CHAPTER 8

Interactions in Plankton Food Webs

Seasonal Succession and Phenology of Baltic Sea Zooplankton

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8.1 Introduction

In the world's largest ecosystems, the oceans, marine plankton form complex communities and interact in many different ways (Lima-Mendez et al. 2015). Food web interactions determine the transfer of energy from primary producers to higher trophic levels, cycling of carbon and energy within the pelagic system, and export of pelagic production to the seafloor, and thus global biogeochemical processes (Falkowski et al. 1998, Steinberg and Landry 2017). Zooplankton perform an important ecosystem service as the main group of grazers on the pelagic primary production and as the main prey of fish, and therefore link lower and higher trophic levels of aquatic food webs. In some systems, the zooplankton level also comprises the largest standing biomass across groups, larger than both the primary producers lower in the food web, and fish and other predator levels higher in the web (Gasol et al. 1997). Zooplankton, particularly copepods, are the major food source for commercially important fish in marine systems, and by grazing on phytoplankton, zooplankton also control phytoplankton and their blooms.

Plankton communities are formed by a large diversity of taxa from viruses, heterotrophic prokaryotes and other unicellular organisms, including flagellates, ciliates to multicellular organisms such as rotifers, diverse crustaceans from copepods to shrimps, chaetognaths and jellyfish. Planktonic organisms range from around 0.02 µm to 200 cm (Sieburth et al. 1978, Steinberg and Landry 2017) (Fig. 8.1), varying with more than six orders of magnitude. The majority of biological activity (> 90%) in aquatic food webs takes place in microorganisms, which includes organisms feeding on at least four different trophic levels (Calbet and Landry 2004). For example, heterotrophic nanoflagellates eat picophytoplankton, that in turn are preyed upon by ciliates (microzooplankton) and further

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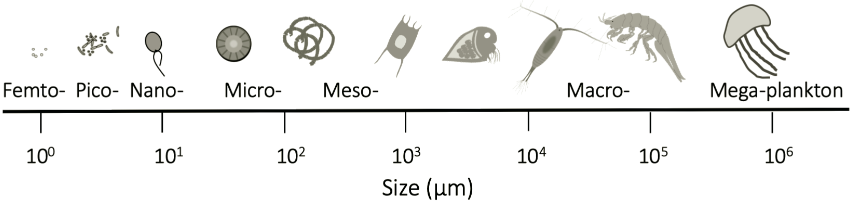

Figure 8.1: Size spectra of plankton illustrated using dominant species of the Baltic Sea. Size range from femto- (0.02–0.2 µm; e.g., viruses), pico- (0.2–2 µm; e.g., heterotrophic prokaryotes, picophytoplankton), nano- (2–20 µm; e.g., phytoplankton), micro- (20–200 µm; e.g., flagellates, ciliates), meso- (0.2–20 mm, e.g., cladocerans, copepods), macro- (2–20 cm; e.g., shrimps) to megaplankton (20–200 cm; e.g., jellyfish) (Sieburth et al. 1978).

consumed by copepods (mesozooplankton), and thus connect the microbial loop with the classical grazing food web (phytoplankton-zooplankton-fish) (Sommer et al. 2002, Basedow et al. 2016). In the interaction network, zooplankton have a key role by concentrating and channelling carbon and essential biochemicals from primary producers to upper trophic levels, such as fish (Varpe et al. 2005, Winder et al. 2017b).

While the seasonal succession of phytoplankton groups and their traits and driving mechanisms are much studied and well described (Sommer et al. 2012, 2017, Weithoff and Beisner 2019), the succession of zooplankton species and their traits is less well synthesized, which is probably a result of more complex behaviours, longer generation times and life cycles in zooplankton (Romagnan et al. 2015). For phytoplankton, increasing abundances are initiated by increasing sunlight and shoaling of the mixed-layer depth, referred to as the critical depth hypothesis (Sverdrup 1953), after intense vertical mixing that redistributes nutrients throughout the water column, although this has been challenged by the critical turbulence and disturbance-recovery hypotheses (Behrenfeld and Boss 2014). The seasonal development of zooplankton follows the spring phytoplankton bloom, with a succession from grazing to predatory organisms (Sommer et al. 2012). Autumn water-column mixing and reduced day length redistribute cells in the water column and terminate the annual succession. Phyto- and zooplankton seasonal succession and species replacement are affected by physical factors, nutrient or food limitation and biotic interactions, such as food quality, parasitism, or fish predation (Sommer et al. 2012, Behrenfeld and Boss 2014, Romagnan et al. 2015).

Understanding the seasonal succession of zooplankton, as well as their responses to changing environmental conditions, requires detailed knowledge of their population dynamics through the annual cycle as well as their interactions with food, competitors and predators. This is particularly so in temperate and polar systems where seasonal cycles of pelagic production are strong.

Zooplankton diversity is large also with respect to life history traits, morphologies, behaviours and feeding modes. Studying the evolutionary drivers behind this diversity, and the underlying trade-offs that have shaped them, is important to understand how different species perform in a seasonal environment, how they interact, and during which periods they are present and abundant. In seasonal environments, the timing of life history events within the annual cycle and their timing with regard to ecological processes require particular attention. This study is called phenology, a word also increasingly used for the actual timing, such as breeding phenology or diapause phenology.

In this chapter, the seasonal aspects of interactions between primary consumers and zooplankton are highlighted and the resulting annual cycles of zooplankton dynamics described. The foci are intra-annual population dynamics as well as the degree that these patterns repeats themselves between years. Particular attention is given to the treatment of temporal interactions in planktonic food webs, the role of phenology and the accompanying life history adaptations to seasonality. Observed dynamics are in turn related to life history traits, likely ecological drivers and environmental constraints. The Baltic Sea is used as a case study. The Baltic Sea is a strongly seasonal ecosystem and one of the best studied brackish water ecosystems with extensive multi-year monitoring programmes, including several stations with sampling designs that have high sampling frequency (Griffiths et al. 2017, Reusch et al. 2018). Such resolution is needed for solid work on plankton phenology (Ji et al. 2010, Mackas et al. 2012) and for comparing model predictions on seasonal timing and life histories with data (Varpe 2012). The Baltic Sea stretches over a considerable latitudinal gradient (about 13 degrees) with strong gradients in temperature and salinity, allowing rich opportunities for illustrating how varying seasonality and physical conditions impact zooplankton (Snoeijs-Leijonmalm et al. 2017).

8.2 Zooplankton Trophic Pathways

Plankton community structure determines energy availability for higher trophic levels (Stibor et al. 2004), global biogeochemical cycles (Litchman et al. 2015) and remineralization of macronutrients (Calbet and Landry 2004). The aquatic food web, the pelagic one in particular, is often size structured where small organisms are eaten by larger ones (Barnes et al. 2010) (Fig. 8.2). The size ratio between primary consumers and phytoplankton is typically assumed to be 10.1 (Hansen et al. 1994); however, prey size vary among different predator groups, and the ratio is smaller within microbial organisms and higher for mesozooplankton species. Consequently, several trophic levels separate small phytoplankton cells from the larger zooplankton organisms (Stibor et al. 2004). There are, however, exceptions to the size-structured food web where predators are smaller than prey, such as pallium feeding (Jacobson and Anderson 2008) or peduncle-feeding heterotrophic dinoflagellates (Ok et al. 2017). Or prey may be orders of magnitude smaller than themselves within mesozooplankton, such as mucous-mesh grazers (e.g., appendicularians, pelagic tunicates) (Conley et al. 2018).

Within the microbial loop, bacteria are being grazed by heterotrophic nanoflagellates (HNF), which together with small-sized phytoplankton cells are being grazed upon by microzooplankton, which are then prey for mesozooplankton. Lager-sized phytoplankton, however, forms a more direct route, the classical algae-zooplankton-fish link (Fig. 8.2). Part of this production is recycled within the

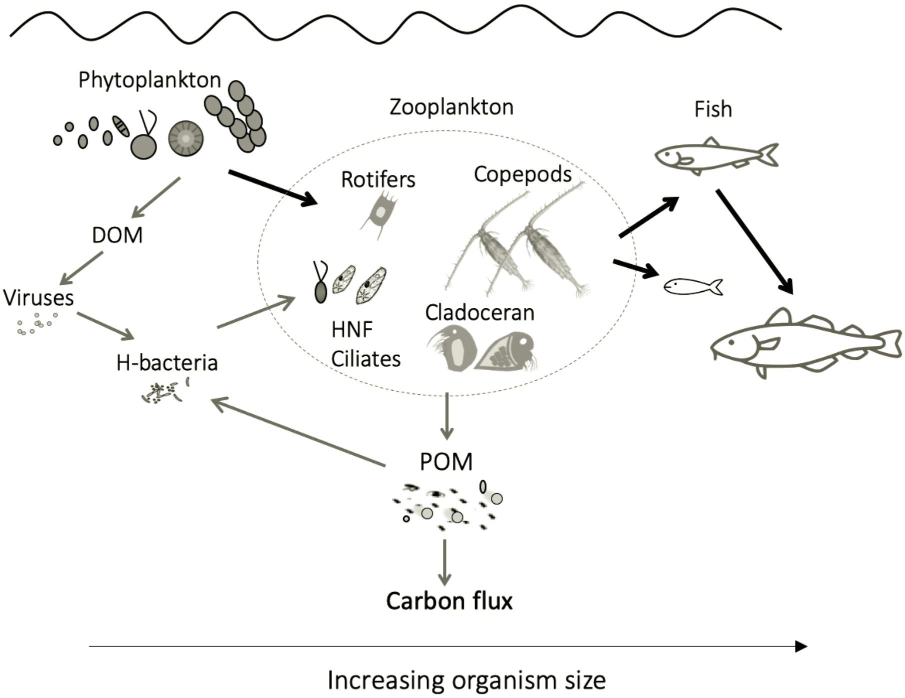

Figure 8.2: A basic model of the pelagic food web with key players, illustrated using dominant taxonomic groups of the Baltic Sea. Trophic (black), detrital (grey) pathways and sedimentation to the seafloor are shown. Organism size increases from left to right. Trophic interactions within the zooplankton assemblage (dashed line) are not shown. DOM = dissolved organic material, POM = particulate organic material, H-bacteria = heterotrophic prokaryotes, HNF = heterotrophic nanoflagellates.

detrital food web through non-living organic matter that is leached out from all organisms (dissolved organic material, DOM) or derived from plant and animal tissue, such as discarded appendicularian houses and crustacean exoskeletons after moulting, or faeces and classified as particulate organic matter (POM) (Fig. 8.2). This non-living organic matter is returned to the food web through its incorporation into bacterial biomass that in turn is grazed by protists or deposited to the seafloor. In addition, mixotrophic organisms that are capable of both photosynthesis and phagotrophy, or the combination of both primary and secondary production in the same organisms, are common within protists, consequently altering carbon and energy flows in food webs (Flynn et al. 2019). Thus, plankton is characterized by a multitude of trophic and non-trophic interactions at the microbial scale (Lima-Mendez et al. 2015, Basedow et al. 2016).

Size-structured trophic interactions imply that the size structure of the phytoplankton community is an important factor determining carbon flow as it affects the relative importance of the microbial and classical food web and consequently food web length and transfer efficiency of zooplankton to upper trophic levels. The size structure of the phytoplankton community is in turn controlled by the supply of growth-limiting dissolved inorganic nutrients, such as nitrogen or phosphorus (Sommer et al. 2002). Under oligotrophic condition, small cells of primary producers have a relative advantage due to their larger surface to volume ratio that facilitates nutrient uptake, compared to larger cells (Falkowski and Oliver 2007). Under eutrophic conditions, the selective pressure for small size is reduced and larger-sized phytoplankton or colony forming species dominate (Sommer et al. 2002). In oligotrophic and eutrophic systems with poorly edible phytoplankton blooms, up to 75% of the daily primary production is transferred within the microbial loop (Landy and Calbet 2004). This implies that the majority of production occurs at the lower end of the size spectrum.

Aquatic food webs are characterized by low transfer efficiency of matter and energy across trophic levels, which is in the range of about 10–20% because of respiration, excretion, egestion or sloppy feeding between trophic levels (Sommer et al. 2002). Given a predator prey size ratio of 10, for consumers in the 1 mm size range, such as copepods occupying trophic level three, less than 1% primary production remains available. Assuming the rules of ecological efficiency, an increase in transfer efficiency is expected with an increasing contribution of larger phytoplankton cell sizes and thus in more productive regions compared to nutrient poor regions. However, other factors than size influence carbon transfer efficiency within the plankton food web, such as food quality, mixotrophy or patchiness. Food quality, including essential macromolecules for consumers that are produced by phytoplankton such as polyunsaturated fatty acids or sterols, varies greatly among phytoplankton organisms and major taxonomic groups (Galloway and Winder 2015). Phytoplankton consisting of species high in essential compounds increase transfer to upper trophic levels (Burian et al. 2019). Common among microzooplankton are mixotrophic plankton that can simultaneously exploit inorganic resources and living prey (Stoecker et al. 2009, Flynn et al. 2019), which enhance trophic transfer (Ward and Follows 2016). In addition, micro-scale variability in plankton distribution (patchiness) and predator-prey overlap enhances trophic transfer in oligotrophic oceans (Priyadarshi et al. 2019).

There are also alternative pathways from primary producers to higher trophic levels. For example, some mesozooplankton, like the cladoceran *Bosmina* are able to feed directly on heterotrophic prokaryotes (bacteria and archaea), reducing the number of trophic steps and energy loss within the microbial loop (Sommer et al. 2002). Filamentous and toxic cyanobacteria are less edible and digestible for zooplankton (Sommer 1989) and the energy (carbon) is reaching higher trophic levels via the microbial food web through cell lysis and excretion, which reduces energy transfer to higher trophic levels by including additional trophic levels.

Nutrient availability and consequently phytoplankton cell size and food web structure are strongly affected by climate change, which affects vertical mixing of the water column (Falkowski and Oliver 2007, Winder and Sommer 2012). Increasing temperature is strengthening vertical stratification and decreasing nutrient supply to the photic zone due to reduced mixing, which is favouring small-sized phytoplankton in oligotrophic regions (Winder et al. 2009a, Winder and Sommer 2012) and is expected to enhance carbon cycling within the microbial loop. In systems with high dissolved phosphorus availability and nitrogen limitation, such as the Baltic Sea, warming favours filamentous cyanobacteria that are able to fix atmospheric nitrogen (diazotrophs, e.g., *Nodularia*) (Paerl and Huisman 2008). Filamentous cyanobacteria are assumed to be less edible for zooplankton organisms and carbon then enters the food web via bacterial decomposition and the microbial loop (Loick-Wilde et al. 2019).

8.3 Zooplankton Life Histories and Adaptations to Seasonality

As for any organism, zooplankton species cannot maximize all traits that contribute to fitness. Instead, there are trade-offs, for instance between offspring size and numbers, adult body size and survival, and between growth and reproduction (Stearns 1992). A large range of solutions to these trade-offs have evolved, giving rise to biodiversity. Allan (1976) illustrated this variation in his analysis of growth rates and life history traits in zooplankton. He focused on the major groups of rotifers, cladocerans, and copepods. These three groups are also among the most central zooplankton groups in the Baltic Sea. In Allan's analysis, rotifers have the highest potential for population growth among the three groups, achieved particularly through short development times from egg to first reproduction. Adult body size is also smallest in the rotifers. Cladocerans are similar to the rotifers with respect to several life history traits, but longer developmental times lead to somewhat lower maximum intrinsic rate of increase, despite higher fecundity and longer lifespan in the cladocerans. Both rotifers and cladocerans have parthenogenetic reproduction when conditions are favourable. Copepods have considerably lower growth potential because of longer developmental times combined with larger adult body size. Copepods have few or only one generation per year and may even use multiple years to reach maturity and reproduction. Also, copepods always reproduce sexually, whereas sexual reproduction in rotifers and cladocerans primarily takes place when resting eggs are produced at the onset of unfavourable conditions.

Allan (1976) stressed the link between life history traits and the seasonal fluctuations of zooplankton, a focus also adopted in this chapter. This section gives a brief overview of life history traits that are important for understanding zooplankton adaptations to seasonality and for interpreting phenology and population dynamics in seasonal environments. In doing so, annual routines are referred to as an organism's regular schedule of activities or behaviours over the annual cycle (McNamara and Houston 2008). The concept of annual routines helps clarify how different activities over the year are linked and how changes in one activity usually lead to changes in others through temporal trade-offs. From an evolutionary perspective, it can be asked what the optimal annual routine would be given the environment (McNamara and Houston 2008, Varpe 2012) and how it may change in response to environmental change, as well as the consequences of no response to expected change (Feró et al. 2008). The ability of zooplankton to respond to changed seasonal timing of food availability vary depending on life history strategy (Winder and Schindler 2004b).

Schematically speaking, it can be useful to group zooplankton adaptations to seasonality as related to two parts of the year: the unproductive part when food is low (often winter like conditions), or productive part when food is high (Varpe 2017). The distinct seasonality of primary production observed in higher-latitude environments (Winder and Cloern 2010, Ji et al. 2013) exemplifies such productivity regimes, and many life history adaptations of zooplankton have evolved in response. The food availability for zooplankton in the Baltic Sea is also highly seasonal (Hjerne et al. 2019).

The unproductive period is usually spent in one of two main forms: a seed like stage, usually referred to as resting eggs, or as a well-developed juvenile or an adult stage. Resting eggs, and the accompanying embryonic dormancy, is common across many taxa including rotifers, copepods and cladocerans (Marcus 1996, Holm et al. 2018). Resting eggs usually sink to the bottom and are in the sediments until hatching, typically prior to the next productive season. However, resting eggs can live long and do not necessarily hatch before after several years (De Meester 1993). Hence, they form the analogy to a seed-bank, which is viewed as a bet-hedging strategy. Resting eggs can for instance remain viable in anoxic sediments and reoxygenation of anoxic sediments activates a large pool of buried zooplankton eggs (Broman et al. 2015). Furthermore, resting eggs have not only evolved as an adaptation to low food availability. Harsh conditions, such as warm or cold temperatures have also been highlighted, both as proximate and ultimate driver (Holm et al. 2018). Furthermore, some species may enter dormancy to avoid periods of high predation risk, such as the summer diapause in some daphnids (Pijanowska and Stolpe 1996). Diapause during summer may also be selected because of warm waters (Chinnery and Williams 2003) or a food bottleneck caused by competition from other species (Santer and Lampert 1995). There are different forms of resting eggs and dormancy. These can be viewed as a continuum from quiescent (facultative) to diapause (obligatory), terms adopted from the literature on insect diapause (Danks 2002). Quiescent eggs are arresting development in direct response to unfavourable conditions but are also resuming development once conditions are favourable again. Diapausing resting eggs on the other hand are produced in order to remain in arrested development for a period of time and may require other cues to get activated—such as photoperiod. Diapausing resting eggs are common in cladocerans and rotifers and require a cooling period before development can resume (Viitasalo and Katajisto 1994). Copepods produce either quiescent eggs that are prevented from hatching by environmental conditions or true diapausing eggs that require a resting period before hatching can proceed (Viitasalo and Katajisto 1994).

The alternative to resting eggs is to spend the unproductive season in a near mature or even adult stage. In many of the world's oceans, such overwintering is found in calanoid copepods (Conover 1988, Atkinson 1998), then often combined with a seasonal migration to great depth. Predator avoidance is regarded a key benefit of the migration, along with metabolic benefits, including metabolic dormancy, and possibly benefits regarding where water currents keep or bring the individual (Kaartvedt 2000, Irigoien 2004, Varpe 2012). The seasonal migration to deeper waters is accompanied by considerable energy storage to fuel metabolic needs during the unproductive winter (Record et al. 2018). Some species may even carry reserves to fuel reproduction after or towards the end of the overwintering period, hence they are capital breeders (Varpe et al. 2009). Even larger and longer-lived zooplankton, such as krill, display several of the same adaptations, notably large body size, wintering in mature stages, and energy storage (Hagen 1999).

The productive season is either started as a well-developed stage that can reproduce early, or in the case of the resting egg solution, as individuals that need time to develop and grow before maturity and the first reproductive spell. Depending on season length and life history, there may be many generations per season, one generation as in the case of an annual life cycle, or it may take more than a year to complete a generation. Many zooplankton species are small and with relatively large growth potential, and able to have multiple generations per year, such as the smaller microzooplankton. Their potential for rapid population growth could lead to top-down control of their food source, the phytoplankton (Landry and Calbet 2004, Boyce et al. 2015). Other forms have one generation per year, but with potential for two generations if conditions change, such as reported for a calanoid copepod (*Leptodiaptomus ashlandi*) in response to climate warming induced environmental changes in Lake Washington (Winder et al. 2009b). Zooplankton with slower growth, larger body size and a multi-year life span can, for instance, be found in colder high-latitude environments (Conover 1988). Some longer lived species are also iteroparous, in the sense that the same individuals may reproduce in consecutive years (Varpe and Ejsmond 2018). Zooplankton species with adult forms living for more than one year are, however, relatively rare.

In addition to seasonality in food availability, temperature clearly impacts growth and thereby annual routines and life histories. Growth and development are faster when water temperatures are higher, impacting key life history traits such as time from egg to first reproduction. Temperature variability also leads to other patterns of life history diversity, such as the intraspecific patterns of larger body size at colder temperatures because of unequal responses of growth and development rates to temperature (Forster and Hirst 2012).

Seasonal food availability often leads to time constraints on development (Sainmont et al. 2014). Interestingly, plastic responses can be expected in response to where in the season an individual is. The light environment may be one source of information organisms can use as cue to base such plasticity on (Johansson et al. 2001). The plasticity can include behavioural responses, such as increased feeding intensity towards the end of a season, but also life history responses such as reduced body size. Similar responses may arise in response to varying predation risk (Bjærke et al. 2014), hence it is also important to understand how risk may vary over the year and through the productive period (Varpe and Fiksen 2010). There are multifaceted predictions on the interactions between environmental conditions (food availability and risk) and life history traits such as body size, energy storage and voltinism (Ejsmond et al. 2018). For instance, as a consequence of fitting more generations into one feeding season, the prediction is that body size will decline and that the potential for energy storage thereby is reduced (Ejsmond et al. 2018).

Some species are also zooplankton only for a relatively short period of their life, and benthic for the rest of their life. This group is called meroplankton. They are planktonic as young, and during a relatively brief time-window within the productive season, before they settle at the seabed. Bivalves, barnacles, snails, crabs or eggs and larval stages of nektonic organisms (e.g., fishes, shrimps) are examples of groups where many have a planktonic stage, with dispersal as the main adaptive value. The benthic form may grow larger and live longer, with indeterminate growth and thereby growth and reproduction co-occurring through large parts of life (Heino and Kaitala 1999).

8.4 The Baltic Sea—A Place where Freshwater and Marine Zooplankton Meet

8.4.1 General Description of the Baltic Sea

The Baltic Sea is a semi-enclosed postglacial sea with a surface of 415,000 km^2 stretching over large latitudinal (53º N to 66º N) and ecological gradients (Snoeijs-Leijonmalm et al. 2017) (Fig. 8.3). The Baltic Sea was gradually formed after the retreat of the ice during the last glaciation and is a young sea, some 14,000 to 10,000 years old. It consists of different basins that vary in temperature, salinity and food web structure, such as primary production or terrestrial carbon input (HELCOM 2007). Besides a strong temperature gradient, the Baltic Sea is also characterized by a strong salinity gradient from near freshwater (salinity of 2) in the innermost parts to marine water (salinity of 30) at the entrance to the North Sea and a permanent halocline that separates the surface water from the more saline bottom water at about 70 m depth (Carstensen et al. 2014). The Baltic Sea is a shallow sea with an average water depth of 58 m and maximum depth of 459 m (Fig. 8.3), and a water residence time above 30 years (HELCOM 2007).

The Baltic Sea has high productivity with intensive fisheries that contributes to 1.2% at a global scale despite its small area (0.11% of the total ocean). Primary productivity is changing along the latitudinal gradient with about 10 times higher primary production in the southern parts compared to the northern parts, primarily due to higher terrestrial input of dissolved organic carbon and reduced underwater light in the north, while heterotrophic prokaryote production varies less along this gradient (Andersson et al. 2017). This results in over 50% bacterial production at the base of the food web in northern basins due to high terrestrial carbon inflow and low phosphorus availability (Sandberg et al. 2004). In addition, there is a strong gradient in eutrophication and reduced phosphorus levels towards the Bothnian Bay, reducing primary production in the north (HELCOM 2009a).

The Baltic Sea is an area that experienced warming over the last century with 1.5ºC between 1871 and 2011 during the spring season (The BACC Teach 2015), which is high compared to other marine areas (Reusch et al. 2018). This effect of global warming has led to many related alterations of the physical environments, such as strengthening of vertical water stratification, expansion of anoxia and sea ice decline (Carstensen et al. 2014, The BACC Teach 2015, Liblik and Lips 2019). A

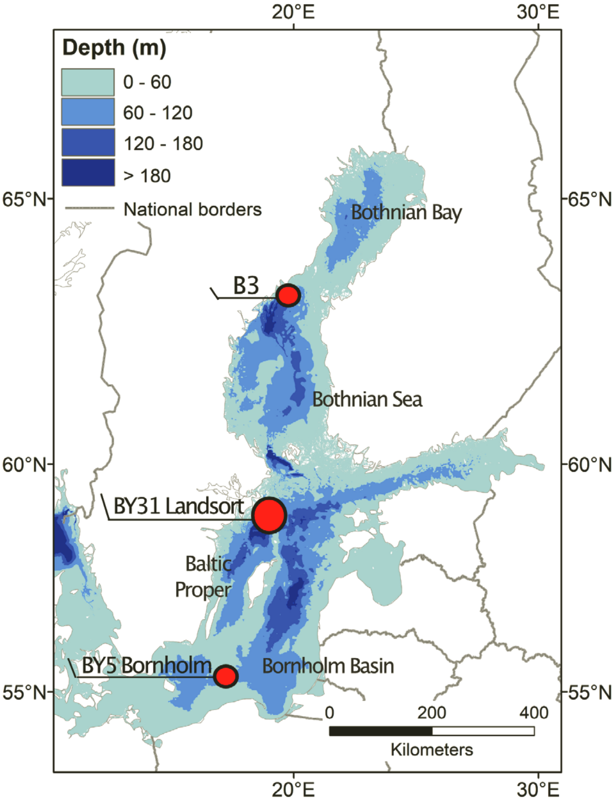

Figure 8.3: Bathymetry map of the Baltic Sea with location of zooplankton sampling stations and major basins. The Baltic proper BY31 Landsort Deep station (large filled circle) is the main focus of this study. The southern Baltic proper station BY5 Bornholm basin and the northern station in the coastal Bothnian Sea B3 are used for spatial comparisons (small circles).

multitude of anthropogenic stressors, including eutrophication, harvesting, and pollutants, have also led to rapid alterations of the system. Environmental conditions also affect zooplankton dynamics, with temperature, food availability and predation pressure being important drivers, which affect abundances of key zooplankton species (Möllmann 2000).

8.4.2 Zooplankton Species Composition of the Baltic Sea

The taxonomic diversity of zooplankton in the Baltic Sea is relatively low due to the young age of the sea and because only few species are endemic to brackish conditions in general, which also holds for the Baltic Sea (HELCOM 2009b, Ojaveer et al. 2010). In this brackish water environment, both limnic and marine species meet their physiological limits. In addition, the strong gradient in salinity and temperature forms physical, physiological or resource-related barriers for crustacean zooplankton to spread (Viitasalo et al. 1990, Vuorinen 1998). Low diversity, however, suggests that species redundancy is in general low and that new introduced species can have big impacts on the ecosystem.

Nano- and Microzooplankton

Phagotrophic protists, including heterotrophic nanoflagellates (HNF; 2–20 µm), dinoflagellates and ciliates ranging in size from about 1 µm to greater than 100 µm are the most numerous and species rich group of zooplankton, both in the Baltic Sea and more generally (Ojaveer et al. 2010).

Phagotrophic protists are important grazers of heterotrophic prokaryotes and picophytoplankton. Their contribution to total zooplankton biomass might be relatively low, but phagotrophic protists contribute substantially to grazing, often consuming more than 50% of the primary production, and carbon cycling within the microbial web can contribute substantially to carbon and nutrient turnover (Sherr and Sherr 2002, Landry and Calbet 2004, Schmoker et al. 2013).

Rotifers are diverse and abundant in the Baltic Sea, as in other coastal and estuarine systems and diversity and abundance decrease with increasing salinity given the freshwater origin of this group (Ojaveer et al. 2010). Two rotifer genera, *Keratella* spp. and *Synchaeta* spp. are most abundant in the central Baltic Sea and can at times dominate the zooplankton assemblage in abundance.

Mesozooplankton

The dominant mesozooplankton groups by biomass in the Baltic Sea are cladocerans (Cladocera) and copepods (Copepoda) (Ojaveer et al. 2010). Cladocerans include the fresh and brackish-water *Bosmina coregoni* as well as the marine cladoceran *Evadne* (dominated by *E. nordmanni* and the less abundant *E. anonyx* species) and *Podon* spp. The introduced carnivorous cladoceran *Cercopagis pengoi* (Ojaveer et al. 2010) appears sporadically in the water column. Small to medium sized (0.6–1.5 mm) copepod species dominate in terms of abundance: *Temora longicornis*, *Eurytemora affinis*, *Acartia* spp. and *Pseudocalanus* spp., and to lesser extent *Centropages hamatus* and *Limnocalanus macrurus* in the low salinity region.

The calanoid copepod *Temora* is a euryhaline and eurythermal species with a wide geographical distribution ranging from sub-tropical to sup-polar coastal marine waters (Continuous Plankton Recorder Survey Team 2004). In the Baltic Sea, this species occurs at its physiological salinity limits and occurs primarily in offshore waters (Viitasalo et al. 1995, Ojaveer 1998). *Temora* is a broadcast spawner and overwinters as active copepodite stages in the water column with no signs of resting stages.

Eurytemora affinis is a euryhaline zooplankton species with a wide distribution in the Northern hemisphere and a dominant species in coastal and estuarine systems, commonly inhabiting brackish waters (Winkler et al. 2011). This species occurs across a wide range of salinities, from freshwater to marine systems (Viitasalo et al. 1994, Lee 2016). This is an egg-carrying species and females carry eggs in a sac until hatching. This copepod is thought to produce diapausing eggs in autumn in the Baltic Sea that overwinter in the sediment (Katajisto et al. 1998). Egg clutch size of this species seems to be unaffected by salinity and temperature, while hatching success is reduced at lower salinity (Karlsson et al. 2018). *E. affinis* is an important grazer and central prey for fish in the Baltic Sea (Diekmann et al. 2012).

Three species of *Acartia* occur in the Baltic Sea, *A. bifolosa*, *A. longiremis* and *A. tonsa*. This copepod is a broadcast spawner and eggs of *Acartia* are found in the sediment, suggesting that a large proportion of eggs spawned by females reach the bottom prior to hatching (Katajisto 2003). Egg production with maximum values of 12 eggs female^{-1} day^{-1} is in general low in the Baltic Sea (Koski et al. 1999). It is thought that *A. bifolosa* produce resting eggs in the Baltic Sea in the form of quiescence, with no obligatory diapausing phase. Egg hatching is thought to occur throughout the year in the Baltic Sea and the hatching success is dependent on bottom temperature, which also affects the development rate of the eggs (Katajisto 2003).

The larger-sized copepod *Pseudocalanus* spp. (mainly *P. acuspes*) is regarded as a glacial arctic relict in the Baltic Sea and is most abundant in deeper water layers below the halocline (Renz et al. 2007). Lower abundances of this species are typically observed in years with low salinities (Möllmann 2000). Egg production of *Pseudocalanus* is highest in April reaching up to 3.6 eggs female^{-1} day^{-1} and is strongly related to food availability during the spring bloom (Koski et al. 1998, Renz et al. 2007). This copepod is an important prey for larval and adult planktivorous fish such as sprat and herring (Möllmann et al. 2003).

Other, less abundant copepod species include the marine larger-sized (ca 1.4 mm) copepod *Centropages hamatus*, which has a coastal distribution pattern (Durbin and Kane 2007) and reaches relatively low abundances in the Baltic Sea, but can at times be an important prey for planktivorous fish (Saage et al. 2009). The copepod *Limnocalanus macrurus* dominates in the Bothnian Bay and Bothnian Sea and with a carnivorous diet in the later copepodite stages (Dahlgren et al. 2012). As a cold-stenothermic species, it prefers temperatures below 11ºC and occurs mainly below the thermocline (Hutchinson 1967). Similar to many high-latitude copepods, this species stores lipids in the form of wax esters (Vanderploeg 1998), which are used for metabolism as well as reproduction in winter to early spring (Dahlgren et al. 2012). Stored wax esters give *Limnocalanus* the possibility to survive starvation periods and reproduce at low food levels (Hirche et al. 2003).

Appendicularians, like *Oikopleura dioica* and *Fritillaria borealis*, appear occasionally in the zooplankton assemblage in the central Baltic Sea, but do not form extensive blooms as in the oceans (Ojaveer et al. 2010, Andersson et al. 2017).

Macroplankton and Megazooplankton

Macrozooplankton is mainly represented by Cnidaria (jellyfish) with the most dominant species being the scyphozoan *Aurelia aurita* that occurs throughout the Baltic Sea and the lion's mane *Cyanea* spp. that are restricted to the more saline waters (Andersson et al. 2017). Comb jellies, Ctenophora, are also present in the Baltic Sea, including the non-indigenous *Mnemiopsis leidyi*. Additional macrozooplankton species are mysids that reside close to the seafloor during the day and ascend in the water column during night (Rudstam et al. 1989). Other macrozooplankton forms common in true marine systems, including chaetognathes, krill and shrimps, are absent from the central Baltic Sea (Ojaveer et al. 2010), and appear occasionally at the entrance of the Baltic Sea after penetration of more saline Atlantic oceanic water bodies (Telesh et al. 2008). Given the absence of these groups, it can be expected that top-down control on mesozooplankton is mainly dominated by fish predation rather than invertebrates. Selection pressures to avoid visually searching predators, such as through diel vertical migration, transparency or small body size should therefore be particularly strong in the Baltic Sea.

Meroplankton

Meroplanktonic groups, including eggs and larvae of benthic and nektonic organisms, are occasionally important components of the zooplankton assemblage. These include mainly planktonic larvae of bivalves (*Macoma balthica*, *Cerastoderma glaucum*, *Mya arenaria*, *Mytilus trossulus*), gastropods, polychaetes and the bay barnacle *Amphibalanus improvises* (Andersson et al. 2017). As such, meroplankton is not a separate size class but spans across the micro-, meso- and macrozooplankton range.

8.5 Seasonal Monitoring, Methods and Environmental Conditions

The responses of plankton species and communities to environmental conditions set the framework for food web interactions that ultimately determine the transfer of energy and nutrients to higher trophic levels. The temporal dynamics of plankton communities are integral to understanding the function of planktonic food webs. The seasonal development and its environmental factors control plankton community dynamics and composition, which is often an annually repeated process depending on biotic community interactions (predation, herbivory, or competition), reproduction, resource availability and top-down control by predation (Winder and Cloern 2010, Sommer et al. 2012). Continuous monitoring programmes over an extended period of the year are needed to understand the complex seasonal patterns of environmental conditions and plankton communities, including interannual variability and how variables respond to changes in the environment (Ji et al. 2010, Cloern et al. 2016).

Seasonal dynamics in the Baltic Sea are here illustrated using a pelagic monitoring dataset with high temporal resolution from monthly sampling during the winter (November–February), weekly during the spring bloom (March–April) and bi-weekly during the remaining season over a decadal time period (12 years; 2007–2018, for phytoplankton the time period 2007–2011 is used) at an offshore monitoring station in the northern Baltic Proper, the central part of the Baltic Sea (station BY31) with a depth of 495 m (Fig. 8.3). For phytoplankton, integrated water samples were taken with a sampling hose from 0 to 20 m depth and preserved with acid Lugol's solution (Hjerne et al. 2019). Phytoplankton > 2 µm were counted after sedimentation using an inverted microscope. Zooplankton samples were collected using a 90 µm-WP2 net with a closing system from the upper 0–30 m and 30–60 m water depth strata. For zooplankton species, data are shown from the upper 0–30 m where most of the species are most abundant, except for *Pseudocalanus* which is most abundant in the 30–60 m water column. Abiotic and chemical variables are measured at a 5 m depth interval from 0–30 m followed by a 10 m interval until 100 m and 25 m interval until 150 m (Hjerne et al. 2019). Seasonal dynamics are further compared to a more southern (southern Baltic proper, station BY5) and a more northern monitoring station (Bothnian Sea, B3) (Fig. 8.3) with a monthly sampling interval during the ice-free period and same sampling procedure. Sampling and counting of phytoplankton and zooplankton is described elsewhere (Telesh et al. 2008, HELCOM 2014). Data are available from the Swedish Meteorological and Hydrological Institute (SMHI) (http.//sharkdata.se/; https.//sharkweb.smhi.se/).

For plankton, seasonal variability in population dynamics and phenology are characterized by changes in abundances, timing of the seasonal peak and season duration (Ji et al. 2010). For the zooplankton assemblage in the Baltic Sea, three phenological indices for zooplankton were identified. Average summer abundance was defined between May and September and calculated for each year. The timing of the seasonal peak was defined as the centre of gravity of abundance, as applied by Edwards and Richardson (2004) and season duration as the number of days between the 25th and 75th percentile of the seasonal year-specific cumulative abundance (Ji et al. 2010). Data were daily linearly interpolated between observation days for calculating the indices, although it is acknowledged that this may not be the best strategy for weekly to monthly sampling frequencies.

8.6 Seasonal Dynamics of Environmental Conditions and Phytoplankton

In the Baltic Sea, physical and chemical conditions vary greatly over the course of the year. The winter period from November to February is typically characterized by vertical water-column mixing, low water temperature, dropping below 4ºC in the upper water column, and reduced light availability, as illustrated for the central sampling station BY31 (Fig. 8.4). Dissolved inorganic nutrients are typically well mixed over the entire water column, and winter mixing redistributes nitrogen (nitrate) from the deep water to the surface, reaching highest seasonal values between January and March (Fig. 8.4b). The northern Baltic Proper has experienced few ice winters over the last decade usually with fewer than 10 ice days, whereas several years in the 80s had close to 100 ice days (Hjerne et al. 2019).

Phytoplankton increases rapidly in March–April as a response to increasing light availability, water temperature (Fig. 8.4b) and water column stratification, resulting in marked spring bloom peaks that typically occur between mid to late April and are dominated by diatoms and dinoflagellates (Hjerne et al. 2019) (Fig. 8.5). As a consequence, dissolved nutrient concentrations (nitrate, phosphate) and Secchi depth are decreasing, while oxygen concentrations are at its highest. Salinity decreases slightly in March due to increased river inflow (Fig. 8.4b).

The summer period is characterized by steep vertical temperature and oxygen gradients, and a stratified water column with average temperature of about 15ºC in the upper 20 m during the

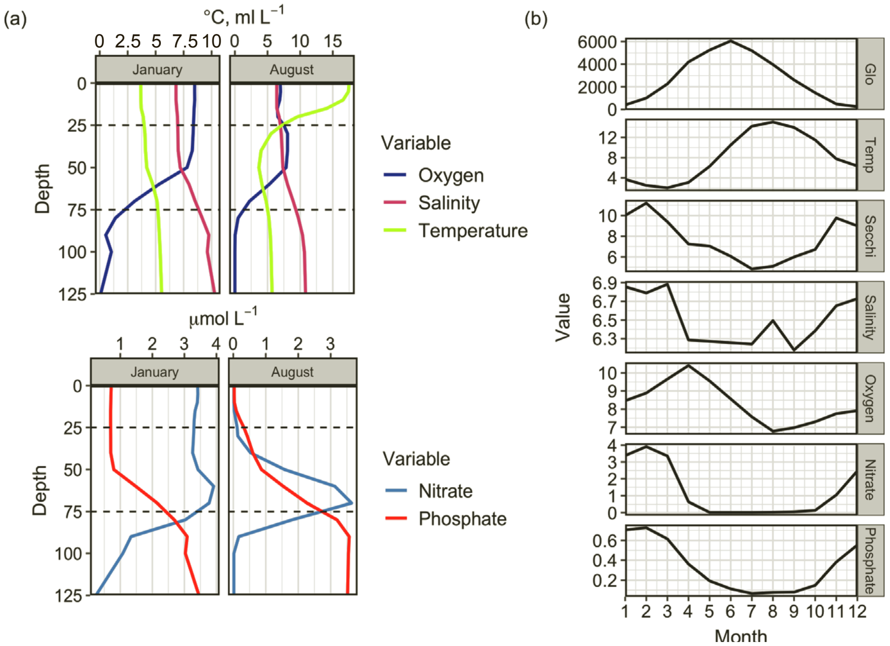

Figure 8.4: Physical and chemical conditions in the Baltic Sea station BY31. Shown are multi-year monthly averages of (a) vertical profiles of temperature (ºC), salinity, oxygen (ml L^{-1}), nitrate (nitrite + nitrate) (µmol L^{-1}) and phosphate (µmol L^{-1}) during January and August, representing the mixing winter and stratified summer period, respectively, and (b) seasonal patterns of global irradiance (Glo, W m^{-2}) as a proxy for PAR, temperature (ºC, Temp), Secchi depth (m), salinity, oxygen (ml L^{-1}), nitrate and phosphate (µmol L^{-1}) from the upper 20 m water strata. The two horizontal dashed lines in (a) represent approximately the upper and lower thermocline depth, respectively. Data are from 2007–2018 (Glo from 2007–2011, see Hjerne et al. 2019 for station description) available from the Swedish Meteorological and Hydrological Institute (SMHI) (https.//sharkweb.smhi.se/).

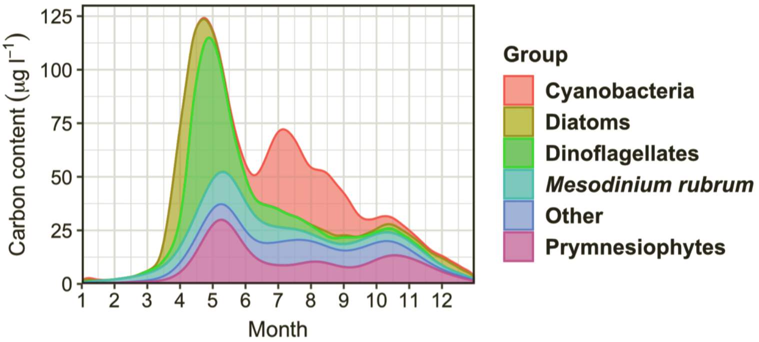

Figure 8.5: Average multi-year seasonal biomass dynamics of major phytoplankton taxonomic groups at the Baltic Sea station BY31. Phytoplankton data include the period 2007–2011 (available at https.//sharkweb.smhi.se/). Data are daily interpolated between observation days and smoothed using a kernel density estimate to generate the graph. The temporal resolution of the underlying sampling is monthly during winter (Nov–Feb), weekly during the spring bloom (Mar–Apr) and bi-weekly during the remaining season.

summer months from June/July to August (Fig. 8.4a). The euphotic zone reaches to about 10–20 m with the thermocline depth at about 25 m. Concentrations of nitrate and phosphate are low in the upper water column and increase with depth below the thermocline (Fig. 8.4). During the summer months, the phytoplankton assemblage is diverse but includes prominent cyanobacteria blooms, with *Aphanizomenon flos-aquae* and *Nodularia spumigena* as abundant species (Fig. 8.5).

8.7 Seasonal Dynamics of the Zooplankton Assemblage: Multi-year Average Perspective

Seasonal fluctuations in zooplankton abundance are a result of how annual routines and life history strategies interact with environmental conditions (Allan 1976, Varpe 2012). There is large diversity in strategies as well as in environmental conditions and preferences, leading to complex dynamics and interactions at the community level. Smaller and fast reproducing zooplankton often show higher temporal variability and sharp peaks, and rapid increases at the order of days, while temporal fluctuations of larger and slower reproducing species are more dampened (Klais et al. 2016).

In the Baltic Sea, the zooplankton assemblage shows strong seasonal fluctuations with distinct peak periods for the different taxonomic groups (Fig. 8.6). This seasonal cycle indicates a set of environmental conditions controlling population abundance, driven by temperature, food availability and predation. Seasonal plankton food web interactions are described below, and the annual cycle is used as a main structure to revisit life history strategies and trophic interactions. Four characteristic periods are identified that divide the annual cycle into: overwintering; stratification onset and the spring phytoplankton bloom period; summer stratification period and the dominance of cyanobacteria bloom; termination of stratification, decline in plankton productivity and onset of autumn mixing.

8.7.1 *Overwintering*

Zooplankton densities in the water column are typically low during the winter period, from November to February (Fig. 8.6), consisting mainly of nauplii and immature copepod stages, while adult stages

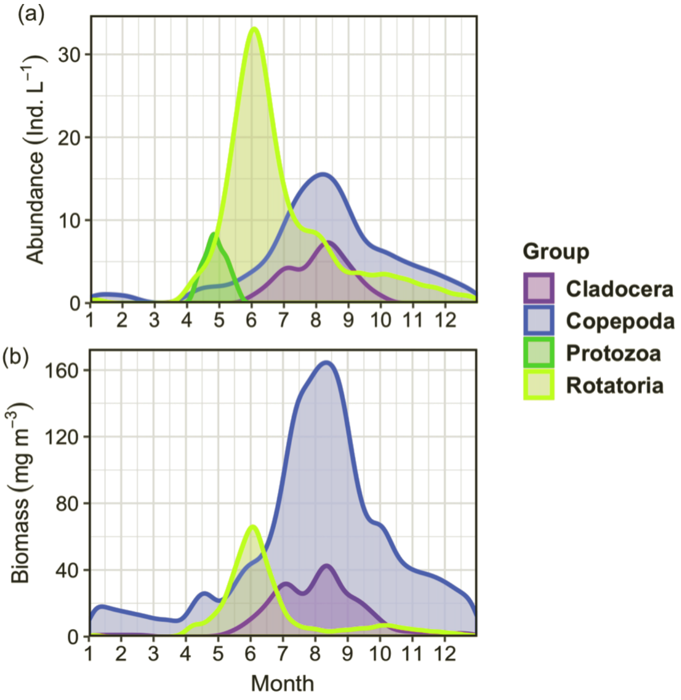

Figure 8.6: Average multi-year seasonal biomass dynamics of the major zooplankton taxonomic groups protozoans, rotifers, cladocerans and copepods at the Baltic Sea station BY31 for (a) abundance and (b) biomass (in wet weight). Protozoans only include the species *Radiosperma* sp. Zooplankton data include the period 2007–2018 available at (https.//sharkweb.smhi.se/). The temporal resolution of the underlying sampling is monthly during winter (Nov–Feb), weekly during the spring bloom (Mar–Apr) and bi-weekly during the remaining season. Data are daily linearly interpolated between observation days and smoothed using a kernel density estimate. Biomass data for *Radiosperma* sp. are not available.

occur in lower abundances (data not shown). Phytoplankton concentrations are low and food limitation affects zooplankton abundances. Cladoceran and rotifer abundances in the water column typically drop to zero, but *Bosmina*, *Synchaeta* and *Keratella* may occur in very low abundances below 0.03 ind. L^{-1} in some winters (Fig. 8.7a). These organisms are known to produce fertilized diapausing eggs at declining temperature and food availability, and eggs of both groups are observed in the sediment (Viitasalo and Katajisto 1994).

Some zooplankton species overwinter as active stages in the water column, but in low abundances such as for the copepods *Acartia* spp. (about 0.5 ind. L^{-1}), or *Temora*, *Eurytemora* and *Pseudocalanus* (with about 0.3 ind. L^{-1}) (Fig. 8.7b). This suggests continuous reproduction by a few individuals at low rate. Most copepods produce overwintering resting eggs and calanoid copepods are the most common eggs identified in Baltic Sea sediments (Viitasalo and Katajisto 1994), belonging to *Acartia* spp. and *Eurytemora*. *Temora*, on the other hand, is thought to hibernate in the water column during the winter as immature and adult stage. Occurrence of copepods in the sediment is also confirmed by metabarcoding analysis of Baltic Sea sediment showing that copepods, particularly *Eurytemora*, dominate DNA sequences in the northern Baltic Proper sediment, although *Temora* dominates in the southern Baltic Proper sediment (Broman et al. 2019). Copepod DNA in the sediment may derive from buried eggs, sinking remains from copepods such as carcasses, and faecal pellets.

Lipid reserves of overwintering copepod species are generally lower for the small-sized copepods in the Baltic Sea compared to the larger copepods of polar regions (Lee et al. 2006, Peters et al.

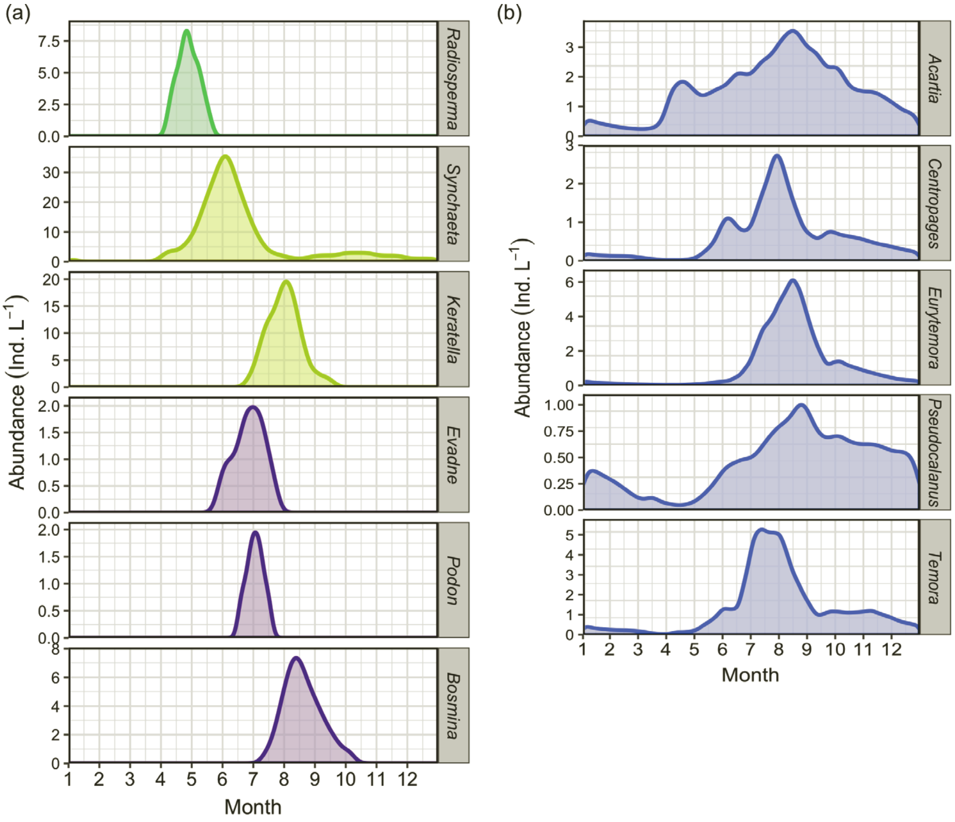

Figure 8.7: Average multi-year seasonal dynamics of zooplankton species abundances at the Baltic Sea station BY31. The left panel, (a) includes the protist *Radiosperma*, the rotifers *Synchaeta* and *Keratella* and cladocerans *Bosmina*, *Evadne* and *Podon*, the right panel (b) are copepod species. Zooplankton data include juvenile and adult stages over the period 2007–2018 available at (https.//sharkweb.smhi.se/). Data are daily linearly interpolated between observation days and smoothed using a kernel density estimate.

2013). *Temora* accumulates lipid reserves in autumn that may buffer against starvation during winter; however, the reserves (in the form of triacylglycerols) may suffice only for a few days or weeks. This suggests that copepods in the Baltic Sea either depend on food availability through the winter or rely on resting egg strategies, with lipid reserves playing a minor role for overwintering and reproduction (Peters et al. 2013), except for *Limnocalanus* (Dahlgren et al. 2012).

8.7.2 Stratification Onset and the Spring Phytoplankton Bloom Period

Phytoplankton spring blooms appear in March–April at low temperature (below 5ºC) (Figs. 8.4 and 8.5) at which development rates and generation times of zooplankton are long. Zooplankton develop in response to food availability and warmer temperature. Protozoans, represented by heterotrophic flagellates and ciliates, are the first ones that build up zooplankton biomass in spring (Arndt 1991) and can make up about 85% of the biomass of the zooplankton spring community (Johansson 2004). Bacterial heterotrophic production increases with the phytoplankton bloom (Bunse et al. 2019), followed by protozoans with brief delays and high abundances reached prior to the establishment of mesozooplankton (Arndt 1991). Protozoans depend on phytoplankton as food resource, either directly or indirectly via grazing on bacteria on phytoplankton. The small-sized protozoans are susceptible to much the same grazing pressures as the phytoplankton and abundances decrease with increase in mesozooplankton (Johansson 2004). Given that protozoan densities are close to zero over winter, the population likely rejuvenates from hatching of pelagic or benthic resting stages.

Radiosperma sp., a protist that was continuously observed in the monitoring, reflect this spring peak pattern and reaches highest abundances during the phytoplankton boom with up to 8 ind. L^{-1} (Fig. 8.7a). The spring peak in *Radiosperma* is short-lived and by June densities of this protist are close to zero. Similar to phytoplankton, protists have short generation times and can double within days. Protozoans also benefit from the spring-bloom condition with abundance of nano-sized phytoplankton prey and low predation by copepods (Johansson 2004). The sharp decline of these herbivores is most likely due to overgrazing of their food resource and suppression by mesozooplantkers that increase in abundance this time of the year (Arndt 1991, Johansson 2004).

Heterotrophic flagellates and ciliates are major consumers of the spring phytoplankton biomass (Arndt 1991) with an estimated ciliate consumption of 15% of the net primary production (Johansson 2004). Microzooplankton grazing may control spring bloom dynamics (Schmoker et al. 2013); however, the effect of phagotrophic protists grazing on seasonal phytoplankton patterns is thought to be minor, compared to cladocerans and copepods (Sommer et al. 2012). This is due to the fast response of protists to food availability and reduced potential of phytoplankton to escape top-down control, a prerequisite for blooms and subsequent crashes. In addition, the diet breadth of many phagotrophic protists species is smaller compared to mesozooplankton, and thus only suppresses specific prey groups. Regulation of phytoplankton dynamics by protists is dampened if predator-prey cycles are fast (associated with high growth rates) and phytoplankton species fall outside the preferred protists prey size. Regardless, phagotrophic protists may have a considerable grazing activity and a strong effect on phytoplankton species replacement, but less influence compared to mesozooplankton grazing (Schmoker et al. 2013, Menden-Deuer and Kiørboe 2016).

During the spring period, rotifers increase about at the same time as protozoans but their peak occurs with some delay. The dominant rotifer *Syncheata* spp. peaks in June, reaching average monthly densities of about 35 ind. L^{-1}, while *Keratella* spp. peak later in the season with average densities of up to 20 ind. L^{-1} in August (Fig. 8.7a). Generations most likely rejuvenate from hatching of benthic resting eggs as densities are very low during the winter season. The two most abundant rotifer species have different feeding behaviour. *Synchaeta* spp. is a predator and feeds mainly on dinoflagellates and ciliates, while *Keratella* spp. is a suspension feeder and preys on degraded detritus material but also ingests protists (Arndt 1993) and ciliates (Weisse and Frahm 2002).

The observed spring phytoplankton declines before the increase in dominating mesozooplankton grazers suggest that the clear water phase is mainly driven by microzooplankton grazing, nutrient limitation and subsequent acceleration of sinking particles. The transition period between the spring and summer phytoplankton bloom is characterized by a diverse community dominated by dinoflagellates, the mixotrophic ciliate *Myrionecta rubra* (formerly *Mesodinium rubrum*) (Hansen et al. 2012, Kim et al. 2016) and Prymnesiophytes (Fig. 8.5).

8.7.3 Stratified Summer Period and the Dominance of Cyanobacteria Bloom

The biomass increases of slower growing cladocerans and copepods are delayed until the stratification period between June and August, with highest abundances of crustacean zooplankton coinciding with the period of the cyanobacteria bloom (Figs. 8.5 and 8.6). Cladoceran abundances are low during the winter months and it is thought that the population rejuvenate from hatching of benthic resting eggs triggered by increasing temperature, light and oxygen or a combination of them (Kankaala 1983). Cladoceran taxa prevail during the summer period and reach densities up to 8 ind. L^{-1} or 40 mg m^{-3} in wet weight biomass (Fig. 8.6). *Evadne* spp. and *Podon* spp. are the first ones to increase in May–June with highest abundances during July with about 2 ind. L^{-1} and decline during August to low abundances (Fig. 8.7a). Abundances of *Bosmina* reveal a seasonal pattern with increase in July, and maxima in August up to 8 ind. L^{-1}, and decline towards September. The introduced carnivorous *Cercopagis* appears only sporadically during June and July at station BY31 (data not shown), likely due to its preference for warm waters.

Copepods exhibit a slow numerical growth response to increasing phytoplankton and temperature in spring, and typically peak during the summer months at BY31 with up to 17 ind. L^{-1} (including all copepodite stages and adults) and dominating the zooplankton biomass with up to 160 mg m^{-3} wet weight (Fig. 8.6). Their population increases coincide with an increase in temperature above about 10ºC. The copepods *Eurytemora* and *Temora* are the most dominant taxa of this group followed by *Centropages* and *Acartia* in the upper 30 m, while *Pseudocalanus* is dominant below 30 m, in the 30–60 m depth layer (Fig. 8.7b).

Temora persists throughout the year in the water column and develops slowly in spring. The development of the first generation is initiated by egg production of overwintering females, and nauplii typically dominate during the spring bloom in April (Dutz et al. 2010). Spring egg production is associated with low levels of storage lipid in *Temora*, and the triacylglycerol reserves that increase in autumn probably serve as a relatively short-term buffer against starvation during winter (Peters et al. 2013). Hence, *Temora* is an income breeder relying on phytoplankton for egg production (Dutz et al. 2012). At BY31, *Temora* abundances typically increase rapidly during June, reach peak abundance in July with about 5 ind. L^{-1} and the species remains in the water column throughout the summer (Fig. 8.7b). The number of generations produced by *Temora* depends on environmental conditions. In the southern Baltic Sea (Bornholm Basin), there are five to six generations a year as deduced from stage structure, copepodite length and stage duration (Dutz et al. 2012) (Fig. 8.8). Secondary maxima may occur in autumn dominated by nauplii or copepodite stages, typical for areas where *Temora* produces four to six generations per year (Digby, PSB 1950). Egg production of *Temora* is strongly affected by the low salinity in the Baltic Sea, and maximum production rates of 12 eggs female^{-1} are about 3–5 times lower compared to areas with higher salinity (> 30) (Holste et al. 2009). *Temora* is a suspension feeder primarily targeting non-motile prey (Tiselius and Jonsson 1990).

The copepod *Eurytemora* is thought to produce diapause eggs in autumn in the Baltic Sea that overwinter in the sediment (Tiselius and Jonsson 1990). At BY31, abundances of this species increase in June with peaks in August of about 6 ind. L^{-1} and densities decline to low abundances by November (Fig. 8.7b). *Eurytemora* shows a selective feeding behaviour on rotifers (Feike and Heerkloss 2009) suggesting that the relatively short period of seasonal durations is caused by this specialised interaction.

Acartia, particularly *Acartia bifolosa*, produces resting eggs in the Baltic Sea in the form of quiescence, with no obligatory diapausing phase (Katajisto 2003). Egg hatching is thought to occur throughout the year in the Baltic Sea and to depend on bottom temperature (that peaks in June),

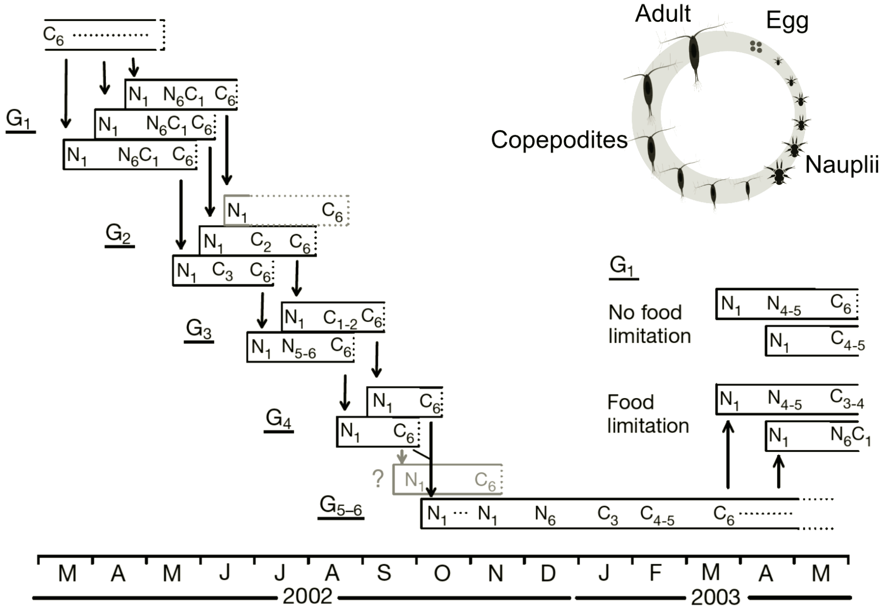

Figure 8.8: Schematic and hypothetical life cycle of *Temora longicornis* in the Bornholm Basin, Baltic Sea during March 2002 to May 2003 based on observed occurrence of nauplii and projected cohort development (after Dutz et al. 2010). The life cycle of copepods and its life stages are illustrated in the insert. Different generations or cohorts are indicated. The projection suggests that the species produced five to six generations in 2002. N = nauplii stage N1 to N6, C = copepodite stage C1–C5 and adult stage C6, G = generation 1–6. Adapted from: Dutz, J., V. Mohrholz and J. van Beusekom. 2010. Life cycle and spring phenology of *Temora longicornis* in the Baltic Sea. Mar. Ecol. Prog. Ser. 406: 223–238, with permission from Inter-Research.

which affects the development rate of the eggs. At BY31, *Acartia* spp. (mainly *A. bifolosa*) occur all year round in the water column and show smaller peaks (around 2 ind. L^{-1}) after the spring bloom and maximum peaks during the warm temperature season in late summer (August) with up to 3.5 ind. L^{-1}. Maximum densities of *A. longiremis* are typically in June, while *A. bifolosa*, the most abundant *Acartia* species, and *A. tonsa* develop peaks in July and August. Densities decline slowly after October and remain low during the rest of the year and at about 0.5 ind. L^{-1} over the winter (Fig. 8.7b). *Acartia* has a prey switching behaviour and is capable of both raptorial and filter feeding, consuming a broad size spectrum of prey from both the classical and microbial food web (Kiørboe et al. 1996, Engstrom 2000).

Pseudocalanus individuals are found in the water column year-round and abundances increase in June and peak during August with average densities of 0.5 ind. L^{-1} in the upper 30 m water column (data not shown) and higher values of 1 ind. L^{-1} in the depth stratum of 30–60 m at BY31 (Fig. 8.7b). Given the wide distribution of this species in the North Sea and Arctic, and its Arctic origin, it is assumed that *Pseudocalanus* is a glacial relict in the Baltic Sea (Ojaveer 1998). Seasonality of stage composition and growth measurements suggest that this copepod produces only one cohort over the annual cycle (Renz et al. 2007). Females show high seasonal variability in size and lipid content (Peters et al. 2006), suggesting that females mature from overwintering copepodite stages in early spring, a development and growth possibly fueled by storage lipids. This species is thought to have the same life cycle as *Pseudcalanus* spp. in the Arctic (McLaren et al. 1989) with high production in spring and the later developmental stages accumulating storage lipids in the form of wax ester, followed by overwintering and then maturation in early spring. Low abundances in late winter and early spring suggest considerable mortality associated with this pelagic overwintering. Seasonal fatty acid analysis indicates an opportunistic feeding behaviour and high dominance of ciliates in the diet (Peters et al. 2006) as well as feeding on sinking detritus particles.

Population densities of the larger-sized (ca. 1.4 mm) copepod *Centropages* increase after the spring bloom, reaching highest density of about 3 ind. L^{-1} during end of July and early August (Fig. 8.7b). Densities drop quickly to below 1 ind. L^{-1} after mid-August. This calanoid copepod produces resting eggs in other areas, such as the North Sea (Viitasalo 1992), which might also be its overwintering strategy in the Baltic Sea, as suggested by the very low abundances in the pelagic during winter and early spring. *Centropages* is omnivorous eating phyto- and microzooplankton as well as other copepods (Calbet et al. 2007), and it can, similar to *Acartia*, select prey and switch between suspension feeding and ambush predation (Tiselius and Jonsson 1990). Given the diverse diet of *Centropages*, it is suggested that food is not the limiting driver of its population dynamics (Tiselius and Jonsson 1990). Its relatively large body size may however make it vulnerable to visual predation by fish.

Among meroplankton taxa, Bivalvia larvae are the most abundant plankton component. Abundances increase with warming waters through the summer and reach peak abundances in June with about 0.8 ind. L^{-1}, prior to the peaks of the other dominant mesozooplankton taxa (data not shown). Given that *Macoma baltica* is the dominant benthic bivalve, most of the larvae likely belong to this species. Cirripedia larvae appear between June and October (data not shown), albeit in very low abundances, probably due to the brackish water conditions of the Baltic Sea.

8.7.4 Termination of Stratification, Decline in Plankton Productivity and Onset of Autumn Mixing

The stratification period starts to break down with water temperature decrease in September and mixing into deeper water layers (Fig. 8.4). Dissolved inorganic nutrients are redistributed in the water column and concentrations increase again in the upper water layer in October. This coincides with a decline in phytoplankton biomass (Fig. 8.5), although diatom peaks of *Coscinodiscus* spp. may occur after inorganic nutrients are redistributed in the water column. Zooplankton experience declines in all taxa, and all species with resting eggs are absent from the pelagic by November and the copepods (except *Acartia* and *Pseudocalanus*) have reached low abundances by then (Fig. 8.7). This suggests that the production of the large-sized diatom in autumn is not much grazed upon by pelagic species and rather sinks out and becomes food for benthic species.

8.8 Interannual Variability in Seasonal Zooplankton Succession and Phenology

Changes in abiotic and biotic factors and variation in environmental factors can modify phenology and population size fluctuations, affecting the timing and duration of peak abundances and magnitude, as well as the timing of production and emergence of resting stages (Mackas et al. 2012). Interannual variation in zooplankton abundance, timing and duration is likely related to temperature, food availability and predation pressure (Winder and Schindler 2004a, Winder et al. 2009b). Temperature is a key parameter affecting physiological rates in ectotherms (Cushing 1990, Forster and Hirst 2012), and zooplankton population growth fluctuates strongly with seasonal temperature variation. Temperature affects metabolic and vital rates, and increasing temperature within the tolerance range of individual organisms accelerates both growth and developmental rates given sufficient resources. However, population dynamics of zooplankton will depend not only on the direct effects of temperature on vital rates but also on the synchronization of key life stages with food availability (Cushing 1990, Winder and Schindler 2004b). This is particularly important for pelagic herbivores in temperate regions where quantity and quality of phytoplankton, their major food resource, is highly variable on a seasonal basis (Sommer et al. 2012). For instance, the onset of the phytoplankton bloom in the Baltic Sea BY31 station varies between mid and end April, and peak phytoplankton bloom can range from about 50 to over 100 µgC L^{-1} (Hjerne et al. 2019).

In addition to bottom-up processes driving the seasonal production cycle, predation by higher trophic levels can be important for structuring zooplankton populations (Fig. 8.2) and is expected to account for 67–75% of total copepod mortality (Hirst and Kiørboe 2002). In the Baltic Sea, the planktivorous clupeid fish species, sprat and herring, are dominant predators on zooplankton, and the predation pressure varies through the year and between years (Möllmann 2000, Möllmann et al. 2008). For instance, Möllmann (2002) described how the increase of the sprat population through the 1990s may have impacted zooplankton mortality and thereby the population dynamics of zooplankton, *Pseudocalanus* and *Temora* in particular. Fish predation on zooplankton is expected to cascade down to primary producers, suggesting a closely interlinked food web (Casini et al. 2008).

Zooplankton peak abundances, timing of seasonal peak and duration fluctuate substantially from year to year in some taxa, particularly for microzooplankton (Fig. 8.9). For example, average summer densities of the protozoa *Radiosperma* range from close to zero to 6 ind^{-1}. Maximum densities of this protazoa occur between April and September with seasonal durations of about 110 days. For the rotifer *Synchaeta*, summer peak averages are around 7 ind. L^{-1} , while *Keratella* reaches lower densities with averages around 2 ind. L^{-1}. Peaks of both rotifer species appear at a narrow time window with both having short seasonal durations of about 30 days and *Synchaeta* peaking end of June and *Keratella* early August. Given that these zooplankton species fluctuate strongly, sampling frequency may contribute to some of the interannual variability.

For the cladoceran *Podon* and *Evadne*, annual average and maximum densities are in a narrower range with average and maximum values ranging from 0.5 to 1.5 ind. L^{-1}, seasonal peaks typically occurring in July and short seasonal durations of less than 50 days (Fig. 8.9). *Bosmina* shows higher interannual variability with averages from 0.5 to 8 ind. L^{-1}. Bloom timing and duration of this cladoceran is more variable, ranging between mid-July and mid-August with a short median seasonal

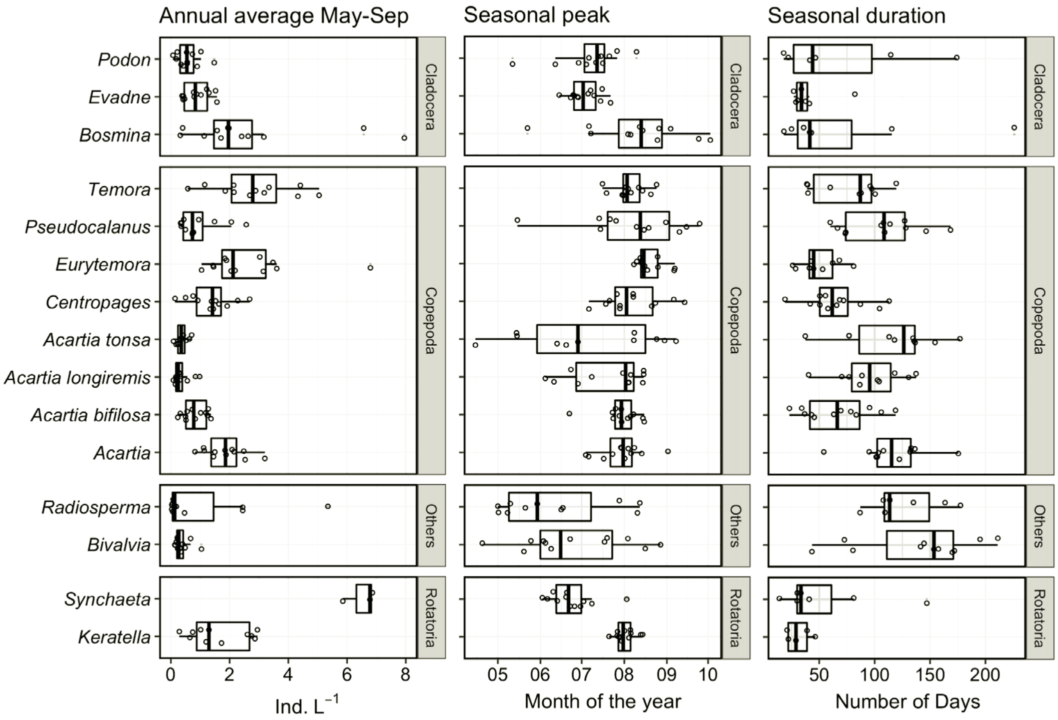

Figure 8.9: Interannual variability of zooplankton multi-year average summer (May–Sept) abundance (left), timing of the seasonal peak (middle) and seasonal duration (right) in the northern Baltic proper station BY31. Plots indicate the median (vertical line), the 25th and 75th percentile (box), the upper and lower whisker (horizontal bars), and individual observations (dots). Seasonal peak is the year day with highest abundance; seasonal duration is the number of days between the 25th and 75th percentile of seasonal abundance.

duration of less than 50 days. The invasive cladoceran *Cercopagis* was only observed sporadically between April and October with average summer abundances below 2 ind. L^{-1} (data not shown).

Within the copepods, *Temora* and *Eurytemora* reach highest summer abundances with interannual variation ranging from averages of 0.5 to 6 ind. L^{-1} (Fig. 8.9). Bloom timing occurs consistently between early and mid-August with *Eurytemora* having short seasonal durations of about 50 days and *Temora* up to 100 days. This confirms earlier observations showing that *Eurytemora* is confined to the warm water season and forms large transitory population peaks in late summer (Möllmann 2000). Average summer densities of *Pseudocalanus* and *Centropages* are around 1.5 ind. L^{-1} with seasonal peaks between July and August. *Centropages* peaks are relatively short (around 75 days), while *Pseudocalanus* peak over a longer time period (more than 100 days).

Among *Acartia*, *A. bifolosa* reaches highest summer densities with about 1.5 ind. L^{-1}. This species shows a narrow bloom timing and typically peaks in early August and with a seasonal duration from 40 to 75 days (Fig. 8.9). Timing of seasonal peak and seasonal duration of *A. tonsa* and *A. longiremis* is more variable, occurring between early June and end of August and with seasonal durations up to 125 days and more. Annual averages of Bivalvia larvae are typically below 0.3 ind. L^{-1} and peaks occur as early as end of April and as late as end of September with longer seasonal duration of about 150 days (Fig. 8.9). This indicates that Bivalvia reproduction is variable between years.

8.9 Spatial Variation in Seasonal Zooplankton Succession and Phenology

Spatial and latitudinal gradients in environmental and biotic factors lead to patterns in zooplankton distributions and community composition, as well as spatial variability in within-species traits and dynamics (Hays et al. 2005, Daase et al. 2013). In the Baltic Sea, copepods typically peak about one to two months earlier in the southern station compared to the central and northern most sampling stations with peaks occurring in June compared to August (Fig. 8.10). In contrast, rotifers and cladocerans vary less across the latitudinal gradient.

Zooplankton species composition in the southern Baltic Proper is similar to the BY31 station; however, species dominance changes, particularly within copepods. In comparison, the northern Baltic Sea comprises more brackish and freshwater species such as *Limnocalanus*. In addition to spatial variability in salinity, food availability and predation are the most pronounced environmental variables structuring the zooplankton assemblage in the Baltic Sea. Zooplankton bloom timing and duration varies across the stations (Fig. 8.11), which for some taxa may lead to a difference in timing of the seasonal peak by up to a month. Some taxa appear considerably earlier in the south whereas differences in timing between the two more northern stations are less clear. Given that BY31 has high sampling frequency (weekly to bi-weekly during the spring and summer period) compared to the monthly sampling at the other stations, differences in variability could be an artefact of the sampling but needs to be verified.

Synchaeta is the most abundant rotifer species in the southern Bornholm basin, whereas *Keratella* is more abundant in the Bothnian Sea. Bloom timing and duration of rotifers are more variable between years in the southern and northern Baltic Sea (Fig. 8.11). *Synchaeta* typically appear before the copepod and cladoceran peaks, while *Keratella* peaks overlap with mesozooplankton. Given that copepods and cladocerans are strong competitors for food, the seasonal dynamics suggests that *Synchaeta* has a temporal niche before crustaceans increase in abundance.

Seasonal peaks of *Bosmina*, the most abundant cladoceran in the Baltic Sea, is quite consistent across the latitudinal gradient with peaks in early August and relatively short seasonal duration. Limited abundances of this cladoceran species early in the season and during mid-summer could be related to intense fish predation by fish larvae, sprat and herring during the spring and early summer period.

Seasonal peaks of most copepods appear in general about one month earlier in the southern Baltic Sea, typically in July compared to August for the central and northern stations (Fig. 8.11). The

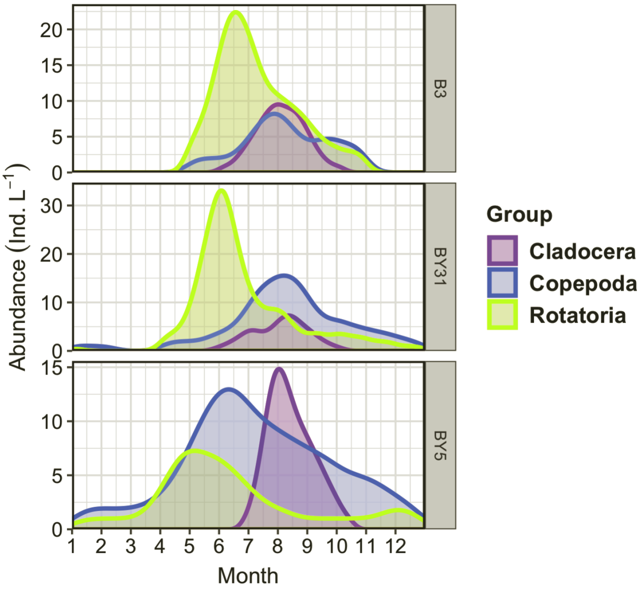

Figure 8.10: Average seasonal abundance of major zooplankton taxonomic groups at the southern (BY5), central (BY31) and northern (B3) sampling stations. Zooplankton data for BY5 include the years 2009–2011, 2013, 2016, 2017, for BY31 the period 2007–2018 and for B3 2012–2017. Data are daily interpolated between observation days and smoothed using a kernel density estimate. Protozoa include only the species *Radiosperma* sp.

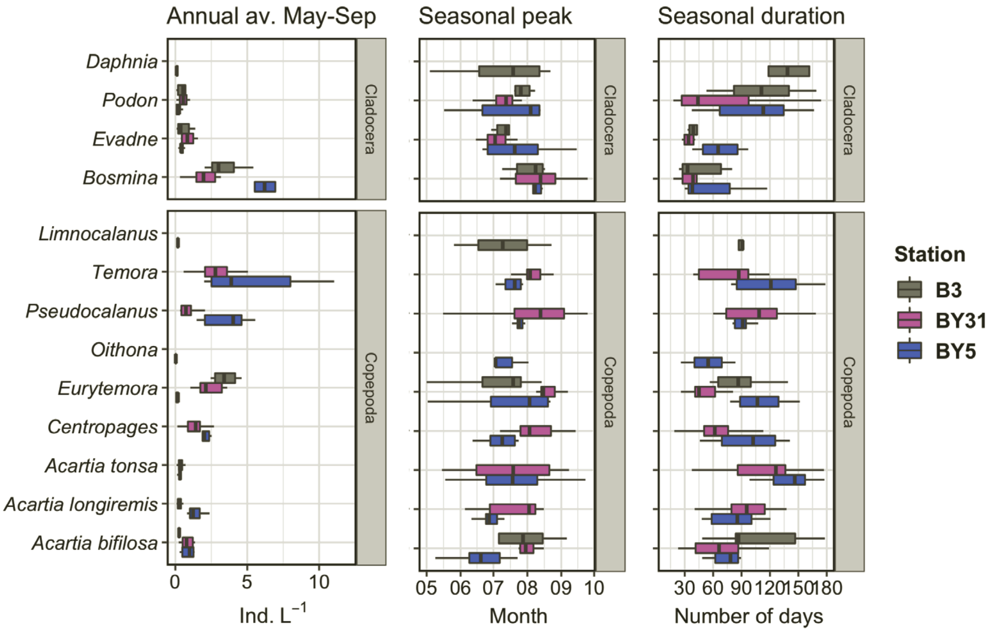

Figure 8.11: Interannual variability of zooplankton multi-year average summer (May–Sep) abundance (left), timing of the seasonal peak (middle) and seasonal duration (right) in a northern (B3), central (BY31) and southern (BY5) sampling location in the Baltic Sea. For description of boxplots, data availability and quantification of plankton phenology see Figs. 8.9 and 8.10.

most abundant copepods, *Temora* and *Pseudocalanus* have a relatively narrow time window of low abundance. The duration of *Pseudocalanus* is about 100 days, while it is more variable for *Temora*. This suggests a narrow prey window for fish species depending on these copepods. *Centropages* is absent in the northernmost station and has similar densities in the central and southern station with seasonal peaks in July in the south and August in the central station. Similarly, *Acartia* spp. copepods typically peak earlier in the southernmost station compared to the central station, except for *Acartia tonsa* that shows high variability in seasonal peak and duration. In the northernmost station, *A. biofolosa* occurs at low abundances. *Eurytemora* is the most abundant copepod in the Bothnian Bay and compared to the central BY31 station has a more variable time window in the northern and southern regions with peaks occurring between May and September. The small-sized *Oithona* species appears only in the southern Baltic Sea with low abundances within a narrow time window in July and seasonal duration below 100 days. Low salinity likely restricts the distribution of this oceanic species.

These latitudinal patterns of zooplankton phenology indicate that the general seasonal succession and species replacement is relatively consistent across the Baltic Sea latitudinal gradient; however, timing of the seasonal peak and duration vary across the gradient. This suggests that environmental conditions of temperature, food availability and predation pressure affect seasonal dynamics across the Baltic Sea and likely affect the interannual and decadal variability in abundance and phenology.

8.10 Plankton Interactions under Changing Environmental Conditions in the Baltic Sea

Zooplankton growth and reproduction rates are sensitive to temperature and food abundance, including the duration of the feeding season, with direct implications for population dynamics (McCauley and Murdoch 1990). For ectotherms in particular, climate warming thus leads to elevated turnover rates, increased number of generations per year, greater population variability, and altered phenology and life history traits, such as timing of dormancy and smaller body sizes (Daufresne et al. 2009, Winder et al. 2009b, Garzke et al. 2015). Moreover, climate change alters the density gradient of the water column and consequently the relative strength of mixing and stratification. Mixing processes are usually accompanied by changes in phytoplankton dynamics that in turn affect the seasonal dynamics of consumers (Winder et al. 2009b). As a result, climate may indirectly affect population dynamics and life histories of zooplankton through its effect on seasonality of resource availability and other components of the ecosystem, such as the extent of the growing season. Such modifications in the environment are expected to affect life cycle responses in zooplankton, particularly in copepods (Drake 2005), given the plasticity of their life histories and their extended longevity compared to cladocerans and rotifers (Allan 1976).

In the Baltic Sea, phytoplankton spring bloom timing, magnitude and composition display high variability from year to year with the peak biomass of the bloom occurring between end of March and end of April at station BY31 (Hjerne et al. 2019). Spring bloom timing occurred about 1–2 weeks earlier over the last 20 years driven by less clouds and less wind. Furthermore, due to warming, the magnitude of spring bloom diatoms decreased, while summer associated cyanobacteria increased (Wasmund and Uhlig 2003, Kahru and Elmgren 2014, Kahru et al. 2016). These changes are expected to affect carbon cycling within the pelagic system and export rates to the benthos.

In addition to temperature, changes in salinity are expected for coastal systems as climate also affects precipitation patterns and freshwater inflow (Käyhkö et al. 2015). For the Baltic Sea, a decrease in salinity was observed and a further decrease is expected for the coming decades due to increasing freshwater inflow and reduced marine water inflow through the narrow entrance (The BACC Teach 2015). Because some zooplankton species are physiologically constrained by salinity, changes in salinity are affecting abundance and distribution. For example, *Pseudocalanus*, an important prey item for larval and planktivorous feeding fish, and as such considered a key species (Möllmann et al. 2003) experienced multi-year declines that coincide with decrease in North Sea water inflow and decreasing salinity in the Baltic Sea. This species is considered a mediator between climate change and herring growth, with consequences for the fisheries (Möllmann et al. 2003, Casini et al. 2008). Similarly, *Temora* serves as the major diet for sprat *Sprattus sprattus* and herring *Clupea harengus*.

The effect of top-down control on *Temora* population dynamics by fish predation is, however, uncertain (Köster et al. 2003, Dutz et al. 2010), and it is thought that hydrographic conditions explain most of the variation in the fluctuations of this copepod species. *Temora* decreased in coastal waters over the last decades with a general trend of decreasing salinity and increase in freshwater inflow in the Baltic Sea (Ojaveer 1998, Vuorinen 1998), and its distribution was shifted westwards into areas of higher salinity.

The light regime of the pelagic domain also determines multiple processes, both photosynthesis and primary production as well as predator-prey interactions involving visually searching predators. Many processes impact the light regime of Baltic Sea waters, including freshwater inflow and the amount of suspended matter, eutrophication and the shading through algae blooms near the surface, and snow-covered sea ice. These processes all have pronounced spatial variability, both with respect to distance from the coast and along latitude, such as for suspended matter (Kyryliuk and Kratzer 2019). Sea ice is more common, and lasts for a longer part of the season, in the northern parts, particularly the Bothnian Bay (Haapala et al. 2015, Hjerne et al. 2019). The amount of sea ice varies considerably between years and has declined over time (Haapala et al. 2015). Runoff processes are also highly dynamic but with no or weaker trends over time (Käyhkö et al. 2015). The net effects on water clarity and light regime are challenging to predict and highly likely to be dependent on region. From other aquatic systems, it is known that increased runoff from land leads to murkier waters and changing ecological interactions (Aksnes et al. 2009, Opdal et al. 2019). Less sea ice leads to more light and may be of particular importance in areas where the sea ice cover historically has lasted well into the well-lit spring period. Such sea ice changes would be expected to have similar implications to those observed and predicted in polar seas (Clark et al. 2013, Langbehn and Varpe 2017). For parts of the Baltic Sea where the net effect is more light for a longer part of the season, we would expect species well adapted to avoid visually searching predators to increase, and selection pressures to shift strategies towards smaller body size, more transparency, and increased diel vertical migration (DVM).

Other human drivers, such as eutrophication, anoxia or fishing that are prominent in the Baltic Sea (Reusch et al. 2018) also have direct effects on the plankton community and likely affect species composition, carbon flow within the food web and seasonal dynamics of zooplankton (Arndt 1991, Casini et al. 2008, 2016). In comparison, many plankton organisms of the Baltic Sea are quite resistant to ocean acidification (Rossoll et al. 2013, Lischka et al. 2017). Given that the Baltic Sea has strong seasonal changes in pH that exceed the predictions for open ocean systems by the end of this century (Reusch et al. 2018), it is assumed that species are adapted to high pH variation (Thomsen et al. 2017). Given that jellyfish are tolerant to low pH levels, ocean acidification and warming may give this group a competitive advantage in the Baltic Sea (Winder et al. 2017a).

Multi-year changes in the annual zooplankton cycle are not well studied in the Baltic Sea but changes can be expected given alterations in phytoplankton seasonal dynamics and abiotic factors (Wasmund and Uhlig 2003, Hjerne et al. 2019). Given that the degree to which individual species respond to changing temperature and salinity varies, it is likely that climate change can significantly alter trophic flows in unpredictable ways. The effect of climate change further depends on the local adaptions of life history traits, as has been shown for *Eurytemora* in the Baltic Sea (Karlsson et al. 2018). This suggests that the extent of physical changes and the potential for species to adapt to changing environmental conditions will greatly influence food web dynamics as future climate warms and becomes more variable.

8.11 Conclusions

Understanding the seasonal succession of zooplankton, as well as their responses to changing environmental conditions, requires detailed knowledge of their population dynamics through the annual cycle as well as their interactions with food, competitors and predators. In this chapter, we have described temporal interactions between primary producers and consumers in plankton food webs of the Baltic Sea. Observed dynamics and patterns have been discussed in relation to driving mechanisms and environmental variables. For our Baltic Sea case, ciliate and rotifer microzooplankton species are the first ones to appear after the spring phytoplankton bloom that occurs around April when water temperatures are low. Mesozooplankton, including cladocerans and copepods, peaks are temporally decoupled from the spring bloom and occur during the cyanobacteria dominated summer blooms in August. Given the strong seasonal overlap of diverse zooplankton, specialized feeding behaviour may allow coexistence of copepod and cladoceran species during the summer season. The absence of some groups of larger and non-visual predatory zooplankton from the Baltic Sea suggests that fish are the main predators on mesozooplankton. Their visual search for food lead to strong selection pressures for anti-predator strategies such as through diel vertical migration, transparency or small body size. The timing of peak abundance of zooplankton species is highly variable from year to year, except for a few species, such as *Eurytemora affinis* that appear during a narrow and similar time window each year. Population peaks in the southern Baltic Sea typically appear one month earlier compared to central and northern stations where the seasonal dynamics of mesozooplankton are more condensed within the summer months. Multi-year changes in zooplankton assemblages are mainly related to abundance declines of some key copepod species driven by salinity declines. However, given alterations in phytoplankton seasonal dynamics and abiotic factors, multi-year changes in zooplankton phenology are expected and the complex interactions with other climate change effects can significantly alter trophic flows.

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