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**Benthic resting eggs
in the life cycles of calanoid copepods
in the northern Baltic Sea**

TARJA KATAJISTO

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Supervised by Doc. Ilppo Vuorinen
 Archipelago Research Institute
 University of Turku
 Finland

Reviewed by Doc. Jari Hänninen
 Archipelago Research Institute
 University of Turku
 Finland

 Doc. Paula Kankaala
 Lammi Biological Station
 University of Helsinki
 Finland

Examined by Prof. Genuario Belmonte
 Department of Biological and Environmental Sciences and Technology
 Lecce University
 Italy

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Egg dormancy was studied in calanoid copepods near Hanko Peninsula, SW coast of Finland, northern Baltic Sea. The seasonal variation in benthic egg abundance and hatching success was assessed by extracting eggs from surface sediments and incubating them at temperatures corresponding to the *in situ* bottom temperatures. This was compared with the seasonal variation in plankton abundance. The depth distribution of viable eggs in sediments was determined from core samples. To reveal the factors behind dormancy and affecting survival, eggs produced by field-collected females were incubated under different temperature, light and oxygen conditions.

The resting eggs of three copepod species, *Acartia bifilosa*, *Eurytemora affinis* and *Acartia tonsa*, were found in the sediments. *Acartia bifilosa* and *E. affinis* are the dominant calanoid species of coastal areas of the northern Baltic Sea and occur in plankton throughout the year, although their numbers in winter are low. *Acartia tonsa*, which has been mostly neglected in earlier studies in the area, was not found in plankton during most of the year but attained high abundances in autumn. The resting eggs of these species represented different types of dormancy: quiescence (facultative dormancy), diapause (obligate dormancy) and an intermediate type.

Acartia bifilosa produces subitaneous, i.e. ready-to-hatch eggs throughout the productive season. Egg abundance in the surface sediments closely followed the variations in abundance of females in the plankton and was in turn followed by the abundance of nauplii in the plankton. This suggests that in shallow areas large fractions of the eggs may sink to the bottom prior to hatching. Some of these continue development and hatch without undergoing arrest, while others are buried and become dormant under the anoxic conditions prevailing under the sediment surface. The dormancy of the eggs represents the quiescent type: their development is arrested due to external conditions and is resumed when favourable conditions are restored. These studies show that the oxygen conditions of the environment regulate the egg dormancy of *A. bifilosa* in the northern Baltic Sea. Temperature affected the development rate, but did not directly affect hatching success or dormancy of the eggs. The eggs were also able to develop in complete darkness. The nauplii hatched at very low oxygen concentrations, but under near-anoxic conditions development ceased and was resumed when the eggs were subsequently incubated in normoxic water. The eggs could retain viability for several months under anoxia, sometimes for periods as long as a year. This is exceptional for subitaneous eggs and ensures survival over seasonal time scales.

Eurytemora affinis carries eggs in egg sacs. In summer the eggs produced are subitaneous and hatch in a few days in the egg sacs. In autumn *E. affinis* produces diapause eggs that are released from the egg sacs and sink to the bottom. Diapause eggs are 'programmed' to arrest their development, which can only resume after a certain refractory phase is completed, if conditions are favourable. In my experiments the diapause eggs of *E. affinis* began to hatch at low temperatures 3–4 months after spawning, but at elevated temperatures (13 °C) hatching was further delayed and viability was eventually depressed, unless first chilled (at 2 °C). The hatching performance of eggs extracted from surface sediments was similar to that of diapause eggs derived from field-caught females, while older eggs from deeper layers hatched readily. Diapause eggs are often capable of long-term dormancy and form egg banks in the sediments. This also applies to *E. affinis* eggs:

there was no apparent loss of viability in 5–6 years, and some viable eggs were extracted from even deeper sediment layers, corresponding to ages more than ten years. Therefore, the eggs can be used as a long-term survival strategy, in addition to securing recruitment after winter.

Acartia tonsa is a warm-water species and an immigrant to the Baltic Sea. Different from *A. biflosa* and *E. affinis*, it only occurs in the plankton in late summer and autumn and spends the rest of the year on the bottom as resting eggs. The egg type produced appears to be intermediate between subitaneous and diapause and resembles the so-called ‘delayed-hatching’ egg type. A fixed refractory phase required in diapause (*sensu stricto*) was lacking: some eggs hatched soon after spawning, and cumulative hatching occurred for up to several months. The temperature and time of the year affected the response in *A. tonsa*. At higher temperatures (18 and 13 °C) and in summer, there was almost no delay in hatching, and the delay was more pronounced at 6 °C and in autumn. The eggs did not hatch at low temperatures (3 °C). The abundance of viable eggs in the sediments was small compared with that of the indigenous species, but appears to be sufficient to support the persistence of local populations of this species. Since the species’ occurrence in the water column is seasonally restricted, *A. tonsa* is dependent on the resting egg strategy for yearly recruitment in the northern Baltic Sea.

Tarja Katajisto, Finnish Institute of Marine Research, P.O. Box 2, FI-00561 Helsinki, Finland

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INTRODUCTION

Plankton in sediments: an overview of the ‘resting egg strategy’

Traditionally, the aquatic environment is divided into habitats, and consequently the organisms are also categorized relative to the habitats they most conspicuously live in. Often the environment of the adult stage is viewed as the ‘proper’ environment of the species. Many organisms, however, occupy different habitats at different stages of their life cycles, or perform repetitive habitat changes, such as diurnal or seasonal vertical migration. For example, many species categorized as ‘benthos’ spend their larval phase in the pelagial and the ‘plankton’ in turn may find a refuge on the bottom as benthic resting stages. The present thesis focuses on the benthic resting eggs of planktonic copepods in the northern Baltic Sea.

Individual organisms often face drastic changes in their environment. The environment can become inhospitable for the inhabitants over various time scales, from cycles < 24 h in length to seasonal or annual variation. In high latitudes, seasonal variation in light regime and temperature as well as food availability pose special demands of flexibility and adaptability for individuals. The environment may also turn unfavourable due to biological interactions, such as competition or predation. Harsh conditions can be avoided by migrating to more hospitable environments or shutting the environment ‘outside’ by entering a dormant state (*‘migration in time’*). Dormancy occurs in different taxa, from unicellular organisms to the animal and plant kingdoms, in terrestrial and aquatic environments, from small and temporary to large and permanent bodies of water. It encompasses various states

of metabolic depression, ranging from a light torpor to a complete arrest in vital functions (Storey & Storey 1990). Different types and phases of dormancy in many invertebrate taxa, e.g. copepods (Williams-Howze 1997), sponges (Fell 1995), branchiopods (Brendonck 1996) and rotifers (Ricci 2001), are often described in terms similar to those of insects, which are well documented (e.g. Danks 1987). Essentially similar physiological processes govern dormancy in insects and copepods (Elgmork & Nilssen 1978).

The term ‘resting eggs’ can refer to different types of dormancy, ranging from *quiescence* (or facultative dormancy) to *diapause* (or obligate dormancy). In referring to eggs, a distinction between *subitaneous* (ready-to-hatch) and diapause eggs is made (Grice & Marcus 1981). Quiescence is a direct response of subitaneous eggs to environmental conditions that are unfavourable for development or hatching. Development may resume as soon as favourable conditions are restored. Diapause, in turn, is a genetically controlled state of arrested development. Diapause eggs are produced by females in response to cues preceding the onset of environmental adversity that may be detrimental to the development of offspring. By definition, diapause includes a ‘refractory phase’ during which development does not resume even under favourable conditions (Watson & Smallman 1971, Elgmork & Nilssen 1978); some species also require a period of chilling or warming before termination of diapause can occur (Marcus 1980, 1989). The refractory phase of copepod eggs may last several months (Marcus 1996), although after completion of this phase dormancy may continue even for years if unfavourable conditions prevail (Watson & Smallman 1971, Grice & Marcus 1981, Hairston & De Stasio 1988, Marcus

et al. 1994). Since postrefractory diapause eggs and quiescent eggs may show similar responses to hatching cues, it is not always possible to distinguish the dormancy type of eggs collected in the field (Grice & Marcus 1981). Both types may also occur in one species (e.g. Castro-Longoria & Williams 1999). In some species diapause and subitaneous eggs differ morphologically from each other (e.g. Pertzova 1974, Kasahara & Uye 1979) but in many they do not (Grice & Marcus 1981). In addition, copepod eggs in shallow coastal areas may also sink to the bottom prior to hatching and if conditions at the sediment/water interface are favourable they may continue development (Landry 1978, Uye 1980); thus at the sediment surface eggs may also be found that have not necessarily experienced dormancy.

Development and/or hatching may be retarded in quiescent and postrefractory diapause eggs, due to adverse temperatures or oxygen deficiency (Kasahara et al. 1975, Uye et al. 1979, Johnson 1980, Sullivan & McManus 1986, Marcus 1989) or (although seldom in copepods) darkness (Landry 1975, Uye & Fleminger 1976, Uye 1980). Diapause egg production is most often triggered by seasonal cues, such as changes in photoperiod and/or temperature (Marcus 1980, 1982, Hairston & Kearns 1995, Chinnery & Williams 2003). However, diapause egg production also occurs as a direct response to avoidable conditions. Diapause egg production in the cladoceran *Daphnia magna* and in the copepod *Eurytemora affinis* was stimulated by the presence of predatory fish (Ślusarczyk 1995, 1999) and crowding (Ban & Minoda 1994).

Diapause eggs are often capable of survival beyond seasonal time scales. The unhatched eggs can remain viable for years or even centuries in the sediments (Mar-

cus et al. 1994, Hairston et al. 1995). They form an 'egg bank', analogous to the seed banks of plants, that acts as a long-term survival strategy against unpredictable catastrophes or in case reproduction fails during one or more consecutive years (Hairston & De Stasio 1988, De Stasio 1989). An egg bank also maintains genetic variation in a fluctuating environment (Ellner & Hairston 1994) and thus slows the rate of evolution (Hairston & De Stasio 1988). A seed pool can greatly reduce the fitness uncertainty produced by cyclic or randomly changing environments, because the years that have good seed production will have more impact on the genetic composition of the population than bad years (Templeton & Levin 1979). The long-term dormancy of the eggs at the individual level lengthens the reproductive life span of the short-lived female to resemble that of an iteroparous species (Hairston & Cáceres 1996).

Life cycles and resting eggs in calanoid copepods

Copepods may be the most numerous multicellular organisms in the world, even outnumbering insects (Hardy 1956, Mauchline 1998). The order Calanoida is mainly pelagic; 75% of the species are marine and 25% are freshwater (Mauchline 1998). In the marine pelagic zone it is the most successful copepod order (Webb & Weaver 1988). Copepods form an essential part of the so-called 'grazing chain'; they feed omnivorously on algae and small heterotrophs (Kleppel 1993) and are important food for planktivores such as mysids and fish (e.g. Hansson et al. 1990, Flinkman et al. 1992). Despite their wide distribution and great numbers, calanoid copepods show remarkably little variation in structure and

life history: they have six successive naupliar stages (NI–NVI) that are followed by six successive copepodite stages (CI–CVI), the sixth of which are the adults.

Complex life cycles with alternating sexual and asexual phases, associated with resting stage production in many other organisms, including cladocerans (Egloff et al. 1997) and rotifers (Birky & Gilbert 1971), do not occur in calanoid copepods. They always reproduce sexually. Most pelagic calanoid species broadcast their eggs freely into the sea – others carry them in ‘egg sacs’, i.e. attached to the ventral side of the genital somite until the nauplii hatch out (Mauchline 1998).

In the Calanoida, dormancy occurs either in the embryonic stage (Superfamily Centropagoidea) or in the copepodid stage (Superfamily Megacalanoidea). In coastal and fresh waters, dormancy is expressed by benthic resting eggs; in the deep oceanic waters many species overwinter as a dormant copepodid stage (CIV/V) that descends to the depths (Williams-Howze 1997). Other copepods, cyclopoids and harpacticoids, mainly aestivate as (encysted) copepodites or adults in sediments (Williams-Howze 1997); embryonic dormancy (resting eggs) is rare in orders other than Calanoida (Dahms 1995, Santer 1998). Currently, 46 marine or estuarine (Marcus 1996 and references therein, Belmonte & Puce 1994, Chen & Marcus 1997, Belmonte 1997, Guerrero & Rodríguez 1998, Newton & Mitchell 1999) and 28 freshwater (Williams-Howze 1997 and references therein, Jersabek & Schabetsberger 1995, Chen & Folt 1996, Parker et al. 1996, Williams-Howze et al. 1998, Pasternak & Arashkevich 1999, Libman & Threlkeld 1999, Couch et al. 2001, Knapp et al. 2001, Hall & Burns 2001, Dharani & Altaff 2004) calanoid copepod species have been reported

to produce resting eggs. [Since the paper of Marcus (1996) was published, *Acartia biflora* in Chinese waters has been classified as a different species, *A. hongii*, from the one in Europe (Soh & Suh 2000)]. Diapause as well as quiescence occurs, although the type of dormancy has not been determined in all studies. The studies covered environments from low to high latitudes but most studies have been conducted in northern temperate waters.

The Baltic Sea: environment and zooplankton

The Baltic Sea is a large semienclosed brackish water sea with restricted water exchange with the North Sea via the shallow and narrow connection in the Danish Sound. The water balance is dependent on the inflow of saline water through the Kattegat and on precipitation, about 2/3 of which enters the sea as river runoff from the large catchment area (Ehlin 1981). As a result, a vertical and horizontal salinity gradient develops. During summer, thermal stratification accompanies and strengthens the vertical salinity stratification. Special meteorological conditions are needed for large saline inflows to occur and the deep water to be replaced. In between the periods of deep water renewal, stagnant conditions develop in the subbasins and oxygen depletion occurs in these areas (e.g. Matthäus 1995). Due to increasing eutrophication, coastal bottoms have also suffered from oxygen deficiency (Weigelt 1991, Bonsdorff et al. 1997, Persson & Jonsson 2000, Laine & Kangas 2004). The conditions at the bottoms significantly affect plankton via the benthic life cycle link.

The biodiversity of the Baltic Sea is low, which can be attributed to the salinity con-

ditions (Segerstråle 1957). The salinity of the largest part of the surface water in the Baltic Sea is between 5 and 10 psu (Kullenberg 1981), whereas 6–8 psu is the salinity range that the lowest number of species can tolerate (Remane 1934). Abundances are, however, high. The species assemblage of the Baltic Sea is a unique mixture of marine, freshwater and estuarine species (Remane 1934, Segerstråle 1957). The mesozooplankton consists mostly of copepods, cladocerans and rotifers; few benthic invertebrate species have planktonic larvae, although these may occur in great numbers (Hällfors et al. 1981). Only eight calanoid copepod species regularly occur in the northern parts of the sea; these include the marine species *Temora longicornis*, *Pseudocalanus minutus elongatus*, *Centropages hamatus* and *Acartia longiremis* as well as the estuarine or brackish water species *A. bifilosa*, *A. tonsa*, *Eurytemora affinis* and *Limnocalanus macrurus* (Hällfors et al. 1981, Silina 1989). The most numerous, both in numbers and biomass, are *A. bifilosa* and *E. affinis* (Viitasalo 1994). Most of these species are known to produce resting eggs in the other seas of Northern Europe (Lindley 1986, 1990, Næss 1991, 1996, Castro-Longoria & Williams 1999, Castro-Longoria 2001).

The northern Baltic Sea is a strongly seasonal environment. Changes in the amount of solar radiation drive the seasonal succession of temperature, salinity and, consequently, water stratification and nutrient availability for primary producers. In winter, the sea is largely covered with ice, but the duration and area of the ice cover varies interannually. Since the sea is relatively shallow (more than half of its area is < 50 m deep), the benthic resting stage strategy is applicable for many planktonic species. It is well recognized that cladocerans (Puras-

joki 1945, 1958, Kankaala & Wulff 1981, Kankaala 1983, Krylov & Panov 1998) and rotifers (Arndt 1988, 1991) spend a significant part of the year on the bottom as resting eggs, since their occurrence in plankton is seasonally restricted (Hernroth & Ackefors 1979). Recently phytoplankton studies have also taken the benthic component into account (e.g. Nehring 1996, Olli 1996, Kremp 2000a,b).

OBJECTIVES

Copepods show seasonal abundance fluctuations in the northern Baltic Sea but, excluding *Acartia tonsa*, do not totally disappear from the water column in winter. However, it has long been assumed that benthic resting eggs are included in their life cycles. In spring, the abundance of *A. bifilosa* nauplii tends to peak before females, which may be attributed to recruitment from the bottom (Hernroth & Ackefors 1979, Viitasalo 1992a). The occurrence of viable eggs of *Acartia* spp. in sediments was verified by Viitasalo (1992a). More detailed knowledge on the species assemblage of benthic eggs and the dynamics of egg deposition to and recruitment from the bottom has, however, been lacking.

To reveal the role of benthic eggs in the life cycles of calanoid copepods in the northern Baltic Sea the following aspects were studied and are summarized in this thesis:

(a) The seasonal dynamics of egg deposition on and recruitment from the bottom was studied by following the variation in egg abundance and hatching activity in surface sediments, together with the planktonic abundance, throughout the year at two sites (I).

(b) The species identity of the benthic

eggs was studied by comparison with eggs produced by females of different calanoid species and by indentifying the nauplii hatching from them to the family level, if possible.

(c) The survival potential of the eggs in the sediments, which defines the role that benthic eggs may play in the life cycles of the copepods, was studied by determining the vertical distribution of viable eggs in sediments, related to the sediment age (IV, V, this summary), by storing eggs in sediment in the laboratory and determining their viability after different time periods (III), and by addressing how long newly produced eggs survive under different conditions (III, this summary).

(d) The egg types and factors behind the dormancy of different species were determined by following the development of eggs produced by females under various conditions (II, III, this summary) and by observing the hatching pattern of eggs sampled from sediments at different times of the year or in different sediment layers (I, V, this summary).

MATERIAL AND METHODS

Two types of study were conducted. First, eggs were sought in sediment samples and incubated to reveal their hatching success and pattern, as well as to identify the species, if possible (I, IV, V). Second, eggs produced by field-collected *Acartia bifilosa* females were incubated under different conditions to reveal the factors behind dormancy (II, III). In addition to the studies presented in I–V, some unpublished results of studies on the egg dormancy of *A. tonsa* and *Eurytemora affinis* are presented in this summary.

Study sites

These studies were conducted in the Tvärminne – Pojo Bay area in the vicinity of Hanko Peninsula, at the entrance to the Gulf of Finland, northern Baltic Sea. To the east of the peninsula, a transition occurs from the open sea to an estuary. Sampling was mainly conducted at two sites: Tvärminne Storffjärden (subsequently referred to as ‘Storffjärden’) in the archipelago zone and the Sällvik deep in the estuary. Additional sampling was conducted at Björholm (depth 20 m), between the estuary and Storffjärden, and Långskär (43 m), Längden (50 m) and Storgadden (50 m) in the open sea area (Fig. 1).

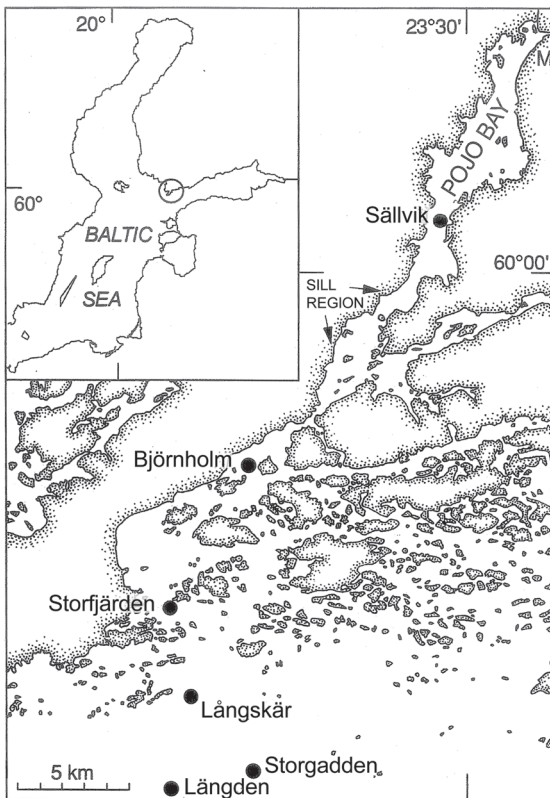


Figure 1. Map of the study area showing the sampling sites.

Storfjärden (max. 33 m) lies in the archipelago zone between the estuary and the open sea. The bulk of the water column is formed by surface water of the open Baltic proper. Meteorological conditions strongly influence the hydrography (Niemi 1973, 1975, Hällfors et al. 1983). Thermal stratification normally develops during summer but easily breaks up, due to upwellings. The temperature near the bottom is below 2 °C in winter and may increase up to 12–14 °C in autumn; the salinity usually varies between 5 and 7 psu. Ice covers the area for variable periods, typically for 2–3 months, in winter, but not necessarily every year. In winter the zooplankton is scarce and composed of copepods, mainly *Acartia bifilosa*; in summer cladocerans and rotifers also occur (Viitasalo 1992b). In addition to *A. bifilosa* the copepod *Eurytemora affinis*, the cladoceran *Bosmina longispina maritima* and the rotifer *Synchaeta baltica* are abundant. The occurrence of permanent benthic infauna indicates that near-bottom oxygen deficiency does not occur (Laine et al. 2003), although the benthos has undergone drastic changes in recent decades (Segerstråle 1933, Karjala & Lassig 1985, Kangas et al. 2001, Laine et al. 2003). However, the depth of the visibly oxygenated (brown) sediment surface layer varies from > 1 cm to only 1–2 mm (IV, Katajisto, pers. obs.).

In the estuary, Pojo Bay, a vertical salinity gradient prevails between the outflowing oligohaline surface water (0–3 psu) and more saline deep water (Niemi 1973, 1978, Stipa 1999). The halocline at ~10-m depths effectively prevents mixing of these layers. Renewal of the deep water is mostly dependent on occasional inflows of saline water over a 6-m-deep sill; major inflows normally occur in winter and spring. The temperature near the bottom is under 1 °C

in winter and rises usually to 4–5 °C in summer; the salinity ranges from 4 to 5.5 psu. The ice cover often persists from December or January until April. Due to stagnant conditions in summer, the deep water becomes very poor in oxygen (Niemi 1978, Stipa 1999), and the macrofauna is missing in the 42-m-deep study site, Sällvik. Due to the lack of bioturbation, the sediment is characterized by a noticeable lamination (IV). The zooplankton community at Sällvik is a mixture of limnic and brackish water species (Levander 1915, Halme 1958, Koski et al. 1999). The large calanoid *Limnocalanus macrurus* occurs almost throughout the year; other more or less frequently occurring calanoids include *E. affinis* and *A. bifilosa*. Cyclopoids are abundant and of the cladocerans *Daphnia cucullata* is the most numerous (Koski et al. 1999).

Sediment sampling and analysis

The sediment cores were taken and sliced with a Limnos sediment corer (diameter 94 mm; described by Kansanen et al. (1991); I, IV, V). During the seasonal study only the surface (1–2 cm) was sampled; otherwise the sediment layers were extruded from the cores down to 10–25 cm, and all or some of the 1-cm layers were further processed in the laboratory (Fig. 2). The eggs were extracted from the sediments by centrifugation in a sugar solution (Onbé 1978) after sonication of the samples (Marcus 1984a, 1989). The egg counts were performed either from ethanol-preserved samples (I) or unpreserved samples (I, IV). The eggs were mostly incubated in 96-well culture plates for about one week or for so long that the hatching ceased (Table 1). The incubations were conducted soon after sampling (I) or after storage of sediment at 3–5 °C

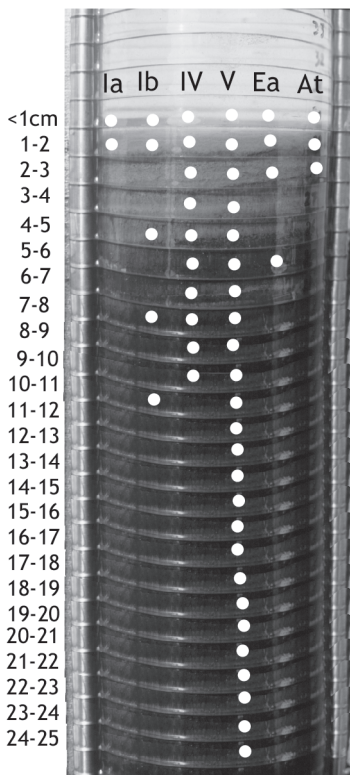


Figure 2. Sediment layers sampled in the studies. Sites: see Table 1.

(Table 1). The incubations were conducted in the dark, because light was not expected to affect hatching at the sediment surface: measurable amounts of light were not detected near the bottom at the study sites (Lindström & Nilsson 1988). The egg species could not be identified in all the experiments. The nauplii were identified to family level when possible, using an inverted microscope.

Since the eggs were extracted from sediments and then incubated to observe hatching, the results cannot be interpreted to represent the actual hatching rate in the field where only those eggs that are on the sediment surface probably get a chance to hatch. Therefore, I did not attempt to convert the egg numbers and hatching activity in the seasonal study to actual emergence rates of nauplii from sediments (I). However, the results show how egg deposition to and naupliar recruitment from the sediments fluctuate seasonally.

The long-term viability of the eggs was assessed by comparing the depth distribution of viable eggs with the sedimentation

Table 1. Sediment sampling: sites, timing and incubation of copepod eggs extracted from the sediments. A. Limnos cores. B. Ockelman sledge. Studies: Ea = *Eurytemora affinis*, At = *Acartia tonsa*. Sites: St = Storfjärden, Sä = Sällvik, Lå = Långskär, Stg = Storgadden

	Study	Site	Time of year	Abundance counts	inc. T °C	inc. d
A	I (a)	St, Sä	throughout	yes	'in situ'	6
	I (b)	Lå, Stg	May	yes	3,13,18	8–14
	IV	St, Sä	May	yes ⁽¹⁾	13,16,19	5–7 ⁽¹⁾
	V	Sä	Nov	estimates only	12	5–14 ⁽²⁾
	Ea	Sä	Nov	yes	3,13	< 270
	At	St	May	yes	(3),8,13,18	≤ 77
B	III	St	Oct	no	13–15	5–15 ⁽³⁾

Storage prior to incubations (and counts) ⁽¹⁾20–82 days (St) and 155–218 days (Sä)

⁽²⁾33–39 days

⁽³⁾up to 6 years

rate in Sällvik, as estimated using several methods. These included distribution of radionuclide ^{137}Cs in a sediment core determined to a depth of 24 cm (IV, V) and the lead concentration, which indicated the consumption intensity of lead-containing automobile fuels as analysed from sediment samples taken to a depth of 40 cm (IV). In addition a crust-freeze sampler (Renberg 1981), which freezes an undisturbed sediment core, was used to visually analyse and count the varves of the sediment (IV). For direct evaluation of egg longevity the sediment, collected from Storfjärden in October 1993 with an Ockelmann sledge, was stored at 3–5 °C for up to 6 years (III). During the storage, the viability of the calanoid eggs was checked at irregular intervals by incubating eggs extracted from the sediments at 13–15 °C.

Plankton sampling

To relate the seasonal abundance fluctuations of the eggs in sediments to the population dynamics of the copepods in the water column, the zooplankton was sampled at 2–6-week intervals between March 1992 and April 1993 from Storfjärden and Sällvik (I). The samples were taken with a 100- μm mesh net and preserved in ~4% hexamin-buffered formalin prior to analysis. The numbers of adults, copepodites (stages I–V) and nauplii (three size categories) were counted under a dissecting microscope.

Egg development and dormancy in *Acartia biflosa*

Eggs produced by field-collected *Acartia biflosa* females were incubated under different conditions to reveal the nature of the

eggs produced as well as to study the induction of dormancy and survival of the eggs (II, III). The females were caught in Storfjärden (II, III), Björholm (II) and Längden (III) in summer (II, III) and autumn (II).

The effect of temperature on development and hatching was studied by incubating the eggs in filtered seawater (FSW) in 96-well culture plates at different temperatures between 1.5 and 18 °C (II). Hatching was checked once or twice per day until no more nauplii appeared. The incubations were mostly conducted in darkness (except for the short exposures to light during the experimental procedure). The eggs were also incubated in a 16h:8h light:dark cycle and in total darkness from production until the final checking of hatching success (II).

The effect of low oxygen concentrations on the viability and induction of dormancy was studied in two types of experiments (III). In short-term experiments the eggs were incubated under hypoxic conditions (0–0.4 ml O₂ l⁻¹) for 8 or 10 days at 13 or 10 °C, respectively, while in long-term experiments the eggs were incubated for up to 441 days under near-anoxic conditions at 4–13 °C (III). The anoxic and hypoxic conditions were created and measured using the gas chromatographic method developed by Lutz et al. (1992). After the hypoxic incubation and at 1-week to 5-month intervals during the anoxic incubations, the oxygen concentration in usually three replicate vials was measured with a Hewlett Packard 5890 Series II gas chromatograph (Jaakkola & Simojoki 1998) and the number of eggs and hatched nauplii checked. The remaining eggs were subsequently incubated in normoxic FSW in 96-well culture plates at 10 or 13 °C to reveal hatching of viable eggs. All the incubations were conducted in the dark.

Egg development and dormancy in *Acartia tonsa*

Egg development in *Acartia tonsa* was studied in autumn 1998, from August, when the females first appeared in the plankton, until October. The animals were caught at Storfjärden with vertical hauls from depths of 25–30-m to the surface with a 200- μ m cod-end net, suspended with ambient seawater in large buckets and taken to the laboratory. Water was taken at 10–20-m depths and filtered (GF/F) for the experiments. The females were transferred to 2-l Erlenmeyer flasks (about 50 females each), fed with a mixture of cultured algae (*Brachiomonas submarina* and *Pseudopedinella elastica*) and acclimated for ~1 day at 13 or 15 °C before egg production for the experiments. The eggs were collected after 5–12-h production periods and incubated at 3, 6, 13 and 18 °C in 96-well culture plates (one egg per well, 3 \times ~30 eggs per temperature). Hatching of nauplii was checked at 1–14-day intervals until the remaining unhatched eggs were seemingly unviable.

Acartia tonsa does not occur in the water column during winter and spring (I), and to reveal its recruitment potential from the benthic egg pool in summer, sediment was collected from Storfjärden in May 1997 and 1998 with a Limnos corer (three cores each year). The loose surface (app. 0.5 cm) was taken with a siphon and 1-cm slices were cut with the device of the corer (1997 to 1.5-cm depths, 1998 to 2.5-cm depths, Fig. 2). Water from 30-m depths was filtered (GF/F) and used for handling the samples and in the experiments. The eggs were extracted with the sugar solution – centrifugation method (3 min at 1000 g) (Onbé 1978, Marcus 1984a, 1989). They were counted under a stereomicroscope and incubated in 96-well plates at 8 and 13 °C (1997) and

at 3, 8 and 18 °C (1998). In both experiments with eggs produced in the laboratory and those collected from the sediment, the plates were transferred to 18 °C in case no nauplii hatched at lower temperatures.

Diapause eggs of *Eurytemora affinis*

Diapause egg production of *Eurytemora affinis* was studied in autumn 1996. The eggs produced by females and collected from sediments were incubated and the hatching patterns observed. The females for the experiments were caught in October in Sällvik deep, Pojo Bay, with a 100- μ m net with a vertical haul from about 25 m to the surface. In the laboratory, the females were collected in 2-l Erlenmeyer flasks with FSW (~50 females and 5 males each) and allowed to stand at 13 °C. The copepods were fed with *Brachiomonas* (200–300 cells/ml). Females that developed egg sacs during the next five days were placed individually in plastic jars with 30 ml FSW. When they had released the eggs, the females were removed, the water in the jars changed and the eggs further incubated at 2, 3 and 13 °C. For the egg incubations, FSW from above the bottom was used. Individual clutches were incubated separately (except for one combined ‘clutch’ of 21 eggs from five females). To check the possible need for chilling, three clutches at a time at one-month intervals, were moved back to 13 °C from 2 °C. After 1–3 months from the start, the clutches were checked for hatched nauplii at 5–16-day intervals. This was continued for ~1.5 years, or until all unhatched eggs in the jars were unviable.

To compare the results obtained by incubating eggs produced by females in the laboratory with the situation in the field, sediment was sampled for about one month after

collecting the females. Three cores were taken from the Sällvik deep with a Limnos corer and cut in 1-cm slices to a 6-cm depth (Fig. 2). The eggs were extracted from the sediments by centrifugation in a sugar solution (Onbé 1978) after sonication of the samples (Marcus 1984a, 1989). They were counted and incubated in 96-well culture plates (one egg per well) at 3 and 13 °C for so long that hatching ceased. Hatching of the eggs was checked mostly at one-week intervals.

RESULTS AND DISCUSSION

Benthic resting eggs of northern Baltic Sea calanoids

Eggs of three copepod species were found in sediments in these studies. These included the two dominant species of the coastal zooplankton, *Acartia bifilosa* and *Eurytemora affinis*, and *A. tonsa*, which was abundant in autumn (I). Eggs of the less abundant species, *Centropages hamatus* and *Temora longicornis*, have been found in sediments in other sea areas, e.g. in the North Sea (Lindley 1986, 1990), and the former also in the southern Baltic Sea (Madhupratap et al. 1996). However, I never observed eggs of these species. Many studies have shown that the eggs of *C. hamatus* have conspicuous spines (Pertzova 1974, Marcus 1989, Madhupratap et al. 1996, Chen & Marcus 1997), and it is unlikely that they should have gone unnoticed in the sediment samples. It may be that their occurrence in the Baltic Sea is restricted to the southern parts. The eggs of *T. longicornis* have not been found in other studies in Baltic Sea sediments, either in the southern Baltic Sea (Madhupratap et al. 1996) or the Bothnian Sea (Albertsson & Leonards-

son 2000, 2001). In the Baltic Sea *T. longicornis* is more abundant in the open sea than in coastal areas (Viitasalo 1992b, Viitasalo et al. 1995), which may restrict the applicability of the benthic resting egg strategy.

Acartia bifilosa

On an annual time scale, *Acartia bifilosa* is the most abundant species of the pelagic mesozooplankton community in the northern Baltic Sea (Viitasalo 1994). In the sediments of the study area (excluding Pojo Bay) it was also the most abundant representative in the inactive fraction, namely the benthic egg pool (I, IV). The high abundance of eggs in the sediment reflects the abundance of the species in the water column. The populations begin to build up in April or May, and several abundance peaks may be observed until the numbers decline in October or November (Viitasalo 1992a, Viitasalo et al. 1995). The females occur from April to November and probably produce eggs during most of this time – eggs were deposited on the bottom throughout the period that females were observed in the plankton (I). In the southern Baltic Sea *A. bifilosa* females maintain egg production, though at a low level, in winter when the water temperature is < 2 °C (Schmidt et al. 1998).

Acartia bifilosa produces only one type of egg in the study area, i.e. subitaneous eggs. The egg development rate is dependent on temperature; the eggs hatched in 2–16 days at 18–1.5 °C, respectively (II). Since the warmest temperatures mostly occur for short periods and are restricted to the upper 5–10 m, development most often requires more than two days. Therefore, it is realistic to assume that a large part of the eggs reaches the bottom prior to hatching

on the shallow coasts of the Baltic Sea. In two days the eggs would sink at least an estimated 26 m, applying the sinking speeds reported for the eggs of marine calanoid copepods (Landry 1978, Uye 1980, Marcus & Fuller 1986, Kiørboe et al. 1988, Miller & Marcus 1994, Wang et al. 2005), although turbulence and water currents may slow the sinking speed (Miller & Marcus 1994). Sinking to the bottom was reflected in the variations in abundance of the planktonic and benthic populations of *Acartia* spp. at Storfjärden in 1992–1993. Egg abundance in the sediment clearly followed the abundance of the planktonic females and was in turn followed by the naupliar abundance in the water column (I).

Assuming that eggs mostly sink to the bottom prior to hatching, the recruitment of *A. biflosa* is linked with benthic conditions. Low temperature or darkness did not hinder development (II), but under anoxic conditions the eggs became quiescent (III). When the sediment surface is oxygenated, the eggs continue development and hatch. However, depending on the sedimentation rate and the physical and biological mixing of the sediment, some of the eggs will be buried and become dormant due to oxygen depletion that prevails beneath a thin surface layer in organically rich coastal sediments (Revsbech et al. 1980). The eggs may be translocated or resuspended in the water column (Marcus & Taulbee 1992), while vertical translocation in the sediment, both upwards and downwards, further occurs due to bioturbation by benthic fauna (Marcus & Schmidt-Gengenbach 1986, Kearns et al. 1996). The eggs can remain viable for periods of from several months to more than a year (III) and wait for an opportunity to be returned to the sediment surface. During most of the year the temperature in the bottom layer is low, thus lengthening the

development time and increasing the probability that some of the eggs will be buried. Hatching probably occurs from the sediment throughout the year. The intensity of hatching is dependent on the egg pool on the sediment surface and on the temperature, which determines the speed of development. There is evidence that the recruitment to a planktonic population is at least seasonally dependent on the processes affecting hatching from benthic eggs: a correlation between naupliar abundance and deep-water temperature in autumn was detected in an analysis of a long-term data series (Viitasalo et al. 1994).

Since some of the eggs become dormant for variable periods on the bottom, the time between laying and hatching varies more in eggs that sink to the bottom prior to hatching than in eggs that hatch already in the water column. This lengthens the reproductive life span of the females. A population may also maintain a more constant perennial population by ‘time-released’ hatching from the sediments (Uye 1980, 1985). This should level down the effects of possible egg production peaks. However, peaks could be observed in *A. biflosa* naupliar abundance (I). In addition to the changes in egg production that lead to differences in the egg pool on the bottom, these peaks can be derived from changes in the benthic conditions that accelerate hatching (in autumn) or perhaps changes in the pelagic conditions that affect survival of the hatched nauplii (in spring).

The abundance of *Acartia* nauplii often peaks in autumn (Viitasalo 1992a, I), when the water column can be mixed to the bottom and the accompanying warming of the deep water accelerates egg development. Resuspension of sediments may also occur during these mixing events and further enhance recruitment from the bottom. Very

few of these autumnal recruits will ever reach the reproductive stage: in 1992, the abundance of the nauplii crashed and did not end up as a substantial increase in copepodite abundance (I). On the other hand, this peak was the seed of the small overwintering population.

In spring, a naupliar peak can be observed clearly before the adults grow in abundance (Hernroth & Ackefors 1979, Viitasalo 1992a, I); the timing of this peak often roughly corresponds to melting of the ice cover (Viitasalo et al. 1994). Although this peak most probably is a result of hatching of the benthic resting eggs, there is no indication that any special event or seasonal condition would promote an abrupt and synchronized hatching from the bottom (I). The eggs do not need a light cue for hatching (II); an increase in the temperature that could speed up development and hatching will not occur before late spring or even early summer. Seasonal oxygen depletion occurs in some coastal environments, but probably not to such an extent that it would explain the observed spring peaks. It is possible that nauplii hatch from the bottom throughout the winter, but they are only observed when conditions in the water column promote survival and growth to the older stages. The food conditions below the ice appear favourable for nauplii early in the season, while the copepodites apparently suffer from insufficient food resources in winter, judging by the decrease in their storage lipids (Werner & Auel 2004).

The possible advantage of this continuous emergence from the bottom is that a species can 'sample' different environmental conditions of the year (De Stasio 1990). This would be particularly useful in environments where the timing of seasonal variation is unpredictable and favourable environmental conditions are not accompanied

by a detectable cue for hatching in the sediment. In the Baltic Sea the ice conditions vary on a yearly basis, accompanying differences in the onset and volume of the spring phytoplankton bloom (e.g. Niemi 1975). However, in such a strategy reproductive losses are necessarily high and it cannot always be concluded that the patterns observed are 'adaptations' or 'strategies'. For example, it was suggested that mistiming of hatching of the resting eggs of the cladoceran *Bosmina longispina maritima* influences the large annual variations in productivity of this species in the Baltic Sea (Kankaala 1983). Resting eggs were observed hatching in late spring, but the high planktonic densities of the cladoceran could not be established before autumn when the conditions were suitable for the species. Continuous hatching from sediments is probably more profitable for *A. bifilosa*, which can maintain high population densities for a large part of the year.

Eurytemora affinis

Eurytemora affinis is the second most abundant copepod in the northern Baltic Sea (e.g. Hernroth & Ackefors 1979, Viitasalo 1992b). It is also the dominant copepod species in the brackish and estuarine waters of Northwestern Europe, or even of the Northern Hemisphere (Mauchline 1998, Lee 1999, Gasparini et al. 1999). In contrast to the other parts of Europe, where the maximum abundance is often observed in spring at relatively low temperatures (e.g. Castel 1993, Escaravage & Soetaert 1995), in the northern Baltic Sea *E. affinis* peaks after *A. bifilosa*, is abundant in summer and declines in late autumn (e.g. Hernroth & Ackefors 1979, Viitasalo et al. 1995).

Several facts suggest that *E. affinis* pro-

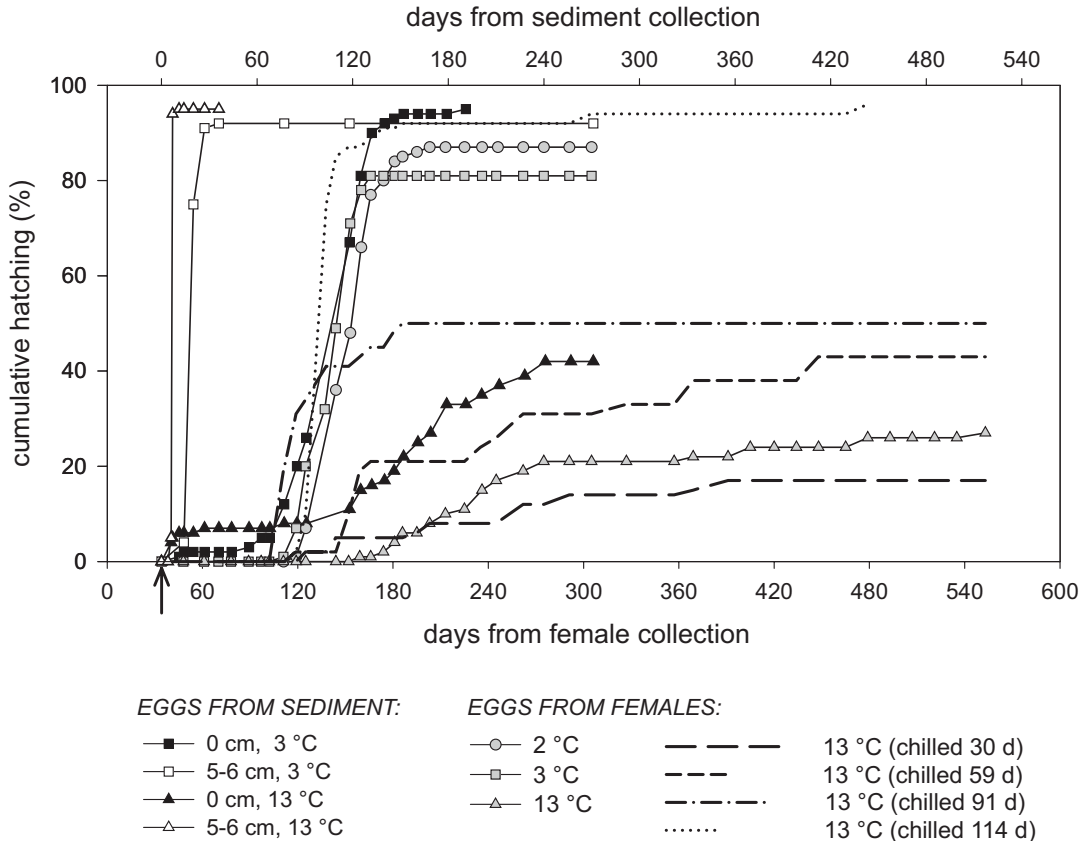


Figure 3. Cumulative hatching of *Eurytemora affinis* diapause eggs at different temperatures. The lower x-axis starts from October 11, which was the sampling date of the females. The arrow shows the sampling date of the sediments. The sediment-egg incubations are drawn to start from this point so that the ‘calendar timing’ of all the curves is similar.

duces diapause eggs in the northern Baltic Sea. Its eggs were found numerously in the sediments, especially in Sällvik (I, V). *Eurytemora affinis* carries an egg sac in which the eggs develop until hatching. Thus, accidental sinking to the bottom is prevented for subitaneous eggs, and those found on the bottom are more probably diapause eggs. Long-term viability is a trait more often associated with diapause than subitaneous eggs (Grice & Marcus 1981): *E. affinis* eggs maintained high viability for at least 6–8 years in sediments (III, V). In addition, eggs taken from the surface sedi-

ments (= newly sedimented) in autumn did not hatch after a short incubation (I, V), whereas older eggs from the deeper layers hatched readily (V).

The production of diapause eggs was verified in experiments with eggs produced by field-collected females in October. The diapause eggs were released from the egg sacs within several (0–8) days. The first nauplii hatched at 2–3 °C after 3–4 months, after which gradual hatching occurred from each individual clutch for up to three months (Fig. 3). The refractory phase took about five months at 2 and 3 °C, de-

terminated as the time when the cumulative hatching had attained 50% of final success. To achieve substantial hatching success at a warm temperature (13 °C), a chilling (at 2 °C) for ~3 months was required. If not chilled or chilled for a shorter time, hatching began later and continued longer (more than a year), resulting in poorer success. In all different 13 °C incubations (except for the group chilled for 114 days), there was at least one clutch with no hatching during the 1.5-year experiment.

The hatching pattern of the eggs sampled from the surface sediments in November was strikingly similar to that of the eggs produced by the females in the laboratory, which confirmed that diapause egg production had occurred at the study site. After the refractory phase, which was over nearly concurrently in both eggs derived from the sediment and those from the females, the cumulative hatching percentage rose to high values at 3 °C while it rose slowly and attained only modest values at 13 °C (Fig. 3), quite similar to the eggs produced by females in the laboratory. In contrast, eggs that originated from deeper sediment layers were deposited during previous years and had already completed the refractory phase and hatched without delay (Fig. 3). The chilling requirement was also met in the sediments: there was no delay or reduction in final hatching success at 13 °C. The majority of the eggs in the surface sediments were probably produced at approximately the same time that the experiments with females were conducted. In preliminary experiments conducted in early October, a smaller fraction of the clutches produced were diapause eggs, also suggesting that a shift to diapause egg production occurs in October. However, the length of the refractory phase may vary, depending on the time of egg production, which can lead

to fairly simultaneous termination of dormancy for eggs produced at different times (Marcus 1987, Ban & Minoda 1991).

The only other study that revealed the development pattern and hatching requirements of *E. affinis* diapause eggs is the one by Ban and Minoda (1991), which was conducted for a lake population of the species in Japan. A refractory phase was observed at all temperatures but, in contrast to my results, it was shorter at high temperatures and no chilling was needed. At 20 °C, a 50% hatch was attained in 36 days and at 4 °C in 45–107 days. In a marine environment, where the water temperature remains high late in autumn and downwellings may occur, the need for chilling ensures that the eggs will not hatch before the onset of winter, while smaller bodies of water cool more rapidly in autumn, making such backup strategy unnecessary. In Pojo Bay, where my study was conducted, the water is strongly stratified and does not warm up on the bottom in autumn (Niemi 1973, 1978, Stipa 1999), but the area is not isolated from the adjacent sea area and the organisms are probably not locally adapted.

For the other European populations of *E. affinis*, the production of diapause eggs was only revealed from the occurrence of the eggs in sediments. In the Bothnian Sea (Albertsson & Leonardsson 2000, 2001) and southern Baltic Sea (Madhupratap et al. 1996), the sediments were collected and hatching observed in spring, when the refractory phase must have been over and chilling accomplished during winter; thus, egg hatching was observed during a short incubation at 13–15 °C. In Norway, Næss (1996) incubated eggs at 10 °C for 10 days after storage of sediment at 4 °C for > 1 month. Resting eggs of *E. affinis* were also found in sediments in an estuary in Oregon, eastern North Pacific Ocean

(Johnson 1980).

The eggs of *E. affinis* form a viable egg bank in the sediments. The abundance as well as hatching success of the eggs was high from the surface to the deeper layers (5–6 cm; Figs. 3,4). The sedimentation rate in the Sällvik deep is approximately 1 cm year⁻¹ (IV, V). The most recent sediment is quite loose, and probably the siphoned surface and the next adjacent layer represent the sedimentation of the study year, the following layer approximately the previous year and the sediment at 5–6-cm depths is probably five years old. The viability did not decrease during these five years (Fig. 3). In eight-year-old sediment ‘high abundance’ and hatching success were also attained; viable eggs were found even deeper (V). In the pioneering study (IV) the observed copepod egg abundances in the 0–10-cm layers in Sällvik were very low compared with these later estimates.

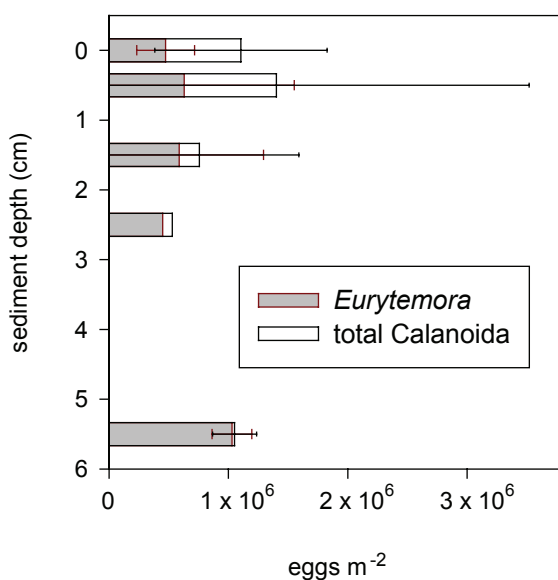


Figure 4. Copepod egg abundance in the sediments of the Sällvik deep. Average of three profiles ± S.D.

This was probably a methodological problem and will be discussed later in connection with oxygen conditions (p. 29).

Although *E. affinis* is not a ‘classical’ example of a species that undergoes dormancy, since it does not totally disappear from the plankton in winter, it produced quite typical diapause eggs that had a clear refractory phase and that also needed chilling prior to development at warm temperatures. As was stated above, *E. affinis* occurs in winter in low numbers and peaks in summer. Small numbers of *E. affinis* were observed in the under-ice water in Santala Bay on the northern coast of the Hanko Peninsula (Werner & Auel 2004). Therefore, production of diapause eggs is not essential for winter survival. The planktonic population can be renewed after winter from two sources: hatching from the bottom and reproduction by those specimens that have survived the winter months in the water column. Diapause eggs probably serve two purposes for *E. affinis*: 1) they ensure recruitment if the planktonic population fails to survive to the next spring and 2) they form a viable egg bank in the sediments in the event of long-term catastrophes.

Acartia tonsa

In contrast to earlier reports, *Acartia tonsa* is abundant in the study area. It occurred in the plankton in late summer and autumn when it equalled *A. biflosa* in abundance in Storfjärden and replaced it in Sällvik (I). *Acartia tonsa* is a cosmopolitan species (Razouls 1995), mentioned as having North American or Indo-Pacific origins (Leppäkoski & Olenin 2000). It is mostly restricted to nearshore environments (e.g. Paffenhöfer & Stearns 1988, Tester & Turner 1991). First observed in Europe in

the early 20th century (Remy 1927, as cited in Brylinski 1981), it has become a permanent and abundant inhabitant of many estuarine habitats (Brylinski 1981). It was already reported from the Gulf of Finland in 1935 (Smirnov 1935), but it has only occasionally occurred in plankton samples in the coastal northern Baltic Sea. At Storfjärden it was rarely seen in plankton samples, at least until 1984 (Viitasalo 1992b). However, in a study conducted in 1983–1988 in the eastern Gulf of Finland, the abundance of *A. tonsa* attained 40–50% of the total copepod abundance in the deep-water areas in autumn (Silina 1989, 1991).

Acartia tonsa is a warm-water species that occurs throughout the year in tropical and warm temperate waters, but seasonally in the northern part of its range in North America (Zillioux & Gonzalez 1972, McAlice 1981) and in Europe from the Baltic Sea to the English Channel (Arndt & Schnese 1986). It can be assumed that *A. tonsa* relies on benthic resting eggs for recruitment in these areas (Zillioux & Gonzalez 1972, McAlice 1981, Arndt & Schnese 1986), although its eggs have been extracted from sediments only in the Baltic Sea (Madhupratap et al. 1996, I) and in Florida (Marcus 1991, Chen & Marcus 1997) where *A. tonsa* occurs throughout the year. In Florida the hatching success was low (10–50%; Chen & Marcus 1997), and the eggs are not assumed to remain viable in the sediments for extended time periods (Suderman & Marcus 2002). In the Baltic Sea the species is dependent on the viability of the benthic resting eggs, and Madhupratap et al. (1996) found the hatching success of the eggs to be high, about 70–90%. In the northern Baltic Sea its survival in sediment can vary widely. Sediment was collected from Storfjärden in May 1997 and 1998: the egg numbers in

the surface sediment (about 0–1.5 cm) were $0.7\text{--}1.9 \times 10^5 \text{ m}^{-2}$ in 1997 and $0.04\text{--}1.7 \times 10^5 \text{ m}^{-2}$ in 1998, which is roughly an order of magnitude lower than the egg abundance of *A. bifilosa* (I). In May 1997 the hatching success was high (50–80%) at 8 and 13 °C and lower in May 1998 (< 40%) at 8 and 18 °C. The eggs did not hatch at 3 °C during the 1.5-month incubation, after which low hatching success (< 20%) was attained at 18 °C. In May 1998 the 1.5–2.5-cm layer was also sampled, and the number of viable eggs was about $0.6 \times 10^5 \text{ m}^{-2}$.

Although records of benthic eggs for *A. tonsa* are scarce, the species is well known to undergo egg dormancy; in fact it was among the first marine copepods for which resting eggs were reported (Zillioux & Gonzalez 1972). It has often been reported to produce diapause eggs (e.g. Marcus 1996), but this has actually been verified in only a single study. In experiments conducted in Southampton, England, *A. tonsa* laid three morphological types of eggs. Two of these types (produced in September) were classified as subitaneous because they attained high hatching success within 24 h after laying, whereas eggs of the third type (produced in October) did not hatch in 90 days at 20 °C and were classified as diapause eggs (Castro-Longoria 2001). However, the viability of these eggs was not verified by further incubating them. Quiescence due to low temperature has been observed in several studies, but the temperature at which development is arrested varies between and within studies, depending on the time of the year or the parental acclimation temperatures. In most cases development is arrested at about 5 °C (Zillioux & Gonzalez 1972, Støttrup et al. 1999, Castro-Longoria 2003; for contrasting observations, see Uye & Fleminger 1976, Chinnery & Williams 2004). Hatching requirements and develop-

ment times in different studies are variable. Differing incubation times make comparison somewhat difficult. Often it is thought that temperatures above 10 °C are needed for significant levels of hatching from benthic resting eggs (McAlice 1981, Arndt & Schnese 1986).

In 1998, the egg development of *A. tonsa* was studied during the time it was found in the plankton. Females first appeared in mid-August and could be caught until early November. The results clearly showed that the eggs of *A. tonsa* experience dormancy in the northern Baltic Sea, but that the pat-

tern differs from that described elsewhere for the species. Two main features could be distinguished: at a low temperature (3 °C) development was inhibited, while at higher temperatures (≥ 6 °C) ‘delayed hatching’ (Chen & Marcus 1997) progressively occurred during autumn (Fig. 5). ‘Delayed hatching’ does not fit into the quiescence/diapause dichotomy, but is an example of an intermediate type of dormancy. A fixed refractory phase required in diapause (*sensu stricto*) is lacking: some eggs hatch soon after spawning and cumulative hatching occurs for up to several months (Chen &

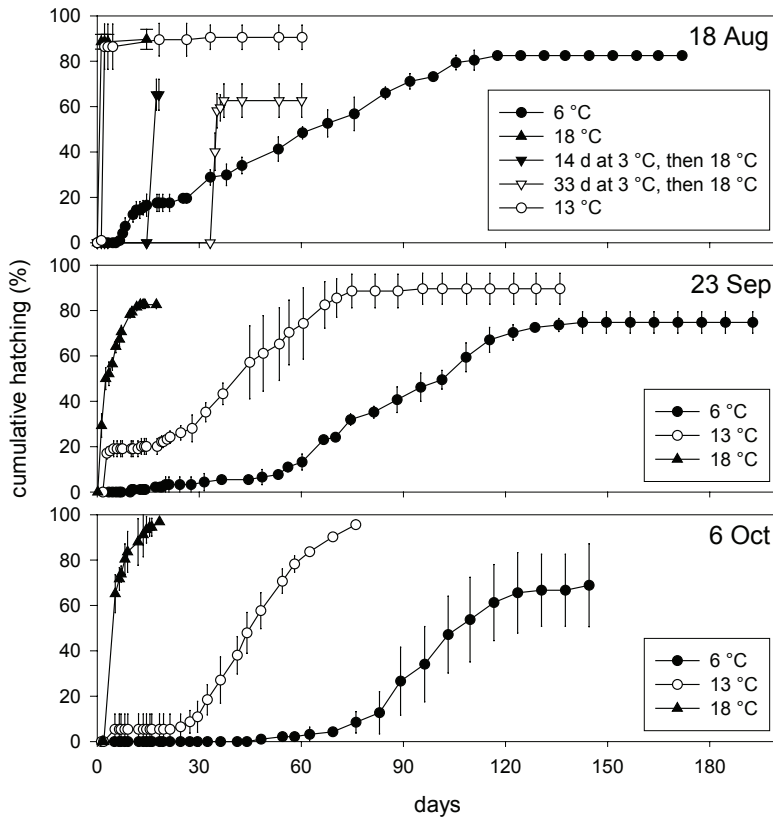


Figure 5. Development of *Acartia tonsa* eggs. Cumulative hatching at different temperatures (means and standard deviations of three replicates of ~30 eggs). Sampling dates for females are shown in each graph. The eggs did not hatch at 3 °C and were transferred to 18 °C after 14- and 33-day incubations (Aug 18).

Marcus 1997). The temperature and time of the year affected the response in *A. tonsa*. At higher temperatures (18 and 13 °C), the eggs in general attained high hatching percentages (> 80%), but the time for the cumulative hatching to reach this final hatching percentage varied. Some of the eggs developed rapidly and hatched in a few days after spawning, while others showed a delayed hatching response. There was almost no delay in hatching of eggs spawned in summer (August), but the delay became more pronounced through autumn. At 6 °C, fewer eggs hatched initially than at 13 and 18 °C, but high cumulative hatching percentages could finally be attained, except in those experiments begun late in autumn (Fig. 5).

Temperature-controlled development affects the recruitment of *A. tonsa* from benthic eggs in summer, the critical temperature being somewhere between 3 and 6 °C. Populations develop in late summer when water near the bottom has also warmed sufficiently. When the first females appear and produce eggs, development at high temperatures is rapid and it may be that most eggs develop to hatching in the water column or soon after sinking to the bottom, depending on the deep-water temperatures. If the water is thermally stratified, the eggs produced in the water column may be separated into two groups: those that soon hatch in the water column and the others that sink to the bottom where low temperatures considerably delay hatching. Chen and Marcus (1997) suggested that delayed hatching may be a 'bet-hedging' (risk-spreading) strategy to spread the recruitment of offspring over time. For *A. tonsa* the applicability of such a strategy under northern conditions is limited to a short period in late summer, since the waters cool towards winter and hatching probably ceases. Delayed

hatching therefore leads to accumulation of eggs on the bottom. In my experiments the eggs were exposed to constant temperatures, which does not reflect the situation in the field where they are exposed to gradually declining temperatures. It is not known how the eggs respond to changing temperatures; possibly they further slow down development when the temperature lowers.

Intra- and interspecies differences

My results show that the resting eggs of *Acartia bifilosa*, *A. tonsa* and *Eurytemora affinis* represent different types of dormancy and that these species differ with respect to life cycle strategy. *Eurytemora affinis* produces two types of eggs: subitaneous eggs in summer and diapause eggs in autumn. The diapause eggs only hatch after a refractory phase (of at least three months) and also need to experience a period of chilling before they can hatch at a warm (13 °C) temperature (Fig. 3). Subitaneous eggs develop in egg sacs until hatching and probably are not capable of dormancy. *Acartia bifilosa* produces subitaneous eggs throughout the productive season (I, II). In shallow areas many eggs sink to the bottom (I), where their development and hatching are inhibited or retarded if they end up in an oxygen-deficient environment (III), e.g. under the sediment. Their dormancy is of the quiescent type (II). The dormancy of *A. tonsa* eggs does not clearly belong to either type, but resembles the delayed-hatching type described by Chen & Marcus (1997) (Fig. 5). The species only occurs in the plankton in late summer and autumn (Silina 1989, 1991, I), and the development of the eggs is affected both by temperature and the time of the year (Fig. 5). Of the three species *A. tonsa* is the only one that is clearly

dependent on the resting egg strategy for yearly recruitment under northern conditions. It occurs in the plankton for only a restricted time period of the year, while the others never totally disappear from the water column.

The life cycles of the indigenous copepods *A. bifilosa* and *E. affinis* share some similar characteristics: they do not disappear completely from the plankton in winter (Hernroth & Ackefors 1979, Viitasalo 1992b, I) and their eggs are able to hatch at low temperatures (I, II, Fig. 3). They face similar stresses during winter – both maintain small populations during winter, but the individuals cannot ‘replace’ themselves by reproduction as they would do under summer conditions. Growth is minimal, even negative if the lipid reserves are utilized (Werner & Auel 2004). Therefore, dormancy on the seabed also offers a good alternative for overwintering for species with no gaps in planktonic existence. This can be seen as a form of ‘bet-hedging’ strategy (cf. Hairston et al. 1985).

Although both species partially overwinter as benthic resting eggs, they differ in the type of dormancy – diapause in *E. affinis* (this summary) and quiescence in *A. bifilosa* (II, III). Quiescence of subitaneous eggs may not be an option for *E. affinis* because it carries the eggs in egg sacs until hatching, so that the eggs do not normally sink to the bottom. An exception to this rule possibly occurs after predation: the eggs may end up on the bottom in fish faeces. The subitaneous eggs are able to survive passage through fish intestines (Flinkman et al. 1994), but during this time their development is not arrested (J. Flinkman & M. Viitasalo, Finnish Institute of Marine Research, unpubl. data). The subitaneous eggs of *E. affinis* may not be capable of dormancy; their viability is soon lost under

anoxia (Ban & Minoda 1992). In contrast, the subitaneous eggs of *A. bifilosa* survived well under anoxia in my experiments, especially at low temperatures (III), and *A. bifilosa* does not need to allocate resources for diapause egg production.

The seasonal dynamics of egg deposition and recruitment from the bottom differ among species. The eggs of *A. bifilosa* are deposited on the bottom almost throughout the year (I), while *E. affinis* produces diapause eggs in autumn (this summary) and the subitaneous eggs produced in summer do not sink to the bottom. Hatching from the bottom may also be more or less continuous for *A. bifilosa* (I), whereas the eggs of *E. affinis* begin to hatch in spring after the refractory phase is completed (Fig. 3). *Eurytemora* eggs that have accumulated in the sediments in previous years should be ready to hatch any time of the year, but most have probably been buried too deep in the sediment to significantly contribute to the seasonal recruitment pattern. The eggs of *A. bifilosa* show remarkable survivability for subitaneous eggs (III), but are still short-lived compared with *E. affinis* diapause eggs which showed no loss in viability for several years (V, this summary).

The warm-water origins can be seen in the seasonal occurrence and egg development pattern of *A. tonsa*. It occurs only for a restricted time in the plankton (I), which makes it totally dependent on benthic resting eggs in maintaining local populations. The egg dormancy of *A. tonsa* represents an intermediate type between diapause and quiescence, and development of its eggs is arrested at low temperatures (this summary). The variability in egg development pattern and survivorship could indicate that it has not totally established itself in the area, or alternatively it can be an expression of the life cycle plasticity in this invasive species.

The wide range of development patterns probably facilitates the establishment of remote populations, and could be an important element behind the success of *A. tonsa* in gaining and maintaining its wide latitudinal distribution.

In addition to interspecies differences intraspecies differences were also evident. My studies revealed that egg dormancy of *A. bifilosa* in the northern Baltic Sea represents the quiescent type and that diapause eggs are not produced (II), while in the English Channel populations of *A. bifilosa* both types occur and, furthermore, quiescence in its subitaneous eggs is induced by low temperatures (Castro-Longoria & Williams 1999). The egg development pattern of *A. tonsa* has varied widely in different studies (although in many cases it was not thoroughly investigated). In contrast to my studies, the eggs of *E. affinis* hatched more readily at warm temperatures in a lake in Japan (the refractory phase was dependent on temperature), and no chilling was needed (Ban & Minoda 1991). However, there is doubt whether '*E. affinis*' in Europe and Asia belong to the same species: recent phylogenetic analysis suggests that *E. affinis* constitutes a sibling species complex (Lee 2000). On the other hand, *A. bifilosa* in the Baltic Sea is the same species as the one in the English Channel, as shown by morphological examinations (Hirst & Castro-Longoria 1998).

It is not unusual for life cycle strategies to vary geographically within a species. Along the NW Atlantic coast, populations of *Labidocera aestiva* (Marcus 1984b) and *Acartia hudsonica* (Avery 2005) differ in relation to the occurrence of diapause, as do those of *Acartia clausi* (*A. omorii*) in different parts of Japan (Uye 1980, 1982, 1985). In ponds, diapause timing may vary within a small geographical area in relation

to special conditions in the ponds (Hairston et al. 1985). The diversity of copepod life cycle strategies in relation to dormancy indicates that there is evolutionary plasticity in the trait. The diapause trait (Wyngaard 1988) and the response to cues for diapause (Hairston & Dillon 1990, Avery 2005) are heritable, and diapause timing may undergo rapid evolution (Hairston & Walton 1986). Thus, dormancy patterns in copepods may readily respond to selection pressures. Quiescence may occur in addition to diapause, possibly because it is more flexible in relation to induction and termination of dormancy (Elgmork 1980).

The evolution of metabolic depression as a means to survive under unfavourable conditions is unclear. The molecular mechanisms of metabolic depression are basically similar over a wide range of taxa (Storey & Storey 1990). Alekseev and Starobogatov (1996) suggested that the dormancy, or diapause, trait is an ancestral feature with monophyletic origins, although there is also abundant evidence suggesting polyphyletic origins (Hairston 1998). If diapause evolved once, then the Baltic populations of *A. bifilosa* would have lost the trait after differentiating from the populations in the English Channel; if it evolved many times, the English Channel populations would have gained the trait after the spreading of the species. In either case, in the Baltic Sea the selection pressure for diapause in *A. bifilosa* is evidently too weak or lacking. First, in contrast to the English Channel (Castro-Longoria & Williams 1999), the planktonic population is not totally absent any time of the year, although it is very small during winter. Thus, recruitment in spring is not totally dependent on benthic resting eggs. Second, the production of diapause eggs is more costly than that of subitaneous eggs (Hairston & Cáceres 1996).

The diapause trait may not be selected for if the quiescent eggs also remain viable in the sediments over winter. The eggs of *A. biflosa* are also capable of survival beyond the seasonal scale, in contrast to the notion that quiescent eggs are not capable of long-term survival (Grice & Marcus 1981): nauplii hatched from eggs stored in sediment in the laboratory for almost two years (III). In Southampton waters *A. biflosa* was absent from the plankton during the warm months in summer and autumn (Castro-Longoria & Williams 1999). Diapause may be essential for survival in such situations, since warm conditions probably depress the survival of quiescent eggs (e.g. Uye & Fleminger 1976, Uye 1980, III).

Induction and maintenance of dormancy and survival under different conditions

Temperature

Temperature is one of the most important factors controlling egg development and dormancy in organisms. The rate of metabolic action is dependent on temperature; in seasonal environments temperature, in addition to photoperiod, indicates the time of the year. The egg development time of copepods is inversely related to temperature, but the relationship is dependent on the species and environmental regime the population is adapted to. In addition, species have specific tolerance limits; generally, species adapted to low-temperature environments develop more rapidly at low temperatures (e.g. McLaren et al. 1969).

Temperature can affect dormancy in several ways. Development of subitaneous eggs may be arrested at an unsuitable temperature. In diapause eggs, the length of

the refractory phase as well as hatching of the eggs after completion of the refractory phase may be affected by temperature (Grice & Marcus 1981). In the Baltic Sea temperature fluctuations are large at the surface, from near 0 °C (and ice cover) in winter to about 16–19 °C in summer (Haapala & Alenius 1994). The variation decreases with depth; e.g. at 30 m the maximum temperatures in general remain between 5 and 10 °C (Haapala & Alenius 1994), but may attain higher values of 12–13 °C, or even as much as 18 °C (Tvärminne Zoological Station, unpubl. data).

The three species studied here responded differently to temperature. The development rate of *Acartia biflosa* eggs is dependent on temperature but the temperature does not directly affect hatching success (II). However, since low temperatures increase the time needed for development, they also increase the probability that the eggs will reach the seafloor and become buried prior to hatching. This will suppress the final hatching success because some of the buried eggs will probably never hatch. On the other hand, if the eggs become quiescent due to oxygen deficiency, they will survive longer in cold than in warm environments (III). Thus, the effect of temperature is two-sided.

Eurytemora affinis lays both subitaneous and diapause eggs. Development of subitaneous eggs was not studied here; development times vary considerably in different studies, e.g. at 5 °C from 7 (Escaravage & Soetaert 1993) to 14 days (Andersen & Nielsen 1997), and at 12 °C from 1 (Vuorinen 1982) to 4 days (Andersen & Nielsen 1997). Low temperatures (2–3 °C) do not inhibit hatching (Vijverberg 1980, Escaravage & Soetaert 1993, Katajisto, pers. obs). Certain temperature regimes are required for the completion of the refractory

phase in diapause eggs of *E. affinis*. High final hatching success was achieved if the 3–4-month refractory phase was spent at 2–3 °C, while shorter or no chilling resulted in poor and slow hatching at 13 °C. This ensures that the eggs do not hatch already in autumn. After completing the refractory phase, diapause eggs respond to temperature in a manner similar to that of subitaneous eggs: hatching is more rapid at higher temperatures, as was seen when incubating ‘old’ eggs extracted from the deeper sediment layers (Fig. 3).

In *Acartia tonsa* temperature also affects the hatching success of subitaneous eggs. The development was arrested at low temperatures (~3 °C). Viability was reduced during the quiescence: about 60% of the eggs hatched at 18 °C following a 2–5-week incubation at 3 °C. In contrast, at 6 °C high hatching success was attained, although development required up to four months. Therefore, the low temperature apparently suppressed viability, not the dormancy itself. Since the seasonal occurrence of *A. tonsa* in the plankton is restricted to late summer and autumn (I), newly produced eggs may not be subjected to very low temperatures, although in some strongly stratified waters, such as Pojo Bay, this may occur. However, it is more likely that the eggs that experience delayed hatching will experience gradually declining temperatures. Overwintering in sediments requires that some of the eggs must retain viability at cold temperatures of < 3 °C. Possibly eggs that already are in a state of dormancy are better able to survive the cold.

Oxygen conditions

Generally, the absence of oxygen means impossible living conditions for most mul-

ticellular organisms. However, a variety of organisms can cope with low oxygen concentrations in their environment and even benefit from them. Dormant organisms may reduce their metabolic activities to a minimum; in the extreme case metabolic depression can be perfect and dormant organisms may survive extended time periods under anoxia (Clegg 1997).

In *Acartia bifilosa*, being exposed to anoxic conditions is a requirement for dormancy (II, III). Unless oxygen deficiency prevails in the bottom water, the eggs must be buried to become quiescent. Typically, only the topmost few millimetres of sediments are oxygenated (e.g. Revsbech et al. 1980). In the other species studied, other factors contribute to dormancy and the requirement for anoxic conditions is not as strict. The delayed-hatching eggs of *A. tonsa* and diapause eggs of *Eurytemora affinis* were observed hatching after an incubation of almost 5 months (Fig. 5) and 1.5 years (Fig. 3) under normoxic conditions, respectively. Dormancy, however, would probably continue longer under anoxic conditions, which may account for the longer-term viability observed in the eggs of these species. The yearly recruitment of *A. tonsa* from benthic resting eggs is possible only if the eggs remain dormant and viable in the sediments for > 6 months; the *E. affinis* eggs that had been extracted from 5–10-year-old sediments hatched successfully (V, this summary).

Great differences occur in the survival potential of copepod eggs. The sediment samples were stored for up to six years in the laboratory, and nauplii that emerged from the eggs that were extracted from these seemingly anoxic samples were almost exclusively *E. affinis*, although this species originally constituted only a minor proportion of the copepod eggs in the samples

(III). In Sällvik, the abundance and viability of *E. affinis* eggs showed no decrease from the sediment surface to 6-cm depths (corresponding to 5–6 years in age), while other species were abundant only in the surface sediments (Figs. 3 and 4). Overall, diapause eggs survive longer than subitaneous eggs (e.g. Grice & Marcus 1981). However, the subitaneous eggs of *A. bifilosa* survive well compared with other species. The subitaneous eggs of *Centropages hamatus* survived three months under anoxia (Marcus & Lutz 1998), and subitaneous eggs of *Acartia steueri*, *A. clausi* (Uye 1980) and *Tortanus forcipatus* (Kasahara & Uye 1979) hatched after 3, 5.5 and 7 months' storage in mud, respectively. The subitaneous eggs of *A. bifilosa* survived notably longer in my studies: up to a year in anoxic water and almost two years in sediment (III). Therefore, the quiescence of subitaneous eggs is an applicable overwintering strategy for *A. bifilosa* in the northern Baltic Sea.

Copepod eggs develop and hatch at oxygen concentrations (0.1–0.3 ml O₂ l⁻¹; Uye & Fleminger 1976, Ambler 1985, Lutz et al. 1992, 1994, Ban & Minoda 1992, III) that can be considered as severely hypoxic (cf. Diaz & Rosenberg 1995). The hatched nauplii probably cannot survive under such conditions (Uye & Fleminger 1976, Ban & Minoda 1992). However, if oxygen deficiency is restricted to a thin layer above the bottom, the nauplii may manage to swim to the upper, oxygenated water layers. In comparison to completely anoxic conditions, low oxygen concentrations below the hatching threshold appear to depress the viability of eggs (Lutz et al. 1994, III). Therefore, risking the survival of nauplii may be a safer strategy than remaining dormant under hypoxic conditions in which the viability of the eggs would quite soon be lost.

The better survival of the eggs under

completely anoxic than hypoxic conditions (III) may explain the low viability of the eggs in some samples. When the sediments were mixed with water during sampling and the samples subsequently stored for five months, the number of eggs found, as well as their hatching success, was low (max. 21%, IV). This could have been due to the probable slight oxygenation of the samples during sampling and storage. It is possible that only in the complete absence of oxygen would all metabolic activity cease and long-term survival become possible (Lutz et al. 1994). If factors other than oxygen conditions induce dormancy, the survival of eggs under anoxic versus oxic conditions can be compared. The diapause eggs of *E. affinis* survived well through the 3–5-month refractory phase at low temperatures and under normoxic conditions, but at the higher temperature dormancy was prolonged and final hatching success poor (Fig. 3). The oxygen may have contributed to the loss of viability during this long storage. The eggs survive much longer in anoxic sediments, as mentioned above. The formation of long-term viable egg banks may require that anoxic conditions prevail in the sediments. For example, the diapause eggs of *Centropages hamatus* survived better under anoxic than normoxic conditions (Marcus & Lutz 1998).

Although copepod eggs are able to survive anoxic conditions – and even benefit from the induction and maintenance of dormancy by them – the increasing occurrence of oxygen deficiency in the bottom water accompanying eutrophication of coastal areas in the Baltic Sea (Weigelt 1991, Bonsdorff et al. 1997, Persson & Jonsson 2000, Laine & Kangas 2004) may have negative effects on species with the benthic life cycle link. Widespread attention has been focused on the negative effects of

anoxic or hypoxic conditions on the benthic fauna (Andersin et al. 1978, Weigelt 1991, Laine et al. 1997, Powilleit & Kube 1999), but the relationships between zooplankton and benthic conditions have not been studied. In other seas, situations that may have been related to occasional or permanent oxygen depletion near the bottom vary from seasonal variations in copepod abundance in Chesapeake Bay (Roman et al. 1993, Keister et al. 2000) to changes in species dominance of the copepod community in eutrophied Tokyo Bay (Uye 1994) and the impoverished zooplankton of a stratified fjord in the Kattegat (Fenchel et al. 1995). Hypoxic conditions may also affect populations even if no direct lethal effects are found, because reproduction may already be affected by sublethal concentrations (Marcus et al. 2004).

Light

The photoperiod is one of the main cues for initiating diapause egg production (Marcus 1980); sometimes the response is modified by temperature (Marcus 1982, Hairston & Kearns 1995). Light conditions may also contribute to finishing the developmental arrest, whether it be diapause or quiescence (Brendonck 1996, Egloff et al. 1997). However, in copepods, the breaking of egg dormancy seldom requires light; only the eggs of *Acartia clausii* have been reported not to hatch in darkness (Landry 1975, Uye & Fleminger 1976). On the other hand, Uye (1980) reported that hatching of *A. clausii* and *A. steueri* was suppressed in darkness but not totally inhibited. In the Baltic Sea light penetrates poorly to the bottom, and eggs of the species studied are able to hatch in darkness (I–V, this summary); the eggs of *A. bifilosa* were also tested in total dark-

ness from production to hatching and this did not affect hatching success (II).

Other factors

Other factors contributing to egg survival on and recruitment from the bottom were not studied but are briefly discussed here. Physical forces affect resuspension as well as mixing of the sediments. The sediment type affects physical mixing of the eggs into the sediments; in coarse sediments the eggs are likely to remain near the surface (Marcus & Taulbee 1992). Resuspension of the sediment may enhance hatching by bringing the eggs to the water column from the sediment but it may also only relocate the eggs (Marcus 1984a, Marcus & Fuller 1989, Lindley 1990). The rates of sinking and emergence are affected by temperature and turbulence, the former by determining the time needed for development and the latter by slowing down sinking and affecting resuspension.

Physical mixing decreases with depth. According to a modelling study performed in the Gulf of Bothnia, high resuspension frequency (> 5–300 times per year) is expected in areas with 0–30-m water depths, and low frequency (≤ 5 times per year) at 30–60 m (Brydsten 1993). Resuspension in the study area may be more frequent. Dinoflagellate cyst resuspension in Storfjärden was affected by storms: strong resuspension of cysts was observed during a stormy winter; in contrast, low resuspension occurred during a calm winter (Kremp 2001). Being a deep surrounded by shallower areas, the study site Sällvik deep is probably an accumulation bottom: Heiskanen and Tallberg (1999) estimated that most of the sedimenting material in the deep originates from secondary sources, i.e. after re-

suspension from the shallower areas. This may contribute to the high abundance of the eggs in the deep. However, the hatching performance of the eggs from the surface sediments indicates that the accumulating material is from recent deposits (I, V, Fig. 3). The high sedimentation rate of the area enhances burial, in combination with low temperatures, and promotes the formation of a large egg bank.

The benthic fauna may affect the eggs indirectly by bioturbation and directly by predation. The effect of benthic animals on the eggs is dependent on species. Kearns et al. (1996) showed that bidirectional movement of eggs (or egg-sized beads) occurs in a lake due to net downward translocation by chironomids and net upward movement by tubificid oligochaetes; both groups are found in coastal sediments of the Baltic Sea (e.g. Karjala & Lassig 1985, Bonsdorff et al. 1996). Albertsson and Leonardsson (2000, 2001) concluded that in the Bothnian Sea the amphipod *Monoporeia affinis* negatively impacts copepod recruitment from benthic eggs, probably because it translocates eggs deeper in the sediment. Polychaetes, in turn, can move eggs to the sediment surface from the deeper layers where they feed – copepod eggs may survive passage through polychaete guts (Marcus 1984a, Marcus & Schmidt-Gengenbach 1986). Recently, the invader polychaete *Marenzelleria viridis* has rapidly extended its area of distribution in the Baltic Sea (e.g. Stigzelius et al. 1997, Olenin & Leppäkoski 1999, Perus & Bonsdorff 2004). The species competes with *M. affinis* (Kotta & Ólafsson 2003, Neideman et al. 2003), which has declined in abundance in some areas at the same time as *M. viridis* has established itself (Perus & Bonsdorff 2004). It has remarkable effects on the sediment structure: it forms deeper burrows than the

indigenous species and changes the sediment surface to a network of burrow openings (A. Laine, Finnish Institute of Marine Research, pers. com.). The effects on benthic resting eggs remain to be seen. The pelagic mysids *Mysis relicta* and *M. mixta* are important zooplanktivores in the northern Baltic Sea (Hansson et al. 1990, Viherluoto et al. 2000), but they may also impact the benthic community and resting eggs because they perform vertical diurnal migrations, residing near the bottom during the day (Salemaa et al. 1986). While foraging on the sediment they cause a remarkable resuspension of benthic material (Viitasalo & Viitasalo 2004). Although this resuspension may favour hatching from benthic eggs, the mysids may negatively impact some taxa; e.g. they are known to feed on cladoceran ephippia (Viitasalo & Viitasalo 2004).

In addition to direct effects, bioturbation by benthic animals enhances physical and chemical processes. Bioturbation mixes the sediment deeper than physical forces (e.g. Sanford 1992) and also makes the sediment more susceptible to resuspension (Rhoads & Young 1970, Graf & Rosenberg 1997). The oxygen conditions near the bottom affect the occurrence of benthic animals, which in turn affect the oxygen penetration depth in sediments. For example, in an archipelago area of the Gulf of Bothnia in sediments with high densities of the amphipod *M. affinis* the oxidized sediment layer extended to about 7 cm in depth, while with the lowest amphipod density it was < 1 cm (Albertsson & Leonardsson 2000). In experiments *M. affinis* created oxygen pockets in anoxic sediments down to about 15 mm (Modig & Ólafsson 2001). Active transport of oxygen through *M. affinis* burrows was evident to a depth that exceeded twice the diffusional penetration depth of oxygen (from about 4 to 7 mm); the amphi-

pods also made sediment material more flocculent than in cores without the amphipods (Tuominen et al. 1999).

Animal burrows form rapidly changing mosaics of oxic microniches and oxygen gradients in the sediment (Forster & Graf 1992, 1995, Fenchel 1996). This thickening of the oxygenated layer may not, however, positively affect the eggs buried in the sediment, since oxygenation of sediments may break up dormancy under unfavourable conditions and it may not be possible for the nauplii to leave the sediment. The duration of oxidation events is typically short (Forster & Graf 1992, 1995), and the eggs may experience successive periods of oxic and anoxic conditions. This may also occur if the eggs are returned to the sediment surface and then back several times in succession. Thus, development could resume and then undergo arrest again. Some insects may re-enter dormancy after diapause (Danks 1987), but it is not known if copepod eggs can arrest development once it has resumed. The eggs of *Acartia bifilosa* can respond to changes in their environment during development at various stages. The development slowed down when the eggs were first incubated at 13 °C and then transferred to 1.5 °C (II). The eggs of *A. bifilosa* collected from sediments hatched less synchronously (I) than eggs derived from females (II), indicating that they may become quiescent at different stages of development. Whether this is possible several times in succession remains to be verified; however, each time development is resumed, the energy stores are reduced.

In addition to the macrofauna, some microorganisms may attack the eggs. In my experiments the eggs were sometimes infested by fungi (II), and sometimes ciliates could be observed swarming around or inside the eggs (Katajisto, pers. obs.). It is

not clear if these microorganisms attacked eggs that were already dying or if they actually promoted death. In oceans, the heterotrophic dinoflagellates *Protoperidinium* cf. *divergens* (Jeong 1994) and *Noctiluca* spp. (Kimor 1979, Daan 1987) are known to prey upon copepod eggs. However, these species do not occur in the study area (H. Kuosa, Tvärminne Zoological Station, pers. com.) and it is not known if dinoflagellates also attack copepod eggs in the Baltic Sea.

Egg bank

Eggs that accumulate in the sediments and retain their viability for years form an egg bank, comparable to the seed banks of terrestrial plants. The existence of egg banks was verified by determining the viability of eggs collected from sediments of known age. The egg bank of *Eurytemora affinis* in the Sällvik deep consisted of eggs up to about ten years old (V). In other environments, a few stray copepod eggs of impressive ages, > 40 years in an estuary (Marcus et al. 1994) and > 300 years in a pond (Hairston et al. 1995), have been successfully hatched. These long survival times may be exceptional, but a high number of eggs remain viable in sediments for several years in marine (Marcus et al. 1994, V, this summary), and even for decades (~100 years) in more temporary environments (Hairston et al. 1995). Prolonged diapause more probably occurs in crustaceans living in inland waters than in the marine environment (Hairston & Cáceres 1996).

The ages of these long-lived egg banks were estimated assuming that mixing of the variously aged sediments and eggs is negligible at the study sites (Marcus et al. 1994, Hairston et al. 1995, V), and thus the oldest eggs may never get a chance to contrib-

ute to the recruitment. Actual evidence for the functioning of long-term egg banks is scarce and is restricted to fresh waters. Most observations show recruitment from benthic egg banks after one (Hairston & Van Brunt 1994) or two years (Hairston & De Stasio 1988, Taylor et al. 1990) of failure in reproduction. Human-induced changes in aquatic environments have offered longer-term ‘experiments’ on the feasibilities and restrictions of using egg banks in the re-establishment of planktonic populations after local extinctions. Recovery of the calanoid copepod *Hesperodiaptomus arcticus* was successful in an alpine lake after disappearance of stocked salmonids: recruitment occurred from diapausing eggs after ~20 years of no new reproduction (Parker et al. 1996). However, recovery may fail if the egg bank is depleted during the disturbance. This could occur due to benthic predation (Parker et al. 1996) or if the eggs are induced to hatch from the egg bank when conditions begin to improve but the animals are still not able to survive in the water column to a reproductive stage, e.g. during recovery of an acidified lake (Arnott & Yan 2002). For successful re-establishment of a population from an egg bank, dioecious species such as copepods need high numbers of almost simultaneously hatched nauplii, compared with asexually or parthenogenetically reproducing species such as cladocerans (Sarnelle & Knapp 2004). In the Baltic Sea, the increasing occurrence of drifting algal mats in shallow coastal areas (Bonsdorff 1992, Vahteri et al. 2000) may locally deplete the benthic egg pool, since the way into the water column will be blocked for nauplii possibly hatching under the hypoxic conditions (see p. 29) that usually develop under the mats.

Resting eggs and invasive species

Although dormancy is seen as an alternative to migration, it may also lead to dispersal. There is evidence that dormant stages can be transported, at least over short distances, by wind or water currents or by animal vectors, although there is controversy over the significance and extent of such dispersals (e.g. Bohonak & Jenkins 2003, Havel & Shurin 2004). Undoubtedly, humans offer far more efficient vehicles. Herbert and Cristescu (2002) estimated that the human-mediated invasion rate of crustacean zooplankton from Europe to the Laurentian Great Lakes has been nearly 50 000-fold compared with invasion at the ‘natural’ rate. The ballast water of long-distance cargo ships is the most important transmission agent across oceanic barriers for estuarine or freshwater aquatic organisms today (Carlton & Geller 1993). Increasing concern has been shown in preventing unwanted immigration of non-indigenous, potentially harmful organisms. Organisms that produce diapausing resting stages are especially difficult to control, because they are able to survive extreme conditions during transport (Panov et al. 2004). This makes them resistant to management options, such as exposure to high salinities when brackish or fresh ballast water is partially replaced with open-ocean water (Gray et al. 2005). In addition, since ballast water tanks cannot be totally emptied, vessels arriving in port with ‘no ballast on board’ also carry residual sediment that can contain viable diapause eggs of several taxa (Bailey et al. 2003). When the tanks are refilled and emptied again the organisms can be released to the recipient areas.

In the list of nonindigenous species recorded in the Baltic Sea, there are two zooplankton species, *Acartia tonsa* and the

cladoceran *Cercopagis pengoi* (Leppäkoski & Olenin 2000). At least *C. pengoi* probably arrived in the ballast water of ships, although it is not known whether as active or resting stages. However, having resting eggs in the life cycles certainly has aided both species in establishing populations in the new areas, as was already discussed for *A. tonsa* (p. 25–26). *Cercopagis pengoi* also originates from temperate waters (Caspian Sea) and produces resting eggs. It was found to allocate a larger part of its reproduction to resting eggs in the Baltic Sea than in the Caspian Sea (Krylov & Panov 1998).

SUMMARY

Resting eggs were found in three dominant calanoid species of coastal areas of the northern Baltic Sea. Since most other zooplankters and many phytoplankters also use benthic refuges during seasonal absence from the water column, it can be concluded that it is a very applicable strategy in the area. Although seasonality is pronounced and the overall yearly pattern is similar, there is wide variation in the timing of spring events (release of the ice cover, the phytoplankton blooms). Therefore, the life cycles are not highly synchronized and variable strategies exist. Both *Acartia bifilosa* and *Eurytemora affinis* occur in the plankton throughout the year, although in winter with low abundance; hatching from resting eggs occurs during extended time periods. *Acartia tonsa* is the only species that is clearly dependent on the resting egg strategy for yearly recruitment under northern conditions.

The resting eggs of *A. bifilosa* represent the quiescent type: the species produces subitaneous eggs throughout the productive

season (II). In shallow areas large fractions of the eggs may sink to the bottom prior to hatching. Some of these continue development and hatch without arrest, while others are buried under the sediment and become dormant (I). Temperature or light do not affect dormancy of the eggs (II), but oxygen deficiency in the environment keeps the eggs dormant (III).

Eurytemora affinis carries eggs in egg sacs. In summer the eggs produced are subitaneous and hatch in a few days in the egg sacs. In autumn the species produces diapause eggs, which are released from egg sacs and sink to the bottom. They can only hatch after a certain refractory phase (3–5 months) if conditions are favourable. If not chilled prior to exposure to elevated temperatures, hatching is further delayed. The eggs are capable of long-term dormancy and can be used as a long-term survival strategy (V).

Acartia tonsa has mostly been neglected in previous zooplankton studies at the southern coast of Finland but it was abundant in the plankton during these studies (I, Katajisto, pers. obs.). Different from *A. bifilosa* and *E. affinis*, *A. tonsa* occurs in the plankton only in late summer and autumn, and spends the rest of the year on the bottom as resting eggs. The egg type produced appears to be intermediate between subitaneous and diapause (this summary) and resembles the so-called ‘delayed-hatching’ egg type. Dormancy in eggs is affected by temperature and probably also by the oxygen concentration in the environment. The eggs do not hatch at low temperatures.

The occurrence of benthic resting eggs in the life cycles of dominant copepods links these planktonic species with the conditions on the bottoms. The eggs retain viability under conditions that would be detrimental to most living things and form a

long-lived egg bank. The eggs of *A. biflosa* remain viable for months, possibly years, under the anoxic conditions (III) that typically prevail under the sediment surface, and the eggs of *E. affinis* remain viable for years in the sediment (V). On the other hand, if the water above the sediment also becomes oxygen-depleted, recruitment from the benthic eggs is prevented. Therefore, eutrophication and the increasing occurrence of near-bottom anoxia may affect the population dynamics of these species.

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