

CHAPTER 5

GENERAL DISCUSSION, CONCLUSIONS AND FUTURE CHALLENGES

5.1 It started with... a change in course

Most European commercial fish stocks are overfished and at the same time fisheries are under substantial financial pressure in several countries (FAO 2012). Beam trawl fisheries dominate the Belgian fishing fleet, although they are subject to high exploitation costs and they execute negative impacts on the marine ecosystem, mainly because of discarding large amounts of non-commercial and undersized commercial species, and the impact on the benthic fauna (Groenewold and Fonds 2000, Depestele *et al.* 2008). To work out a sustainable strategy for the Flemish fisheries sector it is necessary to extend the used fishing methods. This includes developing niche fisheries and a sustainable exploitation of the living marine resources. For many years, potential alternatives for beam trawl fisheries are being investigated at ILVO; examples are the commercial use of trammel nets, fishing pots and fishing lines (Verhaeghe *et al.* 2008). However, although Belgium used to have a pelagic fishery (Lescrauwaet *et al.* 2010), a renewed potential for a 'real pelagic' exploitation has not yet been investigated.

Pelagic fisheries largely contribute to the total fish catch in many open seas (FAO 2012). Moreover, there is a global trend from an ecosystem dominated by demersal fish species towards a system with more and smaller (semi-)pelagic fish, a worldwide phenomenon called 'fishing down the food web' (Pauly *et al.* 1998). As opposed to its benthic ecosystem components (meio-, macro-, epi-, hyperbenthos, benthic and demersal fish), the pelagic ecosystem components (except for sea mammals and harmful algae) are traditionally less studied in the North Sea. Nonetheless, there are many benthic organisms with one or more pelagic life stages, and zooplankton is known to play a crucial role in the pelagic as main food source for higher trophic levels (Harris *et al.* 2000, Richardson 2008). A better knowledge of the spatial and temporal distribution of this zooplankton, in relation to the presence of

pelagic fish species (and seabirds), was therefore necessary to estimate the importance of the pelagic ecosystem and the possibilities of a small-scale (semi-)pelagic fishery in Belgian waters.

Starting in 2009 with this PhD study, we went for monthly sampling campaigns with the R.V. Zeeleeuw, with the intention to map the presence and abundance of pelagic fish in the Belgian part of the North Sea (BPNS). For this, we deployed a pelagic net (4*4 m) that is kept open by two midwater superkrub boards. However, in the choppy waters of the southern North Sea strong currents are a daily phenomenon, and using this larger net type from R.V. Zeeleeuw didn't go very smoothly. The research vessel had to drag its fishing gear from the starboard side (as there was no A-frame at the back), which at least three times led to trawl doors or net material getting into the propeller, and again another lost campaign. Also, in the few cases we were able to deploy the net without problems, we caught very few fish. Does this mean that few pelagic fish were present or that the gear wasn't working properly? Or where these fish outsmarting us? It is no secret that pelagic fish spend a lot of time in school. After four cruises, we decided to stop risking the ship, crew and valuable time of other scientific cruises. We started using a less erratic 3*1 m outrigger semi-pelagic trawl, which delivered us much more fish, but only sampled the near-bottom part of the water column, while we didn't capture any data from the upper part of the water column. Some literature suggests that pelagic fish often reside closer to the seafloor during daytime (Blaxter and Hunter 1982, Köster and Schnack 1994, Cardinale *et al.* 2003), implying we probably sampled a large part of what was there. On the other hand, several studies prove that seabirds that won't dive deep (e.g. terns), catch a lot of pelagic fish at the water surface during daytime, also in the BPNS (e.g. Vanaverbeke *et al.* 2011).

As we were not able to cover the full water column, we dare not present quantitative info on the pelagic fish stocks present in the BPNS. So we changed course, and instead of focusing on the possibilities of a small-scale pelagic fishery in the BPNS, all the time and effort of this PhD study was spent on the first part of the initial work, namely to expand and update our knowledge of the mesozooplankton community in the southern North Sea, and to characterize the trophic role of zooplankton as prey for small pelagic fish.

Remark: anno 2013, the sampling possibilities are very different: the new R.V. Simon Stevin is able to drag a full-sized pelagic net at the back, which will allow us to finally figure out which pelagic fish are swimming where, when and in what numbers in the whole water column. There is opportunity for the future...

5.2 Zooplankton species composition in the Belgian part of the North Sea

This PhD presents a comprehensive study on the zooplankton of the Belgian part of the North Sea, based on monthly sampling campaigns in 2009-2010, taken with a WP2-net at ten locations spread over the entire BPNS on a near-mid-offshore gradient. This study provides zooplankton data with a high taxonomical resolution and a full spatial and temporal coverage of the BPNS. It was nearly forty years ago that a study with such amount of spatial, temporal and taxonomical detail focused on zooplankton as the main ecosystem component in the BPNS (Van Meel 1975). Overall, 137 zooplankton taxa were found in the WP2-net samples, of which nine species were new to the Belgian Register of Marine Species (Vandepitte *et al.* 2010). As such, this study acts as an up-to-date benchmark and reference for future work on zooplankton in the BPNS.

The BPNS zooplankton is year round dominated by calanoid copepods. This corresponds with earlier observations in or near the BPNS made by Van Meel (1975), Daro *et al.* (2006) and Brylinski (2009) as well as with Dutch and German (Helgoland Roads) literature ranking these calanoid copepods as stock-forming plankters, together with echinoderm larvae and appendicularians (Fransz 1975, Greve *et al.* 2004, Wasmund *et al.* 2011, O'Brien *et al.* 2011). At Plymouth L4 station (long-term monitoring station in the western part of English Channel), the most abundant taxa differed from those in the BPNS and occurred at lower densities (see Chapter 2 and Addendum 1, for a thorough overview of the zooplankton composition).

By comparing our findings with literature on Belgian zooplankton, it becomes clear that *Calanus finmarchicus* has disappeared. Van Meel (1975) mentioned this calanoid to still reach high densities in the southern North Sea in the 1970s. In this study, only *C. helgolandicus* and no *C. finmarchicus* was found, corresponding with the recent results of Brylinski (2009) in the Dover strait. This is important, because the virtual absence of *C. finmarchicus* in the southern North Sea has a very negative effect on cod recruitment. This

now vanished large calanoid copepod used to act as an important food source for cod larvae (Beaugrand *et al.* 2003).

The North Sea mesozooplankton, and in particular its copepod communities, is often considered to show 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 very common whilst larger species typical for Atlantic inflow such as *C. typicus*, *C. helgolandicus*, *P. elongates*, *Metridia lucens*, *Labidocera wollastoni* and *Candacia armata* reached much lower densities (Addendum 1), similar to the findings of Brylinski (2009) in the Dover strait.

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), we couldn't separate well-defined communities based on distinct species compositions. Instead, we describe the mesozooplankton assemblage of the BPNS as a neritic community, occasionally influenced by some oceanic species through the inflow of Atlantic water. This differs from other ecosystem components, such as macrobenthos (Van Hoey *et al.* 2004) or hyperbenthos (Dewicke *et al.* 2003), where distinct species assemblages could be delineated in the BPNS region, related to small-scale variability in some structuring environmental parameters (depth, mud content and median grain size in case of the macrobenthos).

5.3 Invasive species and warmer jellyfish infested waters

It is generally considered that concomitant with rising temperatures, plankton biodiversity is increasing in the North Sea, due to an influx of fish larvae and plankton species from warmer waters (Greve *et al.* 2005, Richardson 2008). In terms of ecosystem productivity this change is currently considered detrimental, because the southern/warmer-water species are rarely replacing the colder-water species in similar abundances and phenology (Beaugrand *et al.* 2003, Bonnet *et al.* 2005). This in turn may negatively impact other trophic levels including fish larvae. As shown above, we found that *C. finmarchicus* has disappeared from Belgian

waters and has been replaced by *C. helgolandicus*. Great spatial variation was observed in the distribution of the latter and we found no preference by pelagic fish towards this prey species in comparison with other calanoids (see further). In general, it can be stated that *Calanus* sp. no longer act as staple food for pelagic fish in the southern North Sea, in contrast to previous results from the southern regions and to recent work in the northern part of the North Sea (Beaugrand *et al.* 2003, Prokopchuk and Sentyabov 2006).

Marine invasions are considered a major threat for the world's oceans. Although few species completely vanish from an area, many others pop up out of the blue, albeit often by means of direct human help (Kerckhof *et al.* 2007). While ballast water is crucial for safe and efficient modern shipping operations, it conveys marine species on a worldwide scale. The International Maritime Organization (IMO) estimated that the 3.4 billion tons of ballast water annually move some 7000 species around the world at any given time (Carlton 1985, Clarke *et al.* 2003, Globallast 2007). It is important to know how many 'exotic/non-indigenous' species are present in any system, and which ones are or could be called 'invasive' species, defined as introduced species that adversely affect (be it economically, environmentally or ecologically) the habitats and bioregions they invade.

The Belgian part of the North Sea also received a large number of invading species. Currently, 71 marine 'non-indigenous' species (algae, crustaceans, cnidarians, *etc.*) have established persistent populations in the BPNS (Kerckhof *et al.* 2007, Vandepitte *et al.* 2012). Despite the fact that many non-indigenous species have (mero)planktonic larval stages, only two of the in total 98 zooplanktonic taxa we identified to species level in the BPNS can be considered non-indigenous species, namely *Nemopsis bachei* (a hydrozoan) and *Mnemiopsis leidyi* (a ctenophore). Since their introduction in 1996 and 2007 respectively, these coelenterates now occur along the entire Belgian coastline in well-established populations (Van Ginderdeuren *et al.* 2012a,b).

Are we now heading for warmer waters dominated by invasive species and jellyfish?

We did a search in www.mediargus.be (the daily press monitoring of Belgium) using keywords as "verkwalling", "plankton soep" and "kwallen" (*i.e.* Dutch for gelatinous, plankton soup and jellyfish). The hundreds of Belgian (and international) newspaper articles - and their often frightening headlines - speak for themselves: scientific results on jellyfish

increase have seeped into everyday media. The reader is told that we are heading for a plankton soup, dominated by invasive species and jellyfish, and that jellyfish are bound to dominate the North Sea ecosystem. But do these phenomena, published both in vulgarizing and scientific literature worldwide, (already) take place in the BPNS?

The invasive ctenophore *M. leidyi* is known for its notorious effect on the pelagic ecosystem of the Black Sea in the 1980s (Vinogradov *et al.* 1989). Due to preserving problems (the body tissue dissolves completely in formaline), this ctenophore remained below radar in our first sampling campaigns. Upon the moment of discovery, *M. leidyi* was already distributed along the entire Belgian coastline (Van Ginderdeuren *et al.* 2012b). In 2009-2010, it even survived the coldest winter in fifteen years in Belgian waters, and it remained present along the coastline and in all ports during the following summer (L. Vansteenbrugge, pers. comm.). This suggests that *M. leidyi* has likely established a permanent population in the BPNS, which might even act as a source for the invasion of other colder waters. The observed peak densities and biovolumes are still lower than in Denmark, the Black Sea and its adjacent water bodies, or the natural habitat in the US (Decker 2004, Riisgård *et al.* 2007). For the time being, a scenario similar to that in the Black Sea (which is a very different ecosystem, see discussion in Chapter 2 - Annex 1) is not likely to occur in the BPNS, but cannot be ruled out.

Also, for the sixteen other coelenterate species found in our study (four cnidarians, ten hydrozoans and two ctenophores) no abnormally high densities were observed, albeit rare to find quantitative info on indigenous species. Jellyfish and ctenophores often thrive in areas with high anthropogenic impacts, such as overfishing, eutrophication, translocation and habitat modification (Mills 2001, Purcell *et al.* 2007, Richardson 2008, Richardson *et al.* 2009). Purcell (2005) concluded that temperate jellyfish species might benefit from global warming, whilst tropical species (with a thermal maximum around 34-35 °C) are likely to decline. Studying the distribution edges of important planktonic species is vital and tells a lot about changes in the ecosystem. The fact that little quantitative information on North Sea jellyfish is available yet, and that scientists are not sure how jellyfish populations are evolving, are justifications to conduct more research on the important trophic (and often invasive) group called gelatinous zooplankton. Our findings of *M. leidyi* in the BPNS, already led to the start of a European project (MEMO, Interreg-4A '2 seas', nr. 06-008-BE-MEMO,

2009-2013) that specifically focuses on the threats exerted by *M. leidyi* and other jellyfish on the marine food web in the eastern English Channel and the southern North Sea (Cf. PhD study by L. Vansteenbrugge at ILVO - in prep.).

5.4 Spatial, temporal and phenological patterns in the zooplankton community

Our results point out spatial and temporal distribution patterns in the mesozooplankton abundances in the BPNS.

Average zooplankton densities were highest midshore, then nearshore and lowest offshore. These spatial patterns, characterized by densities not peaking close to the shoreline but some miles away from the coastline, are similar to those recorded in recent studies that focused on other ecosystem components in the BPNS, such as demersal fish, epibenthos or macrobenthos (Van Hoey *et al.* 2004, De Backer *et al.* 2010). Benthos distribution however, is more patchy and changes along the Belgian coastline (west coast - east coast) (Van Hoey *et al.* 2004). In contrast, highest phytoplankton biomass was found nearshore, similar to the chlorophyll *a* results of Muylaert *et al.* (2006).

Most of all, a clear seasonal structuring of the zooplanktonic abundance is observed in our study. 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 (data extrapolated from OSTIA: Stark *et al.* 2007). This might have led to the delayed peak of zooplankton densities in 2010, compared to the highest densities occurring in May in 2009. A similar seasonal pattern in zooplankton abundance is noted in most temperate regions, related to the annual patterns in the phytoplankton distribution, as this phytoplankton is known as the primary food source for zooplankton (Van Meel 1975, Greve *et al.* 2004, Daro *et al.* 2006, O'Brien *et al.* 2011).

At a regional scale, it has been found that trends in phytoplankton are rather correlated with hydro-climatic variability than with anthropogenic input (Richardson and Schoeman 2004, Richardson 2008). However, excessive nutrient loads brought by the discharge of major western European rivers still lead to eutrophication in the shallow southern North Sea (Rousseau *et al.* 2006). The unbalanced nutrient environment, characterized by an excess of nitrate over silicate and phosphate, leads to yearly re-occurring spring algal blooms, with a sudden change in phytoplankton dominance from diatoms to the harmful flagellates

Phaeocystis globosa and *Noctiluca scintillans* (Lancelot 1995, Vasas *et al.* 2007). These are considered a bad food source with a low nutritive value for zooplankton (Antajan 2004), and formation of large colonies by *P. globosa* appears to reduce predation by small copepods such as *Acartia*, *Temora* and *Centropages* (Nejstgaard *et al.* 2007).

Eutrophication may thus lead to less favorable conditions for the zooplankton in coastal regions such as the BPNS. Also, for deeper water masses in the Northeast Atlantic, it is thought that the amount of time phytoplankton cells will spend in the euphotic zone will increase with climate change, because warmer temperatures boost metabolic rates and enhance stratification (Richardson 2008). As such, climate change may even exacerbate the negative effects of eutrophication, if for example, the above would be reflected in an extended period of harmful algae dominance (Richardson 2008).

In spring and summer, the holoplanktonic copepods are typically joined by high numbers of meroplanktonic larvae, including echinoderm larvae (see Chapter 3 and Addendum 1, for a thorough overview of all zooplankton abundances). Long-term monitoring since the 1940s with the Continuous Plankton Recorder (CPR, SAHFOS) reveal large-scale and long-term changes in the abundance and phenology of North Sea plankton (Lynam *et al.* 2004, Greve *et al.* 2005, Richardson 2008). 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). An extreme is noted for *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.

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, 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). Hay *et al.* (2011) further concluded that a high proportion of the year-to-year variability of the zooplankton of the

North Sea 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 confirm this phenomenon.

In January 2013, the monitoring station at Gravelines (nearshore station situated in close vicinity of Dunkirk port, eastern English Channel, sampled by IFREMER) was added to the - publicly available- COPEPODITE zooplankton monitoring metabase. There are no data from this station in the earlier ICES zooplankton status reports but monthly sampling results will be provided shortly (Pers. comm. Elvire Antajan, IFREMER). This is important information, since it implies that nearshore zooplankton data from the eastern English Channel will become available in the near future. If zooplankton sampling in the BPNS is to be continued, we will compare both the Belgian and French nearshore datasets.

5.5 Diet composition of the four pelagic fish species

A study sampling pelagic fish and zooplankton simultaneously every month during consecutive years, spanning nearshore to offshore sampling locations, is unprecedented in the southern North Sea. We focused on the four most abundant small pelagic fish species in the BPNS, namely herring (*Clupea harengus* L., Clupeidae), sprat (*Sprattus sprattus* L., Clupeidae), mackerel (*Scomber scombrus* L., Scombridae) and horse mackerel (*Trachurus trachurus* L., Carangidae). As discussed in Chapter 5.1, the pelagic fish were gathered by means of different nets (pelagic, semi-pelagic outrigger, and extra hand-lining for mackerel), simultaneously with the zooplankton sampling. As such, we were able to investigate the diet of these pelagic fish species with great temporal and spatial detail, and link the diet results directly to the *in situ* zooplankton community present in the Belgian part of the North Sea.

A total of 71 prey taxa were found in 725 stomachs. Copepods (16 taxa) were found in 64 % of all stomachs and represent 77 % of all found prey items. The proportion of fish with empty stomachs over the entire investigated period was low (11 %) for all four pelagic species, indicating that the Belgian part of the North Sea acts as a valuable feeding ground for pelagic fish.

Both numerical and gravimetric analyses showed that the diet of herring and sprat was dominated by calanoid copepods. Only two copepods *Temora longicornis* and *Centropages hamatus* accounted for nearly three quarters of all ingested prey items in the four fish species. In sprat even 93 % of the ingested prey items were calanoid copepods. Herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. The larger adult herring (> 20 cm) all had (nearly) empty stomachs. This may be attributed to the fact that they were caught late autumn, when so-called 'fat' herring temporarily stops feeding before spawning in winter (Hardy 1924, Muus and Nielsen 1999). Mackerel added sandeels to an otherwise planktivorous diet. Horse mackerel consumed both benthic and pelagic prey. Generally, there were many similarities between our findings on prey composition (at least at higher taxon level) with other studies (Hardy 1924, De Silva 1973, Sandström 1980, Last 1989, Arrhenius and Hanson 1992, Huse and Toresen 1996, Dalpadado *et al.* 2000, Darbyson *et al.* 2003, Voss *et al.* 2003, Möllmann *et al.* 2004, Bernreuther 2007, Segers *et al.* 2007). However, many differences were noted as well (see Chapter 4 for an extended discussion on (dis)similarities in diet composition).

Many mackerel stomachs were nearly empty. One may wonder if this is related to the sampling technique, using pole and rod, although this is contradicted by several studies stating that hooked lures select for feeding fish, not for fish with empty stomachs (Dempster *et al.* 2011, Reubens *et al.* 2013). We concluded that the total copepod numbers in mackerel stomachs are too low to fulfill the daily energy demand of these very active fish. This is confirmed by the gravimetric analyses, which showed that fish were a far more important food source than crustaceans for mackerel. At least 20 % of the investigated mackerel had eaten sandeels or fish larvae, and we estimate the importance of sandeels in the diet of mackerel even much higher. Little quantitative information is available on the distribution of sandeels in the BPNS. No less than five species are found (Vandepitte *et al.* 2010): *Ammodytes tobianus*, *Ammodytes marinus*, *Gymnammodytes semisquamatus*, *Hyperoplus lanceolatus* and *Hyperoplus immaculatus*. They are often reported as bycatch in Van Veen bottom grabs and beam trawls, and as important food source for Belgian seabirds (Vanaverbeke *et al.* 2011). More detailed information (with bigger pelagic nets) must be gathered to solidify our thoughts on the trophic relationship between sandeels, small pelagic fish and seabirds in the BPNS.

5.6 Bottom-up control by zooplankton or selective foraging behavior by pelagic fish?

From the > 100 zooplankton species in the water column, only two (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items. Still, pair-wised tests revealed significant differences in prey abundance in the stomachs between the four fish species, as well as significant differences in spatial and temporal patterns. The fact that the spatial and temporal differences in the pelagic fish diet are less pronounced compared to the zooplankton community patterns, is most probably related to a ubiquitous presence of the dominant plankton species in the fish diet.

Also, no correlation between fullness index and prey density was found. This led us to believe that calanoid copepod densities aren't a limiting factor in the feeding ecology of pelagic fish in the BPNS. Herring may show cannibalism on its own eggs and larva (Hardy 1924, Dalpadado *et al.* 2000), especially when zooplankton concentrations are (too) low (Rudakova 1966, Last 1989, Ellis and Nash 1997), which might impact the abundance of these herring year classes (Holst 1992). Similarly, Segers *et al.* (2007) suggested that herring forages on eggs when other prey are scanty. In our study, cannibalistic pressure was limited as clupeid larvae were found in only four herring stomachs and only few fish eggs were eaten, indicating the presence of sufficient other prey. Also, the fact that smaller and faster plankton species were left aside (see below), supports the idea that zooplankton was not restrictive, and that pelagic fish in the BPNS are not bottom-up regulated by their zooplanktonic prey.

However, there was a very different composition of zooplankton species and life stages in the zooplankton samples, compared to those found in the fish stomachs. For example, *A. clausi*, one of the most common zooplankton species in the BPNS, was barely found in the stomachs. This was also observed by Casini *et al.* (2004) in the Baltic, and is probably related to the small size and high escape response of *Acartia* spp. (Viitasalo *et al.* 2001) and possibly also to the fact that the genus is often considered a surface dweller (Hansson *et al.* 1990), thus perhaps not always spatially overlapping with fish whereabouts.

Several species, which are known to constitute an important part of herring and sprat diets in other areas (Hardy 1924, De Silva 1973, Prokopchuck and Sentyabov 2006), are common in the plankton samples (e.g. the urochordate *Oikopleura dioica*, the harpacticoid copepod *E.*

acutifrons, the cladoceran *Evadne nordmanni*, meroplanktonic echinoderm larvae, fish larvae and fish eggs), but they are rarely found in the diet of the four studied fish species.

Just 6 % of all copepods in the diet were copepodites, compared to 62 % of the copepods (taking into account only the species found in the stomachs) in the water column. Of course, the peak abundance of copepodites is clearly limited to certain periods of the year, but the selectivity towards 'bigger' prey was also observed for herring, sprat and mackerel in the Norwegian Sea and in the Baltic (Prokopchuk and Sentyabov 2006, Möllmann *et al.* 2004, Bernreuther 2007).

Much more female copepods were eaten than males, in contrast to the well-balanced distribution of both sexes (of species that were preyed upon) in the water column. Possibly these females with egg sacs swim a bit slower and are easier to catch. These findings are in line with results published on Baltic herring, which showed selective predation on larger individuals and egg-carrying females of copepods and cladocerans (Sandström 1980, Flinkman *et al.* 1992).

All these findings are indicative of a profound selective feeding behavior exhibited by all four pelagic fish species. The omnipresence of the copepod *Temora longicornis* in the diet of herring, sprat, mackerel and horse mackerel speaks for itself. But does it involve an inherent risk to forage on only a very limited number of ubiquitous zooplankton species? What were to happen if the smaller *A. clausi* (the most abundant, but almost not preyed copepod in the BPNS) outcompeted *T. longicornis* in Belgian waters? Would fish just switch to smaller or other prey types? These are important topics given the selective feeding behavior shown above. For the southern North Sea and English channel there is no evidence (yet) that *A. clausi* will be replacing *T. longicornis* (Barnard *et al.* 2004), but for the Baltic a steadily increase in biomass of *Acartia* spp. was noted in the nineties (Möllmann *et al.* 2002, 2003). Still, the spring development of *T. longicornis* is complex and depends not only on prevailing temperatures, but also on spring bloom timing and post-bloom food availability (Dutz 2010). Mismatches may lead to profound changes in prey availability. Actually, we simply don't know how pelagic fish in the southern North Sea would respond to a decreased population of *T. longicornis*.

From a historical perspective the relationships between fish and their planktonic prey clearly remains viable, although substantial changes can be shown. Garrido and Murta (2011) showed interdecadal differences in the diet composition of horse mackerel, proving that predatory fish can change their trophic niche (and the whole food web configuration) as an adaptation to changing prey abundances and prey availability.

This leads us to conclude that even minor changes in the ecology or phenology of the dominant zooplankton species could have profound effects on the pelagic fish stocks. As shown in the previous paragraphs, fish and plankton species typical for warmer waters are moving northwards and increase in the North Sea (Richardson 2008), but they seldom replace the cold-water species in similar abundances (Beaugrand *et al.* 2003, Bonnet *et al.* 2005). Further changes in the zooplankton communities are thus likely to occur in the future (Richardson 2008).

Large scale decadal trends in salinity, temperature and hydrodynamic regimes, caused by Atlantic oscillations (NOA) influence zooplankton communities worldwide (Fransz *et al.* 1991, Reverdin *et al.* 1997, O'Brien *et al.* 2011). Temperate marine environments such as the southern North Sea may even be more vulnerable to these changes, because of a dependence of fish recruitment success on the yearly synchronization with planktonic prey production (Hjort 1914, Cushing 1990, Kirby *et al.* 2007). Pelagic fish are thus influenced directly and indirectly by climate changes, as increasing water temperatures will force them to migrate northwards in eastern Atlantic waters, and will lead to changes in the development of their favored prey (Frederiksen *et al.* 2006, Prokopchuk and Sentyabov 2006).

An important question is how long will the marine ecosystem – already weakened by other anthropogenic stressors- need to resynchronize its phenological relationships to adapt to warmer temperatures? Therefore, it is important to further monitor both pelagic fish and their zooplanktonic prey populations, and to be aware of possible shifts in or mismatches with the plankton, organisms at the basis of marine ecosystems.

5.7 Implications of this pelagic PhD study for policy, conservation and management

European marine waters harbor a tremendous biological diversity, but the biodiversity is also under threat from a multitude of transnational stressors, such as fishing, pollution, ocean

acidification, anoxia and climate change. As such, member states have both the moral and legal obligation to prevent biodiversity loss and to meet the international commitments on biodiversity conservation. However, politicians usually tend to work and think on a national level, and national interests all too often play a dominant role in the decisions that are adopted. Combine this with the fact that zooplankton are a very “international” animal group - many zooplankton species were born in France before passing in Belgian waters and settling or dying in the Dutch part of the North Sea - and one quickly realizes there is an incongruity.

It is important to emphasize that zooplankton can be seen as a very good **indicator of environmental changes** in the North sea for several reasons: zooplankton is highly temperature dependent, with physiological rates doubling or even tripling given a 10 °C temperature rise (Mauchline 1998); zooplankton is not commercially exploited in the North Sea; zooplankton organisms are practically all short-lived (< 1 year), which allows for a tight coupling between climate change and zooplankton population dynamics; and finally, the majority of zooplankton species is free floating during their whole life (Richardson 2008). A high proportion of the year-to-year variability and decadal trends in the zooplankton of the North Sea is related to long-term and large scale climate changes, while except for eutrophication, the effect of land-based activities (e.g. sand extraction, dredging or pollution) is almost neglectible (Fransz *et al.* 1991, Reverdin *et al.* 1997, Richardson 2008, O’Brien *et al.* 2011). This means that the distribution of zooplankton can accurately reflect temperature and ocean currents.

As such zooplankton is a study object capable of answering many of the questions raised by scientists, conservationists but also policy makers. However, it remains difficult to convince politicians of the importance of zooplankton and the continuous monitoring of that zooplankton in our Belgian waters. As shown above, zooplankton plays a major role in the marine food web. In contrast to benthic or sessile organisms (e.g. polychaetes or corals), it is not very useful to create a marine protected area (MPA) to conserve zooplankton biodiversity. One can only ‘protect’ zooplankton by a good management of external factors, such as climate change and eutrophication. This does not mean that a small country such as Belgium should neglect the zooplankton or that we cannot contribute to the conservation of this so important trophic group.

Belgium can prove itself most useful by providing small scale but detailed knowledge, which allows for an upscaling of these results to stakeholders abroad. Our planktonic research has distilled important insights into zooplankton species diversity, community structure and phenology in the small pocket of North Sea we call our own. But in order to further lift the quality and durability of zooplankton research in Belgium, we consider it of utmost importance to maintain a constant supply of data, in the form of continuous zooplankton monitoring.

In Europe, many of the environmental objectives, guidelines and obligations are determined by European legal entities. The Marine Strategy Framework Directive (MSFD, European Commission) obliges member states (including Belgium) to reach good environmental status (GES) by 2020 (Marine Strategy Framework Directive: 2008/56/EC). By reference to the initial assessment, member states will determine a set of characteristics for GES, based on 11 qualitative descriptors, in respect of each marine (sub)region. This includes establishing environmental targets and associated indicators. Zooplankton should be involved in at least four descriptors of the MSFD:

- Descriptor 1: Biological diversity is to be maintained. The quality and occurrence of habitats and the distribution and abundance of species are in line with prevailing physiographic, geographic and climatic conditions;
- Descriptor 2: Non-indigenous species introduced by human activities are at levels that do not adversely alter the ecosystems;
- Descriptor 4: All elements of the marine food webs, to the extent that they are known, occur at normal abundance and diversity, and levels capable of ensuring the long-term abundance of the species and the retention of their full reproductive capacity;
- Descriptor 5: Human-induced eutrophication is minimized, especially adverse effects thereof, such as losses in biodiversity, ecosystem degradation, harmful algae blooms and oxygen deficiency in bottom waters.

One of the priorities of the MSFD is to identify a suite of ecological parameters from the available datasets, which are useful to indicate good or bad environmental status in the

contexts of biodiversity and ecosystem functioning. Up till now, zooplankton is not included in any of these descriptors. For the Belgian 'pelagic' zone, GES is currently only based on eutrophication *s.s.* (Descriptor 5). This includes indicators such as chlorophyll concentrations, density of the harmful alga *Phaeocystis* sp., and total nutrient concentrations.

Our study has proven that mesozooplankton dynamics in the BPNS are complex and that spatial and temporal structure can vary a lot. Highest zooplankton densities for instance were found in areas with lower phytoplankton biomass. Therefore, evaluating the pelagic environment based on phytoplankton info and eutrophication indicators alone (as it is stated in MSFD now), seems inaccurate to us.

The development of a zooplankton biodiversity index, similar to Benthos Ecosystem Quality Index (Van Hoey *et al.* 2007), might be a good step forward to provide useful information on the status and especially the short and long term evolution of the pelagic ecosystem. Especially if reference conditions can be established from climatological time series. If we know the baseline for a degraded ecosystem, we can work to restore it. This index should take into account certain keystone (e.g. *T. longicornis*) and non-indigenous species (e.g. *M. leidyi*.) or species groups (e.g. total jellyfish numbers), and use simple ratios such as abundance of diatoms *vs.* calanoids, phytoplankton *vs.* zooplankton or zooplankton *vs.* chlorophyll *a*. The use of this zooplankton biodiversity index for management and conservation purposes, implies to conduct small scale but permanent monitoring of the zooplankton populations in Belgian waters.

5.8 Main conclusions of this pelagic study

The general aim of this PhD study was to expand and update our knowledge of the mesozooplankton community structure in the southern North Sea, and to characterize the trophic role of zooplankton as prey for pelagic fish. This was established by sampling zooplankton and pelagic fish on a monthly basis for two years in 2009 and 2010 in the Belgian part of the North Sea, and spending quite some time in the lab to identify all zooplankton taxa and to do the stomach content analyses. The scientific value of this thesis lies in the fact that we could not only look into the zooplanktonic community structure with great temporal and spatial detail, but also link these *in situ* plankton results directly to the diet of four pelagic fish species.

In an attempt to close the identified gaps in available data and information, this study concludes as follows:

Which zooplankton species are present in the Belgian part of the North Sea?

The most abundant taxa in the WP2 nets were the calanoid copepods *Temora longicornis*, *Acartia clausi*, *Paracalanus parvus*, *Centropages hamatus*, *Pseudocalanus elongatus*, *Centropages typicus*, *Calanus helgolandicus* and the harpacticoid *Euterpina acutifrons*. In spring and summer these holoplankton species were joined by high numbers of meroplanktonic echinoderm and decapod larvae. Among the 137 taxa encountered, nine were never before reported from Belgian waters: four copepods, two hydrozoans, one cladoceran, one mysid and one polychaete. We found several specimens of the rare monstrilloid *Cymbasoma germanicum*, including several male specimens that had never been observed before. The calanoid copepod *Calanus finmarchicus* seems to have disappeared completely from the Belgian scene. The updated zooplankton species list (the last one dates from some 40 years ago) contributes to the present-day knowledge of the total species richness in the southern North Sea, and forms a valuable basis and checklist for future ecological surveys.

Which non-indigenous zooplankton species are present in the BPNS?

Currently, at least 71 marine 'non-indigenous' species (algae, crustaceans, cnidarians, etc.) have established persistent populations in the BPNS. Despite the majority of these non-indigenous species having meroplanktonic larval stages, only two of the in total 98 zooplankton taxa we identified to species level were holoplanktonic exotic species: *Nemopsis bachei* (a hydrozoan) and *Mnemiopsis leidyi* (a ctenophore). Since their introduction in 1996 and 2007 respectively, both non-indigenous coelenterates have largely expanded their distribution range, and now occur along the entire Belgian coastline in well-established populations. Sightings of adult *M. leidyi* in the coldest winter months, imply that this gelatinous ctenophore species can survive Belgian winters, not only in (semi) enclosed water bodies such as harbors, but also in open sea conditions. The observed peak densities and biovolumes are still lower than in the Baltic Sea, the Black Sea or its natural habitat in the US. However, taking into account the notorious impact of this species in the different invaded

waters, it is recommended to extend the monitoring of *M. leidy* populations in the Belgian part of the North Sea.

How are the zooplankton communities spatially and temporally structured?

Smaller 'neritic' (coastal) copepod species, and especially *T. longicornis* and *A. clausi* dominated the overall zooplankton densities. Because of the ubiquitous presence in time and space of the dominant species, the mesozooplankton in the BPNS can be typified as a single neritic zooplankton community (from species perspective). Yet, these neritic species are often joined by low numbers of 'oceanic' (offshore) copepod species occasionally imported with the inflow of Atlantic oceanic water, such as *C. helgolandicus*, *C. typicus*, *Metridia lucens*, *Labidocera wollastoni* and *Candacia armata*.

Our results indicate distinct temporal and spatial distribution patterns in the mesozooplanktonic community. Months with highest average densities were May-June and September (a smaller secondary autumn peak), lowest densities were noted in December and January. Densities varied between 150 and 15000 ind.m⁻³, and averaged highest midshore, then nearshore and offshore. Similar spatial patterns as those observed for the zooplankton, 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 such as demersal fish, epibenthos and macrobenthos.

What is the diet composition of the dominant pelagic fish in the BPNS?

The most abundant "small pelagic" fish species in the BPNS, caught with a 3*1 m outrigger semi-pelagic fish trawl (and line-fishing), were herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus*, and horse mackerel *Trachurus trachurus*. A total of 71 prey taxa were found in > 700 fish stomachs. The proportion of fish with empty stomachs was low, proving that the BPNS acts as a valuable feeding ground for pelagic fish. The diet of herring and especially sprat was dominated by calanoid copepods, although herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. Mackerel added sandeels to an otherwise planktivorous diet, while horse mackerel consumed both benthic and pelagic prey. Stomach fullness index was highest for sprat, followed by herring, horse mackerel and mackerel.

What can be concluded on bottom-up control and fish feeding behavior?

We observed a very different composition of zooplankton species and life stages in the plankton samples compared to those in the fish stomachs. The calanoid copepod *A. clausi*, one of the most common zooplankton species in the BPNS, was barely found in the stomachs, as was the case for fish eggs, fish larvae and several common planktonic species known to be preyed upon elsewhere. This indicates a clear selectivity of the four fish species towards only a few, mainly larger copepod species. Secondly, only a small percentage of all copepods found in the stomachs were juvenile stages (copepodites), whilst more than half of the copepods dwelling the water column were immature, indicative of a selective feeding behavior towards adult copepods. Moreover, of all adult copepods in the stomachs, clearly more females than males were recorded, whilst we found a well-balanced sex ratio in the water column, again showing a selective feeding behavior towards slower (gravid) females. No correlation was observed between fullness index and total density of planktonic prey species. Plankton densities averaged highest in spring and at midshore stations, while fullness index was highest nearshore and (apart from sprat) in summer. This indicates that zooplankton densities were not restrictive, and that there is no bottom-up control by copepods on the pelagic fish populations in the BPNS.

The impact of eutrophication and climate change on the pelagic environment is to be taken seriously. The differential response of phytoplankton, mesozooplankton and holozooplankton to environmental changes can lead to a mismatch between successive trophic levels, and will influence the synchrony between primary, secondary and tertiary producers. From a historical perspective several predator–prey relationships remained viable, although they underwent substantial changes. Yet the fact that more than 100 plankton species were found in the water column and only two of these (*T. longicornis* and *C. hamatus*) accounted for nearly three quarters of all ingested prey items, leads us to conclude that even minor changes in the ecology or phenology of these dominant zooplankton species could have huge effects on the pelagic fish stocks.

An important question is: how long will the marine ecosystem need to adapt and resynchronize its phenological relationships due to warmer temperatures, knowing that the relationships are already weakened by other concomitant anthropogenic stressors? Long-

term data are needed to better understand the ongoing processes and responses in the pelagic ecosystem. Therefore, we must conclude by stating that it is important to further monitor both pelagic fish and their zooplanktonic prey populations, and to keep track of population sizes and possible shifts or mismatches in the plankton, the basis of many marine food webs.

5.9 Remaining challenges and opportunities for future pelagic research in the BPNS

At least for the recent past, only a few papers touched upon zooplankton in the BPNS. The last detailed zooplankton species lists date some 40 years ago. As such, we started this doctoral work by asking ourselves as many questions as possible. And we knew we wouldn't be able to answer all these questions. Four years of plankton research have distilled important insights into the species diversity, the community structure and the phenology of the zooplankton in the small pocket of North Sea we call our own. We always planned on linking zooplankton with pelagic fish and fish stocks. Yet we were not able to quantitatively study the pelagic fish stocks, nor the potential for a small-scale pelagic fishery in the BPNS, but we got many detailed insights on the diet of the dominant "small pelagic" fish species in the southern North Sea.

Now the time has come to look forward and to state what we think is worth investigating. These challenges may be fisheries related, policy inspired or real fundamental research. We think the following topics must be taken into account, better sooner than later:

- The range of human activities depending upon a healthy North Sea ecosystem, such as fisheries, aquaculture but also tourism, are vast. As already stated, climate change and its impact on the pelagic ecosystem in coastal North Sea waters is a very important problem, that nations large and small must address. The possible changes in the zooplankton community structure and the impact of these changes on the higher trophic levels, are important to investigate over prolonged periods. We need to extend our knowledge of how different species will react to warming temperatures, increased CO₂, acidification, and alterations in primary production and phytoplankton species composition (Richardson 2008, Dam 2013). These phenomena take place in our backyard on a daily basis, so in the foreseeable future the low

countries, including Belgium, must tackle these problems with both field sampling studies (time series) and experimental lab work.

- The jellyfish joyride, which may or may not be occurring, is definitely turning heads of both the scientist, the public, and the local governments (Attrill *et al.* 2007, Richardson *et al.* 2009). The fact that the BPNS recently got introduced to the notorious invasive ctenophore *Mnemiopsis leidyi*, ensured even more bustle. Given the strong interest in jellyfish we encountered during the past four years, we strongly advice that gelatinous zooplankton (*i.e.* jellyfish *s.l.*) are to be followed up. This is already done for the moment in the ongoing PhD research by L. Vansteenbrugge *et al.* within the Interreg IVa – 2 Seas MEMO project, but what about further monitoring after that PhD study? The monitoring will also require special attention on larger scyphozoan jellyfish. Abroad, such research has been successfully conducted using acoustic sounders and optical plankton counters, such as the Video Plankton Recorder (Basedow *et al.* 2013).
- Genetic research on zooplankton is taking place worldwide. The Census of Marine Zooplankton (CMarZ), for example, aims at a global assessment of marine zooplankton biodiversity - including genetic diversity - by developing DNA barcodes (short DNA sequences that can be used for quick species identification) for all zooplankton species. This might also proof useful for microzooplankton and bacterioplankton, two groups that we didn't study.
- The body size of many dominant zooplanktonic crustaceans has decreased in the entire Northeast Atlantic (Pitois and Fox 2006). It would be very interesting to have morphometric measurements of zooplankton in the BPNS (ideal for MSc-thesis work) and to determine to which extent a loss in functional diversity (e.g. feeding, locomotion, biological traits such as body size and longevity) is occurring in the southern North Sea, since a loss in functional diversity would reduce the biological complexity of the pelagic ecosystem (Duffy and Stachowicz 2006) .

- It is also worth investigating whether a relationship is present between biodiversity and size-structure. Increasing biodiversity is often associated with a decreasing size-structure of the community (Pitois and Fox 2006). The distribution of plankton sizes is a fundamental determinant of energy transfer efficiency in marine ecosystems, and a size decrease may impact overall biomass of higher trophic levels and influence ecosystem services such as a reduced carbon drawdown (Sheldon *et al.* 1972, Pitois and Fox 2006).
- Very little is known on diurnal cycles and spatial and temporal patterns in vertical migration of zooplankton in the southern North Sea. For the BPNS region, almost no literature is available (Daro 1985a,b, Fransz *et al.* 1998). Daro (1985a) observed vertical migration of *T. longicornis* and *P. elongatus* during the phytoplankton bloom in May 1981. It would be interesting to investigate whether diurnal patterns still are present or whether our well-mixed waters preclude vertical migration patterns of different zooplankton species. This in turn might help explain fish distribution and foraging patterns.
- Phytoplankton dynamics in the eutrophicated southern North Sea are complex, and changes in the phytoplankton will affect zooplankton dynamics, as phytoplankton is the main food source of zooplankton (Antajan 2004, Rousseau *et al.* 2006). In recent years, phytoplankton studies in the BPNS focused on the harmful algae or studied phytoplankton as an entire group, for example, through remote sensing of phytoplankton biomass by satellite imaging (the Belcolour project, Vanhellemont *et al.* 2011). It might help to explain zooplankton dynamics, if zooplankton densities were related not just to chlorophyll *a* levels in general, but also to densities of key prey groups (e.g. diatoms vs. flagellates, *etc.*). Also, biochemical analyses such as HPLC gut fluorescence analysis can be applied to unravel the feeding ecology of the zooplankton (Antajan *et al.* 2004). Finally, putting zoo- and phytoplankton data together into models, could help explain and forecast zooplankton dynamics in the southern North Sea. Therefore, a collaboration between ecologists and eco-modelers must be supported. The upcoming Lifewatch project (VLIZ) might well provide us with

more detailed phytoplankton monitoring data in the near future (e.g. through the use of a cytosense flow meter). It is important to make wise use of these future data.

- With regards to dietary studies of (pelagic) fish, stable isotope analyses are getting more and more widespread (Pitt *et al.* 2009). Within the MEMO project stable isotope analyses are conducted, to verify whether pelagic fish eat *M. leidyi* ctenophores in the BPNS. Towards the future this should be further expanded since it provides most detailed info on fish feeding ecology and can help to determine the diet of tiny pelagic fish larvae.
- We haven't examined diurnal patterns in the feeding behavior of pelagic fish (*cf.* Darbyson *et al.* 2003). In the future it would be of high interest to verify whether there are diurnal differences in feeding intensity and diet in the permanently mixed water columns of the BPNS. This in turn can be linked to results on diurnal and vertical zooplankton distribution patterns.
- The European Commission and its policy makers are eager to state that biodiversity needs to be maintained, that a Good Environmental Status is vital for the future of the North Sea, that non-indigenous species should be at levels that do not adversely alter the ecosystems, and that all elements of the food web have to occur at normal abundance and diversity and levels capable of ensuring the long-term abundance of species (*i.e.* the descriptors 1, 2 and 4 of the Marine Strategy Framework Directive, Annex I). This obviously requires data on the pelagic ecosystem components: not only a constant supply of data through continuous zooplankton (and pelagic fish, see further) monitoring, but also the development of zooplankton indicators (e.g. the zooplankton biodiversity index) and the assessment of different conservation and management strategies. For this, we propose three stations (near-mid-offshore) to be sampled monthly for mesozooplankton.
- The past four years we took part in the ICES Working group on Zooplankton Ecology (WGZE) and the Working Group on Small Pelagic fish (WGLESP). The continued presence of a Belgian representative in these international working groups in the

future is a must. As shown throughout this PhD, pelagic research is not only interesting, it is also quite useful. Only by working together with other pelagic researchers and by taking part in international projects, we will be able to establish a Belgian center of excellence in pelagic research. This center should merge all pelagic knowhow on phytoplankton, zooplankton, jellyfish, pelagic fish, *etc.*

- Due to severe logistic problems, we were not able to present quantitative info on the pelagic fish stocks of the BPNS. Instead, all the time and effort was spent on fish feeding ecology. Assessing the pelagic fish stocks in the BPNS requires acoustic devices (fish finding sonar) and large pelagic nets towed at significant high speeds (4-5 knots), to be able to catch fast-swimming species such as mackerel (Dommasnes *et al.* 2004, Prokopchuck and Sentyabov 2006). *Anno* 2013, the new R.V. Simon Stevin (VLIZ) is in use, which is a first step to figure out which pelagic fish are swimming where and when in Belgian waters, and in what numbers. It is noteworthy that still, after many decades of Belgian marine research, there is no detailed knowledge what so ever on the distribution of pelagic fish in the water column and near the water surface. It's a pity we couldn't fill that gap, but we really hope to take a prominent role in the assessment of the pelagic fish stocks of the BPNS in the near future.
- Finally, there is an economic and social interest in a small-scale pelagic fishery in the BPNS. *Anno* 2013 Belgian fishermen no longer target pelagic fish, but our study has proven that pelagic species of commercial value occur in the BPNS, so what about a pelagic future for Belgian fisheries?

Nowadays, large-scale pelagic fisheries are usually very profitable and well organized. There is good cooperation with the fisheries policy through the establishment of Regional Advisory Councils (RACs), Total Allowable Catches (TACs) are usually respected, and many (not all!) pelagic fish stocks are at high reproductive capacity or at least they endure the pressure from these large scale fisheries. This cannot be said for most demersal fish stocks worldwide (FAO 2012, ICES advices 2012).

Pelagic fish such as herring, sprat and sandeels are mostly fished in very high numbers for the fishery to be profitable. As Belgian shipping companies never invested in huge freezer trawlers, they will never be able to cope with these large

foreign pelagic fishing companies. The key to success thus lies in a small scale niche fishery targeting pelagic fish (e.g. jigging for mackerel during summer months), and marketing their fresh and high quality products to Belgian customers. We know this can work: several Dutch ship owners bought Belgian licenses and currently fish with flyshooting vessels for non-quoted species, such as mackerel, horse mackerel and red mullet in Belgian waters. They prove that fishing for small pelagics in the BPNS is profitable. It is the moral duty of Belgium to further support and investigate the social, economical and -most important- the ecological aspects of a small scale pelagic fishery in Belgian waters.