

# Diet composition influences the growth of the pelagic mysid shrimp, *Mysis mixta* (Mysidacea)

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We studied the growth, feeding, and elemental composition of *Mysis mixta* from June to September 1997 in the northern Baltic Sea. In June the juvenile population had a unimodal size distribution (mean length ~6 mm), but in July–August, the population was divided into two cohorts. A stomach content analysis showed that the mysids in the larger and faster growing cohort fed significantly more on crustacean zooplankton and pelagic material than the smaller one: the mean ratios of zooplankton:phytoplankton and pelagic:benthic particles in July–August were respectively 0.27 and 0.11 for the small cohort, and 0.54 and 0.36 for the large cohort. This suggests that food quality and its energy content are important in influencing the growth of pelagic mysids in the northern Baltic. The C:N ratio of the two cohorts did not vary much, which shows that ingestion of food items with varying elemental content is not necessarily reflected in the elemental composition of consumers.

## Introduction

Omnivorous feeding behaviour is a common strategy by which freshwater and marine invertebrates cope with varying food conditions (Mauchline 1980, Landry 1981, Wiadnyana and Rassoulzadegan 1989, Stoecker and Capuzzo 1990, Kleppel 1993, Gismervik and Andersen 1997, Hansson *et al.* 1997). Omnivory is profit-

able for consumers when food items are scarce in the environment or there is no large difference between the items' profitability. Omnivores may also switch from one food supply to another depending on the relative abundance of food items in the surrounding environment. In addition to food availability, the quality and energy content of food is also important for growth (Sturner and Robinson 1994, McKinnon 1996).

Generally, a low C:N ratio of food indicates good food quality (Kiørboe 1989, McKinnon 1996, Lindley *et al.* 1997). However, while some studies show a strong effect of the food's chemical composition on the reproductive success of zooplankton (Jónasdóttir 1994), other studies do not (Sanders *et al.* 1996). This is partly because maintenance, growth and reproduction demand different food qualities. Maintenance metabolism requires primarily energy, while growth requires many other essential elements (Sterner and Robinson 1994). However, even though it is well known that food quality affects the growth of marine copepods (e.g. McKinnon 1996), studies on the correlation between food quality and growth or survival of other pelagic invertebrates are scarce.

Mysid shrimps (Mysidacea) are common planktivores that feed on phytoplankton, detritus and small zooplankters by creating a suspension-feeding current. They also prey on actively moving zooplankters by raptorial feeding (Mauchline 1980). Mysids may be able to choose the best way of feeding in varying situations by switching between suspension feeding and raptorial feeding (Viitasalo and Rautio 1998). The diet of mysids usually reflects the availability of different food items (Vihertuoto *et al.* 2000), but consistent patterns of prey preference have also been detected (Rudstam *et al.* 1992, Vihertuoto and Viitasalo 2001). Further, the diet of mysids changes with age. *Mysis* species have a threshold size of 7–8 mm, after which they become capable of capturing zooplankton (Grossnickle 1982, review, Vihertuoto and Viitasalo 2001), which obviously affects the quality of food they ingest.

*Mysis mixta* generally has a one-year life cycle in the northern Baltic Sea (Rudstam *et al.* 1986). Young are released in early spring after the ice break-up. New juveniles grow during summer and autumn, and start to breed in late autumn. Oviparous females carry their brood 4 to 5 months and begin to release them in early spring. Salemaa *et al.* (1986) noticed that some females remain immature during their first winter and breed only in their second autumn. These females start to release their young before the one-year-old females, which may result in two cohorts of juveniles (Salemaa *et al.* 1986).

On the other hand, the other possibility is that the distinct cohorts are due to differential growth rates of individuals within the same population. Could it be that, after attaining the threshold size for zooplankton feeding, juveniles start to grow faster, and can the growth rate be dependent on the quality or energy content of food? These questions were explored by collecting animals in the field, and analysing their length distribution and stomach contents. Further, we also wished to study whether the carbon to nitrogen ratio of mysids remains stable or varies during summer in the northern Baltic Sea.

## Material and methods

The samples were collected between 3 June and 15 September 1997 from an open sea area (59°43'N, 23°13'E) (depth 80 m) south of Hanko peninsula at the entrance to the Gulf of Finland. The mysids were caught at night with a large plankton net of mesh size 500  $\mu$ m, diameter 0.8 m, and length 3 m. The net hauls were taken from near the bottom to the surface. The samples were preserved in 4% buffered formaldehyde (final conc.) immediately after sampling. One bottom sample was also taken in August from the same place as the mysids using a Limnos-bottom sampler (Kansanen *et al.* 1991), in order to identify benthic food particles available to mysids in the surface layer of the sediment. The bottom sample was also preserved in 4% buffered formaldehyde (final conc.).

One hundred juvenile mysids were measured from the tip of the rostrum to the end of the telson (body length, BL) from every sample. The dry weight (DW) was calculated from body length measurements according to the equation:

$$DW = 0.0032 \times BL^{2.85} \quad (1)$$

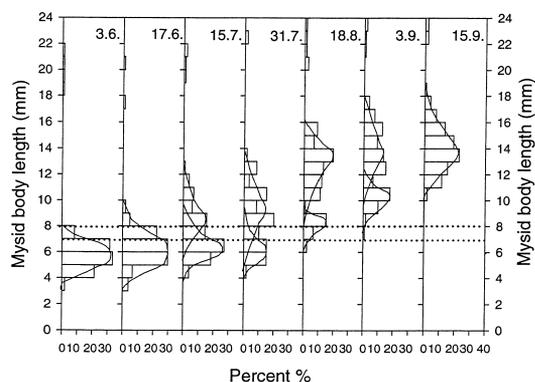
(Gorokhova 1999). To identify the food particles in stomachs, the mysids were carefully dissected, the stomachs and their contents transferred onto a glass slide, and observed with an inverted microscope (100 $\times$  to 400 $\times$  magnification). An average 24 stomachs were studied from every sampling day (total  $n = 168$ ) and

50 food items identified from each stomach. For the sediment sample, 5 subsamples were taken using a syringe, and particles studied and recognised similarly as for the stomach contents.

Since the different prey taxa occurred in stomachs in remains 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. All prey items were additionally classified into two prey categories, pelagic-benthic and zooplankton-phytoplankton. These categories are not mutually exclusive, overlapping to some extent. Phytoplankton particles here considered as benthic material were identified from cells resisting decomposition, such as spores of diatoms and dinoflagellate cysts (as identified in the sediment sample). Other particles were diatoms and crustacean remains in various stages of decomposition. Of the animal taxa, harpacticoids and highly decomposed crustacean remains were considered as benthic particles, whereas all calanoids and cladocerans were considered planktonic.

The length distributions of mysid populations were studied for every sampling day ( $n = 100$ ) separately to discover different cohorts. The best fitted distributions were counted for the mysid population using the program MIX (an interactive program for fitting mixtures of distributions; Macdonald and Green 1988). The program analyses histograms as mixtures of statistical distributions, that is, by finding a set of overlapping component distributions that gives the best fit to the histogram.

The carbon and nitrogen content as well as the C:N ratio of mysids were measured in July and August. Mysids were caught at night with a 'Mysis-net' and placed in an insulated box with water taken from below the thermocline. In the laboratory a total of 34 mysids were measured, washed with Milli-Q water, and put into small tin dishes (1 mysid per dish). The tin dishes

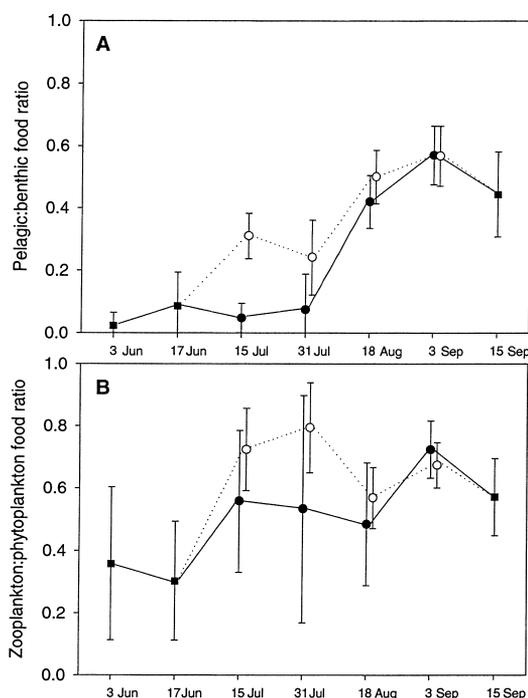


**Fig. 1.** The length frequency distribution of *Mysis mixta* populations in Ajax deep (59°43N, 23°13E) in the northern Baltic Sea in 1997. The best fitting curves are drawn by hand from the results of the MIX program (Macdonald and Green 1988). Dotted lines indicate the threshold size of 8 mm for zooplankton feeding.  $N = 100$  per every sampling date.

were then dried at 60 °C for 24 h, after which C and N contents were analysed using a stable isotope analyser (Europa Scientific ANCA, automatic nitrogen and carbon analyser) (Barrie and Lemley 1989).

## Results

In June 1997 the length distribution of *Mysis mixta* juveniles was uniform, following a normal distribution with one peak frequency (average size of  $5.5 \pm 1.1$  mm, mean  $\pm$  SD; Fig. 1). In contrast, in July, August and in the beginning of September, the population was divided into two different sub-populations (average length from July  $5.8 \pm 0.9$  mm and  $8.4 \pm 1.4$  mm to September  $9.7 \pm 0.9$  mm and  $13.6 \pm 1.7$  mm, respectively). The low frequency area between the two cohorts moved steadily from July to September and distinguished the border of the cohorts. In mid-September the length distribution of juveniles was again unimodal, with only one peak frequency ( $12.9 \pm 1.3$  mm, Fig. 1). When the population formed one cohort, the length range was smaller (4 to 8 mm) than at the time of two cohorts (8–10 mm). Also, a few mature mysids (17 to 23 mm), that probably belonged to the previous year's generation,



**Fig. 2.** (A) Pelagic:benthic and (B) Zooplankton:phytoplankton food ratios in the diet of *Mysis mixta* in June–September 1997. Open circles indicate the large cohort, filled circles the small cohort and filled squares the population before and after the division to two cohorts (means  $\pm$  SD). See text for further information on the division into two cohorts.

were present in the population throughout the summer. The results from the analysis of the best fits, calculated by the MIX program, support our hypothesis of two separate cohorts in July–August (curves drawn by hand from the

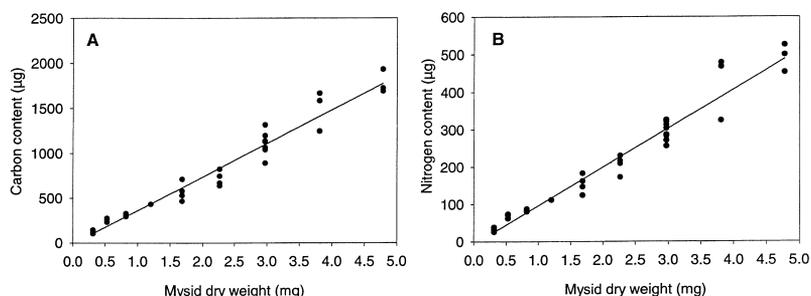
MIX results in Fig. 1). The two-peak distributions fitted much better compared to one-peak distributions from 15 July to 3 September (Table 1).

We compared the diets of the two cohorts of juveniles from 15 July to 3 September, when the cohorts could be clearly separated. The zooplankton part of the diet mainly comprised copepods, while the phytoplankton fraction consisted of decomposed diatoms, dinoflagellates, blue-green algae and green algae. The stomach contents were divided into two categories: pelagic:benthic food and zooplankton:phytoplankton food, and the ratios in the two cohorts were compared. Both food ratios differed between cohorts. The larger cohort ate significantly more pelagic material (Mann-Whitney  $U$ -test:  $z = 4.267$ ,  $p < 0.001$ ,  $n = 96$ ) and zooplankton, though the difference in zoopl:phytopl ratio was not statistically significant ( $z = 1.886$ ,  $p = 0.059$ ,  $n = 96$ ). In July, when the difference in feeding was most clear, the pelagic:benthic ratios were 0.06 and 0.27, and zooplankton:phytoplankton ratios 0.54 and 0.77 respectively for the small and large cohort (Fig. 2A and B). These differences were statistically significant (Mann-Whitney  $U$ -test: pelagic:benthic:  $z = 4.202$ ,  $p < 0.001$ ,  $n = 49$ ; zoopl:phytopl:  $z = 2.282$ ,  $p < 0.05$ ,  $n = 49$ ). The diets became more similar towards September, along with the unification of the size distribution (cf. Fig. 1). Later in September the variation in the diet remained at a low level, pelagic material forming  $\sim 45\%$  and zooplankton  $\sim 55\%$  of the diet.

The carbon and nitrogen contents of *M. mixta* juveniles were measured in July and August.

**Table 1.** Best fitted length distributions for juvenile *Mysis mixta* population during summer 1997 by the MIX program (Macdonald and Green 1988). The table shows fits for all one-peak distributions as well as fits for the 4 distributions where two-peak distribution fitted better. The best fits are printed in bold.

Sampling date	Best fitted distribution	One-peak frequency ( $\chi^2$ )	Goodness of fit ( $P$ )	Two-peak frequencies ( $\chi^2$ )	Goodness of fit ( $P$ )
3 Jun.	Normal	<b>2.22</b>	<b>0.70</b>		
17 Jun.	Normal	<b>4.61</b>	<b>0.59</b>		
15 Jul.	Lognormal	8.49	0.39	<b>2.19</b>	<b>0.79</b>
31 Jul.	Lognormal	13.74	0.11	<b>9.29</b>	<b>0.41</b>
18 Aug.	Weibull	25.31	0.00	<b>10.49</b>	<b>0.23</b>
3 Sep.	Lognormal	22.97	0.01	<b>11.00</b>	<b>0.20</b>
15 Sep.	Lognormal	<b>2.12</b>	<b>0.95</b>		



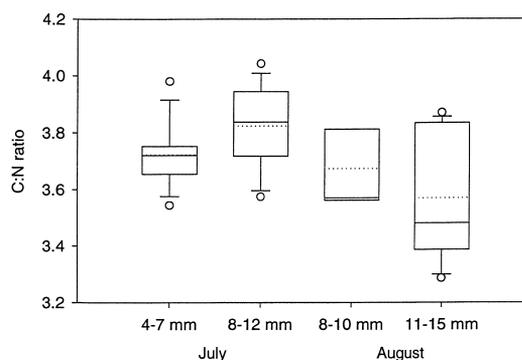
**Fig. 3.** Linear regressions between (A) carbon and (B) nitrogen content and mysid dry weight (A:  $r^2 = 0.96$ ,  $p < 0.001$ ,  $n = 34$ , B:  $r^2 = 0.95$ ,  $p < 0.001$ ,  $n = 34$ ) in July and August, 1997. Mysids are all juveniles, length variation is between 5 and 13 mm. Dry weight is estimated from body length:DW from the equation of Gorokhova (1999).

Regression between both carbon and nitrogen contents and mysid dry weight (mg) was linear (Fig. 3A and B). The variation in C:N ratio was low, from 3.5 to 4.0 in July and from 3.3 to 3.9 in August. The differences were not statistically significant between cohorts in either of the months (Mann-Whitney  $U$ -test:  $p > 0.05$ ) (Fig. 4).

## Discussion

In the northern Baltic Sea, several distinct cohorts of *Mysis* species can be observed during the course of the year. This may be due to females breeding in their first or second autumn, possibly leading to young being released at different times in the following spring. Thus distinct cohorts may be found because of two separate release times of young (Salemaa *et al.* 1986).

Our data provides an alternative explanation for the two cohorts during summer 1997. In the middle of July, a part of the juvenile population started to grow faster and therefore two distinct cohorts could be seen during summer. What can be the reason for these different growth rates when the original situation in June is equal for all mysids? If there were both one- and two-year old breeders in the *M. mixta* population, there should be two distinct juvenile cohorts already in June (cf. Salemaa *et al.* 1986). In our study area, however, the juvenile population was uniform during the whole of June and was divided into two only in July (Fig. 1). A few large females which were present the whole summer



**Fig. 4.** C:N ratios of *Mysis mixta* in July and August 1997. The two cohorts (discussed in the text) are separated. Mean values are shown by a dotted line, the median by a solid line; the lower and upper ends of the box denote the 25 and 75th percentiles, and the ends of the whiskers the 10 and 90th percentiles. Open circles: outliers.  $n = 34$  (20 mysids in July and 14 in August).

were probably too old to breed (Hakala 1978). There were no ovigerous females present in the beginning of June, excluding the possibility that some young could be released still during June which would therefore be smaller and grow slower in the beginning of summer. This suggests that *M. mixta* near the southern coast of Finland had a one-year life cycle with one release time for young in spring, and that therefore some other explanation has to be found for the two separate cohorts during the study period.

In June the whole *M. mixta* population fed more on benthic phytoplankton, but in July there were two different 'feeding lines'. Smaller

mysids fed more on phytoplankton and benthic material, but larger ones switched to a diet richer in zooplankton. The difference was clear in both prey categories. In July, phytoplankton biomass is at its minimum (Niemi 1976), whereas the abundance of cladocerans and copepods species is close to their maximum (Viitasalo *et al.* 1995). Thus, zooplankton availability is good for the mysids over 7–8 mm that are capable of capturing them. In the beginning of July, when the two cohorts started to grow at different rates (large: growth coefficient 3.9, small: 0-growth), both cohorts changed their diet to more zooplankton, but the faster growing mysids changed their nutrition more than the others. Animal food may nutritionally be of better quality for mysids than phytoplankton or detritus, as suggested for copepods (e.g. Conover and Corner 1968, Corner *et al.* 1976, Heinle *et al.* 1977, Stoecker and Capuzzo 1990, review). For instance, it is known that green algae (Dunstan *et al.* 1992) and cyanobacteria (Koski *et al.* 1999) are not 'good' food compared to zooplankton or dinoflagellates. Also decomposing benthic material, for example diatoms, can be low quality food compared to fresh pelagic material (e.g. Lehtonen 1997). Therefore, we suggest that the mysids that fed on pelagic food and zooplankton gained a growth advantage compared to the benthic feeders and phytoplankton grazers.

Mysids have a threshold size of 7–8 mm, after which they become essentially predators (Grossnickle 1982, review; Viherluoto and Viitasalo 2001). In our study area, juvenile mysids were 4 to 13 mm long in July. The population was therefore divided into two groups that differed in their feeding: suspension feeders below 8 mm, and predators over 8 mm. Mysids at the larger end of the size distribution probably started to be large enough to capture zooplankters, and thus gained more protein and amino acid-rich animal food (Stoecker and Capuzzo 1990, review). In contrast, the rest of the population continued to feed mainly on phytoplankton (decomposing diatoms, cyanobacteria and green algae) and their growth rate remained lower (during July growth rate was ~0) than that of individuals already feeding raptorially.

This phenomenon may occur because of differences in migration behaviour. Mysids per-

form diurnal vertical migrations to avoid visual predators such as fish. During the night they migrate upwards for better food supply (Rudstam *et al.* 1989). Probably some mysids spent more time near the bottom, whereas others migrated to the upper water column where zooplankters were available. Raptorial feeding may provide more energy per unit time than phytoplankton grazing (Gifford and Dagg 1988) and may therefore confer a growth advantage on mysids capable of capturing and handling prey. Further, the ingestion rate of mysids increases after attaining the threshold size (Viherluoto and Viitasalo 2001), which also provides more energy per unit time. After getting the growth advantage, the larger mysids had continually better chances to capture larger prey than smaller mysids (Cooper and Goldman 1980), which further kept their size distributions apart and, hence, their diets. In August, the mysids of the smaller cohort also reached the threshold size for zooplankton feeding; their growth rate consequently increased (growth coefficient 3.63), and in mid-September the two cohorts again united. The reason for the decreased growth of the larger cohort in September could be the severe competition for food with herring and sprat. In early autumn planktivorous fish and mysids decrease the abundance of zooplankton (Hansson *et al.* 1990a), which indicates that food supply is limited and this, in turn, may negatively influence the growth of mysids (Hansson *et al.* 1990b).

The quality of food can also be measured by the C:N ratio (Kjørboe 1989, McKinnon 1996, Sanders *et al.* 1996, Lindley *et al.* 1997). A low C:N ratio of food indicates high quality, and the elemental composition of the animal itself is also an indicator of condition. A few studies have investigated nitrogen and carbon content of mysids. Donnelly *et al.* (1993) measured the C:N ratio of three mysid species (*Eucopeia sculpticauda*, *E. unguiculata*, *Gnathophausia ingens*) in the Gulf of Mexico. Compared to these values (5.9 to 7.3) our values for Baltic *Mysis mixta* were very low (3.3 to 4.0), which should indicate good condition. Gorokhova (1999) got similar results for *M. mixta* (juveniles 3.8) in the northern Baltic proper. C:N ratio was similar in both cohorts in our study, so this does not explain the different growth rates. However,

omnivory probably provides a better quality diet for mysids than phytoplankton or detritus alone, as several studies have shown with other zooplankton (e.g. Conover and Corner 1968, Heinle *et al.* 1977, Stoecker and Capuzzo 1990, review).

We recognise that our data cannot distinguish between reason and consequence, i.e. do different feeding modes influence the growth of mysids, or does the growth difference allow for different utilisation of phytoplankton and zooplankton? Possibly mysids in June originated from the same cohort but the largest ones of the population had earlier had the opportunity to start feeding on zooplankton and therefore achieved a higher growth rate. However, our data is the first one to show such a clear difference in growth rates and diets of different sized mysids in the Baltic Sea. Further studies on the effects of food quality are still needed to fully understand the importance of food quality and availability for nectobenthic mysids.

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## References

- Barrie A. & Lemley M. 1989. *Automated  $^{15}\text{N}/^{13}\text{C}$  analysis of biological materials*. American Laboratory, August, pp. 1–7.
- Conover R.J. & Corner E.D.S. 1968. Respiration and nitrogen excretion by some marine zooplankton in relation to their life cycles. *J. Mar. Biol. Ass. UK* 48: 49–75.
- Cooper S.D. & Goldman C.R. 1980. Opossum shrimp (*Mysis relicta*) predation on zooplankton. *Can. J. Fish. Aquat. Sci.* 37: 909–919.
- Corner E.D.S., Head R.N., Kilvington C.C. & Penny-cuick L. 1976. On the nutrition and metabolism of zooplankton X. Quantitative aspects of *Calanus helgolandicus* feeding as a carnivore. *J. Mar. Biol. Ass. UK* 56: 345–358.
- Donnelly J., Stickney D.G. & Torres J.J. 1993. Proximate and elemental composition and energy content of mesopelagic crustaceans from the eastern Gulf of Mexico. *Mar. Biol.* 115: 469–480.
- Dunstan G.A., Volkman J.K., Jeffrey S.W. & Barrett S.M. 1992. Biochemical composition of microalgae from the green algae classes Chlorophyceae and Prasinophyceae. 2. Lipid classes and fatty acids. *J. Exp. Mar. Biol. Ecol.* 161: 115–134.
- Gifford D.J. & Dagg M.J. 1988. Feeding of the estuarine copepod *Acartia tonsa* dana: carnivory vs. herbivory in natural microplankton assemblages. *Bull. Mar. Sci.* 43: 458–468.
- Gismervik I. & Andersen T. 1997. Prey switching by *Acartia clausi*: experimental evidence and implications of intraguild predation assessed by a model. *Mar. Ecol. Prog. Ser.* 157: 247–259.
- Gorokhova E. 1999. Mysid growth, stable isotope fractionation, and energetics: implications for food web studies. Ph.D. thesis, Stockholm University, Stockholm, pp. 1–29.
- Grossnickle N.E. 1982. Feeding habits of *Mysis relicta* — an overview. *Hydrobiol.* 93: 101–107.
- Hakala I. 1978. Distribution, population dynamics and production of *Mysis relicta* (Lovén) in southern Finland. *Ann. Zool. Fennici* 15: 243–258.
- Hakala I. 1979. *Ecology and energetics of a Mysis relicta population in Lake Pääjärvi, southern Finland*. Ph.D. thesis, University of Helsinki, Helsinki, pp. 1–7.
- Hakala I., Ryabinkin A. & Salemaa H. 1993. Population structure and life cycle of *Mysis relicta* in Lake Paanajärvi. *Oulanka Reports* 12: 115–118.
- Hansson S., Larsson U. & Johansson S. 1990a. Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J. Plankton Res.* 12: 1099–1116.
- Hansson S., Rudstam L. G. & Johansson S. 1990b. Are marine planktonic invertebrates food limited? The case of *Mysis mixta* (Crustacea, Mysidacea) in the Baltic Sea. *Oecologia* 84: 430–432.
- Hansson S., Hobbie J.E., Elmgren R., Larsson U., Fry B. & Johansson S. 1997. The stable nitrogen isotope ratio as a marker of food-web interactions and fish migration. *Ecology* 78: 2249–2257.
- Heinle D.R., Harris R.P., Ustach J.F. & Flemer D.A. 1977. Detritus as food for estuarine copepods. *Mar. Biol.* 40: 341–353.
- Heiskanen A.-S. & Tallberg P. 1999. Sedimentation and particulate nutrient dynamics along a coastal gradient from a fjord-like bay to the open sea. *Hydrobiol.* 393: 127–140.
- Jónasdóttir SH 1994. Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar. Biol.* 121: 67–81.
- Kansanen P.H., Jaakkola T., Kulmala S. & Suutarinen R. 1991. Sedimentation and distribution of gamma-emitting radionuclides in bottom sediments of southern Lake Päijänne, Finland, after the Chernobyl accident. *Hydrobiol.* 222: 121–140.
- Kjørboe T. 1989. Phytoplankton growth rate and nitrogen content: implications for feeding and fecundity in

- a herbivorous copepod. *Mar. Ecol. Prog. Ser.* 55: 229–234.
- Kleppel G.S. 1993. On the diets of calanoid copepods. *Mar. Ecol. Prog. Ser.* 99: 183–195.
- Koski M. 1999. Carbon:nitrogen ratios of Baltic Sea copepods — indication of mineral limitation? *J. Plankton. Res.* 21: 1565–1573.
- Koski M., Engström J. & Viitasalo M. 1999. Reproduction and survival of the calanoid copepod *Eurytemora affinis* fed with toxic and non-toxic cyanobacteria. *Mar. Ecol. Prog. Ser.* 186: 187–197.
- Landry M.R. 1981. Switching between herbivory and carnivory by the planktonic marine copepod *Calanus pacificus*. *Mar. Biol.* 65: 77–82.
- Lehtonen K.K. 1997. Ecophysiology of two benthic amphipod species from the northern Baltic Sea. *Monogr. Boreal Env. Res.* 7.
- Lindley J.A., John A.W.G. & Robins D.R. 1997. Dry weight, carbon and nitrogen content of some calanoid copepods from the seas around southern Britain in winter. *J. Mar. Biol. Ass. UK* 77: 249–252.
- Macdonald P.D.M. & Green P.E.J. 1988. *User's guide to program MIX: An interactive program for fitting mixtures of distributions*. Guenther printing, Ontario, Canada.
- Mauchline J. 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.* 18: 1–677.
- McKinnon A.D. 1996. Growth and development in the subtropical copepod *Acartia gibber*. *Limnol. Oceanogr.* 41: 1438–1447.
- Niemi Å. 1976. *Växtplanktonets ekologi och miljö i Tvärminneområdet*. Ph.D. thesis, University of Helsinki, Helsinki. 73 pp.
- Rudstam L.G., 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 L.G., 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 L.G., 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., 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.
- Sanders R.W., Williamson C.E., Stutzman P.L., Moeller R.E., Goulden C.E. & Aoki-Goldsmith R. 1996. Reproductive success of 'herbivorous' zooplankton fed algal and nonalgal food resources. *Limnol. Oceanogr.* 41: 1295–1305.
- Sterner R.W. & Robinson J.L. 1994. Thresholds for growth in *Daphnia magna* with high and low phosphorus diets. *Limnol. Oceanogr.* 39: 1228–1232.
- Stoecker D.K. & Capuzzo J.M. 1990. Predation on Protozoa: its importance to zooplankton. *J. Plankton. Res.* 12: 891–908.
- Urabe J. & Watanabe Y. 1992. Possibility of N and P limitation for planktonic cladocerans: An experiment test. *Limnol. Oceanogr.* 37: 244–251.
- Viherluoto M., Kuosa H., Flinkman J. & Viitasalo M. 2000. Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Mar. Biol.* 136: 553–559.
- Viherluoto M. & Viitasalo M. 2001. Temporal variability in functional responses and prey selectivity of the pelagic mysid, *Mysis mixta*, in natural prey assemblages. *Mar. Biol.* 138: 575–583.
- 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. & Rautio M. 1998. Zooplanktivory by *Praunus flexuosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. *Mar. Ecol. Prog. Ser.* 174: 77–87.
- Wiadnyana N.N. & Rassoulzadegan F. 1989. Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. *Mar. Ecol. Prog. Ser.* 53: 37–45.

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