

Seasonal changes in the population structure and life cycle of *Neomysis integer* in Pärnu Bay, northeastern Baltic Sea

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Abstract. In winter and spring the density of overwintering generations of *Neomysis integer* was low. In spring the increase in the biomass of the generations was due to the growth in length and not due to reproduction. The mysid bred continuously through the summer and had two recruitment peaks. The mortality of the species abruptly increased from September. The timing of reproduction depended on the harshness of winter (NAO winter index) and spring temperature. Reproduction took place earlier in milder winter and spring conditions. Large-scale climate patterns such as the NAO index were a better predictor of the life cycle of *N. integer* in Pärnu Bay than local environmental variables.

Key words: Baltic Sea, nectobenthos, NAO index, *Neomysis integer*, reproduction.

INTRODUCTION

Because of their high abundance and wide distribution, mysids are an important component in the ecosystem of the Baltic Sea. They link benthic and pelagic environments as well as primary and secondary production to higher trophic levels (e.g. Kotta, 2003). *Neomysis integer* (Leach) is considered to be the most widespread mysid species in the Baltic forming large dense schools practically in the whole coastal range of the Baltic Sea (Yarvekyulg, 1979; Köhn, 1992; Kotta & Kotta, 1999). In the northern Baltic *N. integer* has not been found in the eastern part of the Gulf of Finland including Neva Bay (Segerstråle, 1945; Sanina, 1961; Yarvekyulg, 1979), northern Bothnian Bay (Segerstråle, 1945; Yarvekyulg, 1979) but likewise in any smaller bays of low salinity (Yarvekyulg, 1979).

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Knowledge about the life cycle of key species is the first step towards reliable estimates of secondary production and understanding the functioning of the aquatic ecosystem in general. Life cycle characteristics of a species can vary considerably between different sites; hence, knowledge of the local population structure and life cycle is a prerequisite for experimental work and ecosystem modelling. To date there are a few publications on temporal changes in the population structure and life cycle of *N. integer* in the Baltic Sea area. These studies mainly concentrated on the southern or central Baltic Sea (Kinne, 1955; Wiktor, 1961; Jansen et al., 1980; Arndt & Jansen, 1986; Rudstam et al., 1986). In the northern Baltic Sea, however, there is just one dataset available from the 1970s (Kotta, 2003). The aim of this paper is to describe the seasonal variation in the population structure and life cycle of *N. integer* in the Gulf of Riga, compare the timing of generation development between different years, and relate these changes to selected environmental variables.

MATERIAL AND METHODS

Pärnu Bay is a shallow semi-enclosed water basin in the northeastern Gulf of Riga (Fig. 1). The surface area of the bay is about 700 km² and its volume is 2 km³. The maximum depth increases gradually from 7.5 m in its inner part to 23 m in the outer part. The hydrological conditions of the bay are formed under the complex influence of meteorological processes, the river discharge (Pärnu River, freshwater inflow 2 km³ annually), and the water exchange with the open part

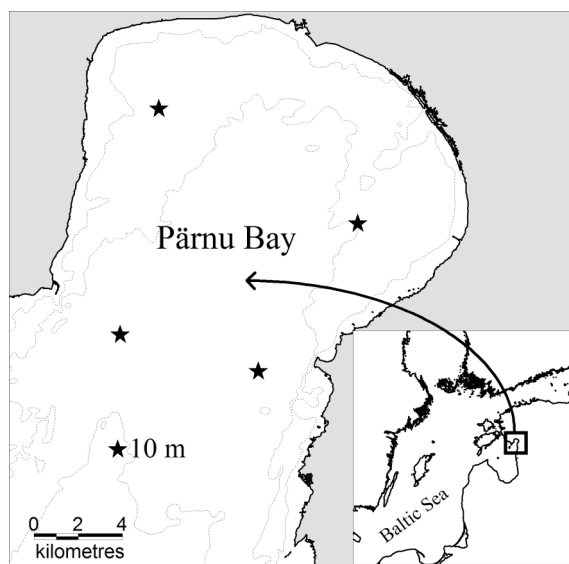


Fig. 1. Study area.

of the Gulf of Riga. The currents are generally weak in the area and are mainly wind induced. The bay is suffering from a heavy anthropogenic eutrophication. The town of Pärnu with its 70 000 inhabitants and the Pärnu River are the major sources of pollution in the bay. The contents of N_{total} , P_{total} , and $\text{SiO}_{\text{silicate}}$ increased on average two times in the seawater and the primary production of phytoplankton increased substantially in the 1970s and 1980s. Since 1990 the wastewater of the town of Pärnu has been mechanically and biologically treated. However, the Pärnu River, which is responsible for about 10% of the total riverine runoff to the Gulf of Riga and annually brings about 40–50 t of P_{total} and more than 4000 t of N_{total} into Pärnu Bay, is still a significant source of nutrients (e.g. Kotta et al., 2007).

As the Gulf of Riga is a shallow water basin the changes in air temperature have a direct influence on the dynamics of both surface and deep water. In a typical year the water is cold and no clear thermocline occurs till May. Later the surface water temperature rises to about 17–20 °C and a thermocline builds up. The thermocline reaches the bottom of the deepest parts of the bay in August and disintegrates in September–October due to intensive wind mixing. In the course of autumn storms the surface water cools down (e.g. Kotta, 2003).

The population structure and life cycle of *N. integer* were studied in 5 stations in Pärnu Bay during 1973 and 2005. A long-term series with fortnightly sampling is available for a 10 m station in the middle of Pärnu Bay from the ice-free seasons of 1973–1987. As *N. integer* spends most of its life in the shallow sea in the Gulf of Riga, this station is considered as the type area for the species (Fig. 1).

The samples for mysid density were collected in daytime during ice-free seasons. A modified Rass dredge (Rass, 1933) was used for sampling. The dredge is made of a nylon netbag, which is attached to a rectangular metal frame. An attached floater at the upper part of the frame keeps the dredge in an upward position and assures that the gear slides gently on the sediment surface without digging into it. The netbag has a mouth size of 20 × 60 cm. The dredge was towed on a rotating metal cylinder (stone, gravel, sand, hard clay bottoms) or sledge (silty hard clay bottoms). The dredge is unsuitable for sampling on silty soft sediment where the mesh will be clogged up.

At the beginning of sampling the dredge was slowly lowered while the ship was moving. The speed was slowed down when the length of the submerged wire exceeded the depth two times. When the dredge touched the bottom, the speed was kept at approximately 1 km h⁻¹. By the end of sampling (100 m, 5 min) the speed was increased so that the dredge raised above the bottom and the wire was pulled in. Earlier estimates have shown that the amount of water that passes through the mesh during the sampling on the bottom is on average 17 ± 3 m³. All samples were stored in 4% buffered formaldehyde–seawater solution. The abundance and biomass (wet weight) of each mysid species were determined.

During sampling the temperature in the bottom layer was measured. The temperature measured six times daily at Kihnu and Pärnu hydrometeorological stations was related to our measurements (nonlinear regressions, $r^2 > 0.95$). This relationship was used to calculate water temperatures on a daily basis. Data on

salinity were obtained from the Estonian Hydrometeorological Institute. Nutrient load values were obtained from Yurkovskis (2004).

As a proxy of atmospheric behaviour (Barnston & Livezey, 1987; Ottersen et al., 2001) the indices of the North Atlantic Oscillation (NAO) were used. The NAO is primarily a winter phenomenon as its connection with the wind, temperature, and precipitation fields is strongest in winter. During the years of high NAO there is a substantial increase in the rainfall and consequently the freshwater inflow into the Baltic Sea (Hänninen et al., 2000). The increased pressure differences result in stronger winter storms and higher winter temperatures in the northern Europe (Rogers, 1984). The NAO data were obtained from the World Monthly Surface Station Climatology. The winter indices of the NAO (NAO December of previous year, NAO December through February, NAO December through March, NAO in March) are based on the difference of normalized sea level pressure (SLP) between Lisbon, Portugal, and Stykkisholmur/Reykjavik, Iceland, since 1864. The SLP anomalies at each station were normalized by division of each seasonal mean pressure by the long-term mean (1864–1983) standard deviation. Normalization is used to avoid the series being dominated by the greater variability of the northern station.

The length–frequency distribution of *N. integer* was estimated from length measurements of 250 mysids selected randomly from a sample on each sampling date in 1973 and 2005. The following classes and developmental stages of mysids were distinguished: juveniles – sexual characteristics are not developed; the distinction of juveniles and the remaining population was made between 6 and 9 mm length-classes; subadult males – the 4th pleopods short; adult males – elongated 4th pleopods reach beyond the posterior edge of the last abdominal segment; females without marsupia (stage 1); females with the marsupia developing but no larvae present (stage 2); females with larvae present in the marsupium (stage 3); females with fully developed but empty marsupia (stage 4). Within each developmental stage we estimated the total length of all mysids measured as the distance from rostrum to telson. The changes in the length–frequency structure were used to describe the generation development of mysid populations in the study area.

For univariate analysis the statistical program Statistica version 6 was used (StatSoft Inc., 2004). We employed correlation and linear regression analyses to describe the relationships between nutrient loads and other abiotic and biotic environmental variables (Sokal & Rohlf, 1981).

RESULTS

In March 1973 the population of *N. integer* consisted predominantly of immature females, which did not have yet completely developed marsupia, together with both subadult and adult males. Two generations could be distinguished with modal classes at 10–11 and 15–16 mm (Fig. 2).

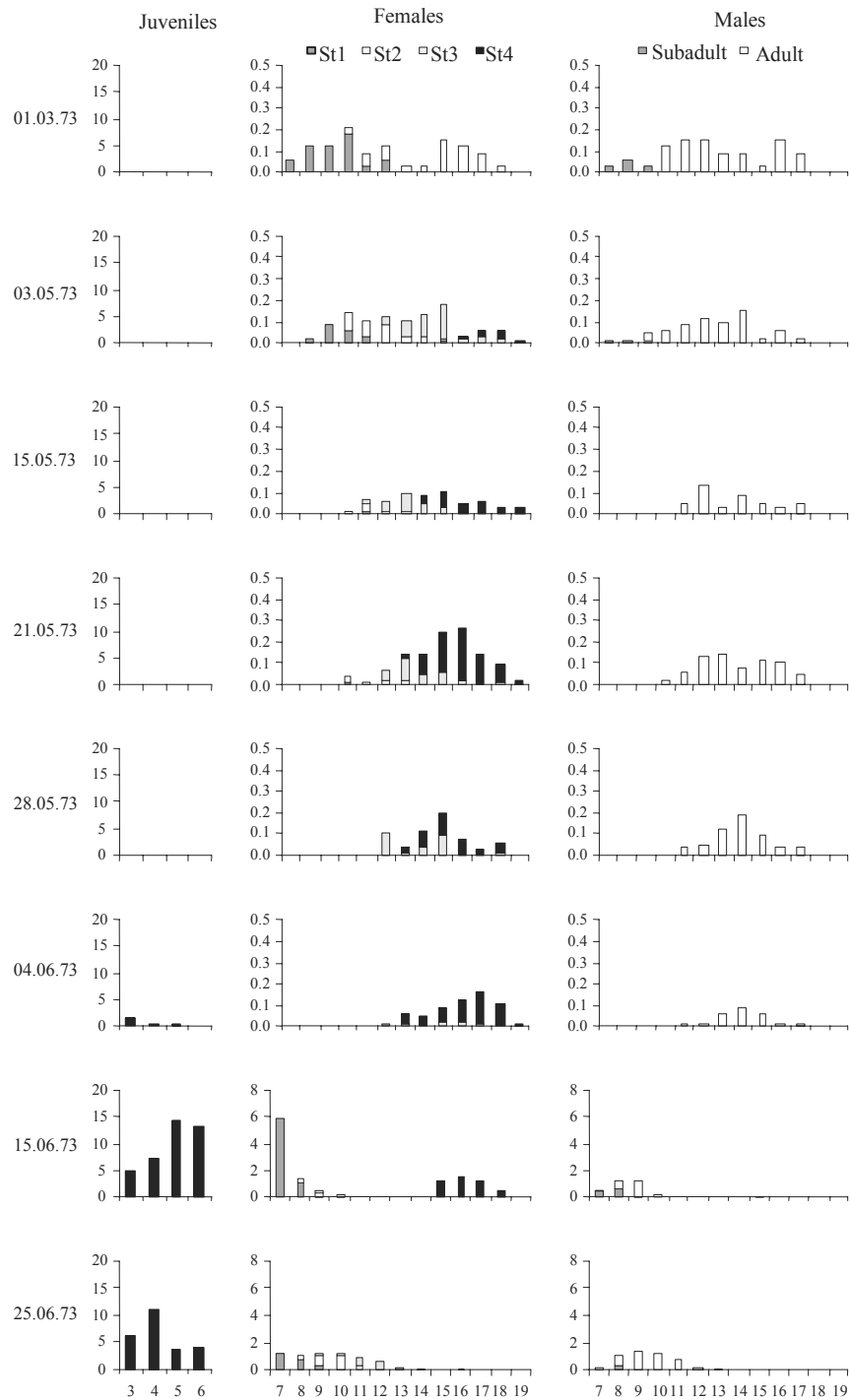


Fig. 2. Seasonal changes in the abundance distribution (y -axis, ind. m^{-3}) by length (x -axis, mm) and developmental stages of *N. integer* in 1973.

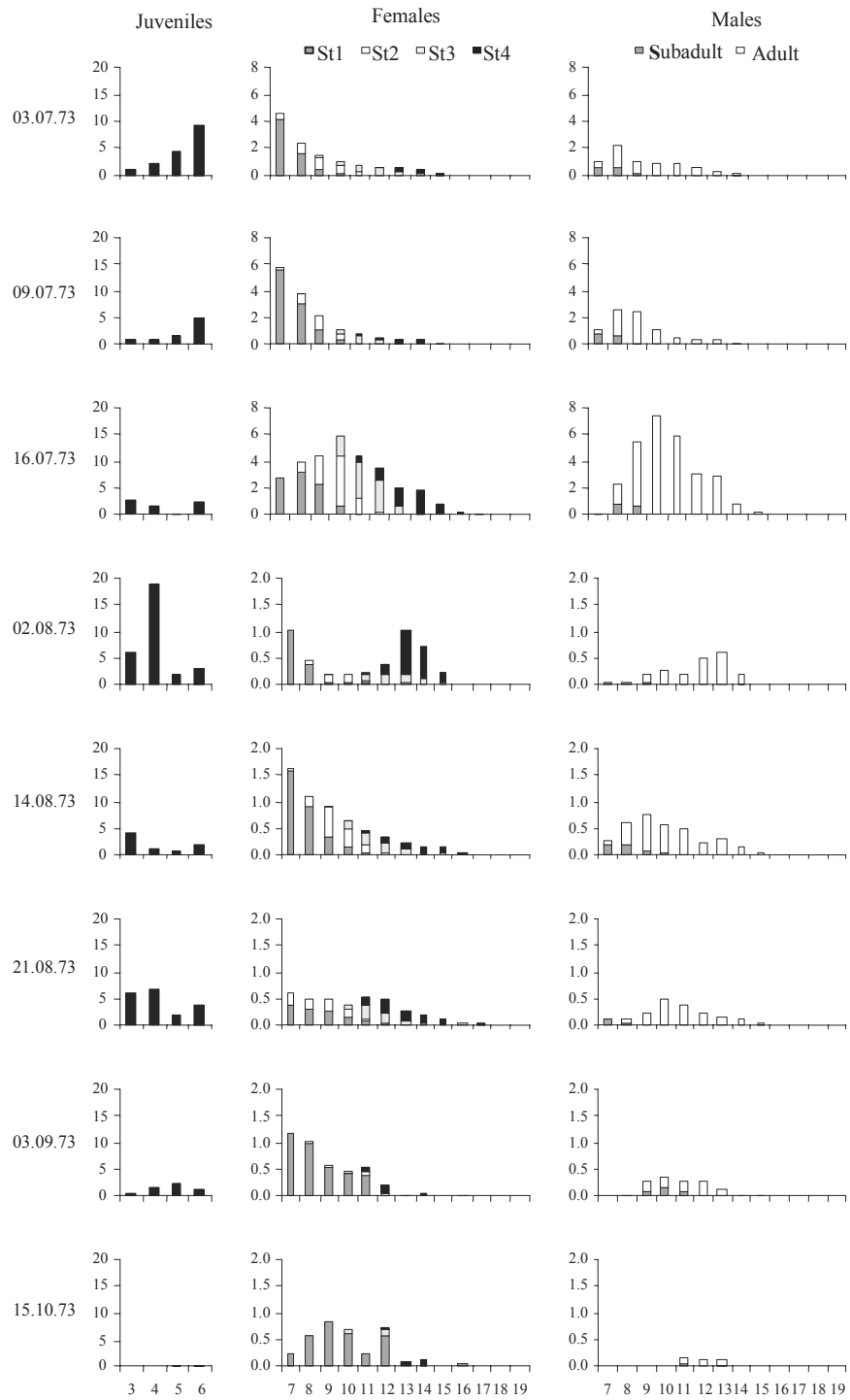


Fig. 2. Continued.

In the course of April–May the overwintering generations grew significantly and bimodalities of the length–frequency distribution disappeared. The modal class of the mixed generations was observed at 14–16 mm. In winter and spring mysid densities remained low and their biomass increased gradually due to growth.

First gravid females were observed at the beginning of May. In mid-May nearly all individuals of *N. integer* were adults and the gravid females accounted for about 27% of the population. Overwintering males were first eliminated from the population. If the sex ratio of males and females was 1 : 1 in March then in early June males accounted for only about 29% of the population of *N. integer*. When females had released their young their mortality increased abruptly. The overwintering generation died out by the end of June.

First juveniles were caught in early June. Throughout June–July juveniles grew gradually into subadult stages. Simultaneously subadults became adult males and females. Breeding took place more or less continuously until early September. Following more intensive breeding, indicated by a higher proportion of gravid females in the population, peaks of juveniles were observed. Recruitment maxima occurred on 15 and 20 June and on 2 and 21 August. Together with recruitment the abundance and biomass values of mysids increased exponentially. The highest abundance was estimated at 65.0 ind. m⁻³ and biomass at 0.424 g m⁻³ in mid-July.

In late August or early September the majority of adults died out. Males had significantly higher mortality than females. By 15 October, the ratio of males to females was only 0.1. Females with undeveloped marsupia dominated in the mysid population. In the same period the number of mysids declined to less than 5 ind. m⁻³ and biomass down to 0.03 g m⁻³.

In 2005 the development of new generations was delayed by about a month. Although first juveniles were found on 15 June, the peak of reproduction occurred from 2 to 8 July. The second peak of reproduction was observed on 28 August. The densities of *N. integer* were substantially higher in 2005 than in 1973 indicating higher productivity of the system in 2005 (Figs 3 and 4).

In 1973–1987 the first juveniles were caught between 23 May and 1 August (Fig. 5). Among the studied variables (temperature, salinity, nutrients, NAO) there was a statistically significant relationship between NAO winter indices and spring temperature and the timing of reproduction. These environmental variables explained about 87% of the reproduction dynamics of the mysid population (polynomial multiple regression analysis, $r^2 = 0.87$, $p < 0.001$). Compared to spring temperature the NAO index gave a stronger relationship with the timing of *N. integer* reproduction. The β values (relative importance of a variable in overall regression analysis) were 0.30 for squared spring temperature, 0.46 for NAO_{December}, 0.62 for squared NAO_{January}, and 0.30 for NAO_{February}. Compared to harsh years (low NAO winter index), the first peak of reproduction took place earlier following a mild winter (high NAO winter index). Reproduction was also shifted earlier with increasing average water temperature between March and June (Fig. 6).

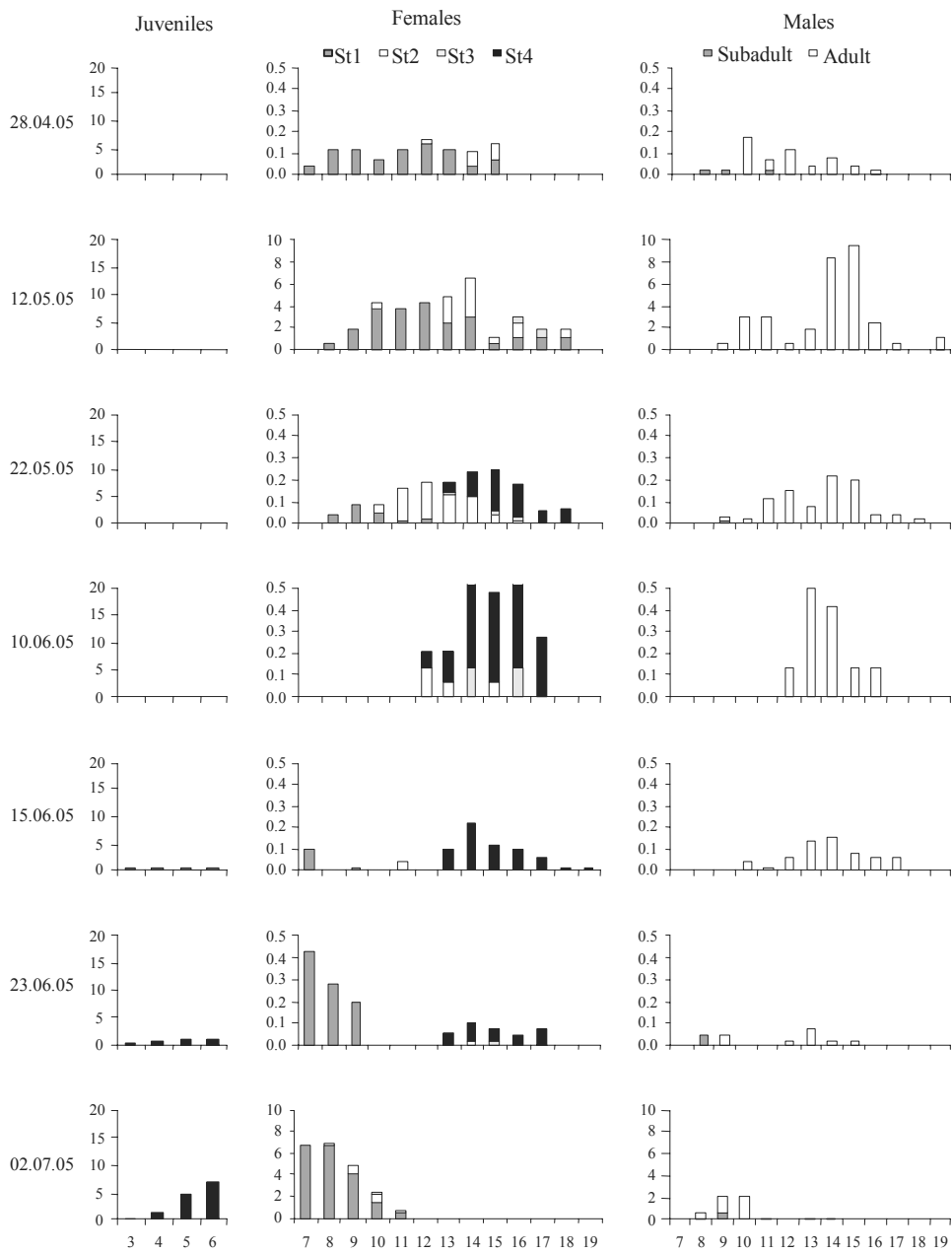


Fig. 3. Seasonal changes in the abundance distribution (y-axis, ind. m⁻³) by length (x-axis, mm) and developmental stages of *N. integer* in 2005.

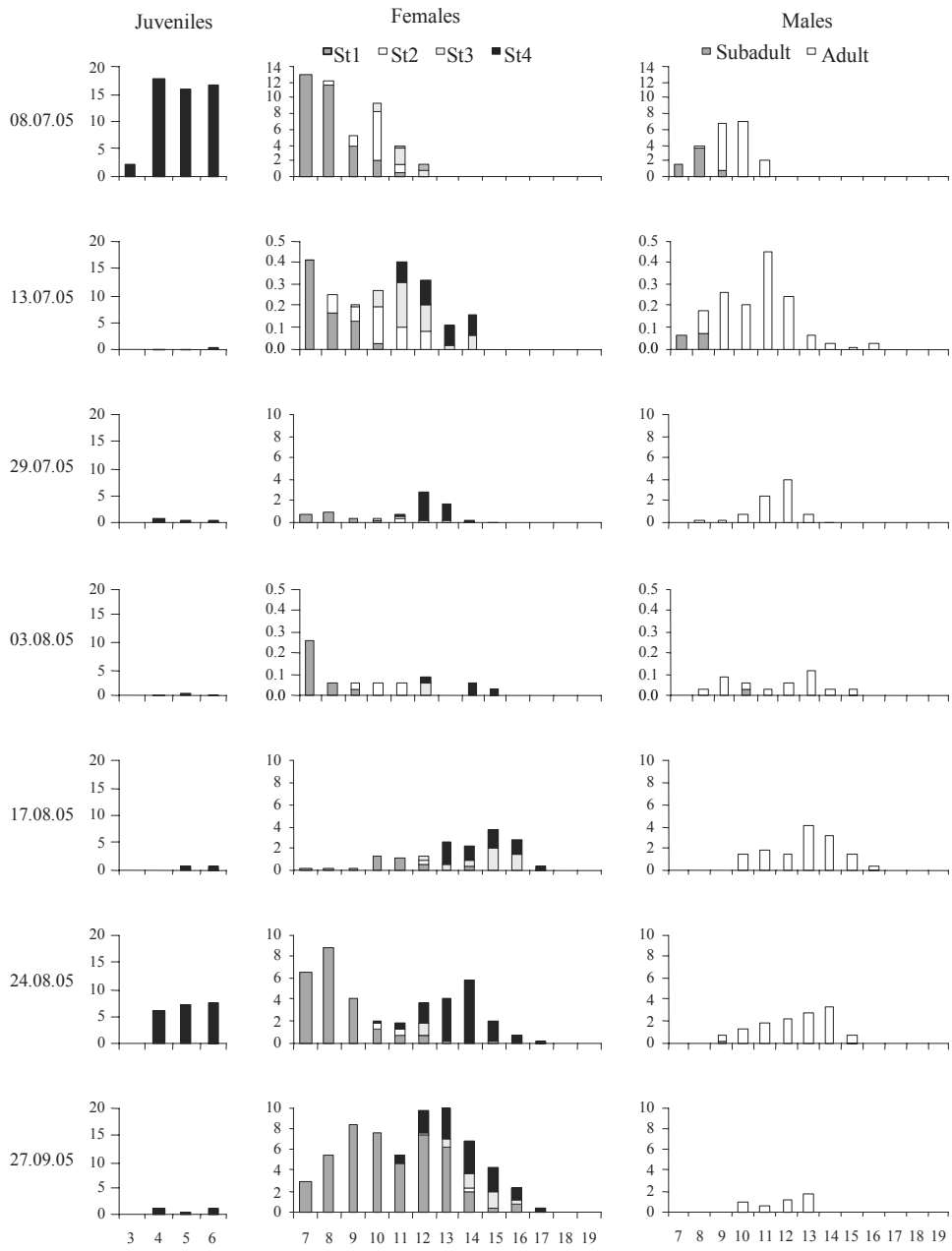


Fig. 3. Continued.

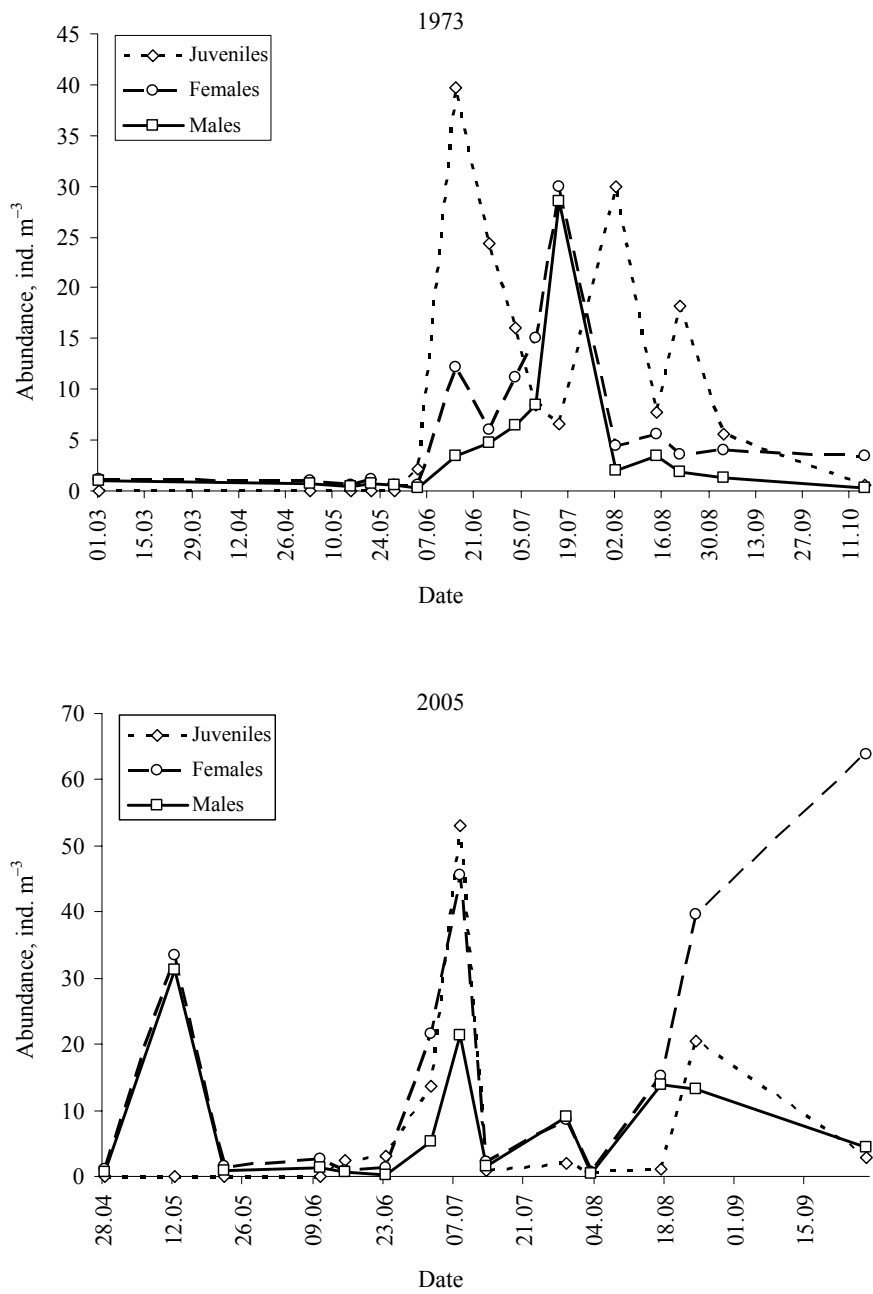


Fig. 4. Seasonal changes in the abundance of different developmental stages of *N. integer* in 1973 and 1975.

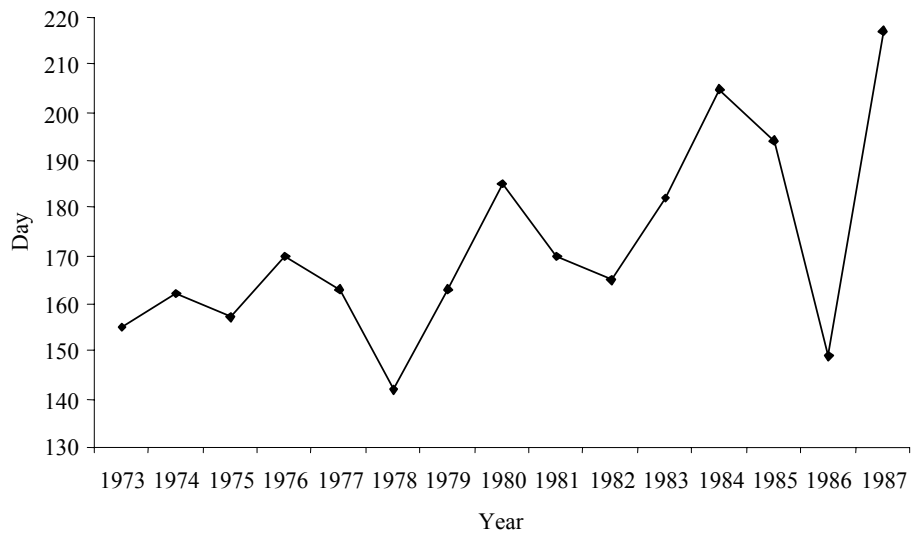


Fig. 5. Interannual variation in the time of the first record of juveniles in a 10 m station during 1973–1987.

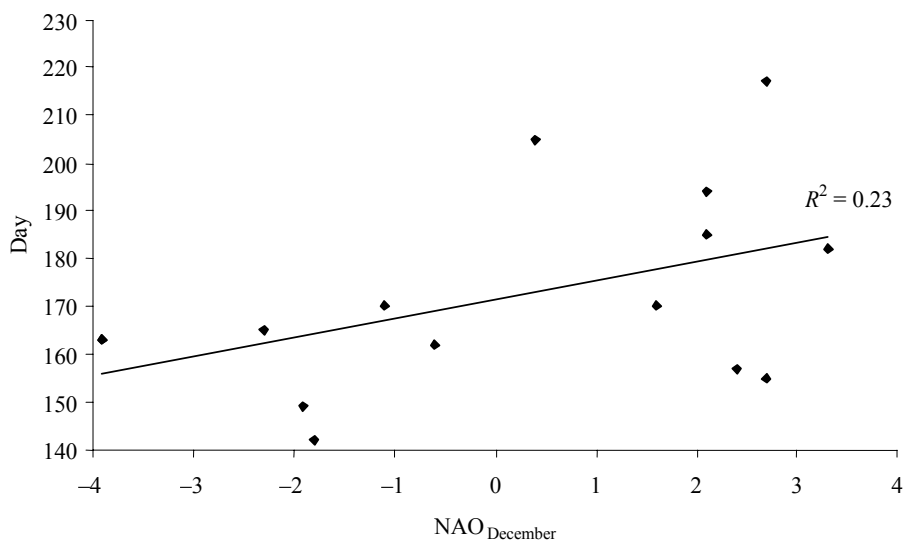


Fig. 6. Regression between the NAO_{December} of the previous year and the time of the first record of juveniles.

DISCUSSION

Among the native mysid shrimps of the Baltic Sea *N. integer* prefers warmer waters than the other mysid species (Kinne, 1955). Therefore, it is expected that the temperature regime in spring and summer may have an effect on the timing and magnitude of the breeding of the species. Our data showed that reproduction of *N. integer* took place earlier in 1973 than in 2005. Compared to multiannual average the spring and summer 1973 were exceptionally warm whereas the spring and summer 2005 corresponded to the typical year of the study period. The NAO winter index was exceptionally high in 1973 and the value resembled the multiannual average in 2005. Thus, besides warm spring and summer conditions, mild and stormy winter characterized the year 1973. Successive breeding of *N. integer* through the summer has been reported elsewhere in European waters. The Baltic population has two recruitment peaks (Kinne, 1955; Wiktor, 1961; Jansen et al., 1980; Arndt & Jansen, 1986; Rudstam et al., 1986) opposed to three generations or even more complex breeding cycles at lower latitudes (Sorbe, 1981; Mauchline, 1980; Mees et al., 1994; Aaser et al., 1995). Differently from its populations in other regions the Baltic population of *N. integer* does not have an early spring generation and the timing of reproduction during summer is slightly shifted.

However, despite the shorter breeding period, *N. integer* is by far the most successful mysid species in the coastal area of the whole Baltic Sea. Thus, it is likely that low temperatures of the Baltic Sea as such do not limit the population growth of *N. integer*. This is also supported by the regression analysis indicating that the NAO values had a higher impact on the mysid population than water temperature. In the northeastern Gulf of Riga the highest abundance and biomass values of *N. integer* are often but not always expected during warm summers (Ojaveer et al., 1999). It is likely that a positive correlation between temperature and the density of zooplankton (i.e. food availability to mysids) is the cause of this relationship (Simm & Ojaveer, 2000; Kotta et al., 2004). There is also experimental evidence that the relationship between temperature and the growth of *N. integer* depends on food availability. At a high food level the growth of mysids increases with temperature whereas the reverse relationship is true at low food levels (Gorokhova, 2002). This study also demonstrated that atmospheric processes in the northern Atlantic, i.e. the NAO values, are more powerful in explaining the seasonal changes in the population structure and life cycle of *N. integer* than locally estimated environmental variables. The NAO values involving complex weather patterns, e.g. temperature and wind effects at high temporal resolution (Ottersen et al., 2001), are likely to describe better the timing and magnitude of phytoplankton and zooplankton spring peaks. Although our previous study indicated that the higher trophic level interactions shade the direct effect of NAO on the biomass level of mesozooplankton and mysids (Kotta et al., 2004), the large-scale climate patterns seem to trigger the spring development of *N. integer* population and thus, control the timing of the life cycles of mysids in Pärnu Bay.

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REFERENCES

- Aaser, H. F., Jeppesen, E. & Søndergaard, M. 1995. Seasonal dynamics of the mysid *Neomysis integer* and its predation on the copepod *Eurytemora affinis* in a shallow hypertrophic brackish lake. *Mar. Ecol. Prog. Ser.*, **127**, 47–56.
- Arndt, E. A. & Jansen, W. 1986. *Neomysis integer* (Leach) in the chain of boddens south of Darss/Zingst (Western Baltic) – ecophysiology and population dynamics. *Ophelia*, **4** Supplement, 1–15.
- Barnston, A. G. & Livezey, R. E. 1987. Classification, seasonality and persistence of low-frequency atmospheric circulation patterns. *Mon. Weather Rev.*, **115**, 1083–1126.
- Gorokhova, E. 2002. Moulting cycle and its chronology in *Mysis mixta* and *Neomysis integer* (Crustacea, Mysidacea): implications for growth assessment. *J. Exp. Mar. Biol. Ecol.*, **278**, 179–194.
- Hänninen, J., Vuorinen, I. & Hjelt, P. 2000. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol. Oceanogr.*, **45**, 703–710.
- Jansen, W., Arndt, E. A., Hahn, W., Bottorf, T. H., Wronna, F. & Raschewski, U. 1980. Untersuchungen zur populationsentwicklung von *Neomysis integer* (Leach) in der Darss-Zingster Boddenkette. *Wiss. Z. Wilhelm-Pieck Univ. Rostock*, **29**, 95–97.
- Kinne, O. 1955. *Neomysis vulgaris* Thompson, eine autökologisch-biologische Studie. *Biol. Zentralbl.*, **74**, 160–202.
- Köhn, J. 1992. Mysidacea of the Baltic Sea – state of the art. In *Taxonomy, Biology and Ecology of (Baltic) Mysids (Mysidacea, Crustacea)* (Köhn, J., Jones, M. B. & Moffat, A., eds), pp. 5–23. Int. Expert Conference, Hiddensee, Germany. Rostock University, Rostock.
- Kotta, I. 2003. Population ecology of mysids (Crustacea, Mysidacea) in the Gulf of Riga, NE Baltic Sea. *Diss. Natural Sci., Tallinn Pedagogical Univ.*, TPU Press, 7.
- Kotta, I. & Kotta, J. 1999. Distribution and migration of mysids in the Gulf of Riga (Northern Baltic). *Proc. Estonian Acad. Sci. Biol. Ecol.*, **48**, 284–295.
- Kotta, J., Simm, M., Kotta, I., Kanošina, I., Kallaste, K. & Raid, T. 2004. Factors controlling long-term changes of the eutrophicated ecosystem of Pärnu Bay, Gulf of Riga. *Hydrobiologia*, **514**, 259–268.
- Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K. & Ojaveer, H. 2007. Gulf of Riga and Pärnu Bay. In *Ecology of Baltic Coastal Waters* (Schiewer, U., ed.), pp. 217–243. Ecological Studies, **197**, Springer, Berlin.
- Mauchline, J. 1980. The biology of mysids and euphausiids. *Adv. Mar. Biol.*, **18**, 681.
- Mees, J., Abdulkerim, Z. & Hamerlynck, O. 1994. Life history, growth and production of *Neomysis integer* in the Westerschelde estuary (SW Netherlands). *Mar. Ecol. Prog. Ser.*, **109**, 43–57.
- Ojaveer, H., Lankov, A., Eero, M., Kotta, J., Kotta, I. & Lumberg, A. 1999. Changes in the ecosystem of the Gulf of Riga from the 1970s to the 1990s. *ICES J. Mar. Sci.*, **56**, 33–40.
- Ottersen, G., Planque, B., Belgrano, A., Post, E., Reid, P. C. & Stenseth, N. C. 2001. Ecological effects of the North Atlantic Oscillation. *Oecologia*, **128**, 1–14.
- Rass, T. 1933. *Guide for the Quantitative Sampling of Roe and Marine Larvae*. GOIN, Moscow (in Russian).

- Rogers, J. C. 1984. The association between the North Atlantic Oscillation and the Southern Oscillation in the northern hemisphere. *Mon. Weather Rev.*, **112**, 1999–2015.
- 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*, **4** Supplement, 225–238.
- Sanina, L. V. 1961. About the biology of *Neomysis vulgaris* Thompson in the Gulf of Riga. *Tr. NIIRKH SNKH Latv. SSR*, **3**, 293–306 (in Russian).
- Seegerstråle, S. G. 1945. Über die Verbreitung der Müsiden in den Finnland umgebenden Meeresgewässern. *Comm. Biol. Soc. Sci. Fenn.*, **9**, 1–15.
- Simm, M. & Ojaveer, E. 2000. Dynamics of copepods and fish larvae in Pärnu Bay (NE part of the Gulf of Riga) in the spring–summer period. *Proc. Estonian Acad. Sci. Biol. Ecol.*, **49**, 317–326.
- Sokal, R. R. & Rohlf, F. J. 1981. *Biometry. The Principles and Practice of Statistics in Biological Research*. 2nd edition. Freeman WH, San Francisco, California.
- Sorbe, J. C. 1981. La macrofaune vagile de l'estuaire de la Gironde. Distribution et migration des espèces. Modes de reproduction, régimes alimentaires. *Océanis*, **6**, 579–592.
- StatSoft Inc. 2004. *Electronic Statistics Textbook*. Tulsa, OK. StatSoft. WEB: <http://www.statsoft.com/textbook/stathome.html>
- Wiktor, K. 1961. Observations on the biology of *Neomysis vulgaris* (Thompson) in Zalew Szczeciński (Stettiner Haff) and Zatoka Pomorska (Pomeranian Bay). *Przegl. Zool.*, **5**, 36–42 (in Polish).
- Yarvekyulg, A. 1979. *The Bottom Fauna in the Eastern Part of the Baltic Sea*. Valgus, Tallinn (in Russian).
- Yurkovskis, A. 2004. Long-term land-based and internal forcing of the nutrient state of the Gulf of Riga (Baltic Sea). *J. Mar. Syst.*, **50**, 181–197.

***Neomysis integer*'i populatsioonistruktuuri ja elutsükli sesoonsed muutused Pärnu lahes Liivi lahe kirdeosas**

Ilmar Kotta, Jonne Kotta ja Kristjan Herkül

Neomysis integer'i ületalvitunud põlvkonna asustustihedus on väike. Müsiidide kevadine biomassi kasv on tingitud loomade pikkuskasvust ja sigimine seda ei mõjuta. *N. integer* sigib kogu suveperioodil ja liigil on kaks paljunemismaksimumi. Septembrist alates suureneb *N. integer*'i populatsiooni suremus oluliselt. Paljunemise ajastus sõltub talve ja kevade karmusest. Peale pehmet talve ja kevadet toimub müsiidide sigimine varem. Suureskaalalised kliimaprotsessid kirjeldavad *N. integer*'i elutsükli Pärnu lahes paremini kui kohapeal mõõdetud parameetrid.