

# CHAPTER 4

## SELECTIVE FEEDING BY PELAGIC FISH IN THE BELGIAN PART OF THE NORTH SEA

---

Adapted from:

*Van Ginderdeuren K, Vandendriessche S, Vincx M, Prössler Y, Matola HD, Hostens K (subm.)*  
Selective feeding by pelagic fish in the Belgian part of the North Sea. *Ices Journal of Marine Science*. Submitted 10/2/2013.

### **Abstract**

Pelagic fish and their planktonic prey are susceptible to a changing climate, giving rise to mismatches and planktonic bottlenecks. A detailed examination of the feeding ecology of pelagic fish can provide valuable insights in the causes and consequences of these phenomena. The present study investigated the diets of both juvenile and adult herring, sprat, horse mackerel and adult mackerel in the Belgian part of the North Sea (BPNS) in relation to the distribution of zooplankton and ambient abiotic conditions. A study sampling pelagic fish and zooplankton simultaneously every month during consecutive years, and spanning nearshore to offshore sampling locations, is unprecedented in the southern North Sea. A total of 71 prey taxa were found in 725 stomachs of fish gathered at ten stations, sampled monthly in 2009 and 2010. The proportion of fish with empty stomachs was low (11 %), and the number of prey species ranged from 0 to 21 sp. per stomach. The diet of herring and sprat was dominated by calanoid copepods, but herring stomachs also contained many decapod larvae, amphipods, cumaceans and mysids. Mackerel added sandeels to an otherwise planktivorous diet. Horse mackerel consumed both benthic and pelagic prey. The highest frequency of occurrence in the stomachs was observed for the calanoid copepods *Temora longicornis* (33408 of all 55004 prey items identified) and *Centropages hamatus* (5003 times found). The fullness index ranged between 0 and 20.6, and averaged highest for sprat (0.86), followed by herring (0.60), horse mackerel (0.26) and mackerel (0.24). We observed a different composition of zooplankton species and life stages in the plankton samples compared to those in the fish stomachs. More adult and female copepods were

eaten than the plankton samples would suggest. Also, the calanoid copepod *Acartia clausi*, the most common zooplankton species in the BPNS, was barely eaten, as was the case for fish eggs and larvae, and for common planktonic species known to be preyed upon elsewhere (e.g. *Oikopleura dioica*, *Evadne nordmanni*, *Euterpina acutifrons*). Additionally, plankton densities averaged highest in spring and at midshore (20-30 km from shore) stations, but fullness index was highest nearshore (< 12 km from shore) and (apart from sprat) in summer. A significant correlation between fullness index and total density of planktonic prey species was not observed, indicating that zooplankton densities were not restrictive.

Yet the fact that more than 100 plankton species occurred in the plankton samples and just 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 zooplankters could have profound effects on pelagic fish stocks.

**KEYWORDS:** herring, sprat, mackerel, horse mackerel, diet, zooplankton, Belgian part of the North Sea

## 1. Introduction

Abundant mid-trophic pelagic fish usually play a central role in marine ecosystems, channeling energy and nutrients between zooplankton and top predators, and being important fishery targets (Frederiksen *et al.* 2006).

Both pelagic and demersal fish species must keep in step with their zooplanktonic food sources, for this is what they or their larvae feed on (Russell 1976, Muus and Nielsen 1999). The identification and quantification of trophic interactions between zooplankton and pelagic fish requires diet and feeding rate studies. Diet compositions reflect feeding ecology, and shifts in diet can be directly linked to an 'actor' such as climate control, anthropogenic impacts, seasonality, and interannual variations. Major changes in the diet of pelagic fish have been documented on diurnal, seasonal and interannual time scales (Köster and Schnack 1994, Albert 1995, Pillar and Barange 1995, Bromley *et al.* 1997, Grant and Brown 1998, Dalpadado *et al.* 2000, Gislason and Astthorsson 2000, Adlerstein and Welleman 2000, Hanson and Chouinard 2002, Darbyson *et al.* 2003).

Spatial and temporal changes in the environment strongly regulate trophic interactions. Sea surface temperature, thermocline depth, and the presence of coastal fronts and currents can have significant effects on the distribution and abundance of fish species (Alheit *et al.* 2012). As such, fluctuations in oceanic conditions due to climate change will have an important impact on several fish stocks. Reid *et al.* (2003) proposed that the presently warm regime of the North Sea should be linked to an increased inflow of North Atlantic water. Iversen *et al.* (2002) demonstrated a positive correlation between the winter volume influx of Atlantic water and the catches of horse mackerel in the North Sea six months later. The large influx of warm and nutrient rich Atlantic water presumably leads to an increased biological production, and hence food availability for pelagic fish (Reid *et al.* 2001).

The present study aimed to examine the interactions between pelagic fish species in the Belgian part of the North Sea (BPNS) and their zooplanktonic food sources. Four important commercial fish species were investigated: herring (*Clupea harengus* L., Clupeidae), sprat (*Sprattus sprattus* L., Clupeidae), mackerel (*Scomber scombrus* L., Scombridae) and horse mackerel (*Trachurus trachurus* L., Carangidae).

Zooplankton communities are crucial to the functioning of marine food webs because of their sheer abundance, high diversity and vital trophic ecosystem functions (Mauchline 1998, Richardson 2008). Zooplanktonic organisms 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), triggering a northward displacement of marine organisms and mismatches between predatory fish and prey (Cushing 1990, Southward *et al.* 1995, Hays *et al.* 2005). In the southern North Sea, small calanoid copepods dominate the zooplankton, with up to 84 % of abundance in spring and summer (Krause *et al.* 1995, O'Brien *et al.* 2011).

Considering the biogeographical and phenological shifts in the distribution of pelagic species, and the vital importance of plankton in the marine food web, an update on pelagic fish feeding ecology in the BPNS, positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly in place.

The aims of this study were: (1) to characterize the diet of four common pelagic fish species in the BPNS, (2) to verify whether selectivity in feeding occurs, by comparing diet results with data on zooplankton from the same areas and periods, and (3) to investigate spatial and temporal patterns in the diet of the four pelagic fish species, indicating which environmental variables (abiotic and biotic) influence feeding ecology.

## **2. Materials And Methods**

### *2.1 Study area*

This study covers the entire Belgian part of the North Sea (ca. 3600 km<sup>2</sup>), 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, 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 is characterized by the presence of several sandbank systems with a high morphological and sedimentological diversity, resulting in different benthic communities (Degraer *et al.* 1999, Van Hoey *et al.* 2004), which produce planktonic larvae (Van Ginderdeuren *et al.* 2012a), subsequently influencing the pelagic ecosystem via benthic-pelagic coupling (Provoost *et al.* 2013).

## 2.2 Data origin

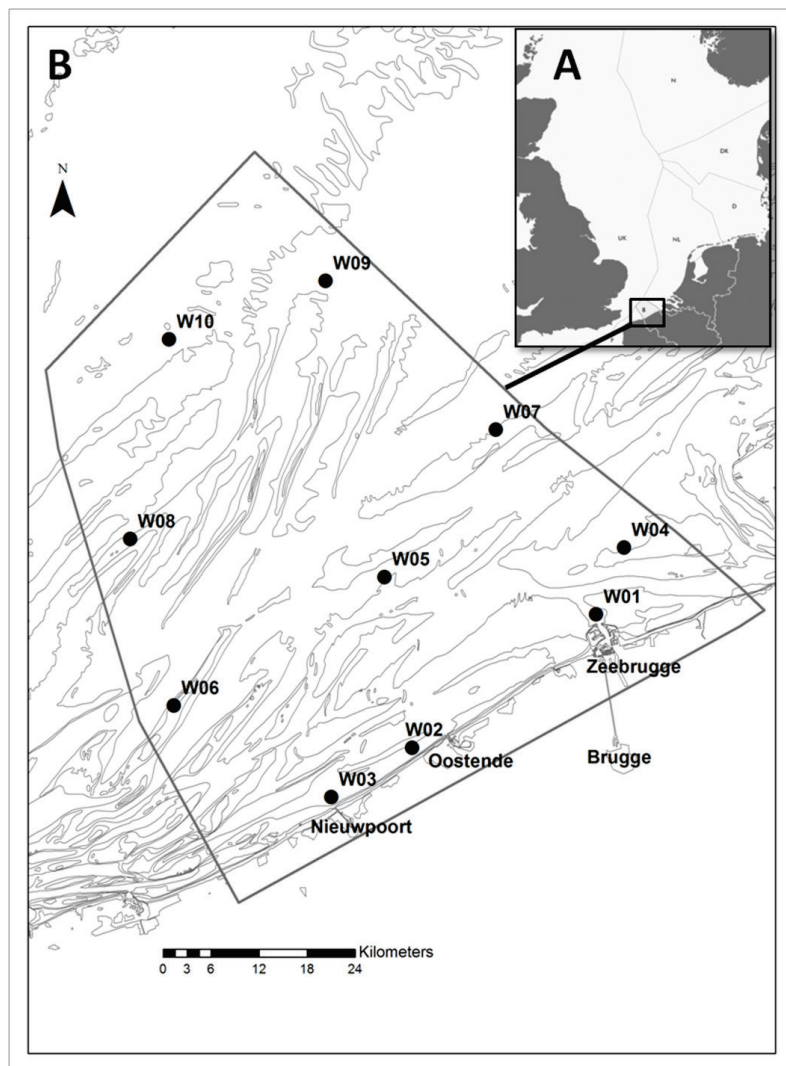


Figure 1: A) North Sea exclusive economic zones; B) Belgian part of the North Sea (BPNS) with ten stations (nearshore W01-04, midshore W05-07, offshore W08-10).

Sampling was carried out monthly in 2009 and 2010 at ten monitoring stations positioned along a nearshore-midshore-offshore axis on the BPNS (Fig. 1). Fish samples were taken with a 3\*1 m outrigger semi-pelagic trawl, trawled for half an hour at 3.5 knots at every station. Mackerel were hand line fished, with simple hooked feathers as lure, as they were too fast swimmers to catch with the trawl net. Line fishing was done for 15 min. at every station using a varying number of hand lines. Large fish were weighed ( $\pm 5$  g) and measured onboard (total length and fork length;  $\pm 1$  mm), their digestive tract was cut off at the oesophagus and the anus, and fixed in 8 % formaline. Small fish were injected with and fully fixed in 8 % formaline and afterwards measured and dissected in the lab. Using optical microscope and stereomicroscope, prey taxa were identified to species level when possible to attain the

highest taxonomical resolution. When hundreds of calanoid copepods were present in a stomach, we identified the first 100 copepods (van Guelpen *et al.* 1982). Calanoid copepods were identified to species level, sex and stage (adults, copepodites). The copepodites of *Centropages hamatus* vs. *Centropages typicus* and those of *Paracalanus parvus* vs. *Pseudocalanus elongatus* were not distinguished.

We made a distinction between holoplanktonic (species that spend their entire life as plankton in the water column, e.g. calanoid copepods), meroplanktonic (early life stages of animals that spend a part of their life as plankters, e.g. decapod larvae) and tycho planktonic (species that are occasionally carried into the water column) prey taxa. Certain species groups such as mysids, amphipods and cumaceans that are often referred to as hyperbenthic, were also counted as tycho planktonic. Prey remains that could not be identified were catalogued as digested matter (with abundance = 1 when present in a stomach). Wet weights (WW), dry weights (DW) and ash weights (AW) of every species of prey were measured to the nearest 0.01 mg. Dry weights were acquired by drying the stomach contents in an oven at 60 °C for 48 hours. Ash weight was obtained by muffling the dry weight samples at 550 °C for 2 hours. When combining these data, the ash free dry weight (AFDW = DW-AW) could be calculated.

After trawling, a WP2 zooplankton net (57 cm diameter, 200 µm mesh size, Fraser 1968) fitted with a flow meter (Smith *et al.* 1968) was towed in an oblique haul from bottom to surface at each station. This allowed for a direct comparison between fish stomach content and zooplankton abundance and species composition. Zooplankton samples were fixed and preserved in a 4 % formaline solution. Using optical microscope and stereomicroscope, taxa were identified to species level when possible. Big and rare animals were initially sorted from the catch in a general sweep. Then subsamples were taken to count and identify the abundant zooplankton species, with at least 100 calanoid copepods identified per sample (van Guelpen *et al.* 1982). A CTD (Seabird 19plusV2) cast was carried out at every station to measure depth, temperature and salinity.

### 2.3 Overall comparison

Prey species richness in fish stomachs was estimated by Hill's diversity number  $N_0$ , which is equal to the number of species in a stomach. The Shannon-Wiener index  $H'$  ( $\log e$ ) was used

to calculate prey species diversity. Both  $N_0$  and  $H'$  were calculated on raw stomach content data.

Based on the stomach content abundance data (fourth-root transformed, following Quinn and Keough 2002), a non-metric multi-dimensional scaling (MDS) analysis was applied to explore the relationship between stomachs from different fish species, years, stations and months. This technique relates zooplankton prey abundance and composition through a matrix of Bray-Curtis similarities. Spatial and temporal differences in stomach content were investigated using PERMANOVA pair wise testing (based on Bray Curtis similarity), using three factors: “year”, “month” and “shore” (grouping the ten stations in nearshore, midshore and offshore groups) for every fish species separately. First, interaction between these factors had to be investigated (Main PERMANOVA test). In most analysis performed, interaction between factors was significant ( $p < 0.05$ ), hence we present significant differences separately for every combination of factors for every fish species within each year (Addendum 4).

Two-way crossed SIMPER analysis (based on Bray Curtis similarity) was performed for each fish species and each year separately, using factors “shore” (near-mid-offshore) and “month”, and identified the prey species primarily contributing to the similarity in the sample clusters.

Finally, the patterns in stomach content compositions in relation to environmental variables (temperature, chlorophyll *a* biomass, salinity and prey density) are linked via distance-based linear models analysis DistLM).

All these analyses were performed using the package PRIMER 6 (Clarke 1993, Clarke and Gorley 2006).

## *2.4 Diet indices*

To determine the dietary importance of each food category and to compare feeding ecology of different fish species and sampling locations, frequency of occurrence and relative abundance methods were used (Hyslop 1980). Secondly, an electivity index  $E$  was calculated, to determine prey preference among the different prey categories. The index  $E$  in equation [4] is based on electivity indices used in zooplankton feeding and clearance experiments,

comparing copepod stomach content with prey densities in the experimental medium (Vanderploeg and Scavia's 1979a,b, Antajan 2004).

The frequency of occurrence of a given prey type is defined as the number of stomachs in which that prey occurs, expressed as a frequency of the total number of stomachs in which prey are present. In equation [1],  $N_i$  is the number of predators with prey  $i$  in their stomach and  $N$  is the total number of stomachs that were not empty.

$$[1] \%FO_i = (N_i/N) * 100$$

The relative prey abundance can be either numerical (% abundance) or gravimetric (% AFDW). In equation [2],  $S_i$  is the abundance or AFDW of prey  $i$  in the stomach and  $S_t$  the total stomach content of the predator:

$$[2] \%R_i = (S_i/S_t) * 100$$

The stomach fullness index (Sigurdsson and Astthorsson 1991) was used as an indicator of feeding activity. In equation [3], AFDW<sub>s</sub> is the weight of the stomach content and AFDW<sub>f</sub> the weight of the entire fish.

$$[3] FI = AFDW_s * 100 / AFDW_f$$

The Electivity index  $E_i$  (Vanderploeg and Scavia's 1979a,b) indicates prey preference among the different prey categories ( $m$ ):

$$[4] E_i = (W_i - 1/m) / (W_i + 1/m)$$

Where  $W_i$  is defined by the following equation:

$$[5] W_i = (r_i/n_i) / \sum_i (r_i/n_i)$$

In equation [5]  $r_i$  signifies prey contribution of a prey species to the fish diet (relative abundance in fish stomachs) whereas  $n_i$  stands for its natural availability (relative abundance in the water column  $\approx$  zooplankton samples). Neutral preference is indicated by an  $E$  of 0, with positive values up to +1 representing increasing preference and negative values down to -1 representing increasing avoidance.

Fish ash-free dry weights were calculated from length-wet weight relationships in literature (Wigley *et al.* 2003 for herring and sprat, Coull *et al.* 1989 for mackerel and horse mackerel). Wet weight of the fish was then converted to AFDW with the common formula AFDW  $\approx$  20 % of WW (Edgar and Shaw 1995, Van Ginderdeuren, unpublished data).

The Schoener index (Schoener 1970) was calculated to assess the proportional overlap in diet of the four pelagic fish species. Values can range from 0 (no overlap) to 1 (perfect



overlap), with an accepted significance value of 0.60. The dietary overlap coefficient (S) of fish species x and y is calculated as in equation [6], with  $P_{x_i}$  the proportion of prey species i in the diet of fish x, and  $P_{y_i}$  the proportion of prey species i in the diet of fish y.

$$[6] S = 1 - 0.5 (\sum |P_{x_i} - P_{y_i}|)$$

### 3. Results

#### 3.1 General characterization of the overall diet

Stomach data were derived from 725 stomachs, of which 84 empty stomachs that were omitted from further analyses, resulting in 209 herring, 247 sprat, 95 mackerel, and 90 horse mackerel stomachs (Fig. 2), sampled mostly during summer months (Fig. 3) and at nearshore stations (Fig. 4).

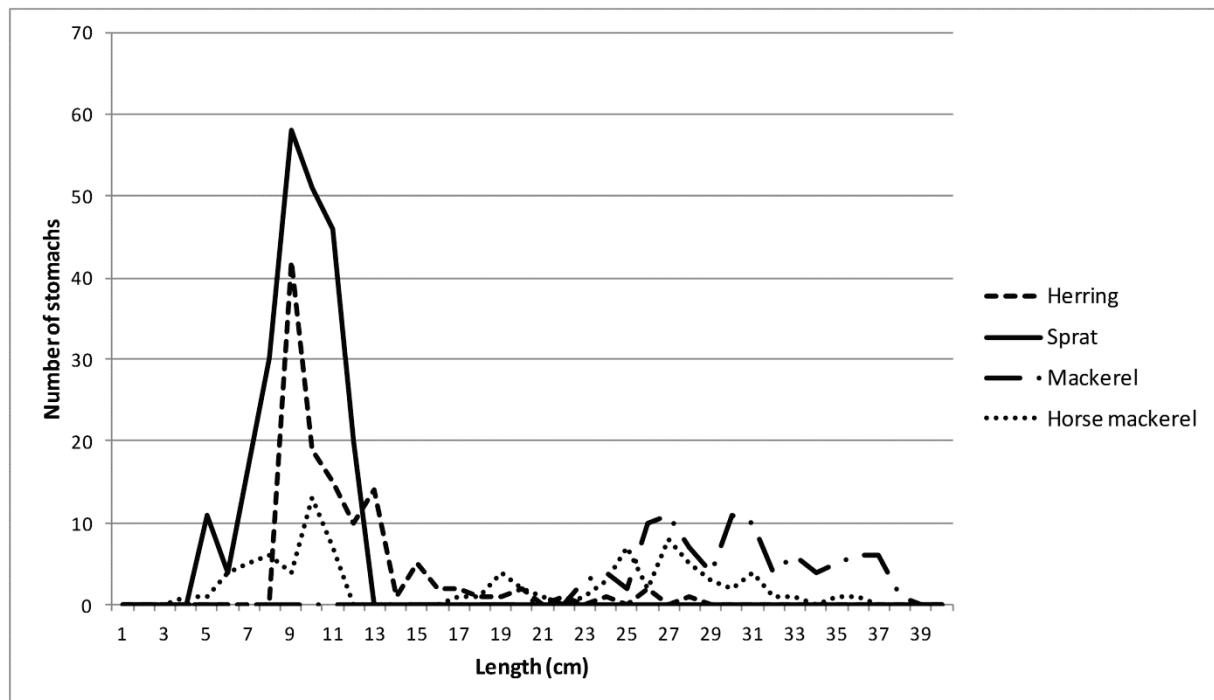


Figure 2: Number of stomachs analyzed per length class (cm) for four pelagic fish species.

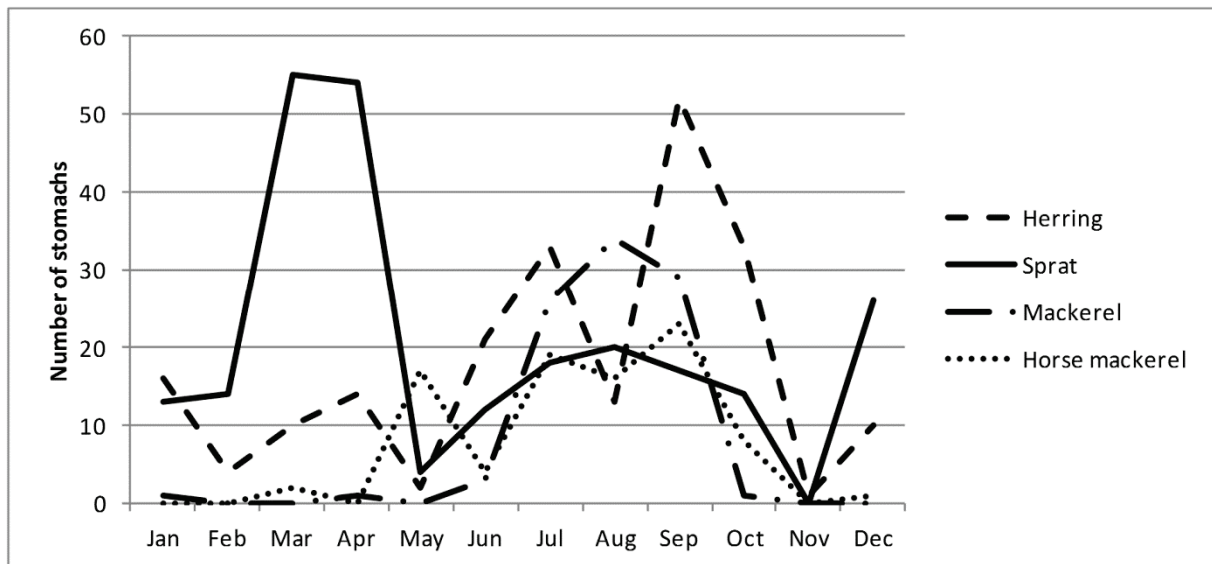


Figure 3: Number of stomachs analyzed per month for four pelagic fish species.

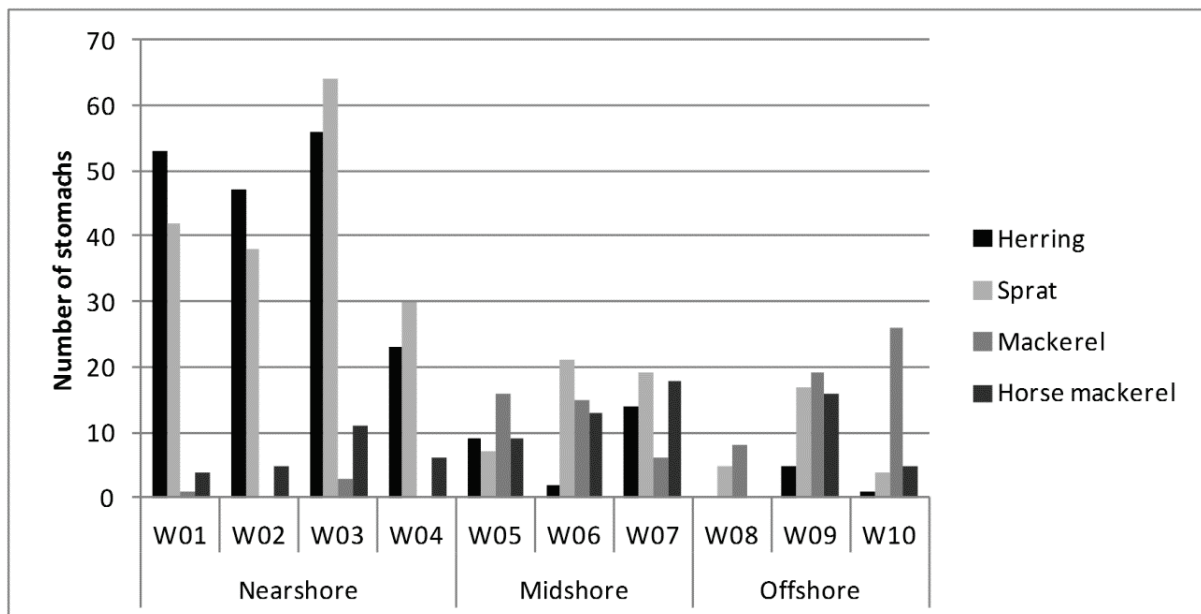


Figure 4: Number of stomachs analyzed per station (grouped in near-mid-offshore clusters) for four pelagic fish species.

In total 71 prey taxa (36 identified to species level) were found (Table 1). Species richness ranged from 0 to 21 sp.stomach<sup>-1</sup> and species diversity (Shannon H') from 0 to 2.2. Stomach contents were dominated by copepods (16 taxa) throughout the year. They were found in 64 % of all stomachs and represent 77 % of all found prey items (Fig. 5). The calanoid copepods *Temora longicornis* and *Centropages hamatus* occurred most frequently in the diet (a whopping 33408 of all 55004 prey items identified were *T. longicornis*). Only 6 % of all copepods in the diet were copepodites, indicating selectivity towards adults. Of all adult

copepods recorded in the diet, 62 % were females and 38 % were males. Fullness indices ranged between 0 and 20.6 and averaged highest for sprat ( $0.86 \pm \text{SD } 1.94$ ), followed by herring ( $0.60 \pm 1.35$ ), horse mackerel ( $0.26 \pm 0.50$ ) and mackerel ( $0.24 \pm 0.45$ ). Fullness indices were highest nearshore (lowest offshore) and in summer (lowest in winter), sprat being the exception with highest FI in spring, and mackerel not caught nearshore (Fig. 4).

Unidentifiable digested material was found in 46 % of all stomachs. Larvae of decapods, cirripeds, fish and polychaetes, as well as amphipods, mysids, chaetognaths, juvenile shrimp and cladocerans only represented a small portion of the diet numerically (Fig. 5,6), but in biomass terms their contribution was higher, due to their bigger size (see further).

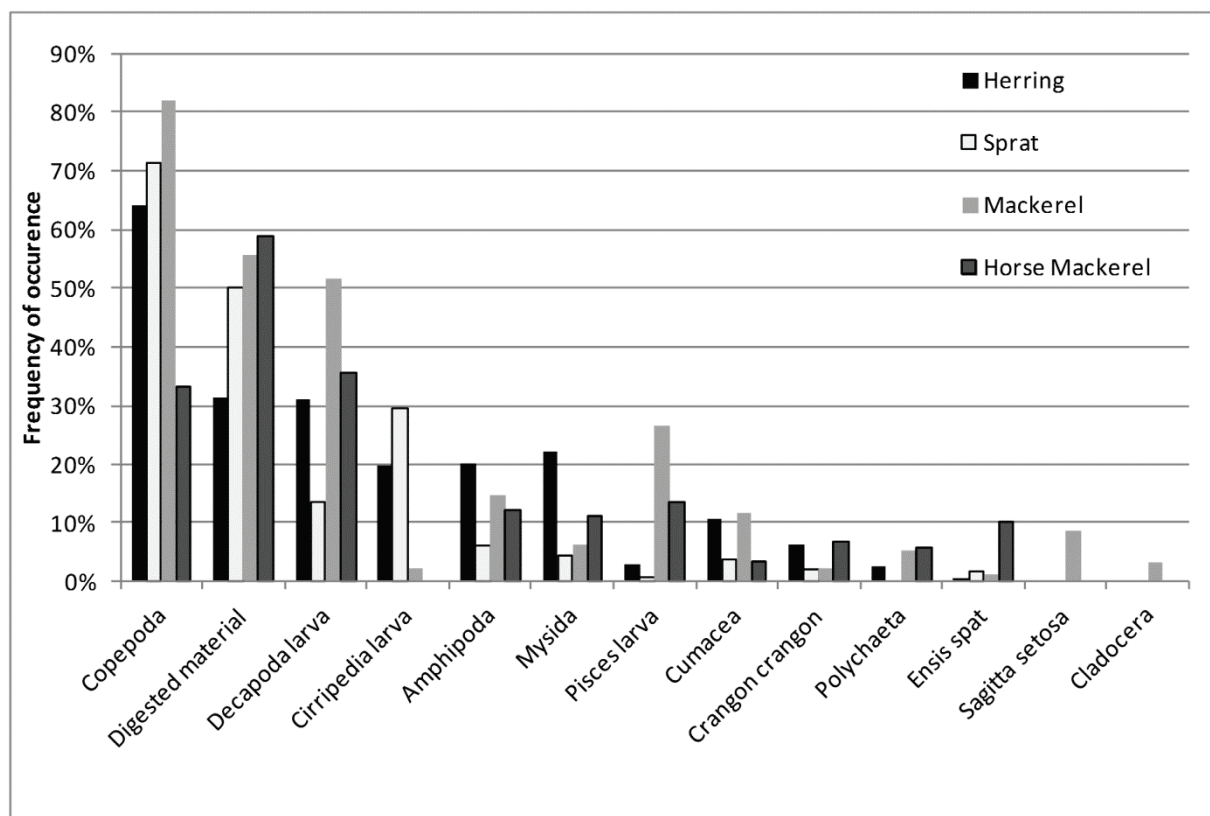


Figure 5: Frequency of occurrence (%) of the most important prey groups for herring, sprat, mackerel and horse mackerel.

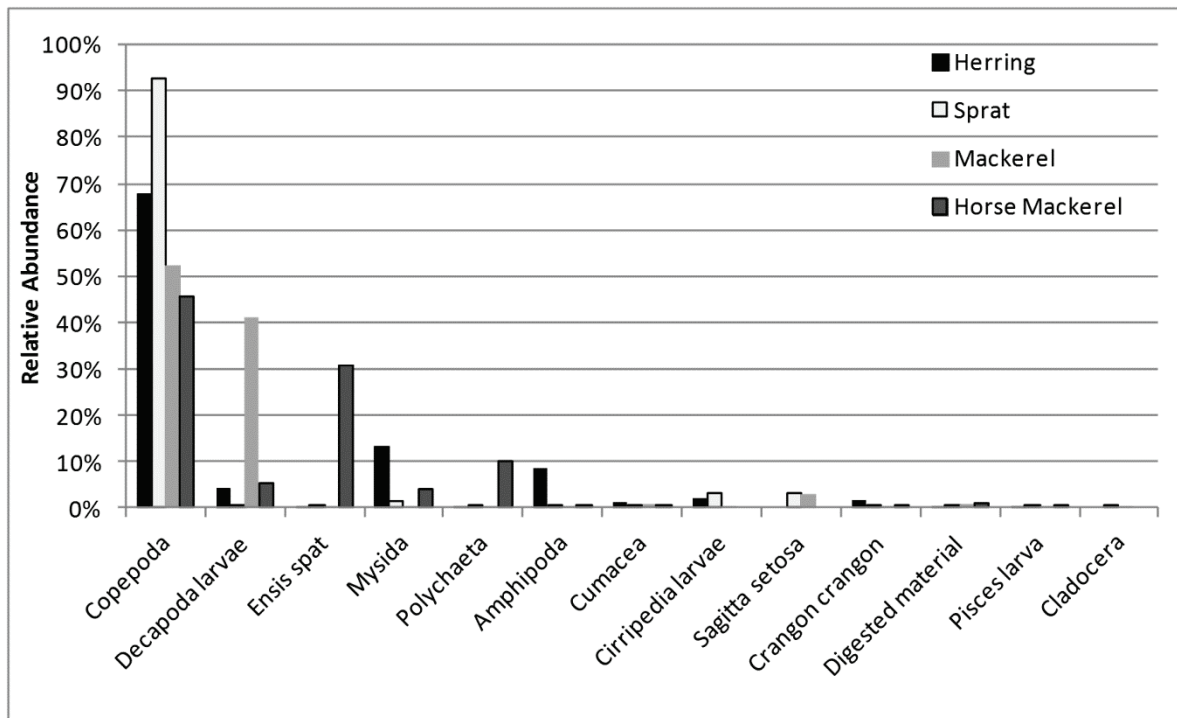


Figure 6: Relative abundance (%) of the most important prey groups for herring, sprat, mackerel and horse mackerel.

Table 1: List of prey items found in the stomachs of herring *Clupea harengus*, sprat *Sprattus sprattus*, mackerel *Scomber scombrus* and horse mackerel *Trachurus trachurus*. %FO: Frequency of occurrence, %RA: Relative abundance.

		Herring		Sprat		Mackerel		Horse mackerel	
		%FO	%RA	%FO	%RA	%FO	%RA	%FO	%RA
<b>HOLOPLANKTON</b>									
<b>Copepoda</b>	Copepoda sp.	25.4	4.6	27.1	6.7	21.1	0.9	14.4	1.4
Calanoida	<i>Acartia clausi</i>	5.7	0.5	2.0	-	28.4	1.6	1.1	0.1
	<i>Acartia clausi</i> copepodite	0.5	-	-	-	-	-	-	-
	Calanoida sp.	1.0	-	0.8	-	6.3	1.2	5.6	0.5
	<i>Calanus helgolandicus</i>	2.9	-	0.4	-	23.2	1.1	4.4	0.1
	<i>Centropages hamatus</i>	25.4	2.7	33.6	15.6	27.4	1.6	7.8	0.5
	<i>Centropages typicus</i>	12.0	0.8	10.9	1.1	23.2	1.2	1.1	0.1
	<i>Isias clavipes</i>	3.8	0.1	5.7	0.1	17.9	0.8	3.3	0.1
	<i>Labidocera wollasteni</i>	1.0	-	0.4	-	4.2	0.1	1.1	-
	<i>Paracalanus parvus</i>	5.3	0.2	2.4	-	11.6	0.8	1.1	-
	<i>Pseudocalanus elongatus</i>	1.4	-	3.6	0.1	9.5	0.5	2.2	0.1
	<i>Temora longicornis</i>	52.2	58.7	65.6	69.0	57.9	41.5	25.6	42.8
Cyclopoida	<i>Oithona</i> sp.	0.5	-	0.4	-	-	-	-	-
Poecilostomatoida	<i>Giardella callianassae</i>	-	-	0.4	-	-	-	-	-
Harpacticoida	<i>Euterpina acutifrons</i>	7.2	0.3	0.4	-	13.7	0.3	1.1	0.1
	Harpacticoida sp.	3.3	0.1	0.4	-	2.1	-	-	-
	<i>Tigriopus</i> sp.	1.0	-	-	-	2.1	0.1	-	-
Siphonostomatoida	<i>Caligus elongatus</i>	-	-	0.4	-	4.2	0.3	-	-
<b>Chaetognatha</b>	<i>Sagitta setosa</i>	-	-	-	-	8.4	3.0	-	-
<b>Cladocera</b>	<i>Evadne nordmanni</i>	-	-	-	-	2.1	0.1	-	-

	<i>Podon</i> sp.	-	-	-	-	1.1	-	-	-
<b>Urochordata</b>	<i>Oikopleura dioica</i>	-	-	0.4	-	1.1	0.1	-	-
<b>MEROPLANKTON</b>									
<b>Echinodermata</b>	<i>Ophiura</i> sp. spat	-	-	-	-	1.1	-	-	-
<b>Bivalvia</b>	<i>Ensis</i> sp. spat	0.5	-	1.6	0.2	1.1	-	1.1	30.8
<b>Cirripedia</b>	Cirripedia sp. cyprid larva	19.1	2.3	27.9	3.3	2.1	-	-	-
	Cirripedia sp. nauplius larva	1.4	-	3.2	-	1.1	-	-	-
<b>Decapoda</b>	Anomura sp. megalopa larva	1.0	-	-	-	-	-	-	-
	Anomura sp. zoea larva	-	-	0.4	-	7.4	0.7	3.3	0.2
	<i>Callinassa</i> sp. megalopa	1.4	-	0.4	-	7.4	0.2	2.2	0.1
	Brachyura sp. zoea	2.4	0.1	4.0	0.1	8.4	0.3	3.3	0.1
	Caridea sp. zoea	5.7	0.2	2.8	-	17.9	3.7	7.8	0.4
	<i>Crangon crangon</i> juvenile	6.2	1.9	2.0	0.2	2.1	-	6.7	0.4
	Decapoda sp. megalopa	25.8	3.7	8.1	0.5	48.4	29.2	27.8	4.8
	Isopoda sp. larva	1.0	-	-	-	1.1	-	-	-
	<i>Pisidia longicornis</i> zoea	-	-	-	-	14.7	7.2	1.1	-
	<i>Lanice conchilega</i> larva	-	-	-	-	1.1	-	1.1	-
	Polychaeta sp. larva	1.4	-	-	-	1.1	-	1.1	-
	Ammodytidae sp. larva	-	-	-	-	14.7	0.3	-	-
<b>Pisces</b>	<i>Callionymus</i> sp. larva	-	-	0.4	-	1.1	-	-	-
	Clupeidae sp. larvae	1.9	0.1	0.4	-	-	-	3.3	0.1
	Pisces sp. eggs	1.0	-	0.8	0.1	-	-	4.4	1.1
	Pisces sp. larva	1.9	-	-	-	6.3	0.1	4.4	0.1
	Pisces sp. tissue	1.0	-	0.4	-	4.2	0.1	7.8	0.1
	<i>Solea solea</i>	-	-	-	-	1.1	-	2.2	-
	<i>Syngnathus</i> sp. larva	-	-	-	-	-	-	1.1	-
		-	-	-	-	-	-	-	-
<b>TYCHOPLANKTON</b>									
<b>Cumacea</b>	Cumacea sp. juvenile	10.5	1.2	3.2	0.1	7.4	0.3	3.3	0.1
	<i>Pseudocuma</i> sp.	-	-	0.4	-	5.3	0.3	-	-
<b>Amphipoda</b>	<i>Abludomelita obtusata</i>	-	-	-	-	-	-	1.1	-
	Amphipoda sp.	9.1	0.9	2.4	0.1	5.3	0.1	4.4	0.3
	<i>Aora gracilis</i>	0.5	-	-	-	-	-	-	-
	<i>Apherusa ovalipes</i>	-	-	-	-	1.1	-	-	-
	<i>Atylus swammerdami</i>	11.0	6.5	4.5	0.3	10.5	0.4	6.7	0.2
	<i>Bathyporeia</i> sp.	1.0	0.1	1.2	-	-	-	-	-
	Gammaridea sp.	3.3	0.6	0.4	-	-	-	-	-
	<i>Gammarus</i> sp.	1.0	0.2	2.0	0.1	-	-	-	-
	<i>Jassa</i> sp.	1.0	-	1.2	-	-	-	-	-
	<i>Megaluropus agilis</i>	1.4	0.1	0.4	-	-	-	-	-
	<i>Pariambus typicus</i>	-	-	0.8	-	-	-	-	-
	<i>Pontocrates altamarinus</i>	-	-	0.4	-	-	-	-	-
	<i>Gastrosaccus spinifer</i>	7.7	1.2	2.8	0.2	3.2	-	4.4	0.6
	<i>Heteromysis morfosa</i>	0.5	-	-	-	-	-	-	-
	<i>Mesopodopsis slabberi</i>	4.3	0.1	0.8	-	-	-	-	-
<b>Mysida</b>	Mysida sp.	7.2	0.8	1.2	-	3.2	0.1	2.2	0.1
	<i>Neomysis integer</i>	0.5	-	-	-	-	-	-	-
	<i>Schistomysis kervillei</i>	8.1	9.7	2.0	1.4	-	-	5.6	2.9
	<i>Schistomysis spiritus</i>	7.7	1.4	1.2	-	-	-	2.2	0.7
<b>BENTHOS</b>									

Brachyura sp.	1.0	0.1	0.8	-	2.1	-	1.1	-
<i>Branchiostoma lanceolatum</i>	-	-	-	-	5.3	0.3	-	-
<i>Eumida sanguinea</i>	1.0	-	-	-	-	-	-	-
<i>Nereis longissima</i>	-	-	-	-	1.1	-	3.3	10.1
<i>Pagurus</i> sp.	0.5	-	-	-	1.1	-	-	-
<i>Thia scutellata</i>	-	-	-	-	1.1	-	-	-
<b>OTHER</b>								
Digested matter	31.6	/	50.2	/	55.8	/	58.9	/

### 3.2 Diet composition per fish species

#### 3.2.1 Herring

In total 237 herring stomachs were analyzed of which 28 were empty. Length varied between 5 and 30 cm with a clear dominance of immature fish being caught at nearshore stations (Fig. 2,4). The larger adult herring (> 20 cm) that were caught in October and November all had empty or nearly empty stomachs.

Copepods formed an important prey taxon for herring, with *T. longicornis* as dominant species, followed by the mysid *Schistomysis kervillei*, megalopa larvae of decapods and the amphipod *Atylus swammerdami*. The importance of *S. kervillei* in the diet of herring (23 %) was even more evident in the gravimetric data (Fig. 7). Fish larvae (clupeids of 2-5 mm) were found in only four herring stomachs and in the absence of other food items. Two-way crossed SIMPER analysis showed that *T. longicornis* (max of 45 % contribution to similarity in June 2009), together with *Schistomysis spiritus* (11 % in January 2009) and barnacle cyprid larvae contributed most to similarity in stomach content. In summer month, decapod megalopa (maximum of 27 % in September 2009) were important contributors as well.

Fullness indices varied between 0 and 13.6. Significant ( $p < 0.05$ ) differences were found between near-mid-offshore sampled stomachs and between stomach content from different months (Tables 1,2 in Addendum 4).

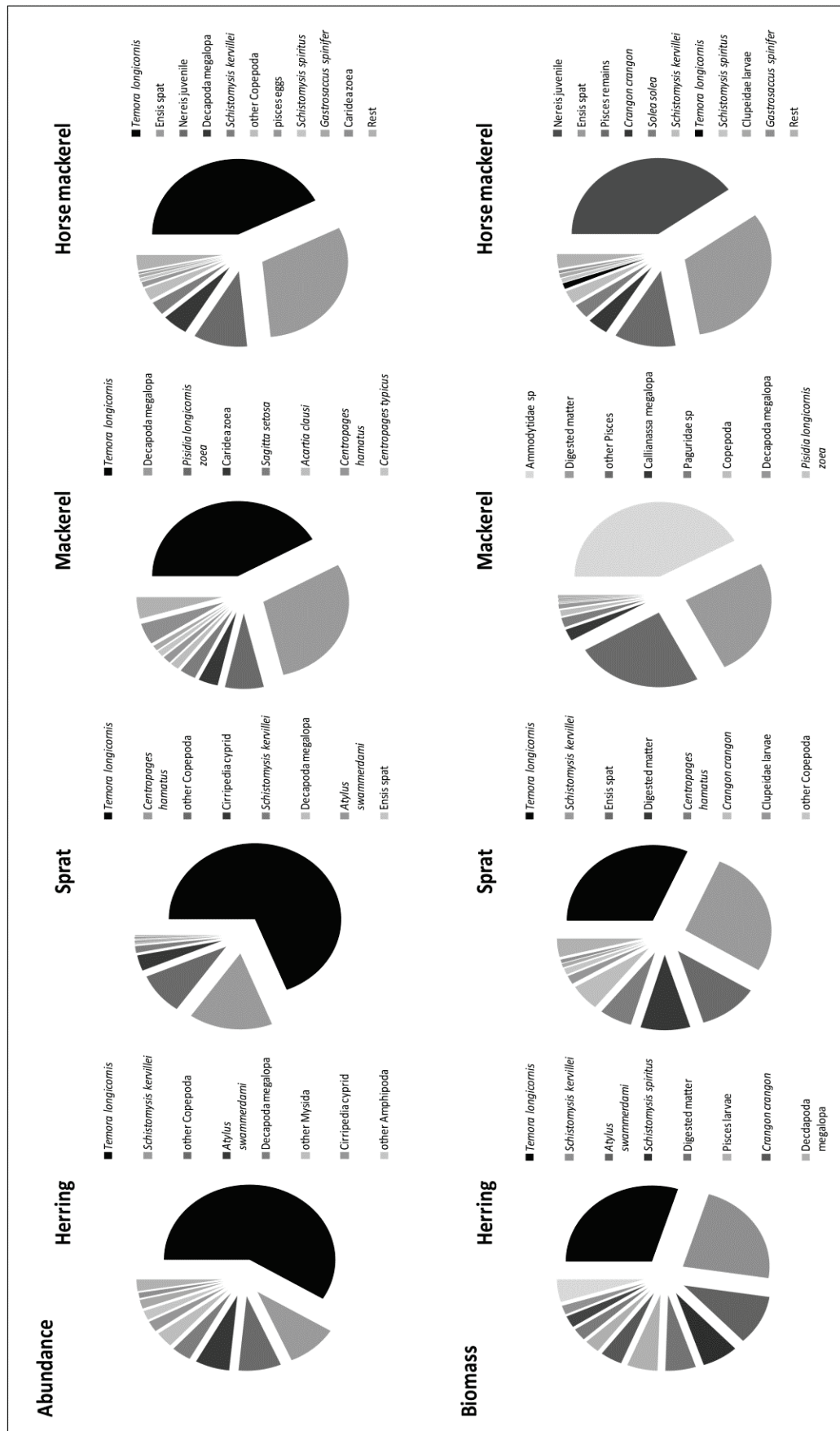


Figure 7: Dominant prey items in the diet of herring, sprat, mackerel and horse mackerel, based on the relative abundances of prey items (top) and on their biomass (AFDW, bottom).

### 3.2.2 Sprat

We analyzed 276 sprat stomachs of which 29 were empty. Length varied between 5 and 14 cm, including many adults (> 10 cm) (Fig. 2). Copepods again constituted the vast majority of prey items in sprat stomachs, with 93 % of all prey items being calanoid copepods (Fig. 7). Especially adult *T. longicornis* dominated the stomach content (both numerically and gravimetrically), followed by *C. hamatus* and cirriped cyprid larvae. Mysids and amphipods were preyed upon as well, but in contrast to herring, almost no megalopa larvae were found. Only one stomach contained clupeid larvae, two stomachs contained fish eggs. Gravimetical analyses showed that *T. longicornis* and *S. kervillei* provided a large part of the daily energy demand (AFDW) of sprat (Fig. 7). Two-way crossed SIMPER analysis showed that sprat had highest similarity in diet composition compared to other fish species (> 40 % in near-mid-offshore areas) and that *T. longicornis* delivered the largest contribution to similarity in every month (each time > 45 %), except for August (highest contribution by decapod megalopa: 37%), and in every zone, followed by *C. hamatus* and barnacle cyprid larvae. Again, pairwise testing resulted in significant differences in stomach content between near-mid-offshore stomachs and stomachs from different months (Table 3 in Addendum 4).

### 3.2.3 Mackerel

In total 96 mackerel stomachs were analyzed, with only one empty stomach. Mackerel was most found in summer months (Fig. 3) and fish (mainly caught with hand lines) measured between 21 and 38 cm (Fig. 2). Nearshore almost no mackerel were caught (Fig. 4). Again, copepods were the dominant prey, with *T. longicornis* as most important (Fig. 7). Other copepods in the diet of mackerel were: *Acartia clausi*, *Calanus helgolandicus*, *Centropages hamatus* and *C. typicus*, *Isias clavipes*, *Pseudocalanus elongatus*, *Paracalanus parvus* and *E. acutifrons*. Other important prey taxa were megalopa larva of decapods. Fourteen mackerel had sandeels Ammodytidae sp. (16 in total) in their stomachs, six had eaten (unidentifiable) fish larvae. Gravimetrically, sandeel seems to be an important energy source for mackerel (Fig. 7). The remainder of the diet consisted of amphipods, cumaceans and cladocerans. Two-way cross SIMPER analysis showed *T. longicornis* and sandeels to contribute most to similarity within midshore samples, whereas decapod megalopa together with *T. longicornis* contributed most in offshore samples. Mackerel were only caught in summer, at mid- and offshore stations and had the lowest fullness indices in this study. No significant differences



were found midshore and offshore sampled stomachs. Several significant differences were found comparing summer with autumn samples (Tables 4,5 in Addendum 4).

#### 3.2.4 Horse mackerel

In total, 116 horse mackerel stomachs were analyzed of which 26 were empty. Total length ranged between 5 and 37 cm (Fig. 2). The diet of horse mackerel included the dominant *T. longicornis*, decapod megalopa larvae and mysid shrimps, but also contained several benthic prey items. Ten adult horse mackerels sampled nearshore in July 2009 had eaten *Ensis* spat (2-4 mm), with on average 146 bivalves per stomach. Four adults had preyed upon juvenile *Nereis longissima* polychaetes (5-10 mm, 480 individuals in total). The importance of these benthic preys becomes even more clear in the gravimetrical results (Fig. 7). Two-way crossed SIMPER showed decapod megalopa larvae and *T. longicornis* as most important contributors to similarity in midshore and offshore samples, whereas nearshore *Ensis* spat contributed most (91 % in 2009 nearshore samples) to similarity within horse mackerel stomachs.

Pair-wise tests (PERMANOVA) revealed significant differences between near- and midshore sampled stomachs and between stomachs sampled in spring and summer months (Table 6, Addendum 4).

The above results indicate that a very limited number of planktonic species constituted the major part of the fish diets. Yet after calculating Schoener indexes between similar length classes of the four fish species, only between the diets of herring and sprat significant (Schoener index > 0.60) overlaps were found. Therefore we calculated Schoener indexes comparing all herring and sprat length classes (Table 2).

Significant spatial and temporal differences in the feeding ecology of herring, sprat, mackerel and horse mackerel in the Belgian part of the North Sea were revealed (see above). Yet variation in temperature (seasonality) only explained 4 % ( $p = 0.001$ ) of the total variation in stomach content (DistLM). Figure 8 shows the summary MDS of all prey abundances in non-empty stomachs (stress value 0.05). Pair-wised tests (PERMANOVA) revealed significant differences in the diets between herring, sprat, mackerel and horse mackerel (Table 7, Addendum 4). Finally, we also conducted hundreds of pairwise tests comparing stomach contents of different length classes within every fish species separately (thus comparing

stomachs from the same year, month and zone for every fish species). Only 18 significant ( $< 0.05$ ) p values were found in 404 pairwise tests (not shown), indicating similarity within the diets of herring, sprat, mackerel and horse mackerel.

Table 2: Schoener index of dietary overlap between herring and sprat. Herring and sprat length classes in cm. Empty stomachs were omitted from this analysis.

		Sprat								
		5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14
Herring	5-6	0.33	0.56	<b>0.68</b>	0.36	0.56	<b>0.60</b>	0.14	0.43	0.03
	6-7	0.31	0.56	<b>0.67</b>	0.34	0.55	<b>0.60</b>	0.39	<b>0.67</b>	0.29
	7-8	0.45	0.35	0.56	0.33	0.38	0.53	0.44	<b>0.64</b>	0.47
	8-9	0.38	0.34	0.48	0.32	0.38	0.48	0.56	<b>0.72</b>	0.54
	9-10	0.16	0.15	0.17	0.14	0.16	0.29	0.40	0.43	0.30
	10-11	0.18	0.18	0.18	0.15	0.18	0.25	0.31	0.35	0.22
	11-12	0.41	0.26	0.32	0.24	0.28	0.44	0.16	0.28	0.23
	12-13	0.05	0.06	0.06	0.06	0.05	0.15	<b>0.88</b>	0.53	<b>0.72</b>
	13-15	0.23	0.41	0.42	0.32	0.41	0.52	0.37	<b>0.67</b>	0.28
	15-20	0.40	0.51	0.57	0.33	0.53	<b>0.64</b>	0.14	0.42	0.20
	>20	0.20	<b>0.68</b>	<b>0.65</b>	0.35	<b>0.67</b>	<b>0.61</b>	0.21	0.50	0.17

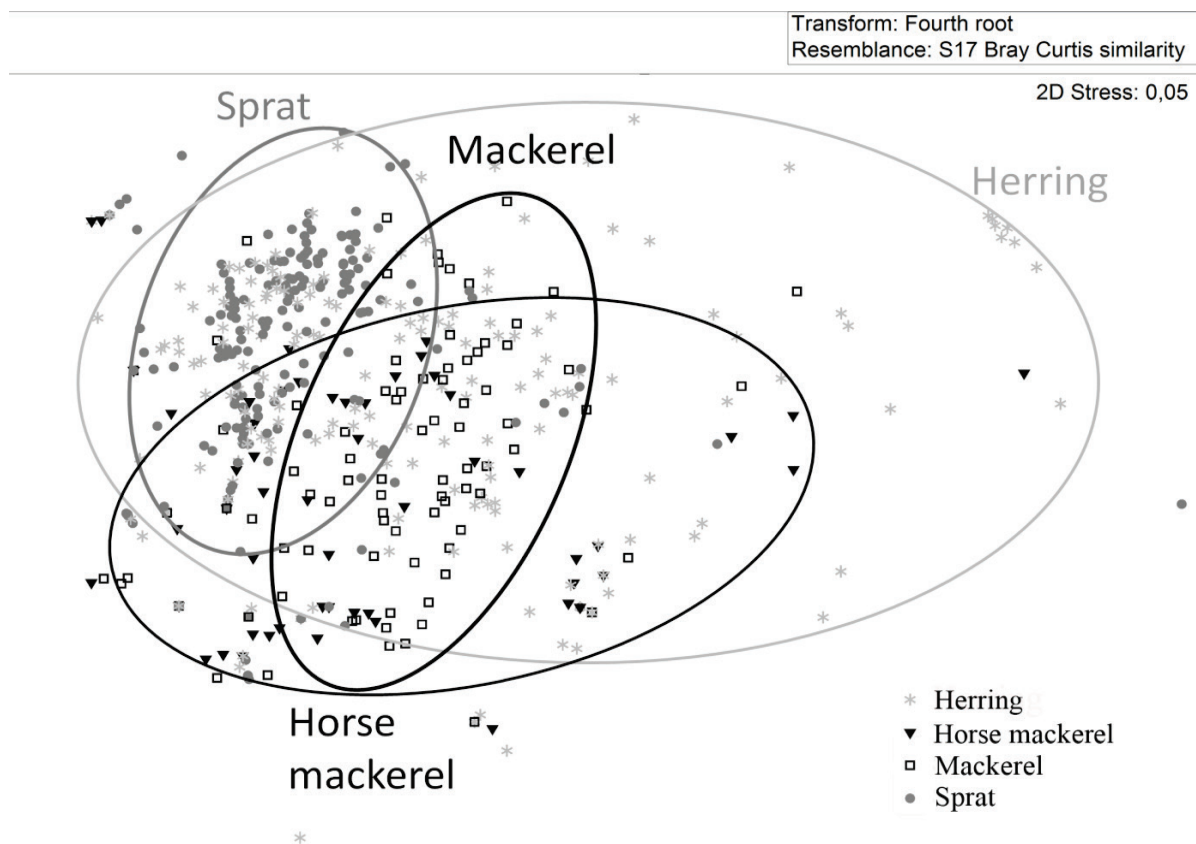


Figure 8: Two-dimensional non-metric MDS plot (stress value = 0.05) of diet composition of 641 non-empty stomachs sampled in 2009 and 2010 in the BPNS, for herring, sprat, mackerel and horse mackerel.

### 3.3 Influencing factors

#### 3.3.1 Abiotic factors

Temperature and salinity profiles revealed that the water column was vertically well-mixed throughout the year (not shown). Sea surface temperature at sampling stations ranged from 2.0 to 20.9 °C, was lowest in February and highest in August (Fig. 6). Due to the cold winter of 2009-2010, sea surface temperatures were lower in early 2010 compared to 2009 (4.9 °C on average in March 2010, compared to 6.1 °C in March 2009). Salinity ranged from 29.9 to 35.0 PSU, with little variation, even at the stations in the vicinity of the Scheldt estuary (Fig. 9). Chlorophyll *a* biomass reached highest values in March (2009) and April (2010), and decreased in an nearshore–offshore gradient. Temperature, Salinity and chlorophyll *a* biomass together explained 8 % ( $p = 0.005$ ) of the total variation (near-mid-offshore, seasonal) in the overall stomach content analysis (DistLM).

#### 3.3.2 Biotic factors – zooplankton

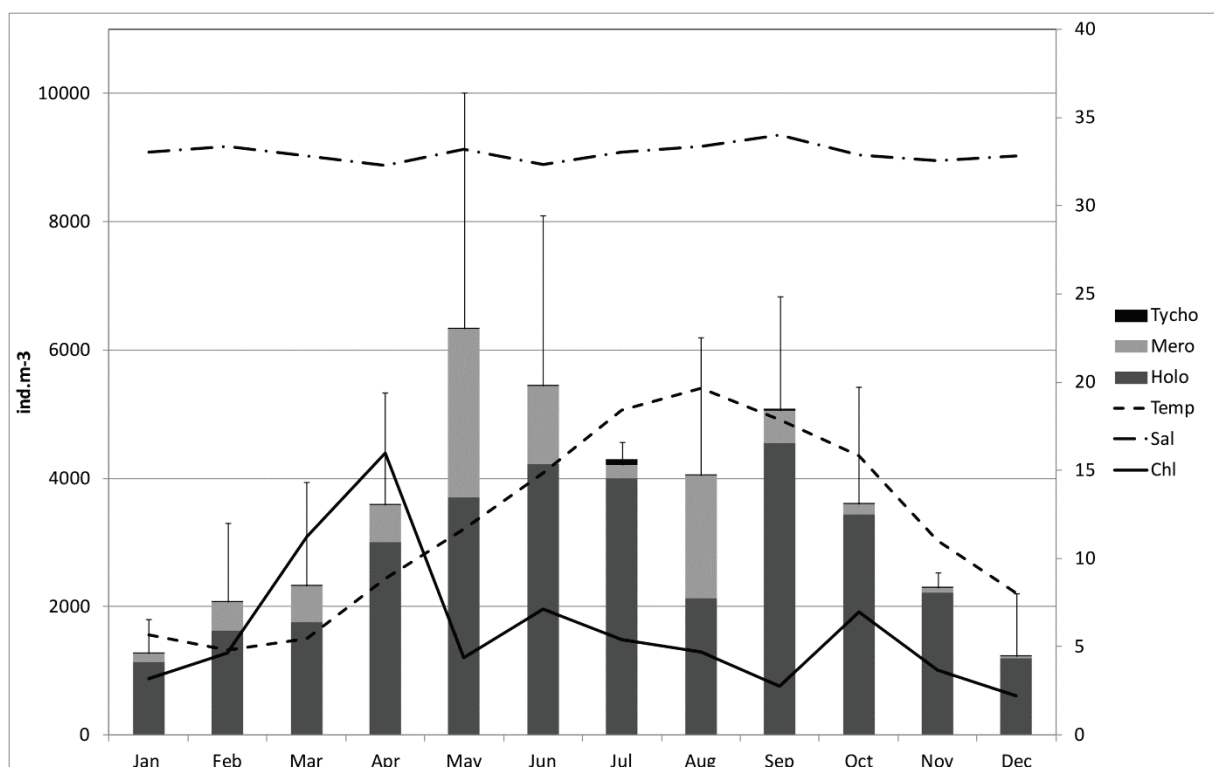


Figure 9: Average monthly zooplankton densities (ind.m<sup>-3</sup>), averaged over all stations and both years (+ SD on total values), divided in holo-, mero- and tycho plankton (left axis). Right Axis: average salinity (PSU), average temperature (°C) and average chlorophyll *a* concentration (mg.m<sup>-3</sup>).

Monthly zooplankton sampling at the ten stations in the BPNS in 2009 and 2010 (53 near, 30 mid, 29 offshore) yielded a total of 137 mesozooplankton taxa (46 holo, 50 mero and 41

tychoplanktonic) of which 98 taxa could be identified to species level, and nine species not previously reported in the area (see Chapters 2,3).

The zooplankton community of the BPNS is characterized by neritic coastal species, but occasionally influenced by species carried with Atlantic water inflow. Zooplankton abundance in the water column was year round dominated by copepods (66 %) and the appendicularian *Oikopleura dioica* (10 %), joined by high numbers of meroplanktonic echinoderm larvae (9 %) in spring and summer (Fig. 9). Calanoid copepods averaged 83 % of all copepods found. Most found were *A. clausi* and *T. longicornis* (present in all samples).

Holoplankton constituted the bulk of the mesozooplankton densities (78 %) in all near-, mid- and offshore stations and in every season (Fig. 6). Meroplankton (mainly echinoderm larvae) was found in lower abundances, but peaked in May and August with respectively 41 % and 47 % of the total plankton densities. Tychoplanktonic taxa were present in much lower densities than holo- and meroplankton in the water column.

### 3.4 Selective feeding behavior: zooplankton vs. stomach content data

Comparing zooplankton data from the water column with the fish stomach contents, allows us to examine selectivity in fish diet. The tychoplankton portion in the diet of herring was much higher than the zooplankton data in the water column would suggest (Fig. 10), while sprat clearly prefers holoplanktonic (copepod) prey. Electivity indices (either negative or positive) were very variable and most absolute values were  $> 0.25$  (Table 3), indicating preference for certain prey species groups (e.g. herring, sprat and horse mackerel targeting mysids and amphipods) and avoidance of others that were ubiquitous in plankton samples (e.g. cladocerans).

Yet no correlation could be found when directly comparing fish stomach fullness with zooplankton prey species density (food supply), calculated from the same date and station as the fish stomach (Fig. 11). This was also proven by a DistLM analysis (not shown), where zooplankton prey density only explained 0.7 % ( $p = 0.029$ ) of the total variation in fish stomach contents.

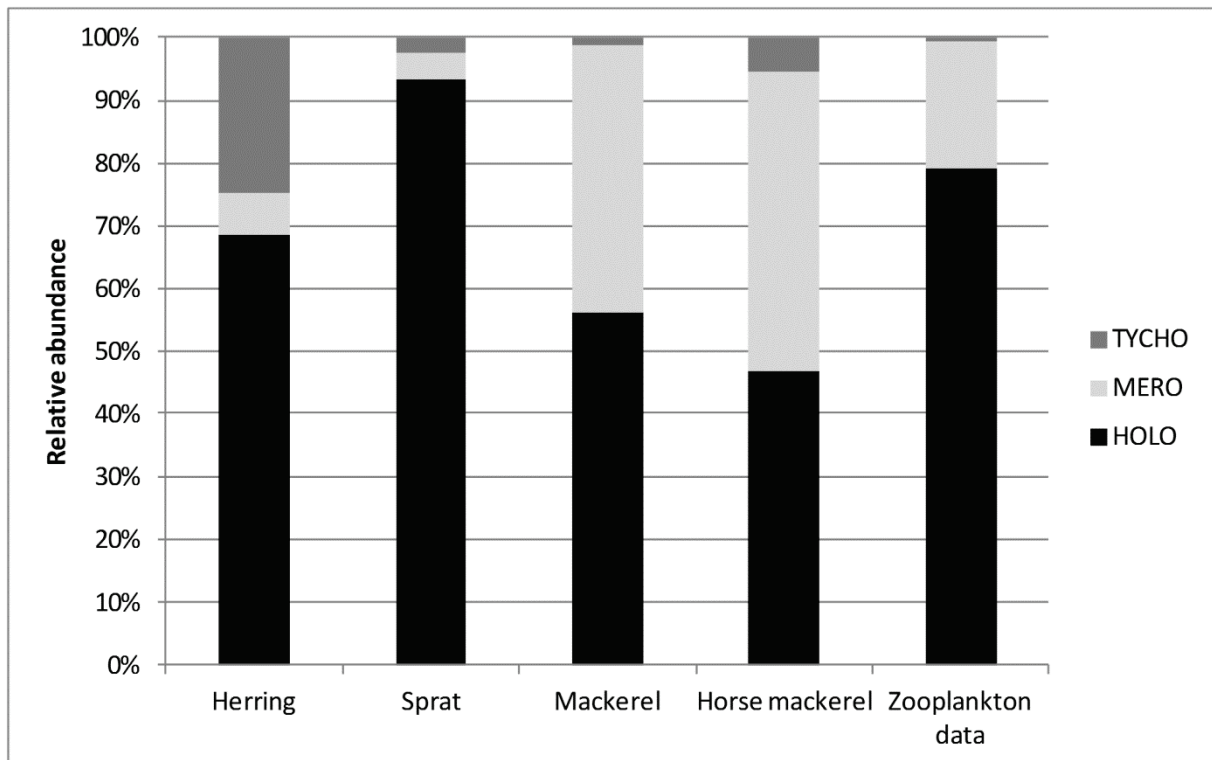


Figure 10: Relative importance of holo-, mero- and tychoplankton in the diet of herring, sprat, mackerel and horse mackerel (based on abundances), displayed against the distribution of these species groups in the water column (zooplankton samples).

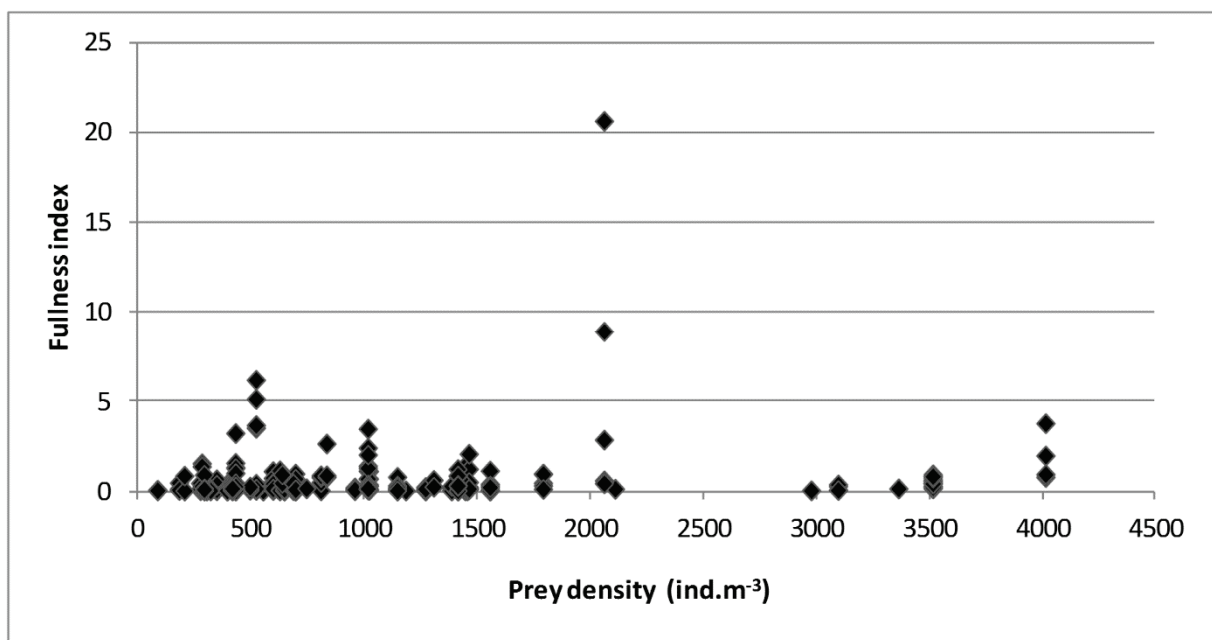


Figure 11: relationship between fish stomach fullness index (all non-empty stomachs) and the summed densities of all prey species (only those prey species that were preyed upon) in the plankton samples ( $\approx$  food supply). As such every prey density originates from a plankton sample, taken at the same time and station as the fish stomach fullness it is plotted against.

Table 3: Electivity index E for the most important prey groups of herring, sprat, mackerel and horse mackerel.

	Herring	Sprat	Mackerel	Horse mackerel
<b>Copepoda</b>	-0.80	0.00	-0.79	-0.62
<b>Decapoda larva</b>	-0.15	-0.20	<b>0.81</b>	<b>0.51</b>
<b>Ensis spat</b>	-1.00	-0.93	-1.00	<b>0.35</b>
<b>Mysida</b>	<b>0.59</b>	<b>0.53</b>	-0.92	<b>0.60</b>
<b>Polychaeta</b>	-1.00	-0.99	-1.00	-0.47
<b>Amphipoda</b>	<b>0.71</b>	<b>0.45</b>	-0.34	<b>0.02</b>
<b>Cumacea</b>	-0.55	<b>0.01</b>	-0.65	-0.85
<b>Cirripedia</b>	-0.91	-0.40	-1.00	-1
<b>Chaetognatha</b>	-1	<b>0.13</b>	-0.58	-1
<b>Pisces larva</b>	-0.98	-0.23	-0.77	-0.71
<b>Cladocera</b>	-1	-0.95	-0.99	-1

Comparing the stomach content data with the zooplankton results shows what the fish were not preying upon. Most striking is the fact that *A. clausi*, a very dominant copepod in the zooplankton samples, was barely found in the stomachs (only 188 individuals on a total of 42461 copepods). Mackerel was the only fish in this study that predated more than occasionally on *A. clausi* (102 specimen found in 27 mackerel stomachs). *Acartia clausi* seemed to be most dominant in September, yet only 3 % of all copepods found in the stomachs in September concerned *A. clausi*.

Around 6 % of the copepods in the diet were juvenile copepodites. This is very different from the situation in the water column, where around 62 % of the copepods (species that were preyed upon) were copepodites. Yet, Only 81 *Calanus helgolandicus* (biggest copepod species in BPNS) were found in 38 stomachs (22 mackerel). As such, 0.19 % of all eaten copepods was a *C. helgolandicus*, which is very similar to the results of the plankton samples where 0.21 % of all copepods concerned this very large calanoid, proving there was no increased selection towards this particular species. Meroplanktonic larva of echinoderms were very abundant in the water column during summer. Pluteus larvae of *Ophiothrix fragilis* reached peak numbers of 10861 ind.m<sup>-3</sup>, yet only one *Ophiothrix* juvenile was found in all analyzed stomachs. Similarly, the urochordate *O. dioica*, averaged 10 % of all plankton densities, but was only found five times in a stomach.

## 4. Discussion

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. As such, we were able to investigate the diet of four pelagic fish species (herring, sprat, mackerel and horse mackerel) with great temporal and spatial detail, and link these *in situ* diet results directly to the zooplankton community present in the Belgian part of the North Sea.

### 4.1 The Belgian part of the North Sea as a feeding ground

The proportion of fish with empty stomachs was low (11 %) for the entire investigated period for all four pelagic species. Similar high numbers of filled stomachs were observed for sprat in the Baltic by Bernreuther (2007) and by Shvetsov *et al.* (1983) in the Eastern and South-Eastern part of the Baltic Sea. Other studies found much more empty stomachs. At the Scottish west coast, *ca.* half of the sprat and herring had some content in their stomachs in the period November-January (De Silva 1973). Last (1989) found that less than 25 % of sprat from the English east coast were feeding, and less than half of the sampled herring had fed. This indicates that the Belgian part of the North Sea acts as a valuable feeding ground for pelagic fish.

### 4.2 Diet composition, overlap and stomach fullness

In total 71 prey taxa were found in 725 stomachs. For every fish species separately, stomach contents rarely differed significantly between different length classes, but when comparing stomach content between herring, sprat, mackerel and horse mackerel, some significant differences were found. Also, significant spatial and temporal differences in stomach content could be shown, following temporal and spatial structuring in zooplanktonic prey populations (see further).

#### 4.2.1 Herring

Copepods formed an important prey of herring with *Temora longicornis* as dominant species, although gravimetrical analysis also showed the importance of *Schistomysis kervillei* (23 %) in the diet. Electivity indices correspond with these gravimetrical results and show increased preference for mysids and amphipods. This is in broad agreement with other

studies (Hardy 1924, Last 1989, Arrhenius and Hanson 1992, Huse and Toresen 1996, Dalpadado *et al.* 2000). De Silva (1973) stated that the diet of herring of the west coast of Scotland was mostly composed of calanoid copepods. Segers *et al.* (2007) also found that crustaceans dominated the food of herring in the southern North Sea. Diet of herring in the Baltic sea was dominated by *Temora* spp., *Centropages* spp. and *Euterpina* spp. (Sandström 1980, Bernreuther 2007). Studies in the Gulf of Lawrence (USA) and in the Norwegian sea found that *Calanus* copepods dominated the diet of herring, accounting for 80 % by mass of the prey consumed (Darbyson *et al.* 2003, Dommasnes *et al.* 2004). We didn't find any proof of increased selectivity for *C. helgolandicus* in our study. Möllmann *et al.* (2000) identified *T. longicornis* and *Pseudocalanus acuspes* as most dominant prey species in the Baltic sea, along with cladocerans. The latter was not found in the stomachs we investigated, despite the fact that the cladocerans *Evadne nordmanni* and *Podon leuckartii* reached densities  $> 1000 \text{ ind.m}^{-3}$  in our plankton samples.

The larger adult herring ( $> 20 \text{ cm}$ ) all had empty or 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). Fullness indices mostly ranged between 0 and 1 in our study. Other European studies found higher fullness indices for herring, ranging between 1.2 and 3.7 in the Norwegian sea (Prokopchuk and Sentyabov 2006), and even mounting to a maximum of 13.4 (Huse and Toresen 1996). Herring caught in summer and nearshore samples had a higher fullness. This might be explained by the fact that decapod zoea and megalopa larvae reached highest numbers in summer and mysids occurred mostly nearshore.

#### 4.2.2 Sprat

No less than 93 % of all sprat prey items were calanoid copepods (holoplankton), with adult *T. longicornis* as dominant prey item. This is supported by other authors who also identified calanoid copepods as most important prey species for sprat (De Silva 1973, Arrhenius and Hansson 1992, Voss *et al.* 2003, Möllmann *et al.* 2004, Bernreuther 2007).

Sprat had the highest fullness index in this study, with peak values in spring, which might be attributed to the fact that copepods peaked in spring. Several authors pointed out the potential control by clupeids on zooplankton communities (Flinkman *et al.* 1992, Möllmann



and Köster 2002). For instance, Möllmann and Köster (2002) indicated a strong inter-annual variability in zooplankton abundance due to clupeid predation pressure. This top-down control is of large ecological importance.

The Schoener index only showed a significant overlap between herring and sprat diets. In the Baltic Sea, a high diet niche overlap was observed between herring and sprat, and hence a strong competition for food resources (Bernreuther 2007). Yet, in an MDS plot sprat stomachs in our study clearly clustered together, whereas stomachs of herring, mackerel and horse mackerel were more scattered. Also the SIMPER analysis showed more similarity in diet of sprat. Electivity indices indicate that sprat showed higher preference for copepods compared to the other pelagic fish species. It can be concluded that herring behaves more opportunistic, with a more varied diet composition than sprat. Interspecific competition between sprat and herring in the BPNS might be present, but seems to be limited.

#### 4.2.3 Mackerel

Many copepod species were found in mackerel stomachs, next to several other prey taxa, which is in agreement with other studies (Cabral and Murta 2002, Darbyson *et al.* 2003, Prokopchuk and Sentyabov 2006). Cabral and Murta (2002) found that the diet of mackerel in summer in Portugal was characterized by zooplankton, while the diet in autumn was composed of fish and megalopa larvae. Electivity indices only showed increased preference for decapod larvae, but it has to be noted that fish were not present in zooplankton samples, hence gravimetrical results are more reliable in the case of mackerel.

Although, overall low fullness indices were calculated for mackerel, a peak was noted midshore, possibly related with the higher copepod and decapod larva densities in this zone. In the present study 23 % of mackerel stomachs contained *C. helgolandicus*, with a maximum of 20 per stomach. Prokopchuk and Sentyabov (2006) found up to 30000 *C. finmarchicus* in a single mackerel stomach, with an average fullness index of 2.6, which is much higher than in our study. Zooplankton numbers found in the mackerel stomachs seemed to be too low to fulfill the daily energy demand of these very active fish. Gravimetrical analyses showed that fish were far more important a food source than crustaceans. Twenty mackerel had eaten sandeels or fish larvae. No less than five sandeel species are found (Vandepitte *et al.* 2010), yet little quantitative information is available on the distribution of sandeels in Belgian waters. There is evidence that suggests that sandeels

are a common fish species in the BPNS: they are often reported as bycatch in Van Veen grabs and beam trawl samples and several studies have showed sandeel to constitute an important part of Belgian seabird diets (Vanaverbeke *et al.* 2011). However, their capabilities to wriggle into the sediment allows them to escape from all but fine meshed fishing nets. More detailed information (with bigger and fine meshed pelagic nets) must be gathered to solidify our thoughts on sandeel distribution in the BPNS.

#### 4.2.4 Horse mackerel

There was very low similarity in horse mackerel stomach contents, indicating a wide range of prey species taken. Next to the dominant holoplanktonic pelagic crustaceans *T. longicornis*, decapod megalopa larvae and mysid shrimp, also benthic prey items were preyed upon. Several adult horse mackerels had eaten *Ensis* spat or juvenile *N. longissima* polychaetes (5–10 mm), resulting in a higher fullness index. Several studies showed a diverse feeding ecology in horse mackerel. In the North Sea, horse mackerel seemed to have a piscivorous diet (Dahl and Kirkegaard 1987), while in the Adriatic Sea euphausiid crustaceans and teleosts dominated the diet (Santic *et al.* 2005). Cabral and Murta (2002) indicated copepods and euphausiids as important prey species for horse mackerel off Portugal. Garrido and Murta (2011) compared horse mackerel diets between areas, seasons and decades in Portugal. The most important prey in 1990–1992 were euphausiids while in 2005–2006 the most important prey were fishes. Their results showed that periods of different feeding intensity for horse mackerel were concomitant with diets characterized by different dominant prey items.

#### 4.3 Selective feeding behavior

The copepod *Temora longicornis* was omnipresent in the diet of herring, sprat, mackerel and horse mackerel, and dominated even more compared to the results from other studies (De Silva 1973, Arrhenius 1996, Möllmann *et al.* 2004), indicating extensive foraging on this particular calanoid. For the rest, we observed a very different composition of zooplankton species and life stages in the zooplankton samples compared to those found in the stomachs of the four fish species. The most common zooplankton species in the BPNS, *A. clausi* was barely found in the stomachs. This was also observed by Casini *et al.* (2004) in the Baltic, and might be related to the small size and high escape response of *Acartia* spp. (Viitasalo *et al.*

2001). Secondly, the genus *Acartia* is often considered a surface dweller (Hansson *et al.* 1990), thus perhaps not always spatially overlapping with fish whereabouts.

The harpacticoid copepod *E. acutifrons*, the urochordate *Oikopleura dioica* (found to constitute an important part of herring and sprat diet by several studies: Hardy 1924, De Silva 1973, Prokopchuk and Sentyabov 2006), the cladoceran *E. nordmanni*, meroplanktonic echinoderm larvae, fish larvae and fish eggs were all ubiquitous in the water column, but very rare in the diet of the four studied fish species in the BPNS. Pelagic fish such as herring and mackerel have been known to shift from particulate to filter feeding at higher prey concentrations (Pepin *et al.* 1988). Yet the fact that few species dominated stomach content whilst many ubiquitous plankters were virtually absent from the diet, indicates that filter feeding was limited.

Only 6 % of copepods in the diet were copepodites, much differing from the situation in the water column, where 62 % of the copepods were copepodites. This selectivity towards 'bigger' prey was also observed by Prokopchuk and Sentyabov (2006) for herring in the Norwegian Sea. Bernreuther (2007) and Möllmann *et al.* (2004) found that herring and sprat in the Baltic Sea mainly preyed on copepodite stage c5 and adults of *T. longicornis* and *P. acuspes*. Prokopchuk and Sentyabov (2006) found immature stages of copepodites in the diet of mackerel in the Norwegian Sea, but c3-5 copepodites of *C. finmarchicus* are still much bigger than adult *T. longicornis*.

Much more female copepods were eaten than males, in contrast to the well-balanced distribution of both sexes of the different copepod species (that were preyed upon) in the water column. This corresponds with results published on Baltic herring (Sandström 1980, Flinkman *et al.* 1992), showing selective predation on larger individuals and females of copepods and cladocerans carrying eggs. Gravid females might swim a bit slower, making them easier to catch.

These findings are indicative of a profound selective feeding behavior exhibited by the four examined fish species. Yet the fact that more than 100 plankton species were found in the water column and just 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 plankters could have huge effects on pelagic fish stocks.

#### 4.4 Bottom-up control by zooplankton

Clear temporal structuring and small-scale spatial variation within the mesozooplankton community was observed, with plankton densities averaging highest in spring and midshore. However, apart from sprat, fullness indices peaked in summer and nearshore, and no correlation between fullness index and prey density was found. Given the fact that calanoids were favorite preys and that these calanoids (especially *T. longicornis*) were more abundant midshore than nearshore, led us to believe that calanoid copepod density is not a limiting factor in the feeding ecology of the four pelagic fish species in the BPNS.

Herring can show cannibalism (Hardy 1924, Dalpadado *et al.* 2000). Especially when zooplankton concentrations are (too) low, predation on clupeid larvae will increase (Rudakova 1966, Last 1989, Ellis and Nash 1997), with an impact on the abundance of these herring year classes (Holst 1992). In our study, cannibalistic pressure was limited as clupeid larvae were found in only four herring stomachs, indicative of sufficient other prey. Also, the fact that few fish eggs were eaten (Segers *et al.* (2007) suggested that herring forages on eggs when other prey are scanty), and that smaller and faster plankton species known to be preyed upon elsewhere (e.g. *O. dioica*, *E. nordmanni*, *A. clausi*) were left aside, supports the idea that zooplankton was not restrictive, and that pelagic fish in the BPNS are not bottom-up regulated by their zooplanktonic prey.

#### 4.5 Foraging in a sea in motion

Literature shows that fish diet can significantly differ in between decades. Garrido and Murta (2011) showed interdecadal differences in the diet composition of horse mackerel, proving that predatory fish can change their trophic niche and therefore the whole configuration of the food web as an adaptation to changing prey abundance and availability. As such, two years of sampling only unraveled part of the feeding ecology of pelagic fish in the BPNS.

Large scale decadal trends in salinity, temperature and hydrodynamic regimes, caused by Atlantic oscillations are thought to influence zooplankton communities worldwide (Fransz *et al.* 1991, Reverdin *et al.* 1997, O'Brien *et al.* 2011). Temperate marine environments like the

southern North Sea may be particularly vulnerable to these changes, as the recruitment success of fish is highly dependent on the yearly synchronization with the production of their planktonic prey (Hjort 1914, Cushing 1990, Kirby *et al.* 2007).

Richardson (2008) showed that holozooplankton abundance peaks earlier by 10 days in the North Sea, diatoms by 22 days, and meroplankton by 27 days compared to 45 years ago. Echinoderm larvae (particularly *Echinocardium cordatum*) even appeared 47 days earlier in the North sea plankton community than they did 50 years ago (Edwards and Richardson 2004). The differential response of phytoplankton, merozooplankton and holozooplankton to changes in the environment is likely to lead to mismatches and will influence the synchrony between primary, secondary and tertiary producers (Edwards and Richardson 2004, Richardson 2008). Pelagic fish are thus influenced directly and indirectly by climate change, as increasing water temperatures force them to migrate northwards in eastern Atlantic waters, and as changes occur in the development of their favored prey (Frederiksen *et al.* 2006, Prokopchuk and Sentyabov 2006).

Of course, over time several predator–prey relationships remained viable, although they underwent substantial changes. An important question is how long will the marine ecosystem need to adapt and resynchronize these phenological relationships, knowing that they are already weakened by other concomitant anthropogenic stressors.

It is noteworthy that still, after many decades of Belgian marine research, there is no detailed knowledge on the distribution of pelagic fish in the water column and near the water surface in the BPNS. Therefore, it is important to further monitor both pelagic fish and their zooplanktonic prey populations, to figure out how fish stocks and fish feeding ecology are evolving, and to be aware of possible shifts in or mismatches with the plankton, the basis of all marine food webs.

### **Acknowledgements**

The first author was funded through a PhD grant by the Institute for Agricultural and Fisheries Research. The authors are grateful to the Flanders Marine Institute, especially Dr. André Cattrijse, for planning the sampling campaigns with RV Zeeleeuw. This study could not have taken place without the adept help of different taxonomical experts verifying our work. We want to express our gratitude to Prof. Dr. Jean-Michel Brylinski (ULCO-LOG) for

help with *Giardella* copepodites, Dr. Elvire Antajan (Ifremer) for help with copepods, Jan Wittoeck (ILVO) for checking tychoplanktonic species, and Dr. Christophe Loots (Ifremer) for verifying fish larvae. Dr. Annelies De Backer and Dr. Gert Van Hoey (both ILVO) are to be thanked for help with the statistical analyses.