

# Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses

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**ABSTRACT:** Zooplankton feeding rates and prey selection of the mysid shrimp *Praunus flexuosus* were studied in single and multiple prey species experiments. Functional responses of *P. flexuosus* were determined for 2 copepod species, *Acartia* spp. (adults) and *Eurytemora affinis* (adult females), and 2 cladoceran species, *Pleopsis polyphemoides* and *Bosmina longispina maritima*. Feeding rates were highest with *P. polyphemoides*, intermediate with *B. longispina maritima* and *Acartia* spp. and lowest with *E. affinis*. Videofilming of the prey species subjected to an artificial water flow confirmed that *E. affinis* displays a stronger escape response than *Acartia* spp., and that cladocerans cannot withstand a water current. In a prey selection experiment with *Acartia* spp. and *E. affinis*, *P. flexuosus*' clearance rates of *Acartia* spp. were suppressed in the presence of *E. affinis*, suggesting an interference effect from *E. affinis*. In another multiple prey species experiment with *Acartia* spp. and *P. polyphemoides*, the mysids fed intensively on cladocerans, regardless of whether the cladocerans occurred alone or with copepods. In contrast, predation on *Acartia* spp. significantly declined when cladocerans were offered as alternative food (at high concentration). We suggest that *P. flexuosus* can capture cladocerans by creating a suspension feeding current, whereas the evasive copepods need to be perceived and attacked individually. At low prey concentration, *P. flexuosus* feeds opportunistically by using both feeding modes, and the apparent 'selectivity' mainly reflects the escape capabilities and morphological defences of the prey species; at high prey concentration, *P. flexuosus* may show true selection by switching from omnivorous feeding to suspension feeding on cladocerans.

**KEY WORDS:** Mysid shrimps · *Praunus flexuosus* · Zooplanktivory · Functional response · Prey selection · Prey switching · Escape reaction · Baltic Sea

## INTRODUCTION

The general 'predation vulnerability' (Pastorok 1981, Greene 1986) of different planktonic prey species can be estimated from planktivores' functional responses to each prey. However, extrapolating functional responses determined in single prey situations to more natural conditions is not straightforward, because

predators may modify their behaviour when several prey species become available. A potential way of adapting to multi-species situations is prey switching, i.e. preying disproportionately more intensively on the most abundant prey species (e.g. Murdoch 1969, Lawton et al. 1974). This behaviour will enable efficient feeding on one prey type at a time, but it will also allow sufficient dietary variation for the predator (Kjørboe et al. 1996). In the pelagic environment, prey switching has been reported in predators that can alter their feeding behaviour from one mode to another. For instance, certain omnivorous copepods switch from suspension feeding on phytoplankton cells (diatoms) to

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raptorial feeding on animal prey (ciliates or copepod nauplii) in response to changes in prey availability (Landry 1981, Kiørboe et al. 1996). Among larger planktivores, similar flexibility has been observed for northern anchovy *Engraulis mordax*, which shifts from zooplanktivory to filter feeding on phytoplankton when zooplankton densities are exceptionally low (Leong & O'Connell 1969).

Mysid shrimps are abundant nectobenthic and sublittoral crustaceans in many lacustrine and marine ecosystems. In the Baltic Sea, their impact on zooplankton populations has been considered significant (Rudstam et al. 1989, 1992, Hansson et al. 1990, Rudstam & Hansson 1990, Uitto et al. 1995, Nordström 1997), but their prey selection has not been extensively studied. The existing marine studies are also somewhat at odds with lacustrine studies: while many freshwater studies suggest that mysids prey more readily on cladocerans than on copepods (Lasenby & Langford 1973, Cooper & Goldman 1980, Bowers & Vanderploeg 1982, Grossnickle 1982, Ramcharan et al. 1985, Nero & Sprules 1986), certain Baltic results suggest that mysids (*Mysis mixta*) prefer a number of copepod taxa over cladocerans (Mohammadian et al. 1997). Furthermore, mysids are predators which have the potential to show prey switching, because they feed on small prey items by suspension feeding but capture larger prey raptorially (Bowers & Grossnickle 1978, Cooper & Goldman 1980, Mauchline 1980, Siegfried & Kopache 1980, Grossnickle 1982). However, prey switching has not previously been explicitly studied in mysids.

The purpose of the present study was to investigate prey selection and prey switching in mysid shrimps. Also, we wanted to find out how mysids may cope with changes in Baltic zooplankton community composition. There are 7 mysid species in the Baltic Sea. Of these, *Mysis mixta* and the 2 sibling species of *M. relicta* are confined to the open sea, whereas *Neomysis integer*, *Praunus flexuosus*, *P. inermis* and *Hemimysis anomala* occupy shallower habitats (e.g. Segerstråle 1962, Rudstam et al. 1986, Salemaa et al. 1986, 1990, Väinölä 1992, Salemaa & Hietalahti 1993). We chose to experiment with *P. flexuosus*, because it is abundant, easy to collect and handle in the laboratory, and able to feed on a range of different prey types, including copepods and cladocerans (Nordström 1997). All mysids feed omnivorously on zooplankton, phytoplankton and detritus, but we wanted to study interactions with animal prey, because these are important food for *P. flexuosus* during its main growth period in summer (Nordström 1997). Following Landry (1981) and Kiørboe et al. (1996), we hypothesised that prey switching may occur in situations where different prey need to be captured with different foraging modes. With relatively similar prey types, in contrast, the ingestion rates

should simply reflect the differences in prey escape capabilities and morphological defences. These hypotheses were examined by single and multiple prey species experiments and by investigating the escape capabilities of the prey species with videographic methods.

## MATERIALS AND METHODS

**Mysid and zooplankton collection.** The material for our experiments was collected in the SW archipelago of Finland (59°47'N, 23°16'E) during July 1997. Mysids were collected from the sublittoral using an arm net which was pulled through macroalgal vegetation (mainly *Fucus vesiculosus*). After capture, mysids were immediately brought into a 13°C temperature-controlled room where adult females with a marsupium (2.2 to 2.5 cm total length) were transferred into filtered seawater ~12 h before the experiments.

Zooplankton was collected daily from a 35 m deep archipelago area (ca 500 m from the shore) using a Hensen-type plankton net (diameter 60 cm, mesh size 200 µm, 1 l cod end), which was hauled 3 to 5 times from ~30 m depth to the surface. Water was stratified and temperature varied between 4 and 23°C in the 0 to 30 m layer. The zooplankton sample was placed in an insulated box with 15 l of seawater collected at ~5, 10 and 20 m depths. Within 30 min after capture, zooplankton was brought into the 13°C room. The dominant calanoids *Acartia* spp. and *Eurytemora affinis* and cladocerans *Pleopsis polyphemoides* and *Bosmina longispina maritima* were chosen as prey. The copepods mainly represented adult stages that were abundant in the water during the experiments. In *Acartia* spp., females and males (but also some Stage 5 copepodites) were selected; in *E. affinis* only egg-carrying females were chosen. Copepods were carefully transferred into filtered seawater and were left to acclimate to the experimental temperature overnight. Cladocerans were left in an aerated container overnight, and actively swimming individuals were transferred to the experimental bottles ~30 min before the experiments. During selection of the cladocerans, the bottles were lit from below, which prevented the specimens from being trapped by the film at the water's surface.

Carbon contents of the prey species were determined using the high temperature combustion method (Salonen 1979) from live individuals that represented sizes and developmental stages similar to those used in the experiments. The carbon contents (in µg C ind.<sup>-1</sup>) were 3.08 for *Acartia* spp. (SD = 0.62, n = 16), 5.14 for *Eurytemora affinis* (SD = 1.12, n = 10), 1.27 for *Pleopsis polyphemoides* (SD = 0.40, n = 10) and 1.82 for *Bosmina longispina maritima* (SD = 0.34, n = 18).

Table 1. Functional response experiments with *Acartia* spp., *Eurytemora affinis*, *Pleopsis polyphemoides* and *Bosmina longispina maritima*: numeric (ind. l<sup>-1</sup>) and carbon concentrations (µg C l<sup>-1</sup>, in parentheses) of prey in the experiments

<i>Acartia</i> spp.	<i>E. affinis</i>	<i>P. polyphemoides</i>	<i>B. longispina maritima</i>
4.3 (13.4)	4.3 (22.3)	13.0 (16.6)	13.0 (23.7)
13.0 (40.2)	13.0 (67.0)	43.5 (55.2)	43.5 (79.1)
26.1 (80.3)	26.1 (134.1)	87.0 (110.4)	87.0 (158.3)
43.5 (133.9)	43.5 (223.5)	130.4 (165.7)	130.4 (237.4)
60.9 (187.5)	60.9 (312.9)	173.9 (220.9)	173.9 (316.5)
87.0 (267.8)	87.0 (447.0)	260.9 (331.3)	260.9 (474.8)

**Functional response experiments.** All predation experiments were conducted in 1.15 l bottles in 0.2 µm-filtered seawater, under dimmed room lighting. Concentrations of *Acartia* spp. and *Eurytemora affinis* were varied from 5 to 100 ind. bottle<sup>-1</sup> and concentrations of *Pleopsis polyphemoides* and *Bosmina longispina maritima* from 15 to 300 ind. bottle<sup>-1</sup> (Table 1). Most of these concentrations may occur in the field (Viitasalo 1992, Viitasalo et al. 1995), although the highest concentrations may only occur in very localised patches. Because mysids apparently interfere with each other's predation in experimental containers (S. Hansson, University of Stockholm, pers. comm.), only 1 *Praunus flexuosus* was placed in each bottle. Bottles were sealed with a plastic film to prevent air bubbles and placed in a plankton wheel rotating at 0.5 rpm. Three to 5 replicates were made with copepods and 3 to 7 with cladocerans. After the incubation, the specimens were killed with Lugol's solution, the mysids were measured, and the remaining copepods and cladocerans were counted under a binocular microscope.

The functional response curves were determined by fitting 3 alternative models to the data: linear ( $y = y_0 + ax$ ), exponential rise to maximum [ $y = a(1 - e^{-bx})$ ] and a sigmoidal model [ $y = a/[1 + (x/x_0)^b]$ ]. These models represent Holling Type 1, 2 and 3 functional response models, respectively (Holling 1959). A more complicated model was chosen only if the variation explained ( $r^2$ ) was >5% higher than the  $r^2$  of the simpler model. The function parameters and  $r^2$  values were estimated using the graphing program SigmaPlot 4.0.

A problem with studying functional responses in bottles is that the prey concentration cannot be kept constant. The experiments therefore need to be relatively short, so that prey are not depleted before the end of the incubation, but long enough to provide a clear predation signal at each concentration. The duration of our experiments was 2 h, which was chosen as most appropriate according to preliminary experiments with durations of 1, 2 and 4 h.

Table 2. Prey selection experiment 1 Ratio of *Acartia* spp. to *Eurytemora affinis* and numeric (ind. l<sup>-1</sup>) and carbon concentrations (µg C l<sup>-1</sup>, in parentheses) of prey in various treatments

<i>Acartia</i> spp.: <i>E. affinis</i> ratio	<i>Acartia</i> spp.	<i>E. affinis</i>	Total conc.
85:15	73.9 (227.6)	13.0 (66.8)	87.0 (294.4)
70:30	60.9 (187.6)	26.1 (134.2)	87.0 (321.8)
50:50	43.5 (134.0)	43.5 (223.6)	87.0 (357.6)
30:70	26.1 (80.4)	60.9 (313.0)	87.0 (393.4)
15:85	13.0 (40.0)	73.9 (379.8)	87.0 (419.8)

**Prey selection experiments.** Prey selection of *Praunus flexuosus* was investigated with 2 different multi-species experiments: *Acartia* spp. with *Eurytemora affinis*, and *Acartia* spp. with *Pleopsis polyphemoides*. The first experiment was designed to examine possible prey switching in a situation where the dominant copepod species (here, *Acartia* spp.) is gradually replaced by a subdominant one (*E. affinis*). In this experiment the total prey density was always 100 ind. bottle<sup>-1</sup>, but the *Acartia* spp.:*E. affinis* ratio was varied as follows: 85:15, 70:30, 50:50, 30:70, 15:85 (Table 2). Four replicate experiments were done for each combination. The effect of the alternative prey species on *P. flexuosus*' clearance rates was analysed with the analysis of covariance (ANCOVA, in the statistical package SYSTAT 5.03). In this analysis, we compared the clearance of *Acartia* spp. with and without *E. affinis* (i.e. results of the multiple prey experiment were compared with results of the functional response experiment); concentration of *Acartia* spp. was used as a covariate. A similar analysis was done also for *P. flexuosus*' clearance of *E. affinis* with and without *Acartia* spp. (with *Eurytemora* concentration as a covariate). Because saturation may hamper the interpretation of ANCOVA, clearly saturating prey concentrations (>50 ind. l<sup>-1</sup>) were excluded from the analyses.

Cladoceran populations often increase very rapidly in the field (e.g. Viitasalo et al. 1995). We therefore designed the second prey selection experiment to examine how mysid feeding rates change when cladocerans are introduced 'on top' of the copepod community. To reveal if prey concentration affects *Praunus flexuosus*' selectivity, the experiment was performed at 2 prey densities: 30 *Acartia* spp. with 60 *Pleopsis polyphemoides* per bottle, and 100 *Acartia* spp. with 200 *P. polyphemoides* per bottle (Table 3). Five replicates were done for both combinations. These 2 prey concentrations are hereafter referred to as 'low food' and 'high food' conditions, respectively. The concentrations were chosen according to the single species functional response curves to represent situations where foraging on *Acartia* spp. should result in approximately similar

Table 3. Prey selection experiment 2 with *Acartia* spp. and *Pleopsis polyphemoides*. Total numeric (ind. l<sup>-1</sup>) and carbon concentrations (µg C l<sup>-1</sup>, in parentheses) of prey in various treatments

Treatment	Total prey concentration
<b>'Low food' conditions</b>	
Treatment 1 (30 <i>Acartia</i> spp. bottle <sup>-1</sup> )	26.1 (80.3)
Treatment 2 (60 <i>P. polyphemoides</i> bottle <sup>-1</sup> )	52.2 (66.3)
Treatment 3 (30 <i>Acartia</i> spp. and 60 <i>P. polyphemoides</i> bottle <sup>-1</sup> )	78.3 (146.6)
<b>'High food' conditions</b>	
Treatment 1 (100 <i>Acartia</i> spp. bottle <sup>-1</sup> )	87.0 (267.8)
Treatment 2 (200 <i>P. polyphemoides</i> bottle <sup>-1</sup> )	173.9 (220.9)
Treatment 3 (100 <i>Acartia</i> spp. and 200 <i>P. polyphemoides</i> bottle <sup>-1</sup> )	260.9 (488.7)

carbon ingestion as foraging on *P. polyphemoides* ('low food' conditions), and foraging on *P. polyphemoides* should give more carbon due to *Acartia* spp. saturation ('high food' conditions) (cf. Table 3 and 'Results').

**Experiments with artificial flow.** To investigate the escape capabilities of the prey species, we video-filmed the behaviour of *Bosmina longispina maritima*, *Acartia* spp. (adults) and *Eurytemora affinis* (ovigerous females) when subjected to an artificially created water flow. *Pleopsis polyphemoides* could not be filmed because it did not occur in plankton at the time these experiments were carried out. The experimental specimens were collected and handled as in the predation experiments. A Pasteur pipette (diameter of the opening = 1.5 mm) was fixed vertically in a cubic 1 l Plexiglas aquarium filled with filtered sea-water so that the tip of the pipette was 3.5 cm above the bottom of the aquarium. The pipette was connected to a silicon tube with the free end hanging 46 cm below the aquarium, which created a water flow to which the zooplankton reacted. When the water level was close to the tip of the pipette, more water was added and filming was continued (after the water turbulence had calmed down) until a sufficient number of observations was made. The filming was done in a 13°C temperature-controlled room, with 'Mintron' closed-circuit video cameras, using infrared light emitting diodes as a light source (Viitasalo et al. 1998). To enable measurements of velocities and distances in 3 dimensions, 2 cameras were fixed at right angles at 90 cm distance from the aquarium. The 2 images were combined on a monitor with a Panasonic digital image mixer, and recorded with a Panasonic video cassette recorder producing 50 frames s<sup>-1</sup>. Time in 1/100 s was recorded with a FOR-A video timer. After filming, the fre-

quency of escapes and captures by the pipette during each interaction were determined from the films. An 'interaction' was here defined as a film sequence starting with an individual plankter being entrained in the flow and ending with the prey either escaping from the flow field, or being sucked into the pipette (after 1 or several sequential escapes). The reaction distance of the plankters from the pipette and their escape speeds (during the first 0.06 s of the escape) were measured using an image analysing program, 'Fisk-Pos' (L. W. Pedersen, Danish Institute for Fisheries Research). Positions of the plankters were followed frame by frame on the 2 perpendicular views, which resulted in x-y-z and time coordinates for each escape and capture.

## RESULTS

### Functional responses

In most of the functional response experiments, the food consumption of *Praunus flexuosus* increased linearly with increasing prey abundance. In *Acartia* spp., however, a sigmoid (Holling Type 3) model explained 75% of the variation (Fig. 1A), whereas the linear and Holling Type 2 models explained 67 and 70%, respectively; saturation was approached at *Acartia* spp. concentrations exceeding ~50 ind. l<sup>-1</sup>. With *Eurytemora affinis*, *Pleopsis polyphemoides* and *Bosmina longispina maritima*, a linear model explained as much of the variation (within ~1%) as the more complicated models (Fig. 1B–D). There was large variation in the consumption rates between *P. flexuosus* individuals: the ingestion rates varied 2- to 4-fold at the highest prey concentrations (Fig. 1).

Fig. 2 shows the functional responses transformed to carbon ingested versus carbon available. The slope of the functional response was highest with *Pleopsis polyphemoides*, intermediate with *Bosmina longispina maritima* and lowest with *Eurytemora affinis*. *Acartia* spp. carbon ingestion was first similar to that of *P. polyphemoides*, but, with saturation at carbon concentrations above ~150 µg C l<sup>-1</sup>, *Acartia* spp. ingestion approached that of *B. longispina maritima*. From the sigmoid regression of *Acartia* spp., we can predict that *Acartia* ingestion will decline below that of *B. longispina maritima* at prey concentrations exceeding ~300 µg C l<sup>-1</sup> (Fig. 2).

### Prey selection

In the first prey selection experiment, *Acartia* spp. was eaten at a higher rate than *Eurytemora affinis*, as

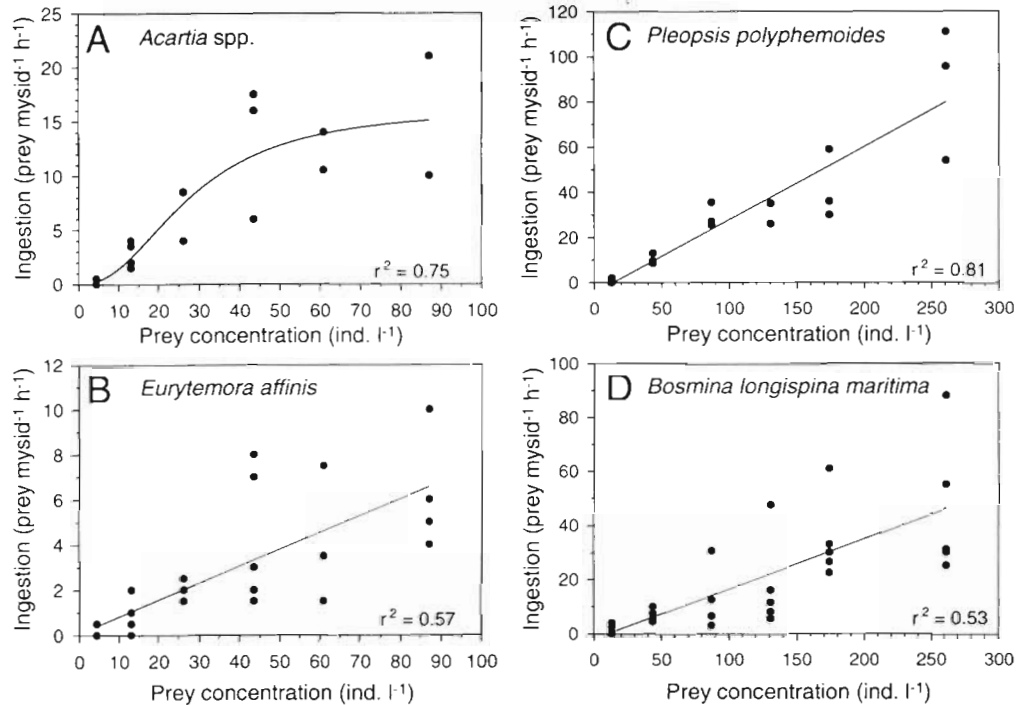


Fig. 1 *Praunus flexuosus*. Functional responses with (A) *Acartia* spp. adults, (B) *Eurytemora affinis* ovigerous females, (C) *Pleopsis polyphemoides* and (D) *Bosmina longispina maritima*. Lines denote regressions through data;  $r^2$ : variance explained

expected from the single prey experiments. *Praunus flexuosus*' feeding rate on *E. affinis* exceeded that on *Acartia* spp. only when the proportion of *E. affinis* was >70% of the population density or carbon concentration (Fig. 3). Consequently, the total ingestion of copepods was significantly higher with an *Acartia* spp.-dominated diet (>50% of the biomass in *Acartia* spp.) than with a *E. affinis*-dominated diet (Student's *t*-test value = 2.05,  $p = 0.049$ ,  $df = 28$ ) (Fig. 4).

The data do not clearly support the hypothesis of a stepwise switching from one prey species to another, although a curvilinear regression fits the *Eurytemora affinis* data (Fig. 3) somewhat better than a linear one ( $r^2 = 0.32$  and  $0.38$  for the linear and third order polynomial regressions, respectively). We may examine the occurrence of prey switching in this experiment by studying the ratio of clearance rates ( $F$ ) of the 2 prey species (cf. Landry 1981). Fig. 5 shows the ratio of *Acartia* spp. and *E. affinis* clearance rates ( $F_{Acartia}/F_{Eurytemora}$ ) as a function of *Acartia* spp. concentration (expressed as percentage of total prey availability). The ratio does not increase, which suggests that *Praunus flexuosus* did not show prey switching between these 2 species. We may further examine this result by comparing the clearances of the 2 prey in single and multiple prey species experiments. Fig. 6 shows that the clearance of *Acartia* spp. was significantly lowered when *E. affinis* was provided as alternative food (ANCOVA,  $p = 0.0015$ ), whereas the clearance of *E. affinis* remained unchanged regardless of

whether they were offered alone or together with *Acartia* spp. (ANCOVA,  $p = 0.837$ ). This suggests that there was a 1-sided interference effect: the presence of *E. affinis* interfered with predation on *Acartia* spp. but the presence of *Acartia* spp. did not interfere with predation on *E. affinis*.

The second multiple prey experiment was designed to find out if *Praunus flexuosus* suppresses its feeding on copepods (*Acartia* spp.) when cladocerans (*Pleopsis polyphemoides*) are provided as additional food (or

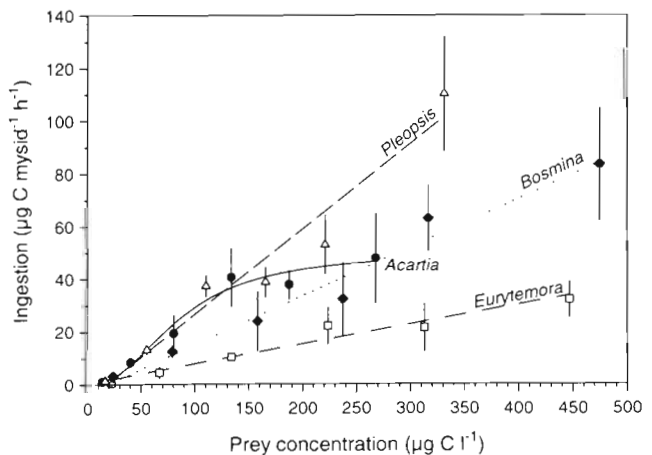


Fig. 2 *Praunus flexuosus*. Functional responses with *Acartia* spp., *Eurytemora affinis*, *Pleopsis polyphemoides* and *Bosmina longispina maritima*, shown as carbon weight ingested vs carbon weight available

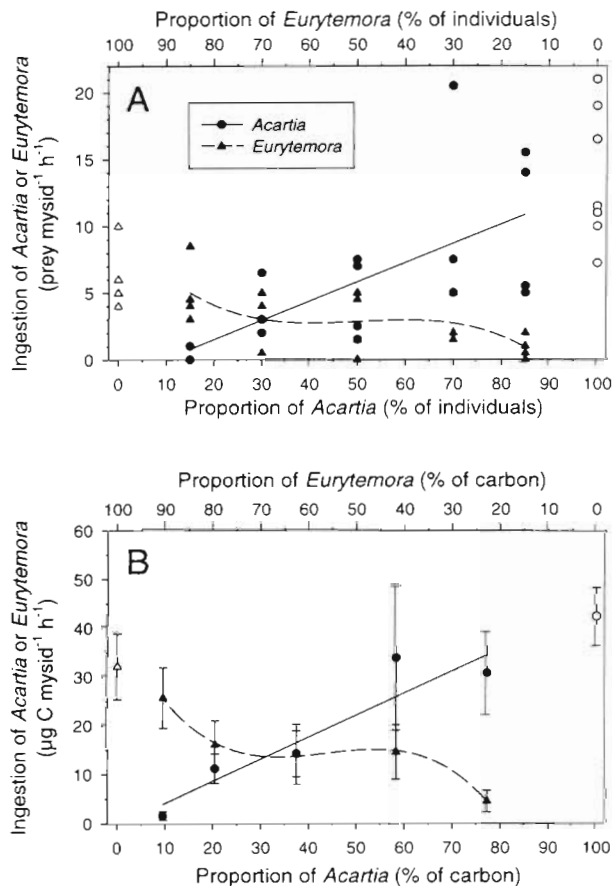


Fig. 3. *Praunus flexuosus*. Prey selection experiment 1 with *Acartia* spp. and *Eurytemora affinis*. Ingestion of *Acartia* spp. (●) and *E. affinis* (▲) in relation to their proportional availability: (A) expressed as individuals ingested; (B) expressed as carbon weight ingested. Solid lines: linear regression through *Acartia* spp. data; dashed lines: a third order polynomial regression through *E. affinis* data. (○, △) Ingestion rates of *Acartia* spp. and *E. affinis* in single prey experiments (cf. Fig. 1), respectively. Symbols and vertical lines in (B): means and standard errors, respectively

vice versa). In 'low food' conditions (Fig. 7A), the ingestion of both prey remained at the same level, regardless of whether they were offered alone or together with the alternative prey species (Student's *t*-test,  $p > 0.10$ ). In 'high food' conditions, in contrast, *Acartia* spp. ingestion significantly decreased in the presence of *P. polyphemoides* (Student's *t*-test value = 3.67,  $p = 0.006$ ,  $df = 8$ ), while *P. polyphemoides* ingestion remained at a similar level with or without *Acartia* spp. (Fig. 7B). However, if we take into account that the prey availability in the different treatments varied from 66 to 489 µg C l<sup>-1</sup>, we note that the total ingestion showed a Holling Type 3 functional response (Fig. 8). Thus, in terms of carbon ingested, *P. flexuosus* seemed to be able to 'optimise' its foraging, regardless of prey mixture.

### Experiments with artificial flow

The experiments with artificial flow revealed significant differences in the escape capabilities of the prey species. Both copepod species showed strong escape responses. The reaction distance from the opening of the pipette was very similar in *Acartia* spp. and *Eurytemora affinis* (averages = 0.52 and 0.53 cm, respectively; Fig. 9A), but the escape speed (Fig. 9B) was significantly higher in *E. affinis* than in *Acartia* spp. (averages = 5.51 and 4.05 cm s<sup>-1</sup>, respectively; Student's *t*-test value = 2.29,  $p = 0.026$ ,  $df = 51$ ). Due to its higher initial speed, *E. affinis* also travelled a longer distance than *Acartia* spp. during each escape (averages = 0.34 and 0.26 cm, respectively).

A closer inspection of copepod behaviour revealed that the escaping *Eurytemora affinis* first performed a long series of small jumps and were finally released from the flow with a longer jump. In contrast, *Acartia* spp. were often repeatedly drawn towards the pipette, with the distance to the pipette gradually diminishing, and were finally captured. Consequently, the escape success of *E. affinis* was 91% (51 of 56 interactions), whereas *Acartia* spp. escaped only in 67% of the cases (33 of 49 interactions).

In complete contrast to the copepods, *Bosmina longispina maritima* were not able to resist the water current, and were always caught by the pipette if entrained in the flow. The escape success of *B. longispina maritima* was thus 0%. The ability

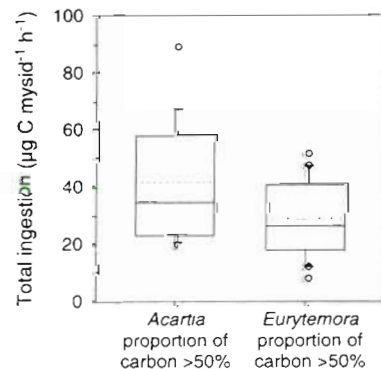


Fig. 4. *Praunus flexuosus*. Prey selection experiment 1 with *Acartia* spp. and *Eurytemora affinis*. Total carbon ingestion in treatments where the proportion of *Acartia* spp. of available carbon was >50%, and when the proportion of *E. affinis* of available carbon was >50% (cf. Fig. 3B). Difference between data sets is statistically significant (Student's *t*-test value = 2.054,  $p = 0.049$ ,  $df = 28$ ). Ends of boxes: 25th and 75th percentiles; ends of whiskers: 10th and 90th percentiles of the data; middle horizontal lines: medians; dotted lines: averages; circles: outliers outside 10th and 90th percentiles



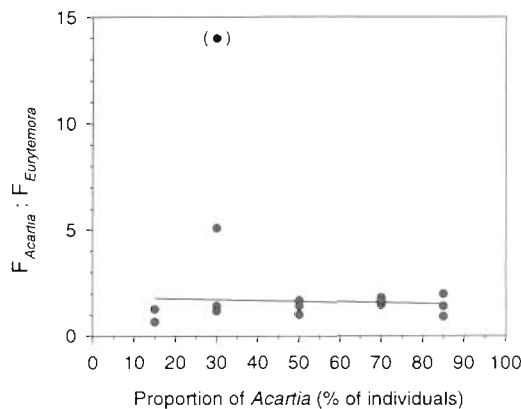


Fig. 5. *Praunus flexuosus*. Prey selection experiment 1 with *Acartia* spp. and *Eurytemora affinis*. Ratio of clearance rates of *Acartia* spp. and *Eurytemora affinis* ( $F_{Acartia} : F_{Eurytemora}$ ), as a function of *Acartia* spp. concentration (expressed as percentage of prey available). Solid line: linear regression through data; the outlier (in parentheses) is not included in the regression

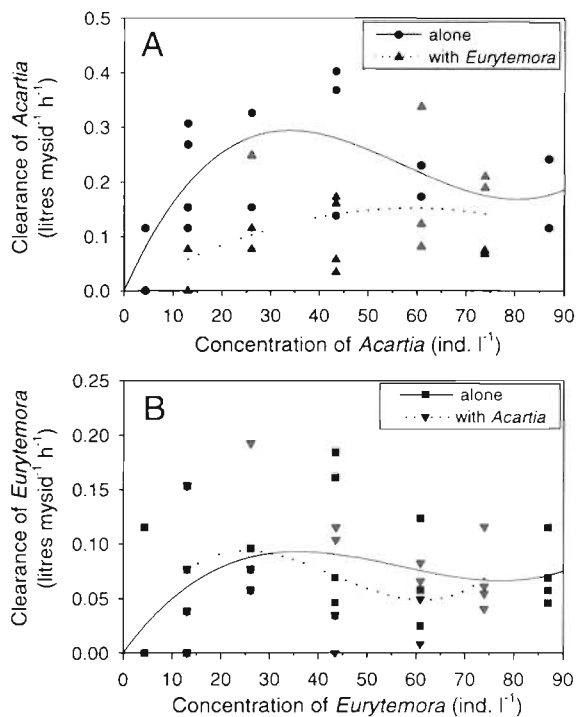


Fig. 6. *Praunus flexuosus*. Mysid clearance rates of (A) *Acartia* spp. and (B) *Eurytemora affinis* as a function of *Acartia* spp. and *E. affinis* availability, respectively. (●, ■) Clearance rates in single prey experiments (cf. Fig. 1A, B); (▲, ▼) clearance rates in prey selection experiment 1. Lines drawn as third order polynomial regressions through respective data

of *Pleopsis polyphemoides* to escape from pipette suction could not be investigated, but previous experiments (Viitasalo unpubl.) have shown that their locomotory powers are similar to or weaker than those of

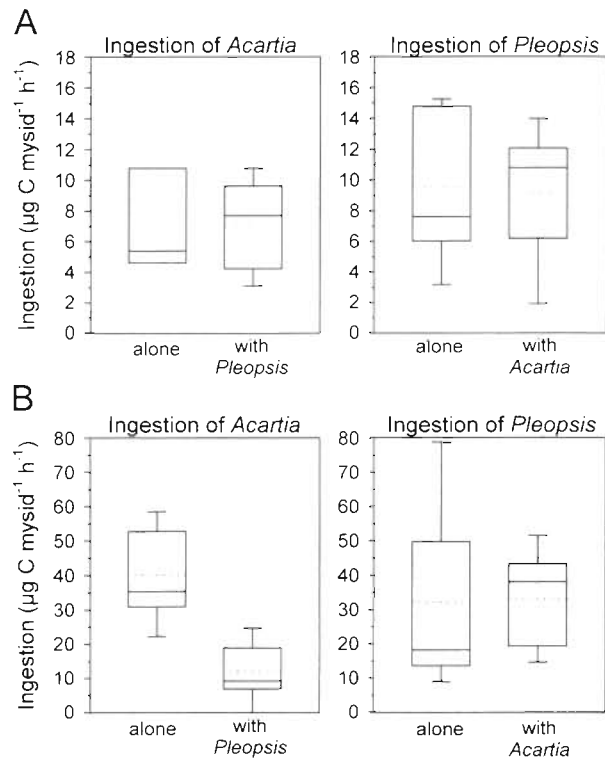


Fig. 7. *Praunus flexuosus*. Prey selection experiment 2 with *Acartia* spp. and *Pleopsis polyphemoides*. Ingestion rates when the prey were offered alone and when together with the alternative prey species. (A) 'Low food' conditions; (B) 'high food' conditions (see text for explanation). The difference between the ingestion of *Acartia* spp. data sets in (B) is statistically significant (Student's *t*-test value = 3.67,  $p = 0.006$ ,  $df = 8$ ). Box-and-whisker plots as in Fig. 4

*B. longispina maritima*. We therefore believe that, with an identical experimental setup, the escape success of *P. polyphemoides* would have been 0% as well.

## DISCUSSION

### Functional responses

The functional response of a predator reflects the efficiency of the components of the predatory interaction, i.e. search, location, pursuit, attack, handling and ingestion (e.g. Holling 1959, Kerfoot 1978). Below the saturation level, the ingestion rate depends on the product of the encounter rate between predator and prey and the capture success of the predator. In the case of mysids feeding on zooplankton, the speed of the mysid (or its feeding current) mainly determines the encounter rate, because the mysid velocity is generally much higher than zooplankton swimming speed. If we assume a relatively constant mysid speed, the ingestion rate at each prey concentration thus depends

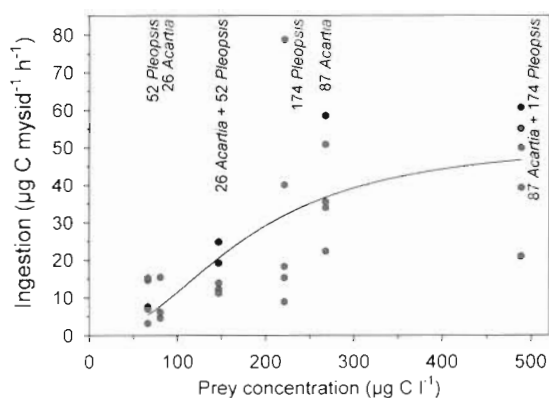


Fig. 8. *Praunus flexuosus*. Prey selection experiment 2 with *Acartia* spp. and *Pleopsis polyphemoides*. Total carbon ingestion plotted against carbon availability in various *Acartia* spp.-*P. polyphemoides* combinations. Solid line: sigmoidal (Holling Type 3) regression line through data;  $r^2 = 0.514$ . Prey concentration (ind.  $l^{-1}$ ) indicated above each treatment

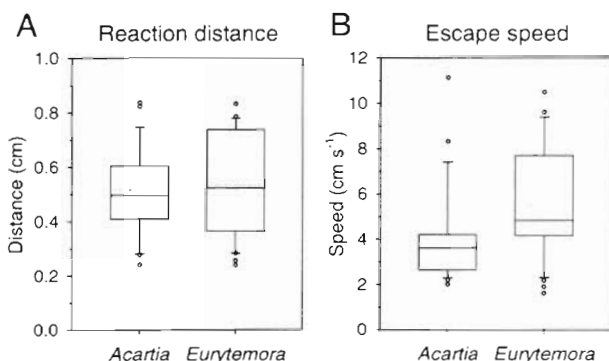


Fig. 9. *Acartia* spp. and *Eurytemora affinis*. Artificial flow experiment: (A) copepod reaction distances from the opening of the pipette; (B) escape speeds of the copepods during the first 0.06 s of the escape. The difference between the data sets in (B) is statistically significant (Student's *t*-test value = 2.29,  $p = 0.026$ ,  $df = 51$ ). Box-and-whisker plots as in Fig. 4

on the mysid's perceptive radius, capture success and handling time (Gerritsen & Strickler 1977). These parameters, in turn, depend on prey characteristics, such as escape performance and body size and shape, as well as other morphological defences. In a single prey species experiment, we can therefore interpret the initial slope of the functional response to reflect the 'predation vulnerability' (sensu Pastorok 1981, Greene 1986) of each prey type to mysid predation.

The functional response experiments showed clear differences between predation vulnerabilities of the 4 prey species. *Pleopsis polyphemoides* was the most profitable species, both in terms of number of prey captured and amount of carbon ingested, *Eurytemora affinis* was the least profitable species, and *Acartia* spp. and *Bosmina longispina maritima* were intermedi-

ate. With the wide range of prey concentrations studied, the functional responses were near-linear in *E. affinis*, *P. polyphemoides* and *B. longispina maritima*. This suggests that *Praunus flexuosus* feeding on these species rarely saturates in the field. In contrast, feeding on *Acartia* spp. saturated above  $\sim 50$  ind.  $l^{-1}$ . Average concentrations of *Acartia* spp. normally remain below this level (e.g. Viitasalo 1992, Viitasalo et al. 1995), but many copepod species, including *Acartia* spp., occasionally show swarming behaviour, with densities reaching 500 to 2000 ind.  $l^{-1}$  (Hamner & Carleton 1979, Ueda et al. 1983). If *Acartia* spp. form similar swarms in the Baltic Sea, *P. flexuosus* feeding on *Acartia* spp. could easily saturate.

The different prey vulnerabilities observed in predation experiments were consistent with the results of the pipette experiments. Whether the fluid flow created by a pipette simulates mysid feeding current can of course be questioned. However, in another experiment (Viitasalo et al. 1998), the reaction distance of *Eurytemora affinis* females from freely swimming mysids (*Neomysis integer*) was 0.45 cm, which corresponds with the reaction distance of *E. affinis* observed in the present study (0.53 cm). This suggests that we can use pipette experiments to simulate mysid feeding current and to make comparisons between the escape capabilities of prey species. Based on our experiments, we suggest that, although *Acartia* spp. and *E. affinis* possessed similar sensory abilities (as characterised by their reaction distances to the pipette), *E. affinis* is a more difficult prey for *Praunus flexuosus* because of its stronger escape jump and better endurance during a long series of escapes. The difference between the vulnerabilities of copepods and *Pleopsis polyphemoides* can also be explained by the pipette experiments, which showed that small cladocerans (i.e. *Bosmina longispina maritima*) cannot resist the water flow. This agrees with the results of Szlauer (1965), Drenner et al. (1978) and Drenner & McComas (1980), who have shown that cladocerans have less developed escape reactions than copepods. The higher survival of *B. longispina maritima* compared to *P. polyphemoides*, on the other hand, may be partly explained by its morphological and behavioural defences. *Bosmina* spp. possess a carapace that can be closed to protect the vulnerable appendages and soft abdomen, which provides some protection against predation (Kerfoot 1978). *P. polyphemoides* does not have a similar bivalve morphology, which probably makes it more vulnerable to invertebrate predation.

Our results agree with another Baltic study, in which the feeding of *Mysis mixta* was studied in mesocosms. Mohammadian et al. (1997) found that *M. mixta* ingests prey in the following order of preference: *Pseudocalanus* juveniles  $\approx$  *Acartia* adults  $\geq$  *Bosmina*  $\approx$  *Acartia* juveniles  $>$  *Eurytemora* adults and juveniles.



These results, as well as ours, differ from North American lake studies, which suggest that *Mysis relicta* favours cladocerans over copepods (Lasenby & Langford 1973, Cooper & Goldman 1980, Bowers & Vanderploeg 1982, Grossnickle 1982, Ramcharan et al. 1985, Nero & Sprules 1986). This difference could be explained by assuming that the Baltic *B. longispina maritima* possesses more effective defences against predation than its freshwater relatives.

### Prey selection

When investigating prey 'selection' it is important to distinguish *true* selectivity from *apparent* selectivity. Apparent selectivity mainly reflects prey characteristics, such as escape behaviour and morphological defences, whereas true selection implies an active choice by the predator. True selectivity has been demonstrated in fish which can visually select prey according to prey size (Gardner 1981), colour contrast (Thetmeyer & Kils 1995) or swimming pattern (Zaret 1980). To show true (pre-attack) selectivity, the predator must be able to identify each prey prior to attack and 'memorise' the profitability of different prey types. It is therefore less likely that invertebrate predators, especially those with less developed vision, show true selection. Invertebrate predators may instead optimise their foraging by more mechanistic behavioural patterns, such as prey switching.

Our experiments confirmed that, although *Praunus flexuosus* in most situations feeds opportunistically, it may under certain food conditions show true prey selection. In the experiment where *Pleopsis polyphemoides* and *Acartia* spp. were offered together (at high prey concentration), *P. flexuosus* clearly suppressed its feeding rates on copepods, whereas predation on cladocerans remained unchanged. We suggest that this was due to mysids switching to suspension feeding on cladocerans while decreasing capture attempts on the more evasive copepods. This kind of behavioural switching is analogous to that observed in the copepods *Calanus pacificus* and *Acartia tonsa*, which switch from suspension feeding on diatoms to raptorial feeding on animal prey (copepod nauplii or ciliates) when the phytoplankton concentration decreases (Landry 1981, Kiørboe et al. 1996). In the case of mysids, the suspension feeding mode and the raptorial mode are probably mutually exclusive, because small cladocerans are not effectively collected without a strong feeding current, whereas the feeding current will provide a fair warning signal for the hydromechanically sensing copepods.

We may ask why *Praunus flexuosus* switched from raptorial feeding of copepods to suspension feeding of

cladocerans, and not vice versa. There are several possible explanations. First, suspension feeding on cladocerans may be energetically advantageous because the same water current that is used in swimming and respiration draws the prey to the feeding appendages. Creating a feeding current also increases encounter rates with the prey in suspension, which may be especially beneficial for littoral mysids like *Praunus* spp. that during daytime remain in the shadow of macroalgae. Also, small cladocerans are easier and faster to handle and ingest than copepods. For instance, an egg-carrying *Eurytemora* female was handled for ~2 min by *Neomysis integer* (Viitasalo et al. 1998), whereas *Bosmina* spp. can be swallowed whole (whole *Bosmina* spp. individuals have been found in the guts of *Mysis* spp.; M. Viherluoto pers. comm.).

When the mysids were provided 2 copepod prey species at the same time (*Acartia* spp. and *Eurytemora affinis*), prey switching did not occur. This is plausible because both copepod species need to be captured raptorially, and so a behavioural exclusion of the other prey type will not take place. On the other hand, in the presence of *E. affinis*, the clearance of *Acartia* spp. was significantly lower than found in the single prey experiments. It is possible that the large body and egg sac of *E. affinis* females, or the hydrodynamic disturbance the species produces, stimulated *Praunus flexuosus* to make frequent unsuccessful attacks on the evasive *E. affinis*. In accordance, Ramcharan et al. (1985) found that *Mysis relicta* most frequently attacked *Limnocalanus macrurus* and *Senecella calanoides* (which were the largest prey available), although they never captured *S. calanoides* and caught *L. macrurus* in 4% of the attempts only.

In summary, we suggest that the selectivity of *Praunus flexuosus* increases with increasing prey availability. At low prey concentrations, *P. flexuosus* feeds flexibly and opportunistically by using both suspension and raptorial feeding modes. The apparent 'selectivity' thus mainly reflects the escape capabilities and morphological defences of the different prey species. At high prey concentrations, in turn, *P. flexuosus* may show true prey selection by switching behaviourally to suspension feeding on cladocerans. If copepods are the only prey type available, the total ingestion depends on how frequently the mysids are stimulated to unsuccessfully attack the more evasive prey species.

### Implications for Baltic plankton communities

Our results show that all prey species are not equally profitable for *Praunus flexuosus*. Small cladocerans were preyed on more efficiently than copepods, and

*Acartia* spp. were easier to prey on than *Eurytemora affinis*. This implies that long-term changes in the proportions of these taxa may affect the food gain of *P. flexuosus*, and possibly also other Baltic mysid species. In this context we note that many crustacean zooplankton species respond to variations in Baltic hydrography. An increase in water temperature and stratification and lowering of salinity favour small cladocerans (*Bosmina longispina maritima* and *Pleopsis polyphemoides*), whereas a decrease in water stratification and an increase in water salinity favour neritic copepod species, such as *Pseudocalanus elongatus*, *Temora longicornis* and *Centropages hamatus* (Vuorinen & Ranta 1987, Lumberg & Ojaveer 1991, Viitasalo et al. 1995). Our experimental results therefore imply that a decrease in salinity might improve food conditions for Baltic mysids, due to the associated increase of easily preyed on cladocerans.

The matter is not simple, however. Mysids do not feed exclusively on zooplankton, and the hydrographical changes that favour cladocerans (increase in temperature and lowering of salinity), also tend to favour *Eurytemora affinis* and disfavour the neritic copepods. *E. affinis* was shown to be difficult prey for mysids, whereas *Pseudocalanus elongatus* and *Temora longicornis* are less evasive than *E. affinis* and *Acartia* spp. (Mohammadian et al. 1997, Viitasalo et al. 1998, present study, Viitasalo unpubl.). Therefore, we suggest that long-term changes in hydrography may have different effects on shallow water and open sea mysids. In shallower archipelago areas, a decline in salinity and increase in water temperature and stability would increase the biomass of the easily preyed on *Pleopsis polyphemoides* and intermediately profitable *Bosmina longispina maritima*, which would benefit the littoral mysids *Praunus* spp. and *Neomysis integer*. In the open sea, where *P. polyphemoides* is not as abundant as in coastal areas (e.g. Viitasalo 1992), similar hydrographical changes would favour *B. longispina maritima* and the evasive *E. affinis*, and disfavour the less evasive neritic copepods. This might lead to a decrease of zooplankton in the diet of the open sea mysids *Mysis mixta* and *M. relicta*.

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## LITERATURE CITED

- Bowers JA, Grossnickle NE (1978) The herbivorous habits of *Mysis relicta* in Lake Michigan. *Limnol Oceanogr* 23:767–776
- Bowers JA, Vanderploeg HA (1982) *In situ* predatory behavior of *Mysis relicta* in Lake Michigan. *Hydrobiologia* 93: 121–131
- Cooper SD, Goldman CR (1980) Opossum shrimp (*Mysis relicta*) predation on zooplankton. *Can J Fish Aquat Sci* 37: 909–919
- Drenner RW, McComas SR (1980) The roles of zooplankton escape ability and fish size selectivity in the selective feeding and impact of planktivorous fish. In: Kerfoot WC (ed) *Evolution and ecology of zooplankton communities*. University Press of New Hanover, New Hanover, p 587–593
- Drenner RW, Strickler JR, O'Brien WJ (1978) Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *J Fish Res Bd Can* 35:1370–1373
- Gardner MB (1981) Mechanisms of size selectivity by planktivorous fish: a test of hypotheses. *Ecology* 62:571–578
- Gerritsen J, Strickler JR (1977) Encounter probabilities and community structure in zooplankton: a mathematical model. *J Fish Res Bd Can* 34:73–82
- Greene CG (1986) Patterns of prey selection: implications of predator foraging tactics. *Am Nat* 128:824–839
- Grossnickle NE (1982) Feeding habits of *Mysis relicta*—an overview. *Hydrobiologia* 93:101–107
- Hamner WM, Carleton JH (1979) Copepod swarms: attributes and role in coral reef ecosystems. *Limnol Oceanogr* 24:1–14
- Hansson S, Larsson U, Johansson S (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J Plankton Res* 12: 1099–1116
- Holling CS (1959) The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can Entomol* 91:293–320
- Kerfoot WC (1978) Combat between predatory copepods and their prey: *Cyclops*, *Epischura*, and *Bosmina*. *Limnol Oceanogr* 23:1089–1102
- Kjørboe T, Saiz E, Viitasalo M (1996) Prey switching behaviour in the planktonic copepod *Acartia tonsa*. *Mar Ecol Prog Ser* 143:65–75
- Landry MR (1981) Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Mar Biol* 65:77–82
- Lasenby DC, Langford RR (1973) Feeding and assimilation of *Mysis relicta*. *Limnol Oceanogr* 18:280–285
- Lawton JH, Beddington J, Bonser R (1974) Switching in invertebrate predators. In: Usher MB, Williamson MH (eds) *Ecological stability*. Chapman and Hall, London, p 141–158
- Leong RJH, O'Connell CP (1969) A laboratory study of particulate and filter feeding of the northern anchovy (*Engraulis mordax*). *J Fish Res Bd Can* 26:557–582
- Lumberg A, Ojaveer E (1991) On the environment and zooplankton dynamics in the Gulf of Finland in 1961–1990. *Proc Estonian Acad Sci Ecol* 1:131–140
- Mauchline J (1980) The biology of mysids and euphausiids. *Adv Mar Biol* 18:1–677
- Mohammadian MA, Hansson S, De Stasio BT (1997) Are marine planktonic invertebrates food limited? The functional response of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Mar Ecol Prog Ser* 150:113–119
- Murdoch WW (1969) Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol Monogr* 39:335–354

- Nero RW, Sprules WG (1986) Predation by three glacial opportunists on natural zooplankton communities. *Can J Zool* 64:57–64
- Nordström H (1997) Rantavyöhykkeen halkoisjalkaäyriäisten (Mysidacea) ravinnonkäyttö Itämeressä. MSc thesis, University of Helsinki, p 1–57
- Pastorok RA (1981) Prey vulnerability and size selection by *Chaoborus* larvae. *Ecology* 62:1311–1324
- Ramcharan CW, Sprules WG, Nero RW (1985) Notes on the tactile feeding behaviour of *Mysis relicta* Lovén (Malacostraca: Mysidacea). *Verh Int Verein Limnol* 22:3215–3219
- Rudstam LG, Hansson S (1990) On the ecology of *Mysis mixta* (Crustacea, Mysidacea) in a coastal area of the northern Baltic proper. *Ann Zool Fenn* 27:259–263
- Rudstam LG, Hansson S, Larsson U (1986) Abundance, species composition and production of mysid shrimps in a coastal area of the northern Baltic proper. *Ophelia Suppl* 4:225–238
- Rudstam LG, Danielsson K, Hansson S, Johansson S (1989) Diel vertical migration and feeding patterns of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Mar Biol* 101:43–52
- Rudstam LG, Hansson S, Johansson S, Larsson U (1992) Dynamics of planktivory in a coastal area of the northern Baltic Sea. *Mar Ecol Prog Ser* 80:159–173
- Salemaa H, Hietalahti V (1993) *Hemimysis anomala* G.O. Sars (Crustacea: Mysidacea)—immigration of a Pontocaspian mysid into the Baltic Sea. *Ann Zool Fenn* 30:271–276
- Salemaa H, Tyystjärvi-Muuronen K, Aro E (1986) Life histories, distribution and abundance of *Mysis mixta* and *Mysis relicta* in the northern Baltic Sea. *Ophelia Suppl* 4:239–247
- Salemaa H, Vuorinen I, Välipakka P (1990) The distribution and abundance of *Mysis* populations in the Baltic Sea. *Ann Zool Fenn* 27:253–257
- Salonen K (1979) A versatile method for rapid and accurate determination of carbon by high temperature combustion. *Limnol Oceanogr* 24:177–183
- Segerstråle SG (1962) The immigration and prehistory of the glacial relicts of Eurasia and North America. A survey and discussion of modern views. *Int Rev Ges Hydrobiol* 47: 1–25
- Siegfried CA, Kopache ME (1980) Feeding of *Neomysis mercedis* (Holmes). *Biol Bull* 159:193–205
- Szlauer L (1965) The refuge ability of plancton animals before models of plancton-eating animals. *Pol Arch Hydrobiol* 13: 89–95
- Thetmeyer H, Kils U (1995) To see and not to be seen: the visibility of predator and prey with respect to feeding behaviour. *Mar Ecol Prog Ser* 126:1–8
- Ueda H, Kuwahara A, Tanaka M, Azeta M (1983) Underwater observations on copepod swarms in temperate and sub-tropical waters. *Mar Ecol Prog Ser* 11:165–171
- Uitto A, Kaitala S, Kuosa H, Pajuniemi R (1995) Effect of nutrient addition and predation of mysid shrimp (*Neomysis integer*) on a plankton community in a short-term enclosure experiment in the northern Baltic. *Aqua Fenn* 25: 23–31
- Väinölä R (1992) evolutionary genetics of marine *Mysis* spp. (Crustacea: Mysidacea). *Mar Biol* 114:539–550
- Viitasalo M (1992) Mesozooplankton of the Gulf of Finland and northern Baltic Proper—a review of monitoring data. *Ophelia* 35:147–168
- Viitasalo M, Vuorinen I, Saesmaa S (1995) Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *J Plankton Res* 17: 1857–1878
- Viitasalo M, Kiørboe T, Flinkman J, Pedersen LW, Visser AW (1998) Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities. *Mar Ecol Prog Ser* (in press)
- Vuorinen I, Ranta E (1987) Dynamics of marine mesozooplankton at Seili, Northern Baltic Sea, in 1967–1975. *Ophelia* 28:31–48
- Zaret TM (1980) The effect of prey motion on planktivore choice. In: Kerfoot WC (ed) *Evolution and ecology of zooplankton communities*. University Press of New Hanover, New Hanover, p 594–603

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