealed that *S. proboscideus* can consume these up to its own body weight per day (Dumont *et al.*, 1994). However, single prey tests may not reveal the diet-breadth of predators under natural conditions. As can be seen from Table 4, virgin stages consumed a maximum of three

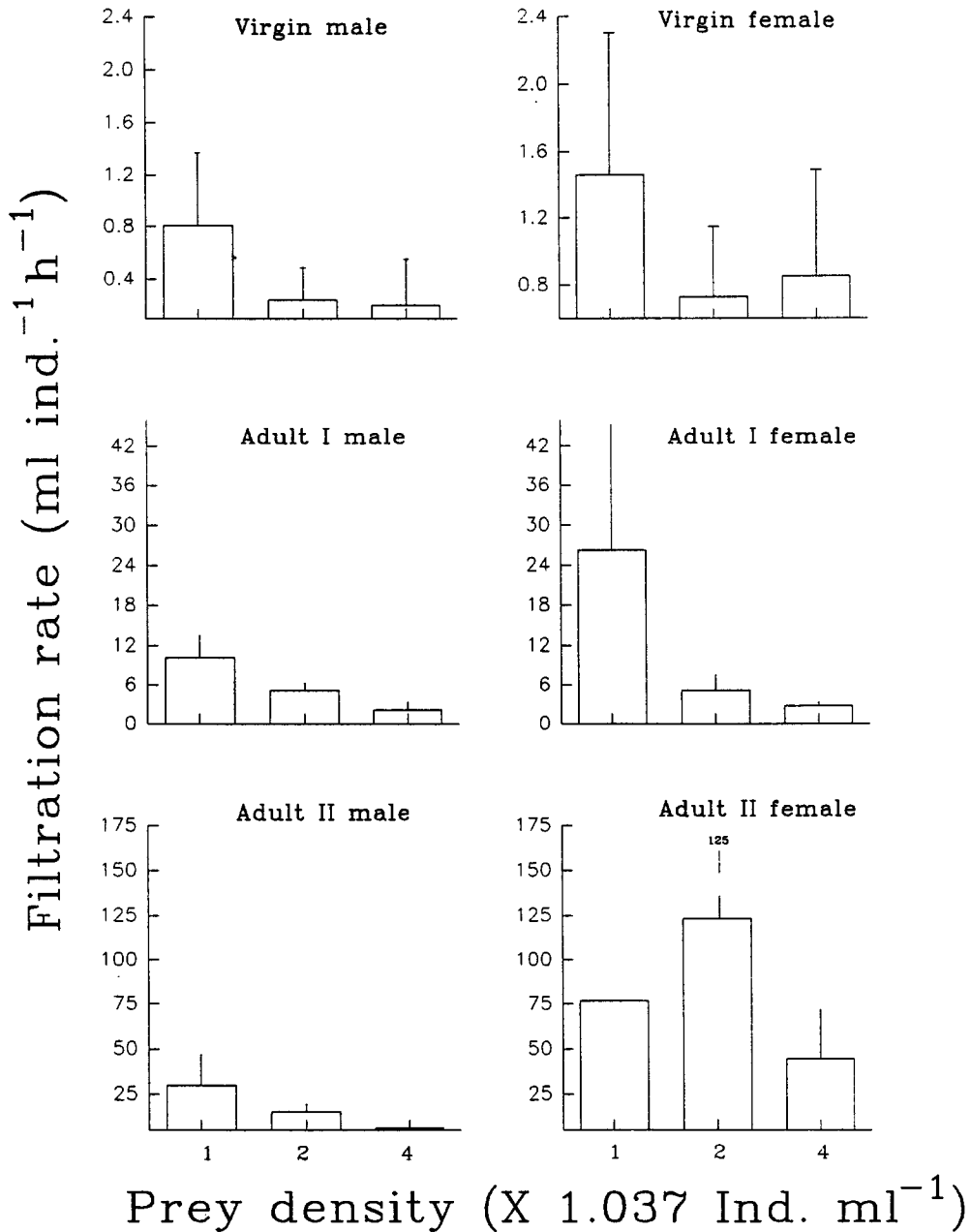


Fig. 6. Filtration rates (ml ind.⁻¹ h.⁻¹) in *S. proboscideus* as function of prey concentration. Values shown were mean \pm S.D. for three replicate recordings. Note the difference in scale in Y axis.

prey types, whereas advanced stages ate as many as 7 prey types.

Numerically, *K. cochlearis* were abundant in ambient water (Table 1) as well as in the gut (Fig. 2). How-

ever, Chesson's electivity index for this species was lower in large stages indicating that selection was not operative in adults (Fig. 3). Although statistical properties of Chesson's index (Chesson, 1983) have not

Table 6. Filtration rate by *S. proboscideus* in relation to predators size and sex as function of zooplankton prey concentration. Three-way ANOVA.

Variable	Source of variation	df	SS	MS	F
Filtration rate					
	Stage	2	24429.64	12214.82	12.8***
	Sex	1	7425.68	7425.68	7.8**
	Conc.	2	2762.17	2762.17	1.4 ^{ns}
Interactions					
	Stage* sex	2	11276.76	5638.38	5.9**
	Stage*conc.	4	4032.73	1008.18	1.1 ^{ns}
	Sex*conc.	2	1231.28	615.64	0.6 ^{ns}
	Stage*sex* conc.	4	3362.38	840.59	0.5 ^{ns}
	Error	36	34385.14	955.14	--

*** = $p < 0.001$; ** = $p < 0.01$; ns = non-significant ($p > 0.05$)

been established, it can be used for displaying prey preferences. Thus, when its value (Σ) becomes zero, this indicates no preference. From Fig. 3, it is evident that copepods (and their nauplii) and the jumping rotifer, *Polyarthra vulgaris*, were not consumed by *S. proboscideus*, where Σ was -1. For *Pompholyx sulcata*, except three cases, Chesson's index was positive (ranging from +0.072 to +0.997). Similarly, *B. longirostris* was positively selected in several cases (Fig. 3). The fact that rotifers were prominent, but *Bosmina* largely unused by virgin but used by adult predators illustrates a prey size constraint rather than rejection. In addition, large (*Daphnia*), and large, rapid swimming copepods were absent from the diet. Again, we conclude that this was not due to selectivity by the predators, but to an efficient escape mechanism of the prey (Hassell, 1978; Drenner & McComas, 1980; Mertens *et al.*, 1990). Copepod nauplii and *Polyarthra* avoided being preyed upon, presumably by a jumping escape reaction (Gilbert, 1985). Only in the case of *E. macrourus*, we do not, at this time, have an explanation for their absence from the gut. Earlier studies (Green & Lan, 1974; Sarma, 1993), have also shown a low preference or even rejection of *E. macrourus* by *Asplanchna brightwelli*.

This implies that adult *Streptocephalus* is a non-selective, prey size-limited predator, with the earlier stages having a restricted animal diet-breadth. The food consumption values of *S. proboscideus* here recorded varied from a minimum of 0.01 $\mu\text{g DW ind.}^{-1}$

h.^{-1} to a maximum of 43.3 $\mu\text{g DW ind.}^{-1} \text{h.}^{-1}$. These values are within the range recorded for this species using algae (Brendonck, 1993b) and rotifers (Dumont *et al.*, 1994). Adult stages (I & II) consumed on average 90% more dry weight than virgins. But the body length increment of adult (I & II) stages over virgins was only 50%. Thus, consumption increases nonlinearly with body size. In freshly formed temporary ponds, the combination of mass hatching and rapid growth, accompanied by a high consumption and broad prey spectrum must cause a rapid depletion of prey. In natural conditions, hunger is therefore the rule, and it is no wonder that mortality among growing fairy shrimps is often exponential (Hildrew, 1985). This is one of the reasons why we starved animals prior to our feeding experiment: Fig. 1 shows a hyperbolic decrease of consumption rate with time. Continuously well fed animals consume about half of the amount of food as hungry animals during the first half hour of feeding, but this latter rate likely more closely reflects their hunger state in natural conditions.

The duration of feeding time in laboratory experiments is important for other reasons as well. In our study, we worked with experiments of 30 minutes duration because: (1) freshwater anostracans have a minimum gut retention time of 30 minutes (Brendonck, 1993b) and (2) our aim was to measure prey size and type present in the gut. Durations in excess of 30 minutes would produce difficulties in correctly identifying and quantifying prey in the gut, as it would be at least partly digested (in addition to the problem of excretion).

Predator sex, stage and their interaction had a significant effect on prey consumption, but no interaction of stage with prey concentration was found (Tables 2a, b). This apparent absence of a functional response may relate to the complexity of the food mixtures offered, since functional responses did occur when single feed items (*A. fissa*) were offered (Dumont *et al.*, 1994). The fact that filtration rates tended to decrease rather than to increase with prey density, further, suggests that the lower food quantity offered may have been close to satiation level.

Females filtered significantly higher volumes of water than corresponding males (Table 6), with adult II females filtering almost 5 times more than males (Fig. 6). Dumont *et al.* (1994) recorded a filtration rate of about 90 $\text{ml ind.}^{-1} \text{h.}^{-1}$ for such large-sized females in *S. proboscideus*, using rotifers as prey. Brendonck (1993b) reported a maximum of around 18 $\text{ml ind.}^{-1} \text{h.}^{-1}$ for small-sized (14 mm) male *S. proboscideus*.

Here, we observed about 12 ml ind.⁻¹ h.⁻¹ for males of the same size. That females also consumed a proportionately higher quantity of prey than males (27 to 91%) at any stage, is consistent with earlier observations too (Dumont *et al.*, 1994), and reflects the higher energetic needs of this sex, which allocates more resources to reproductive output than males (Glazier & Calow, 1992).

Acknowledgements

AJA thanks Belgian Administration for Development and Cooperation (A.B.O.S) Belgium. SSSS and GM are grateful to World Laboratory (Switzerland) and the Vlaamse Gemeenschap (Belgium) for financial support, respectively.

References

- Belk, D. & G. A. Cole, 1975. Adaptational biology of desert temporary pond inhabitants. In *Environmental physiology of desert organisms*. N.F. Hadley (ed.), Dowden, Hutchinson and Ross, Inc, Stroudsburg, Pennsylvania: 207–226.
- Bernice, R., 1971. Food, feeding and digestion in *Streptocephalus dichotomus* Baird (Crustacea: Anostraca). *Hydrobiologia* 38: 507–520.
- Bottrell, H. H., A. Duncan, Z. M. Gliwicz, E. Grygierek, A. Herzog, A. Hillbricht-Ilkowska, H. Kurusawa, P. Larson & T. Weglenska, 1976. A review of some problems in zooplankton studies. *Norw. J. Zool.* 24: 419–456.
- Brendonck, L., 1993a. Feeding in the fairy shrimp *Streptocephalus proboscideus* (Frauenfeld) (Branchiopoda: Anostraca). 1. Aspects of the feeding biology. *J. Crust. Biol.* 13: 235–244.
- Brendonck, L., 1993b. Feeding in the fairy shrimp *Streptocephalus proboscideus* (Frauenfeld) (Branchiopoda: Anostraca). 2. Influence of environmental conditions on feeding rate. *J. Crust. Biol.* 13: 245–255.
- Brown, L. R. & L. H. Carpelan, 1971. Egg hatching and life history of a fairy shrimp *Branchinecta mackini* Dexter (Crustacea: Anostraca) in a Mohave desert playa (Rabbit Dry Lake). *Ecology* 52: 41–54.
- Cannon, H. G. & F. M. C. Leak, 1933. On the mouth parts of the Branchiopoda. *Phil. Trans. r. Soc. Lond. B* 222: 340–352.
- Cannon, H. G., 1935. A further account of the feeding of *Chirocephalus diaphanus*. *Proc. r. Soc. Lond. B* 117: 455–470.
- Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. *Ecology* 64: 1297–1304.
- Dierckens, K. R., S. S. S. Sarma, J. Mertens & H. J. Dumont, 1995. Feeding the fairy shrimp *Streptocephalus* (Anostraca-Crustacea) with the rotifer *Anuraeopsis*. *Hydrobiologia* 308: 29–33.
- Drenner, R. W. & S. R. McComas, 1980. The role of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In W. C. Kerfoot (ed.), *Evolution and Ecology of Zooplankton Communities*. The University Press of New England, Hanover, New Hampshire: 587–593.
- Dumont, H. J., I. Van de Velde & S. Dumont, 1975. The dry weight estimate of biomass in a selection of Cladocera and Rotifera from the plankton, periphyton and benthos of continental waters. *Oecologia* 19: 75–97.
- Dumont, H. J., J. G. Tundisi & K. Roche (eds), 1990. *Intrazooplankton predation*. Developments in Hydrobiology 60 (Reprinted from *Hydrobiologia* Vol. 198).
- Dumont, H. J., A. J. Ali, S. S. S. Sarma & J. Mertens, 1994. Predatory filter-feeding in freshwater fairy shrimps: Functional response of *Streptocephalus proboscideus* (Crustacea: Anostraca) fed *Anuraeopsis fissa* (Rotifera). *Int. Rev. ges. Hydrobiol.* 79: 511–519.
- Fryer, G., 1966. *Branchinecta gigas* Lynch, a non filter-feeding raptatory anostracan, with notes on the feeding habits of certain other anostracans. *Proc. Linn. Soc. Lond.* 177: 19–55.
- Fryer, G., 1983. Functional ontogenetic changes in *Branchinecta ferrox* (Milne-Edwards) (Crustacea: Anostraca). *Phil. Trans. r. Soc. Lond. B* 303: 229–343.
- Gilbert, J. J., 1985. Escape response of the rotifer *Polyarthra*: a high speed cinematographic analysis. *Oecologia* 66: 322–331.
- Glazier, D. S. & P. Calow, 1992. Energy allocation rules in *Daphnia magna*: clonal and age differences in the effects of food limitation. *Oecologia* 90: 540–549.
- Green, J. & O. B. Lan, 1974. *Asplanchna* and the species *Brachionus calyciflorus* in two Javanese sewage ponds. *Freshwat. Biol.* 4: 223–226.
- Hall, D. J., S. T. Threlkeld, C. W. Burns & P. H. Crowley, 1976. The size-efficiency hypothesis and the size structure of zooplankton communities. *Ann. Rev. Ecol. Syst.* 7: 177–208.
- Hartland-Rowe, R., 1972. The limnology of temporary waters and the ecology of the Euphyllipoda. In R. B. Clarke & R. J. Wootton (eds), *Essays in Hydrobiology*. University of Exeter, UK.
- Hassell, M. P., 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, USA.
- Hildrew, A. G., 1985. A quantitative study of the life history of a fairy shrimp (Branchiopoda: Anostraca) in relation to the temporary nature of its habitat, a Kenyan rainpool. *J. anim. Ecol.* 54: 99–110.
- Kerfoot, W. C. & A. Sih (eds), 1987. *Predation. Direct and indirect impacts on aquatic communities*. University Press of New England, Hanover.
- King, C. E., 1967. Food, age, and the dynamics of a laboratory population of rotifers. *Ecology* 48: 111–125.
- Lynch, M., 1979. Predation, competition, and zooplankton community structure: an experimental study. *Limnol. Oceanogr.* 24: 253–272.
- Mainly, B. F. J., P. Miller & L. M. Cook, 1972. Analysis of a selective predation experiment. *Am. Nat.* 106: 719–736.
- Mertens, J., N. Munuswamy, C. De Walsche & H. J. Dumont, 1990. On predatory tendencies in the feeding ecology of the fairy shrimp *Streptocephalus proboscideus* (Frauenfeld) (Crustacea: Anostraca). *Hydrobiologia* 198 (Dev. Hydrobiol. 60): 119–123.
- Pastorok, R. A., 1981. Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62: 1311–1324.
- Peters, R. H., 1984. Methods for the study of feeding, grazing, assimilation by zooplankton. In J. A. Downing & F. H. Rigler (eds), *A manual on methods for the assessment of secondary production in freshwaters*. Blackwell Scientific Publications, Boston, Massachusetts. IPM Handbook 17, 2nd edn.
- Reeve, M. R., 1963a. The filter feeding of *Artemia* I. In pure culture of plant cells. *J. Exp. Biol.* 40: 195–205.
- Reeve, M. R., 1963b. The filter feeding of *Artemia* II. In suspension of various particles. *J. Exp. Biol.* 40: 207–214.
- Rutner-Kolisko, A., 1977. Suggestions for biomass calculation of plankton rotifers. *Arch. Hydrobiol. Beih.* 8: 71–76.

- Sarma, S. S. S., 1989. Effect of *Chlorella* density and temperature on somatic growth and age at maturity of the rotifer *Brachionus patulus* (Muller) (Rotifera). *Current Science* 58: 788–791.
- Sarma, S. S. S., 1993. Feeding response of *Asplanchna brightwelli* (rotifera): laboratory and field studies. *Hydrobiologia* 255/256 (Dev. Hydrobiol. 83): 275–282.
- Sih, A., P. Crowley, M. McPeck, J. Petranka & K. Strohmeier, 1985. Predation, competition, and prey communities: a review of field experiments. *Ann. Rev. Ecol. Syst.* 16: 269–311.
- Streams, F. A., 1994. Effect of prey size on attack components of the functional response by *Notonecta undulata*. *Oecologia* 98: 57–63.
- White, G. E., G. Fabris & R. Hartland-Rowe, 1969. The method of prey capture by *Branchinecta gigas* Lynch, 1937 (Anostraca). *Crustaceana* 16: 158–160.
- Wiggins, G. B., R. J. Mackay & I. M. Smith, 1980. Evolutionary and ecological strategies of animals in annual temporary pools. *Arch. Hydrobiol. (suppl.)* 58: 97–206.
- Williams, D. D., 1987. *The ecology of temporary waters*. Croom Helm. London and Sydney. Timber Press, Portland, Oregon.
- Williams, W. D., 1985. Biotic adaptations in temporary lentic waters, with special reference to those in semi-arid and arid regions. *Hydrobiologia* 125 (Dev. Hydrobiol. 28): 85–110.
- Zaret, T. M., 1980. *Predation and freshwater communities*. Yale University Press, New Haven/London.