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Selective feeding by pelagic fish in the Belgian part of the North Sea

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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. In all, 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* (33 408 of all 55 004 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 with 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 calanoid 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: Belgian part of the North Sea, diet, herring, horse mackerel, mackerel, sprat, zooplankton.

Introduction

Abundant mid-trophic pelagic fish usually play a central role in marine ecosystems, channelling 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 a "driver" 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; Adlerstein and Welleman, 2000; Dalpadado *et al.*, 2000; Gislason and Astthorsson, 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 currently 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 6 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).

Zooplankton communities are crucial to the functioning of marine foodwebs 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 foodweb, an update on pelagic fish feeding ecology in the Belgian part of the North Sea (BPNS), positioned in the transitional region between the Atlantic Ocean and the North Sea, is certainly in place. More specifically, the aims of this study were: (i) to characterize the diet of four common pelagic fish species in the BPNS, (ii) to verify whether selectivity in feeding occurs, by comparing diet results with data on zooplankton from the same areas and periods, and (iii) 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.

Material and methods
Study area
This study covered the BPNS (ca. 3600 km^2), situated in the southern bight of the North Sea (Figure 1). The BPNS has a maximum seaward extent of 87 km, is bounded by a 67 km sandy coastline, and bordered eastwards by the Westerschelde estuary (Degraer *et al.*, 2003). Prevailing marine currents convey saline Atlantic water in NE direction through the Channel towards the BPNS where it meets the SW oriented Westerschelde outflow (Nihoul and Hecq, 1984; Howarth, 2001). There is a macro tidal current regime (tidal amplitude averages 4 m) and a well-mixed water column, which is on average 30 m deep (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.*, 2012), subsequently influencing the pelagic ecosystem via benthic–pelagic coupling (Provoost *et al.*, 2013).

Data origin
Sampling was carried out monthly in 2009 and 2010 at ten monitoring stations positioned along a nearshore–midshore–offshore axis on the BPNS (Figure 1).

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). 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 handline fished, with simple hooked feathers as lure, as they were too fast swimmers to catch with the trawlnet. Line fishing was done for 15 min at every station using a varying number of handlines. Large fish were weighed (± 5 g) and measured onboard (total length; ± 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 thereafter dissected in the lab. Only stomachs and not intestines were investigated. Using the 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*
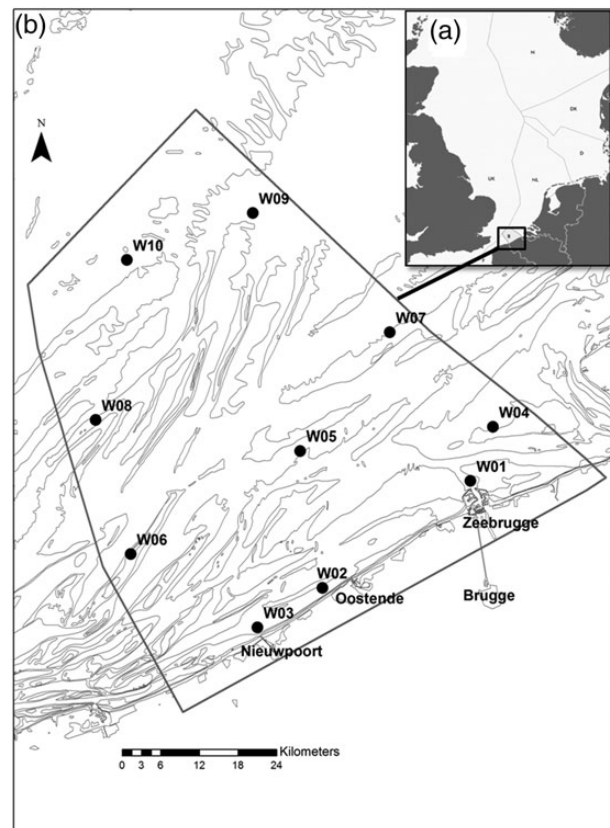

Figure 1. (**a**) North Sea exclusive economic zones; (**b**) BPNS with ten stations (nearshore W01–04, midshore W05–07, offshore W08–10).

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 tychoplanktonic (species that are occasionally carried into the water column, e.g. cumaceans or mysids) prey taxa. Prey remains that could not be identified were catalogued as digested matter (with abundance = 1 when present in a stomach). Wet weights (WWs), dry weights (DWs), and ash weights (AWs) of every species of prey were measured to the nearest 0.01 mg. DWs were acquired by drying the stomach contents in an oven at 60°C for 48 h. AW was obtained by muffling the DW samples at 550°C for 2 h. When combining these data, the ash-free DW (AFDW = DW − AW) could be calculated.

After trawling, a WP2 zooplankton net (57 cm diameter, 200 μm mesh size) fitted with a flowmeter (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 the 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. Chlorophyll *a* data were attained via MODIS and MER satellite imaging systems (Vanhellemont *et al.*, 2011).

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 multidimensional 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 pairwise 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 (Supplementary Tables).

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).

Diet indices

To determine the dietary importance of each food category and to compare feeding ecology of different fish species and sampling locations, the frequency of occurrence and relative abundance methods were used (Hyslop, 1980). Second, 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 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 is present. In the below equation, N_i is the number of predators with prey *i* in their stomach and N the total number of stomachs that were not empty.

$$\%FO_i = \frac{N_i}{N} \times 100. \tag{1}$$

The relative prey abundance can be either numerical (% abundance) or gravimetrical (% AFDW). In the below equation, S_i is the abundance or AFDW of prey *i* in the stomach and S_t the total stomach content of the predator:

$$\%R_i = \frac{S_i}{S_t} \times 100. \tag{2}$$

The stomach fullness index (Sigurdsson and Astthorsson, 1991) was used as an indicator of feeding activity. In the below equation, *AFDWs* is the weight of the stomach content and *AFDWf* the weight of the entire fish.

$$FI = \frac{AFDWs \times 100}{AFDWf}.$$

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

$$E_i = \frac{W_i - 1/m}{W_i + 1/m}. \tag{4}$$

where W_i is defined by the following equation:

$$W_i : \frac{r_i/n_i}{\Sigma_i(r_i/n_i)}. \tag{5}$$

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 ≈ 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 DWs were calculated from length−WW relationships in the literature (Wigley *et al.*, 2003 for herring and sprat,

Coull *et al.*, 1989 for mackerel and horse mackerel). WW of the fish was then converted to AFDW with the common formula AFDW ≈ 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 the below equation, with Px_i the proportion of prey species *i* in the diet of fish *x*, and Py_i the proportion of prey species *i* in the diet of fish *y*.

$$S = 1 - 0.5(\Sigma |Px_i - Py_i|). \tag{6}$$

Results
General characterization of the diet
Stomach data were derived from 725 stomachs. This included 84 empty stomachs omitted from further analyses, 209 herring, 247 sprat, 95 mackerel, and 90 horse mackerel stomachs (Supplementary Figure S1), sampled mostly during summer (Supplementary Figure S2) and at nearshore stations (Supplementary Figure S3).

In total, 71 prey taxa (36 identified to species level) were found (Table 1). Species richness ranged from 0 to 21 sp. stomach^{-1} 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. The calanoid copepods *Temora longicornis* and *C. hamatus* occurred most frequently in the diet (no less than 33 408 of all 55 004 prey items identified were *T. longicornis*). Only 5.8% 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), followed by herring (0.60), horse mackerel (0.26), and mackerel (0.24). Fullness indices were highest nearshore (lowest offshore) and in summer (lowest in winter), sprat being the exception with highest fullness index in spring, and mackerel not caught at nearshore stations (Figure 2).

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, but in biomass terms, their contribution was higher, due to their bigger size.

Diet composition per fish species
Herring
In total, 237 herring stomachs were analysed; of which, 28 were empty. Length varied between 5 and 30 cm with a clear dominance of immature fish being caught at nearshore stations (Supplementary Figures S1 and S3). 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 gravimetrical

data (Figure 3). 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, 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 (Supplementary Tables S1 and S2).

Sprat
We analysed 276 sprat stomachs; of which, 29 were empty. Length varied between 5 and 14 cm, including many adults (>10 cm) (Supplementary Figure S1). Copepods again constituted the vast majority of prey items in sprat stomachs, with 93% of all prey items being calanoid copepods (Figure 3). Especially adult *T. longicornis* dominated the stomach content, both numerically (69%) and gravimetrically (32%), 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. Gravimetrical analyses showed that *T. longicornis* and *S. kervillei* provided a large part of the energy demand of sprat (Figure 3). Two-way crossed SIMPER analysis showed that sprat had highest similarity in diet composition compared with other fish species (>40% in near-mid-offshore areas). This can also be observed in the MDS plot in Figure 4 where sprat stomachs clearly cluster together. *Temora longicornis* delivered the largest contribution to similarity (SIMPER) 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 (Supplementary Table S3).

Mackerel
In total, 96 mackerel stomachs were analysed, with only one empty stomach. Mackerel was most found in summer (Supplementary Figure S2) and fish (mainly caught with handlines) total length varied between 21 and 38 cm (Supplementary Figure S1). Nearshore, almost no mackerel were caught (Supplementary Figure S3). Again, copepods were the dominant prey, with *T. longicornis* as most important. Other copepods in the diet of mackerel were: *Acartia clausi*, *Calanus helgolandicus*, *C. 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 (Figure 3). 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

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*.

	Herring		Sprat		Mackerel		Horse mackerel	
	%FO	%RA	%FO	%RA	%FO	%RA	%FO	%RA
Holoplankton								
Copepoda								
Copepoda sp.	25.4	4.6	27.1	6.7	21.1	0.9	14.4	1.4
Calanoida								
Acartia clausi	5.7	0.5	2.0	–	28.4	1.6	1.1	0.1
Acartia clausi copepodite	0.5	–	–	–	–	–	–	–
Calanoida sp.	1.0	–	0.8	–	6.3	1.2	5.6	0.5
Calanus helgolandicus	2.9	–	0.4	–	23.2	1.1	4.4	0.1
Centropages hamatus	25.4	2.7	33.6	15.6	27.4	1.6	7.8	0.5
Centropages typicus	12.0	0.8	10.9	1.1	23.2	1.2	1.1	0.1
Isias clavipes	3.8	0.1	5.7	0.1	17.9	0.8	3.3	0.1
Labidocera wollasteni	1.0	–	0.4	–	4.2	0.1	1.1	–
Paracalanus parvus	5.3	0.2	2.4	–	11.6	0.8	1.1	–
Pseudocalanus elongatus	1.4	–	3.6	0.1	9.5	0.5	2.2	0.1
Temora longicornis	52.2	58.7	65.6	69.0	57.9	41.5	25.6	42.8
Cyclopoida								
Oithona sp.	0.5	–	0.4	–	–	–	–	–
Harpacticoida								
Giardella callianassae	–	–	0.4	–	–	–	–	–
Euterpina acutifrons	7.2	0.3	0.4	–	13.7	0.3	1.1	0.1
Harpaticoida sp.	3.3	0.1	0.4	–	2.1	–	–	–
Tigriopus sp.	1.0	–	–	–	2.1	0.1	–	–
Siphonostomatoida								
Caligus elongates	–	–	0.4	–	4.2	0.3	–	–
Chaetognatha								
Sagitta setosa	–	–	–	–	8.4	3.0	–	–
Cladocera								
Evadne nordmanni	–	–	–	–	2.1	0.1	–	–
Podon sp.	–	–	–	–	1.1	–	–	–
Urochordata								
Oikopleura dioica	–	–	0.4	–	1.1	0.1	–	–
Meroplankton								
Echinodermata								
Ophiura sp. spat	–	–	–	–	1.1	–	–	–
Bivalvia								
Ensis sp. spat	0.5	–	1.6	0.2	1.1	–	1–	30.8
Cirripedia								
Cirripedia sp. cyprid larva	19.1	2.3	27.9	3.3	2.1	–	–	–
Cirripedia sp. nauplius larva	1.4	–	3.2	–	1.1	–	–	–
Decapoda								
Anomura sp. megalopa larva	1.0	–	–	–	–	–	–	–
Anomura sp. zoea larva	–	–	0.4	–	7.4	0.7	3.3	0.2
Callianassa 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
Crangon crangon 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	–	–	–
Pisidia longicornis zoea	–	–	–	–	14.7	7.2	1.1	–
Polychaeta								
Lanice conchilega larva	–	–	–	–	1.1	–	1.1	–
Polychaeta sp. larva	1.4	–	–	–	1.1	–	1.1	–
Pisces								
Ammodytidae sp. larva	–	–	–	–	14.7	0.3	–	–
Callionymus 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

Continued

Table 1. *Continued*

	Herring		Sprat		Mackerel		Horse mackerel	
	%FO	%RA	%FO	%RA	%FO	%RA	%FO	%RA
Solea solea	–	–	–	–	1.1	–	2.2	–
Syngnathus sp. larva	–	–	–	–	–	–	1.1	–
Tychoplankton								
Cumacea								
Cumacea sp. juvenile	10.5	1.2	3.2	0.1	7.4	0.3	3.3	0.1
Pseudocuma sp.	–	–	0.4	–	5.3	0.3	–	–
Amphipoda								
Abludomelita obtusata	–	–	–	–	–	–	1.1	–
Amphipoda sp.	9.1	0.9	2.4	0.1	5.3	0.1	4.4	0.3
Aora gracilis	0.5	–	–	–	–	–	–	–
Apherusa ovalipes	–	–	–	–	1.1	–	–	–
Atylus swammerdami	11.0	6.5	4.5	0.3	10.5	0.4	6.7	0.2
Bathyporeia sp.	1.0	0.1	1.2	–	–	–	–	–
Gammaridea sp.	3.3	0.6	0.4	–	–	–	–	–
Gammarus sp.	1.0	0.2	2.0	0.1	–	–	–	–
Jassa sp.	1.0	–	1.2	–	–	–	–	–
Megaluropus agilis	1.4	0.1	0.4	–	–	–	–	–
Pariambus typicus	–	–	0.8	–	–	–	–	–
Pontrocrates altamarinus	–	–	0.4	–	–	–	–	–
Mysida								
Gastrosaccus spinifer	7.7	1.2	2.8	0.2	3.2	–	4.4	0.6
Heteromysis morfosa	0.5	–	–	–	–	–	–	–
Mesopodopsis slabberi	4.3	0.1	0.8	–	–	–	–	–
Mysida sp.	7.2	0.8	1.2	–	3.2	0.1	2.2	0.1
Neomysis integer	0.5	–	–	–	–	–	–	–
Schistomysis kervillei	8.1	9.7	2.0	1.4	–	–	5.6	2.9
Schistomysis spiritus	7.7	1.4	1.2	–	–	–	2.2	0.7
Benthos								
Brachyura sp.	1.0	0.1	0.8	–	2.1	–	1.1	–
Branchiostoma lanceolatum	–	–	–	–	5.3	0.3	–	–
Eumida sanguinea	1.0	–	–	–	–	–	–	–
Nereis longissima	–	–	–	–	1.1	–	3.3	10.1
Pagurus sp.	0.5	–	–	–	1.1	–	–	–
Thia scutellata	–	–	–	–	1.1	–	–	–
Other								
Digested matter	31.6	/	50.2	/	55.8	/	58.9	/

%FO, frequency of occurrence; %RA, numerical relative abundance.

stomachs. Several significant differences were found comparing summer with autumn samples (Supplementary Tables S4 and S5).

Horse mackerel

In total, 116 horse mackerel stomachs were analysed; of which, 26 were empty. Total length ranged between 5 and 37 cm (Supplementary Figure S1). 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. Gravimetrical results (Figure 3) show the importance of predation on juvenile *Nereis longissima* polychaetes (5–10 mm, 480 individuals in total), though only four stomachs that contained these polychaetes. 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. Pairwise tests (PERMANOVA) revealed significant differences between near- and midshore sampled

stomachs and between stomachs sampled in spring and summer (Supplementary Table S6).

The above results indicate that a very limited number of planktonic species constituted the major part of the fish diets. Yet after calculating Schoener indices 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 indices 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 BPNS were revealed. Yet variation in temperature (seasonality) only explained 4% ($p = 0.001$) of the total variation in stomach content (DistLM). Pairwised tests (PERMANOVA) revealed significant differences in the diets between herring, sprat, mackerel, and horse mackerel (Supplementary Table S7). 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
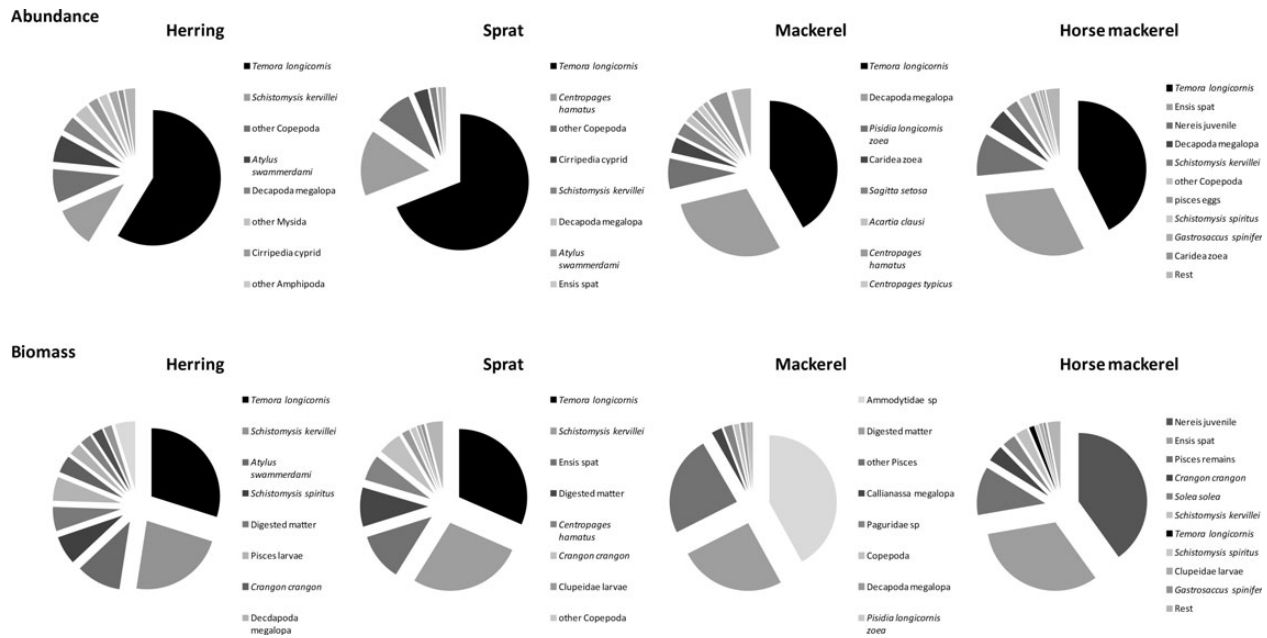
Figure 2. Dominant prey items in the diet of herring, sprat, mackerel, and horse mackerel, based on the relative numerical abundances of prey items (top) and on their biomass (AFDW, bottom).
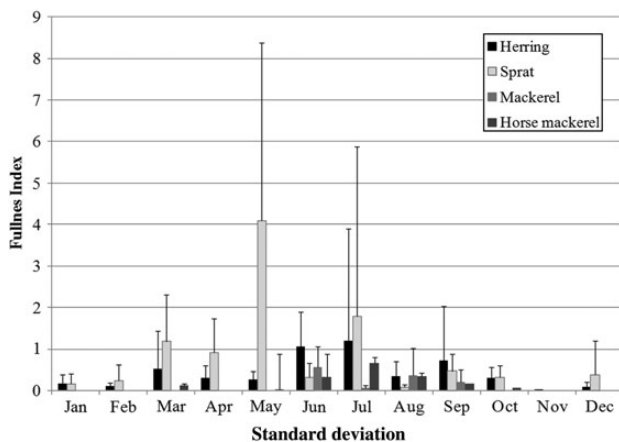

Figure 3. Temporal variation in fullness index for herring, sprat, mackerel, and horse mackerel.

Figure 4. MDS plot of all 641 non-empty stomachs sampled in 2009 and 2010 in the BPNS, for herring, sprat, mackerel, and horse mackerel.

found in 404 pairwise tests (not shown), indicating similarity within the diets of herring, sprat, mackerel, and horse mackerel.

Influencing factors

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 (Figure 5). Due to the cold winter of 2009/2010, sea surface temperatures were lower in early 2010 compared with 2009 (4.9°C on average in March 2010, compared with 6.1°C in March 2009). Salinity ranged from 29.9 to 35.0 PSU, with little variation, even at the stations near the Scheldt estuary (W01 and W04, Figure 5). Chlorophyll *a* biomass reached highest values in March (2009) and April (2010), and decreased in a nearshore–offshore gradient. Temperature, salinity, and chlorophyll *a* biomass together explained
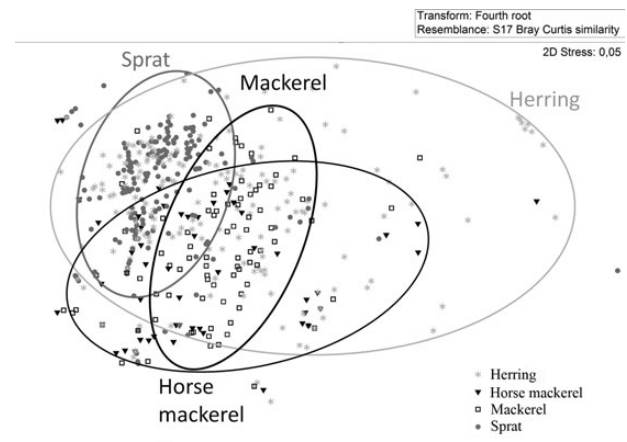
8% ($p = 0.005$) of the total variation (near–mid–offshore, seasonal) in the overall stomach content analysis (DistLM).

Biotic factors: zooplankton

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.

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 *O. dioica* (10%), joined by large numbers of meroplanktonic echinoderm larvae (9%) in spring and summer (Figure 5). Calanoid copepods averaged 83% of all copepods

Table 2. Schoener index of dietary overlap between herring and sprat.

	Sprat								
Herring	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14
5–6	0.33	0.56	**0.68**	0.36	0.56	**0.60**	0.14	0.43	0.03
6–7	0.31	0.56	**0.67**	0.34	0.55	**0.60**	0.39	**0.67**	0.29
7–8	0.45	0.35	0.56	0.33	0.38	0.53	0.44	**0.64**	0.47
8–9	0.38	0.34	0.48	0.32	0.38	0.48	0.56	**0.72**	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	**0.88**	0.53	**0.72**
13–15	0.23	0.41	0.42	0.32	0.41	0.52	0.37	**0.67**	0.28
15–20	0.40	0.51	0.57	0.33	0.53	**0.64**	0.14	0.42	0.20
>20	0.20	**0.68**	**0.65**	0.35	**0.67**	**0.61**	0.21	0.50	0.17

Herring and sprat length classes in centimetres. Empty stomachs were omitted from this analysis.
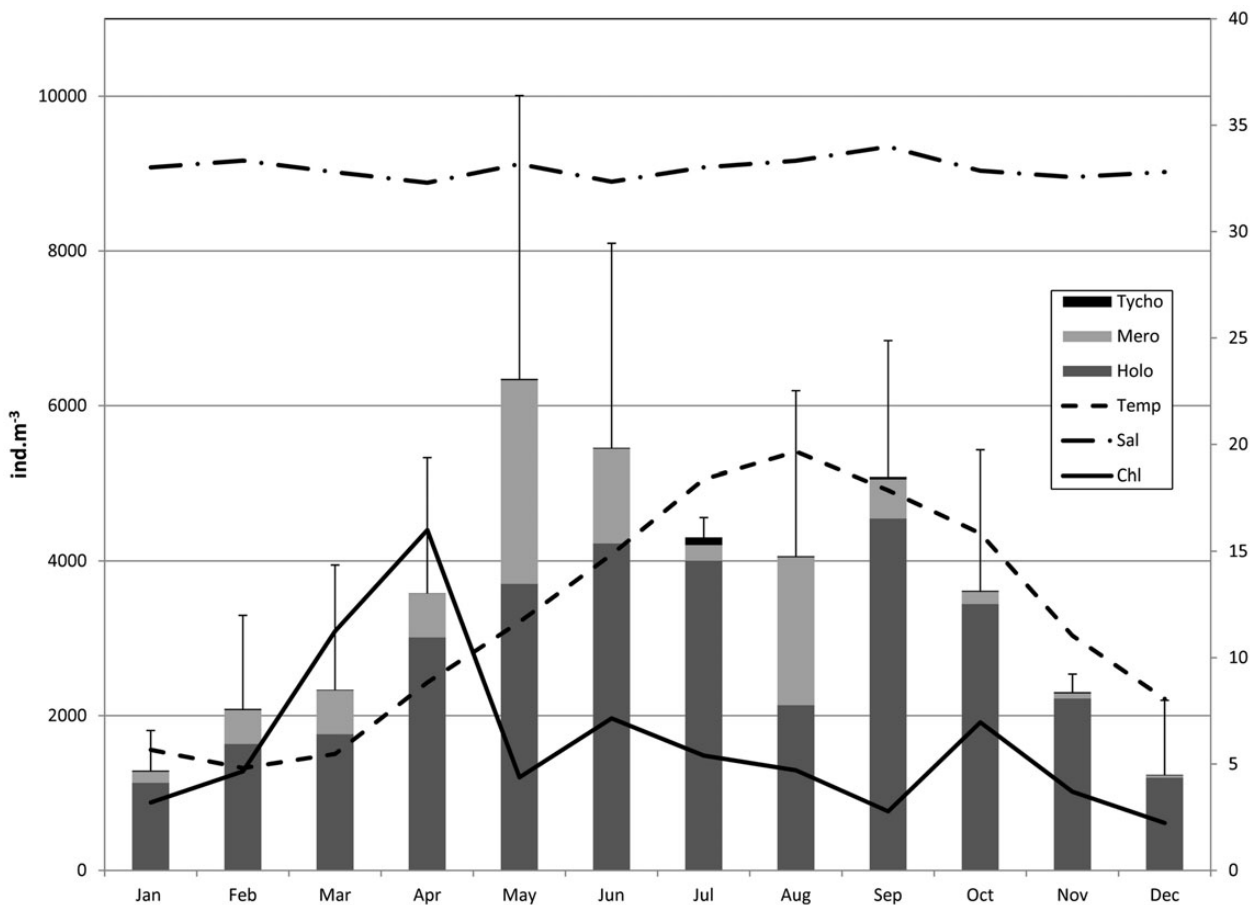

Figure 5. Average monthly zooplankton densities (ind. m^{-3}), averaged over all stations and both years (+SD on total values), divided in holo-, mero-, and tychoplankton (left axis). Right axis: salinity (PSU), temperature (°C), and chlorophyll *a* concentration (mg m^{-3}).

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 (Figure 5). Meroplankton (mainly echinoderm larvae) was found in lesser 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.

Selective feeding behaviour: 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 (Figure 5), 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. 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.

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 42 461 copepods). Mackerel was the only fish in this study that predated more than occasionally on *A. clausi* (102 individuals 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. Only 81 *C. helgolandicus* (biggest copepod species in BPNS) were found in 38 stomachs (22 of which were mackerels).

Meroplanktonic larva of echinoderms were very abundant in the water column during summer. Pluteus larvae of *Ophiothrix fragilis* reached peak numbers of 10 861 ind. m^{-3}, yet only one *Ophiothrix* juvenile was found in all analysed stomachs. Similarly, the urochordate *O. dioica*, averaged 10% of all plankton densities, but was only found five times in a stomach.

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 compare these *in situ* diet results directly with the zooplankton community present in the BPNS.

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

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

The BPNS 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 large numbers of filled stomachs were observed for sprat sampled all year-round 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 <25% of sprat from the English east coast were feeding in winter, and less than half of the sampled herring had fed. This suggest that the BPNS acts as a valuable feeding ground for pelagic fish, since stomachs always contained prey, regardless of the investigated period.

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, given the number of stomachs sampled per species, prey abundance differed significantly between the four species, and significant spatial and temporal differences were shown, following temporal and spatial structuring in zooplanktonic prey populations.

Herring

Copepods formed an important prey of herring with *T. longicornis* as dominant species, although gravimetrical analysis also showed the importance of *S. kervillei* (23%) in the diet. Electivity indices correspond to 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 Hansson, 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. (Sandstrom, 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 did no'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 were not found in the stomachs we investigated, although the cladocerans *Evadne nordmanni* and *Podon leuckartii* reached densities >1000 ind. m^{-3} in our plankton samples.

The larger adult herring (>20 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.

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 interannual variability in zooplankton abundance due to clupeid predation pressure. This top-down control is of large ecological importance (Möllmann and Köster, 2002).

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 clearly clustered together, whereas stomachs of herring, mackerel, and horse mackerel were more scattered. Also the SIMPER analysis showed more similarity in the diet of sprat. Electivity indices indicate that sprat showed higher preference for copepods compared with 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 is limited.

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 Portugal varied seasonally: in summer, it 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 for 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 30 000 *C. finmarchicus* in adult mackerel stomachs (average size of 36 cm), 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 fulfil 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 allow 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.

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, euphausid crustaceans and teleosts dominated the diet (Santic *et al.*, 2005). Cabral and Murta (2002) indicated copepods and euphausids 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 euphausids while in 2005/2006, the most important prey were fish. Their results showed that periods of different feeding intensity for horse mackerel were concomitant with diets characterized by different dominant prey items, indicative of opportunistic feeding behaviour.

Selective feeding behaviour

The copepod *T. longicornis* was omnipresent in the diet of herring, sprat, mackerel, and horse mackerel, and dominated even more compared with 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 with 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). Second, the genus *Acartia* is often considered a surface dweller (Hansson *et al.*, 1990), thus perhaps not always spatially overlapping with fish whereabouts.

Yet, only 81 *C. helgolandicus* were found. 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 were this very large calanoid, proving there was no increased selection towards this large copepod species.

The harpacticoid copepod *E. acutifrons*, the urochordate *O. dioica* (found to constitute an important part of herring and sprat diet by several studies: Hardy, 1924; De Silva, 1973; Prokopchuck 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. Though that some of these items may seem rare simply due to rapid digestion. 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 while

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 predated 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 to results published on Baltic herring (Sandstrom, 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.

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 favourite 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. Although larval prey might disintegrate fast after ingestion, the fact that we found such small numbers compared with high larval densities in the WP 2 samples taken the same day (Van Ginderdeuren *et al.*, 2012) further indicates that fish were not targeting fish larvae. Also, the fact that few fish eggs were eaten [Segers *et al.* (2007) suggested that herring forages on eggs when other prey is 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.

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 foodweb as an adaptation to changing prey abundance and availability. As such, 2 years of sampling only unravelled 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 with 45 years ago. 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 favoured prey (Frederiksen *et al.*, 2006; Prokopchuk and Sentyabov, 2006).

This study found that of all pelagic fish investigated, the proportion with empty stomachs was low, proving that the BPNS acts as a valuable feeding ground. Also we observed a very different composition of zooplankton species and life stages in the plankton samples compared with those in the fish stomachs, indicative of clear selectivity in fish diets. Few juvenile copepodites and less adult males were eaten, vs. more adult and slower (gravid) females. 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.

Therefore, it must be emphasized 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 foodwebs.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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