Are marine planktonic invertebrates food limited? The functional response of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea

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ABSTRACT· The mysid shrimp *Mysis mixta* is an important zooplanktivore in the Baltic Sea and has been suggested to contribute in structuring the zooplankton community. To describe this predation quantitatively, its functional response was determined in laboratory feeding experiments using as prey a sample of the natural zooplankton assemblage from the Baltic Sea. Experiments were made in darkness in 27 l black plastic bags, incubated 24 h at 13°C and with prey concentrations between 7 and 300 ind. l⁻¹ *M. mixta* was a selective predator, consuming prey in the following preference order: *Pseudocalanus* juveniles ≈ *Acartia* adults ≥ *Bosmina* ≈ *Acartia* juveniles > *Eurytemora* adults ≈ *Eurytemora* juveniles. A Type II functional response model was fitted to consumption data, although the saturation level (i.e. maximum consumption rate) was not reached in the experiments. Combining a bioenergetics model, the individual *in situ* growth rate of *M. mixta* and our functional response model indicates that ambient abundances of zooplankton (10 to 20 ind. l⁻¹ in August, which is the annual maximum) are too low to maintain observed growth rates without taking prey patchiness into account. To explain the observed growth of *M. mixta* in the Baltic Sea, zooplankton patches with densities 3.5 to 6 times that of average ambient densities are necessary. The consumption rates also indicate that even when the zooplankton abundance is at its annual maximum, Baltic Sea *M. mixta* is food limited.

KEY WORDS: *Mysis mixta* · Functional response · Zooplankton · Prey selectivity · Baltic Sea

INTRODUCTION

Much ecological research is aimed at improving our understanding of the effects of trophic interactions in structuring natural communities and ecosystems. This interest in trophic interactions has a long history and has been an important basis of studies for many decades (e.g. Lindeman 1942, Hairston et al. 1960, Hairston & Hairston 1993). In recent years, concepts such as 'top-down', 'bottom-up' and 'cascading trophic' interactions (Carpenter et al. 1985) have revitalized this research and made it a central theme in

ecology (e.g. see the 'Special Feature' section in the June 1992 issue of *Ecology*).

To understand food web structure and dynamics, knowledge of limiting factors for different organisms is crucial. If food consumption by a species is limited by factors other than food availability, the consumer will be unable to respond to changes in food abundance. Under such circumstances, the consumer will have no direct effect on food web dynamics; marine zooplankton may be one example of this. Huntley & Boyd (1984) and Huntley & Lopez (1992) suggest, based on literature reviews, that marine zooplankton growth (mainly for copepods but also for other groups such as krill) is generally limited by temperature and not food. This perspective has, however, been questioned by Kleppel

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et al. (1996, see also references therein and the response by Huntley 1996), and in an earlier article (Hansson et al. 1990b) we reported on field data indicating food limited growth of the mysid shrimp *Mysis mixta* Lilljeborg in the Baltic Sea.

One approach for evaluating whether or not a consumer can be expected to be influenced by food availability is to determine its functional response (Holling 1959). If the *in situ* food abundance is so high that the consumer has likely reached its consumption plateau (maximum food consumption), it is no longer food limited. In this paper, results from functional response experiments with *Mysis mixta* and its natural zooplankton prey are reported. These experiments support our earlier finding (Hansson et al. 1990b) that *M. mixta* in the Baltic Sea is food limited, and the results also imply that the mysid is dependent on patchily distributed prey.

MATERIALS AND METHODS

This study was conducted in the northern Baltic proper (58° 49' N, 17° 35' E), where the pelagic community is comparatively simple (Elmgren 1984) and hence well suited for analyses of food web interactions. There are only 3 dominant zooplanktivores in this area: herring (*Clupea harengus* L.), sprat [*Sprattus sprattus* (L.)] and a mysid shrimp (*Mysis mixta* Lilljeborg) (Hansson et al. 1990a, Rudstam et al. 1992, Arrhenius & Hansson 1993). The 4 experiments reported on in this article were conducted during the period August 7 to 23, 1993, which is the time of year when the Baltic Sea zooplankton biomass, and consequently mysid prey availability, peaks in this coastal area (Johansson et al. 1993) as well as in the Baltic proper in general (Hernroth & Ackefors 1979).

Mysid and zooplankton collection. All animals were collected the night before the experiments were started, using a plankton net (mesh size 90 µm) which was pulled below the thermocline and between 17 and 32 m (bottom depth of 25 to 35 m). Within 3 h after being captured, the mysids were placed in sand-filtered seawater (13°C) without food for 12 to 16 h before the experiments. Only mysids 15 to 17 mm in length and which appeared healthy at the end of this period were used.

Within 2 h of collection, the zooplankton to be used as prey were transferred to a large aquarium containing approximately 700 l of 12°C sea water. After 12 h, the surface of the aquarium was skimmed with a 90 µm mesh sieve to remove cladocerans trapped by surface tension, while the bottom of the aquarium was siphoned to remove dead zooplankton. By diluting this 'zooplankton concentrate' with sand-filtered sea
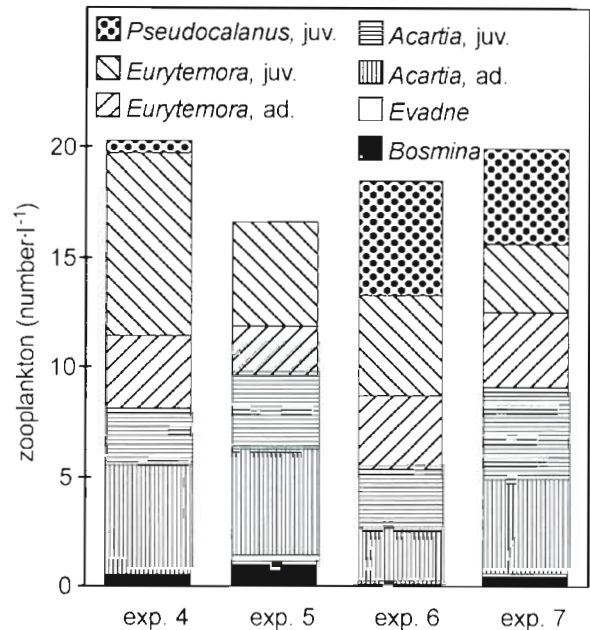

Fig. 1 Zooplankton density and species composition in the start bags (1 × S in Table 1). *Evadne* and *Bosmina* are cladocerans and the remaining genera copepods

water, we created a zooplankton density gradient in each experiment. This density gradient ranged from ca $\frac{1}{3}$ to 15 times the ambient zooplankton density, which is ~20 ind. l[-1] at the depths in which mysids occur during July and August (Rudstam et al. 1989, Hansson et al. 1990a, Johansson et al. 1993). The zooplankton were strongly dominated by copepods (Fig. 1), which is normal for this area (Johansson et al. 1993). Hardly any naupliar stages of copepods occurred in the samples, as these are mainly above the thermocline (Hansson et al. 1990a).

Experimental procedures. The experiments were conducted in suspended black, non-transparent polyethylene bags. To each bag, we added 26.6 l of the sand-filtered sea water with different densities of zooplankton (see above). Ten mysids were also added to all bags, except for 'start bags' and 'control bags' (see below). The air was removed from each bag, which was then closed and incubated for 24 h (3 h for start bags) at 13°C, which is in the upper range of temperatures encountered by *Mysis mixta* during the summer months in this part of the Baltic (Rudstam et al. 1989, Hansson et al. 1990a). The 24 h incubation period was used to eliminate possible effects of diel variation in feeding (e.g. Cooper & Goldman 1982). Preliminary experiments, as well as later studies (Gorokhova & Hansson in press), indicate that the feeding rate of *M. mixta* is at least as high in darkness as in light, and with the relatively large volume used, the container

size probably had no or only marginal effects on feeding rates. A summary of the experiments is given in Table 1.

The start bags were used to estimate starting densities of zooplankton, and these bags were sampled (as described below) as soon as the incubation of the other bags had started. The control bags were used to determine the mortality of zooplankton in the absence of mysids, and they were treated in the same way as the bags with mysids.

After 24 h of incubation, each bag was cut open, rinsed and the water filtered through a 90 µm mesh. Mysids were classified as alive or dead and their dry weight was determined by drying at 60°C to a constant weight. The carbon content of *Mysis mixta* was assumed to be 40% of the dry weight (Mauchline 1980). The dominant zooplankton were counted and classified into groups (Table 2).

Calculations. The background mortality rate of zooplankton was estimated from differences between start and control bags. This background mortality was on average 7%. In bags with mysids, the decrease in zooplankton was on average 37%, so the dominant cause of mortality in these bags was predation. It is possible, however, that the mysids also fed on already dead or dying zooplankton, which is included in the background mortality. We estimated the mysid food consumption rates from the average zooplankton density of start and control bags. A pilot experiment without mysids and with 4 zooplankton densities ($\frac{1}{3}\times$, $1\times$, $3\times$ and $9\times$ ambient zooplankton density) and 5 replicates each, did not indicate any density-dependent background mortality.

To standardize consumption rates, taking into account both size differences among the zooplankton and variation in mysid size, both consumption and zooplankton densities are given in carbon weight instead of number (individual carbon biomasses of zooplankton are given in Table 2). For each bag containing mysids, the daily weight-specific consumption (g C

Table 1. Experimental design in studies of the functional response of *Mysis mixta* from the Baltic Sea. Experiments were conducted in black plastic bags with a volume of 26.6 l, with 10 mysids added to each bag except for the start and control bags to which only zooplankton was added. Expts 1 to 3 were pilot studies on effects of incubation container size, light conditions during the experiment and possible density dependence in the background mortality of zooplankton. Mysid weights given are average individual dry weights (DW). Zooplankton densities are given as no. l^{-1}, with standard deviations given for start and control bags. The variation was much higher among bags incubated with mysids, and this variation is reported as standard errors in Fig. 2. 'Prey decline' shows the decrease in zooplankton biomass during incubation. Abbreviations in the 'Density treatment' column are: $A\times$ = density treatment factor, approximately A times the ambient zooplankton abundance; C = control bag, incubated 24 h without mysids; S = start bag, treated like the control bags, but incubated for only 3 h; M = incubated 24 h with 10 mysids

Expt	Date and mysid DW	Density treatment	No. of replicates	Zoopl. l^{-1}, mean	Prey decline (%), mean	Incubation time (h)
4	Aug 7, 6.0 mg	$1 \times S$	4	21.1 ± 0.8	–	3
		$1 \times C$	4	19.5 ± 0.8	11	24
		$\frac{1}{3} \times M$	3	7.0	45	24
		$1 \times M$	5	21.1	41	24
		$3 \times M$	5	63.3	34	24
		$9 \times M$	5	190	26	24
5	Aug 12, 6.8 mg	$1 \times S$	5	15.7 ± 2.7	–	3
		$1 \times C$	5	16.9 ± 1.3	3	24
		$\frac{1}{3} \times M$	4	5.2	33	24
		$1 \times M$	5	15.7	37	24
		$3 \times M$	5	47.1	34	24
		$9 \times M$	5	141	21	24
6	Aug 20, 7.4 mg	$1 \times S$	3	19.2 ± 0.7	–	3
		$1 \times C$	4	18.6 ± 1.7	4	24
		$1 \times M$	3	19.2	58	24
		$3 \times M$	4	57.7	56	24
		$5 \times M$	4	96.1	46	24
		$9 \times M$	4	173	40	24
		$15 \times M$	4	288	30	24
7	Aug 23, 7.2 mg	$1 \times S$	4	22.5 ± 2.1	–	3
		$1 \times C$	4	19.8 ± 2.6	11	24
		$1 \times M$	4	22.5	44	24
		$3 \times M$	4	67.5	36	24
		$5 \times M$	4	112	32	24
		$9 \times M$	4	202	34	24
		$15 \times M$	4	337	29	24

Table 2. Predominant groups of zooplankton, which together constituted >98% of the number of potential prey in the experiments. Individual biomasses, in µg C ind.$^{-1}$, are from Kankaala (1987)

Species and age stage	Biomass
Cladocerans	
Bosmina longispina maritima (P. E. Müller), adult	0.80
B. l. maritima, juvenile	0.61
Evadne normandii Lovén	1.43
Podon spp.	0.42
Copepods	
Acartia bifilosa Giesbrecht and	
A. longiremis Lilljeborg, adult female	2.81
A. bifilosa and *A. longiremis*, adult male	1.88
A. bifilosa and *A. longiremis*, copepodite IV–V	2.13
A. bifilosa and *A. longiremis*, copepodite I–III	0.68
Eurytemora affinis (Poppe), adult female	2.81
E. affinis, adult male	1.88
E. affinis, copepodite IV–V	2.13
E. affinis, copepodite I–III	0.68
Pseudocalanus minutus elongatus (Boeck), adult	4.69
P. m. elongatus, juvenile	1.43

g^{-1} C d^{-1}) was estimated using the formula below. Consumption was estimated for both total zooplankton and for each taxonomic group.

$$CR_{i,n} = \frac{A \times Z_{control,i} - Z_{mysid,i,n}}{\dfrac{M_{start,i,n} + M_{stop,i,n}}{2} \times W_{i,n}} \times 26.6$$

where $CR_{i,n}$ = the weight-specific consumption rate of mysids in bag n in experiment i (g C g^{-1} C d^{-1}); A = the density treatment factor ($\frac{1}{3}$ to 15, see Table 1); $Z_{control,i}$ = the average zooplankton density (g C l^{-1}) in the start and control bags (1×S and 1×C) in experiment i; $Z_{mysid,i,n}$ = zooplankton density (g C l^{-1}) at the end of the incubation in the *Mysis*-containing bag n in experiment i; $M_{start,i,n}$ = number of mysids in bag n at the start of experiment i (always 10); $M_{stop,i,n}$ = number of mysids in bag n, experiment i, at the end of the incubation (usually 10, only 1% of the mysids died during the experiments); $W_{i,n}$ = average weight (g C) of a mysid in bag n in experiment i; 26.6 = the bag volume, as zooplankton densities are given per litre.

As the zooplankton density decreased during the incubation period, consumption rates were correlated to the estimated density in the middle of the incubation period. Assuming a constant instantaneous mortality rate, this abundance was calculated as:

$$Z_{mean,i,n} = e^{\left(\frac{\ln(A \times Z_{start,i}) + \ln(Z_{mysid,i,n})}{2} \right)}$$

where $Z_{start,i}$ is the average zooplankton density in the start bags in experiment i and the other parameters are

as defined above. If the mysids have a functional response of Type II (Holling 1959), as assumed below, their efficiency will increase as the prey abundance decreases and the equation above will underestimate average prey abundance. However, simulation analyses (authors' unpubl.) showed that with the relatively linear relationships that we found between prey abundance and consumption, these underestimations were at most a few percentage points and thus they will not significantly influence our conclusions.

Using the nonlinear regression module in SPSS for Windows (release 7.0), functional response models of Type II (Holling 1959, Begon et al. 1990) were fitted to the consumption rates (CR) at different zooplankton densities (Z_{mean}):

$$CR = \frac{k_1 \times Z_{mean}}{1 + k_2 \times k_1 \times Z_{mean}}$$

where the constants k_1 and k_2 measure the prey capture rate and prey handling time respectively. When estimating prey capture rates for the different prey categories a linear model ($CR = k_1 \times Z_{mean} + k$, where k is the intercept; linear regression module in SPSS) was applied, as consumption data at this taxonomic level were generally so scattered that no tendencies of decreased consumption rates with increased prey densities could be seen. Instead of using indirect estimates of relative prey 'preferences', such as the Ivlev or Chesson indices (Ivlev 1961, Chesson 1983), we use the prey capture rates (k_1) of different prey to describe the 'preferences' of the mysid.

RESULTS AND DISCUSSION

In all experiments, the food consumption of *Mysis mixta* increased significantly with increased prey density (Fig. 2). The differences among the 4 experiments were small and the 95% confidence intervals for the functional response constants (k_1 and k_2) overlapped among the experiments. Though we manipulated zooplankton densities over a large range, up to 15 × ambient zooplankton abundances, we were unable to detect food saturation levels. As we never reached saturation levels, the estimated values of k_1, k_2 and maximum food consumptions (Fig. 2) must be interpreted with caution. The range of estimated maximum consumption rates (0.19 to 0.41 g C g^{-1} C d^{-1}, for mysids of 6 to 7 mg dry wt, temperature 13°C) is, however, comparable to estimates presented in other studies. Toda et al. (1987) found that 6 to 7 mg dry wt individuals of *Neomysis intermedia*, at temperatures between 10 and 15°C, had maximum consumption rates of 0.1 to 0.3 g C g^{-1} C d^{-1}. For ~5 mg dry wt *Neomysis mercedis* at 10°C,

Chigbu & Sibley (1994) reported maximum consumption rates of 0.7 to 1.6 g $C g^{-1} C d^{-1}$ (as stressed by the authors these values might be overestimates as they are extrapolated from 1 to 3 h experiments; cf. Grossnickle 1978, Gorokhova & Hansson in press).

The maximum food consumption of an animal is curtailed by physical limitations: prey handling time or physiological constraints such as gut passage time. The average individual prey handling time for the calanoid copepod *Diaptomus minutus* by *Mysis relicta* was 18.4 s (Ramcharan et al. 1985). *Neomysis mercedis*, slightly smaller (length 13 mm) than our *M. mixta* (15 to 17 mm), handled cladocerans (*Daphnia*) twice the size of our average zooplankton in 1.4 min (Chigbu & Sibley 1994). As our calanoid copepods are larger than *D. minutus* but smaller than *Daphnia*, a handling time of 60 s per individual prey seems reasonable. From this, a maximum consumption range of 1440 calanoids mysid^{-1} d^{-1} or >1 g C g^{-1} C d^{-1} can be expected, which exceeds our range of estimates of the maximum daily food consumption. Hence, *M. mixta* most likely is not limited by handling time but by other processes.

The functional response relationships described above, together with *in situ* growth data, can be used to evaluate the mysid's natural feeding conditions. From a review on mysid data from the present study area (Rudstam & Hansson 1990), specific daily growth rate in August can be estimated at 0.02, and a 7 mg dry wt *Mysis mixta* would thus grow 0.14 mg in 1 d. In his bioenergetics analyses for *M. mixta* in this area, Rudstam (1989) found a growth conversion efficiency of 26% based on energy. From this, and assuming that the carbon to energy ratio is roughly the same in mysids as in its main food (crustacean zooplankton), the *in situ* food consumption can be estimated at 0.08 g C g^{-1} C d^{-1}. This consumption rate is lower than the maximum consumption rates found in our experiments, supporting our earlier conclusion based on *in situ* growth (Hansson et al. 1990b), that Baltic *M. mixta* is food limited.

Based on the functional responses shown in Fig. 2, zooplankton densities needed to meet this *in situ* consumption (0.08 g C g^{-1} C d^{-1}) can be estimated as 140 to 240 µg C l^{-1}, which is roughly 3.5 to 6 times the ambient zooplankton density (40 µg C l^{-1}). Errors in the bioenergetics model cannot explain this discrepancy, as consumptions predicted from our data and assumed
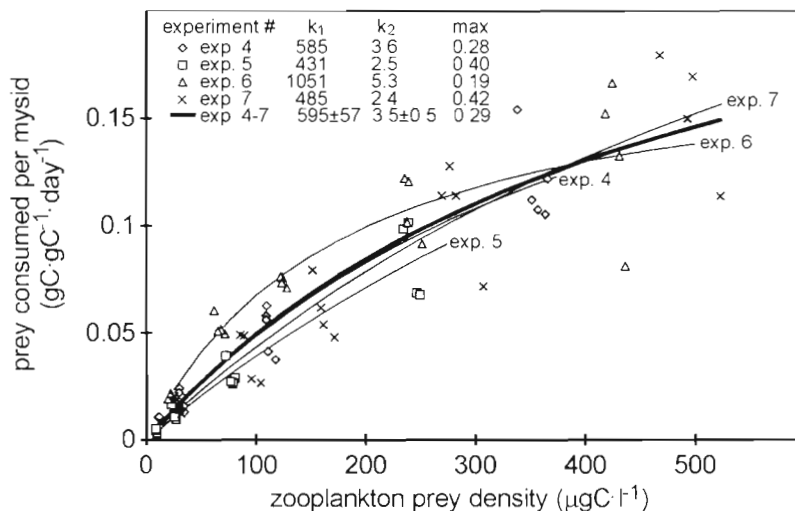

Fig. 2. Results of feeding experiments with *Mysis mixta* and its natural zooplankton prey. The curves show the functional responses (Type II) estimated from each experiment separately and the 4 experiments combined (bold line). The constants in the functional responses (±SE for the combined dataset) and the maximum specific food consumption expressed in carbon ('max.', g g^{-1} d^{-1}) are also given

ambient zooplankton densities would be 0.01 to 0.03 g C g^{-1} C d^{-1} and would result in growth efficiencies over 100%. Another possible explanation is errors in the functional response. As it is hard to determine a functional response without interfering in some way with the mysids or their prey, such errors are difficult to evaluate. A likely explanation to the discrepancy is, however, that zooplankton have a small-scale patchy distribution which is exploited by the mysids and allows them to have a higher food consumption rate than expected from the average zooplankton abundance. The importance of this aspect of food patchiness has previously been discussed and described for various organisms, from plankton to marine mammals (e.g. Morris 1987, Rose & Leggett 1990, Brandt et al. 1992, Noda et al. 1992, Folt et al. 1993, Goyke & Brandt 1993, Saiz et al. 1993, Tiselius et al. 1993, Boyd 1996). Another possibility is that *Mysis mixta*, more than previously thought, uses alternative food sources such as phytoplankton, rotifers, and nanoplankton which are difficult to detect in the stomachs. This explanation is supported by nitrogen isotope analyses of mysids and their zooplankton prey (Hansson et al. in press).

There was a significant variation in capture rates (k_1) for the different prey categories (Kruskal-Wallis test, $\chi^2 = 15.5$, df = 5, p < 0.01; estimated with SPSS for Windows release 7.0). Pairwise tests between prey group had, however, low power due to few observations per group. In general, *Pseudocalanus* juveniles and *Acartia* adults were consistently 'preferred' prey (Fig. 3). *Bosmina* and juveniles of *Acartia* also had relatively
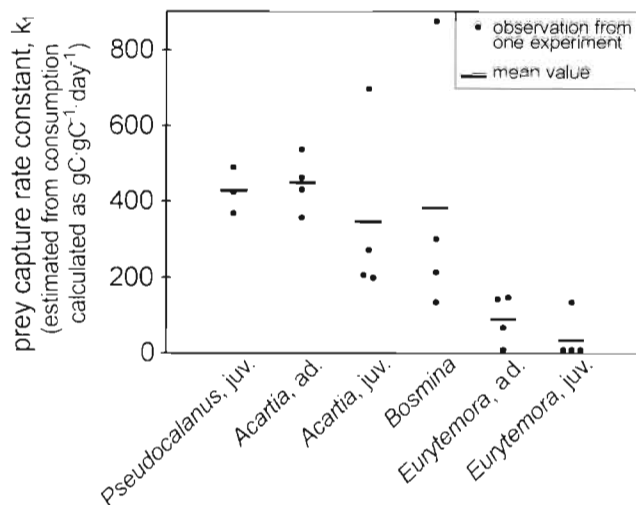
Fig. 3. Prey 'preferences' of *Mysis mixta* for different prey groups, expressed as prey capture rate constants (k_1) estimated from the relationship $CR = k_1 \times Z_{mean} + k$, where CR is the consumption rate, Z_{mean} is the prey abundance and k_1 and k are constants

high average k_1 values, but the variation among experiments was considerable. Consistently low capture rates were shown for both adults and juveniles of *Eurytemora* (both groups had statistically significantly lower k_1 values than *Pseudocalanus* and *Acartia*: Mann-Whitney test, $U = 0$, $p < 0.05$; estimated with SPSS for Windows release 7.0). This order of 'preferences' was the same, whether based on biomass capture rates (g C g^{-1} C d^{-1}) or number of prey consumed per mysid. These preferences differ from field data from this study area according to which *Bosmina* was the highest ranked prey, and *Eurytemora* more preferred than *Acartia* (Rudstam et al. 1989, 1992, based on analyses of simultaneously sampled zooplankton abundances and mysid stomach content; *Pseudocalanus* was not included in these studies as it was very uncommon in the samples). One possible explanation for the disagreement in order between *Acartia* and *Eurytemora* is that mysids *in situ* may forage in patches of zooplankton and that the zooplankton species composition in such patches are poorly represented by zooplankton samples integrating large volumes of water. In the stomachs analyzed by Rudstam et al. (1989, 1992) there was a large proportion of unidentifiable material, and if *Acartia* is more easily digested than *Eurytemora*, this could also have skewed these earlier estimates of preferences.

The prey selectivity of *Mysis relicta* has been studied repeatedly (Cooper & Goldman 1980, Bowers & Vanderploeg 1982, Grossnickle 1982, Ramcharan et al. 1985). In general, it has been reported that 'selected' prey often are small and slow or have less effective predator escape responses, and the order of prey selectivity is generally cladocerans > copepod nauplii and copepodites > adult cyclopoid and calanoid copepods. Our results disagree with these findings for *M. relicta*, as *M. mixta* preferred large copepods (*Pseudocalanus* juveniles and adult *Acartia*) over the cladocerans, and large copepods over small copepods.

In conclusion, we have shown that *Mysis mixta* in the Baltic Sea is food limited even during the annual late-summer peak in zooplankton abundance. This supports our earlier finding (Hansson et al. 1990b), which was based on the correlation between *in situ* growth rates and zooplankton abundances. Furthermore our study suggests that *M. mixta* is able to exploit patches of zooplankton where the abundances are considerably higher than indicated by traditional zooplankton samples. *M. mixta* is a selective predator with the following order of prey preference: *Pseudocalanus* juveniles ≈ *Acartia* adults ≥ *Bosmina* ≈ *Acartia* juveniles > *Eurytemora* adults ≈ *Eurytemora* juveniles.

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