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The feeding ecology of pelagic fish in the southwestern Norwegian Sea – Inter species food competition between herring (*Clupea harengus*) and mackerel (*Scomber scombrus*)

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Abstract

The Nordic Seas are the main feeding area for the three large pelagic fish stocks, Norwegian Spring Spawning herring (NSS herring), North East Atlantic mackerel (NEA mackerel) and blue whiting. In this paper we focus on the southwestern Norwegian Sea. This area is dominated by two different water masses separated by the Iceland-Faroe Front that due to its high productivity attracts large amounts of pelagic fish during their summer feeding migration. After spawning, NSS herring migrate westward into the Norwegian Sea to feed, and in the last couple of years an increasing amount has been observed to reside in the southwestern Norwegian Sea for a prolonged time during summer. At the same time NEA mackerel has increased in stock size and expanded its feeding area, and has been observed in large amounts overlapping with NSS herring during summer. In this paper we focus on the foraging ecology of NSS herring and NEA mackerel in May during the period 2007 – 2011. We investigate the spatio-temporal variations in the diet of NSS herring and NEA mackerel in relation to hydrography. We analyze potential inter-species food competition between NSS herring and NEA mackerel and relate it to inter-annual variations in hydrography and plankton composition. Possible food selectivity is furthermore analyzed by comparing stomach content to the *in situ* prey composition.

Key words Herring, mackerel, feeding, food competition, southwestern Norwegian Sea, spatio-temporal variations

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Introduction

The area north of the Faroes is a productive area. Recent work by Stenevik et al., (2007) showed that the area north of the Faroes had high reproduction rates of *Calanus finmarchicus* on both sides of the Iceland-Faroe Front. Studies by ICES (2011b) have shown that the very same region is an important feeding habitat for large quantities of pelagic fish, such as herring, mackerel, blue whiting during their summer feeding-migration.

The Norwegian spring-spawning herring is the largest herring stock in the northeast Atlantic, and performs large-scale feeding-migrations in the Norwegian Sea in search of planktonic resources. After spawning, mainly off the Norwegian coast during spring, they migrate into the Norwegian Sea, searching for food. Its main prey item is copepods, particularly the large oceanic copepod *Calanus* (e.g. Misund et al., 1996; Dalpadado, et al., 1998; 2000; Dommasnes et al., 2004).

The feeding-migration of the Norwegian spring spawning herring expanded during the 1990s and 2000s to resemble the pattern from the prior to the stock collapse in late 1960s early 1970s (e.g. Hamilton et al. 2004). In the past few years it has been observed to reside for a prolonged period north of the Faroes during summer, feeding on their preferred prey, *C. finmarchicus* (ICES, 2011a).

The other major pelagic stock performing a summer feeding migration into the Norwegian Sea during summer is the North East Atlantic mackerel. They spawn mainly to the west of the British Isles during spring, but migrate northwards during spring/summer in search of their main food *C. finmarchicus* (e.g. Misund et al. 1996; Nøttestad et al. 1999; Gislason and Astthorsson 2002). During the last years a substantial expansion in distribution has occurred towards north and west and large amounts of mackerel are now observed in Faroese waters during summertime (ICES 2011a; ICES 2011b).

Blue whiting also migrates northwards from their spawning ground to the west of the British Isles into Faroese waters during spring/summer. Although their preferred prey is somewhat different than for herring and mackerel, *C. finmarchicus* can at times make up a substantial part of their ingested food (e.g. Prokopchuk and Sentyabov 2006; Langøy et al. 2012).

These fish stocks are all exploited by international fleets, and are of great economic importance for their respective home countries. However, there have been large variations in stock-sizes of all three species during the last decades. At the moment the NSS herring and the NEA mackerel stocks are large while the blue whiting stock has reduced drastically due to low recruitment and high fishing pressure. The biomass of fish using the Norwegian Sea and adjacent waters as their feeding area has been close to record high during recent years (ICES 2009), and during the same period the zooplankton has been on a declining trend to a record low in 2009 (ICES 2011b)

It is thus of great importance to increase the knowledge of the ecological dynamics in the area, in order to be able to understand the mechanisms behind these variations.

The objective of this paper was to study the feeding ecology of two of the major pelagic fish species in the Nordic Seas, herring and mackerel. All data is based on cruises performed by Faroe Marine Research Institute (FAMRI) targeting pelagic fish in early May in the South-western Norwegian Sea during the period 2007- 2011.

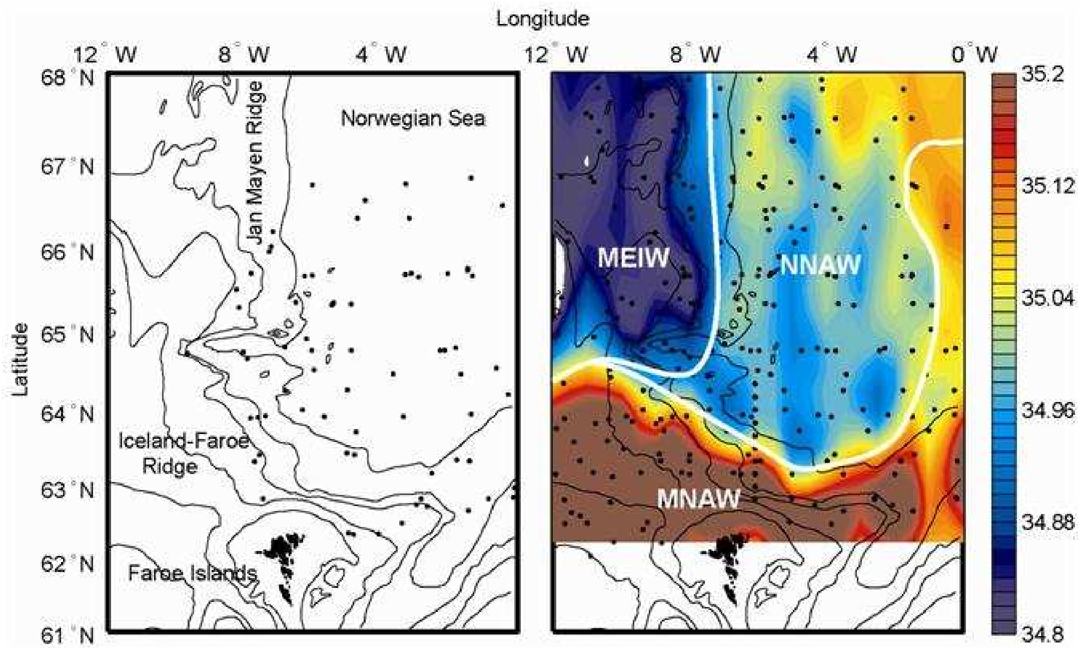

Figure 1. Map of the study-area. Left: the position of all trawl-stations 2007-2011; right: average salinity in the top 200 m of the water column (black dots are all CTD positions in the area during the study period). White lines indicate borders between the three pre-defined water masses.

Materials and methods

The data presented in this paper was collected with RV Magnus Heinason operated by Faroe Marine Research Institute (FAMRI) during five cruises in May 2007 – 2011 covering the Southwestern Norwegian Sea (Figure 1). Plankton samples and hydrography (CTD profiles) were collected at regular intervals along a predefined survey grid, heading from the Faroe Islands and north into the Norwegian Sea. Approximately the same area was covered every year. A pelagic trawl (Vónin 640m) with a mesh-size of 40 mm in the cod end was used for fish collection, and trawling was mostly carried out during the day along the survey grid, 2-3 stations each day. Trawl depth was opportunistic from 0 m to 400 m depth according to acoustic recordings and towing speed was 3 – 4 knots depending on weather conditions

Biological samples

Zooplankton was collected as vertical hauls from 200m depth to the surface, using a WP2 net with an area of 0.25m^2 and a mesh size of 200µm. During the five years 27, 21, 18, 21 and 22 plankton samples were collected respectively. The plankton samples were split into two equal fractions immediately after sampling, using a Motoda plankton splitter. One fraction was oven dried at 60°C until constant weight, in order to estimate the zooplankton biomass. The other fraction was preserved in buffered formaline (4%), and identified to lowest taxonomic level possible at FAMRI.

Biological data of herring and mackerel was obtained from 100 randomly collected fish of each species. The measurements include body length, weight, sex, maturity, and age from otoliths. Stomachs were collected from 5 – 15 fish per station and immediately frozen for further analysis. A total of 561 stomachs were collected during the 5 cruises (Table 1).

Table 1. Number of stations and stomachs sampled, and feeding index (F) for herring (n = 470) and mackerel (n = 91) in the three predefined water masses during the five year period 2007 – 2011.

Year	Water Mass	Species	No. stn.	No. Stomach	F-index
2007	MNAW	Herring	1	10	100
	NNAW		6	84	100
2008	MNAW	Herring	3	41	90
	NNAW		6	70	96
	MEIW		3	31	100
	MNAW	Mackerel	2	16	100
2009	MNAW	Herring	3	34	88
	NNAW		6	86	100
	MNAW	Mackerel	2	30	87
2010	MNAW	Herring	2	8	63
	NNAW		7	37	95
	MEIW		1	6	100
	MNAW	Mackerel	2	11	100
2011	MNAW	Herring	5	26	96
	NNAW		6	27	100
	MEIW		2	10	100
	MNAW	Mackerel	5	27	66
	NNAW		1	5	100
	MEIW		1	2	100

Stomach analysis was carried out in the laboratory at (FAMRI). The stomach was carefully opened and the content (or a subsample when stomach was full) identified to lowest taxonomic level possible. In order to obtain the weight of the stomach content, the stomach was weighted prior to and after emptying the content. In this paper the prey-groups for herring and mackerel were categorized into 7 groups: *Calanus finmarchicus*, *C. hyperboreus*, *Pseudocalanus* sp., other copepods, krill (Euphausiids), amphipods, and other.

Stomach content in this paper is presented as average per station including empty stomachs.

Stomach fullness index was calculated as the weight of the stomach contents (in grams) divided by the length (in cm) of the predator cubed and multiplied by 10000 (similar method as DeBlois and Rose, 1995).
Feeding index (F-index) for each year and water mass was calculated for herring and mackerel as the percentage of stomachs containing food relative to all stomachs from that particular water mass that year.

Hydrography

Vertical CTD profiles from the surface to 1000 m depth were collected using a Seabird x probe on all cruises. Three main water masses occupy the survey area in the upper 200 meter water column. These are the relatively warm and saline Modified North Atlantic Water (MNAW, temperatures between 7.0 and 8°C and salinities between 35.10 and 35.30) approaching from the south, the cold and fresh Modified East Icelandic Water (MEIW, 1.0-3°C, 34.70-34.90)(Hansen and Østerhus, 2000) approaching from the west and the Norwegian North Atlantic Water occupying the central Norwegian Sea (NNAW, ~ 3°C, 35.00)(Read and Pollard, 1992) (Fig. 1).

Since different water masses often contain different biota, there is a rationale to allocate all biological data into water masses. This was difficult with the trawl stations, since they were conducted at varying depths and between CTD stations. To overcome this challenge, the CTD data were averaged onto 50 m depth bins (0-50m, 50-100m etc.) and each layer was subsequently objectively mapped (Bohme and Send, 2005) onto a regular grid. By visual inspection of the mapped hydrographic field near each station (maps, sections, profiles and TS diagrams), and guided by, but not strictly adhering to the abovementioned water mass characteristics, all trawl stations and plankton samples were categorized as either MNAW, NNAW or MEIW.

Results

Zooplankton

The zooplankton biomass varied both within and between years. In general the abundance seemed to be highest in the northern areas, but this was not a consistent pattern or all years (Figure 2).

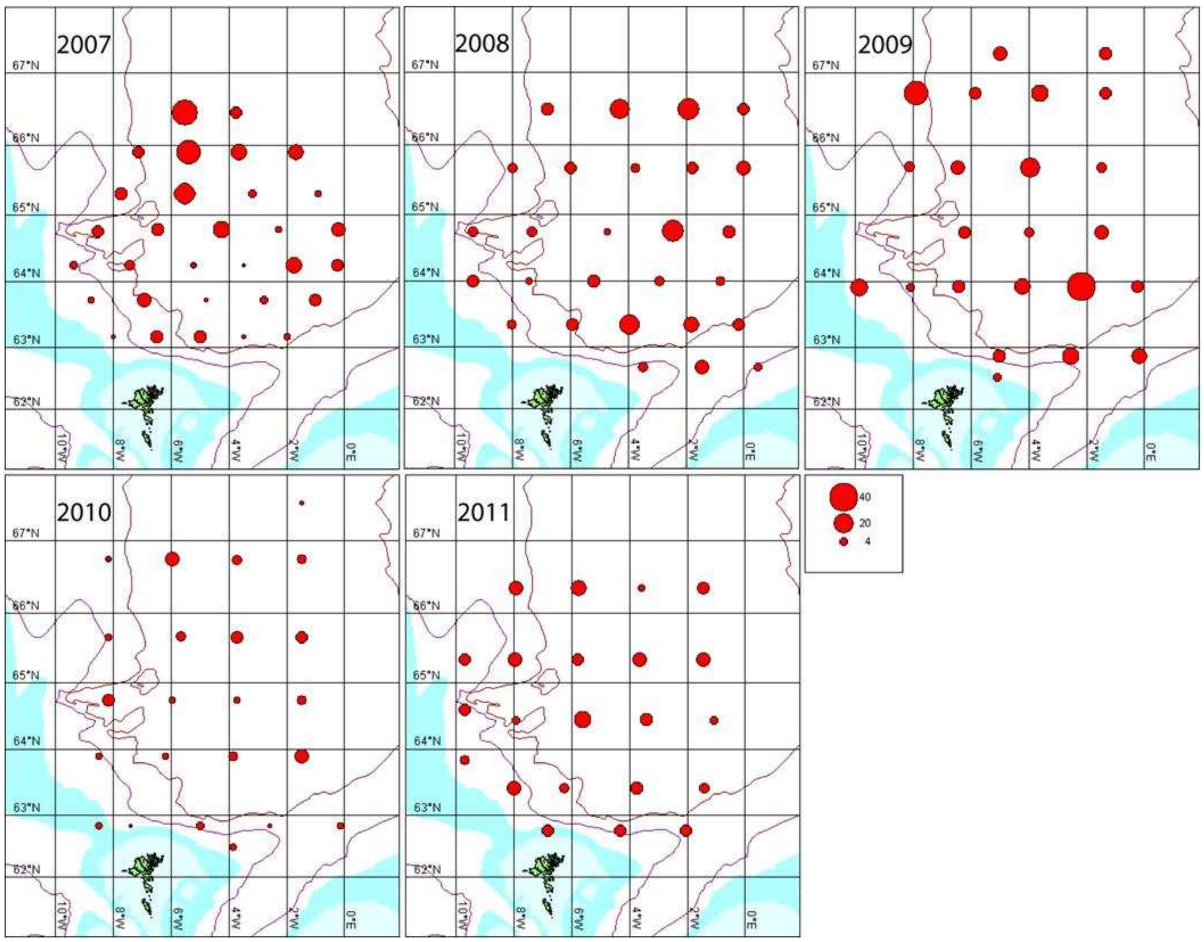

Figure 2. Zooplankton dry weight (mg/m^2) in the survey area in early May during the 5 years study period.

The zooplankton species composition was dominated by the large oceanic copepod *Calanus finmarchicus* (Figure 3). The abundance of *C. finmarchicus* was to a large degree reflected by the developmental stage composition, with high abundances coinciding with high abundances of juveniles (developmental stages CI-CIII). This was especially the case in the two warmer water masses MNAW and NNAW, where juveniles made up a substantial part of the *C. finmarchicus* community by numbers. By excluding the juveniles, the abundance pattern was more even with only small differences between water masses. Another abundant copepod species was *Pseudocalanus* sp. which at some stations dominated the zooplankton community, especially in 2009. The group "Other copepods" was mainly dominated by the very small oceanic copepod *Oithona* sp and at some stations *Metridia* sp and *Microcalanus* sp.

By excluding the small copepod species (incl. juveniles of *C. finmarchicus*), the abundance pattern to a large degree reflected the total zooplankton biomass pattern (not shown).

Due to the fact that a WP2 net with a mesh size of 200 µm does not sample the larger zooplankton like krill and amphipods representatively, they are excluded from all the zooplankton data

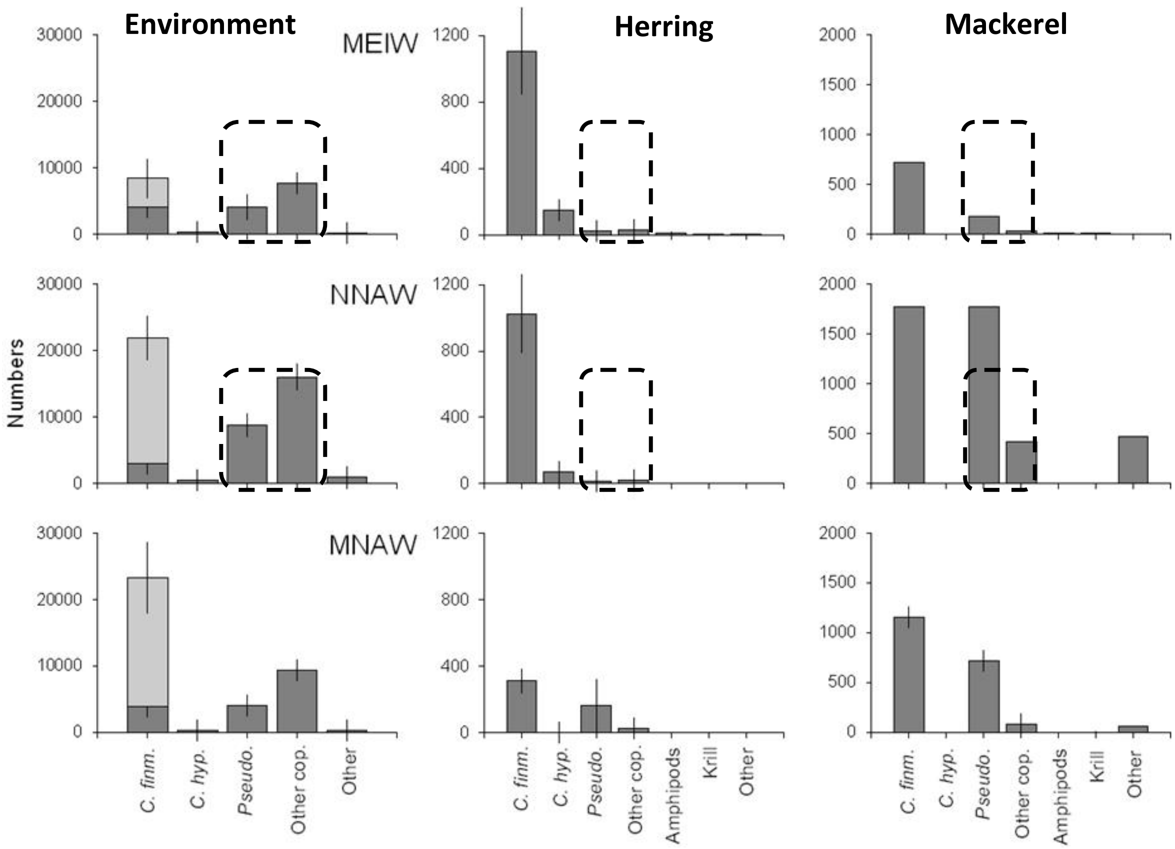

Figure 3. Pooled abundance of key zooplankton groups in the three predefined watermasses during the study period. Left: Abundances in the environment (Dark-grey is adults and light-grey is juveniles); middle: Average stomach content (abundance) of herring; right: Average stomach content (abundance) for mackerel. Vertical lines indicate standard error. The dashed rectangles emphasize deferred prey species.

Herring

Herring were caught at 51 stations during the period 2007 – 2011, and a total of 470 stomachs were analyzed (Table 1).

The stomach content for herring varied both spatially and temporally without any clear pattern. Maximum average stomach content per station approached 5000 prey items per stomach (not shown).

Calanus finmarchicus was by far the most frequent prey in the herring stomachs, and on average made up approximately 85% of the total prey items by numbers (Figure 3 and 4, and Table 2). Other important prey species for herring were *C. hyperboreus* in the NNAW and MEIW water mass and in the warmer MNAW water mass *Pseudocalanus* sp. especially in 2011 when it occasionally dominated the herring stomach content by numbers. All *C. finmarchicus* found in the herring stomachs at all stations during all five years, belong to the group adults (developmental stages CIV-CVI).

Table 2. Relative abundance (percent) of key prey groups in the herring and mackerel stomach in the three predefined water masses for all five years together.

Species	WM	C. finm.	C. hyper.	Pseudo	Other cop.	Amphipods	Krill	Other
Herring	MNAW	85.9	0.3	11.4	1.8	0.1	0.6	0.0
	NNAW	87.9	7.0	1.3	2.5	0.6	0.6	0.1
	MEIW	84.8	6.6	2.0	5.0	0.8	0.6	0.2
Mackerel	MNAW	67.4	0.0	27.0	2.1	0.1	0.0	3.3
	NNAW	57.1	0.0	33.3	3.8	0.1	0.0	5.8
	MEIW	49.5	0.0	39.4	5.1	0.3	0.3	5.4

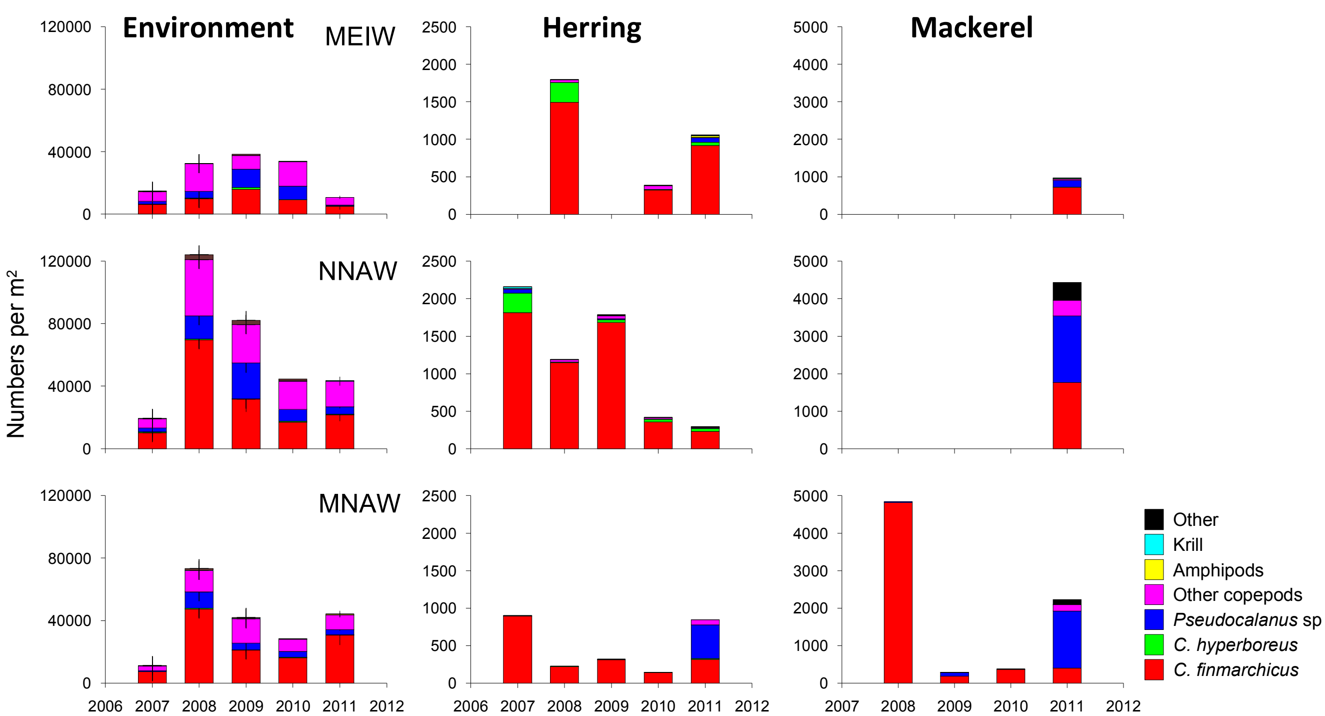

Figure 4. Abundance of key zooplankton groups in the three predefined water-masses during the study period. Left: Abundances in the environment; middle: Average stomach content (abundance) of herring; right: Average stomach content (abundance) of mackerel. Vertical lines indicate standard error.

Average stomach fullness per station reflected to a large extent the stomach content in numbers. However, stations with a relatively large fraction of the large copepod *C. hyperboreus* in the stomach (not shown) seem to stand out as stations with relatively higher stomach fullness (Figure 5).

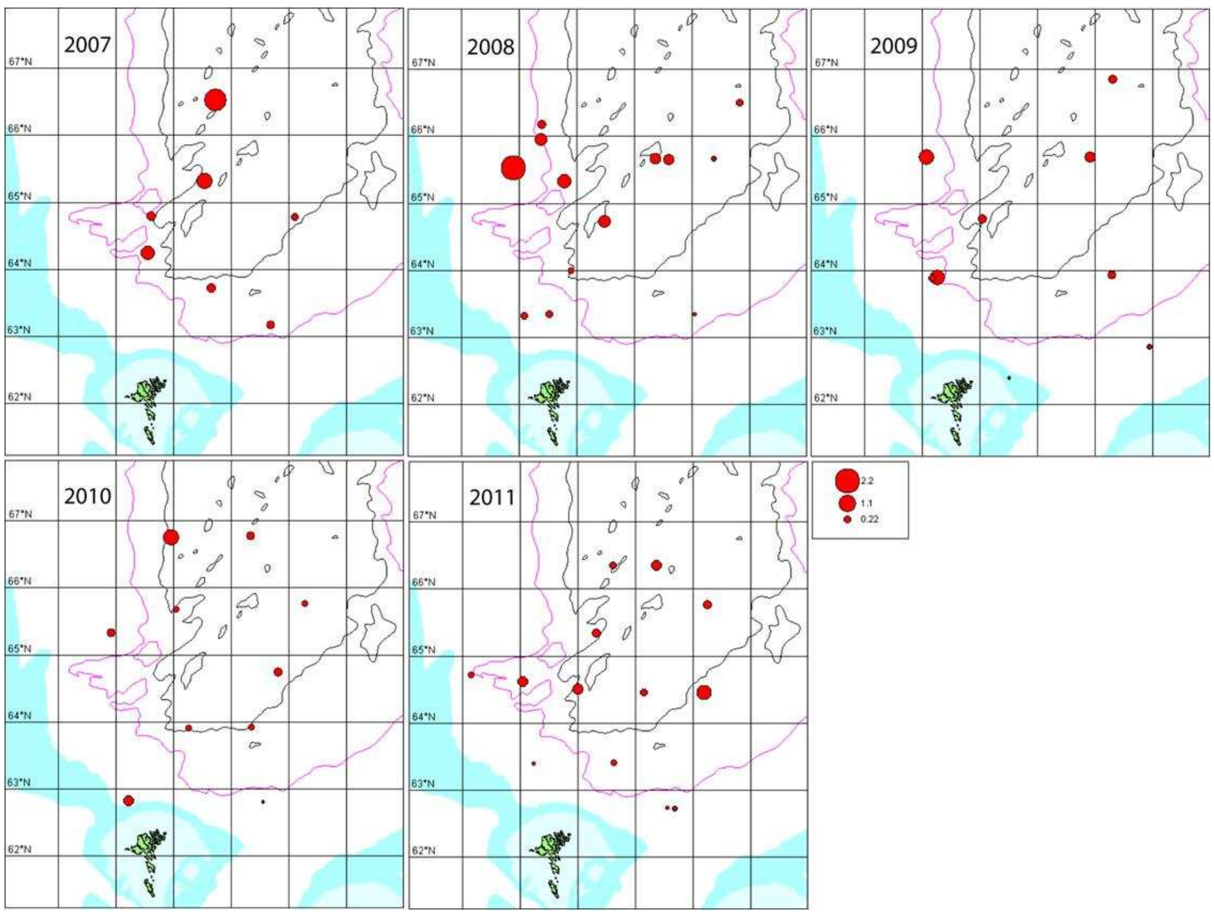

Figure 5. Herring stomach fullness.

Average stomach fullness per water mass for all years together was highest in the cold MEIW and lowest in the warm MNAW (Figure 6). The standard error (vertical lines) was high in the MEIW but this is partly due to the reduced data material from this water mass, with only 6 stations and 47 stomachs during the five years period (Table 1).

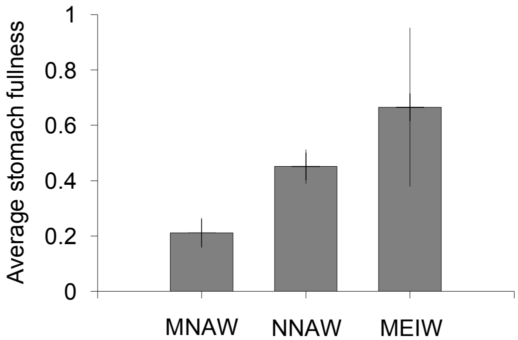

Figure 6. Average stomach fullness for herring in the three predefined water masses for all years pooled. Vertical lines indicate standard error.

The herring F-index (percentage of feeding herring) was generally high, but varied between water masses (Table 1). In the cold MEIW the feeding index was 100% at all stations all years, but in the warmer water masses it varied between years ranging from 100 to a minimum of 63 in MNAW in 2010.

Mackerel

Mackerel were caught at seven stations in 2011 and two stations in 2008, 2009 and 2010, and a total of 91 mackerel stomachs were analyzed. No mackerel were caught in 2007.

There were large stations-to-station as well as inter annual variations in the average stomach content for mackerel. *C. finmarchicus* was the most frequent prey species in the mackerel stomachs, but especially in 2011 *Pseudocalanus* sp. made up a large part of the prey by numbers (Figure 3 and 4 and Table 2). On average *C. finmarchicus* made up between 49% and 76% and *Pseudocalanus* sp. between 27% and 39% of the prey species by numbers, respectively. Younger stages of *C. finmarchicus* were also frequently found in the mackerel stomachs in 2011. The small copepod *Oithona* sp. and *Temora* sp. were the most frequent prey species in the group “other copepods”, while in the group “other” it was decapods.

Average stomach fullness per station for mackerel showed large variations both between stations as well as inter annually (Figure 7). The mackerel feeding index varied between years from 100 to a minimum of 66% in the warm MNAW water mass in 2011 (Table 1).

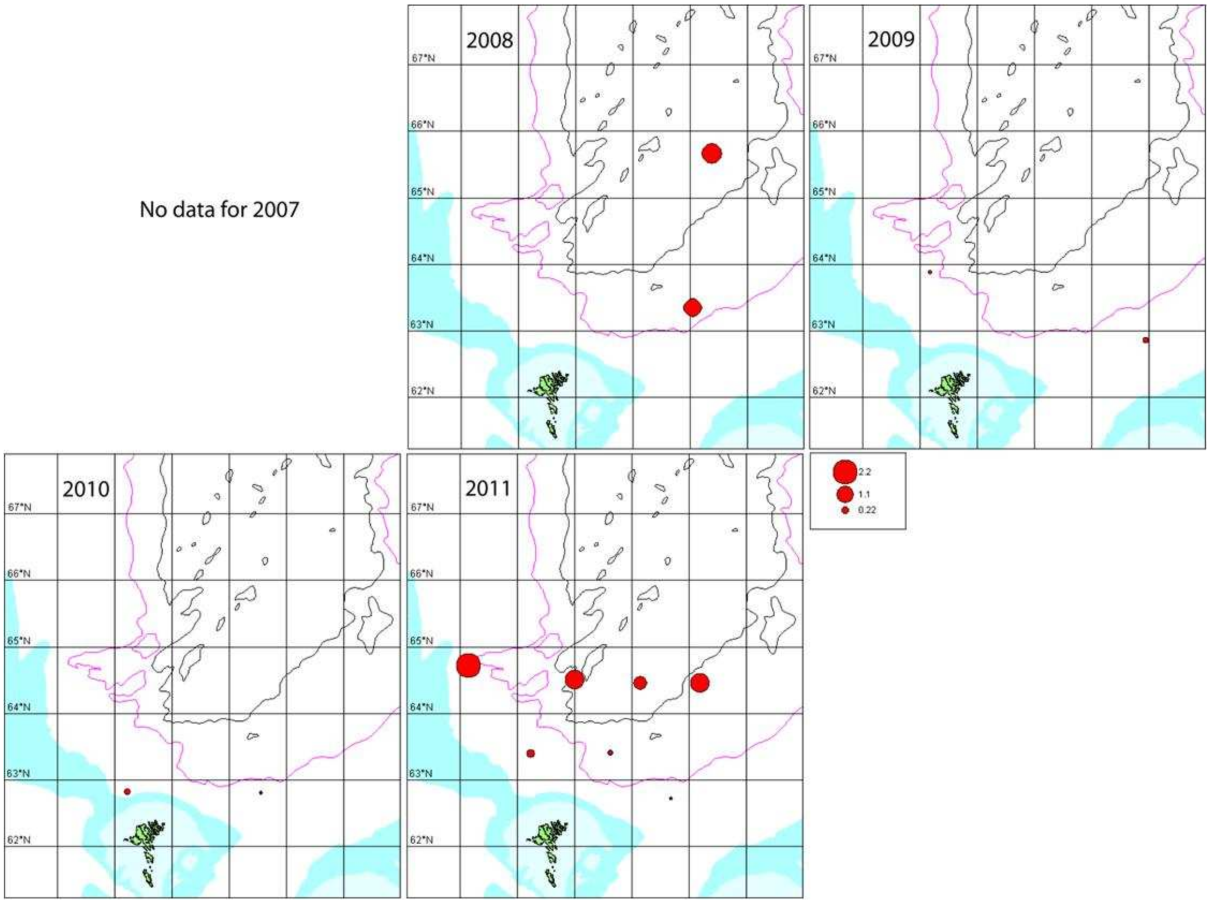

Figure 7. Mackerel stomach fullness.

Herring and mackerel

The preferred prey for herring and mackerel were similar. Both rely on *C. finmarchicus* as their main food, but mackerel to a larger degree also preys on other copepod species (Figure 8).

Herring and mackerel were caught in the same haul at 13 stations during the period 2007 – 2011; two stations in 2008, 2009 and 2010, and seven stations in 2011. On average, mackerel fullness was higher than herring fullness (Figure 8 and Table 3), and generally herring fullness seemed to be more regular low, while mackerel fullness varied from low to high values between stations (Table 3). Although all mackerel stomachs at station 15 in 2011 appear empty (Table 3), they were filled with the amphipod *Themisto* sp., but it was not possible to count the stomach content due to advanced digestion.

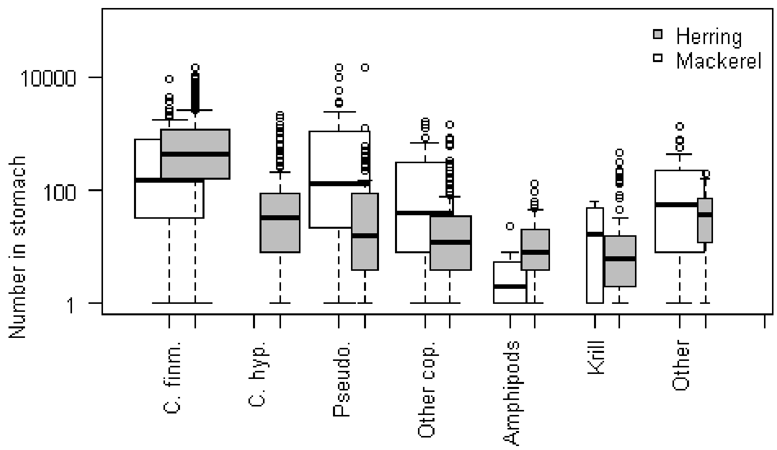

Figure 8. Boxplot of main prey types of herring (grey) and mackerel (white). The horisontal lines indicate the median abundance in stomachs with the specified prey. The boxes indicate the interquartile range (i.e. median +/- 25% of the values). The width of the boxes indicate relative numbers of stomachs with the specified prey (i.e. stomachs that did not contain the specified prey were excluded). The whiskers indicate minimum and maximum abundance - unless the range exceeded 1.5 times the interquartile range from the box. Values outside this limit are indicated with circles.

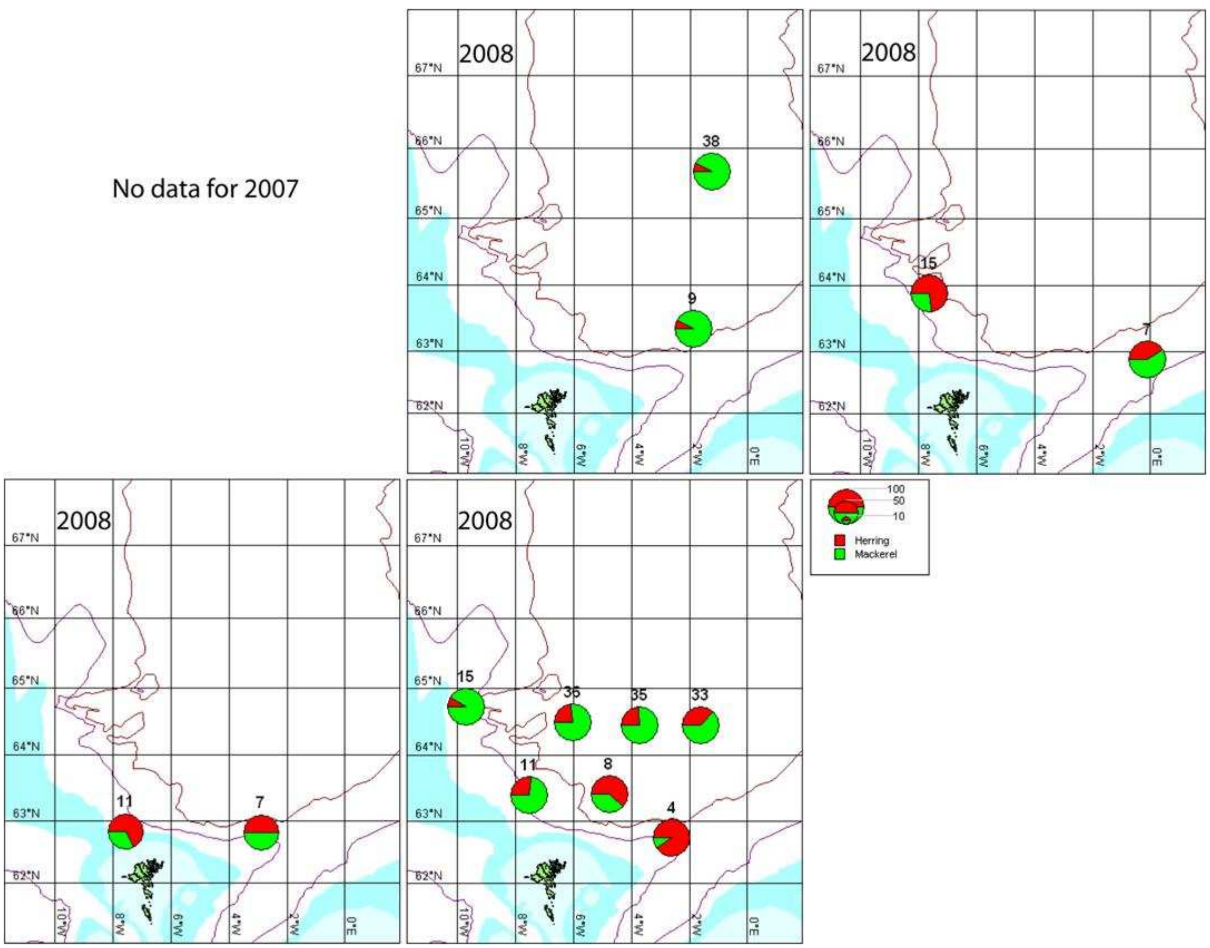

Figure 9. Relative stomach fullness for herring and mackerel at stations where both species were caught in the same haul. Numbers indicate stations number.

Generally both herring and mackerel stomach contents were dominated by *C. finmarchicus,* even though mackerel stomachs to a larger degree also contained *Pseudocalanus* sp. as well as other prey species (Figure 10, Table 3). Not included in the Table are the large amounts of amphipods in the mackerel stomachs at station 15 in 2011.

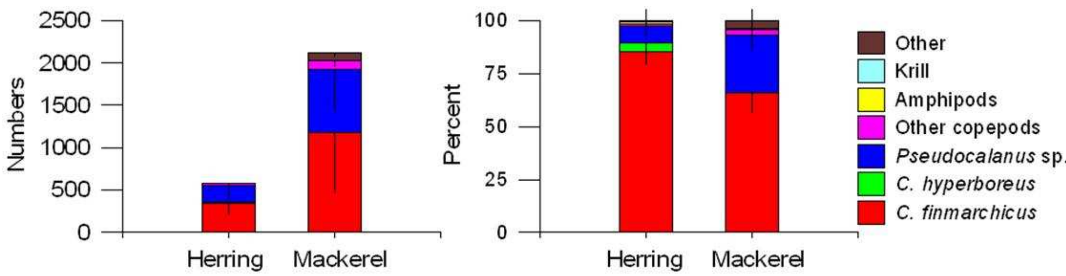

Figure 10. Average abundance of key prey groups in herring and mackerel stomachs, at stations where both species were caught in the same haul. Left: average abundance; right: relative abundance. Vertical lines indicate standard errors.

Table 3. Average stomach fullness and average number of each prey group per station, at stations where both species were caught in the same haul. WM denotes the water mass, stn is the station number, and N is the number of stomach analyzed. (*) denotes that we have no data from this station, but only observations that showed all stomachs to be filled with the amphipod *Themisto* sp., but it was not possible to count the number of individuals due to advanced digestion. Empty stomachs are included when calculating the stomach fullness.

Year	WM	Stn	Species	N	Fullness ± SE	*C. finm.*	*C. hyper.*	*Pseudo.*	Other cop.	Amphipods	Krill	Other
2008	MNAW	9	Herring	11	0.10 ± 0.02	298	0	0	0	0	0	0
			Mackerel	1	1.26	9408	0	0	0	0	0	0
		38	Herring	15	0.12 ± 0.02	114	0.03	13	1.2	0	0	0
			Mackerel	15	1.55 ± 0.28	228	0	49	0.8	0.1	0.1	3.2
2009	MNAW	7	Herring	15	0.11 ± 0.02	448	0	0.1	0.3	0.4	0	0
			Mackerel	15	0.16 ± 0.04	186	0	184	3.2	0.1	0	0
		15	Herring	15	0.23 ± 0.04	485	0.1	19	2.2	1.8	9	0
			Mackerel	15	0.09 ± 0.02	194	0	8	2.3	1	0	0
2010	MNAW	7	Herring	5	0.05 ± 0.02	157	0	0	0.8	0	0.8	0
			Mackerel	5	0.05 ± 0.02	56	0	7	0.4	0.4	0	0.2
		11	Herring	3	0.38 ± 0.24	130	0	0	0	0	5.3	0
			Mackerel	6	0.18 ± 0.06	687	0	7	0	0	0	0
2011	MNAW	4	Herring	5	0.11 ± 0.02	107	0	0	0.6	2.2	0	0
			Mackerel	6	0.01	2	0	0.2	0	0	0	0
		8	Herring	4	0.20 ± 0.05	115	43	2	1.5	0	0	0
			Mackerel	6	0.12 ± 0.06	109	0	523	51	1.3	0	160
		11	Herring	5	0.10 ± 0.01	320	7	12	0.4	0.8	0	0.4
			Mackerel	5	0.26 ± 0.08	763	0	738	52	1.6	0	158
		15	Herring	5	0.19 ± 0.07	222	0	3.2	0.8	1.6	3.2	0
			Mackerel	5	2.20 ± 0.23	*	*	*	*	*	*	*
		33	Herring	7	0.84 ± 0.49	825	4.6	2230	333	0	0	0
			Mackerel	5	1.38 ± 0.40	1139	0	6342	755	0	13	326
		35	Herring	5	0.23 ± 0.04	259	72	33	0	18	0.2	0
			Mackerel	5	0.73 ± 0.18	1771	0	1771	420	0	0	465
		36	Herring	5	0.44 ± 0.10	1054	36	125	0	22	0.8	14
			Mackerel	2	1.46 ± 0.12	724	0	184	32	16	16	0

Discussion

Hydrography and zooplankton

The hydrography in the study area is complex with a convergence of several water masses creating fronts both horizontally and vertically. The fronts between these water masses continuously change location making this a highly dynamic area. The results from our two week May cruises are thus to be interpreted as snap-shots of a highly changing environment. However, our results showing large differences in the zooplankton species composition in these three water masses, verifying the need for grouping all biological stations into different biogeographical zones. In the two warmer water masses (MNAW and NNAW), the *C. finmarchicus* community was dominated by juveniles (developmental stages CI – CIII), while adults (developmental stages CIV – CVI) dominated in the cold MEIW. This clearly indicates an earlier phytoplankton spring-bloom and thus also an earlier zooplankton reproduction in MNAW and NNAW. The abundance of *Pseudocalanus* sp was also consistently highest in NNAW, indicating different zooplankton ecology amongst the water masses.

Herring

After spawning along the Norwegian coast the herring migrates towards west into the Norwegian Sea in search of food. Our results show that in the area north of the Faroe Islands, the main food for herring in May is the large copepod *Calanus finmarchicus*. Other studies have come to the same result in adjacent areas during different times of the herring feeding season (e.g. Dalpadado et al. 2000; Gislason and Astthorsson 2002; Dommasnes et al. 2004; Iversen 2004; Prokopchuk and Sentyabov 2006; Langøy et al. 2012). While most of these results are based on biomasses, our results are based on numbers. This has to be taken into consideration when comparing the results. Converting our numbers into biomass would most likely alter the relative importance of certain small species, so as to reduce the importance of *Pseudocalanus* and increase the importance of the larger krill and amphipods. However, due to the high abundance and the relatively large size of *C. finmarchicus,* it would most likely still rank as the most important prey species for herring. While large prey species like krill and amphipods were only occasionally found in the herring stomachs, *C. finmarchicus* dominated the stomach content at all stations in all water masses during all five years. So even though the large prey species sometimes might be important locally for some herring, *C. finmarchicus* must be regarded as the most important prey species which the herring relies on for the build up of the depleted fat reserves after spawning earlier in the spring.

Our results show that there is an obvious difference between the spectrum of zooplankton found in the environment (WP2) and what is observed in the herring stomach content. Although species like *Pseudocalanus* sp. and the group “other copepods” make up a substantial part of the copepod community, especially in NNAW and MEIW, these are nearly absent in the herring stomachs in these water masses (Figure 3). Our results also show that during early May, herring do not feed on the new generation of *C. finmarchicus*, even in the warmer water masses (MNAW and NNAW) where the *C. finmarchicus* community was dominated by juveniles (by numbers). Rather the herring select the larger individuals of *C. finarmchicus* (developmental stage CIV – CVI) that have ascended from winter diapause in the depth.

The herring feeding activity varied between water masses. This is seen in the stomach fullness which was highset in the cold MEIW and lowest in the warmer MNAW. It is not clear why this is so, especially considering that the zooplankton abundance was lower in this area, or at least equal to the other water masses if we focus on *C. finmarchicus* adults alone. However, this might be a result of size of the herring. Larger herring are known to migrate furthest to the west/north-west and enter the colder water masses like the MEIW (Nøttestad et al 1999; Slotte and Fiksen 2000; Langøy et al. 2012). The difference in the observed stomach fullness might be due to the larger herring being more active or more successful in catching their prey than the smaller herring further south-west

Langøy et al. (2012) reported that species like *Appendicularia* sp and *Limacina* sp are important prey species for herring at certain times during the feeding season. These prey species were only found sporadically in the herring stomachs in our data, and did not contribute significantly to the overall total consumption in the area investigated. However, later during the feeding season, when *C. finmarchicus* start their descent to winter diapause and become unavailable as prey, the herring might rely more on these species as food.

Mackerel

Mackerel enter the area north of the Faore Islands from their spawning grounds in the south. Being a species associated with warm water, they are usually observed in warmer water masses than e.g. herring (REF). The mackerel caught in May during our research period were mostly taken at stations located in the two warmer water masses, MNAW and NNAW. Our results show that for mackerel, as for herring, the main prey species was *C. finmarchicus*, although not to the same extent. Although *C. finmarchicus* dominated the stomach content, *Pseudocalanus* sp. were found in larger numbers and dominated the stomach content at some stations, especially in 2011. And contrary to herring, mackerel fed on *C. finmarchicus* juveniles, which in some stomachs dominated the content by numbers. Again as for herring, we have to take into consideration that our results are in numbers and not biomass (see above). Large prey species like krill and amphipods were rarely found in the mackerel stomachs. However, at a single station located in MEIW the mackerel were full of *Themisto* sp, indicating that these prey organisms can be locally important for mackerel as well as herring.

As for herring, our results show that there was an obvious difference between the spectrum of zooplankton found in the environment and in the mackerel stomach content (Fig. 8). This indicates that mackerel is also a selective feeder, althoug to a slightly lesser extent than herring, since *Pseudocalanus* sp. as well as *C. finmarchicus* juveniles were frequently found in the mackerel stomachs. Herring and mackerel might have different feeding mechanisms with herring as the more selective, picking their prey (visually) while mackerel filter the water by swimming with their mouth open.

However, the trawl sampling depth all five years was opportunistic from zero m to 400 m depth while the plankton samples integrated the uppermost 200 m. Fish might have fed at deeper depths before they were caught in the trawl hauls. We should therefore be careful when comparing stomach content with the zooplankton composition at the nearest net sample location.

Herring and mackerel

Our results confirm previous reports that herring and mackerel prey on similar prey organisms. However, our results based on the trawl hauls where herring and mackerel were caught together show that the mackerel stomachs on average have a much higher content and fullnenss. Langøy et al (2012) came to the same result later during summer in the Norwegian Sea. They concluded that this probably was because the mackerel were in the middle of their feeding season while the herring were approaching the end of their feeding season and therefore had a lower state of hunger. However, our results indicate that mackerel is also a more active feeder in May than herring, even though this is the peak of the herring feeding season. This indicates that mackerel might generally be a more active feeder than herring through the entire feeding season.

The prey composition in the stomachs of the two species was slightly different. This slight differences might indicate different feeding ecology or feeding behaviour. While mackerel stay close to the surface both day and night, herring are known to carry out daily vertical migration staying at depth during day and migrating towards the surface during the night (Misund et al. 1996, Nøttestad et al. 2007), and thus mirroring the behaviour of their main prey, *C. finmarchicus*. The smaller copepod species, as well as *C. finmarchicus* juveniles, do not perform daily vertical migrations to the same extent as the *C. finmarchicus* adults. Herring and mackrel will therefore experience different prey environment during day and night. This will most likely be reflected in the stomach content of the two species. Broms et al (2004) showed that the gut evacuation rate for herring is in the order of 1-2 day. Assuming that the gut evacuation rate for mackerel does not differ much from that of herring, the gut content we analyze is a sum of what the fish has been eating for the last 1-2 days, and not necesarily what they ate just before they were caught. Our observed difference in the herring and mackerel stomach content for herring and mackerel therefore indicates that although they compete for the same main prey, they only partially overlap vertically in the water column which thus reduces their inter-species food competition.

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