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Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea

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Abstract The dietary habits of the pelagic mysid *Mysis mixta* were studied during its growing season at an open sea location in the Gulf of Finland, the northern Baltic Sea. Stomach samples were taken twice a month from June to September 1997. The most abundant phytoplankton taxa in the stomachs were diatoms and dinoflagellates, and copepods and cladocerans were the most abundant zooplankton identified. A clear change was found in the diets during the study period. Small mysids (3 to 6 mm) fed on sedimented phytoplankton in the early summer (90% benthic particles in June) but shifted gradually to a more pelagic and carnivorous diet (>40% pelagic particles, consisting of ca. 60% zooplankton in September). Seasonal changes in mysid capture ability as well as food availability were suggested to affect the diet composition of mysids during their growth. The ratio of pelagic and benthic food particles could – irrespective of the season – be explained by mysid size, whereas the zooplankton:phytoplankton ratio was better explained by season. The stomach analysis suggests that the mysids needed to attain a threshold size of 8 to 11 mm to initiate feeding on the more evasive copepods. Mysids also started to grow faster at the same time as the proportion of copepods increased in the diet, which suggests that copepods are an important energy source for *M. mixta* in late summer. Finally, a comparison was made between the *M. mixta* diet and that of the less

abundant *M. relicta*. The diets of the two pelagic mysid species overlapped by 75% (Schoener's index). The main difference was due to *M. mixta* eating more zooplankton and pelagic material than *M. relicta*.

Introduction

Mysids are found in littoral, sublittoral, pelagic and benthic habitats in oceans as well as in the Baltic Sea (Mauchline 1980; Salemaa et al. 1986). In the Gulf of Finland, northern Baltic Sea, there are seven species of mysids, of which *Mysis mixta* and *M. relicta* live in the open sea areas (Rudstam et al. 1986; Salemaa et al. 1986; Väinölä 1986). They are an important part of the food chain as they are omnivorous, utilising both phyto- and zooplankton as food. By using both pelagic and benthic food, they also provide a link between these environments. Mysids are food for pelagic fish, such as Baltic herring and sprat (Aneer 1980; Wiktor and Szaniawska 1988; Rudstam and Hansson 1990), and they are thus of great ecological importance in the pelagic communities of the Baltic Sea.

Mysids feed on various food items depending on the time of the year. They feed on phytoplankton and detritus by creating a suspension-feeding current, and also prey actively on evasive zooplankters by raptorial feeding (Mauchline 1980; Grossnickle 1982). Johannsson et al. (1994) suggested that crustacean mesozooplankton cannot fulfil the energy requirements of freshwater *Mysis relicta*, and that part of the nutrition has to be phytoplankton and possibly rotifers. On the other hand, phytoplankton cannot be the only energy source for mysids because it is not available in adequate amounts throughout the year.

Most of the feeding studies on *Mysis* spp. have dealt with freshwater *M. relicta* (e.g. Cooper and Goldman 1980; Lasenby and Fürst 1981; Grossnickle 1982; Johannsson et al. 1994; Almond et al. 1996). In the Baltic Sea, the feeding of *M. mixta* has been studied by Hansson et al. (1990), Rudstam et al. (1992) and

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Mohammadian et al. (1997), with the conclusion that *M. mixta* is predominantly carnivorous. Little is however known about the importance of phytoplankton for *M. mixta*, and, to our knowledge, there have been no studies on the diet of *M. relicta* in the Baltic. The diet composition of *Mysis* spp. during their growth is also not fully understood. Earlier studies were restricted to late summer and autumn (Hansson et al. 1990; Rudstam et al. 1992) or were experimental (Mohammadian et al. 1997). Mysids have a 1-year (Rudstam et al. 1986) or a 2-year life cycle (Salemaa et al. 1986) in the northern Baltic, which means that mysids grow from small (3 to 5 mm) to large (15 to 20 mm) individuals during their first summer (June to September) and breed either during their first or second autumn (Salemaa et al. 1986). Major changes in the food preferences of mysids may occur during their growing season, because during this period the availability of different plankton groups changes significantly, and because the small mysids may be less able to capture evasive zooplankton species than the larger individuals (cf. Cooper and Goldman 1980). A shift from a herbi- or detritivorous diet to a more zooplanktivorous one might thus occur in the late season.

We investigated the stomach contents of *Mysis* spp. in an open sea area in the northern Baltic Sea, in order to reveal how the diet of Baltic mysids changes during their main growing period and to determine if small mysids feed, irrespective of season, on different food than large individuals. Our objective was to find out if both effects of prey capture ability and food availability influence the diet composition of the dominant mysid species of the northern Baltic, *M. mixta*. Furthermore, we made a preliminary comparison of the *M. mixta* diet with that of the other congeneric pelagic species, *M. relicta*.

Materials and methods

The material for the study was collected on seven occasions between 3 June and 15 September 1997, from the Ajax deep (59°43'N; 23°13'E) (depth 80 m), situated in an open sea area south of Hanko Peninsula, at the entrance to the Gulf of Finland. The sampling period covers the most intensive growing season of pelagic mysids in the study area (Salemaa et al. 1986). The mysids were caught in the dark (between 22:00 and 02:00 hrs) with a large plankton net (mesh size 500 µm, diameter 0.8 m, length 3 m). The net was lowered to the bottom and then lifted to the surface at a speed of ~0.5 m s⁻¹. The samples were preserved in 4% buffered formaldehyde immediately after sampling. One bottom sample was taken from Ajax in August with the "Limnos" bottom sampler (Kansanen et al. 1991), in order to identify food particles available to mysids in the surface layer of the sediment. The bottom sample was conserved in 4% buffered formaldehyde.

To compare the seasonal changes in mysid diets to the availability of zooplankton, zooplankton data were obtained from a permanent zooplankton monitoring station of the University of Helsinki and the Finnish Institute of Marine Research (Storfjärden, depth 32 m). This station is situated in an archipelago area ~15 km NE of the mysid sampling station, but the seasonal succession of the main taxonomic groups is similar at these two stations (Koski et al. 1999). Storfjärden data may thus be used to get an overall idea of the availability of different food items in the water. The

zooplankton samples were taken with a Hensen type net (mesh size 100 µm, diameter 0.6 m) by a single haul from 25 m depth to the surface, preserved in 4% buffered formalin, and subsampled with a "Folsom" splitter before analysing with an inverted microscope.

All mysids were measured from the tip of the rostrum to the end of the telson. Mysids were classified into four groups according to their size and stage of sexual maturity: small (3 to 6 mm), medium-sized (8 to 12 mm), large (13 to 16 mm) and adults (sexually mature, 8 to 23 mm). *Mysis mixta* were abundant in every sample, and ten stomachs were examined for each size class, thus it was possible to use statistical analyses in comparisons between size groups. *M. relicta* were rare throughout the summer, and all individuals found were analysed. Thus only a general comparison with the *M. mixta* diet was possible. Altogether 180 *M. mixta* and 74 *M. relicta* were analysed. *M. relicta* individuals in the study area belong to Sibling Species II (Vainölä 1986).

To identify the food particles in stomachs, the mysids were carefully dissected and stomachs and their contents transferred onto a glass slide and observed with an inverted microscope (100× to 400× magnification). The first 50 food items were identified from each stomach. For the sediment sample five subsamples were taken with a syringe, and particles were recognised as for the stomach contents. The sediment sample contained, in order of decreasing abundance, sedimentary diatoms, dinoflagellate cysts and remnants of zooplankton.

Since the different prey taxa occurred in stomachs in pieces of various sizes, their biomass could not be accurately quantified. All the results concerning stomach contents are therefore presented as proportions of counted food items. In copepods, the species/taxon identification was based on legs, antennae and furca, in cladocerans on carapaces and legs, and in rotifers and ciliates on loricas. Phytoplankton taxa were identified from whole cells or smaller cell parts in which distinctive features were found. Furthermore, all prey items were classified in two pairs of prey categories, pelagic-benthic and zooplankton-phytoplankton. These pairs are not mutually exclusive, but overlap to some extent. The "zooplankton" category also includes harpacticoids, although they are not generally part of the plankton. Phytoplankton particles that were considered "benthic" material were identified from cells resisting decomposition, such as diatom spores and dinoflagellate cysts (as identified in the sediment sample). Other benthic particles were diatoms, harpacticoids and crustacean remains in various stages of decomposition, whereas all calanoids and cladocerans were considered planktonic.

The percentage overlap of diets (P_{jk}) of the mysid species and different size classes of *Mysis mixta* and different months were calculated with the Schoener overlap index (Schoener 1970):

$$P_{jk} = \left[\sum^n (\text{minimum } P_{ij}, P_{ik}) \right] 100 ,$$

where P_{ij} and P_{ik} are proportions of a certain food item/particle i of the total number of food particles used by mysid species j and species k , and n is the total number of all food particles.

Results

Taxonomy of food items

Stomachs of *Mysis mixta* and *M. relicta* contained phytoplankton, zooplankton and unidentified dead organic material. Phytoplankton species found belonged to diatoms (Diatomophyceae), dinoflagellates (Dinophyceae), green algae (Chlorophyceae) and blue-green algae (Cyanobacteria) (Table 1). In both *Mysis* species, diatoms were the most abundant and dinoflagellates the second most abundant phytoplankton group identified. Zooplankton found in the stomachs belonged to the

Table 1 *Mysis mixta* and *M. relicta*. Phytoplankton and zooplankton particles found in the stomachs from June to September 1997, in the Gulf of Finland. Species names are in alphabetical order, * particles only found in *M. mixta*

Phytoplankton		Zooplankton
Chlorophyceae	<i>Epithemia</i> spp.*	Ciliata
<i>Monoraphidium contortum</i>	<i>Nitzschia</i> spp.	<i>Helicostomella subulata</i>
<i>Oocystis</i> spp.	<i>Synedra</i> spp.	Cladocera
<i>Planktonema lauterbornii</i>	<i>Thalassiosira baltica</i>	<i>Bosmina longispina maritima</i>
Cyanobacteria	Dinophyceae	Other cladocerans
<i>Aphanizomenon</i> spp.	<i>Dinophysis acuminata</i>	Copepoda
<i>Merismopedia</i> spp.	<i>Protoperidinium granii</i>	<i>Eurytemora affinis</i>
<i>Nodularia spumigena</i>	Cysts of dinoflagellates	Harpacticoida
<i>Pseudanabaena</i> spp.*		Other copepods
Diatomophyceae	Others	Rotifera
<i>Achnanthes taeniata</i>	<i>Ebria tripartita</i>	<i>Keratella cochlearis</i>
<i>Chaetoceros</i> spp.	<i>Radiosperma corbiferum</i>	<i>Keratella cruciformis</i>
<i>Coscinodiscus granii</i>	Pollen	<i>Keratella quadrata</i>
<i>Diatoma tenuis</i> *		<i>Notholca</i> spp.*

following groups: calanoid copepods, harpacticoids, cladocerans, rotifers and protists. Of these taxa, the calanoid *Eurytemora affinis*, cladoceran *Bosmina longispina maritima* and rotifer *Keratella* spp. were abundant and could be reliably identified. The loricate ciliate *Helicostomella subulata* only occurred in the stomachs in September, but then it was numerous. Detritus and unidentified remains of crustacean zooplankton were present in all mysid size categories throughout the study period. Changes during the most intensive growing season in the diet of *M. mixta*, the more abundant of the mysid species in the Gulf of Finland (Simm and Kotta 1992), are treated below in more detail.

Zooplankton availability and stomach contents and growth of *Mysis mixta*

The total zooplankton abundance (in the 0 to 25 m water layer) was highest in July and decreased gradually towards October (Fig. 1A). The abundance of rotifers and cladocerans peaked in July, whereas that of copepods increased until early September. The diet composition of mysids also changed during summer (Fig. 1B). In June, phytoplankton was the main component of the diet (69 to 79% of all particles), with diatoms the most abundant taxon (58% of the phytoplankton particles). Other phytoplankton taxa, especially dinoflagellates and cyanobacteria dominated the phytoplankton fraction in stomachs in September, while green algae occurred in the diet steadily throughout the summer. In July the proportion of zooplankton in the *M. mixta* diet increased rapidly. The share of copepods in stomachs increased sharply in August, and in September they constituted 36 to 39% of all particles in stomachs. Cladocerans and rotifers were found in stomachs from July onwards, but their proportion remained low (2 to 7% of all food particles). In July a large fraction of the diet consisted of unidentified crustacean zooplankton parts.

The average body length of *Mysis mixta* increased from 5.8 mm in early June to 13.8 in mid-September

(Fig. 1C). The mysids grew slowly in June and July, significantly faster in early August (from 8.2 to 11.7 mm in 2 weeks), and slower again in late August and Sep-

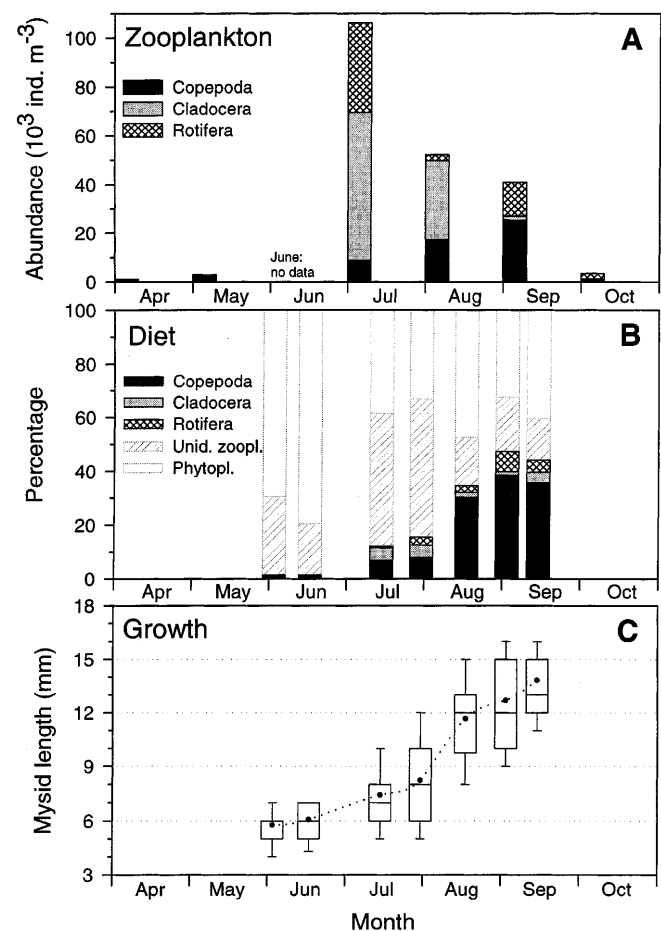


Fig. 1 **A** Zooplankton abundance from April to October 1997. **B** Diet composition of *Mysis mixta* from June to September 1997. **C** Body lengths of *M. mixta* from June to September 1997. Mean values are denoted by solid circles connected by the dotted line and median by the solid line in the middle of the boxes; the lower and upper ends of the box denote 25 and 75th percentiles and the ends of the whiskers the 10 and 90th percentiles

tember. Throughout the study period, a small fraction (2 to 5%) of the population consisted of large (17 to 23 mm long) mature mysids, which probably belonged to the previous year's generation (data not shown).

Pelagic versus benthic feeding

The proportion of pelagic food particles in the diet of *Mysis mixta* increased from 0–40% in June to ~35–75% in August and September (Fig. 2A). In early summer the mysids (most of which were 3 to 6 mm long) fed almost solely on benthic food, and, irrespective of the season, the larger mysids utilised more pelagic food than the smaller mysids. The medium-sized and mature mysids were present throughout the season, and the difference in their diets was statistically significant (Tukey's test, $w = -10.6$, $p < 0.001$, $N = 110$). Fig. 3A shows the pelagic:benthic ratios of *M. mixta* plotted against mysid length. The data show an almost linear increase in the utilisation of pelagic food (ratio from 0 to 0.5) in 5 to 15 mm long mysids; after this the proportion of pelagic food stabilised to ~0.6. A total of 81% of the variation in the pelagic:benthic ratio of *M. mixta* diet could be explained by body length, using a non-linear (logistic) regression depicted in Fig. 3A. The 18 to 21 mm long mature mysids clearly ate more benthic food than the juvenile population in June (cf. the two black circles in

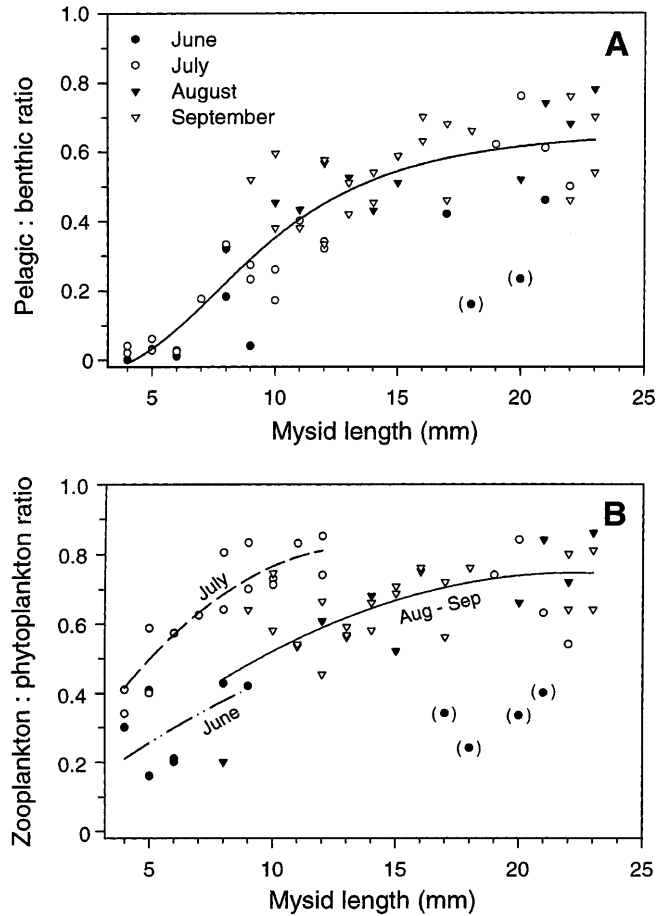


Fig. 3 *Mysis mixta*. A Pelagic:benthic ratio and B zooplankton:phytoplankton ratio in the diet plotted against mysid length. Months are denoted by different symbols. Each symbol denotes one monthly average food particle ratio for one size class (resolution 1 mm). The continuous lines show the regressions between food particle ratios and mysid length. Symbols in parentheses (discussed in "Results") show food particle ratios for large, mature mysids, which are not included in the regressions

parentheses in Fig. 3A), and they were therefore excluded from the regression.

Carnivory versus herbivory

The zooplankton:phytoplankton ratio of the *Mysis mixta* diet increased during the growing season, but the pattern was less clear than with the pelagic:benthic ratio. Generally, the small individuals (3 to 6 mm) consumed less zooplankton than the medium-sized ones (8 to 12 mm), while these consumed less zooplankton than the large individuals (13 to 16 mm) (Fig. 2B). The only exception was mature (17 to 21 mm long) adults of the previous generation, which in June and July consumed, on average, less zooplankton than the medium-sized individuals (Fig. 2B).

Plotting zooplankton:phytoplankton ratios against mysid length (Fig. 3B) shows that, within each sampling

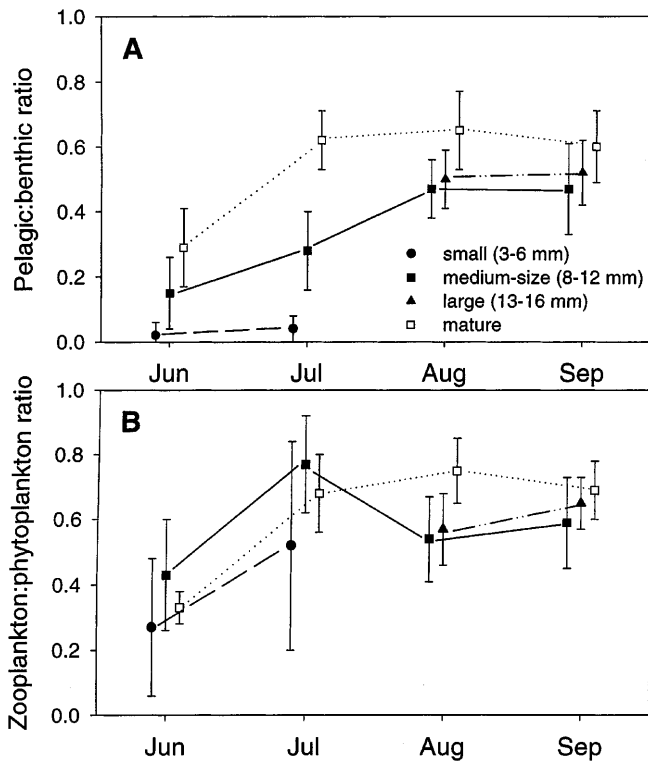


Fig. 2 *Mysis mixta*. A Pelagic:benthic ratio and B zooplankton:phytoplankton ratio in the diet from June to September. Mysids are divided to four size classes. Symbols denote the means and vertical lines denote standard deviations

month, zooplanktivory increased with mysid growth, but that the different months displayed different patterns (i.e. the slopes of the monthly curves are different). Especially in July the proportion of zooplankton in the diet with respect to mysid length was clearly larger than during the other months: in July 65 to 85% of the food particles of the medium-sized (8 to 12 mm) mysids consisted of zooplankton, whereas in August and September the mysids needed to be >15 mm long to reach a similar level of carnivory.

Spearman's correlation test revealed that both season and body length of *Mysis mixta* correlated significantly with the diet composition. Both variables, sampling date and body length, correlated with the pelagic:benthic food ratio ($r_s = 0.686$, $p < 0.0001$ and $r_s = 0.809$, $p < 0.0001$, respectively); as for the zooplankton:phytoplankton ratio the correlation was lower ($r_s = 0.290$, $p < 0.0005$ and $r_s = 0.269$, $p < 0.0005$, respectively).

Comparison of *Mysis mixta* and *M. relicta* diets

Individuals of *M. mixta* and *M. relicta* were approximately of the same size in June and July (mean \pm SD: length 7.2 mm \pm 2.3 and 6.1 mm \pm 1.8, respectively), whereas in August and September *M. mixta* were longer than *M. relicta* (12.6 mm \pm 1.9 and 7.4 mm \pm 1.4, respectively). The overall diet overlap in *M. mixta* and *M. relicta* was 75% in juveniles and 77% in adults (Schoener's index), but clear differences in the diets could be seen. *M. relicta* foraged significantly less on pelagic material than *M. mixta* in all months studied (Mann-Whitney U -test: $z = -4.871$, $p < 0.001$, $N = 254$). Benthic particles dominated *M. relicta* stomach contents throughout the study period, whereas for *M. mixta* this was the case only in June and July (Fig. 4A). Also, *M. relicta* ate significantly less zooplankton than *M. mixta* in all months but June (cf. Fig. 4B), and the difference between the zooplankton:phytoplankton ratios was statistically very significant (Mann-Whitney U -test: $z = -4.939$, $p < 0.001$, $N = 254$).

Discussion

The diet of *Mysis mixta* changed clearly as they grew from the beginning of summer to autumn, from juveniles to sub-adults. The most evident change was the increase of the proportion of pelagic material in stomachs. In June the mysids foraged almost exclusively on benthic material, mainly sedimentary diatoms and other benthic phytoplankton particles. In July the length variation in the mysid population was more pronounced than in June, which was also reflected in the more variable stomach contents. The medium-sized mysids (8 to 12 mm) foraged almost equally on phyto- and zooplankton and benthic and pelagic food, and were thus a

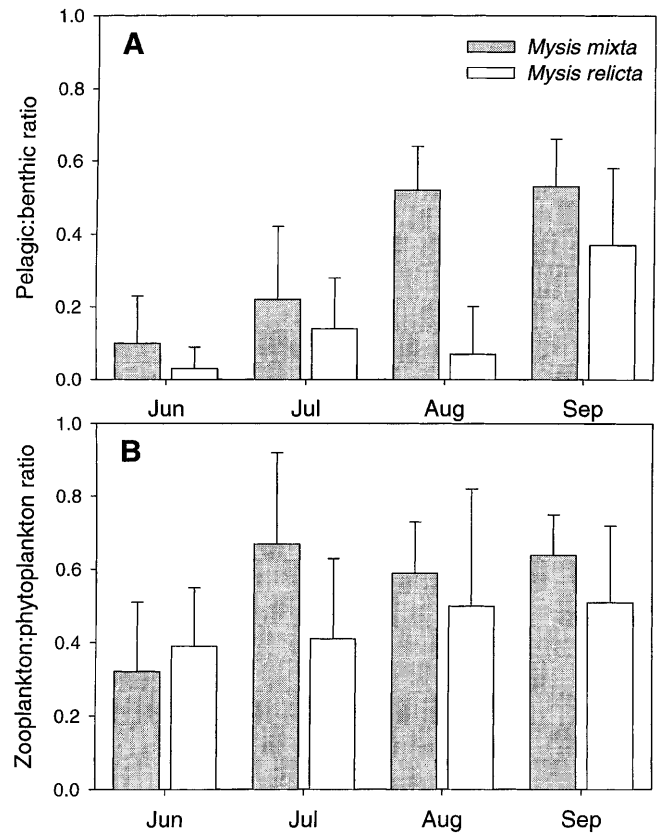


Fig. 4 Monthly averages of **A** pelagic:benthic ratio and **B** zooplankton:phytoplankton ratio in the diet of *Mysis mixta* and *M. relicta*. Vertical lines at the end of bars indicate standard deviations

transition group between small and large mysids. In August and September, the mysids had grown to 8–16 mm long sub-adults, and the proportion of pelagic zooplankton, especially copepods, significantly increased. The observed change in mysid diets could thus be either due to changes in food availability, or due to an increase in the mysids' abilities to capture zooplankters. These two alternative explanations are discussed below.

Changes in diets of growing mysids

In freshwater the food utilisation of mysids is known to vary with seasons (e.g. Adare and Lasenby 1994). In early summer, when mysids are a few millimetres long, small phytoplankton cells are suitable food for them, while the larger mysids, which dominate in late summer and autumn, also feed on zooplankton (Cooper and Goldman 1980). This was also the case in our study area, where 65 to 80% of the food particles in June consisted of sedimentary phytoplankton. This is plausible because in June the diatom spring bloom has settled onto the bottom (e.g. Heiskanen 1998). The dominance of benthic particles in mysid stomachs in early summer may also be due to relatively low microphytoplankton biomass in the pelagial during this period. On the other

hand, we cannot exclude the possibility that the mysids foraged on unarmoured flagellates and other nanophytoplankton, which are probably rapidly digested in mysid stomachs.

Plotting the pelagic:benthic and zooplankton:phytoplankton ratios against mysid body length showed that there is a fairly close relationship between pelagic feeding habits and mysid size (Fig. 3A). In contrast, the shift to zooplankton food seemed to be relatively more closely related to season (i.e. food availability) than to mysid body size (Fig. 3B). However, the share of copepods in the diet increased abruptly in August, although they were already abundant in the plankton in June. We therefore suggest that the mysids needed to attain a threshold size (8 to 11 mm) to initiate pelagic feeding on planktonic copepods. In freshwater, *Mysis relicta* become essentially predators after they attain the size of 7 to 8 mm (Grossnickle 1982). For an omnivore, availability of food items in the water obviously determines the selection of possible food items, but if both phyto- and zooplankton are available, mysid size probably defines the extent of zooplankton utilisation. The fact that, irrespective of season, the smaller mysids ate less zooplankton than the larger mysids proves that mysids need to attain a threshold size to initiate zooplankton feeding. We conclude that both food availability and mysid growth probably affected food utilisation by *Mysis* spp. in our study area, and that changes in both factors drove their feeding habits in the same direction, i.e. zooplanktivory.

Behavioural and energetic factors may also contribute to the seasonal shift in the diets of *Mysis* spp. Mysids migrate towards surface waters for foraging at dusk and descend to escape visual predation by fish at dawn (e.g. Hakala 1978; Salemaa et al. 1986; Rudstam et al. 1989). Seasonal changes in day-length therefore influence the duration of the period spent in the upper water layers (e.g. Beeton and Bowers 1982; Hansson et al. 1990). In the high latitudes of the study area, the night-length is ~5 h in mid-June, but increases to ~11 h in mid-September. In early summer the dark period may be too short to allow efficient utilisation of pelagic food, while the autumnal light conditions are obviously more favourable for pelagic foraging. Also, feeding in the pelagic realm in late summer may be beneficial because the nutritional quality of the organic material in the surface sediment decreases towards autumn (Lehtonen 1997).

Differences in *Mysis mixta* and *M. relicta* diets

M. mixta and *M. relicta* co-occur throughout the northern Baltic Sea, with the exception of the Bothnian Bay, where only *M. relicta* are present (Salemaa et al. 1986, 1990). This may be partly because *M. relicta* survives in lower salinity water better than *M. mixta*, but differences in food utilisation may also influence their distribution limits. The feeding of *M. relicta* has not previously been studied in the Baltic, but freshwater

studies suggest that it is omnivorous, feeding especially actively on diatoms (Grossnickle 1982). In contrast, Baltic studies on *M. mixta* suggest that it is predominantly a carnivore (Rudstam et al. 1989, 1992; Hansson et al. 1990), although Hansson et al.'s (1997) results, based on the nitrogen isotope ratio, suggested that *M. mixta* do feed more on phytoplankton than previously anticipated. Our results corroborate both of these hypotheses. We found that *M. mixta* is more carnivorous than *M. relicta* and that *M. mixta* also feeds actively on phytoplankton, especially during the early life stages. The more carnivorous habits of *M. mixta* may be due to the larger size of *M. mixta*, and also due to *M. mixta* migrating higher in the water column than *M. relicta* (Salemaa et al. 1986). More studies are, however, needed to better understand the feeding behaviour of Baltic mysids with respect to their life cycles. Food utilisation during the winter, brood-carrying period under ice remains unclear.

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