

Title: Identification of critical stages in the population dynamics of key copepod species in the Bornholm Basin (Baltic Sea): potential linkages to physical forcing and climate variability.

Authors: Jörg Dutz, V. Mohrholz, J. Peters, J. Renz, J. Alheit

Abstract:

Previous long-term investigations in the Baltic Sea documented large inter-decadal fluctuations in the standing stock of dominant copepod species and a concomitant regime shift in the composition of the fish fauna. Against this background, the German GLOBEC Project aims to clarify trophodynamic interactions between key zooplankton species and planktivorous herring and sprat and their link to regime shifts under physical forcing. A major goal of the project is to identify critical life-stages and/or processes that determine the seasonal development of a copepod stock size and its vulnerability to changes in the physical environment. We have studied spatio-temporal distribution and stage composition of Baltic *Acartia* populations, seasonal variation of the reproductive success and hatching rates of resting eggs. Hatching of nauplii from the sediment is by far the most important source for *Acartia* recruitment in spring while *in-situ* egg production in the pelagic dominates recruitment during summer. Laboratory experiments revealed a strong temperature control of egg hatching from the sediment and suggest that the recruitment through hatching of resting eggs is a critical process in the population dynamics of *Acartia* spp. in the Baltic with regard to physical forcing. With the onset of the warm season, the temperature control is replaced by food availability as the controlling factor of recruitment. Potential linkages of biomass fluctuations of *Acartia* spp. to prevailing hydrographic conditions and climate variability will be discussed.

Key words: copepod population dynamics, *Acartia* spp. Bornholm Basin, physical forcing

Jörg Dutz, V. Mohrholz and J. Alheit: Institute for Baltic Sea Research Warnemünde, Seestraße 15, D-18119 Rostock, Germany [tel.: +49 381 5197 358, fax.: +49 381 5197 211, e-mail: first.name.surname@io-warnemuende.de], J. Peters: University of Bremen, Bremen, Germany [[tel.: +49 421 2189508, fax.: +49, e-mail: janna.peters@uni-bremen.de], J. Renz: Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Germany [tel.: +49 471 4831 1318, fax.: +49, e-mail: jrenz@awi-bremerhaven.de]

Introduction

The pelagic ecosystem of the central Baltic Sea has considerably changed during the last two decades. Long-term investigations documented large inter-decadal fluctuations in the standing stock of pelagic biota. Several studies demonstrated, for instance, a decline in the abundance of large neritic copepod species like *Pseudocalanus acuspes* or *Temora longicornis* since the 1980s and a significant decrease in the copepod/cladocera ratio in the coastal areas of the Northern Baltic Sea (Viitasalo et al. 1995, Ojaveer et al. 1998, Vuorinen et al. 1998). These observations generally match findings from long-term studies of zooplankton abundance in the open Central Baltic Sea (Vuorinen et al. 1998, Möllmann et al. 2000, Hänninen et al. 2003, Vuorinen et al. 2003). These time series of Finnish, Latvian and Estonian monitoring programmes revealed substantial changes in the standing stocks of important copepod species. A steady decrease in the standing stocks of the formerly dominant species *Pseudocalanus acuspes* during the 1990s contrasts with the increasing/decreasing biomass of *Temora longicornis* and *Acartia* spp. Similar changes have been observed in the composition of the fish fauna of the Baltic Sea. The stock of the major planktivore sprat increased drastically during the last decade presumably due to a release in the predation pressure by cod and high reproductive success (e.g. Köster et al. 2003).

Although there is not always an agreement on the direction of the observed trend in zooplankton standing stocks (cf. Möllmann et al. 2000 vs. Vuorinen et al. 2003), statistical analyses of the long-term data sets relate the biomass fluctuations primarily to changes in the hydrographical environment. Particularly, the decrease in the abundance of *Pseudocalanus acuspes* or *Temora longicornis* correlates well with a decrease in salinity of the Baltic Sea due to a reduced frequency of inflows of saline water from the North Sea and increased river runoff (Möllmann et al. 2003, Vuorinen et al. 2003). The dynamics of the standing stocks of *Acartia* spp., in contrast, was found to reflect temperature conditions in the surface waters of the Baltic. Recently, it was shown that the changes in the physical environment are regulated by climatic conditions (Hänninen et al. 2000, Dippner et al. 2000, Vuorinen et al. 2003).

Despite this recent progress, the mechanisms and processes that relate the observed environmental changes to the pelagic biota are rather unclear. Decreased growth rates or increased mortality resulting from physiological stress due to changing environmental conditions have been invoked as direct mechanism behind the observed effects on copepod populations. Changes in the top-down control by planktivorous fishes like sprat and herring or eutrophication and associated changes in the trophic structure of the Baltic may similarly affect the long-term dynamics of the copepod standing stocks (e.g. Flinkmann et al. 1998, Möllmann & Köster 2002, Hänninen et al. 2003). Within this context, the German GLOBEC Project aims to clarify trophodynamic interactions between zooplankton key species and planktivorous herring and sprat and their link to regime shifts under physical forcing. A major goal of the project is the identification of critical life-stages or processes that determine the seasonal development of the copepod stock size and its vulnerability to changes in the physical environment. Here, we report the first results of a comparison of the spatio-temporal distribution of Baltic *Acartia* spp. populations with the seasonal variation of *in-situ* reproduction and hatching of resting eggs. These results demonstrate that the recruitment through hatching of resting eggs is a critical process in the population dynamics of this species with regard to physical forcing.

Material and Methods:

Seasonal abundance of Acartia longiremis and A. bifilosa

Horizontal and vertical sampling of zooplankton was conducted during a series of cruises between January and December 2003 on a station grid in the Bornholm Basin of the central Baltic Sea (Figure 1). Horizontal sampling was performed using a Babybongo net with a 0.12m² mouth-opening and 150µm mesh size. Double-oblique hauls were conducted from the surface to 5m above the sea floor. The net was equipped with a calibrated flowmeter and was towed with a speed of 3kn. Vertical sampling was conducted with a 0.25m² multiple opening and closing net (Multischließnetz, Hydrobios). The gear was towed vertically from 5m above the sea floor to the surface. The sampling was performed with a vertical resolution of 10m. On each station, vertical profiles of the temperature, conductivity and oxygen were recorded with a CTD probe mounted on a rosette water sampler (ME, Kiel, Germany). All samples were immediately fixed in borax-buffered formalin (4% final concentration). In the laboratory, the taxonomic composition was analysed with a compound microscope at a 50-120x magnification. Individuals of the the target species *Acartia longiremis* or *A. bifilosa* were identified to the developmental stages. The subsample size was adjusted to provide at least 200 counts of the target species. Abundances (per m²) were calculated based on filtered volumes and water depth at the sampling station.

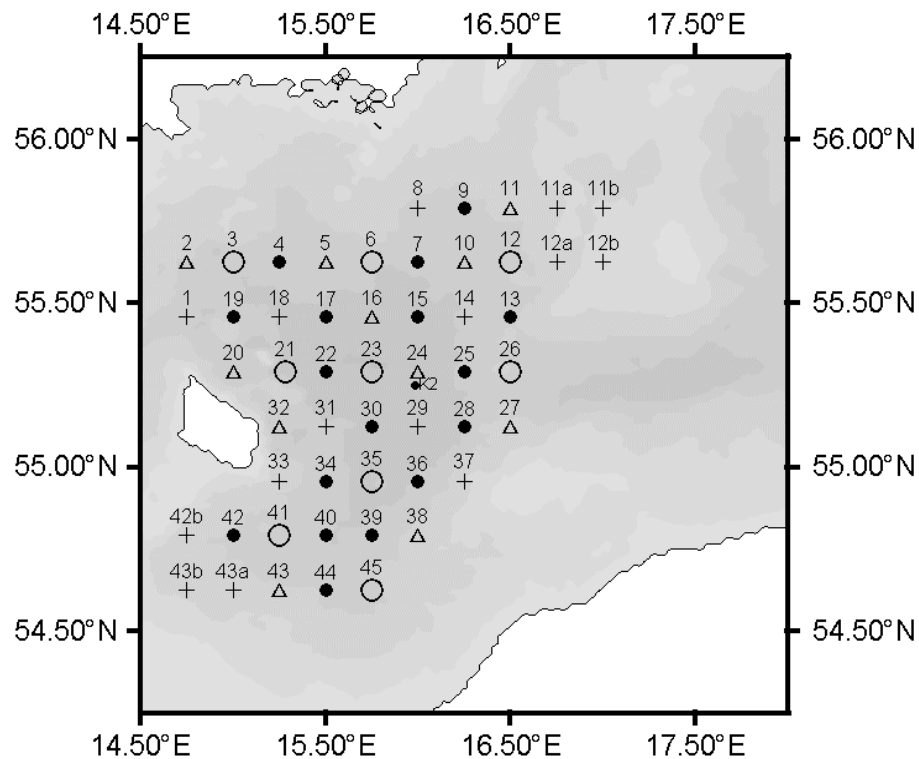


Figure 1: Map of the Central Baltic Sea with sampling stations in the Bornholm Basin.

Hatching of resting eggs

Sampling for resting eggs was conducted at selected stations of the sampling grid in January-March 2003. Stations were chosen to reflect changing water depth and sediment types in the investigation area. Sediment samples were taken with a Multi-Corer equipped with 8 corers made of Plexiglas. After retrieval of the corer, the first 3cm of each core were sliced into discs of 1cm height (approx. volume of 78cm³) and carefully transferred into 500 ml Kautex bottles. The subsamples of 3-5 cores were fixed in borax-buffered formalin (4% final concentration) for later determination of resting egg abundance. The top 1cm of the other subsamples of the was carefully topped-up with ambient seawater (GF/C filtered) to minimize resuspension of the sediment and incubated at 4 or 10 °C in a walk-in cooling chamber. In the laboratory, incubation continued for a period of 3-6 months. Every 2nd or 3rd day, the overlaying water in the Kautex bottles was replaced by new GF/C-filtered ambient seawater. The exchanged water was sieved through a 50 µm mesh and analysed for the presence of nauplii hatched from the sediment. The species composition and the development stage of the nauplii was determined with a compound microscope at a 120x magnification. Nauplii of the genus *Acartia* were not further differentiated into the 3 different species occurring in the investigation area (*A. bifilosa*, *A. longiremis*, *A. tonsa*).

Egg production, egg hatching success and food limitation of egg production

The seasonal variation of egg production rates (EPR) of *Acartia bifilosa* and *A. longiremis* were determined on selected stations of the sampling grid in 2003. As long as the water column was vertically mixed, zooplankton for experiments was collected by vertical tows of a WP-2 net equipped with 100 µm mesh and a closed cod end. With onset of the seasonal warming of the surface layer, stratified sampling was conducted below and above the thermocline with a multiple opening and closing net (Hydrobios). The catches were transferred to large buckets and carefully diluted with ambient sea water. In a walk-in cooling chamber, females of the three species were sorted and incubated individually at *in-situ* temperatures. After 24 hours, produced eggs were collected, enumerated and transferred together into a 250 ml glass bottle for further incubation for hatching.

Limitation of egg production of *Acartia* females by food availability was studied in incubation experiments conducted in February/March, April and August. In general, egg production of females under ambient food conditions was compared with that of females fed a diet of ambient food supplemented with the diatom *Thalassiosira weissflogii* at a concentration of 100 µg C L⁻¹ or females fed a diet of ambient food in which the size fraction bigger than 10 µm has been doubled by reverse filtration. Females were incubated in groups of 7-10 individuals and daily transferred to new food suspensions for a period of 6 days. Experiments were conducted in triplicate. After every day eggs were enumerated and incubated for hatching.

Results

Seasonal abundance of Acartia longiremis and A. bifilosa

During 2002, both *Acartia* species displayed a rather similar and characteristic variation in the seasonal abundance at station 23 in the Bornholm Sea (Fig. 2). In the transition period from winter to spring standing stocks were generally low, particularly those of copepodites and adults. Most characteristic, a pronounced peak in naupliar abundance generally precedes those of copepodites and adults of both species. During the late spring and early summer, the abundance of nauplii decreased while the standing stocks of copepodites and adults increased considerably. A second peak of nauplii of *A. longiremis* and *A. bifilosa* occurred in late summer, this time in close temporal correlation with peaks in copepodites and adults. Throughout the year, the size of the standing stock of both species was similar.

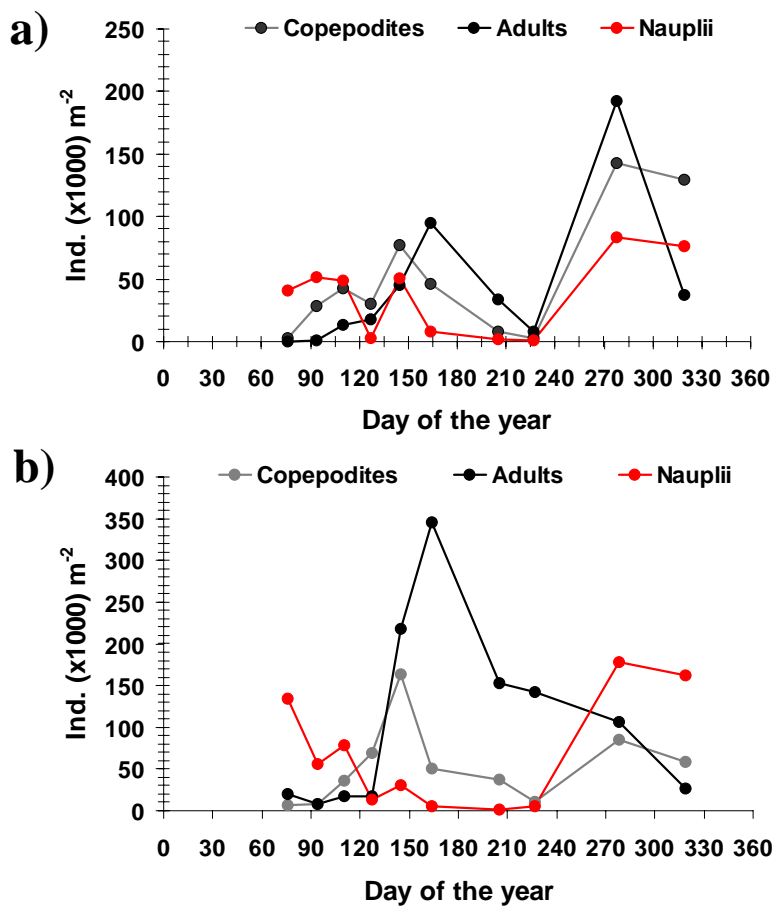


Figure 2: Seasonal abundance of different developmental stages (nauplii, copepodites, adults) of *Acartia bifilosa* (a) and *A. longiremis* (b) in the Bornholm Sea in 2002.

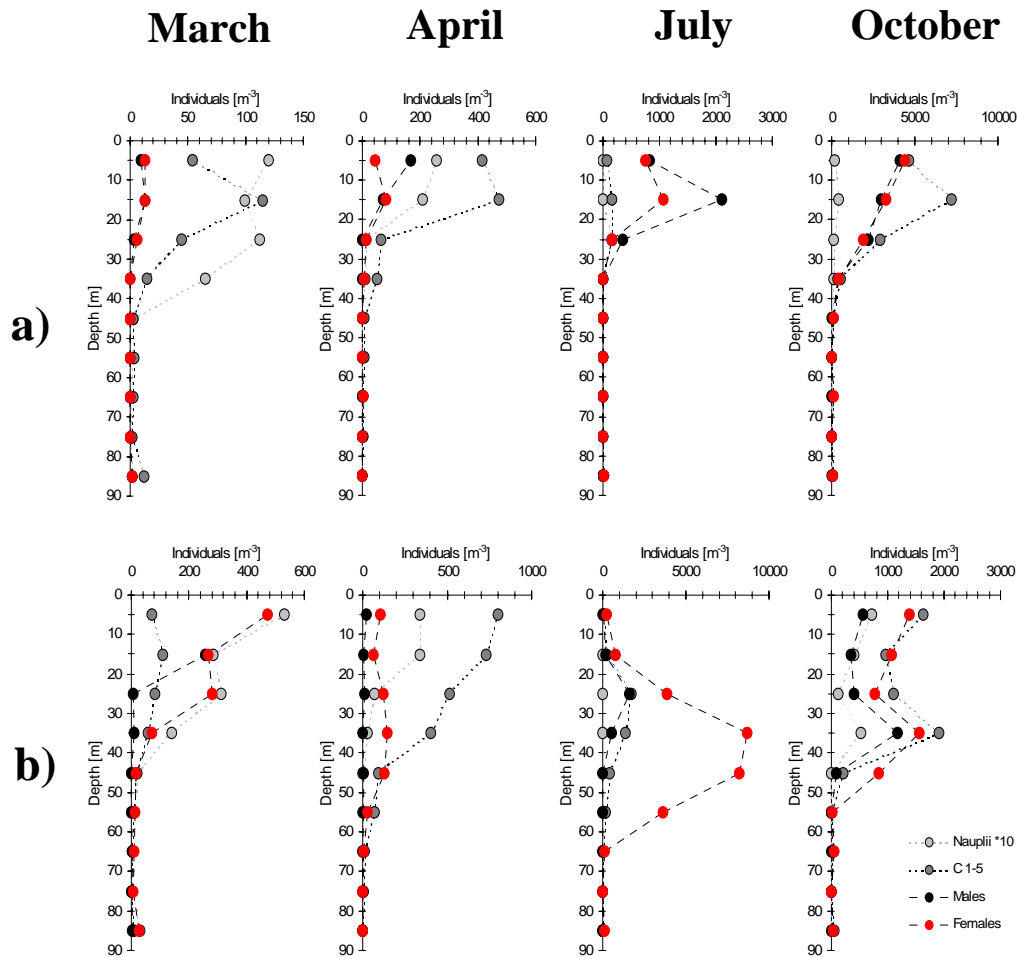


Figure 3: Vertical distribution of different developmental stages (nauplii, copepodites, females, males) of *Acartia bifilosa* (a) and *A. longiremis* (b) in the Bornholm Sea in 2002.

In contrast to the seasonal variation in the abundance, major differences were observed in the vertical distribution of the developmental stages of both species (Fig. 3). The abundance of *A. bifilosa* nauplii, copepodites and adults was generally highest in the surface and subsurface layers. In the winter-spring transition particularly nauplii and copepodites were distributed in the upper 40m of the water column. In spring, and summer, all developmental stages concentrated in the uppermost 20m, whereas a wider distribution of copepodites and adults was observed again in autumn. Similar to *A. bifilosa*, copepodites and especially nauplii of *A. longiremis* showed a wide distribution in winter and spring when the highest abundances were found in the upper 40 m of the water column. However, after the establishment of the seasonal stratification all developmental stages avoided the warm surface layer and were found below the thermocline at depths from 30 to 60 m. After the autumn cooling of the surface waters, the broad distribution of nauplii, copepodites and adults over the upper 40 to 50 meters re-established.

Egg production/hatching and food limitation of egg production

Egg production of both the *Acartia* species was low during winter (Fig. 5). Together with the increase in the water temperature in spring egg production of *A. bifilosa* increased from 5 eggs in late March to the maximum of 21 eggs in June. A sharp decrease in the egg production rate was observed in August. The hatching success of the eggs produced by *A. bifilosa* was variable during the seasons. From January to March average hatching rates were low and did not exceed 50%. Only during the summer hatching rates were higher than 80%.

Compared to *A. bifilosa*, the reproductive potential of females of *A. longiremis* in the Bornholm Sea was low. During the winter-spring transition egg production rates remained below 1 egg day⁻¹. In spring, an increase in egg production was observed, but rates never exceeded 5 eggs female⁻¹ day⁻¹. Pronounced differences were observed in the seasonal variation of the hatching rates of eggs produced by *A. longiremis*. During the period January to April, hatching rates were very low and never exceeded 30% of the total number of eggs. A sharp increase in the hatching rates to more than 80% was then observed from April to May. Until August, hatching rates remained high.

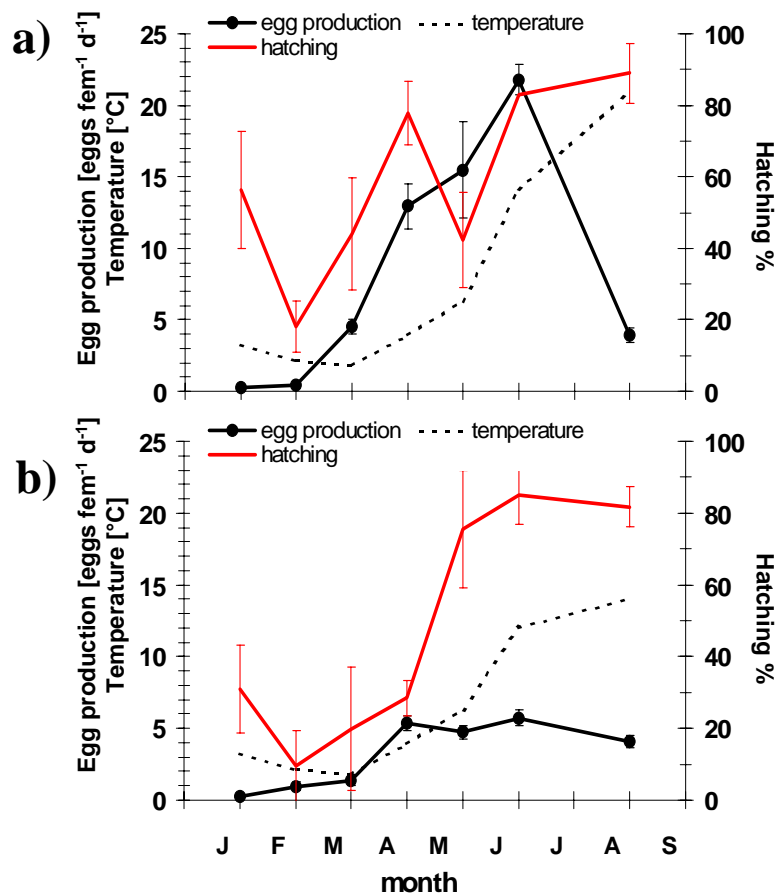


Figure 4: Seasonal variation in egg production and egg hatching of *A. bifilosa* (a) and *A. longiremis* (b) in the Bornholm Sea during 2003.

In the experiments conducted to investigate the seasonal limitation of egg production of *Acartia* spp. evidence for a limitation was found for *A. bifilosa* only. Egg production rates of females of *A. longiremis* fed ambient food with and without supplementation of additional food reflect generally those rates measured *in-situ* (compare Fig. 5 to 4). Only in August, the supplementation of ambient food by the addition of the diatom *T. weissflogii* lead to higher egg production rates. However, the observed difference results rather from a decrease in egg production in the ambient 1x and 2x treatments compared to *in-situ* egg production than an increase in egg production due to the diatom addition.

In *A. bifilosa*, the development of a strong limitation of egg production by the food availability was observed. While the supplementation of ambient food did not show any effect on reproduction in winter, egg production was limited in spring, and most severely, during summer (Fig. 5). Most characteristic, egg production in April and August increased only by the addition of *T. weissflogii* and not by supplementation of the size fraction > 10 μm . This may indicate that egg production was not only limited by the concentration of the ambient food, but probably also by the quality of the available food.

Hatching of resting eggs from the sediment

The results of hatching experiments conducted with sediment cores incubated in the laboratory demonstrate that hatching of resting or subitaneous eggs from the sediment is a significant source for nauplii (Fig. 6). Characteristic for all the sediment cores taken in the Bornholm Sea is an apparent depth dependence of hatching or survival of resting eggs (results not shown). Significant numbers of nauplii hatched only from those cores taken at water depths below 50m. In addition to the heterogeneous distribution, a temporal pattern in the emergence of nauplii from the sediment was observed. Hatching was high from January to March and ceased thereafter. Finally, hatching of resting or subitaneous eggs showed a strong temperature dependence. About 2-5 times more nauplii hatched from sediment cores incubated at 10 °C compared to cores incubated at 4 °C (Fig. 6).

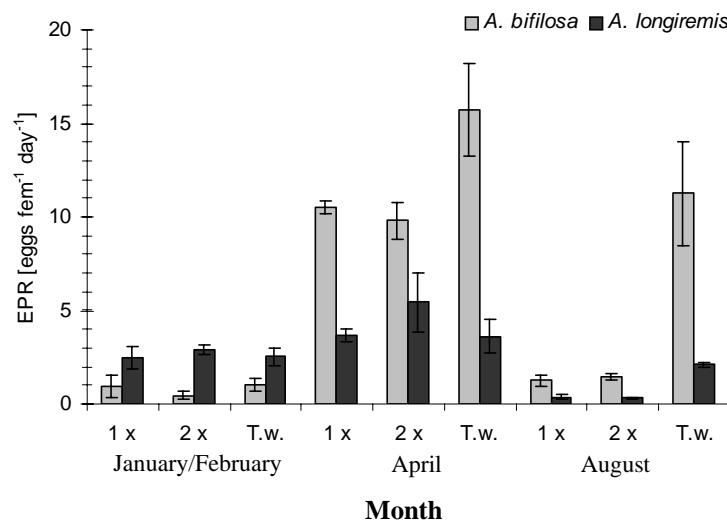


Figure 5: Seasonal variation in egg production of *A. bifilosa* and *A. longiremis* females at ambient food concentrations (1x), at ambient food concentrations with a doubling in the amount of particles bigger than 10 μm (2x) and at ambient food concentrations supplemented with the diatom *T. weissflogii* (T.w.).

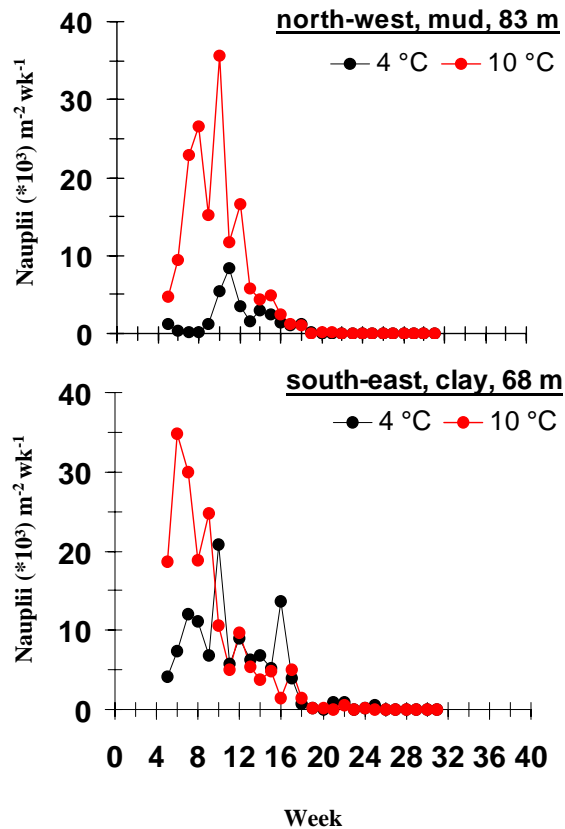


Figure 6: Hatching of *Acartia* spp. nauplii from two sediment cores taken in the Bornholm Basin and incubated at 4 and 10 °C.

Discussion and Conclusions

The comparison of the seasonal abundance of developmental stages of *A. bifilosa* and *A. longiremis* with the *in-situ* egg production and the hatching of benthic resting eggs allows the identification of major process for the seasonal recruitment of both species and those factors potentially controlling their population dynamics in the Bornholm Basin. With regard to the critical periods and processes in the life cycle of both *Acartia* species two different phases can be distinguished.

In the winter-spring transition, the results demonstrate a strong benthic-pelagic coupling in the recruitment of both *Acartia* populations. Hatching of hibernating eggs from the sediment is by far the most important source for *Acartia* nauplii in spring. Egg production by females in the water column is not only very poor during the period from January to April, but hatching success of these eggs is also very low. The reason for the observed low hatching rates remain to be investigated and may be related to physical factors, inhibition of hatching by the diatoms dominating the phytoplankton community in spring or a lack of essential biochemical compounds in the food (e.g. Jónasdóttir 1994, Ianora 1998). In contrast to egg production, very high hatching rates of nauplii have been observed from sediment incubated in the laboratory. Hatching of hibernating eggs was particularly important during the period when *in-situ* egg production and egg hatching was low. Roughly calculated between 120.000 and 205.000 nauplii m^{-2} hatched from the sediment in the period January to April, whereas only 8000 nauplii m^{-2} can be derived from *in-situ* egg production. Thus, hatching of resting eggs explains the

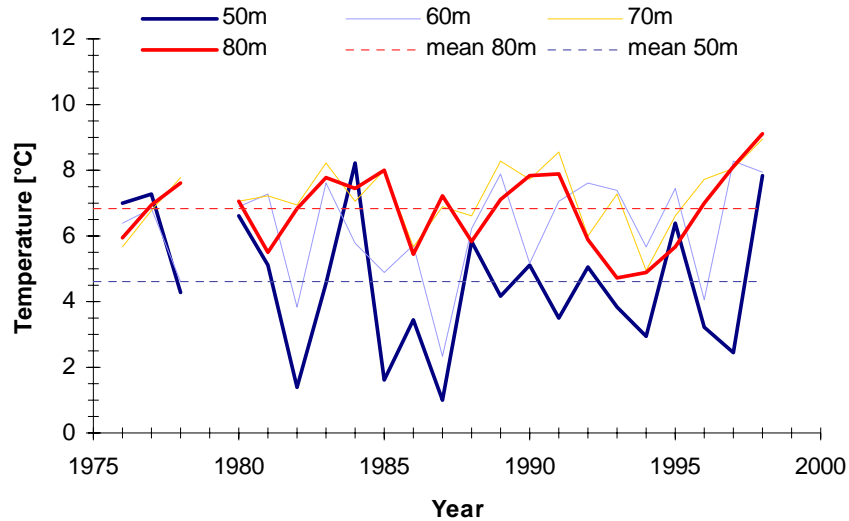


Figure 6: Long-term variation of the water temperature at different depths in the Bornholm Sea.

early occurrence of nauplii in the water column observed in the field samples from the Bornholm Basin. Most important, the laboratory experiments revealed a strong temperature control of egg hatching from the sediment. When sediment cores were incubated at 4 °C, hatching rates were on average about a factor of 2 to 5 lower than those observed at 10 °C.

With the progression of the productive phase in the pelagic, the recruitment of both species shifts from the strong benthic-pelagic coupling towards a domination of *in-situ* egg production and hatching. In spring, hatching rates remain still low, despite increasing egg production rates. During this time of the year, probably most of the eggs sink out of the water column and provide the stock of resting eggs for the recruitment in the following year. In summer, recruitment of the populations depends strongly on *in-situ* production. The low egg production of *A. longiremis* during this time of the year is explained by the vertical distribution of this species. Most of the population, particularly the females avoid the warm surface layers and stay below the thermocline in the cooler intermediate water. Production in *A. longiremis*, thus, might be rather controlled by temperature than food availability. In contrast to *A. longiremis*, females of *A. bifilosa* remain in the warm surface layer where egg production is controlled by food availability.

In conclusion, the results from the Bornholm Basin suggest that the recruitment through hatching of resting eggs is a critical process in the population dynamics of *Acartia* spp. in the Baltic Sea with regard to physical forcing. Firstly, resting eggs are a major source for the first generation of *Acartia* spp. in the Bornholm Sea as demonstrated for this genus for the northern Baltic (e.g. Katajisto et al. 1998). Secondly, hatching of resting eggs is restricted to a short time period in winter-spring. And finally, hatching depends strongly on the *in-situ* temperature in deep areas of the Bornholm Sea. These characteristic patterns in the early life cycle of *Acartia* spp. potentially relate fluctuations in the biomass of these species to the prevailing hydrographical conditions and, thus, to climate variability. The incubation temperatures chosen for the incubations represent generally the upper and lower limit of the naturally occurring range above the sediment in the Bornholm Sea (Fig. 6). The temperature variations at different depths are complex and not always in phase because they are influenced by both the depth of the vertical mixing in winter-spring and inflows of saline water from the North Sea via the Kattegat. Nevertheless, both processes are mainly controlled by climatic factors (Hänninen et al. 2000). A lack of deep vertical mixing during warm winters or of major inflows of cold water and consequently high temperatures in the deep water may explain the increasing biomass of *Acartia* spp. in the 1990's.

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