CHAPTER 3

THE MESOZOOPLANKTON SPECIES ASSOCIATION

IN THE BELGIAN PART OF THE NORTH SEA

Abstract

This manuscript presents the mesozooplankton community structure and its spatial and temporal variability in the Belgian part of the North Sea (BPNS), a first thorough study on this topic in nearly 40 years. Monthly sampling campaigns at ten stations in the BPNS in 2009 and 2010 yielded a total of 137 mesozooplankton taxa (46 holoplanktonic, 50 meroplanktonic and 41 tychoplanktonic), of which nine species had never been reported in the area. Smaller neritic copepods, especially *Temora longicornis* and *Acartia clausi,* were present in all samples and dominated zooplankton densities (66 %), together with the appendicularian *Oikopleura dioica* (10 %). They were joined by high numbers of meroplanktonic echinoderm larvae (9 %) in spring and summer. Based on diversity alone, the mesozooplankton could be typified as one neritic zooplankton community, due to the ubiquitous presence in time and space of the dominant copepods. Yet, these neritic species were often joined by low numbers of oceanic species that are occasionally imported with the inflow of Atlantic oceanic water in the BPNS. Based on a combination of abundance and diversity, our results indicate distinct seasonal and spatial distribution patterns in the mesozooplankton. Months with highest average densities were May, June and July, lowest densities were noted in December and January. Only limited long-term zooplankton data are available for the BPNS from the Continuous Plankton Recorder surveys or the long-term monitoring stations in the vicinity of our research area. However, our data suggest that nowadays zooplankton species appear earlier in the BPNS, comparable with other areas in the North Sea. Densities varied between 150 and 15000 ind.m^{-3}, and averaged highest midshore, then nearshore and

offshore. This is partially comparable with the spatial patterns recorded for other ecosystem components, such as demersal fish, epibenthos and macrobenthos, of which densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS.

KEYWORDS: zooplankton, marine biodiversity, Belgian part of the North Sea, community, phenology

1. Introduction

The vast majority of fish species have a pelagic larval phase (Russell 1976), which depends on the zooplankton as an important food source. For this reason, and because of their sheer abundance, high diversity and vital ecosystem functions (Richardson 2008), zooplankton communities are crucial in the marine food web. Since zooplankton can be considered as the major grazers in ocean food webs, they provide the principal energy pathway from primary producers to consumers at higher trophic levels, including fish and marine mammals (Mauchline 1998, Richardson 2008). In the southern North Sea, small calanoid copepods dominate the zooplankton, up to 84 % of the spring and summer abundance (Krause *et al.* 1995). Copepods fulfill a key role in marine food webs, not only transferring energy to higher trophic levels, but also to the bottom through sedimentation of faecal pellets (Nielsen *et al.* 1993).

Zooplanktonic organisms also help to shape the extent of climate change through carbon fixation via the biological pump, but are, paradoxically, themselves very susceptible to a changing climate (Richardson 2008). In the North Sea and the English Channel, temperature has increased by 1.1 °C since 1962 (Wiltshire and Manly 2004), leading to a northward displacement of marine organisms and match-mismatches between predator and prey (Cushing 1990, Southward *et al.* 1995, Hays *et al.* 2005). The replacement of the cold water *Calanus finmarchicus* species assemblage in the North Sea by the warm water *Calanus helgolandicus* dominated copepod assemblage with lower biomass and smaller species, is a classic example of the severe consequences of a warming climate on marine ecosystems (Richardson 2008).

In a healthy marine ecosystem, herbivorous zooplankton can control natural phytoplankton blooms and keep the system in balance (Rousseau *et al.* 2006). However, the southern North Sea, including the Belgian part of the North Sea (BPNS), is known as an eutrophicated

ecosystem, due to anthropogenically induced nutrient inputs through the discharge of the major western European rivers (Lancelot *et al.* 1998, Rousseau *et al.* 2006). The unbalanced nutrient environment is characterized by an excess of nitrate over silicate and phosphate, leading to spring algal blooms, with a major and sudden change in phytoplankton dominance from diatoms to the flagellates *Phaeocystis globosa* and *Noctiluca scintillans* (Lancelot 1995, Peperzak *et al.* 1998, Vasas *et al.* 2007). Because *P. globosa* is resistant to grazing, it is considered a trophic dead end in the planktonic food chain (Daro *et al.* 2006, Nejstgaard *et al.* 2007). This may lead to a reduced abundance of bottom-up controllers, which might have far-reaching and long-term effects throughout the food web (Lancelot *et al.* 2007). It seems to be an intrinsic property of temperate pelagic ecosystems strongly affected by human activities, to stimulate the microbial network while inhibiting the higher trophic levels, an effect that is exacerbated by overfishing of planktivorous fish (Vasas *et al.* 2007).

Considering the climate change with concomitant biogeographical and phenological shifts in the distribution of planktonic species, and the vital importance of plankton in the marine food web, an update of zooplankton community dynamics in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly in place.

For the BPNS few historic studies on zooplankton are available. The oldest known marine zooplankton samples date from the early 20th century (Gilson collection, discussed in Van Loen and Houziaux 2002). However, there was little to nothing published about the zooplankton species in these samples, as the main focus was on benthic organisms. Daro (1974, 1985a,b) studied diurnal zooplankton behavior in the Sluice dock (Ostend port) and at a station in the BPNS (25 m depth), where she observed vertical migration of the calanoid copepods *Temora longicornis* and *Pseudocalanus elongatus* during the spring phytoplankton bloom. Van Meel (1975) was the first to report a zooplankton species list from the BPNS and adjacent waters. The data in most of these older (benchmark) studies are qualitative rather than quantitative, hence they serve best for presence-absence comparisons (see Van Ginderdeuren *et al.* 2012a). More recent zooplanktonic research in Belgium focused on hyperbenthic species (Dewicke *et al.* 2003) or on a limited number of zooplankton species, like the work on floating seaweed inhabitants by Vandendriessche *et al.* (2006) and on *Lanice conchilega* larvae by Van Hoey (2006). Several studies investigated the calanoid copepod interactions with the harmful algae *P. globosa* (e.g. Gasparini *et al.* 2000, Antajan

2004, Daro *et al.* 2006, Rousseau *et al.* 2006). M'Harzi *et al.* (1998) investigated zooplankton from the BPNS, but used different gears at one fixed depth in only one month, which makes it difficult to compare results. Zooplankton dynamics in the Westerschelde estuary (the Netherlands), at the border of the BPNS, received considerably more attention (e.g. Bakker and De Pauw 1975, Soetaert and Van Rijswijk 1993, Maes *et al.* 2002, Appeltans *et al.* 2003, Azémar *et al.* 2004, Tackx *et al.* 2004, Tackx *et al.* 2005), but up till now, recent data on the marine part of the BPNS remained extremely scarce.

Abroad, a vast amount of North Sea zooplankton data have been gathered by the Continuous Plankton Recorder (CPR) surveys (SAHFOS, conducted since the 1940s). The CPR covers a large area but faces several impracticalities: only a limited part of the North sea is studied on a yearly basis, only the surface water layers are sampled, and the device has a very narrow entrance aperture (1.6 cm^2), which makes it less likely to catch big and faster zooplankton species (Haddock 2008). Moreover, there is a clear lack of CPR samples from the English Channel and the southern North Sea (see Fig. 5 and 6 in Chapter 1). Also no monthly monitoring station exists in the vicinity of Belgian waters, which could allow for a detailed temporal analysis (Fig. 7 in Chapter 1). The nearest zooplankton monitoring stations are the Plymouth L4 survey area in the western part of the English channel and Helgoland roads in the German bight (O'Brien *et al.* 2011).

The aims of this manuscript are: (1) to characterize the mesozooplanktonic (> 200 μm) community structure in the BPNS on the basis of zooplankton species composition, abundance, species richness and habitat preferences; (2) to investigate whether calanoid copepods dominate the food web, and which patterns in temporal and spatial patterns can be noted in the zooplankton community structure; (3) to compare the zooplankton community structure with plankton data from other parts of the North Sea and the English Channel and with the few available Belgian 'historic' data.

2. Materials And Methods

2.1 Study area

This study covers the entire Belgian Exclusive Economic Zone (ca. 3600 km^2), referred to as the Belgian part of the North Sea (BPNS), and is situated in the Southern Bight of the North Sea. The BPNS has a maximum seaward width of 87 km and is bounded by a 67 km long

sandy coastline, bordered eastwards by the Westerschelde estuary (Degraer *et al.* 2003). The prevailing marine currents convey saline Atlantic water in a NE direction through the Channel towards the BPNS (see Chapter 1), where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq 1984, Howarth 2001). The current regime is macro-tidal (tidal amplitude averages 4 m) and keeps the water column (with an average depth of 30 m) well mixed (MUMM 1996).

The BPNS seabed contains several sandbank systems with a high morphological and sedimentological diversity, resulting in different benthic communities (Degraer *et al.* 1999, Van Hoey *et al.* 2004), producing planktonic larvae (Van Ginderdeuren *et al.* 2012a) and subsequently influencing the pelagic ecosystem via benthic-pelagic coupling (Provoost *et al*. 2013).

2.2 Data origin

Sampling was carried out monthly in 2009 and 2010 with RV Zeeleeuw (apart from January and February 2010 due to RV maintenance) at up to ten monitoring stations covering the entire BPNS, positioned along a nearshore-midshore-offshore axis (Fig. 1). A WP2 zooplankton net (57 cm diameter, 200 µm mesh size, Fraser 1968) fitted with flow meter (Smith *et al*. 1968) was towed in an oblique haul from bottom to surface at each station. Samples were fixed and preserved in a 4 % formaldehyde solution. A CTD (Seabird 19plusV2) cast was carried out at every station for measuring depth, temperature and salinity. Chlorophyll *a* data were attained via MODIS and MER satellite imaging systems (Vanhellemont *et al*. 2011).

Data are derived from 112 samples (53 nearshore, 30 midshore, 29 offshore; 74 in 2009, 38 in 2010), taken in salinity ranges from 30 to 35 PSU and temperature ranges from 2 to 21 °C. Data were added to the database of the Bio-Environmental Research unit (ILVO).
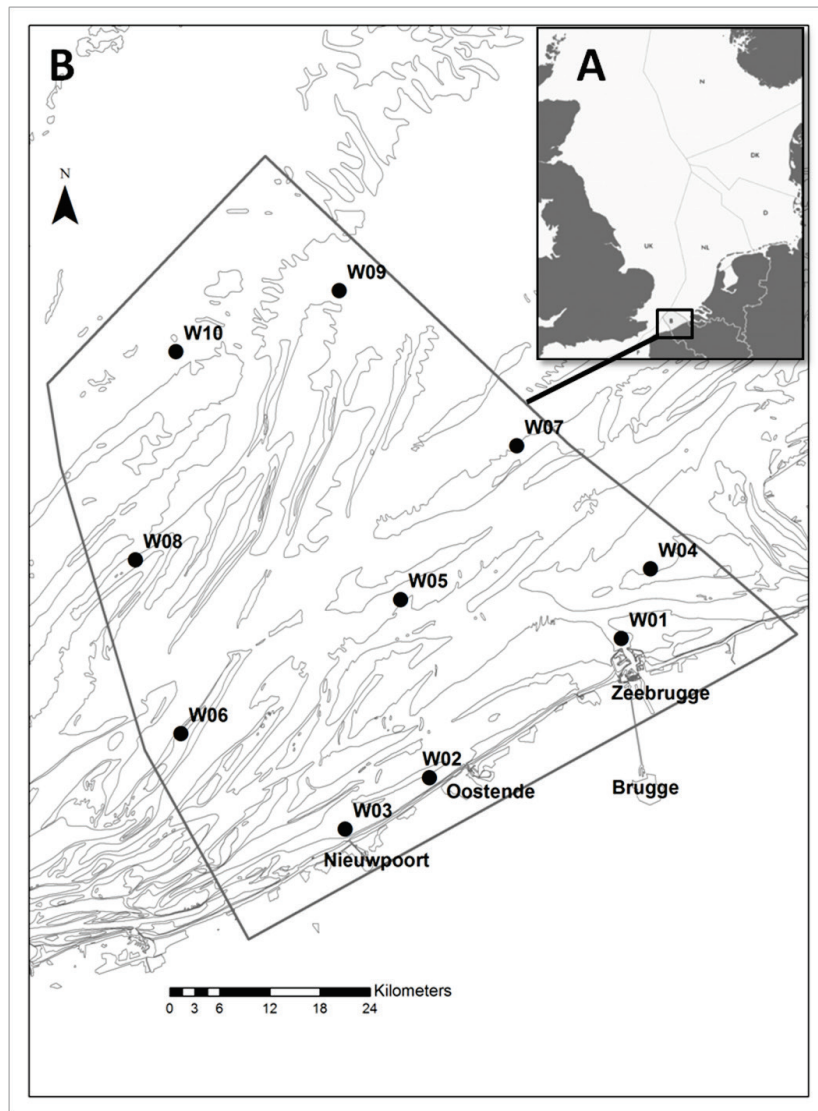
Figure 1: A) North Sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten stations (nearshore W01-04, midshore W05-07, offshore W08-10).

In the lab, taxa were identified to species level when possible, using optical microscope and stereomicroscope equipment. Animals too big or too rare to subsample were initially sorted from the catch in a general sweep. Then subsequent subsamples (small volumes) were taken from the remainder of the sample, for counting and identification of abundant zooplankton species (often present in thousands). When at least 100 calanoid copepods were identified, also that last subsample was further worked out completely (van Guelpen *et al.* 1982). As such, subsample densities could then be converted to total abundances for every species. Calanoid copepods were identified to species level and staged as adults (sexed) or copepodites. Copepodites of *Centropages hamatus* were not distinguished from those of *Centropages typicus*, nor those of *Paracalanus parvus* from *Pseudocalanus elongatus*.

All sample data yielded an original set of 145 taxa. After exclusion of species that were not sampled quantitatively (e.g. benthic species) and lumping taxa due to inconsistent identification (e.g. Caridea and Polychaeta larvae), a set of 137 taxa (further referred to as 'species') was used for multivariate analyses. The different taxa were further classified according to their lifestyle as holoplanktonic (organisms spending their entire life as plankton in the water column, e.g. calanoid copepods), meroplanktonic (early life stages, mainly from larger animals, that spend part of their life as plankters, e.g. decapod larvae) and tychoplanktonic (species that are occasionally carried into the water column, e.g. benthic species and hyperbenthic groups such as Mysida and Cumacea) (for a thorough definition, see Chapter 1).

2.3 Numerical analysis

Noctiluca scintillans (dinoflagellate) was omitted since its very high numbers skewed the data analyses. *N. scintillans* was often found as a brown slick on the water surface, where cells reached abundances up to 50 times higher than the total abundance of the rest of the plankton sample. This caused a sampling bias, hence we omitted the species from further analysis. The spatial and temporal distribution of this dinoflagellate can be found in Addendum 1.

Species richness was estimated by Hill's diversity number N_0, which is equal to the number of species in a sample. The Shannon-Wiener index H' was used to calculate the species diversity. Both N_O and H' (log e) were calculated on raw density data.

Based on the zooplankton density data (fourth-root transformed, following Quinn and Keough 2002), a non-metric multi-dimensional scaling (MDS) analysis was applied to explore the relationship between samples from different years, stations and months. This technique relates zooplankton density and species composition through a matrix of Bray-Curtis similarities. Spatial and temporal differences in zooplankton distribution were investigated using PERMANOVA pair wise testing (based on Bray-Curtis similarity), using three factors: "year", "month" and "shore" (the latter to group the ten stations in nearshore, midshore and offshore groups). As the interaction between factors (main PERMANOVA test) was significant ($p < 0.05$), we present separate significance tests for every combination of factors

within each year. Spatial and temporal differences for species diversity were also verified using PERMANOVA, based on Euclidean distance resemblances. The PERMANOVA designs for both univariate and multivariate data analyses were similar.

Two-way crossed SIMPER analyses (based on Bray-Curtis similarity) were performed for each year separately, using factors "shore" (near-mid-offshore) and "month", to identify the species primarily contributing to the similarity in the sample clusters. Finally, the patterns in species composition and abundance are related to the environmental variables (temperature, salinity and chlorophyll *a* biomass) via distance-based linear models (DistLM). All these analyses were performed using the package PRIMER 6 (Clarke 1993, Clarke and Gorley 2006).

3. Results

3.1 Environmental influence

Temperature and salinity profiles showed that the water column was vertically well-mixed throughout the year. Sea surface temperature at sampling stations ranged from 2 to 21 °C, was lowest in February and highest in August (Fig. 2). Due to an exceptionally cold winter in 2009-2010, sea surface temperatures remained lower for a longer period in early 2010 compared to 2009 (e.g. 4.9 °C in March 2010 *vs.* 6.1 °C in March 2009). Salinity ranged from 30 to 35 PSU, showing little variation, even at the stations in the close vicinity of the Scheldt estuary. Chlorophyll *a* biomass reached highest values in March (2009) and April (2010), and decreased in an nearshore – offshore gradient.
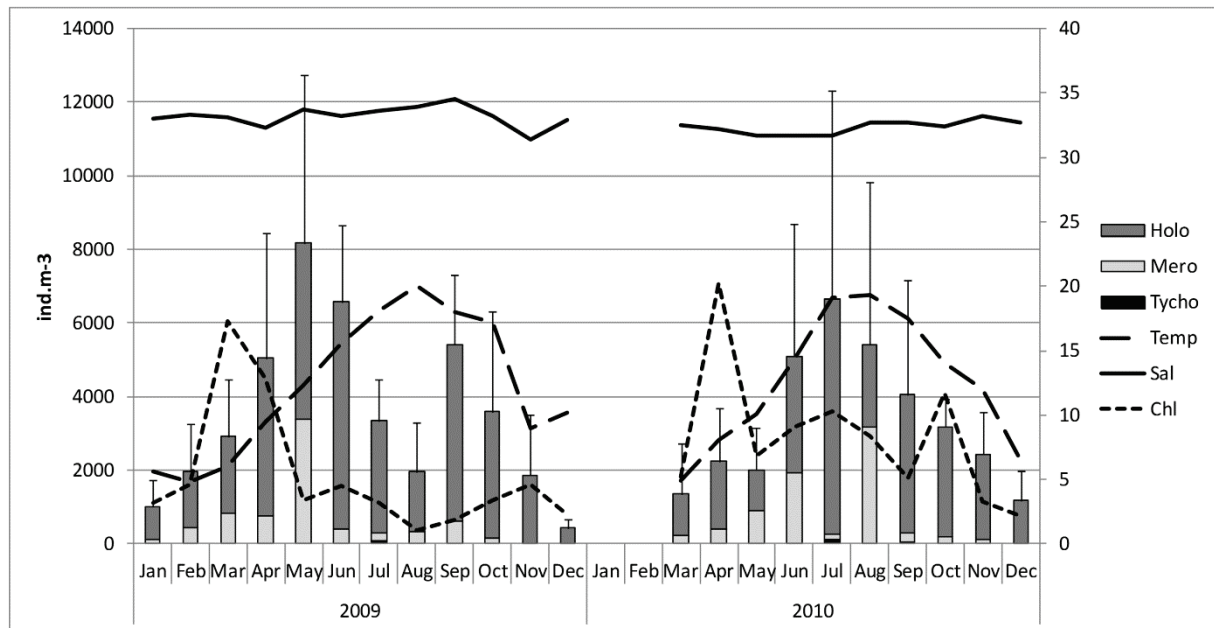
Figure 2: Monthly zooplankton densities (ind.m^{-3}), averaged over all stations (+ SD on total values), divided in holo-, mero- and tychoplankton (left axis). Right Axis: Salinity (PSU), Temperature (°C) and chlorophyll *a* biomass (mg.m^{-3}).

3.2 General characterization of the zooplankton

In total 137 taxa (98 identified to species level) were found in the BPNS in 2009 and 2010, of which 46 are considered holoplanktonic, 50 meroplanktonic and 41 tychoplanktonic. With 70 species (51 % of all species recorded), crustaceans were most found, followed by 24 species of fish larvae (19 %) and 18 species of Coelenterata (13 %). Species richness ranged from 12 to 45 species per sample and species diversity (Shannon H') from 0.5 to 2.5. Zooplanktonic abundance was dominated year round by copepods (66 %) With the calanoid copepods *Acartia clausi* and *Temora longicornis* present in 100 % of the samples. Also the appendicularian *Oikopleura dioica* was year round present (10 %), while in spring and summer high numbers of echinoderm larvae (9 %) were found in the water column (Fig. 3).

This study revealed several species that are new to the Belgian marine species list: the calanoid copepod *Metridia lucens*, the cyclopoid *Oithona similis,* the poecilostomatoid copepod *Giardella callianassae*, the hydrozoans *Amphinema dinema* and *Eutima gracilis*, the mysid *Acanthomysis longicornis*, the polychaete worm *Tomopteris helgolandica*, the cladoceran *Penilia avirostris* and the monstrilloid copepod *Cymbasoma germanicum* (for a complete species list, see Chapter 2).
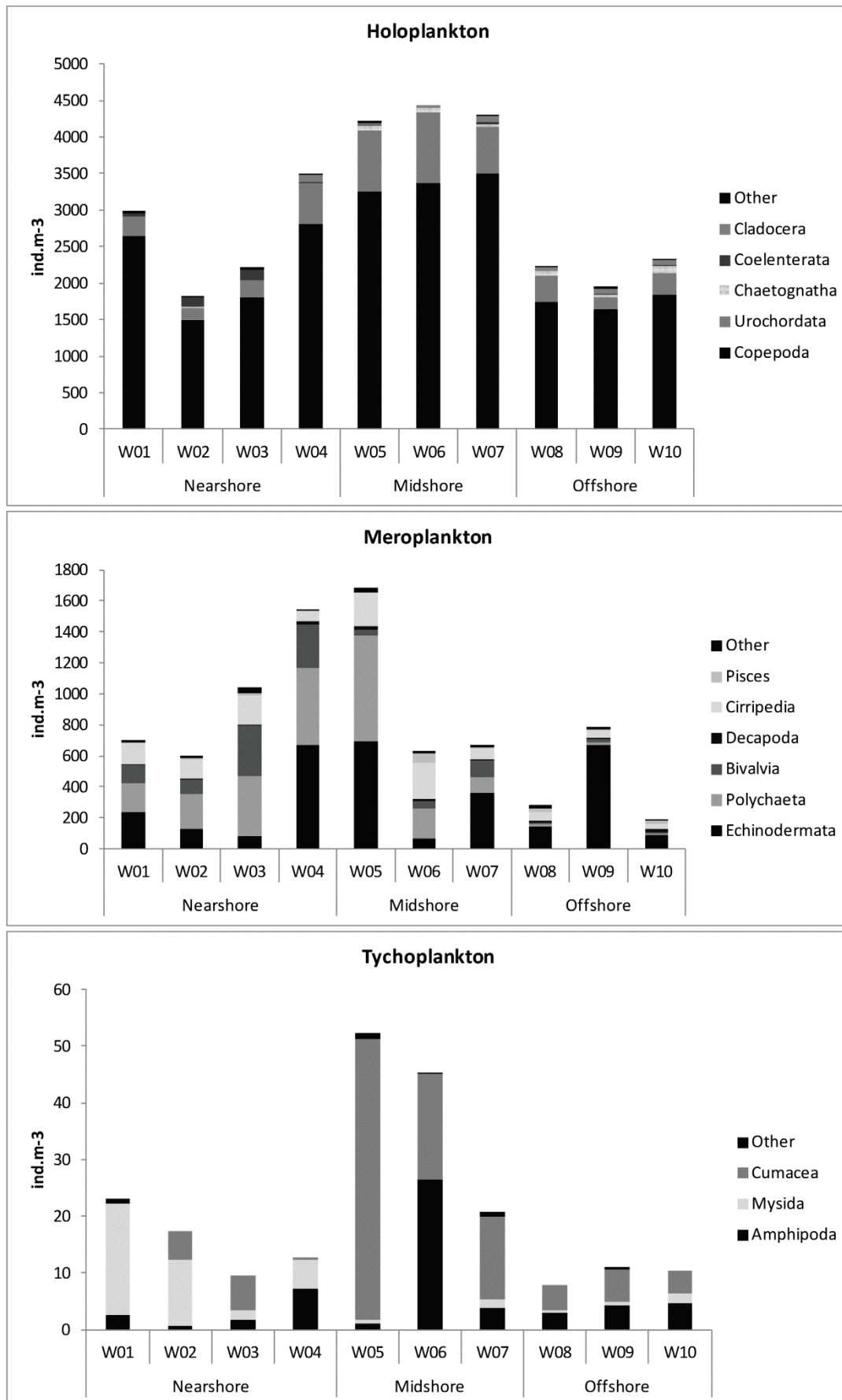
Figure 3: Average zooplankton density (ind.m^{-3}) per station for the main holo-, mero- and tychoplanktonic taxa.

3.3 Copepod abundance and community structure

Calanoid copepods were most abundant, on average 83 % of the total copepod density. Only in autumn, also a peak of harpacticoid copepods (mainly *Euterpina acutifrons*) was noted. Cyclopoida remained scanty all year round (Fig. 4). Highest cyclopoid densities were observed for *Oithona similis, Oithona nana, Cyclopinoides littoralis and Corycaeus anglicus*. Total copepod numbers increased from 720 ind.m^{-3} in January 2009 to 4220 ind.m^{-3} in June 2009 and 6050 ind.m^{-3} in July 2010 (see Addendum 1 for average densities and maximum densities of each species found). The most found calanoid copepods were *T. longicornis, A. clausi, Paracalanus parvus and Centropages hamatus*, year round and at every station (Fig. 4)*,* followed by *Pseudocalanus elongatus, Centropages typicus* and *Calanus helgolandicus*. Detailed taxonomical analysis of *Calanus* copepods revealed that *Calanus finmarchicus* was not present in the BPNS during our study period. *Calanus helgolandicus* on the other hand, was found most in offshore and midshore stations with an average density of 5 ind.m^{-3}, and peaking in March and June with a maximum observed density of 96 ind.m^{-3} at W07.
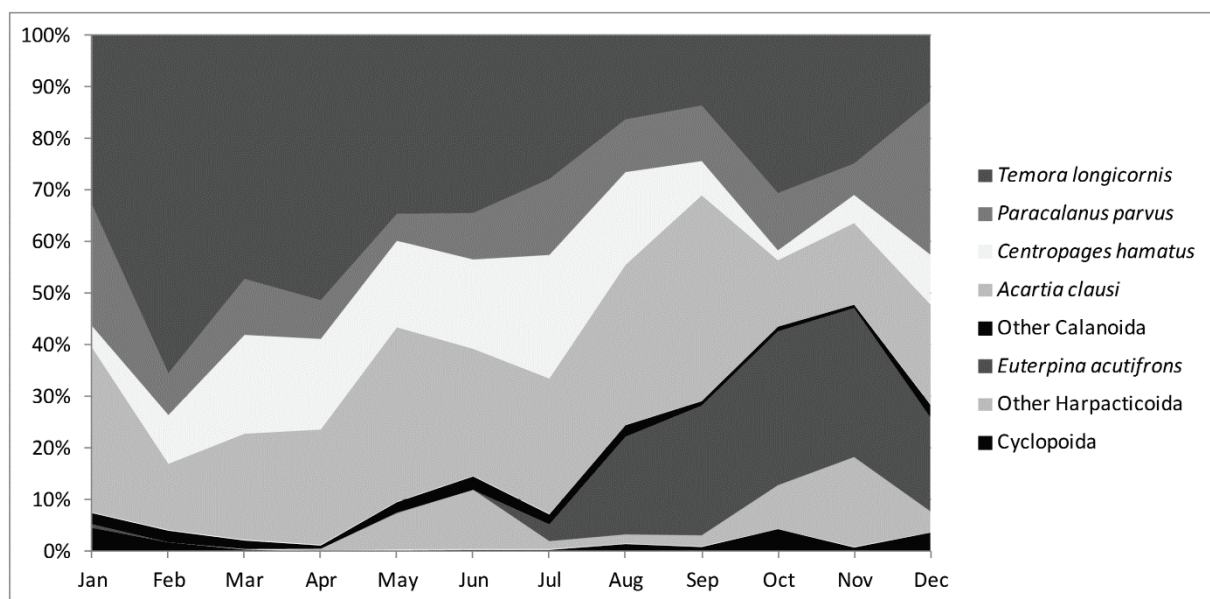

Figure 4: Relative seasonal abundance (%) of the most abundant copepods in the BPNS.

3.4 Community characteristics

3.4.1 Holoplankton

Holoplankton constituted the bulk of the mesozooplankton densities (78 %), in all near-, mid- and offshore stations and in every season (Fig. 3). Highest densities were observed midshore, lowest offshore (Fig. 3).

Highest densities were reached by the dinoflagellate *Noctiluca scintillans* with a peak density of 39800 ind.m^{-3} midshore and an overall average of 1290 ind.m^{-3}. Also, the most abundant species, *i.e.* the omnipresent calanoids *A. clausi* and *T. longicornis*, the urochordate *Oikopleura dioica* and the autumn peaking harpacticoid *Euterpina acutifrons* all belong to the holoplankton. Eighteen species of coelenterates were found in this study, 4 cnidarians, 11 hydrozoans and 3 ctenophores. The Hydrozoa *Clytia hemisphaerica, Margelopsis haeckeli* and *Rathkea octopunctata* were most common. Two invasive coelenterates were reported: *Nemopsis bachei* (Hydrozoa) and *Mnemiopsis leidyi* (Ctenophora), occurring in stable populations and reaching maximum densities of respectively 24 and 0.8 ind.m^{-3} (Van Ginderdeuren *et al.* 2012b). Sightings of adult *M. leidyi* in the coldest winter months imply that the species can thrive in Belgian waters throughout the year (Van Ginderdeuren *et al.*2012b). Chaetognaths were less abundant (Fig. 3) but reached high numbers midshore and offshore (autumn peak densities of *Parasagitta setosa* up to 490 ind.m^{-3}).

3.4.2 Meroplankton

Meroplankton was found in lower abundances compared to the holoplankton, and peaked in May and August with respectively 41 % and 47 % of the total plankton densities (Fig. 3). The most abundant taxa belong to the Echinodermata, more specifically bipinnaria and pluteus larvae of *Echinocardium cordatum* and *Asterias rubens* (peaking in May), *Ophiothrix fragilis* (August-September), *Ophiura* sp. (May) and *Psammechinus miliaris* (June). In general, the highest meroplankton abundance was noted midshore, although echinoderms were more abundant offshore (Fig. 3), with a maximum of 10860 ind.m^{-3} for *O. fragilis* pluteus larvae at W09 in August 2010. Polychaeta larva were abundant in nearshore and midshore samples, particularly during spring with peak densities up to 2810 ind.m^{-3}. Also, barnacle nauplius and cyprid larvae and bivalve spat were relatively abundant (Fig. 3). Fish larvae were the most diverse meroplankton group with 24 species, mostly found during winter and spring.

3.4.3 Tychoplankton

Tychoplanktonic taxa were present in the water column in much lower densities than holo- or meroplanktonic taxa (Fig. 3). Most found were mysids, juvenile Cumacea and 18 species of Amphipoda. Seventy percent of the amphipod densities could be attributed to just one species, *Atylus swammerdami*. Tychoplankton densities peaked midshore and in July (Fig. 3).

Noticeable is the fact that mysid shrimps were most common in the station located in the turbid outflow of the Westerschelde estuary (W01).

3.5 Temporal/seasonal variation in the zooplanktonic community

Monthly densities ranged between 440 ± 240 ind.m^{-3} (December 2009) and 8170 ± 4570 ind.m^{-3} (May 2009). Peaks were noted from May to August, lowest values in December and January (Fig. 2). The high value of July 2010 for holoplankton was due to one sample with high *Temora* densities (> 7000 ind.m^{-3}), whilst the high meroplankton value for August 2010 was caused by an aberrant W09 offshore sample containing thousands of *Ophiothrix* pluteus larvae (> 10000 ind.m^{-3}).
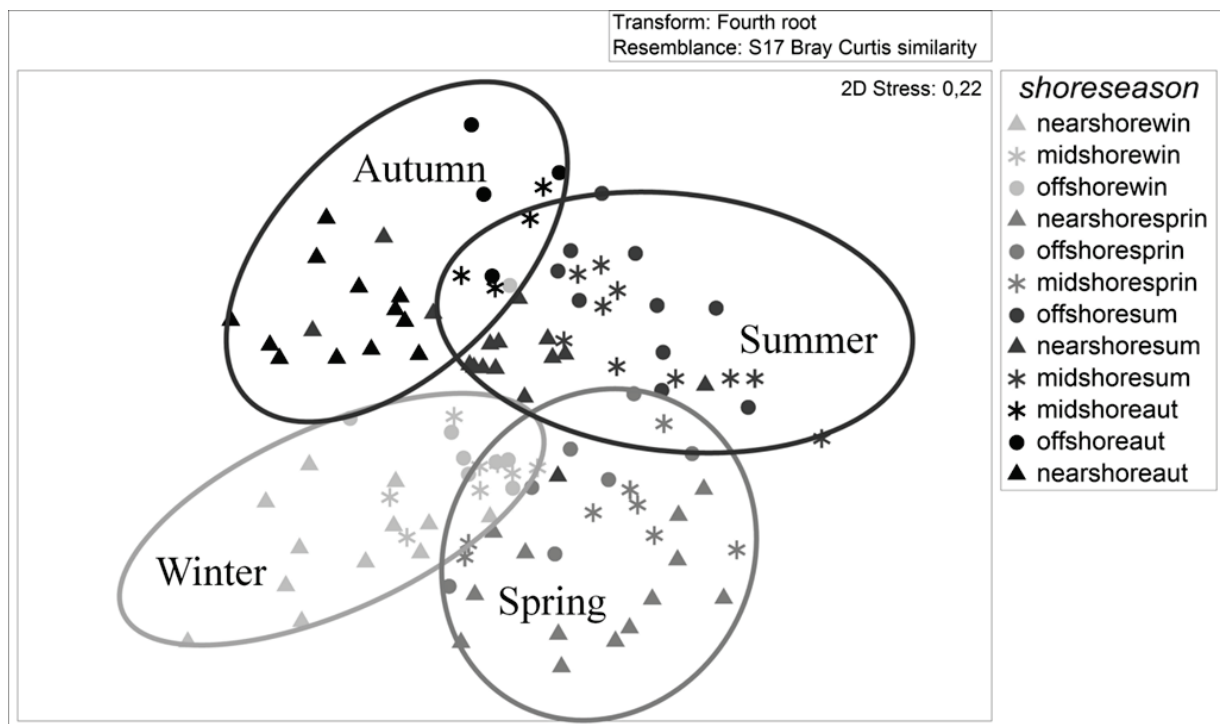

Figure 5: Two-dimensional non-metric MDS plot (stress value = 0.22) of all samples, with indication of different shades of grey for spring (April-June), summer (July-September), autumn (October-December) and winter (January-March) samples and different symbols for near-mid-offshore samples (nearshore W01-04, midshore W05-07, offshore W08-10).

Different multivariate techniques (summary MDS in Fig. 5) revealed distinct patterns in temporal/seasonal variation in the mesozooplankton community. Temperature (seasonality) explained 12 % (p = 0.001) of the total variation in the DistLM analysis (not shown). Together with salinity (6%, p = 0.001) and chlorophyll *a* biomass (2%, p = 0.001), 20% of the observed variation (DistLM) was explained by these three environmental variables. Pair-wise tests

(PERMANOVA) revealed many significant differences between samples from different months (see Table 1 in Addendum 3), indicating clear temporal structure in the zooplankton community of the BPNS. Also, the species diversity H' differed significantly between many months (Pairwise tests in Table 2, Addendum 3). Two-way crossed SIMPER analyses showed *T. longicornis, A. clausi* and to lesser extent *C. hamatus* and polychaete larvae as the most important contributors to similarity in plankton samples from December to July (maximum 13 % for *T. longicornis* in April 2009). From August to October, the abundant harpacticoid copepod *E. acutifrons* contributed most to similarity (maximum 15 % for *E. acutifrons* in August 2009), followed by *Paracalanus parvus*. In November, copepodites from *Giardella callianassae* contributed most to similarity (14%), followed by *E. acutifrons* and *T. longicornis*.

Finally, no significant p-values were obtained from the ten pairwise tests we could run (not shown) for zooplankton samples from the same month and zone (near-mid-offshore) between 2009 and 2010. As such, we are allowed to combine data from 2009 and 2010 samples from the same month and station.

3.6 Spatial variation in the zooplanktonic community

Next to clear temporal patterns, also spatial patterns were observed. Densities often differed significantly between nearshore, midshore and offshore sample clusters (See Table 1 in Addendum 3). Average densities were highest midshore (4660 ± 2380 ind.m^{-3}), then nearshore (3150 ± 2280 ind.m^{-3}) and offshore (2620 ± 1510 ind.m^{-3}) (Fig. 3). The density per station varied between 150 and 15000 ind.m^{-3}. Also for several months, species diversity H' differed significantly between nearshore, midshore and offshore samples (Table 2, addendum 3). Two-way crossed SIMPER analyses again showed *T. longicornis* and *A. clausi*, followed by *O. dioica*, *E. acutifrons* and *P. parvus*, as most important contributors to similarity for both nearshore, midshore and offshore sample clusters, with a maximal contribution to similarity of 11 % for *A. clausi* in nearshore samples.

4. Discussion

This manuscript presents the first zooplanktonic spatial and temporal monitoring study with high taxonomical resolution in the Belgian part of the North Sea (BPNS) in nearly forty years. Overall, 137 -mainly neritic- taxa were found in the WP2 net samples, largely in accordance

with older references (e.g. Van Meel 1975, Rousseau *et al.* 2006, Brylinski 2009). However, as discussed in Van Ginderdeuren *et al.* (2012a), nine species (four copepods, two hydrozoans, one cladoceran, one mysid and one polychaete worm) were new to the Belgian marine species list (Vandepitte *et al.* 2010).

The term community is widely used and the definition usually includes the idea of a collection of species found in a particular place (Mills 1969). Morin (1999) provided tangible methods to delineate communities: (1) physically, by discrete habitat boundaries, (2) taxonomically, by the identification of dominant indicator species, (3) interactively, by the existence of strong species interactions, or (4) statistically, by patterns of species assemblages. Because of the ubiquitous presence in time and space of the dominant species (*T. longicornis* and *A. clausi* occurring at every station in every month and acting as most important contributors to similarity in SIMPER analyses), we couldn't separate well-defined communities based on biodiversity alone. As such, we can describe the mesozooplankton assemblage of the BPNS as one neritic community, with some oceanic species occasionally added through the inflow of Atlantic water (see further). This differs from other ecosystem components, such as macrobenthos (Van Hoey *et al.* 2004) or hyperbenthos (Dewicke *et al.* 2003), in which distinct species assemblages could be delineated in the BPNS (and the adjacent water bodies in case of the hyperbenthos), with typical species for every assemblage, related to the small-scale variability in the structuring environmental parameters for these ecosystem components (such as depth, mud content and median grain size in case of the macrobenthos).

4.1 Copepod community structure

The zooplankton in the BPNS was dominated year round by copepods (all calanoids in this study were identified to species level), making them a key component in the pelagic ecosystem. Most abundant were the calanoids *Temora longicornis, Acartia clausi*, *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus*, *Centropages typicus*, *Calanus helgolandicus* and the harpacticoid *Euterpina acutifrons*. This corresponds with earlier observations in or near the BPNS made by Van Meel (1975), Daro *et al.* (2006) and Brylinski (2009). Also in Dutch coastal waters, *T. longicornis, P. elongatus, A. clausi* and *C. hamatus* have been ranked as the stock-forming copepod species (Fransz 1975).

By comparing our findings with recent and older literature on zooplankton in the BPNS region, it became clear that we lost *Calanus finmarchicus.* In the 19th century, Canu (1892) reported *C. finmarchicus* from the northern French coast (close to the BPNS). Van Meel (1975) mentioned high densities of *C. finmarchicus* in the southern North Sea in the 1970s. It is known that shifts in the NAO index (linked to increasing temperatures) pushed *C. finmarchicus* progressively northwards, while *Calanus helgolandicus* became more abundant and widely distributed in the 1980s in the North Sea (Reid *et al.* 2003, Bonnet *et al.* 2005). In our present study, only *C. helgolandicus* and no *C. finmarchicus* was found, corresponding with the results of Brylinski (2009) in Dover Strait.

The North Sea mesozooplankton, and in particular its copepod communities, shows pronounced regional differences in species composition, related to the bathymetry and hydrography of the area. In shallow/coastal areas, copepods are usually dominated by smaller 'neritic' (coastal) species (e.g. *Acartia* sp., *T. longicornis*), whilst *Calanus* and *Pseudocalanus* sp. are the dominant species in deeper waters, related to Atlantic water influx (Fransz 1975, Van Meel 1975, Fransz *et al.* 1991, Nielsen and Munk 1998, Brylinski 2009, O'Brien *et al.* 2011). In the present study, *C. hamatus* - a coastal species according to Fransz (2000) - was ten times more common than *C. typicus*; the latter mainly being reported from offshore areas by Fransz *et al.* (1991). The presence of *C. typicus* clearly indicates a flux of Atlantic waters in the North Sea. Several other copepod species typical for Atlantic inflow were observed in this study, such as *C. helgolandicus, P. elongates, Metridia lucens*, *Labidocera wollastoni* and *Candacia armata*. All these larger, so-called 'oceanic' (offshore) copepod species reached much lower densities in the BPNS than the smaller calanoids, similar to the findings of Brylinski (2009) in the Dover Strait. Other non-copepod ocean wanderers found in Belgian waters that indicate Atlantic inflow, were *Tomopteris helgolandica*, *Parasagitta elegans* and *Nyctiphanes couchii*. *T. helgolandica* is the only (rare) polychaete in the southern North Sea that can be called holoplanktonic, and is known from Dutch and French waters (Fransz 2000, Dauvin *et al.* 2003). *P. elegans* is a chaetognath from the Atlantic Ocean and the more boreal parts of the North Sea (Fraser 1965). This species used to be more common (Van Meel 1975), but was only found once in the present study. *N. couchii* is the only euphausid we recorded, usually occurring in high densities in the central and northern North Sea, straying into the BPNS (Russell 1935, Van Meel 1975). It has

previously been reported from Belgian waters by Cattrijsse and Vincx (2001) and Lock *et al.* (2011).

Calanoid copepods comprised the majority of copepods all year round. Only during autumn, harpacticoid copepods increased in abundance, while Cyclopoida remained scanty all year round. This confirms the results of other studies (Van Meel 1975, Fransz *et al.* 1991, Halsband-Lenk *et al.* 2004, Wesche *et al.* 2007, Brylinski 2009), and proves that calanoid copepods are well adapted to the cold winter conditions of the southern North Sea. Total copepod numbers increased from January to September with lower peaks in April and July. *T. longicornis* showed a moderate peak in March, at the moment that diatoms still prevail on *Phaeocystis* colonies (Rousseau *et al.* 2006).

However, most calanoids became really abundant after the *Phaeocystis* bloom later in spring, with highest densities in early summer and autumn. Other studies showed that *P. globosa* is not an adequate food source for calanoids (Daro 1985, Gasparini *et al.* 2000, Antajan 2004, Nejstgaard *et al*. 2007), and it has been hypothesized that copepods switch to heterotrophic (microzooplankton) food to compensate for the low phytoplankton ingestion (Daro 1985a,b, Hansen and van Boekel 1991, Antajan 2004). In midsummer there was a clear decrease in copepod numbers. A similar decrease has been observed for diatoms, with a dominance of large species such as *Guinardia delicatula*, *Guinardia striata*, and *Rhizosolenia shrubsolei* (Daro *et al.* 2006*).* Both diatom and copepod summer minima co-occurred with a massive development of the toxic dinoflagellate *Noctiluca scintillans,* which usually starts blooming at the decline of *Phaeocystis* colonies (June-July).

4.2 Spatial, seasonal and phenological patterns in the zooplanktonic community

Our results indicate distinct but small-scale spatial patterns in the mesozooplanktonic abundance of the BPNS. Average zooplankton densities were highest midshore, then nearshore and lowest offshore. Similar spatial patterns, where densities peak in a stretch almost parallel to but some miles away from the coastline in the BPNS, have been recorded for other ecosystem components including demersal fish, epibenthos and macrobenthos (Van Hoey *et al.* 2004, De Backer *et al.* 2010). In contrast, highest phytoplankton biomass was found very close to the coast, similar to the chlorophyll *a* results given in Muylaert *et al.* (2006).

The nearest long-term monitoring stations in the vicinity of the BPNS are the Plymouth L4 survey area and Helgoland roads (O'Brien *et al.* 2011). At Plymouth L4, the most abundant taxa were *Pseudocalanus* spp. (mean abundance of 410 ind.m^{-3}), *Oncaea* spp., *Oithona* spp., *Paracalanus* spp., cirriped larvae and *Temora* spp. (270 ind.m^{-3}). This is different from the calanoid dominated BPNS, where the dominant taxa occurred in higher average densities. At Helgoland roads (German bight), calanoid copepods were omnipresent as well, together with appendicularians (*Fritillaria borealis*) and echinoderm larvae (Greve *et al.* 2004, Wasmund *et al.* 2011), conform with our results.

Next to spatial patterns, clear seasonal structuring in the zooplankton community was observed. highest average densities were noted in May-July, followed by a smaller autumn peak in September, and lowest densities in December and January. As already said, the 2009-2010 winter was the coldest in fifteen years (KMI 2010) with an average estimated SST of 4.1 °C on the BPNS (OSTIA data, Stark *et al.* 2007). This might have led to the delayed peak of zooplankton densities in 2010, compared to the highest densities occurring earlier in 2009. The long term monitoring data of the zooplankton station at Helgoland roads (German bight) also showed highest average copepod abundance in June (O'Brien *et al.* 2011).

Similar seasonal patterns in the zooplankton community structure were noted in other temperate regions, and related to the annual patterns in the phytoplankton distribution, as this constitutes the primary food source for zooplankton (Van Meel 1975, Greve *et al.* 2004, Daro *et al.* 2006, O'Brien *et al.* 2011). Reid *et al.* (1990) stated that phytoplankton dynamics in the North Sea are a very complex matter, and that algal successions and blooms often don't follow classical patterns. Greve *et al.* (2004) observed the onset of this yearly phytoplankton bloom in the German bight in April, just like in our study. Antajan (2004) also found highest phytoplankton biomasses in the BPNS in April, attributable to *Phaeocystis globosa*, after a (smaller) first diatom peak in March.

In spring and summer, the holoplanktonic copepods were typically joined by high numbers of meroplanktonic larvae, including echinoderm larvae. Long-term monitoring since the 1940s, mainly during the Continuous Plankton Recorder surveys (CPR, SAHFOS), revealed large-scale and long-term changes in the abundance and phenology of North Sea plankton

(Beaugrand 2003, Lynam *et al.* 2004, Greve *et al.* 2005, Richardson 2008). Temperate marine environments such as the southern North Sea may be particularly vulnerable to these changes, because the recruitment success of higher trophic levels is highly dependent on synchronization with the pulsed planktonic production (Hjort 1914, Cushing 1990, Eilertsen and Wyatt 2000, Kirby *et al.* 2007).

In general, holozooplankton are peaking earlier by 10 days in the North sea, diatoms by 22 days, and meroplankton by 27 days over the past 45 years (Richardson 2008). The changes in the abundance and phenology of the meroplankton appear to be related to temperature increase. North Sea SST increase has been greatest in the winter and spring months, but temperatures in general are now higher throughout the year (Kirby *et al.* 2007). Egg size and number in poikilotherms can be seen as phenotypically plastic traits that can vary according to temperature. Sheader (1996) and Fischer *et al.* (2003) have shown that higher temperatures during gametogenesis are usually associated with smaller eggs but larger clutches. This relationship may contribute to a larger reproductive output for taxa that produce meroplanktonic larva (Brante *et al.* 2003). Meroplankton is also likely to be influenced by temperature during the planktonic phase. For example, higher temperatures will shorten larval development time and larval survival will increase (Fenaux *et al.* 1994, Lindley and Kirby 2007). In this way, increases in temperatures can influence reproductive output in a wide variety of organisms with similar life-history strategies.

An extreme is noted for (meroplanktonic) *Echinocardium cordatum* larvae, which are nowadays appearing in the plankton 47 days earlier than they did 50 years ago (Edwards and Richardson 2004). The density of echinoderm larvae has increased steadily, and now they are the most abundant taxon in the CPR samples (Lindley and Kirby 2007). Also, in our study *E. cordatum larvae* are found to be the most abundant meroplanktonic species, with a peak in May. It is known that temperature promotes growth and reproduction (larval release) in echinoderms (Kirby *et al.* 2007).

Detailed info on decadal trends in zooplankton community structure in the North Sea is given in the ICES zooplankton status report (O'Brien *et al.* 2011). At Helgoland Roads, a long-term monitoring station in the German bight, the time series started with a negative phase in 1975, followed by a copepod increase with consistent higher than average abundances

during much of the 1980s. After a period of transition (1990–1997), copepod densities decreased and remained in a negative phase, with lower than average abundances. A negative correlation was found between SST and copepod abundance anomalies, with the lowest abundances noted in the periods with highest water temperatures (Greve *et al.* 2004, Hay *et al.* 2011).

A comparison with the long-term CPR-data in the vicinity of Helgoland Roads, suggested a time-lagged synchrony in copepod abundance, with the Helgoland Roads abundance anomalies being ahead of the CPR anomalies by 3–5 years (Hay *et al.* 2011). Hay *et al.* (2011) concluded that water temperature increased more dramatically in the shallow waters at Helgoland Roads than in the North Sea as a whole, possibly explaining why the changes occurred more rapidly in the Helgoland copepod population.

These findings illustrate that a high proportion of the year-to-year variability of the North Sea zooplankton is determined by a physical mechanism related to long-term and large scale climate changes. Probably also in the shallow Belgian waters zooplankton species nowadays appear earlier, but unfortunately almost no long-term CPR or monitoring data exist for the BPNS to unequivocally confirm this phenomenon.