

# On the ecology of *Mysis mixta* (Crustacea, Mysidacea) in a coastal area of the northern Baltic proper

Lars G. Rudstam & Sture Hansson

*Askö Laboratory, University of Stockholm, S-106 91 Stockholm, Sweden*

In the northern Baltic proper, the mysid shrimp *Mysis mixta* has a one year life cycle. The young are released in early spring and grow from about 4 mm in May to 15–20 mm in December, when they are mature. The abundance in 25–40 m deep coastal waters is between 20 and 100 ind./m<sup>2</sup>, although sometimes over 200 ind./m<sup>2</sup> has been recorded. The mysid undertake nocturnal vertical migrations, from the bottoms where they are found during the day, and up in the pelagic zone at night, however avoiding light intensities above 10<sup>-4</sup> lux. The diet of *M. mixta* is dominated by zooplankton, mainly copepods, and together with fish they probably contribute to the autumn decline in the abundance of zooplankton.

## 1. Introduction

The introduction of the freshwater mysid shrimp *Mysis relicta* Lovén into lakes has in some cases caused dramatic changes in both zooplankton species composition and in the relative abundances of the different fish species present (e.g. Goldman et al. 1979, Kinsten & Olsen 1982, Lasenby et al. 1986). There is also increasing evidence for the importance of mysids as zooplankton predators in estuaries (Fulton 1983, Siegfried & Kopache 1980). Mysids must be abundant in the Baltic since they are major forage species of herring and smelt (Aneer 1975, Cortés

1988). It is therefore likely that mysids are important zooplankton predators in the Baltic Sea too.

We have been studying mysids in a coastal area of the northern Baltic proper since 1983. The study area, located 100 km south of Stockholm (58°50'N, 17°40'W), includes a bay influenced by nutrient discharge from a sewage treatment plant and a reference area not directly influenced by this discharge. Chemical and physical parameters, primary production, and zooplankton abundances are being measured in the study area in conjunction with other projects at the Askö Laboratory, University of Stockholm. In this short review, we

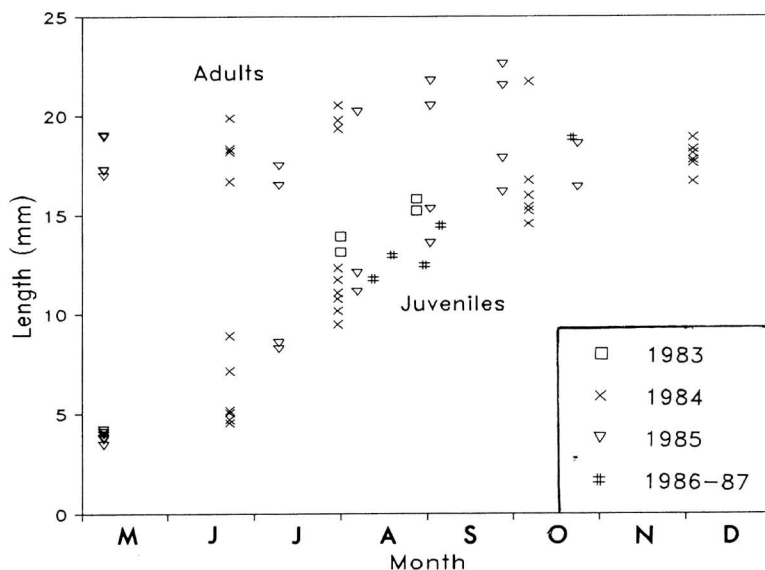


Fig. 1. Total length (tip of rostrum to tip of telson) of *M. mixta* caught in 1983 to 1987 at different stations.

summarize our results to date concerning the ecology of the dominant mysid, *Mysis mixta* Lilljeborg, in this area.

## 2. Life history, abundance and vertical migration

In our area *M. mixta* has a one year life cycle (Rudstam et al. 1986). Young are released in the early spring. 70% of the females caught at the end of April, 1985, had released their young. The juveniles grow through the summer and mature at the beginning of December. Males do not survive the winter and probably die shortly after copulation. The seasonal growth pattern was similar in the years 1983 to 1987 (Fig. 1).

Mysids were the dominating organisms in night-time Bongo net samples (collected from a depth of 25–40 m, 300 µm mesh, Rudstam et al. 1986, 1989, Hansson et al. 1990a) and often constituted over 90% of the animals caught (excluding copepods and cladocerans). *M. mixta* was the most common species throughout the year but small *Neomysis integer* (Leach) were abundant in the summer and early autumn. *M. relicta* was present in smaller numbers, primarily in the inner part of the bay where salinities are slightly lower

(0.05%) than in the outer areas. The abundance of *M. mixta* ranged between 20 and 100 ind/m<sup>2</sup> in the summer and autumn, although we have sometimes obtained abundances of over 200 ind/m<sup>2</sup> (Fig. 2). Comparable densities are found in other parts of the Baltic (Kotta & Simm 1979, Salemaa et al. 1986). Lower abundances in the open water were obtained in the winter and early spring (probably due to low food availability in the water column), as well as in the summer when light nights inhibit vertical migration (Rudstam et al. 1989).

The nutrient enriched bay has greater spring diatom blooms (which should enhance survival of newly released mysids) and higher zooplankton abundances than the reference area. We therefore expected to find increased abundances of *M. mixta* in the nutrient enriched bay compared to the reference area. Though larger abundances of *M. mixta* were found in the bay in 1983 and 1984, this was not the case in 1985 and 1986 (Hansson et al. 1990a, Rudstam et al. 1986, 1989). Thus, we did not find any clear relationship between mysid abundance and nutrient enrichment.

*M. mixta* undertake nocturnal vertical migrations into the water column (Hansson et al. 1990a, Rudstam et al. 1989). The upper limit of this ascent varied with season. Changing light levels

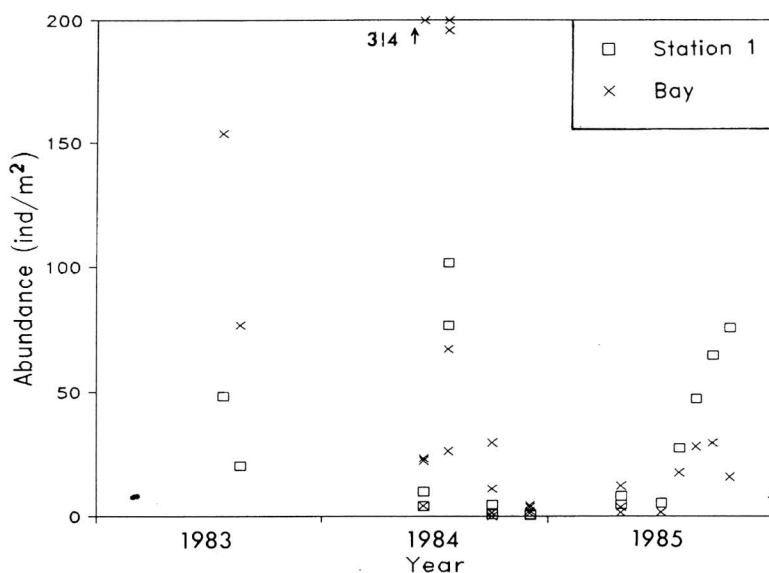


Fig. 2. Abundances of *M. mixta* in the water column from 1983 to 1985. Mysids were sampled with Bongo nets at night in the nutrient enriched bay (Bay, stations 2–5) and in the reference area (station 1).

were sufficient to explain these differences as the mysids avoided light levels above  $10^{-4}$  lux from early summer to late autumn. Compared to light levels, water temperature was a poor predictor of the upper limit of mysid ascent.

We also found high densities of *M. mixta* at the bottom during the night (Rudstam et al. 1989). We do not know whether these mysids move back and forth between the bottom and the water column during the night or if part of the population remains close to the bottom both day and night. In any case, the occurrence of these benthic individuals at night complicates attempts to quantify mysid abundances since we have to rely on results from two different sampling gears.

### 3. Diet and effects on zooplankton

The freshwater *M. relicta* is an opportunistic omnivore capable of utilizing zooplankton, phytoplankton, detritus and benthos (Grossnickle 1982). There is little comparable literature data on the diet of *M. mixta*. We found open water zooplankton (primarily copepods and cladocerans) to be the dominating food item by weight (90–100%) in *M. mixta* larger than 7 mm, although phytoplankton, detritus and benthic cope-

pods were present in small amounts (Hansson et al. 1990a, Rudstam et al. 1989). This was true whether the animals were caught at the bottom in the evening, at the bottom at night, or in the water column at night. Gut fluorescence from animals caught in August showed small amounts of chlorophyll-a compared to primarily herbivorous zooplankton. Herbivory could still be important for the newly released individuals as we did not find zooplankton remains in 3–4 mm long juveniles caught in April, 1985. In laboratory experiments using 1–3 L aquaria, Wennberg (1987) found that juvenile *M. mixta* ingested more algae (the diatom *Skeletonema costatum*) than adults, but the predation rates were not affected by the presence of algae (experiments with juvenile *M. mixta* and the rotifer *Synchaeta* sp. as prey).

We used the observed growth rates in 1983 to 1985 to calculate consumption rates using a bioenergetic model structured after the model presented by Kitchell et al. (1977) (Rudstam 1988, 1989). Consumption rates increased with increasing food availability (biomass of cladocerans and copepods) which show that *M. mixta* is food limited in this part of the Baltic (Hansson et al. 1990b).

Our initial analysis indicated that *M. mixta* may consume between 20 and 50% of the zoo-

plankton production in this area on an annual basis (Rudstam et al. 1986). Calculations based on data from 1983 (Hansson et al. unpubl.), 1984 (Rudstam et al. 1986) and 1985 (Rudstam et al. 1988) show that *M. mixta* consumed a larger proportion of the zooplankton production in the reference area than in the nutrient enriched bay. Mysid annual consumption of zooplankton in 1985 equalled that of fish in the reference area and was about half that of fish in the bay. Mysids and clupeid fish together consumed the whole annual zooplankton production both in the bay and in the reference area in 1985 (Rudstam et al. 1988).

Predation by mysids varied with season (data from 1985, Rudstam et al. 1988). Predation pressure was low during early summer because light nights inhibited mysid vertical migration. As the nights became darker and longer in late summer, we found more mysids in the water column and predation pressure increased. Clupeid fish (herring and sprat), the other major zooplanktivores in this area, also exhibited an increase in predation rates in late summer. This resulted in low total rates of zooplanktivory during the early summer build-up phase of the zooplankton populations (when estimated consumption was lower than estimated production) and high rates during the autumn decline (when consumption was higher than production).

*M. mixta* was a selective zooplanktivore and preferred the copepod *Eurytemora affinis hirundoides* (Nordquist) and cladocerans over the other common copepod species (*Acartia* sp.) (Hansson et al. 1990a, Rudstam et al. 1988). Young clupeids had similar prey preferences. Since we observed higher annual zooplankton consumption (by both mysids and fish) in the nutrient enriched bay compared to the reference area, we expected the relative proportion of the selected zooplankton species would decrease in the bay. However, the proportion of these species increased. Hence, the differences in zooplankton species composition between the nutrient enriched bay and the reference area appear to be determined by other factors early in the season when predation rates are low, whereas the autumn decline in abundances of all zooplankton and the faster decline of cladocerans compared to copepods may be caused by increased predation from mysids and fish in late

summer and autumn (Rudstam et al. 1988, Hansson et al. 1990a).

#### 4. Final remarks

Our results show that *M. mixta* is one of the major zooplanktivores in coastal areas of the northern Baltic proper. It is also an important prey species for herring, the other major zooplanktivore in this area. *M. mixta* then is both a potential competitor to young herring and a major prey of older herring. The predator-prey interactions affecting the structure of the pelagic community in the Baltic are therefore complex and several concepts currently popular in community ecology, such as indirect interactions (Kerfoot & Sih 1987), life history omnivory (Werner & Gilliam 1984, Sprules & Bowerman 1988), and interactions in size structured populations (Persson & Ebenman 1989), have to be invoked to understand these interactions. Further studies on the glacial relict *M. mixta* in the Baltic will therefore increase our understanding of both the Baltic ecosystem and of processes important for the structure of aquatic communities in general.

*Acknowledgements.* The studies reviewed in this paper have been supported by the Swedish Environmental Protection Board and by contributions from the following foundations: Salén, Trygger, Engqvist, Hierta-Retzius, Längman, Helge A:son Johnson, Liljevalch, and SAS. We also wish to thank Ulf Larsson, Sif Johansson and Karin Danielsson, our co-authors on papers included in this review, and H. Hill for linguistic corrections.

#### References

- Aneer, G. 1975: Composition of food in the Baltic herring (*Clupea harengus* v. *membras* L.), fourhorn sculpin (*Myoxocephalus quadricornis* L.) and Eel-pot (*Zoarces viviparus* L.) from deep soft bottom trawling in the Askö-Landsort area during two consecutive years. — Merentutkimuslaitoksen Julkaisuja/Havsforskningsinstitutets Skrifter 239:146–154.
- Cortés, A. 1988: Possible segregation along niche axis (food, space and time) within a pelagic fish community in the northern Baltic proper. — Mimeographed report, University of Stockholm. 25 pp.
- Fulton, R. S. 1983: Interactive effects of temperature and predation on an estuarine zooplankton community. — J. Exp. Mar. Biol. Ecol. 72:67–83.

- Goldman, C. R., Morgan, M. D., Threlkeld, S. T. & Angeli, N. 1979: A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California, Nevada. — *Limnol. Oceanogr.* 24:289–297.
- Grossnickle, N. E. 1982: Feeding habits of *Mysis relicta* — an overview. — *Hydrobiologia* 93:101–107.
- Hansson, S., Larsson, U. & Johansson, S. 1990a: Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. — *J. Plankt. 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* (in press)
- Kerfoot, W. C. & Sih, A. 1987: Predation. Direct and indirect impacts on aquatic communities. — University Press New England, Hanover, NH, USA. 385 pp.
- Kinsten, B. & Olsen, P. 1982: Impact of *Mysis relicta* introduction on the plankton of two mountain lakes, Sweden. — *Rep. Inst. Freshw. Res. Drottningholm* 59:64–74.
- Kitchell, J. F., Stewart, D. J. & Weininger, D. 1977: Applications of a bioenergetic model to yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum vitreum*). — *J. Fish. Res. Board Can.* 34:1922–1935.
- Kotta, I. A. & Simm, M. A. 1979: On the seasonal population dynamics of planktonic and nektobenthic crustaceans in the northeastern Gulf of Riga and the Gulf of Parnu. (In Russian) — *Rybokhoz. Issled. Bass. Balt. Morya* 14:54–62.
- Lasenby, D. C., Northcote, T. G. & Fürst, M. 1986: Theory, practice and effects of *Mysis relicta* introductions to North American and Scandinavian lakes. — *Can. J. Fish. Aquat. Sci.* 43:1277–1284.
- Persson, L. & Ebenman, B. 1989: Dynamics of size (age) structured populations. — Springer Verlag. 284 pp.
- Rudstam, L. G. 1988: Patterns of zooplanktivory in a coastal area of the northern Baltic proper. — Ph.D. Thesis, Department of Zoology, University of Stockholm, Stockholm, Sweden. 164 pp.
- 1989: A bioenergetic model for *Mysis* growth and consumption applied to a Baltic population of *Mysis mixta*. — *J. Plankt. Res.* 11:971–983.
- 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., Hansson, S., Johansson, S. & Larsson, U. 1988: Seasonal dynamics of zooplanktivory along a nutrient gradient in the northern Baltic proper. — In: Rudstam, L. G. (ed.), Patterns of zooplanktivory in a coastal area of the northern Baltic proper. Ph.D. Thesis, Department of Zoology, University of Stockholm, Stockholm, Sweden. 164 pp.
- Rudstam, L. G., Danielsson, K., Hansson, S. & Johansson, S. 1989: Vertical migration, diet and diel feeding patterns of *Mysis mixta* in the Baltic Sea. — *Mar. Biol.* 101:43–52.
- 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.
- Siegfried, C. A. & Kopache, M. E. 1980: Feeding of *Neomysis mercedis* (Holmes). — *Biol. Bull., Woods Hole* 159:193–205.
- Sprules, W. G. & Bowerman, J. E. 1988: Omnivory and food chain length in zooplankton food webs. — *Ecology* 69:418–426.
- Wennberg, L. 1987: Effekten av en alternativ födokälla på predationshastigheten hos *Mysis mixta*. — Mimeographed report, University of Stockholm. 13 pp.
- Werner, E. E. & Gilliam, J. F. 1984: The ontogenetic niche and species interactions in size-structured populations. — *Ann. Rev. Ecol. System.* 15:393–426.