

CHAPTER 2

Zooplankton of the Baltic Sea

2.1 General characteristics of the Baltic Sea zooplankton

The Baltic Sea as a brackish water system with a horizontal salinity gradient from south-west to north-east and a permanent vertical salinity stratification of the central basins is a unique pelagic ecosystem with limited distribution ranges of marine and freshwater species. The location of the Baltic Sea in the temperate climatic zone with oceanic impact in the south-western part and continental impact in the north-eastern areas affects the whole ecosystem through seasonality by causing a pronounced seasonal succession of plankton populations.

Zooplankton in the Baltic Sea has been described routinely in terms of dominant species of certain groups (mainly copepods) and/or size fractions (mesozooplankton) that are identified and counted for monitoring purposes. Therefore, the mixoplankton (Flynn et al., 2019) that embrace the unicellular organisms capable of combining autotrophy and phagotrophy as their feeding modes, usually are not considered in these studies. Meanwhile, precise assessment of zooplankton species diversity provides important information on the marine ecosystem structure, functions, trophic webs and their natural and human-induced alterations. In many zooplankton groups, major functional characteristics responsible for the animals' behaviour and the interactions within communities are species-specific; therefore, the importance of the correct taxonomic identification of zooplankton, especially of key species, indicators of water quality, and non-indigenous species can hardly be overestimated.

Zooplankton of the Baltic Sea is a mixture of marine species and diverse brackish water and limnetic faunas typical for the vast estuarine and coastal areas located mainly in the southern and north-eastern parts of the Baltic. Some genuine brackish water zooplankton species are also known in the Baltic Sea (Remane, 1934). In addition to native species, there are several nonindigenous mesozooplankton species occurring temporarily or even establishing the permanent populations in the Baltic Sea (Gollasch & Nehring, 2006).

Since the publication of the "species minimum curve" by Remane (1934, 1940), it has been generally accepted that "the number of species in the Baltic is small" (Jansson, 1972, p. 12). This conclusion commonly was applied to and supported mainly by the data on benthic macrofauna (Zenkewitch, 1963). Meanwhile, already in the 1960-s Hans Ackefors proposed that "if the microfauna in the water and at the bottom are included the number of species will be much higher" (Ackefors, 1969, p. 5). In other words, according to an exceptionally evocative affirmation of Jansson (1972), "the diversity is there but it is found on a microscale" (p. 14). Thus, already in the second half of the 20th century scientists around the Baltic were admitting that the real

diversity of microscopic invertebrates in plankton might happen to be much higher when special biodiversity investigations are performed.

This idea was later supported by the results of the long-term plankton diversity research in the open and coastal Baltic waters that demonstrated high species richness of pelagic communities (for details see the review publications: Telesh, 1987, 1988, 2001, 2004, 2006a, 2006b, 2008; Telesh & Heerkloss, 2002, 2004; Telesh et al., 2008, 2009, 2011a, 2011b, 2013, 2015; Telesh & Skarlato, 2009; Mironova et al., 2009, 2012, 2013, 2014). Based on these and other published data we can conclude that the earlier existing conception of the low species diversity of planktonic communities in the Baltic Sea had resulted from the insufficient knowledge on the species composition of zooplankton, particularly its small-size fraction. Specifically, the new biodiversity concept was developed: the protistan species maximum concept for the horohalinicum (Figure 2.1), which substantiates high species richness of planktonic auto- and heterotrophic protists in the brackish Baltic waters, with maximum at the critical salinities of 5–8 psu (Telesh et al., 2011a, 2011b, 2013, 2015). The applicability of Remane’s species minimum concept for the biodiversity of mesozooplankton in the Baltic Sea is currently a challenging issue of the ongoing discussion (Cognetti & Maltagliati, 2000; Ptacnik et al., 2011; Telesh et al., 2011a, 2011b; Postel, 2012; Whitfield et al., 2012).

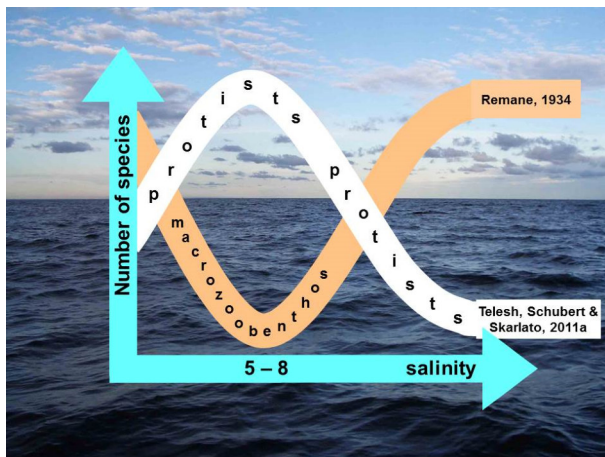


Figure 2.1: The protistan species-maximum concept (Telesh et al., 2011a) describes high diversity of photo- and heterotrophic protists in plankton of the Baltic Sea, with maximum at the critical salinities of 5 to 8 psu, which mirrors the *Artenminimum* curve for macrozoobenthos (Remane, 1934).

In general, zooplankton organisms range in size from few micrometers to meters. It is commonly accepted that a marine zooplankton community is formed by the following size fractions: picoplankton (size of organisms 0.2–2.0 μm , mainly heterotrophic bacteria), nanoplankton (2.0–20.0 μm , heterotrophic nanoflagellates, nanociliates), microplankton (20–200 μm , ciliates and a large part of rotifer species), mesozooplankton (0.2–20.0 mm, larger rotifers, mainly planktonic crustaceans, meroplanktonic larvae of some benthic invertebrates, etc.), and macrozooplankton (organisms larger than 20 mm: Cnidaria, Ctenophora, Chaetognatha, Mysidacea, Euphausiacea, Decapoda, Polychaeta and others) (Lenz, 2000).

Since the present publication is focused on mesozooplankton species that are most common in the Baltic Sea, we skip the information about macrozooplankton, as well as nano- and microzooplankters, major part of which are ciliates. However, it is important to mention that ciliates of the Baltic Sea are represented by more than 740 species (Mironova et al., 2014), they can be very abundant, and their functional role in planktonic communities has been substantially underestimated so far (Figure 2.2). Unlike the dominant mesozooplankters, microplanktonic ciliates usually are not considered in the regional monitoring programs; nevertheless, they are good indicators of water quality. They contribute significantly to energy fluxes (for example, through the microbial loop or due to mixotrophy) and water purification in the Baltic Sea ecosystem. The most recent data on species composition, diversity, spatial

distribution, seasonality, abundance, biomass and productivity of ciliates in the Baltic Sea can be found elsewhere (Mironova et al., 2009, 2012, 2013, 2014, and references therein).

Mesozooplankton (0.2–20 mm) is the dominating group in the Baltic Sea in terms of biomass. It may constitute up to 76% (i.e. >1000 kg C/m²) of the average annual carbon mass, as measured in the western Gdańsk Bay during the 1980s (Witek, 1995). The remaining 18% and 6% were contributions of protozoans and macrozooplankton, respectively. The percentage of the average annual production of mesozooplankton in this region reaches 39%. Within the mesozooplankton fraction, copepods *Pseudocalanus* spp. (Figure 2.3), *Temora longicornis*¹, *Acartia* spp. (Figure 2.4), rotifers *Synchaeta* spp., and cladocerans *Evadne nordmanni* (Figure 2.5) are the most important taxa in terms of biomass and production. The ctenophore *Pleurobrachia pileus*, the copepod *Eurytemora affinis* (Figure 2.6) and rotifers *Keratella* spp. (Figures 2.5, 2.7) play a minor role, while the appendicularian *Fritillaria borealis* (Figure 2.8), Polychaeta larvae (Figure 2.9), the cladocerans *Bosmina* spp. (Figure 2.10), *Podon* spp. (Figure 2.5), the copepods *Centropages hamatus* (Figure 2.11), and Bivalvia larvae (Figure 2.8) range in between (Figure 2.12).

¹ Authors of the Latin species names are mentioned in the zooplankton checklist (Table 5.1 in Chapter 5).

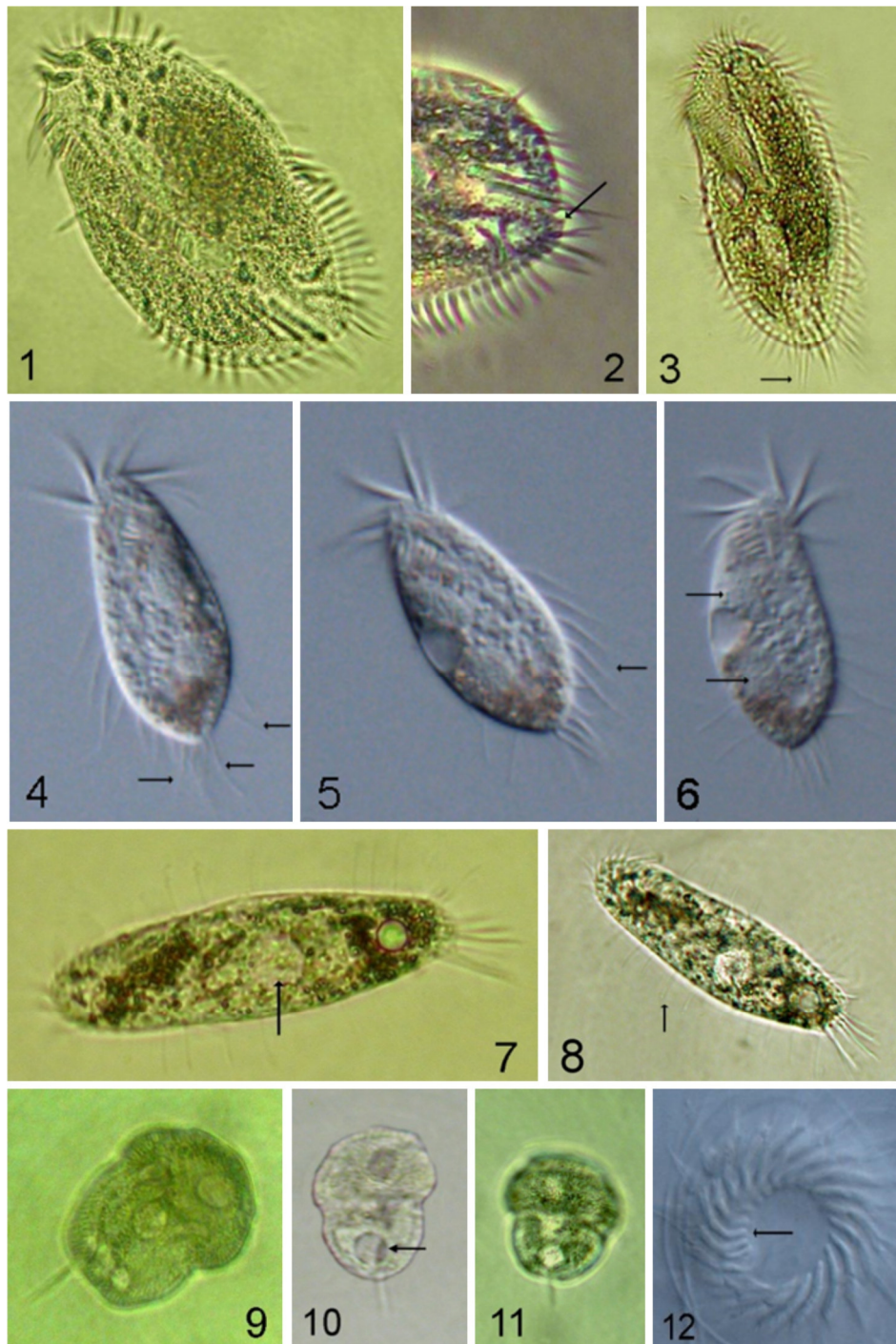


Figure 2.2: Ciliates (Ciliophora). **1**, *Histriculus vorax*, with large adoral zone of membranelles and two macronuclear nodules, body length 210 μm ; **2**, *Histriculus vorax*, posterior body end is broadly rounded and notched (arrow); **3**, *Sterkiella histriomuscorum*, with short inconspicuous caudal cirri (arrow) and contractile vacuole located in the mid-body, body length 105 μm ; **4**, **5**, **6**, *Oxytricha setigera*, with inconspicuous caudal cirri (**4**, arrows), dorsal cilia (**5**, arrow) and contractile vacuole located in mid-body between two macronuclear nodules (**6**, arrows), body length 38 μm ; **7**, **8**, *Tachysoma pellionellum*, with contractile vacuole located in mid-body (**7**, arrow) and stiff dorsal cilia (**8**, arrow), body length 65 μm ; **9**, **10**, **11**, *Urocentrum turbo*, dumbbell-shaped ciliate, with a tuft of caudal cilia and a single contractile vacuole located posteriorly (**10**, arrow), body length 55 μm ; **12**, *Strobilidium caudatum*, top view of adoral zone, with prominent external and internal (arrow) adoral membranelles, live, differential interference contrast (DIC); photos E. Mironova (from Telesh et al., 2009).



Figure 2.3: Copepoda. 1, *Pseudocalanus elongatus*, female, abdomen, lateral view, vertical arrow shows genital segment, horizontal arrow shows spermatophores; 2, *P. elongatus*, P5 of male, lateral view; 3, *P. elongatus*, copepodite C4, lateral view, length $716.9 \pm 24.4 \mu\text{m}$ (Postel et al., 2007), red inclusions – lipids stocked for diapausing; 4, *P. elongatus*, nauplius ventrally, length $306.9 \pm 14.0 \mu\text{m}$ (Postel et al., 2007); 5, *P. elongatus*, nauplii at different stages in the sample (1, 2, 4, 5, photos H. Sandberg; 3, photo courtesy of P. Snoeijs-Leijonmalm).

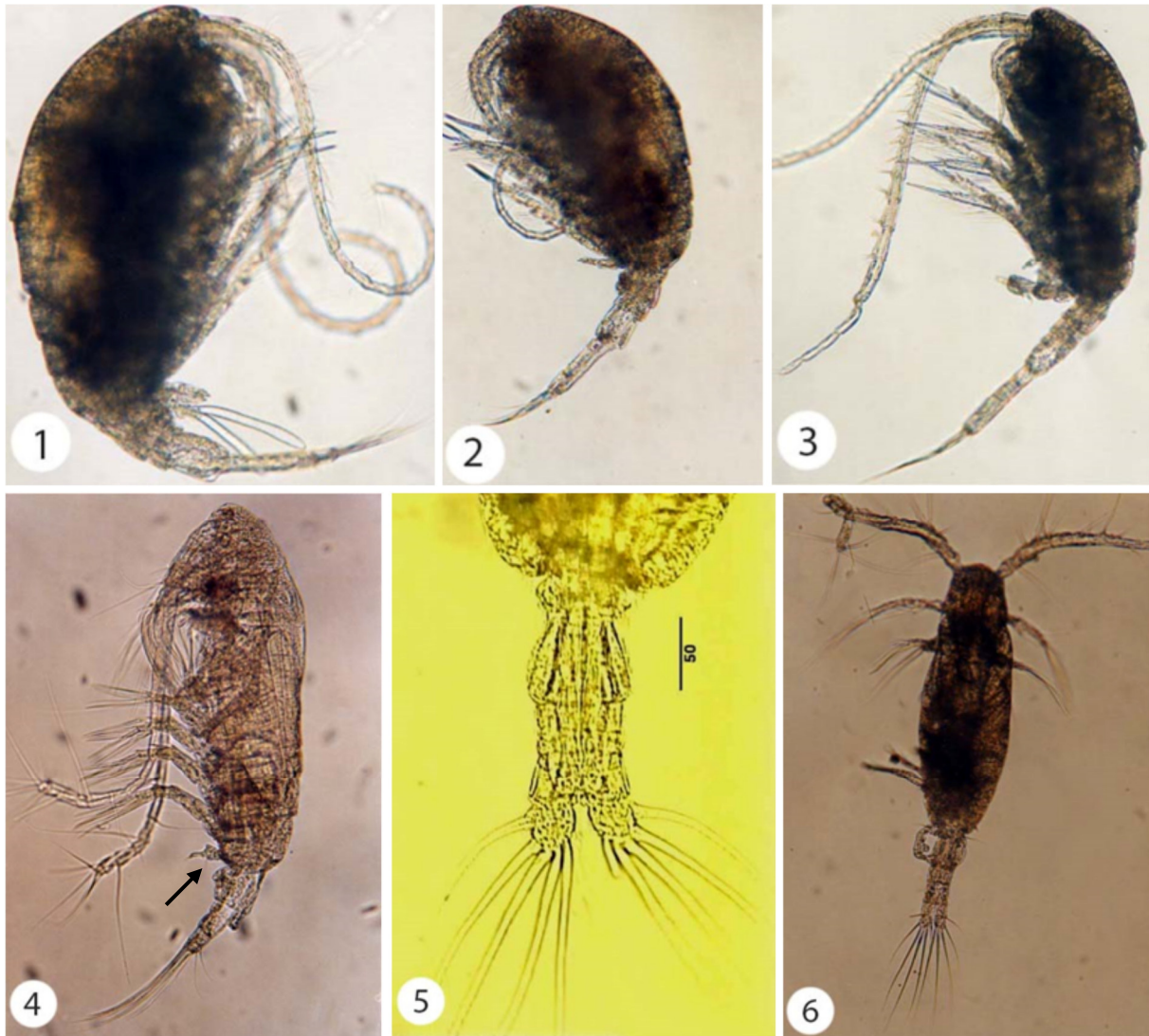


Figure 2.4. Copepoda. **1, 2**, *Temora longicornis*, female, lateral view, prosome length $709.3 \pm 6.7 \mu\text{m}$ (Postel et al., 2007); **3**, *T. longicornis*, male, lateral view, prosome length $690.8 \pm 6.0 \mu\text{m}$ (Postel et al., 2007) (photo courtesy of P. Snoeijs-Leijonmalm); **4**, *Acartia tonsa*, female laterally, prosome length ca. $620 \mu\text{m}$, arrow shows P5 (photo H. Sandberg); **5**, *A. tonsa*, male urosome (after Telesh & Heerkloss, 2004); **6**, *Acartia longiremis*, male, ventral view, prosome length ca. $600 \mu\text{m}$ (photo H. Sandberg).

About forty mesozooplankton species are regularly occurring in the Baltic Sea in significantly high abundances. Ten to twelve of them are dominating taxa. Their spatial occurrence is explained mainly by the salinity patterns. According to hydrographic regime with prevailing outflow of low saline water in the upper layer and temporary inflows of higher saline water below the halocline, species with relevant salinity preferences inhabit the western and the eastern parts and the open Baltic Sea, respectively.

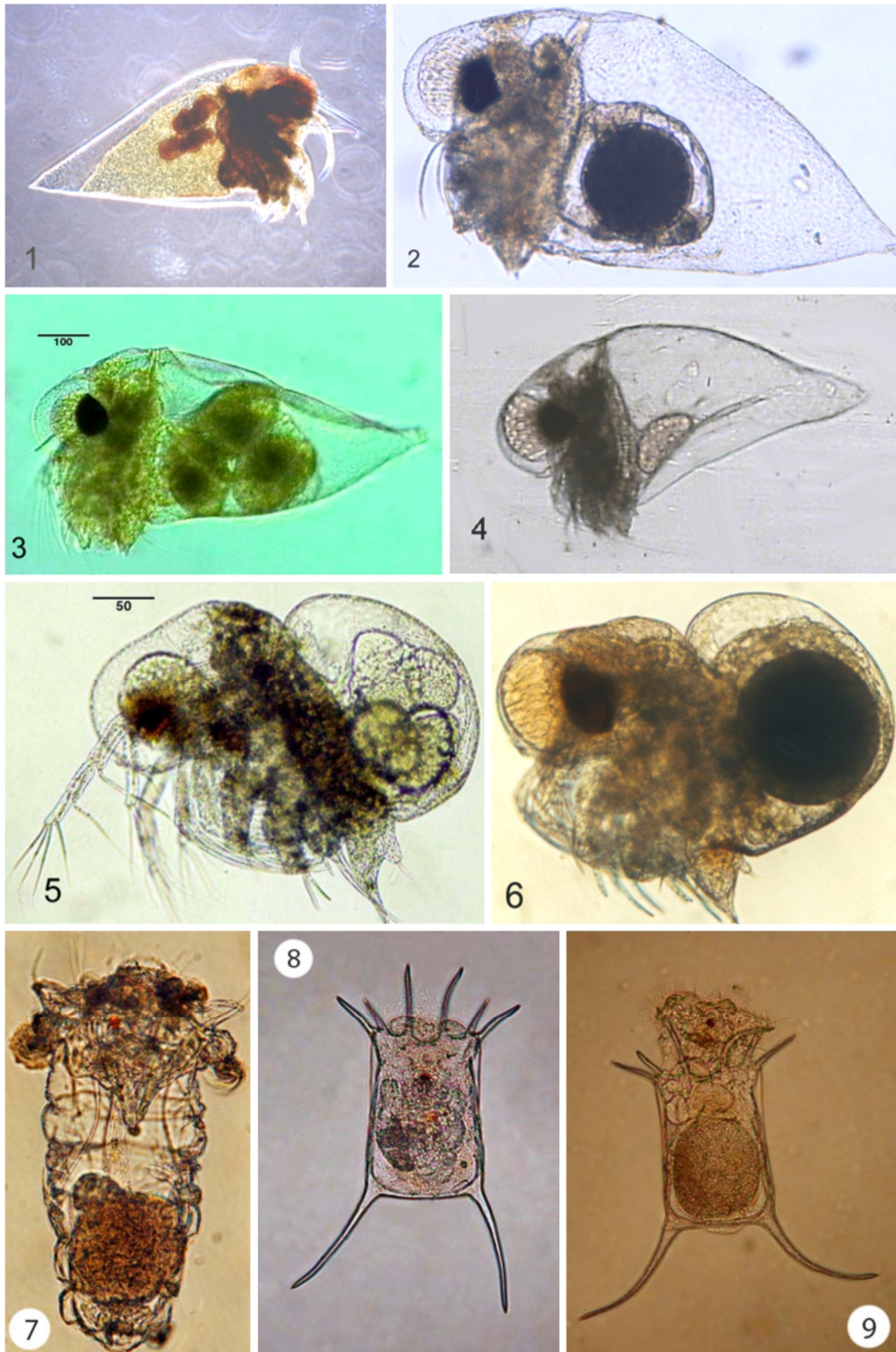


Figure 2.5: Cladocera. 1, *Evadne nordmanni*, young female, lateral view (photo courtesy of P. Snoeijs-Leijonmalm); 2, *E. nordmanni*, female with resting egg, lateral view, body length ca. 700 µm (photo H. Sandberg); 3, *E. nordmanni*, female with embryos, lateral view; 4, *E. nordmanni*, male, body length ca. 500 µm, lateral view (photo H. Sandberg); 5, *Podon leuckartii*, female with eggs, lateral view; 6, *Podon leuckartii*, female with resting egg, lateral view (3, 5, 6 after Telesh & Heerkloss, 2004). **Rotifera:** 7, *Synchaeta* sp., live female, semi-contracted, body length up to 600 µm (photo H. Sandberg); 8, 9, *Keratella quadrata platei*, female, dorsal view, body length up to 350 µm (photo courtesy of P. Snoeijs-Leijonmalm).

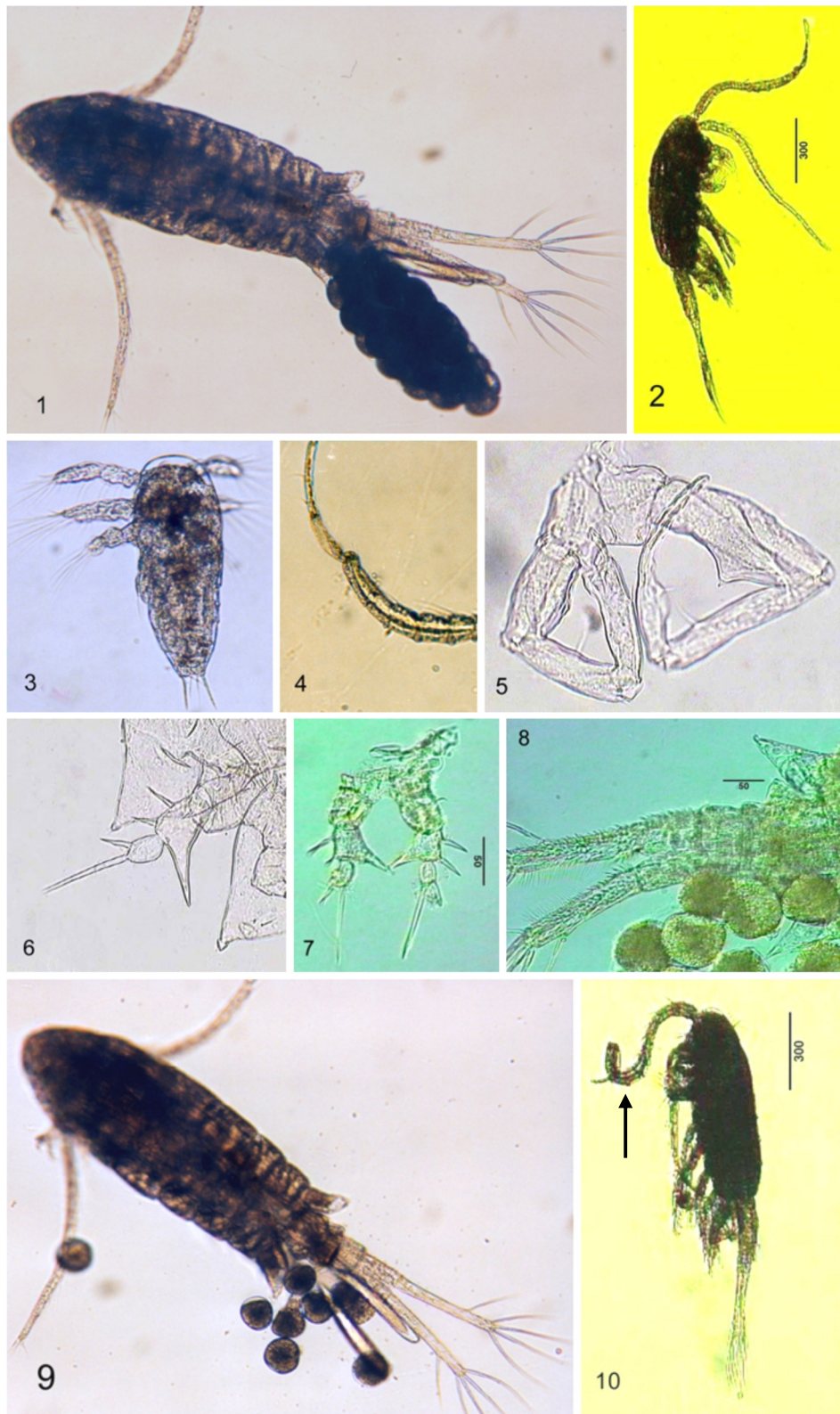


Figure 2.6: Copepoda. 1, *Eurytemora affinis*, female with egg sack, ventral view, prosome length ca. 650 µm; 2, *E. affinis*, male, lateral view; 3, *E. affinis*, nauplius N6 ventrally, body length 260 µm; 4, *E. affinis*, male, articulation of the antenna; 5, *E. affinis*, P5 of male; 6, 7, *E. affinis*, P5 of female; 8, *E. affinis*, posterior end of female, with eggs; 9, *E. affinis*, female with few loose eggs; 10, *E. affinis*, male, lateral view, arrow shows the articulated antenna (after Telesh & Heerkloss, 2004; 1, 3, 4, 9, photos H. Sandberg).

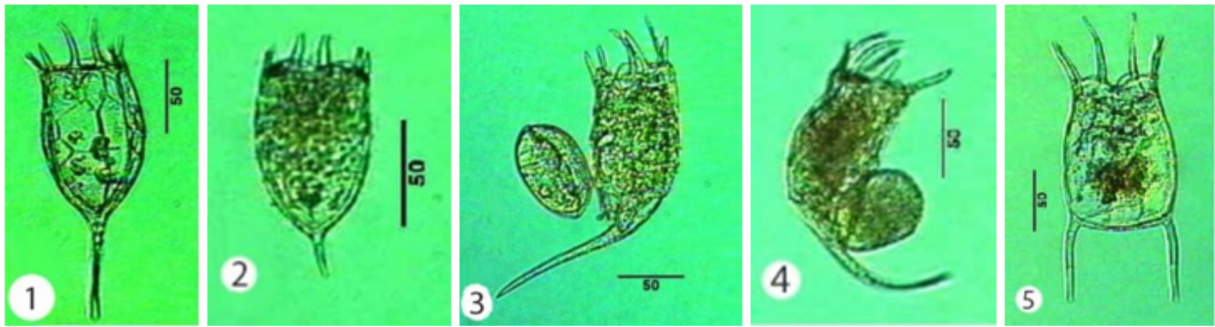


Figure 2.7: Rotifera. 1, *Keratella cochlearis typica*, female, lorica with long spine, dorsal view; 2, *K. cochlearis typica*, female, lorica with short spine, dorsal view; 3, 4, *Keratella cochlearis baltica*, female, lateral view, with egg; 5, *K. quadrata*, live female, dorsal view (after Telesh & Heerkloss, 2002).

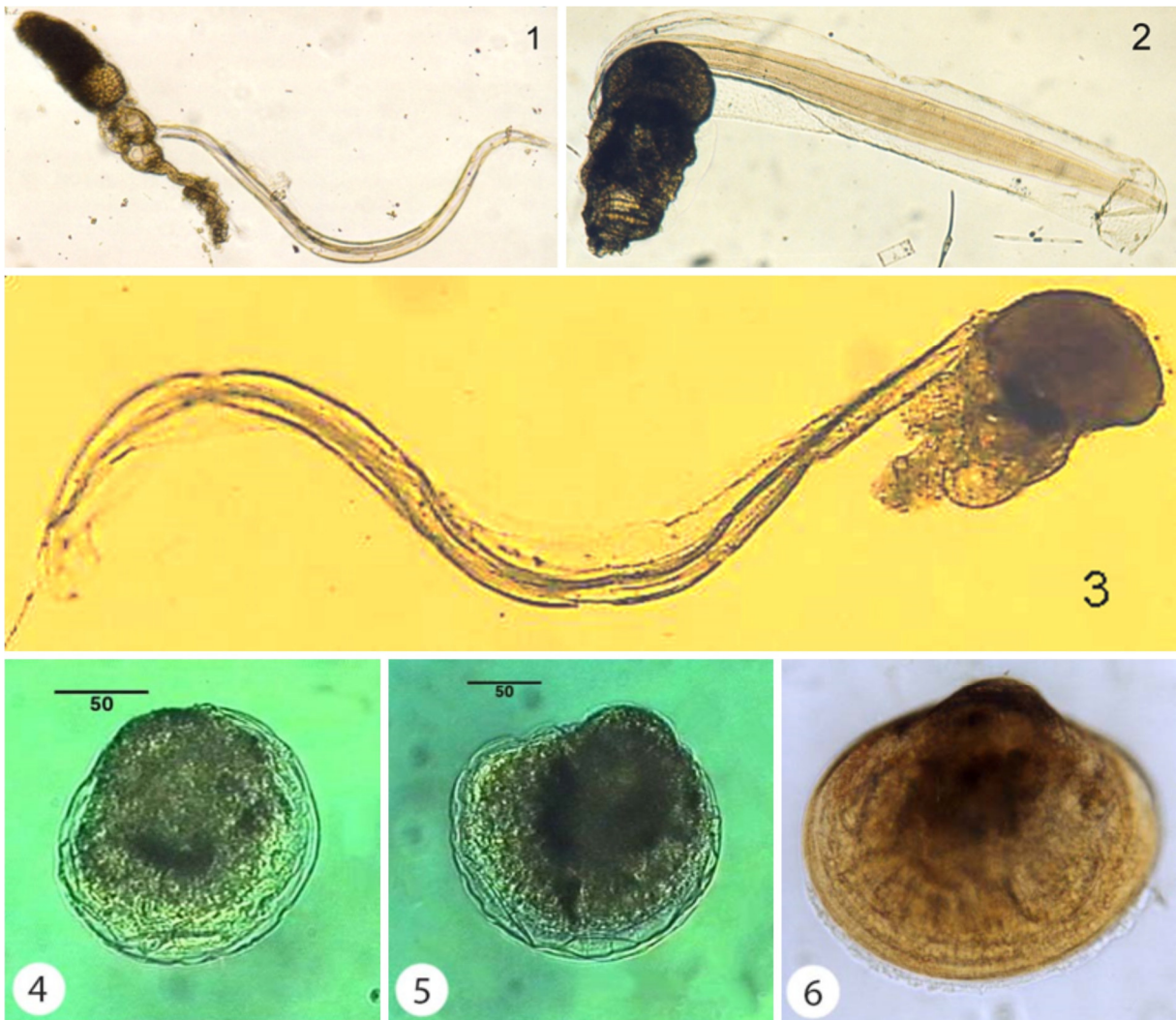


Figure 2.8: Copelata. 1, *Fritillaria borealis*, body length $758.5 \pm 59.1 \mu\text{m}$ (Postel et al., 2007); 2, 3, *Oikopleura dioica*, adult with fertile gonad, total length ca. $1200 \mu\text{m}$, body length ca. $700 \mu\text{m}$ (photos H. Sandberg). **Larvae of bivalve molluscs:** 4–6, different larval stages of *Bivalvia* (4, 5, larvae of *Dreissena polymorpha*, after Telesh & Heerkloss, 2004).

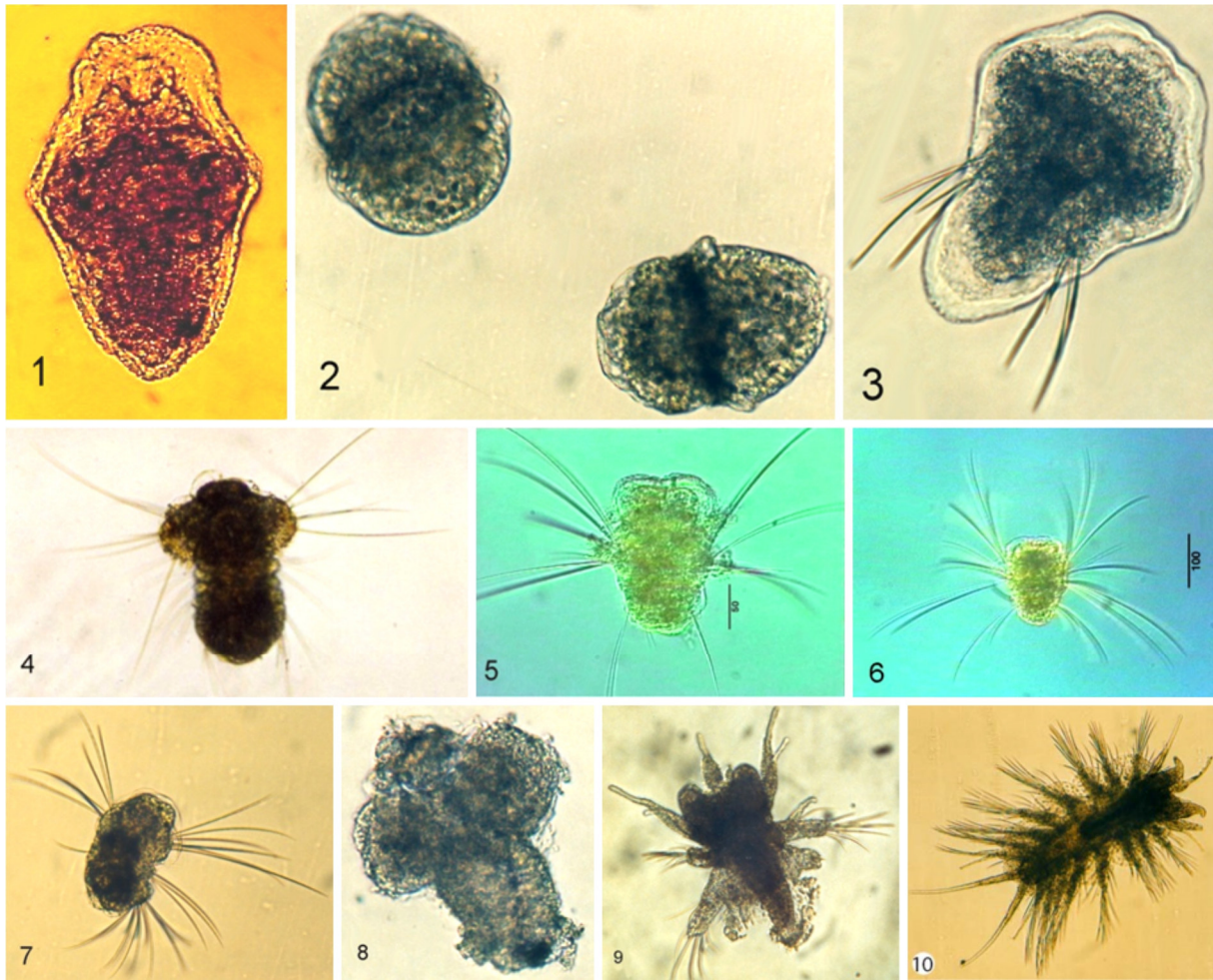


Figure 2.9: Polychaeta, larvae at different stages of development. **1, 2**, Trochophore, length ca. 200 μm ; **3–7**, nectochaete of different species (**5, 6**, *Marenzelleria viridis*, after Telesh & Heerkloss, 2004); **8, 9**, larvae of unidentified polychaete species; **10**, *Harmothoe* sp., young specimen, length ca. 800 μm (photos H. Sandberg).

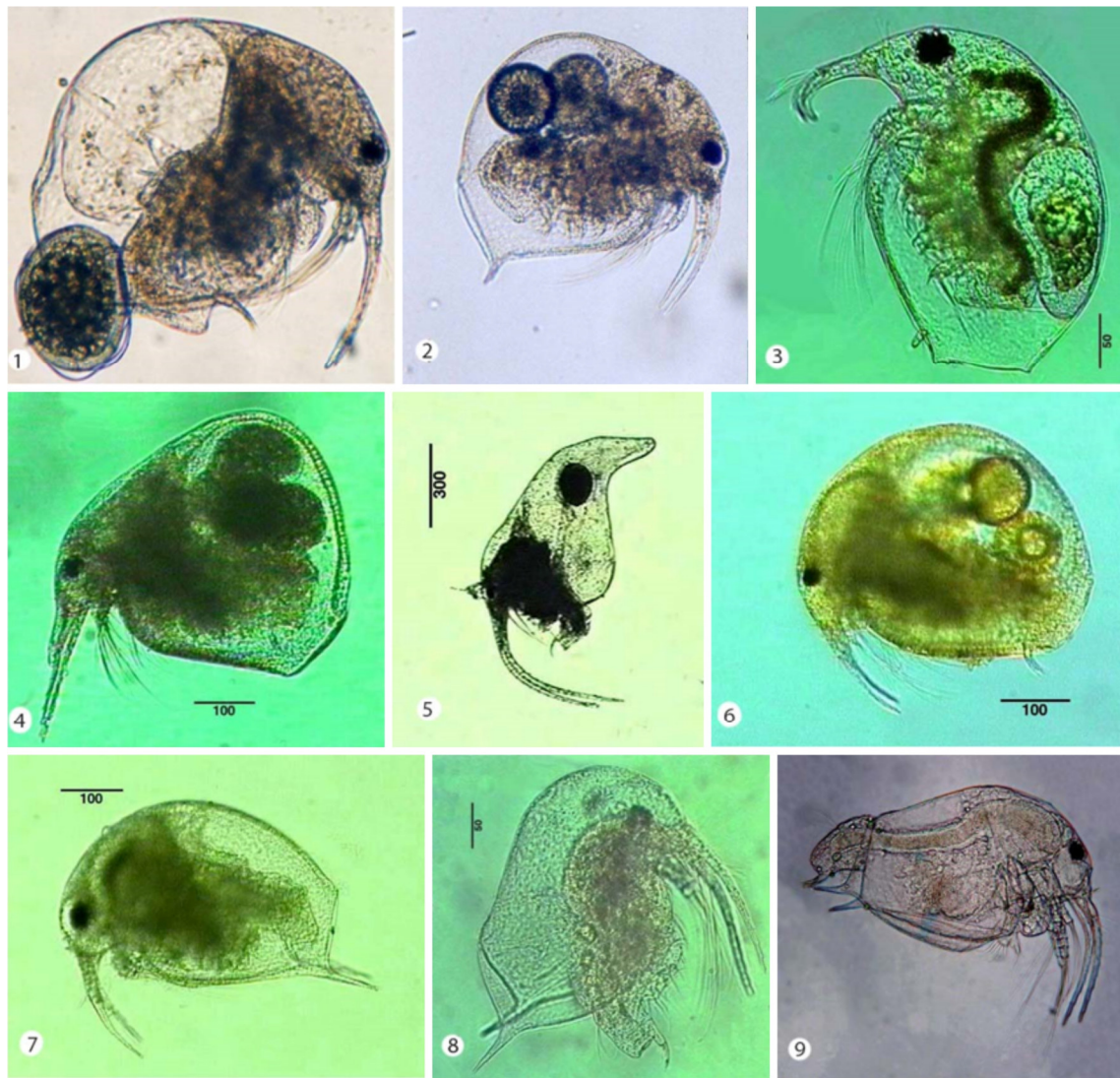


Figure 2.10: Cladocera. 1, *Eubosmina maritima*, female with an embryo, lateral view, body length 250–620 μm ; 2, *E. maritima*, female with eggs, lateral view (1, 2 photo courtesy of H. Sandberg); 3, *Bosmina longirostris curvirostris*, female with an embryo in the brood chamber, lateral view; 4, *Eubosmina coregoni gibbera*, female with embryos, lateral view; 5, *Eubosmina coregoni thersites*, female with resting egg, lateral view; 6, *Bosmina crassicornis*, female with eggs, lateral view; 7, *Eubosmina longispina*, young female, lateral view; 8, *E. longispina*, juvenile, lateral view; 9, *E. longispina*, male, lateral view, body length 400–600 μm , photo courtesy of P. Snoeijs-Leijonmalm (3–8 after Telesh & Heerkloss, 2004).

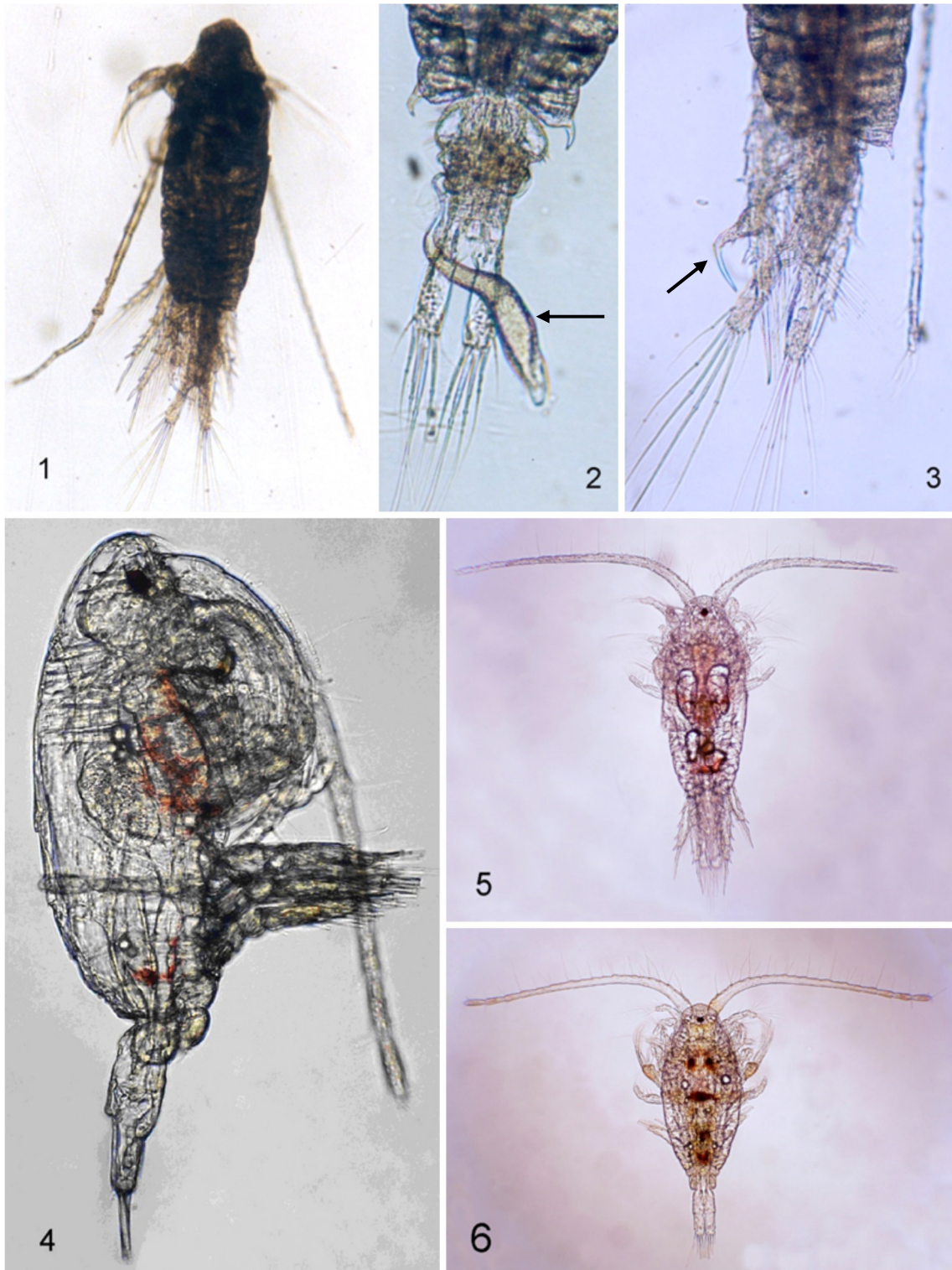


Figure 2.11: Copepoda. 1, *Centropages hamatus*, male, dorsal view, total length ca. 1400 μm , cephalothorax length $802.8 \pm 8.6 \mu\text{m}$ (Postel et al., 2007); 2, *C. hamatus*, abdomen of female, with spermatophore (arrow); 3, *C. hamatus*, abdomen of male, P5 seen at left side (arrow); 4, *C. hamatus*, copepodite C4, lateral view, length of prosome $655.8 \pm 12.1 \mu\text{m}$ (Postel et al., 2007); 5, 6, *C. hamatus*, copepodite C2, ventral view, length of prosome $478.4 \pm 16.4 \mu\text{m}$ (Postel et al., 2007) (1–3, photos H. Sandberg; 4–6, photo courtesy of P. Snoeijs-Leijonmalm).

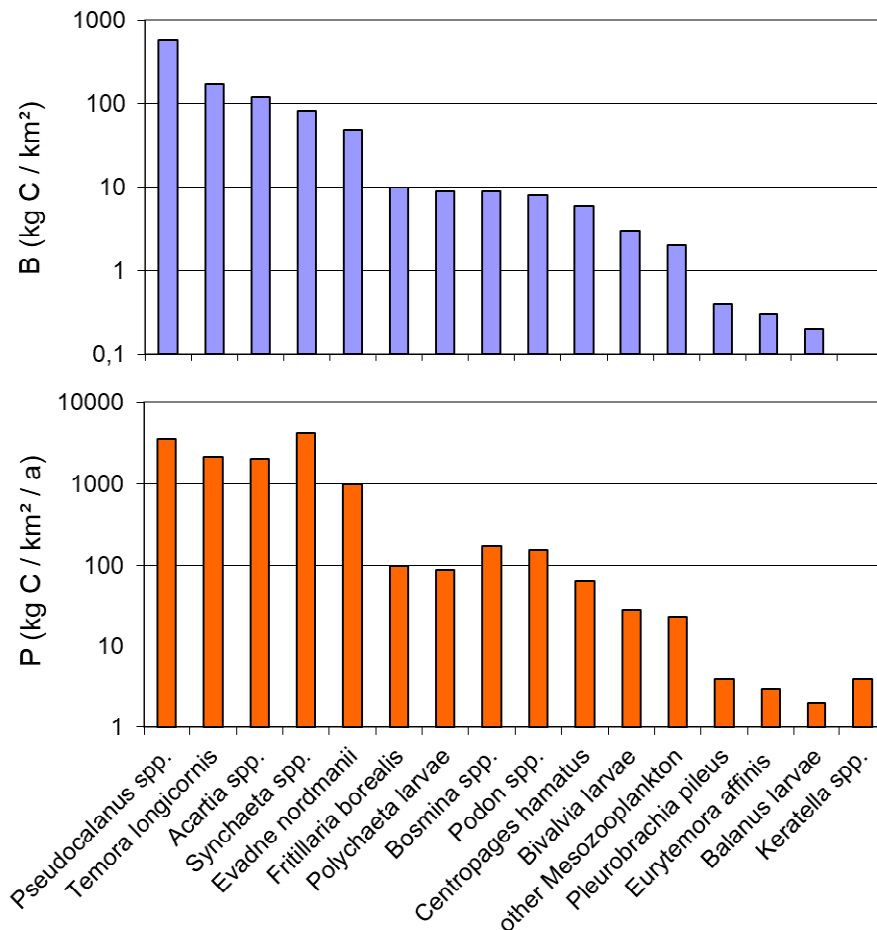


Figure 2.12: Contribution of various taxa to zooplankton biomass (B, above) and annual production (P, below) in Gdańsk Bay during the 1980s (after Witek, 1995).

Additionally, there is a remarkable shift in the dominating taxonomic groups throughout the Baltic Sea. Thus, *Paracalanus parvus*, *Pseudocalanus* spp. (Figure 2.13) and *Oithona similis* (Figure 2.14) dominantly occur in the entire water column of the western Kattegat, while *Calanus finmarchicus* and *Centropages typicus* occasionally appear there. Predominant cladocerans are the carnivorous *Evadne nordmanni*, *Podon* spp. (Figure 2.5) and *Pleopsis polyphemoides* in this area. The brackishwater filter feeding cladocerans from the genera *Eubosmina* and *Bosmina* (Figure 2.10) are dominant in the Baltic proper during summer.

Partly in the eastern Kattegat and especially in the Sound, the zooplankton species composition demonstrates similarities to that in the near-surface waters of the Arkona Sea, for example, by the occurrence of *Acartia* species, which is a result of the Baltic Sea water outflow. Copepods *Acartia bifilosa* that tolerate a salinity of 0.30 psu (Sewell, 1948), and *Eurytemora affinis* (Figure 2.6), which survives at 0.50 psu (Busch & Brenning, 1992), are the key species in the Gulf of Finland and the Bothnian Sea. Behrends et al. (1990) described a two-layer distribution of zooplankton in the Bay of Bothnia. While the glacial relict copepods *Limnocalanus macrurus* (Figure 2.15) inhabit the cooler and low-saline deep waters, *Daphnia* (Figure 2.16) species appear in the surface layers, in nearly freshwater conditions. *Centropages hamatus* (Figure 2.11) is a subdominant; it occurs at maximum population densities from Kattegat to the Arkona Sea. The Baltic proper is the area where *Acartia* species, *Temora longicornis* and *Bosmina* spp. (in summer) are dominating.

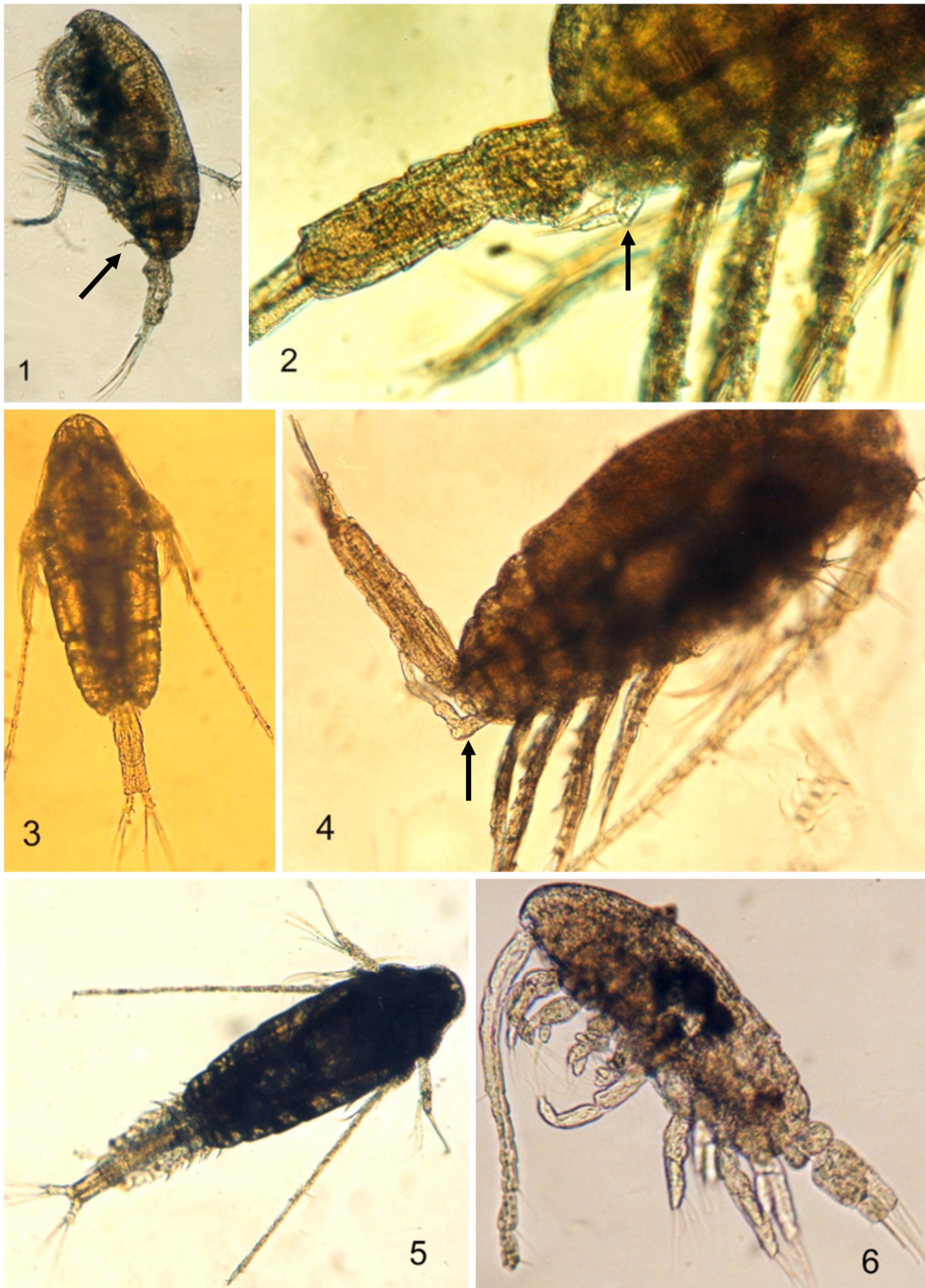


Figure 2.13: Copepoda. 1, 2, *Paracalanus parvus*, female, lateral, body length ca. 1000 μm , arrow shows P5; 3, *P. parvus*, male, ventral view, prosome length $789.8 \pm 10.4 \mu\text{m}$ (Postel et al., 2007); 4, *P. parvus*, male, lateral view, arrow shows P5; 5, *Pseudocalanus elongatus*, female, dorsal view, prosome length $887.0 \pm 9.5 \mu\text{m}$ (Postel et al., 2007); 6, *P. elongatus*, copepodite C3, lateral view, prosome length $573.5 \pm 41.9 \mu\text{m}$ (Postel et al., 2007) (photos H. Sandberg).

The seasonality is a pronounced reason for structural variability in plankton communities of temperate regions like the Baltic Sea. It is exposed in the reproduction cycles that are linked with the species' demands for food availability and for certain

temperature. Rotifers typically dominate in May (*Synchaeta* spp.) and in August (*Keratella* spp.) when their parthenogenetic reproduction mode allows for utilizing optimal food conditions within a short period of time. Cladocerans proceed in the same way. *Bosmina* spp. peak using a small temporal “window” in summer, when temperature rises above 15 °C (Ackefors, 1969).

There are two species of appendicularians in the Baltic Sea, *Oikopleura dioica* and *Fritillaria borealis* (Figure 2.8). The first one prefers the higher salinity in the western Baltic Sea. Its reproduction maximum is in autumn while *F. borealis* inhabit all regions of the Baltic proper, mainly in spring. Bivalvia larvae (Figure 2.8) also peak in a bimodal way, probably depending on different reproduction periods of various species, which is likely, because two of four co-occurring species are more abundant (Ackefors, 1969) and have their reproduction time span from May to August (*Macoma balthica*) or from August to October (*Mytilus edulis*) (Hernroth & Ackefors, 1979).

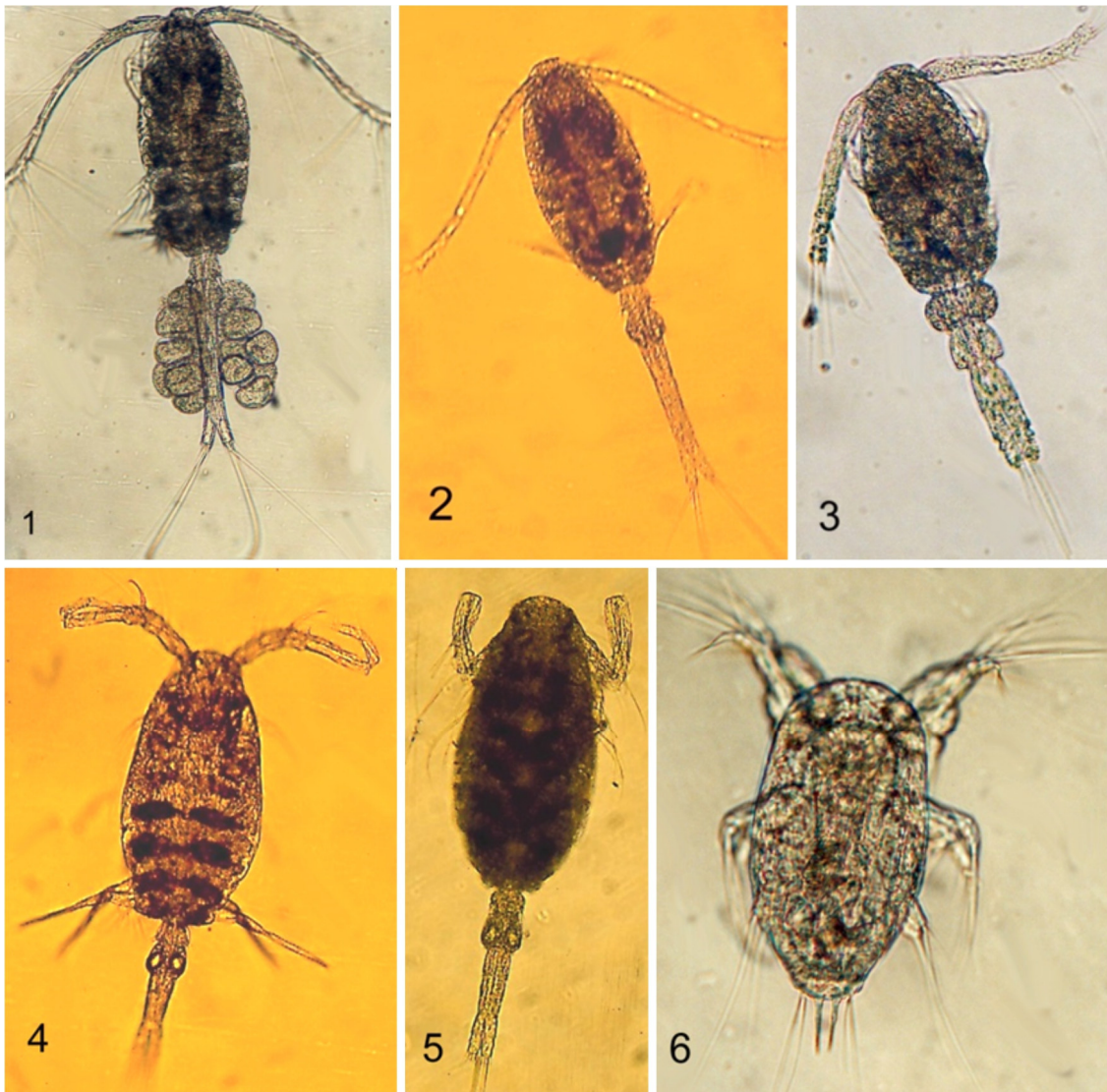


Figure 2.14: Copepoda. 1, 2, *Oithona similis*, female ventrally, total length ca. 800 μm , CPHT length $432.3 \pm 10.0 \mu\text{m}$ (Postel et al., 2007); 3, *O. similis*, young copepodite, CPHT length $293.8 \pm 26.6 \mu\text{m}$ (Postel et al., 2007); 4, *O. similis*, male ventrally, total length ca. 600 μm ; 5, *O. similis*, male dorsally; 6, *O. similis*, nauplius dorsally, length $235.4 \pm 1.4 \mu\text{m}$ (Postel et al., 2007) (photos H. Sandberg).

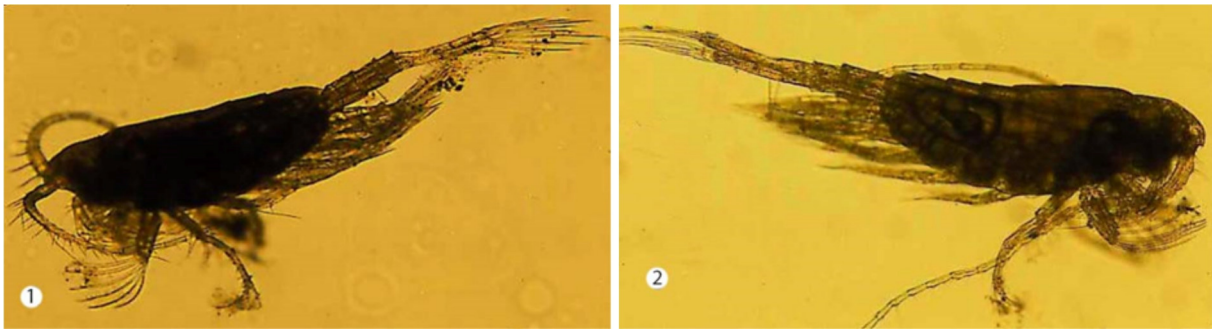


Figure 2.15: Copepoda. 1, *Limnocalanus macrurus*, male, dorso-lateral view, prosome length 1.7–1.8 mm (Hernroth, 1985); 2, *L. macrurus*, female, lateral view, total length 2.4–2.9 mm, prosome length 1.7–1.9 mm (Czaika, 1982; Balcer et al., 1984; Hernroth, 1985) (photos H. Sandberg).



Figure 2.16: Cladocera. 1, *Daphnia longispina*, female with embryos, lateral view; 2, *Daphnia cristata*, female with egg, lateral view; 3, 4, *Daphnia cucullata*, females with eggs, lateral view, difference in helmet morphology is due to cyclomorphosis; 5, *Daphnia cucullata procurva*, female, lateral view (after Telesh & Heerkloss, 2004).

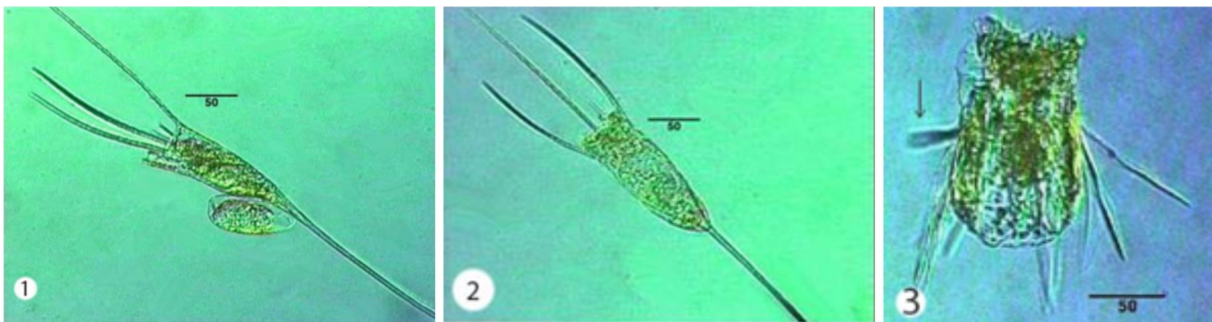


Figure 2.17: Rotifera: 1, *Kellicottia longispina*, female, lateral view, with egg; 2, *K. longispina*, female, ventral view; 3, *Polyarthra vulgaris*, female, lateral view, arrow shows ventral finlet (after Telesh & Heerkloss, 2002).

The amount of co-occurring *Cardium* species and *Mya arenaria* is normally negligible (Ackefors, 1969). Polychaeta larvae are more abundant during the phytoplankton spring bloom than in the remaining time of the year. Finally, the seasonal patterns of the adult calanoid copepods density demonstrate one peak in March and another period of higher abundances during several months in summer and autumn.

Taking the key species with maximal abundance of several thousand individuals per cubic meter separately, the seasonal pattern of calanoids is more differentiated

and explains the annual course of the total zooplankton abundance. *Pseudocalanus* spp. (Figure 2.13) become mature in March, April and May; they are followed by *Acartia bifilosa* in May, July and August, *Eurytemora affinis* (Figure 2.6) in July and August, *Temora longicornis* (Figure 2.4) in July and August, and finally, by *Acartia longiremis* (Figure 2.4) – mainly in August. Copepods *Pseudocalanus* spp. are probably responsible for the total zooplankton peak in May, while the majority of calanoids become adult in summer. This could be explained by different temperatures in the habitats. Meridional shifts in seasonality are possible.

Decadal and multi-decadal variability in the atmospheric and consequently in the hydrographic regime also causes changes in mesozooplankton abundances and sometimes in species composition. Salinity and temperature changes are the main driving forces here. For example, the longer period of missing salt-water inflows and rising river runoff in the Northern Baltic proper and the Gulf of Finland in the late 1980s corresponded to the appearance of eight *Keratella* species and other rotifers, e.g. *Polyarthra* spp. and *Kellicotia longispina* (Figure 2.17), as well as the cladocerans *Bythotrephes longimanus* (Postel et al., 1996). Consequently, the number of taxonomic groups increased. At the same time, the key species changed in the Central Baltic proper. The former dominant halophilic representatives of the cold-water genus *Pseudocalanus* were substituted by the *Acartia* species. In the northern parts of the Baltic proper, the former dominance of *Acartia* spp. was replaced by the brackish water species *Eurytemora affinis*. These results based on the HELCOM data set for the entire Baltic Sea were in accordance with the reports on the regional shifts published by Vuorinen and Ranta (1987), Viitasalo et al. (1990), Lumberg and Ojaveer (1991), Flinkman et al. (1998), Ojaveer et al. (1998), Vuorinen et al. (1998), Dippner et al. (2000, 2001) and Möllmann et al. (2000, 2003).

2.2 Dominant species and mesozooplankton community composition

The most abundant mesozooplankton species that dominate in the Baltic proper in terms of biomass belong to the calanoid copepods (*Acartia*, *Temora*, *Pseudocalanus*, *Centropages*, *Eurytemora*). Marine copepods found in the Baltic Sea are small-sized, compared to those occurring in the fully marine environments, and they are able to adapt to mesohaline or oligohaline conditions. Thus, truly marine species such as representatives of the genus *Calanus* do only occur sporadically in the most western part of the Baltic Sea, as a consequence of saltwater intrusions from the North Sea. The occurrence and reproduction success of the marine copepods *Pseudocalanus* sp. depend strongly on high salinity and oxygen content in the water system. This species is the most important and energy-rich food source for zooplanktivorous fish such as herring (Flinkmann et al., 1998; Möllmann et al., 2003). Holmborn et al. (2010) confirmed by the genetic analyses that *Pseudocalanus acuspes* is the only species of this genus with a resident population in the Baltic Sea. Copepods from the other above mentioned genera are less sensitive to salinity changes and brackish water conditions. Especially *Acartia* spp. and *Eurytemora affinis* are the coastal and estuarine marine species with high capacity of adaptation to oligohaline or even freshwater environments. A truly freshwater copepod, distributed in low-salinity habitats such as the Gulf of Finland, the Åland Sea and the Bothnian Bay, is *Limnocalanus macrurus* (HELCOM, 2009).

The circumglobally distributed marine cyclopoid copepod *Oithona similis* has been described as a eurythermal, euryhaline, omnivorous species since it can be adapted to a wide range of habitats (Fransz et al., 1991). In the Baltic Sea, the distribution range of this small-sized species is mainly restricted by salinity conditions.

The cosmopolitan marine tunicates *Fritillaria borealis* and *Oikopleura dioica* are common members of the zooplankton communities in temperate climate zones, although the distribution range of the former extends to the Polar Regions whereas the latter is rather adapted to warm and even subtropical habitats (Fenaux et al., 1998; Schulz & Hirche, 2007). Both species are euryhaline and able to occur in salinities as low as 6 psu (*Fritillaria*) and >11 psu (*Oikopleura*) (Ackefors, 1969).

Most Cladocera are of freshwater origin, such as the family Bosminidae, which is represented by a variety of species in the Baltic Sea, some of which can hardly be distinguished morphologically. In the central Baltic Sea, *Bosmina (Eubosmina) coregoni maritima* is registered very often (e.g. Ackefors, 1971; Möllmann et al., 2005; Schulz et al., 2012), although other authors determine this species as *Bosmina longispina maritima* (e.g. Kankaala, 1983; Rudstam et al., 1992; Telesh & Heerkloss, 2004). In coastal waters, other Bosminidae are also known: *Bosmina longirostris*, *Eubosmina coregoni*, *Bosmina coregoni typica* (Wiktor, 1964; Arndt, 1989; Telesh & Heerkloss, 2004; Semenova, 2011). The second cladoceran family inhabiting coastal waters of the Baltic Sea are the Podonidae, represented by *Evadne nordmanni*, *Podon intermedius*, *Podon leuckarti*, *Pleopis polyphemoides* and *Penilia avirostris* (e.g. Hällfors et al., 1981; Viitasalo et al., 1995; Durbin et al., 2008). It is commonly agreed that the early ancestors of the Podonidae lived in freshwater like all other Cladocera (Richter et al., 2001). For the cosmopolitan species *Evadne nordmanni* a genetically distinct Baltic Sea population was found and discussed as Baltic Sea post-glacial evolution (Böckmann et al., 2018). The Ponto-Caspian invader *Cercopagis pengoi* is a brackish-water Cladocera species, which invaded the Baltic Sea during the late 1980s–early 1990s (Ojaveer & Lumberg, 1995; Panov et al., 1996). Since the mid-1990s, it established permanent populations in the Gulf of Finland and the Gulf of Riga (Avinski, 1997; Krylov et al., 1999; Uitto et al., 1999) and is still further expanding its distribution range southwards (Bielka et al., 2000; Litvinchuk & Telesh, 2006). For more information about the invasive species in plankton of the Baltic Sea, see Section 2.7 below.

Rotifers are especially diverse and abundant in the Baltic coastal ecosystems (Telesh & Heerkloss, 2002; Telesh, 2004). Rotifers decrease in diversity and in numbers with increasing water salinity, due to the freshwater origin of this group. The most species-rich rotifer families in the Baltic Sea are Synchaetidae (*Synchaeta* spp., *Polyarthra* spp.) and Brachionidae (*Brachionus* spp., *Keratella* spp.). These rotifers contribute significantly to the total zooplankton biomass and production, also in the open Baltic waters (Ojaveer et al., 2010). It is very difficult to discriminate between the species of *Synchaeta* in the preserved samples; therefore, they are often lumped together as *Synchaeta* spp. Common species in coastal and offshore waters of the Baltic Sea are *Synchaeta baltica* and *Synchaeta monopus* (Johansson, 1992; Viitasalo et al., 1995; Telesh & Heerkloss, 2002; Telesh et al., 2009). The second most abundant rotifer genus in the coastal waters of the Baltic Sea is *Keratella*, occurring with several species. Identification of these species is based on the characteristics of the lorica. The most common species of this genus are *Keratella quadrata*, *Keratella cochlearis* and *Keratella cruciformis* (Johansson, 1992; Viitasalo et al., 1995; Telesh & Heerkloss, 2002; Telesh et al., 2009). Relative abundance of different forms from the *Keratella cochlearis*-group can be converted into eutrophication index (the *Keratella*-index, KIN),

which is a convenient tool for evaluation of the trophic state in coastal waters of the Baltic Sea (Gopko & Telesh, 2013).

2.3 Why zooplankton composition varies spatially?

The variable salinity conditions in the Baltic Sea, with horizontal and vertical gradients as well as mixing processes, affect the physiological functions of zooplankton organisms by causing osmotic stress. Depending on their origin, species live in a hypo- or hyper-osmotic milieu. These organisms are either osmoregulators, maintaining a certain internal ion concentration, or they are osmoconformers and adjust their intracellular osmolarity to the surrounding medium. The regulation of the osmolarity of euryhaline marine organisms is often facilitated by low water temperatures. In any case, acclimatization to variable salinities is energy consuming and thus shapes the distribution ranges of zooplankton species differently, depending on their specific physiological performance.

2.4 Horizontal distribution patterns

The salinity gradient from the south-western (mesohaline) to the north-eastern Baltic Sea (oligohaline) is an important factor regulating the horizontal distribution range of zooplankton species and the biodiversity of the zooplankton community (Figure 2.18).

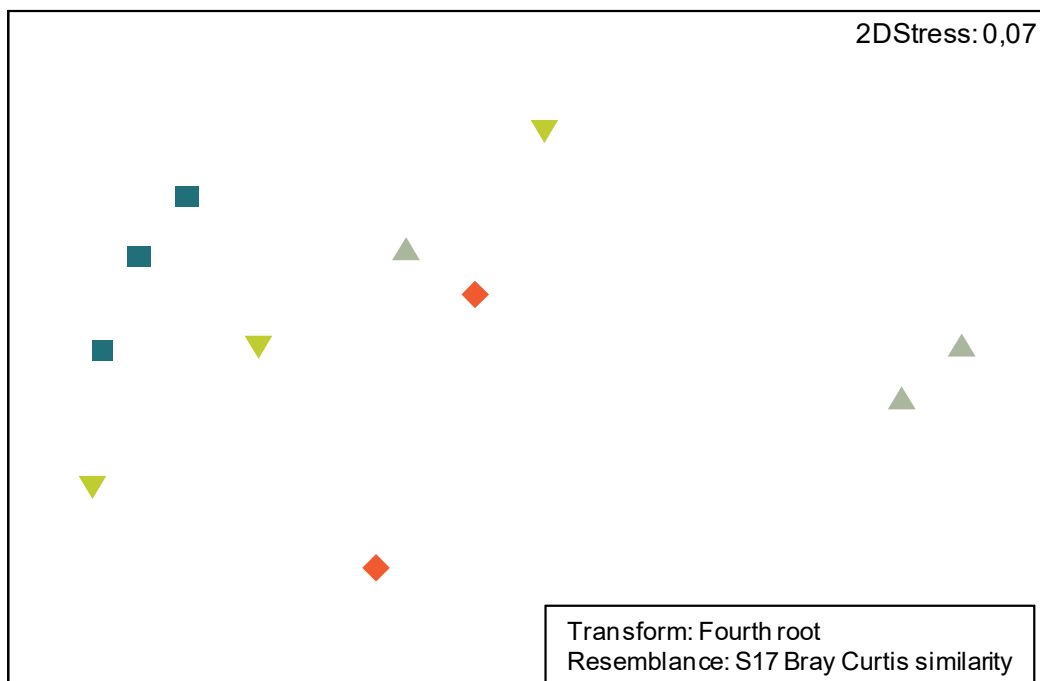


Figure 2.18: The mesozooplankton community composition in the western Baltic Sea above the halocline changes from west to east. MDS-plot of zooplankton community of four geographical areas in July 2009; blue squares: Great Belt; green triangles: Fehmarnbelt; red rhomb: Mecklenburg Bight; grey triangle: Darss Sill (from FEMA-FEHY, 2013).

In the most south-western part of the Baltic Sea, the Belt Sea, the zooplankton community composition is strongly influenced by the saline water inflow from the North Sea and outflow of low saline water in the surface layer. Key species of saltwater inflows are, for instance, the marine copepods *Calanus helgolandicus* and *Calanus finmarchicus*, as well as the marine cladocerans *Penilia avirostris*, which can reach the Kiel Bight and the Mecklenburg Bight by the advection of organisms with water masses from the North Sea but do not establish reproducing populations there because of the mesohaline conditions in the Belt Sea (Postel, 1995). In the western Baltic Sea, the prevalent marine calanoid copepod is *Pseudocalanus acuspes*. The abundance of this species shows a strongly decreasing trend east of the Darss Sill, which is known as a faunistic distribution limit for the marine species in the Baltic Sea (Flinkmann et al., 2007).

Marine taxa, such as Tunicata (mainly *Oikopleura dioica*) and the cyclopoid copepod *Oithona similis*, are quite abundant in the Belt Sea where they frequently account for up to a half of the total biomass in summer and autumn, but occur only rarely east of the Darss Sill (Figure 2.19). In contrast, the brackish-water Cladocera from the family Bosminidae increase in their abundance from the west to the east and account for up to a half of the total zooplankton biomass in summer at Darss Sill (Figure 2.19).

East of the Darss Sill, brackish-water species dominate the mesozooplankton community. Rotifera such as *Synchaeta* spp. and *Keratella* spp. as well as Copepoda such as *Acartia bifilosa*, *Acartia longiremis*, *Eurytemora affinis* and Cladocera of the family Bosminidae occur in high abundances in the surface water layer of the central Baltic Sea and further north-east (Viitasalo, 1992; Postel, 1995). In estuaries and in the most north-eastern coastal areas, the Bothnian Bay and the Gulf of Finland, the freshwater copepod *Limnocalanus macrurus* as well as freshwater species of the genera *Cyclops* and *Daphnia* are regular members of the zooplankton community (Hällfors et al., 1981; Telesh & Heerkloss, 2004).

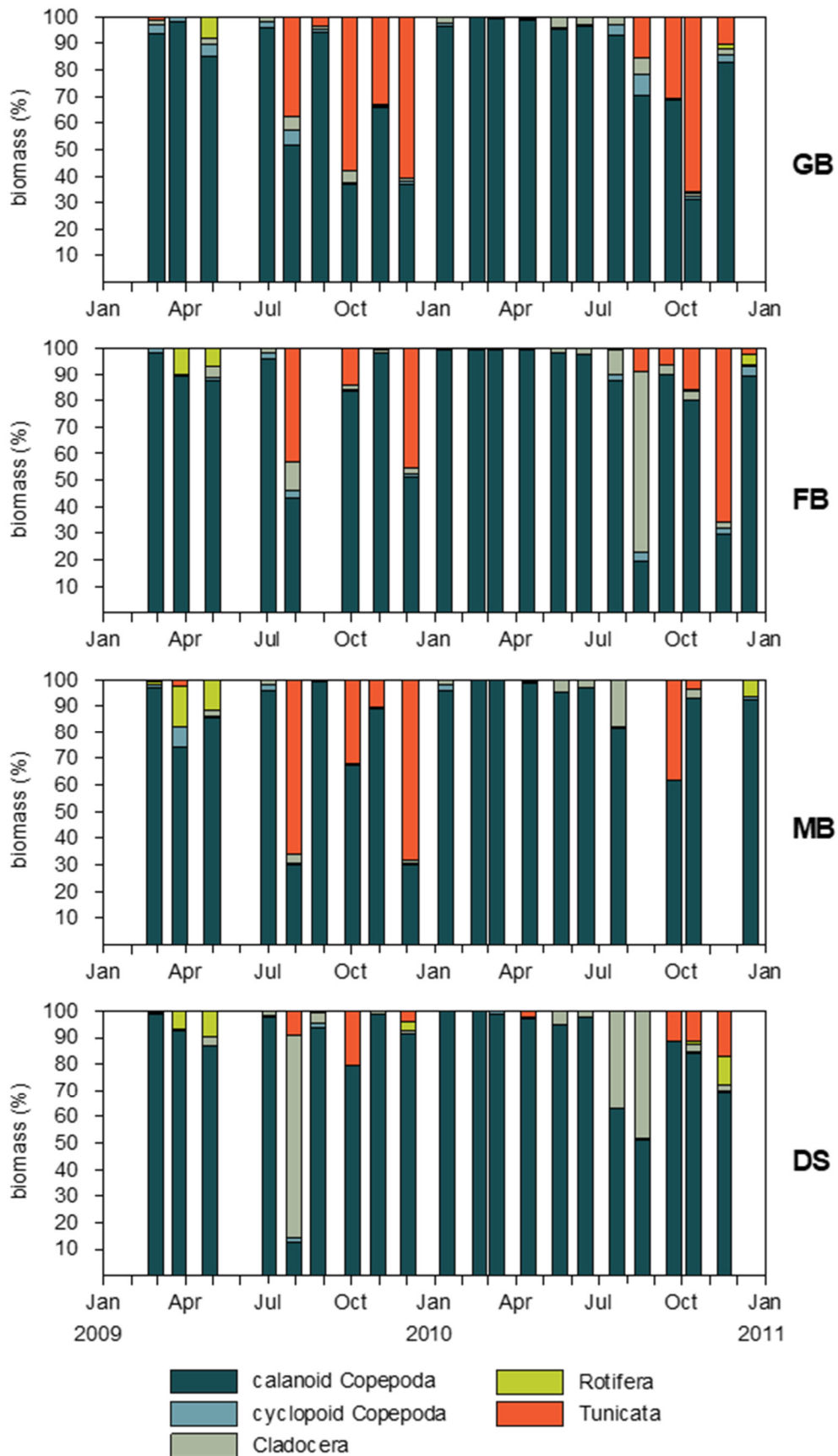


Figure 2.19: Proportion of biomass (%) of zooplankton taxonomic groups in the south-western Baltic Sea in 2009 and 2010; arranged from west (top) to east (bottom). GB: Great Belt; FB: Fehmarnbelt; MB: Mecklenburg Bight; DS: Darss Sill (from FEMA-FEHY, 2013).

2.5 Vertical distribution patterns

The vertical distribution of mesozooplankton species in the Baltic Sea is greatly affected by the abiotic factors: salinity, temperature, oxygen and light. Varying conditions regarding food and the occurrence of predators at different depths are of high importance as well.

One of the most influential factors regulating the vertical distribution patterns of the zooplankton community is the vertical salinity stratification and presence of the halocline (Figure 1.3). The mesozooplankton community shows significant differences between the water layers above and below the halocline, especially during the stagnation periods (in summer and early autumn). In stratified brackish-water systems, marine species can extend their distribution ranges by inhabiting saline deep water layers below the halocline as long as oxygen concentration is sufficient (“brackish water submergence”; Remane, 1940). In the central Baltic Sea, the suitable habitat for marine species is thus limited from above by low salinity and from below – by low oxygen concentration. This phenomenon is confirmed by the spatial distribution patterns of several marine zooplankton species in the Baltic Sea such as the copepods *Pseudocalanus acuspes* and *Oithona similis* that do occur in the water layer between the halocline at salinities >11 psu and the hypoxic zone (<1 ml l⁻¹) as far east as the Bornholm and Gotland Basins (Postel, 1995; Hansen et al., 2004; Renz & Hirche, 2006; Schulz et al., 2007; Schulz & Hirche, 2007; Figure 2.20).

Copepods with a high physiological tolerance of salinity fluctuations, such as *Temora longicornis* and *Centropages hamatus*, show generally a broad vertical distribution range within the whole water column (Hällfors et al., 1981). *Acartia bifilosa* and *Acartia longiremis* are brackish-water species and, therefore, they are well adapted to low salinities. They can inhabit the upper part of the water column, where growth conditions due to food availability are assumed to be better, if compared to the deeper regions (Fransz et al., 1991; Hansen et al., 2006).

Besides the impact of salinity on vertical distribution patterns of zooplankton, the thermal stratification shapes the distribution ranges of certain species as well. As a consequence of its adaptation to low temperatures, the Baltic glacial relict species *Fritillaria borealis* shows, for instance, a seasonal submergence to avoid warm surface water layers in summer (Ackefors, 1969; Ojaveer et al., 1998). In contrast, the production of the surface zooplankton community of the central Baltic Sea, consisting generally of small species such as cladocerans (*Bosmina* spp., *Podon intermedius*) and rotifers (*Synchaeta* spp., *Keratella* spp.), depends mainly on the seasonally high water temperatures and favorable feeding conditions in the surface water layer (Viitasalo et al., 1995; Schulz et al., 2007; Figure 2.21).

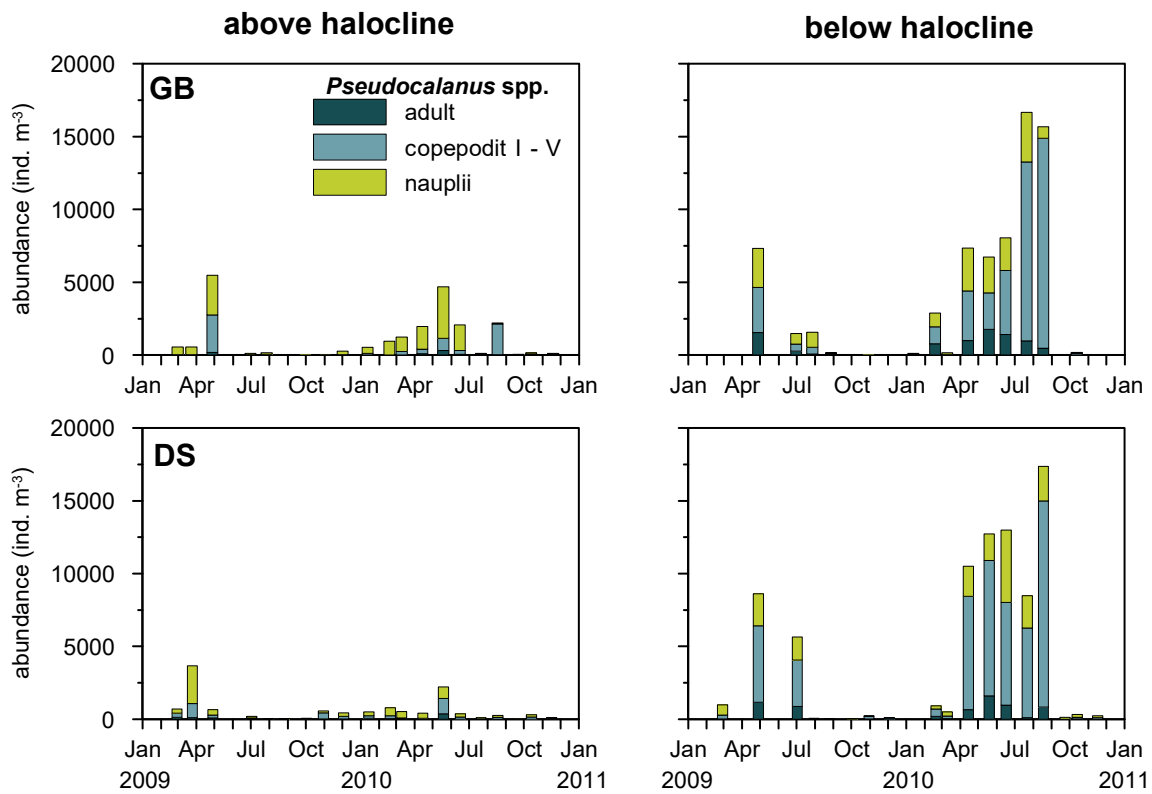


Figure 2.20: Abundance of *Pseudocalanus* spp. developmental stages and adults in 2009 and 2010 above and below the halocline in the Great Belt area (above, GB) and the Darss Sill area (below, DS) (from FEMA-FEHY, 2013).

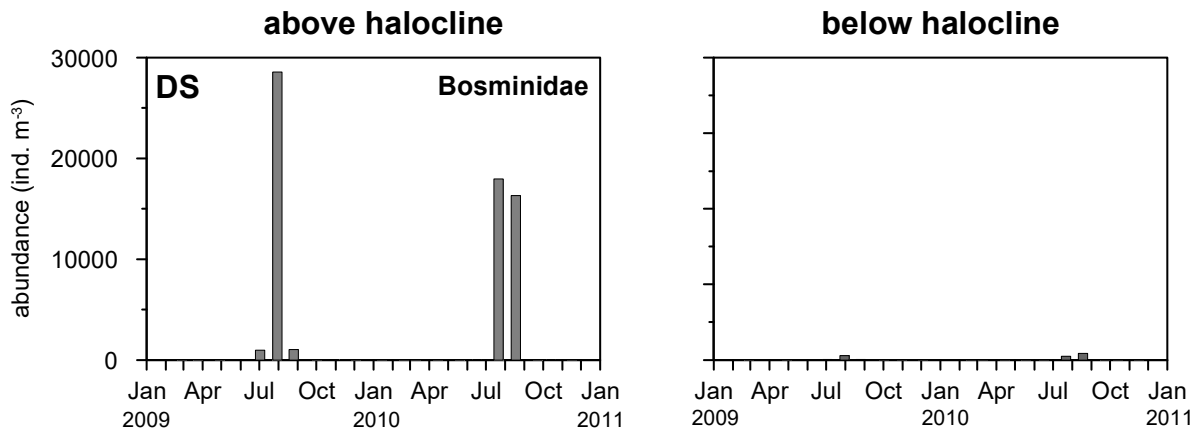


Figure 2.21: Abundance of *Bosminidae* in 2009 and 2010 above and below the halocline in the Darss Sill area (DS) (from FEMA-FEHY, 2013).

Many species of planktonic crustaceans, especially the adult forms of copepods, conduct diurnal vertical migrations through the water column. Vertical migrations are mainly affected by the environmental factors. The ultimate reason for vertical migrations is diminishing mortality through predator avoidance. Therefore, the general migration pattern involves rising to the surface at dusk and grazing on phytoplankton during the night, prior to descending to deeper water layers before dawn to avoid visually feeding predators. Due to the strong relationship between the migration behavior and light conditions, the zooplankton migration patterns change seasonally.

When comparing vertical distribution patterns of zooplankton during the day and at night, obvious differences can be observed. Considering, for instance, the Eastern Gotland Basin with its stable salinity stratification and a pronounced thermal stratification during summer, diurnal migration is expected for certain species (Hällfors et al., 1981). In midsummer, the euryhaline copepods *Centropages hamatus* and *Temora longicornis* accumulate within the thermocline or below the thermocline in daytime but occur mainly in surface waters above the thermocline at night. *Pseudocalanus acuspes* generally prefers deeper water layers because of their higher salinity. Nevertheless, an upwards movement and accumulation in the mid-water layer between the halocline and the thermocline can be observed during the night. Other species such as the cladocerans *Pleopsis polyphemoides* and *Evadne nordmanni* likely do not perform a pronounced diurnal migration; they stay generally in the surface water layers within or above the thermocline (Hällfors et al., 1981). Observations in the Arkona Sea in summer showed that the biomass of mesozooplankton, mainly consisting of the cladocerans *Bosmina* spp., doubled at midnight if compared with the mid-day values in the uppermost 25 m water layer (Postel, 1995).

Diurnal vertical migration (DVM) of zooplankton is not restricted to deep and stable stratified Baltic Sea basins but occurs also in shallow coastal waters. For instance, in shallow macrophyte habitats zooplankton is using dense submerged vegetation above the sediment surface as a daytime refuge from predation (Meyer et al. 2019). The light condition was found an important factor triggering vertical migration in lagoons at the isle of Rügen (Germany). During days with bright sunlight migration was observed, but not during cloudy days (Gerbersdorf & Schubert, 2011). Light dependent diurnal migration patterns were also observed in nearshore waters of the Mecklenburg Bight at depths of only 12 m. After sunset, especially the adult specimens of the copepods *Acartia* spp., *Pseudocalanus* sp. and *Temora longicornis* were migrating to higher water levels (Böckmann, 2013).

The migration behavior of certain zooplankton species is affected by body size, ontogenetic developmental stage, and sex (Titelman & Fiksen, 2004). For the common calanoid copepods *Eurytemora affinis* and *Acartia* spp. it was shown that the migration activity intensified with the increasing body size and older developmental stage, and it was the greatest in adult males (Holliland et al., 2012). However, adult females of *Eurytemora affinis* remained at deeper water layers with only slight upward movement at night, especially in spring. This phenomenon is attributed to the predator-avoidance effect due to high vulnerability of egg-carrying females to predation (Vuorinen, 1987; Flinkman et al., 1992; Holliland et al., 2012).

2.6 Seasonal variations in zooplankton

In temperate climatic zones, pelagic ecosystems are strongly influenced by the seasonality in temperature and light conditions, which regulates primary production and therewith the length of the growing period of the organisms at higher trophic levels, such as zooplankton. To some extent, the biomass and production of zooplankton is directly regulated by temperature conditions. As a consequence, mesozooplankton species of the Baltic Sea show specific annual developmental cycles, causing a pronounced seasonal succession of the composition of the zooplankton community. The annual duration of the growing season of zooplankton in the Baltic Sea depends on the geographic latitude. In the south-western Baltic Sea, the duration of the growing season is from March to October. In the northern Gotland Basin, the season starts one

month later and ends one month earlier. Further to the north, in the Gulf of Bothnia, the growing period is reduced to 4 months and lasts from May through August (Postel, 1995). Depending on the length of the growing season, the biomass of zooplankton shows one or two annual maxima that develop subsequently to the spring and autumn phytoplankton blooms (Figure 2.22).

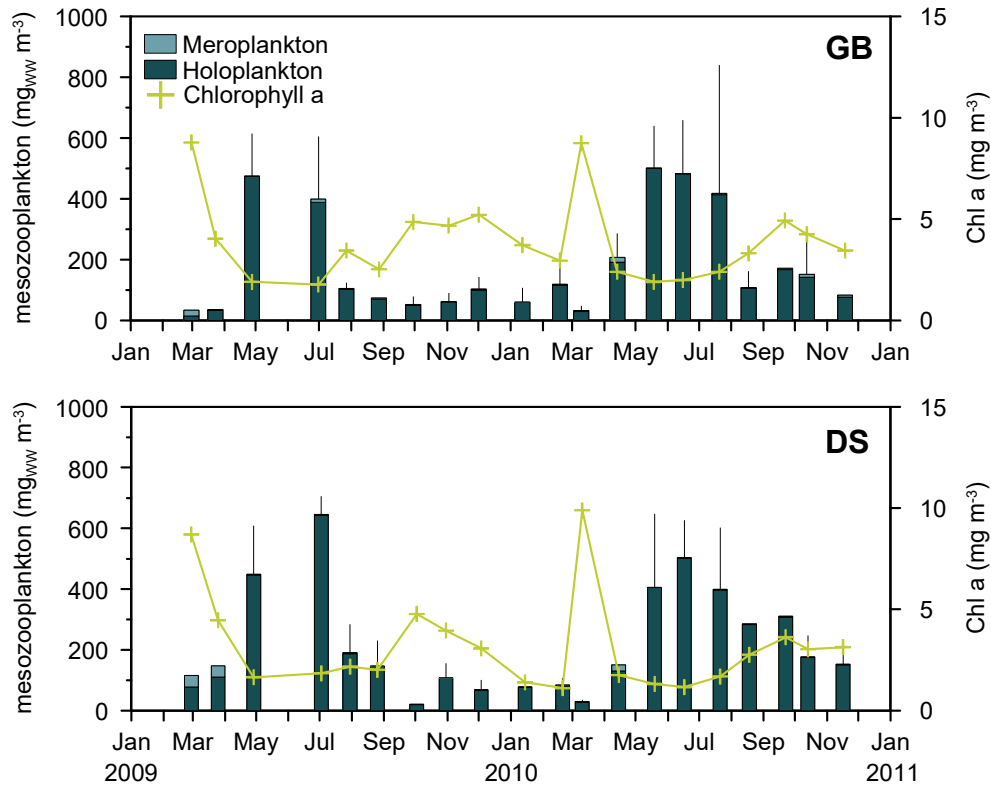


Figure 2.22: Mesozooplankton biomass and chl-a concentration in the south-western Baltic Sea in 2009 and 2010. GB: Great Belt; DS: Darss Sill. Mesozooplankton biomasses are calculated for the whole water column, while chl-a concentrations represent the upper 10 m of the water column (from FEMA-FEHY, 2013).

Besides the annual cycle of the mesozooplankton biomass, the composition of the zooplankton community changes throughout the year. A pronounced succession of the community structure can be recognized from April to September as a consequence of seasonal recruitment and community succession of the dominating taxa (Figure 2.23). In contrast, the winter/early spring community (October to March) appears to be more stable.

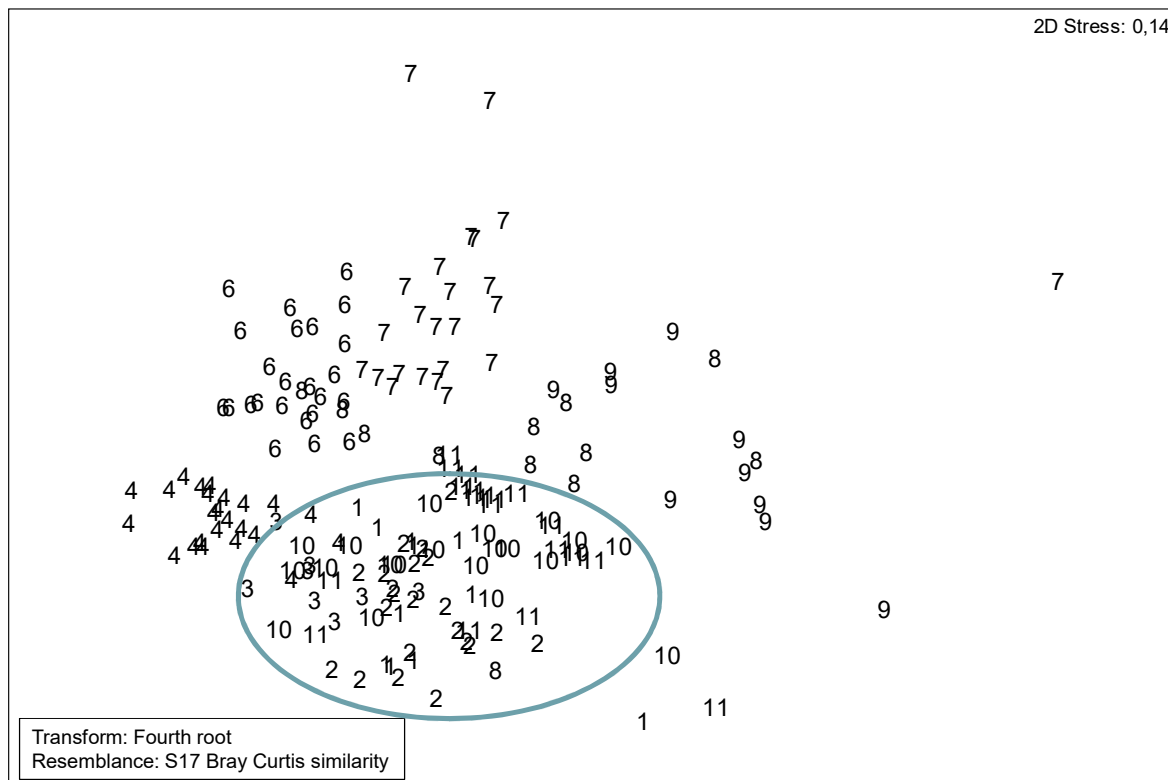


Figure 2.23: The zooplankton community composition in the western Baltic Sea changes throughout the year. MDS-plot of mesozooplankton community in 2009. Data were obtained monthly at 12 stations in the south-western Baltic Sea. Numbers indicate months. The blue ellipse indicates late autumn to early spring season (from FEMA-FEHY, 2013).

The seasonal cycle of the zooplankton community is mainly structured by the developmental cycle of the dominant calanoid copepods. The start of the spawning period with significant number of nauplii is correlated with increasing temperature during spring and early summer: *Acartia* spp. at 0–4 °C, *Pseudocalanus* sp. at 4–8 °C, *Temora longicornis* at 6–10 °C, *Centropages hamatus* and *Eurytemora* sp. at 8–10 °C (Hällfors et al., 1981). A seasonal increase in abundance is also typical for the cyclopoid *Oithona similis*, which shows the annual abundance peaks in late summer/autumn in the central Baltic Sea (Hansen et al., 2004).

Cladocerans reproduce very rapidly by parthenogenesis, developing high population densities very fast in summer when environmental conditions are optimal (Figures 2.24, 2.25). A variety of investigations demonstrate clearly that high temperatures have positive effects on the population dynamics of these crustaceans (Kankaala, 1983; Viitasalo et al., 1995; Möllmann et al., 2002). The dominant species in summer are *Bosmina* spp., whereas the marine cladocerans *Evadne nordmanni* and *Podon* spp. reach population peaks already in spring (Poggensee & Lenz, 1981; Viitasalo et al., 1995; Möllmann et al., 2002).

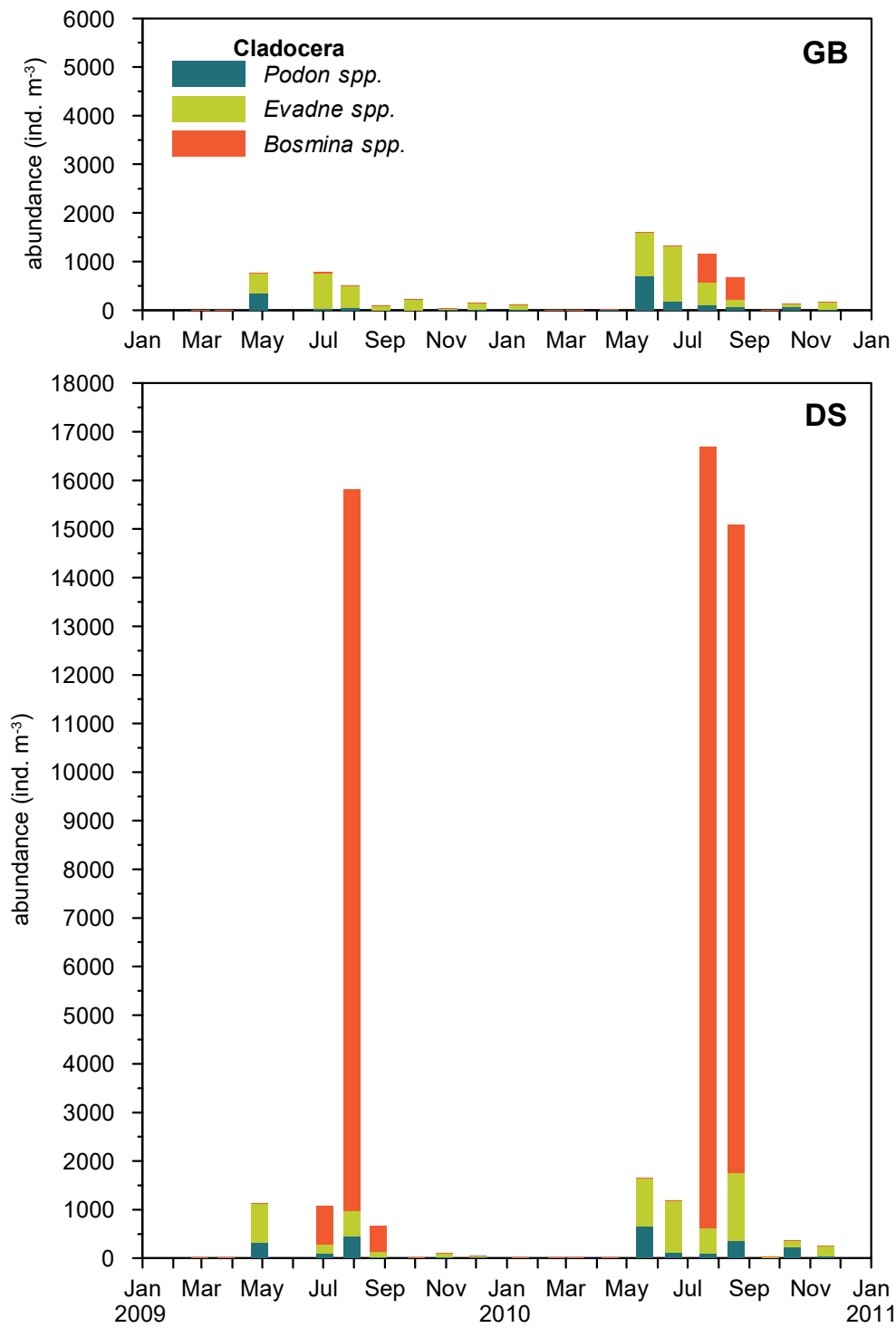


Figure 2.24: Abundance of Cladocera in 2009 and 2010 in Great Belt (GB) and Darss Sill (DS) (from FEMA-FEHY, 2013).

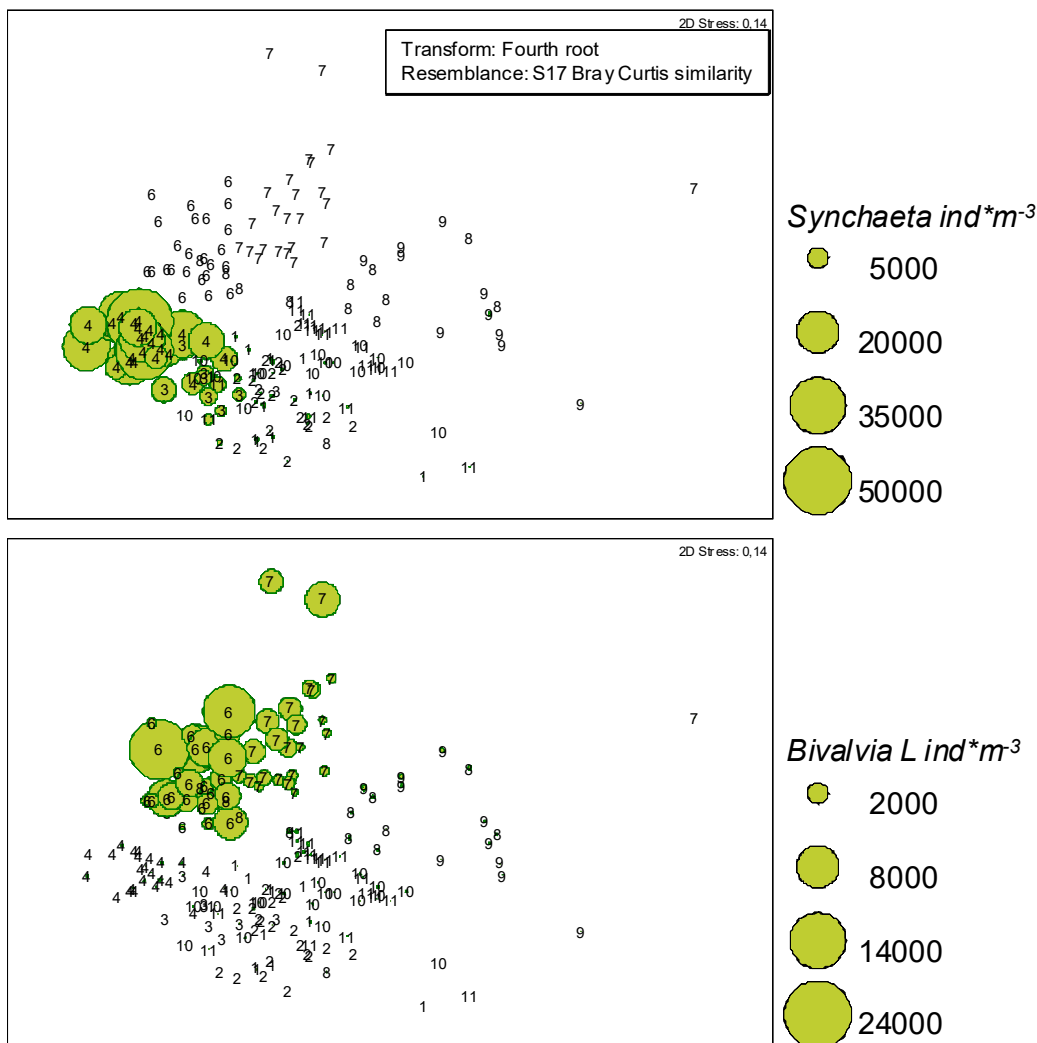


Figure 2.25: Example for the seasonal occurrence of two mesozooplankton taxonomic groups in the south-western Baltic Sea. MDS-plot of mesozooplankton community in 2009. Data were obtained monthly at 12 stations in the south-western Baltic Sea, numbers indicate months. The green bubbles show the seasonal distribution of *Synchaeta* (above) and larvae of *Bivalvia* (below) (from FEMA-FEHY, 2013).

Rotifers are seasonally dominating components of the zooplankton community in offshore and coastal habitats of the Baltic Sea. In the south-western and central Baltic Sea, mass development of the rotifers *Synchaeta* spp. is common in April and May following the phytoplankton spring bloom. Another abundance peak, although smaller, is occasionally observed in autumn. The inter-annual variations are quite high (Dippner et al., 2000). Due to parthenogenetic reproduction, rotifer populations increase fast as soon as the environmental conditions are suitable. The optimum temperature for *Synchaeta* spp. is 4–10 °C. Corresponding to the shifted vegetation period in the northern part of the Baltic Sea, abundance peaks of *Synchaeta* spp. and *Keratella* spp. occur in June (Viitasalo et al., 1995).

The seasonal occurrence of a range of less abundant taxa also contributes to the intra-annual zooplankton community succession. The thermophile Tunicata *Oikopleura dioica* occurs annually in summer (Schulz & Hirche; 2007). Besides the holoplanktonic species, meroplanktonic larvae of benthic invertebrates occur strongly seasonally, correlated with the abundance peaks of Polychaeta larvae in March/April,

larvae of the common starfish *Asterias* in June, Bivalvia and Gastropoda larvae in June/July (Figure 2.25), and Gymnolaemata (Bryozoa) larvae in December–February (FEMA-FEHY, 2013).

2.7 Invasive species

Number of the invasive (nonindigenous or alien) zooplankton species in the Baltic Sea has increased during the recent decades (Leppäkoski & Olenin, 2000; Ojaveer et al., 2010, 2021). Currently, a number of cladoceran species from the Ponto-Caspian area, e.g. *Cercopagis pengoi* (Figure 2.26), *Evadne anonyx* and *Cornigerius maeoticus*, and a ctenophore from the American east coast *Mnemiopsis leidyi* (Figure 2.27) are the examples of alien zooplankters in the Baltic Sea. As obligatory or facultative planktonic predators, they can affect the Baltic pelagic ecosystem (Telesh & Naumenko, 2021). Therefore, such introductions must be monitored very carefully.



Figure 2.26: Cladocera. 1, *Cercopagis pengoi*, general view of a female at stage II (with 2 claws) with resting egg, lateral view; 2, *C. pengoi*, body of a female with embryos in brood chamber, lateral view; 3, *C. pengoi*, body of a female with resting egg, lateral view (after Telesh & Heerkloss, 2004).

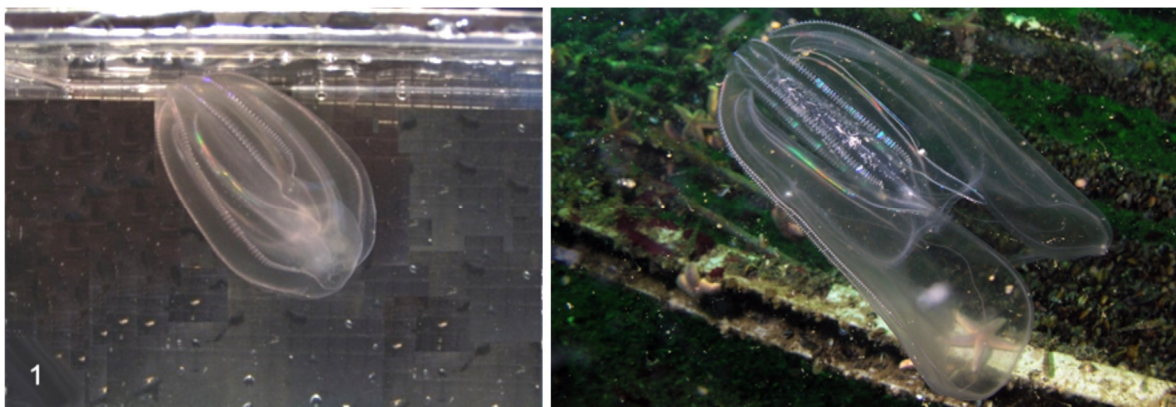


Figure 2.27: Ctenophora. *Mnemiopsis leidyi*, adult, average body length 4–6 cm (1, in aquarium, photo L. Postel, 2006); 2, in the sea (photo G. Niedzwiedz, 2008).

By now, the population of fishhook water flea *C. pengoi* has been established in the greater part of the Baltic Sea. *C. pengoi* occurs more often in coastal waters, but it is also present in the open Baltic Sea (Uitto et al., 1999; Telesh & Ojaveer, 2002; Karasiova et al, 2004; Litvinchuk & Telesh, 2006; Olszewska, 2006; Naumenko & Telesh, 2019; Telesh & Naumenko, 2021). This predatory cladoceran causes a significant impact on the native zooplankton community by feeding on dominant native species such as *Eurytemora affinis*, their nauplii and eggs (Lehtiniemi & Gorokhova, 2008; Naumenko & Telesh, 2019). They consume also *Bosmina* spp. (Pollumäe &

Väljataga, 2004; Gorokhova et al., 2005) and other planktonic filtering crustaceans (Laxson et al., 2003) that are normally dominant in the central Baltic Sea during summer. Finally, due to elimination of other crustaceans by *C. pengoi*, planktivorous pelagic fishes often feed on *Cercopagis* (Antsulevich & Välipakka, 2000). The predation impact of *C. pengoi* can be numerically evaluated (Telesh et al., 2001) and used for monitoring of this successful invasion and its effect on the natural zooplankton community in the Baltic Sea (Telesh & Naumenko, 2021). The predatory planktonic invaders make the food chain longer by one level, which allows expecting additional energy losses during the general energy flow through the pelagic ecosystem of the Baltic Sea. This phenomenon can affect energy balance in general and the size of pelagic fish stocks in particular (Naumenko & Telesh, 2019).

The influence of the most recent invader – the alien ctenophore *Mnemiopsis leidyi* on the pelagic food web of the Baltic Sea is likely limited so far due to its low abundances in the Baltic proper and the northern regions (Kube et al., 2007a, 2007b; Lehtiniemi & Flinkman, 2007). Certain danger to the ecosystem might be expected from a spatial and temporal overlap between a potential mass occurrence of *M. leidyi* and cod eggs below the halocline of the Bornholm Basin (Haslob et al., 2007). This case requires further attention of the researchers (for more details see Section 6.2).

Another invader, formerly known as *Eurytemora affinis* (Poppe, 1880), has happened to be a group of sibling species (Alekseev et al., 2009; Sukhikh et al., 2013). *Eurytemora affinis*, which is originally native to the Ponto-Caspian region, is an important example of the invasive zooplankton in the Baltic Sea. It is the euryhaline copepod species that has been reported from the western European coast, parts of Asia, and within North America from the Atlantic coast, including the Gulf of Mexico, to the Pacific coast (Kipp & Benson, 2010). This species represents a set of cryptic species in the northern hemisphere (Lee, 1999) and was recently defined as a sibling species among copepods in the Baltic Sea (Alekseev et al., 2009). One of the cryptic species of this group inhabiting North America was recently described as the new species *Eurytemora carolleae* Alekseev and Souissi, 2011 (Sukhikh et al., 2013).

The sibling species are a special group of invaders: they are hardly distinguishable morphologically from the local species, but they can be influential for the stability of aquatic ecosystems (Gelembiuk et al., 2006). At the beginning of the invasion, the sibling species can cause an unidentifiable change in the biological diversity, further followed by a rearrangement of the aquatic communities. Sympatric sibling species often exhibit distinct habitat preferences defined by depth, salinity or exposure (Sukhikh et al., 2013). Successional differences between sibling species, reflecting temporal partitioning of resources in response to seasonal change or disturbance, were also documented (Knowlton, 1993). For the North American and European *Eurytemora* species, there are some differences in egg production rate and the reproductive lifespan (Beyrend-Dur et al., 2009). Hence, the *Eurytemora* species complex needs to be studied in a detailed and precise way with monitoring programs that may allow conservationists to combat the invasion (Sukhikh et al., 2013, 2020).

Molecular genetic diagnosis is the most efficient way to identify or confirm the sibling species' penetration to new habitat (Goetze, 2003). Morphological differences among sibling species can also be found but they have to be preceded by the molecular confirmation. In the recent studies, the results of the molecular genetic diagnosis based on the analysis of mitochondrial DNA nucleotide sequence (bar-coding) in the populations of a common circumpolar species *Eurytemora affinis* (Poppe, 1880) and *Eurytemora carolleae* Alekseev and Souissi, 2011, as well as their comparison with the morphological data have revealed the co-occurrence of both

species in the Gulf of Finland, the Baltic Sea (Sukhikh et al., 2013). Interestingly, the proportion of the North-American invader *E. carolleeae* in the Gulf of Finland was ca. 20% of the entire *Eurytemora* abundance, while in the Vistula Lagoon and the Gulf of Riga, the native European *E. affinis* dominated (Sukhikh et al., 2013). Thus, we can conclude that at present the Baltic Sea hosts two genetically divergent clades (now species) of *Eurytemora*: the Atlantic *E. carolleeae* (possibly invasive) and the European *E. affinis* (native) that overlap in their distribution (Alekseev et al., 2009; Sukhikh et al., 2013).

In the Baltic Sea, invasions are registered also in microplankton. There, a vast functional group of microscopically small organisms, the protists, is currently categorized as “mixoplankton”, or mixotrophic plankton, due their mixotrophic feeding mode, i.e. the combination of autotrophic feeding (phototrophy) and phagotrophy (Flynn et al., 2019, and references therein). These organisms can be attributed to both phyto- and zooplankton because they combine the morphological and functional features of an alga (presence of chloroplasts and photosynthetic activity) and a „perfect beast“, feeding phagotrophically (Flynn & Mitra, 2009). At the microplankton level, the invasions of alien species may seem “invisible”; however, microplankton introductions also can have evident (and fast) nuisance ecosystem consequences (Telesh & Skarlato, 2022). A good example of the delayed though devastating effects of a protistan alien is the peculiar history of invasion of the Baltic Sea by the bloom-forming potentially toxic dinoflagellates *Prorocentrum cordatum* (Ostenfeld) J.D.Dodge, 1975 (Telesh et al., 2016). Nowadays, these unicellular planktonic protists form harmful blooms (red tides) in the marine coastal waters globally (Skarlato et al., 2018b; Glibert, 2020).

In the brackish-water Baltic Sea, which is the area of intensively ongoing invasion processes (Olenin et al., 2017), the mixotrophic dinoflagellate *P. cordatum* is generally accepted as the only one truly invasive protistan species because the dynamics and importance of only this unicellular alien meets the major established requirements of the “invader” (Olenina et al., 2010).

The mixotrophic dinoflagellates *P. cordatum* form an important component of pelagic ecosystems since they are involved in a variety of trophic interactions in plankton food webs. These interactions, food sources, and major grazers of *P. cordatum* in the trophic network were summarized recently using the Black Sea case studies (Khanaychenko et al., 2019); they are represented schematically in Figure 2.28.

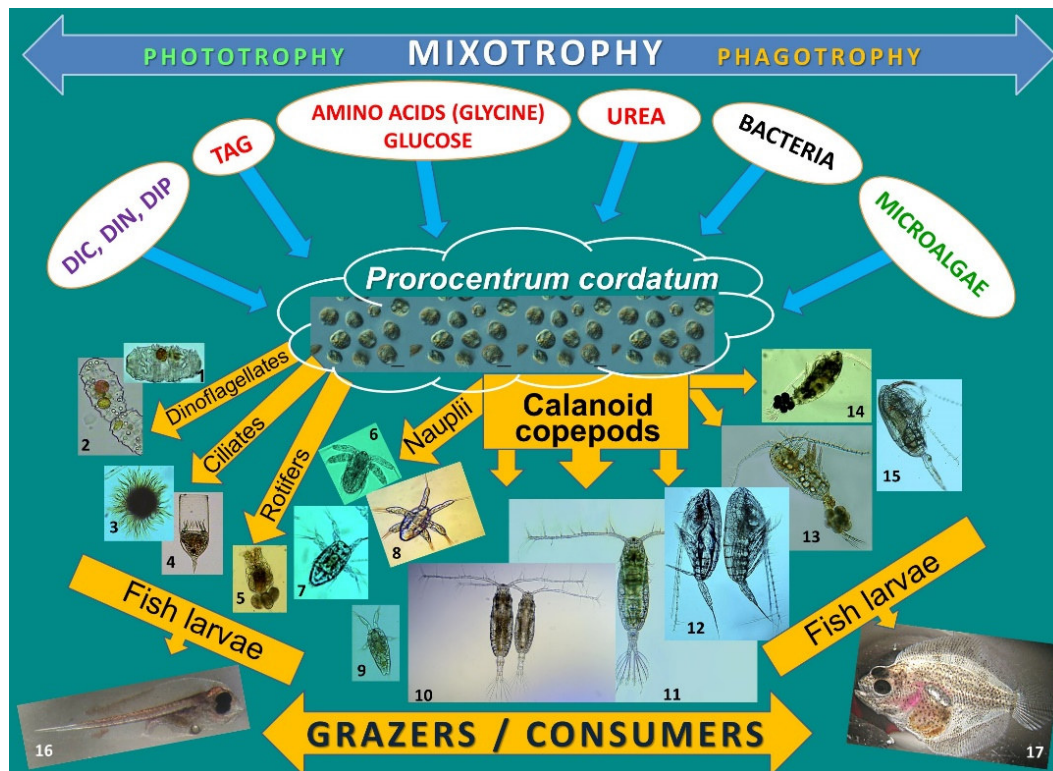


Figure 2.28: Mixotrophic dinoflagellates *Prorocentrum cordatum* in the pelagic food web: their feeding substrates/sources and major grazers/consumers. Heterotrophic dinoflagellates: 1, 2, *Polykrikos kofoidii*. Ciliates: 3, *Strombidium* sp.; 4, *Favella ehrenbergii*. Rotifers: 5, *Brachionus plicatilis*. Larvae of calanoid copepods: 6, 7, *Acartia tonsa*, nauplii; 8, *Calanus helgolandicus*, nauplius; 9, *Calanipeda aquaedulcis*, nauplius. Adult calanoid copepods: 10, *Acartia clausi* (left – female, right – male); 11, *Acartia tonsa*, female; 12, *Calanus helgolandicus* (left – male, right – female); 13, *Calanipeda aquaedulcis*, female with egg sac; 14, *Arctodiaptomus salinus*, female with egg sac; 15, *Pseudocalanus elongatus*, female. Fish larvae: 16, *Scophthalmus maximus* var. *maeoticus*, early larvae (4 days); 17, *Scophthalmus maximus* var. *maeoticus*, metamorphosing larvae. Photo courtesy of N.A. Gavrilova (1, 2, 4), T.V. Rauen (5), and L.S. Svetlichny (7, 10–14). Photo A.N. Khanaychenko (3, 6, 8, 9, 15–17). *Prorocentrum cordatum*, live cells in culture (photo courtesy of M.A. Berdieva). DIC, dissolved inorganic carbon; DIN, dissolved inorganic nitrogen; DIP, dissolved inorganic phosphorus; TAG, triacylglycerides. From Khanaychenko et al., 2019, with modifications.

Recent studies discuss the possible interplay of planktonic invaders in the Baltic Sea. One of the examples is a probability of the cases when harmful blooms of the potentially toxic dinoflagellates *Prorocentrum cordatum* might be downregulated by the neritic copepods *Acartia tonsa* – another alien species in the region (Telesh et al., 2020, and references therein). The preliminary analysis of the available published data revealed that in the Baltic Sea, the populations of both invaders, the protist *P. cordatum* and the copepod *A. tonsa*, are currently increasing in abundance. At present, the major ecological requirements of *P. cordatum* and *A. tonsa* in the Baltic Sea coastal waters partially juxtapose. However, with the on-going eutrophication and global warming, the population of the invasive copepods *A. tonsa* will likely proliferate in the Baltic Sea in the near future and can react positively to the possible shifts in phytoplankton community structure and dynamics, particularly to those changes caused by the enhancing water temperature and/or decreasing salinity. The related shifts in the dominant mixoplankton in favor of the bloom-forming species and the projected enhanced magnitude of blooms could likewise affect their grazers and cause the overall plankton community restructuring in the Baltic Sea (Telesh et al., 2020).

Currently, the multiple negative ecosystem effects of red tides caused by *P. cordatum* are well identifiable: those are displacement of the native *Prorocentrum* species from the dominants due to effective competition for food, oxygen depletion in water due to high concentrations of metabolites after the bloom decay, water quality deterioration, etc. The ecological niche dimensions of this invader in the Baltic Sea were determined since they are largely responsible for the species' range expansion (Telesh et al., 2016). Moreover, fine mechanisms of the invasive success of *P. cordatum* such as mixotrophic feeding, high adaptability of cells to external stresses, and intra-population heterogeneity in the uptake of different nutrient substrates have been largely unveiled in recent years (Matantseva et al., 2016, 2018; Skarlato et al., 2018a, 2018b; Pechkovskaya et al., 2020; Telesh et al., 2020, 2021). However, linkage of this knowledge with predictive invasion theories and forecasts of nuisance ecosystem effects is still in its natural infancy because the integration of microplankton biology into invasion science has been insufficient so far (Ricciardi et al., 2021). Moreover, a large array of studies attempted at finding traits to predict invasiveness, i.e. establishment and spread of new aliens (e.g., see Dickey et al., 2020). Many of those, however, have failed to robustly predict ecological impact of alien species spanning diverse habitats, taxonomic categories and trophic groups, and no correlations between invasiveness and ecological impact were detected so far (Ricciardi et al., 2021, and references therein).

2.8 Long-term trends

Zooplankton diversity, distribution and abundance are closely related to hydrographic conditions in the Baltic Sea, salinity and temperature being the most pronounced driving forces. Hydrological conditions are controlled by climate through the combined effect of river-runoff and occasional intrusions of saline water from the North Sea. Although hydrographic effects are considered as the key factors to the long-term dynamics of zooplankton, the long term changes of the food web with bottom-up effects (eutrophication and food availability; HELCOM, 2009) and top-down effects (changes in fish stocks, e.g. sprat, Möllmann & Köster, 2002) are crucial for the inter-annual variability as well. Changes of the whole entity of these environmental constraints are reflected by the structure and dynamics of zooplankton communities on different timescales.

The biomass of dominant calanoid copepods changed pronouncedly during the last decades in the central Baltic Sea. Namely, *Pseudocalanus acuspes* was reported as the most abundant calanoid copepod during the 1980s in the Baltic proper south of Gotland (Witek, 1995; Postel et al., 1996). Since then, the abundance of this species decreased significantly, most likely as a result of decreasing salinity due to less frequent saltwater inflows (Lass & Matthäus, 2008; HELCOM, 2009). At the same time, warmer thermal conditions during the 1990s have positively affected the thermophile calanoid copepods *Temora longicornis* and *Acartia* spp., which increased in their abundance in the central and northern Baltic Sea (Dippner et al., 2000; Möllmann et al., 2000; Aleksandrov et al., 2009; HELCOM, 2009).

The negative trend of salinity and the positive trend of water temperature in the Baltic Sea since the 1980s have also affected the long-term dynamics of cladocerans, even though these trends for the latter zooplankters were less significant than for copepods. In the 1990s through the 2000s, the density and biomass of cladocerans increased, for instance, in the south-eastern Baltic Sea. Higher water temperatures

create favorable conditions for the development of the thermophile *Bosmina* spp. in summer and the eurytherm *Evadne nordmanni* in spring (Aleksandrov et al., 2009). Further to the north, in the Gotland Basin, these trends are less pronounced. A slight rise in the summerly abundances of *Bosmina* spp. were reported between the 1960s and 1980s. However, this trend did not continue in later decades (Möllmann et al., 2002). Similarly, spring abundances of *E. nordmanni* and *Podon* spp. increased between the 1960s and 1990s (Möllmann et al., 2002).

Recent investigations show that currently an area of about 65% of the Baltic Sea surface water (including the Gulf of Bothnia) has sea surface salinity of less than seven. However, according to the projected models, virtually the whole Baltic Sea surface layer will have the salinity of horohalinicum after some decades with proceeding climate change, while species distribution will change accordingly (Rajasilta et al., 2014; Vuorinen et al., 2015). Considering this trend, it is especially important to obtain the precise data on the actual zooplankton species composition, abundance, biomass and productivity, which is essential for the prognostic modelling of the future biological diversity and the ecosystem stability in the Baltic Sea.