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Temporal variability in functional responses and prey selectivity of the pelagic mysid, *Mysis mixta,* in natural prey assemblages

Abstract Predation rates and prey selection of the pelagic mysid shrimp, *Mysis mixta*, were studied experimentally in the northern Baltic Sea in 1998 during their most intensive growth period, from June to October. Functional responses during 5 months were determined by providing the mysids with a natural zooplankton assemblage, diluted to several different concentrations. The results show that ingestion rate increased, along with mysid growth, from early summer to autumn and that saturation level was reached between 400 and 500 μg C l^{-1}. Ingestion rates increased with increasing prey concentration, and sigmoidal curves explained mostly the variation in ingestion rates (explanatory levels of 86–97%). Prey selection was evident in June, July and August, though weaker during the latter 2 months. Selection differed between the studied months but, generally, copepods were more positively selected than cladocerans. Rotifers were the main prey during June and July, when mysids were small, while larger mysids fed on copepods and cladocerans. Of the copepods, *Eurytemora affinis* was a truly selected species. This study shows that mysids feed on many zooplankton taxa and that they undergo ontogenetic diet shifts.

Introduction

Selective predation by invertebrate predators can influence zooplankton communities by controlling popula-

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tion sizes (Murtaugh 1981; Nero and Sprules 1986; Branstrator 1995; Spencer et al. 1999) and by affecting behavioural patterns in prey, such as vertical migration (Pastorok 1981; Rudstam et al. 1989). On the other hand, changes in prey densities also affect predators' consumption rates, as described by Solomon (1949) and Holling (1959). Prey preference and prey abundance together, influence the feeding rates and success of predators.

Mysid shrimps are common planktivores in the Baltic, as well as in other marine, brackish water and limnetic ecosystems. They feed on phytoplankton, detritus and small zooplankters by creating a suspension-feeding current and can also prey on actively moving zooplankters like copepods, by raptorial feeding (Mauchline 1980). Mysids may be able to choose the most appropriate way of feeding in varying circumstances, by switching between suspension feeding and raptorial feeding (Viitasalo and Rautio 1998). The diet of mysids usually reflects the availability of different food items, but consistent patterns of prey preference have also been detected (Rudstam et al. 1992). Fulton (1982) showed that, in an estuary in North Carolina, the effect of mysid predation upon species composition appeared to depend on the relationship between prey selection and the dominant copepod species in the community. If the preferred copepod species was present, mysid predation tended to reduce its dominance and to increase species diversity in the estuary. In the Baltic Sea, mysid predation is considered to be an important factor affecting zooplankton communities (Rudstam et al. 1989; Rudstam and Hansson 1990; Rudstam et al. 1992); however we still lack a comprehensive picture of prey selection and feeding rates of mysids, especially in regard to the seasonal change.

Four factors influence the prey selection of mysids: prey availability, predator-prey encounter frequency, the vigour of prey escape response and the mysid's capture and handling ability (Cooper and Goldman 1980; Ramcharan et al. 1985). Nero and Sprules (1986) showed that mysids prefer prey which move slowly and

are therefore easy to capture. For the same reason, larger mysids, with increasing prey capture and handling abilities, select larger prey species than do smaller mysids. Somewhat in contrast to this, Mohammadian et al. (1997) found that, in the northern Baltic proper, *M. mixta* preferred copepods to cladocerans. However, there were no large changes in the prey assemblages in their experiments and therefore prey switching could not be studied.

Usually, prey-selection experiments are done using just a few prey species (see, for example, Lasenby and Fürst 1981; Folt et al. 1982; Fulton 1982; Ramcharan et al. 1985; Viitasalo and Rautio 1998). The functional responses in such experiments indicate either stabilizing or destabilizing effects of predators on prey populations (Holling 1959). We have chosen another perspective: to study prey selection by *M. mixta*, using natural prey assemblages, where many factors may affect the selection of different prey species. The null hypothesis is that there are easy and difficult prey for mysids and that neither the total concentration nor the existence of alternative prey affects this preference. Furthermore, we studied the functional responses by changing the offered zooplankton concentration of the natural zooplankton assemblages. The experiments were performed during summer and autumn, so we also incorporated the effects of seasonal changes in the zooplankton assemblage and mysid growth in the experiments. Functional responses for the natural zooplankton community indicate the overall feeding patterns of the predators studied, but the influence on individual prey species cannot be elucidated.

Materials and methods

Mysid and zooplankton collection

Mysids and zooplankton were collected in an open-sea area (depth 65–80 m), south of the Hanko Peninsula, at the entrance to the Gulf of Finland, from June to October 1998. Mysids were collected with a large plankton net, with a mesh size of 0.5 mm, a diameter of 0.8 m and a length of 3 m, which was lowered to near the bottom and then lifted slowly to the surface. The sampling was done at night, during darkness. Zooplankton was collected with several hauls of a zooplankton net (100-μm mesh size) at the same time and from the same place as the mysid samples. Mysids and zooplankton were placed in insulated containers, with sea water from below the thermocline. Mysids and zooplankton were transported within an hour to a cool room (13 °C), with a 16-h:8-h light:dark cycle. Mysids were gently transferred into 0.2-μm-filtered sea water using a sieve and a pipette. The mysid species were identified and *M. mixta* were kept under aeration in filtered sea water without food for about 24 h before the experiments.

Predation experiments

The experiments were performed at the beginning of each month from June to October. The experiments were conducted in 1.18-l glass bottles, with one mysid in each. The zooplankton used in the experiments was a natural assemblage (individual size > 100 μm), with all the species normally present at that time in the sea. To prepare the experimental concentrations, we counted the zooplankton density in the insulated container (individuals per litre) and diluted it to represent from 0.1- to 15-fold densities of the natural concentration. This "natural" (×1) concentration was fixed at 20 copepods l^{-1}, which is a normal concentration in the study area during the summer (Viitasalo et al. 1995). When rotifers were absent from the zooplankton community, the smallest concentration was × 0.5 and the largest concentration was × 15 (i.e. 300 copepods). When rotifers were present, smaller concentrations (×0.1 and ×0.25) were also included, in order to determine the exact numbers of rotifers. We made three replicates from denser concentrations (×5x–×15) and four to six replicates from sparse concentrations. The carbon content of the zooplankton was measured with a stable isotope analyser (RoboPrepTracerMass ANCA-MS), to obtain accurate information on the amount of carbon ingested by mysids during different seasons.

At the beginning of each experiment, filtered sea water (0.2 μm) was placed in the bottles before adding the zooplankton. The water in the container with the zooplankton was carefully stirred and exact volumes of water (and plankton) were added to the bottles. The mysid was added to the bottle using a sieve, the bottles were filled and sealed with a plastic film to prevent air bubbles and placed on a plankton wheel and rotated at 0.5 rpm for 12 h. The experiments were always started in the evening, ensuring darkness throughout most of the experiment (8 h). Mysids and zooplankters that remained in the bottles after the experiment were preserved using acid Lugol's solution. Mysids were measured to the nearest millimetre and the state of sexual maturity was determined. Mysids of approximately the same size, sex and state of maturity were selected for the experiments. Zooplankters were counted using a binocular microscope and classified into groups.

The carbon contents of the zooplankters were partly analysed and partly taken from the literature (Table 1). Three different types of functional responses (Holling 1959) were fitted to the ingestion data using regression modules in the SigmaPlot 4.0 graphics programme for Windows.

Table 1 Carbon content (μg ind^{-1}) of zooplankton groups present in the community in the study area from June to October 1998

Species	Carbon content	Source of information
Acartia spp. adult	2.99	This study
Acartia spp. copepodite	1.83	This study
Eurytemora affinis adult	2.63	This study
E. affinis copepodite	1.85	This study
Temora longicornis adult	2.59	This study
T. longicornis copepodite	1.92	This study
Pseudocalanus elongatus copepodite	1.43	This study
Evadne nordmanni	1.43	Kankaala 1987
Pleopsis polyphemoides	0.86	This study
Bosmina longispina maritima	0.80	Kankaala 1987
Synchaeta spp.	0.24	This study

Selectivity index

We calculated the chi-square selectivity index C using Yate's correction for continuity (Pearre 1982): $C = \pm \left[(|a_d b_e - b_d a_e| - n/2)^2 / abde \right]^{1/2}$, where

	Species		
	A	Others	Total
Diet	a_d	b_d	$a_d + b_d = d$
Environment	a_e	b_e	$a_e + b_e = e$
Total	$a_d + a_e = a$	$b_d + b_e = b$	$a_d + a_e + b_d + b_e = n$

with A the code for the species of interest (e.g. A = *Acartia*) and a_d the number of the given species (e.g. *Acartia*) in the diet, etc.
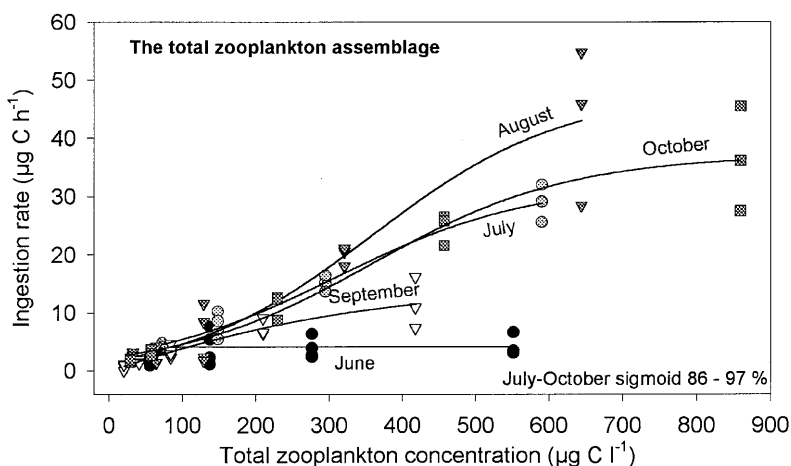
The selectivity index was calculated for each prey group, to determine the selection intensity for different prey, using the average-abundance percentages derived from the carbon content of prey in the diet and in the environment. The significance of selection for different prey groups during each month was tested with Fisher's exact test, as recommended by Pearre (1982), using the Systat 6.0 statistical programme for Windows.

Results

Total ingestion rates

Ingestion rate increased with increasing zooplankton concentration (Fig. 1). Sigmoid functional responses (Holling type III) explained mostly the variation in ingestion rates from July to October. This model explained 86–97% of the variation. In June, the ingestion rate remained linear at a low level. Rotifers were abundant in June and July but in the other 3 months they were scarce (×1 concentration only from 0.5- to 1 µg C l^{-1}). In July, rotifer ingestion was at its highest, at over 25 µg C h^{-1} (×1 concentration ~50 µg C l^{-1}). The feeding of mysids started to saturate at food concentrations of 400–500 µg C l^{-1} (Fig. 1), which is equivalent to 140–170 adult copepods l^{-1}.

Mysids grew from 3 to 19 mm during the study period (Fig. 2). The most rapid phase of growth was observed from July (5–8 mm) to August (9–13 mm). Also at this time, the ingestion rate increased remarkably, achieving the highest level of the whole study period in August. In September, mysids had their first sexual characteristics and growth started to slow down (Fig. 2). When the total ingestion rates of different months were compared, it was found that the rate in August differed significantly from the rates in June, July and September, and June differed from October (Tukey's HSD test: $P < 0.05$).

Zooplankton composition and ingested carbon

The zooplankton community during the study period was dominated by four taxa: Rotifera (mainly *Synchaeta*
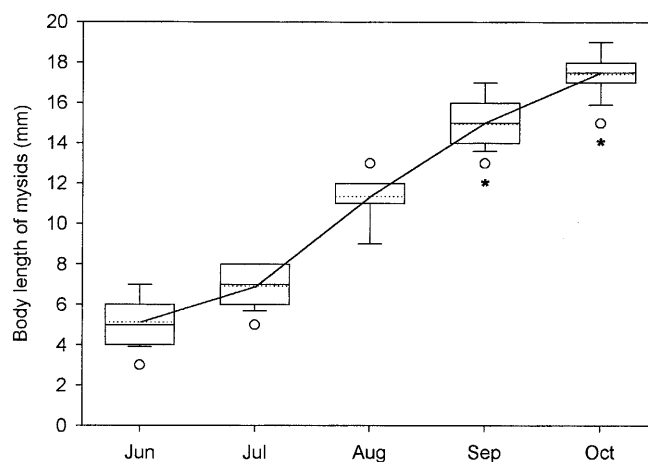

Fig. 2 *Mysis mixta.* Body-lengths (mm) of mysids used in the experiments from June to October 1998. * indicates sexually mature mysids. Mean values are shown by *dotted lines* connected with the *solid line*; the median, by the *solid line* in the middle of the boxes; the lower and upper ends of the box denote 25th and 75th percentiles; the ends of the whiskers, the 10th and 90th percentiles; and *open circles*, the outliers

Fig. 1 *Mysis mixta.* Ingestion rates of the natural zooplankton assemblage in the Gulf of Finland from June to October in 1998. Sigmoid curves are fitted to the ingestion data. The equation of the curves is $y = a / 1 + e^{-(x - x_0/b)}$, where a, b and x_0 are constants and y and x are values from the y and x axes

Fig. 3 *Mysis mixta*. Percentages of **A** available and **B** ingested carbon by zooplankton groups during the study period. Ac, *Acartia*; Eur, *Eurytemora*; Tem, *Temora*; Pseudoc, *Pseudocalanus*; cop, copepodite; ad, adult
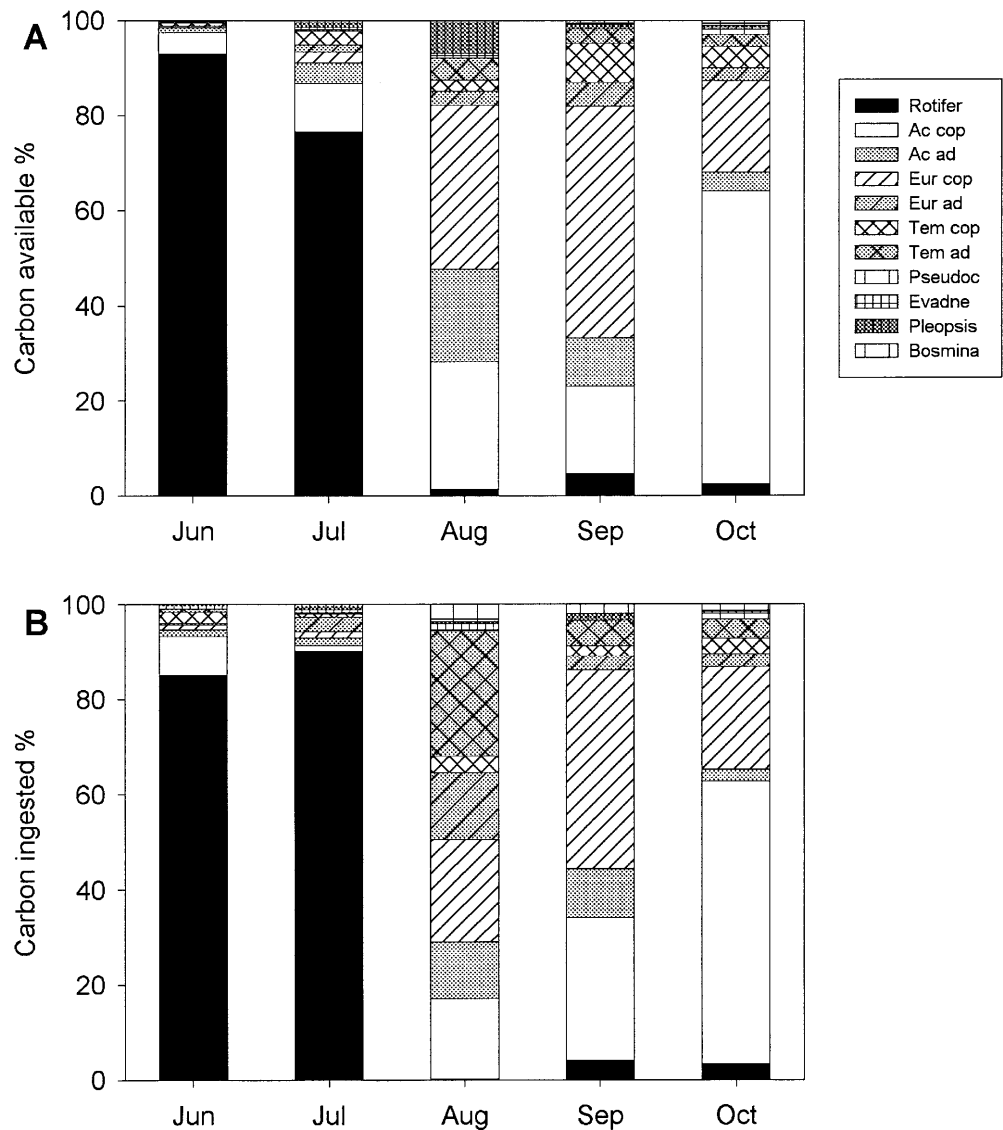
spp.), *Acartia* spp., *Eurytemora affinis* and *Temora longicornis* (Fig. 3A). Other species were the cladocerans, *Pleopsis polyphemoides*, *Evadne nordmanni* and *Bosmina longispina maritima*, and the copepod *Pseudocalanus elongatus*. In June and July, 77–93% of the available carbon consisted of rotifers, while *Acartia* spp. dominated the copepod community. In August, rotifers were sparse, *Acartia* spp. and *E. affinis* were almost equally abundant and *P. polyphemoides* was the dominant cladoceran. In September, *E. affinis* was the most abundant copepod. In October, *Acartia* spp. constituted over 60% of the available carbon, and the second most abundant was *E. affinis*.

The sources of ingested carbon varied throughout the summer (Fig. 3B), largely following the composition of available carbon (Fig. 3A). In June and July, most (85–90%) of the ingested carbon came from rotifers. In August, copepods (all three common species, almost equally, 30–35% each) were the principle source of

carbon, although *T. longicornis* constituted only 11% of the available carbon. In September, *Acartia* spp. and *E. affinis* were the main sources and in October, over 60% of the ingested carbon consisted of *Acartia* spp. The cladoceran proportion of available and of consumed prey was negligible.

Selection of prey groups

Prey preference can be studied by two methods: by comparing the slopes of the specific ingestion-rate curves, or better, by calculating prey-selectivity indices, which make it possible also to take into account the other prey available (Pearre 1982). The ingestion rates of the various prey groups differed from each other. The average ranking of the regression coefficients for ingestion for each prey taxon (Fig. 4A) was as follows, when all studied months were included: *B. longispina*
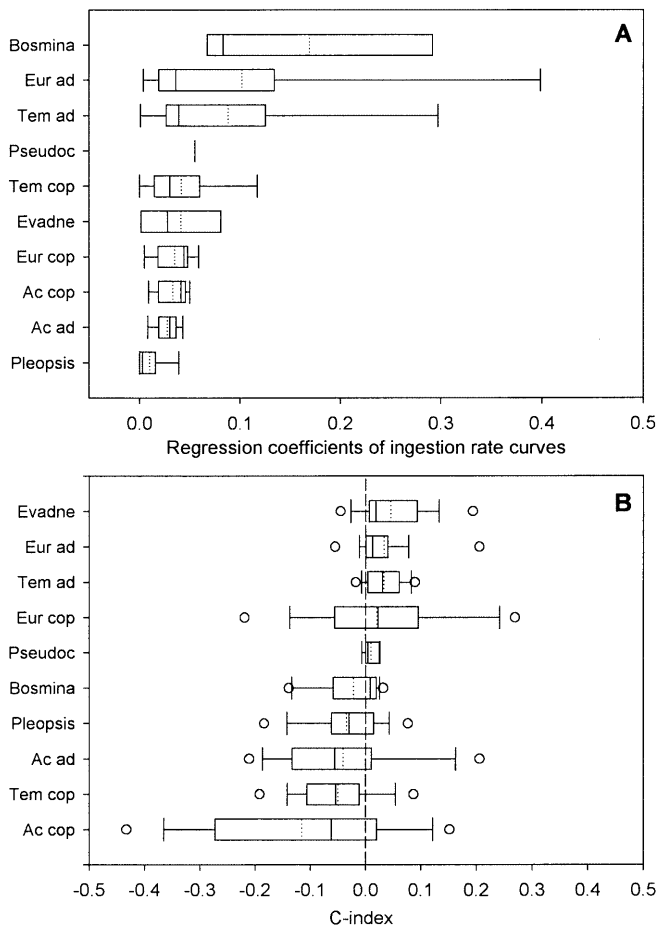
Fig. 4 *Mysis mixta*. **A** Regression coefficients of the slopes of ingestion-rate curves and **B** C-indices (Pearre 1982) for different zooplankton groups. Other designations as in Fig. 2 and abbreviations as in Fig. 3

Comparison of regression coefficients and selection indices (Figs. 4A, B) shows that, when the relative concentration of prey is taken into account (C-index), the ranking changes slightly. *E. nordmanni* was the most positively selected species, but its ingestion rate was low when the relative concentration was not taken into consideration. The ranking of other prey groups remained almost constant regardless of whether regression coefficients or selection indices were used.

There was no correlation between the relative abundance of the prey species in the sea and their selection, nor between mysid length and prey selection. This indicates that selection indices did not change linearly with mysid growth nor with prey availability. Therefore, the only factors that affected selection were the zooplankton concentration offered in the experiment and alternative prey species; i.e. the null hypothesis can be rejected. The null hypothesis was that there are both easy and difficult prey for mysids and that neither the total concentration offered nor the existence of alternative prey affects this preference. This is partly true: there are differences in prey-capture success, which means that there are easy and difficult prey for mysids but, in addition to this preference, the zooplankton concentration offered and alternative prey also have an influence on the selection patterns.

Monthly variation in selection of different prey species

Selection indices ranged from –0.44 to 0.45 during the studied months (Fig. 5). Selection was significant in the first months, in June, July and August (Fisher's exact test; $P < 0.05$), although the variation was large. In September and October, there was no significant selection for any of the prey groups available. The most preferred prey group was different almost every month. Significant selection, either positive or negative, was mostly found with the most abundant prey, the copepodites of *E. affinis* and *Acartia* spp. The third copepod species that was present throughout the summer, *T. longicornis*, was selected only as an adult. *E. nordmanni* was the only cladoceran that was clearly selected in every month during which it is present in the zooplankton community. The most selected prey were *E. nordmanni* in June and *E. affinis* adults in July and copepodites in August (Fisher's exact test; $P < 0.005$, Fig. 5) and the least selected was *Acartia* spp. (Fisher's exact test; $P < 0.001$). In September, the most selected prey were *Acartia* spp. copepodites and the least selected were *T. longicornis* copepodites, though no significant differences were found. In October, the selection indices were close to zero and therefore no specific group could be distinguished from the rest. The variation in selection indices stabilized towards denser concentrations and also towards larger mysid body length, i.e. autumn. In sparse concentrations, selection varied greatly between mysids within each prey group.
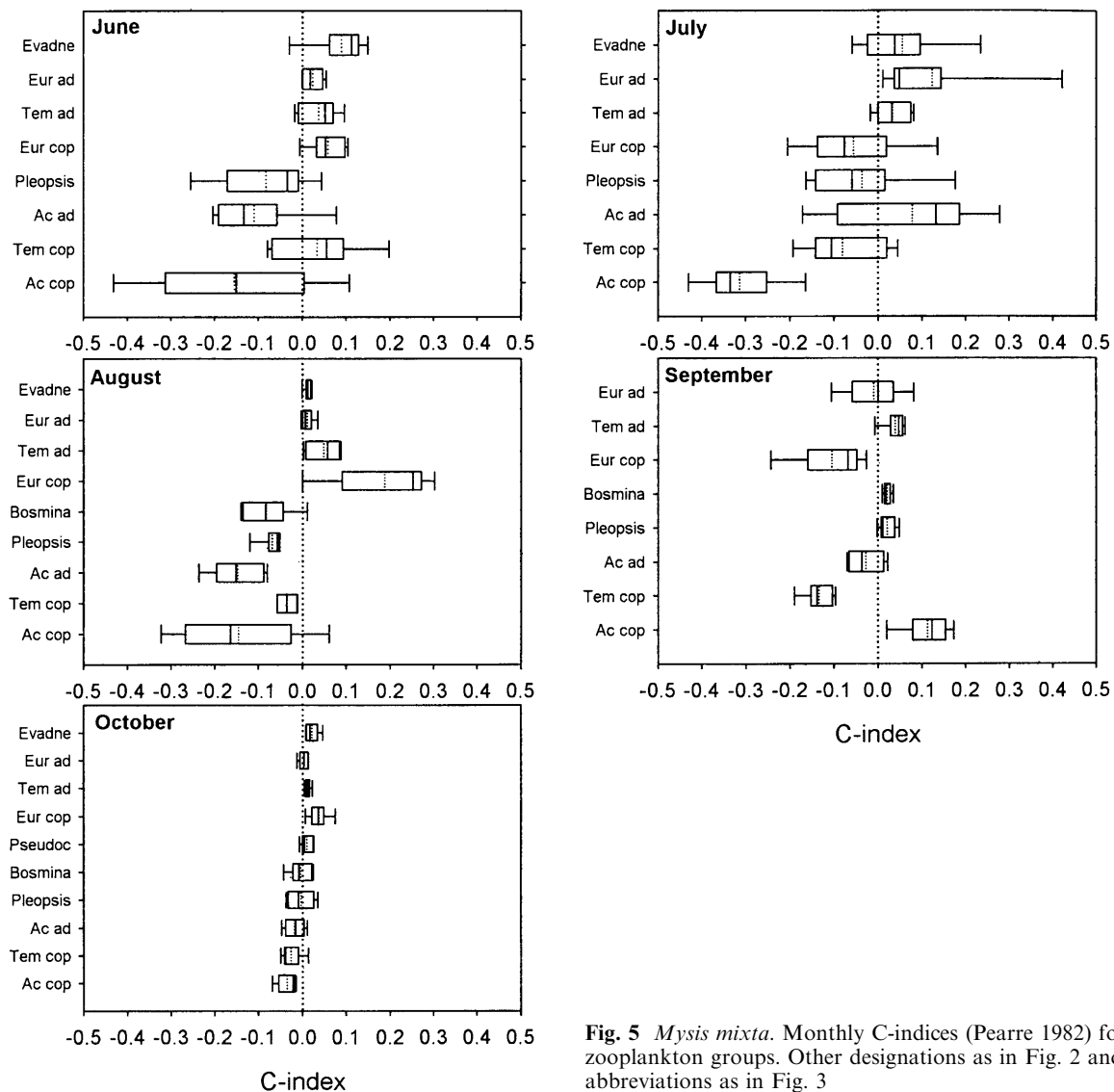
maritima > *T. longicornis* adults ≈ *E. affinis* adults > *P. elongatus* copepodites > *T. longicornis* copepodites > *E. nordmanni* > *E. affinis* copepodites > *Acartia* spp. copepodites > *Acartia* spp. adults > *P. polyphemoides*.

Selection indices were calculated for cladocerans and copepods (Fig. 4B). Rotifers were excluded because they are small prey that are captured incidentally in the feeding current (Viitasalo and Rautio 1998), which does not constitute active selection of this prey from the environment. The order of selection (from most to least selected group) was: *E. nordmanni* > *T. longicornis* adults ≈ *E. affinis* adults > *E. affinis* copepodites > *P. elongatus* copepodites > *B. longispina maritima* > *P. polyphemoides* > *Acartia* spp. adults > *T. longicornis* copepodites > *Acartia* spp. copepodites. The most-selected prey groups also had the smallest standard deviations, which implies that they were preferred to the other prey in almost every month. The variation in selection was largest for the copepodites of *E. affinis* and *Acartia* spp. (Fig. 4B), which means that the most abundant prey were selected quite differently throughout the study period.

Fig. 5 *Mysis mixta*. Monthly C-indices (Pearre 1982) for zooplankton groups. Other designations as in Fig. 2 and abbreviations as in Fig. 3

Discussion

Ingestion rate and functional responses

The ingestion rate of the pelagic mysid, *Mysis mixta*, was lowest at the beginning of summer and increased with increasing mysid length. In September, the ingestion rate was lower than expected and a few of the possible reasons for this may be discussed. Firstly, mysids acquired their first sexual characteristics (females: marsupium) at that time and therefore the attainment of sexual maturity could affect their feeding efficiency. Secondly, September was the only time when *Acartia* spp. were clearly selected and *E. affinis* was not, which indicates that these mysids exceptionally chose prey other than mysids in other months, which clearly had an effect on the feeding rates.

Functional responses followed sigmoidal curves, with saturation levels of approximately 400–500 µg C l^{-1}.

June was the only exception; the saturation levelled out at a food concentration of 50 µg C l^{-1}. During June, mysids were small (average 5 mm) and therefore their predatory abilities were probably still quite undeveloped. In fact, in early summer, they feed mainly on small phytoplankton cells (Viherluoto et al. 2000), which were not available in these experiments. If we compare the saturation level of the feeding of *M. mixta* and the zooplankton density in the Baltic Sea (~40 µg C l^{-1}, Mohammadian et al. 1997), we may conclude that mysids cannot attain their maximal feeding capacity unless they are able to detect and forage in denser zooplankton patches. Zooplankton density decreases towards autumn (Viitasalo et al. 1995) and therefore the feeding and saturation of mysids may be even less likely later in the season. In addition, competition with pelagic fish for food is also greatest during the autumn (Hansson et al. 1990), which further decreases the availability of food for mysids.

Most of the previous studies have investigated functional responses of mysids for particular prey types (e.g. Cooper and Goldman 1980; Lasenby and Fürst 1981; Folt et al. 1982; Chigbu and Sibley 1994; Chapman and Thomas 1998; Viitasalo and Rautio 1998). We found a sigmoidal response in feeding to increasing concentrations of natural zooplankton assemblages. This kind of functional response may occur if the ability of the predator to capture prey increases with the number of encounters with the prey (prey density) (Landry 1981). An alternative functional response could be a type II curve where, at low prey concentrations, the slope rises towards saturation level without any phase of acceleration, as Mohammadian et al. (1997) reported for *M. mixta* in a natural prey assemblage in the northern Baltic proper. A type II response could also be possible for the ingestion rates of this study if prey depletion at low concentrations has influenced the ingestion rates.

Ingestion concentrated on the most available prey types: rotifers, *Acartia* spp. and *E. affinis* copepodites (Figs. 2A, B). The most-ingested prey group varied from month to month, depending on the relative abundance of prey in the water. This has also been reported from lakes Tahoe and Michigan, where *M. relicta* changes its preference according to the relative availability of prey species (Bowers and Vanderploeg 1982; Folt et al. 1982). This kind of predator behaviour may form a refuge for the rare species in the plankton community (Landry 1981).

Prey selection

Almost all selection experiments with natural prey assemblages have been done with freshwater species, with the conclusion that cladocerans are preferred over copepods (Cooper and Goldman 1980; Bowers and Vanderploeg 1982; Vanderploeg et al. 1982; Nero and Sprules 1986). Mohammadian et al. (1997) performed mesocosm experiments with natural prey, and their results showed that *M. mixta* preferred copepods to cladocerans. Our results are similar to those of Mohammadian et al. (1997), with the exception that the most-selected species was the cladoceran, *E. nordmanni*. Since it was rare throughout the study period, it did not contribute much to the overall carbon budget. Therefore, we would say that copepods were generally selected over cladocerans, because all other selected species were copepods (Fig. 4B). Few reasons may be found for copepod selection by mysids, which are generally considered to be non-visual, cruising predators (Viitasalo and Rautio 1998; Viitasalo et al. 1998). The most important signals are hydrodynamic, because mysids cannot hunt prey visually, as fish do (e.g. Zaret and Kerfoot 1975; Drenner et al. 1978; Gardner 1981). Copepods generate stronger signals than cladocerans (e.g. *Pleopsis polyphemoides* and *Bosmina longispina maritima*) because they are larger in size (Kiørboe and Visser 1999) and they perform escape jumps, compared to the smoothly swimming cladocerans. Secondly, faster-swimming prey are encountered more frequently than slower prey (Gerritsen and Strickler 1977).

The most favoured of copepods were *E. affinis* and *T. longicornis*, and the most rejected were *Acartia* spp. Copepods have different escape capabilities (Viitasalo et al. 1998), which are also important for non-visual predators (Drenner et al. 1978). *Acartia* spp. are not as effective in escaping as *E. affinis* (Viitasalo et al., in press) which means that it is an easier prey to capture. However, *Acartia* spp. were only selected by larger mysids, whereas *E. affinis* was also selected by smaller ones. This indicates that *E. affinis* was truly a selected species, despite its strong escape reaction. *E. affinis* also swims more abruptly, creating stronger hydromechanical signals compared to *Acartia* spp. (personal observation) and may therefore be noticed more easily by a mysid. *T. longicornis* was rare compared to *E. affinis* but was also clearly selected in the experiments as an adult. The escape capabilities of these two prey are different; the escape speed and reaction distance of *T. longicornis* are both lower than those of *E. affinis* (Viitasalo et al. 1998), which may explain the favouring of this rare prey.

Differing escape capabilities may also explain the more pronounced variation in copepod selection, compared to the quite stable selection of cladocerans. Cladocerans do not perform escape jumps, as copepods do, and swim more slowly than copepods do (Drenner et al. 1978), thus their vulnerability was more determined by predator activity than by prey response. *E. nordmanni* was the most selected cladoceran and, compared to other species available (*B. longispina maritima*, *P. polyphemoides*), also the largest. Thus, the reason for its preference may be the same as for *E. affinis*: that larger prey creates stronger hydrodynamic signals and is therefore easier to detect.

Relative importance of different prey groups

Prey preference changed considerably during the study period. The most obvious explanation for this is the size variation of mysids from June (~5 mm) to October (~17 mm). Small mysids cannot capture large copepods as effectively as large mysids can (Cooper and Goldman 1980); therefore they feed mostly on phytoplankton (Viherluoto et al. 2000) and, probably, on small and easy prey, such as rotifers and cladocerans. *M. mixta* obtained most of its carbon (80–90%) from rotifers in June and July. It is possible for mysids to filter-feed on rotifers (Viitasalo and Rautio 1998) and if rotifers are numerous (as in the first months of our study), they may fulfil the energy requirements of small mysids. After that, the most important prey group was the copepods (~95% of ingested carbon; Fig. 3A). Mysids in fresh water have a threshold size of 7–8 mm, after which it is easier for them to capture large zooplankters (Gross-

nickle 1982). In August, when large copepods displaced rotifers in the diet, mysids had attained an average size of 11 mm (compared to < 7 mm in July) and therefore copepods were a feasible prey for them. At the same time, the growth rate of mysids increased, perhaps owing to the higher energy content of copepods compared to rotifers.

Variation in prey selection was large from June to September, but was low in October. Small mysids are not capable of capturing the most evasive prey and therefore their preference is based on apparent selectivity, i.e. escape-ability of prey regulates their foraging (Greene 1986). This is also supported by Cooper and Goldman (1980) and Murtaugh (1981). Larger mysids, however, have the possibility to choose between prey, because they can consume prey of a broad size range. On the other hand, their capability of capturing almost anything may explain their much reduced selectivity in October.

Our results indicate firstly that predation success most probably depends on prey escape-capabilities and the ability of mysids to capture and handle prey, but that true selection of some species of prey also exists. Secondly, that different prey species and groups are important at different stages of mysid growth. There seems to be large individual differences in ability to capture prey, which causes difficulties in interpreting selectivity in mysids. It is especially difficult to rank the prey species near the zero line of selection and to say whether these prey are selected by mysid, not selected, or neither. However, our data provide general information on the species that are most selected or not and how these preferences changed during summer and autumn in the northern Baltic Sea.

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