Feeding ecology of Atlantic mackerel (*Scomber scombrus*) in the Norwegian Sea

Herdis Langøy[1,2*], Leif Nøttestad[1], Georg Skaret[1], Cecilie T. Å. Broms[1], and Anders Fernö[1,2]

[1] Institute of Marine Research, P. O. Box 1870, 5817 Bergen, Norway.
[2] Department of Biology, University of Bergen, Thormøhlensgate 55, 5020 Bergen, Norway.

Abstract

Previous studies on Atlantic mackerel (*Scomber scombrus*) feeding during the highly migratory summer period are scarce. In this study we present detailed diet analyses and investigations of prey selection for Atlantic mackerel in relation to zooplankton distribution and hydrographical conditions in the Norwegian Sea in July 2004. A wide variety of prey organisms were found in the stomachs of mackerel in all water masses. According to dry weight was *Limacina retroversa* the principal prey in Coastal and Atlantic water masses. *L. retroversa* was presumably abundant in the Norwegian Sea and taken as secondary prey in the quest for more nutritious prey. *Calanus finmarchicus* was less important in all water masses than previously documented, also when combined with calanoidae copepod remainders, indicating that their descend to overwinter in deeper waters had already started in late July. Mackerel showed a size selective feeding behaviour and preferred larger prey species over smaller prey. Small copepods (< 1 mm) were numerous in the zooplankton samples in all water masses, especially Coastal and Atlantic, but were not present in the stomach samples. Furthermore, the three largest copepodite stages of *C. finmarchicus* (CIV – CVI) were selected over the three smallest stages (CI – CIII). Pronounced prey and size selection strongly suggests that mackerel performed particulate feeding. The potential feeding competition between mackerel and herring was also investigated. There was a clear difference in the diets of the two species. *C. finmarchicus* and *L. retroversa* were the main prey of mackerel, whereas herring preferred euphausiids and amphipods. These latter species normally swim in deeper waters and only enter the upper layers for feeding when protected by the dark. Moderate feeding by herring at the end of their feeding season and more active feeding by mackerel could explain the pronounced differences in the diet and lack of feeding competition between these two important planktivorous species.

*Contact author:

Herdis Langøy: Department of Biology, University of Bergen, Thormøhlensgate 55, 5020 Bergen, Norway, tel: +4795758255, e-mail: herdis.langoy@imr.no

Introduction

The Atlantic mackerel (*Scomber scombrus*) is the third most abundant species in the Norwegian Sea, but still there is little information on its feeding behaviour and ecological interactions with other pelagic planktivorous species during summer. The adult mackerel start migrating in June – August from the spawning grounds off the coast of Spanish and Portuguese waters in the south and around Ireland and west of the UK in the north (Iversen 2002; Ringuette et al. 2002; Iversen 2004) to the early feeding areas in the southern and central part of the Norwegian Sea. Little is known about the feeding migration of mackerel, but it has been found to cover the Norwegian Sea from 62°N to 72°N (Iversen 2004). In warm years mackerel may be distributed up to 73°N (Holst and Iversen 1992; Iversen 2004). The feeding areas are difficult to locate precisely, and the abundance of fish in the Norwegian Sea depends on sea temperature, location of water masses, prey biomass and species composition (Iversen 2004, Skjoldal et al. 2004). Mackerel migrate eastwards in August/September to overwinter along the Norwegian coast (Iversen 2004). After the collapse of the herring population in the area and increased fishing on the mackerel stock, more information is needed to exploit the stock in a precautionary and responsible way.

There are two dominating oceanographic fronts in the central part of the Norwegian Sea (Rey 2004). The fronts separate water masses that provide different growth environments and feeding conditions for the pelagic fish species. The Coastal Front is created and maintained where the fresher Coastal current flowing northwards along the Norwegian coast meets the parallel flowing saltier North Atlantic Current, resulting in a sharp gradient in salinity and temperature (Rey 2004). West of the Coastal Front lies the Arctic Front, separating Atlantic water from the colder and less saline Arctic water (Rey 2004). The three water masses Coastal, Atlantic and Arctic are typically found in the Norwegian Sea (Rey 2004). Mackerel biology is likely to be dependent on the characteristics of the water masses. Consequently, including and linking structured data on water masses to mackerel feeding ecology should therefore be a proper scientific approach.

We know very little about mackerels preference for specific water masses in the Norwegian Sea as well as its general feeding selection. Mackerel is like many other fish species an opportunistic feeder, but when available some prey are preferred above others (Maurer 1976; Pepin et al. 1987; Pepin et al. 1988). The main prey groups of mackerel in the Norwegian Sea have previously been found to be Copepods, *Limacina* spp. and Appendicularia in decreasing order of importance (Skjoldal et al. 2004). Pelagic fish such as mackerel are also important predators on fish eggs and larvae especially in Coastal waters.

The Norwegian spring-spawning herring (*Clupea harengus*) is probably the main competitor of mackerel as their diets are more similar than those of the other pelagic planckivores species (Maurer 1976; Skjoldal et al. 2004). The extensive herring feeding migrations covering large areas of the Norwegian Sea from early May until late July (Dalpadado et al. 2000; Skjoldal 2004), and large size and biomass (Holst et al. 2004), increases their importance as a potential competitor for available food. However, knowledge of the actual feeding competition compared to prey availability

in the Norwegian Sea is limited. Copepods, particularly *Calanus finmarchicus,* have previously been found important in the diet of both species (Maurer 1976; Iversen 2004; Skjoldal et al. 2004), while Euphausiids and Amphipods are seasonally eaten (Maurer 1976; Skjoldal et al. 2004; Prokopchuk and Sentyabov 2005).

The present study aimed at:
1) Quantifying mackerel diet and feeding selection of prey species, sizes and maturity stages by comparing zooplankton samples with stomach content according to water masses.
2) Quantifying potential feeding competition between mackerel and herring.

Material and Method

Stomach content from mackerel and herring, zooplankton samples and CTD data were collected at selected stations, during a cruise undertaken in the Norwegian Sea in July 2004 with the commercial fishing vessel M/V "Libas". Fish were sampled with a large commercial blue whiting pelagic trawl (Egersund trawl) with a large trawl opening, between 45-63 m when applying 200-220 m warp length. Towing speed varied between 4.0-5.3 knots depending on current speed and direction and wind and wave conditions. Previously, trawling has not been used to any extent for sampling mackerel by Norwegian scientists, due to the small trawl opening, about 30 m, of the standard research Åkra trawl, and low to moderate trawling speed, maximum about 3 knots, of the research vessels to avoid rupturing the trawl net (Korneliussen et al. 2003). Large trawl opening increased the areas sampled and high towing speed decreased the possibility of mackerel to escape the trawl opening.

A total of 100 mackerel and 25 herring were sampled individually from each station for full biological samples as a standard procedure (time permitting) including length, weight, sex, special maturation stages, degree of stomach fullness and otoliths for age analysis. Stomach samples were taken from all herring and 25 randomly selected individuals of mackerel. Length, weight, age, and maturity were recorded according to the instructions given in Fotland et al. (2000). Analyses of the stomach content were done at the Institute of Marine Research (IMR), Norway. The scales given by Fotland et al. (2000) were used for finding stomach fullness and state of digestion. The content were carefully taken apart and all identifiable prey identified to the lowest taxonomic group and counted. Developmental stages (copepodite I-VI) were determined for copepods, while total length was recorded for all other organisms. Length of prey organisms was measured to the nearest 0.1 mm. Total species or group dry weight from each stomach was found to the nearest 1 mg after oven-drying at 70°C until constant weight was obtained.

To find out which prey were available to mackerel and herring and the zooplankton biomass, zooplankton samples were obtained by using the WP2 plankton net with a diameter of 56 cm and mesh size of 180 μm. The net was towed vertically from 100 to 0 m and from 25 to 0 m at the location of trawl start at each station. Only zooplankton samples from the 100 to 0 m hauls were used in the present analyses. Each zooplankton sample was separated into two halves. One half was preserved on formalin for taxonomic classification utilizing standard methods at the Institute of Marine Research, while the other half was dried at 70°C for 24 hours before dry weight was used to find the zooplankton biomass.

Based on the collected CTD depth profile data obtained at each station during the cruise, the survey area was divided into three water masses; Coastal, Atlantic and Arctic. M/V "Libas" was equipped with a Seabird 911 probe recording temperature, salinity, and pressure (depth) from the surface down to 500 m depth. The sensor was programmed to record data every two seconds and the speed of the wire during measurements was set to 0.5 m/s, providing data approximately every 1 m in the water column.

Due to time restrictions only part of the cruise track was used in the present study. The geographical area selected was in the central part of the Norwegian Sea (64ºN - 67.5ºN) and covered S→N and E→W areas and included biological stations 7 – 27 (Figure 1). This was the most interesting area of the cruise track as it contained most of the distributed and aggregated mackerel in the Norwegian Sea.
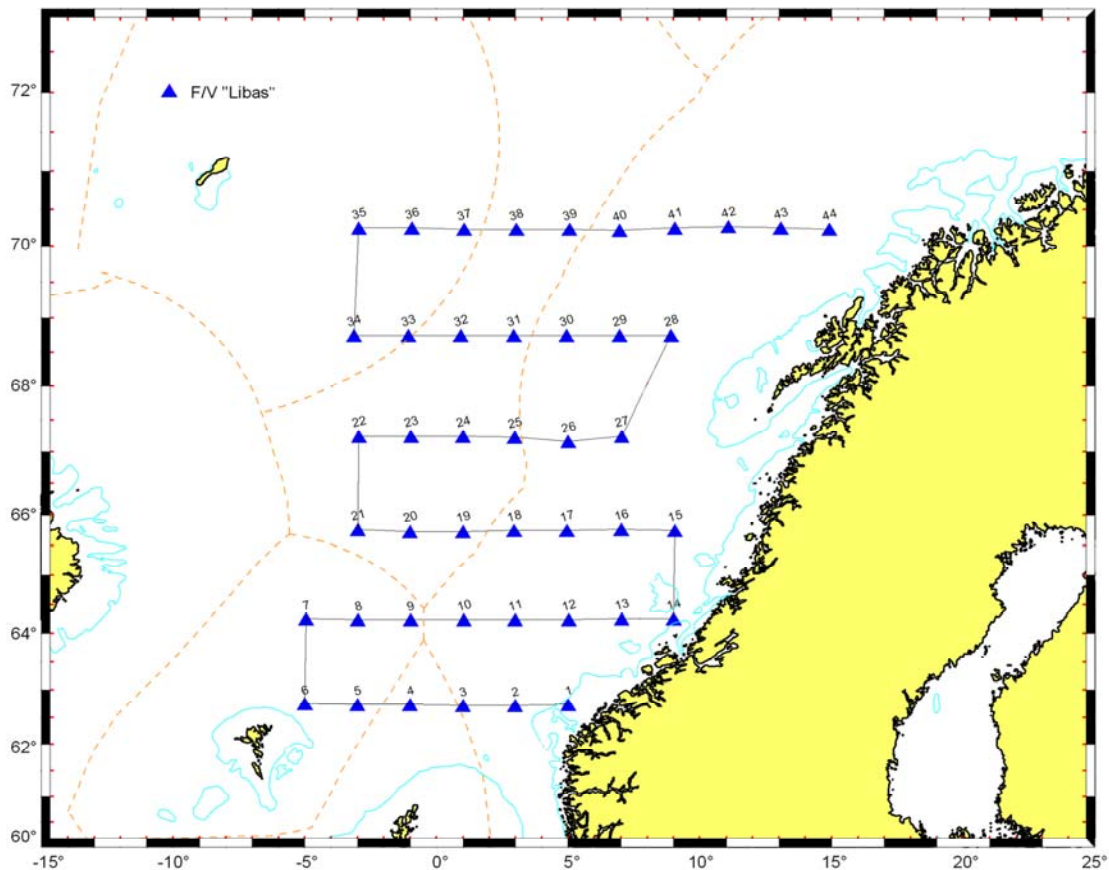
Figure 1. Cruise-tracks and biological and physical stations for M/V "Libas", 15-30 July 2004 in the Norwegian Sea. Data from station 7-27 were used in the present study.

Results

Feeding selection
Prey availability must be compared with diet in order to investigate feeding selection. Both the WP2 samples and the diet of mackerel were similar when comparing Coastal and Atlantic water samples, while the samples from Arctic water differed (Figure 2). Oithona was the most abundant zooplankton according to numbers in Coastal water

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(39%) but it was not found in the diet of mackerel in this or the other water masses (Figure 2). *Limacina retroversa* was the dominant zooplankton species both according to potential (60%) and actual prey (48%) in Atlantic water, and as actual prey in Coastal water (34%) (Figure 2). *Calanus finmarchicus* was the main potential prey in Arctic water (53%), while the group Others, here Appendicularia dominated the diet (32%) (Figure 2). Appendicularia was not found in the other two water masses. *C. finmarchicus* was the second most important prey in Arctic water (Figure 2). The group others from the WP2 samples includes a high number of low percentage potential prey groups, while the others group from the diet includes a low number of low percentage prey groups. Krill and Amphipods were significant in the diet in all water masses (Figure 2). The group Calanoidae Copepods were likely to consist of a high percentage of *C. finmarchicus,* increasing its importance in all water masses.

Interestingly, Copepoda < 1 mm, especially Oithona and Microcalanus CI - III, dominated most of the WP2 samples in numbers, but were not at all present in the stomach samples, while Copepoda > 1 mm, mostly Calanoidae remainders, made up an important part of the stomach samples (Figure 2). Individuals < 1 mm were important in most WP2 samples, while individuals > 1 mm were important in stomach samples (Figure 2). *Calanus finmarchicus* and *Limacina retroversa* made up high percentages in several WP2 and stomach samples (Figure 2).
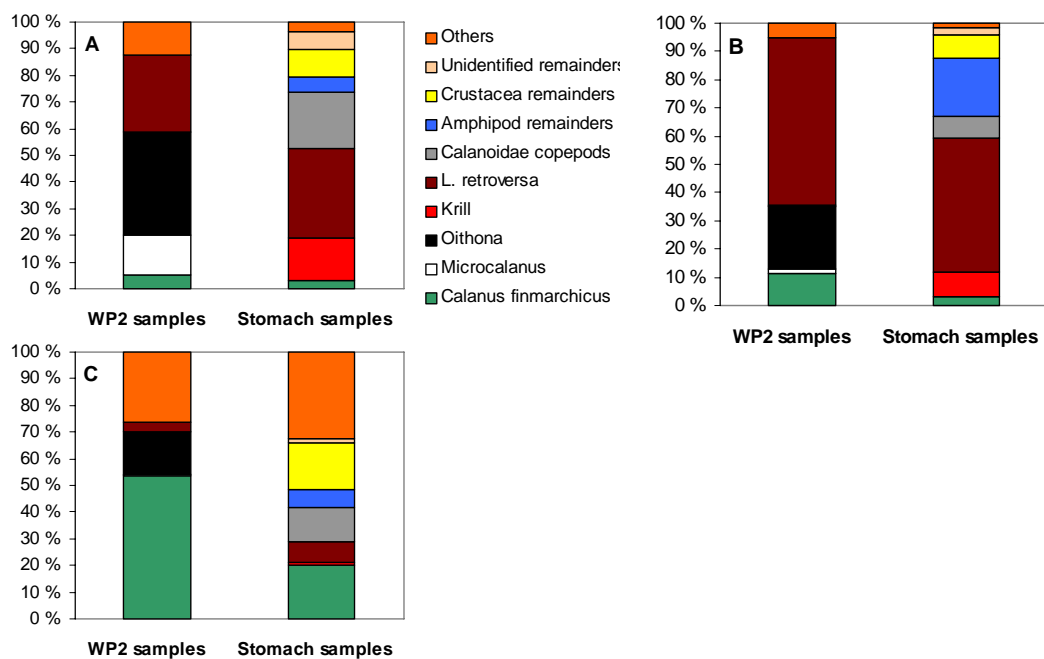
Figure 2. Percent comparison of number of individuals from the WP2 samples, and dry weight of prey from the mackerel diet in the three water masses; A) Coastal, B) Atlantic and C) Arctic.

To examine whether mackerel was opportunistic or selective in it's feeding on the different *Calanus finmarchicus* stages a chi-square test was performed. In the stomachs, the six stages were divided into two major groups I – III and IV – VI. Interestingly, selective feeding on the largest *C. finmarchicus* stages IV-VI was found (p<0.05). The highest developmental stages were frequent both in stomach content and in WP2 samples (Table 1). In the WP2 samples many individuals of

developmental stage III were present, but few of I and II (Table 1). Only one stomach contained *C. finmarchicus* of stages I – III.

Table 1. Total number of individuals of *Calanus finmarchicus* of different copepodite stages in WP2 and stomach samples. Number in the diet was fund by dividing total weight of *C. finmarchicus* by average individual weight.

C. finmarchicus stage	WP2 samples	Stomach samples
I - III	4092	9
IV - VI	294208	45632

Statistical tests were only performed on *Calanus finmarchicus* and *Limacina retroversa,* as they were the only zooplankton found important in both mackerel stomachs and WP2 samples. The number of *C. finmarchicus* in stomach samples was not correlated with the number in the WP2 samples when all stations were tested against each other (correlation test, $p = 0.84$, $r = 0.05$). There was a positive correlation in Coastal water ($p < 0.05$, $r = 0.83$), but not in Atlantic water ($p = 0.26$, $r = - 0.35$). Only stages IV – VI were tested since only one stomach contained stages I – III (Table 1).

Table 2. Comparison of average number of individuals of *C. finmarchicus* of different copepodite stages from WP2 and stomach samples in the three water masses.

Area	CF I - III in WP2 samples	CF I - III in stomachs	CF IV - VI in WP2 samples	CF IV - VI in stomachs
Coastal	2	1	6827	722
Atlantic	329	0	17428	466
Arctic	11	0	18640	17494

Limacina retroversa could not be tested according to water mass as it was only found in the stomachs at six stations. No correlation was found between the amount in the stomachs and WP2 samples (correlation test, $p = 0.81$, $r = 0.05$).

Feeding competition
Co-occurrence of mackerel and herring was investigated to see whether they preferred the same physical environment, and if competition for prey species and size groups appeared at the same trawl stations. Highest abundances of both species were found in the same water masses when all stations were combined (correlation test, $p < 0.01$, $r = 0.63$). When divided into water masses there was no correlation between mackerel and herring catches in Coastal or Atlantic water ($p = 0.77$, $r = 0.14$ and $p = 0.40$, $r = - 0.27$). Mackerel was found alone in four stations, herring in one, and they were found together in 14 out of 21 stations (Figure 3). Mackerel dominated the catches in eight stations, herring dominated in three stations, while three stations had similar catches of both species (Figure 3).
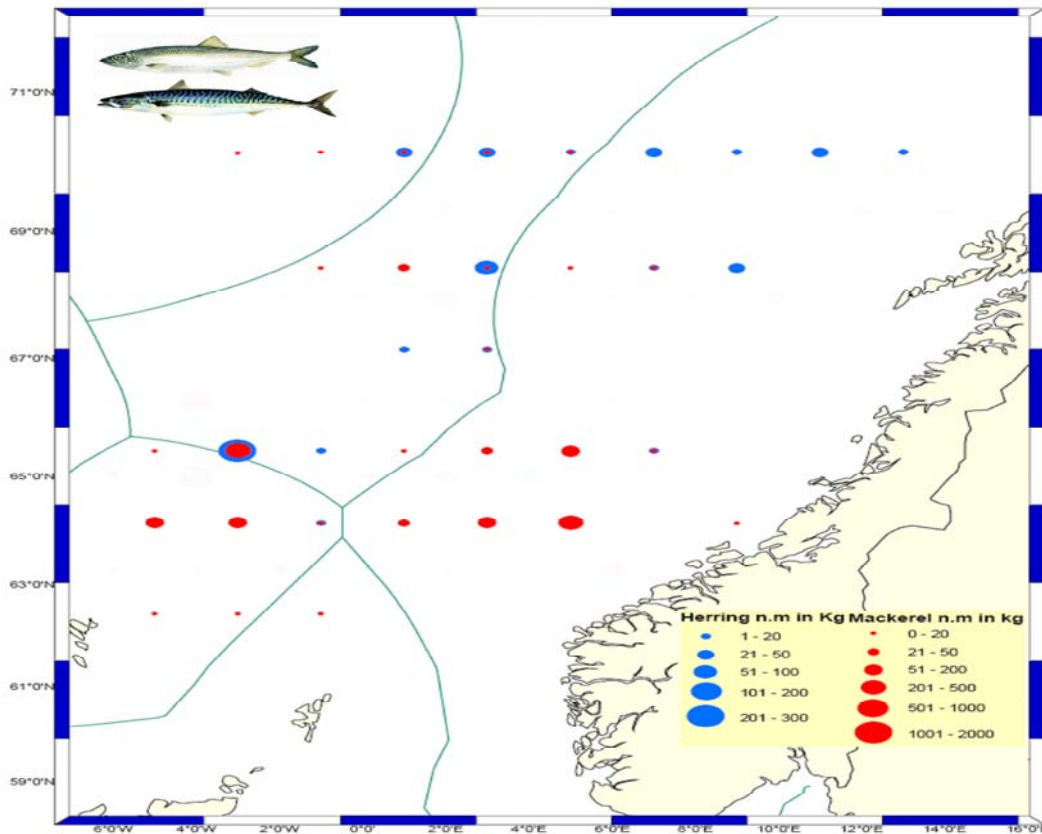
Figure 3. Mackerel and herring catches in kg / n.m. from M/V "Libas" shown together at the belonging stations.

In order to investigate possible feeding competition, herring diet was compared to mackerel diet at stations containing both species with stomachs content. Interestingly, there were clear differences in the stomach contents of herring and mackerel (Figure 4). While mackerel mostly fed on individuals > 1 mm, Copepoda >1 mm, *Limacina retroversa* and *Calanus finmarchicus*, herring mostly ate Euphausiids and Amphipods (Figure 4). Euphausiids and Amphipods were also consumed by mackerel but to a smaller extent than the other prey groups (Figure 4).
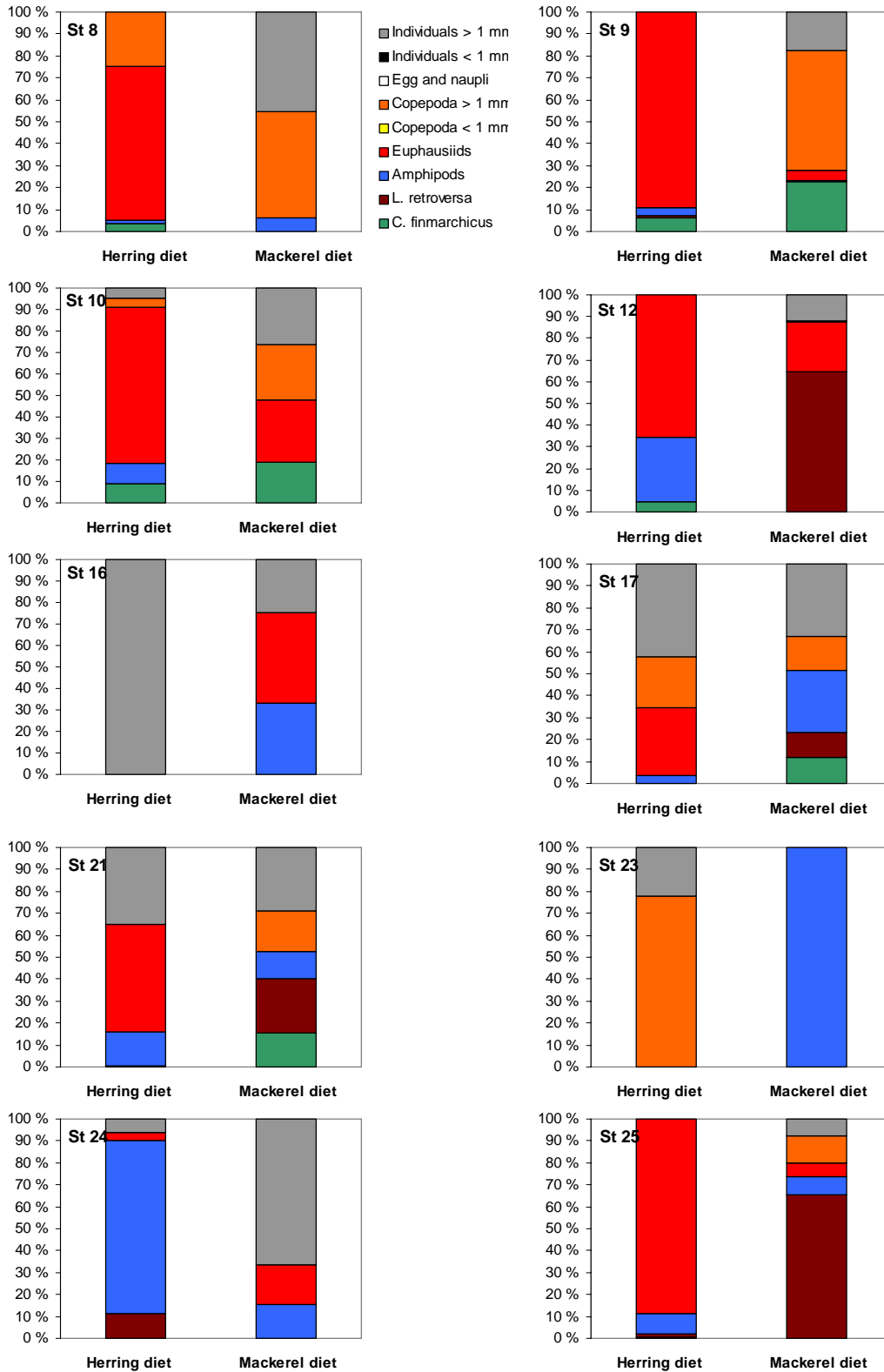
Figure 4. Percentage comparison of the dry weight of the diet of mackerel and herring at the stations containing both species with stomach content. Stations with only empty herring stomachs (18, 19, 26 and 27), and station 20 with only empty mackerel stomachs were not included in the comparison.

Mackerel had higher weight of stomach content compared to herring at all stations (Wilcoxon Rank sum test, p < 0.05) (Figure 5). Fish weight was divided by weight of stomach content and the fractions tested, so that specific tests could be performed without considering fish weight.

Discussion

Feeding selection
Selection for larger prey strongly suggests that mackerel performed particulate feeding during the day. Filter feeding behaviour was indicated by the higher weight of the small *Limacina retroversa* during the few hours of darkness in northern latitudes (64ºN-70ºN). *Limacina retroversa* was rarely found alone but most often in small numbers mixed with other prey. This strongly indicated that it was not intentionally selected but taken as "bycatch" in the quest for other prey. If a prey was numerous throughout the area, like *L. retroversa*, but dispersed within other more preferred prey it could be eaten by mistake in the pursuit for others.

Calanus finmarchicus, often identified as Copepoda >1mm, was usually eaten as the only prey group and seldom mixed with other prey, indicating deliberate prey selection. Prominent species and size selection was supported by selective feeding on larger copepodite stages (CIV-CVI) compared to smaller copepodite stages (CI-CIII). Even after adding Copepoda >1mm to *C. finmarchicus* this species had restricted importance in the weight percentage of the diet compared to previous results where it has been found to constitute more than 50 % (Skjoldal et al. 2004; Prokopchuk and Sentyabov 2005). Also in terms of zooplankton biomass was the share constituted by *C. finmarchicus* in this study lower than previous results (Skjoldal et al. 2004; Prokopchuk and Sentyabov 2005). The restricted importance in the diet compared to previous results, and the frequent occurrence of other prey species indicated that the Calanoidae had started its vertical migration to overwintering habitats in deep water at the time of this study (Pavshtiks and Timokhina 1971). *C. finmarchicus* dominated the zooplankton community only in Arctic waters during the time period of this study. As the plankton spring starts from southeast and spreads northwest the descend is expected to follow the same pattern (Pavshtiks and Timokhina 1971; Rey 2004), explaining the distribution and availability of *C. finmarchicus* for mackerel.

Amphipods and Euphausiids were also intentionally selected, and seldom mixed with other prey species. Amphipods made an important contribution to the dry weight of the diet in all water masses, but especially in Atlantic water. The highest biomass of Amphipods in the Nordic Seas are usually found in cold Arctic water masses (Dalpadado et al. 1998), but the most abundant species in this study, *T. abyssorum* is mainly a sub-Arctic species thriving in cold Atlantic water masses (Dalpadado et al. 2001). Euphausiids were important prey in both Coastal and Atlantic water masses. Different species of Euphausiids are known to be abundant in the entire Norwegian Sea (Dalpadado et al. 1998), and their size is equal to that of the Amphipods.

The importance of zooplankton in this study may be related to a high availability of this prey during the period of high production in the summer (Anon 1998), with few fish larvae or young post-larval stages within the study area. Fish eggs and larvae have previously been found important in the diet of mackerel (Maurer 1976; Dalpadado 1993), but in this study very few fish larvae and no eggs were found in the

stomachs. The absence of eggs could also be caused by digestion, or the small size could have made them difficult to locate, but even then the abundance could not have been high, as traces from these prey groups would otherwise have been found. The most likely explanation was that the abundance of fish larvae and eggs in the study area was low, as it was offshore the main spawning areas.

There was little doubt that selective particulate feeding was performed, and much less so when viewed together with the high frequency of occurrence of small Copepods and individuals <1 mm in the WP2 samples compared to their non-existence in the stomach samples. Size selective feeding has previously been observed for mackerel in the laboratory (Pepin et al. 1987; Pepin et al. 1988), where it showed clear preferences for the largest prey regardless of abundance when presented with prey of different sizes (Pepin et al. 1987; Pepin et al. 1988). Furthermore, the upper limit of prey size increases with increasing size of mackerel (Anon 1998). The upper size of prey that will run through mackerels gill rakers with the water, and the lowest size that is restrained and eaten are unknown. As previous studies on mackerel diet have disregarded the question, and it is not easily investigated, no conclusions were drawn on the subject in this study. To investigate the size of prey that is retained several detailed in situ underwater video-observations and/or carefully designed laboratory studies should be performed.

Feeding competition
Most trawl catches were small (< 10 kg/n.mi) when including all stations from the cruise track and contained both mackerel and herring. Larger catches (> 10 kg/n.mi) were dominated by one of the pelagic planktivorous species, except at two stations with high mixed catches of both mackerel and herring. Godø et al. (2004) found a similar tendency, where small catches were a mix of pelagic fish and large catches (> 10 kg) were dominated by mackerel when including the entire Norwegian Sea. Competition may be the underlying reason for the spatial divergence between the two species, but due to the likely co-evolution that has taken place competition between mackerel and herring in July in the central Norwegian Sea seems unlikely. With this co-evolution mackerel has probably developed to concentrate and feed in areas containing high abundances of *Calanus finmarchicus*, while herring has adapted to concentrate in areas with high abundance of Euphausiids and Amphipods during dark hours. When considering feeding competition between mackerel and herring it is important to remember the complex environment where both prey and predators have the potential to migrate both vertically and horizontally, strongly complicating the matter. Euphausiids and Amphipods were eaten by blue whiting in deep waters during the day, and by herring in the surface layers during dark hours. *C. finmarchicus* was eaten by mackerel in the top layers during the day, and by Euphausiids and Amphipods during dark hours. Competition between mackerel and herring was very limited if not non-existent in July in the central part of the Norwegian Sea, and their diet were consistent and similar even at stations containing only one of the species. This strongly indicates no feeding competition between mackerel and herring during this period. Dominance of one species in large catches was evident in our study and was also found by Godø et al. (2004). Other investigations have concluded high degree of overlap in the diet of these two species during summer (Skjoldal et al. 2004; Prokopchuk and Sentyabov 2005), and therefore likely strong feeding competition. However, very few previous studies have investigated feeding competition at a

relevant scale where individual fishes and single school/shoals experience direct feeding competition with other planktivorous fish species.

There was very little spatio-temporal overlap in the diet of mackerel and herring. While mackerel mostly ate *Calanus finmarchicus* and *Limacina retroversa*, the diet of herring consisted predominantly of Euphausiids and Amphipods. Prior investigations have found high degree of overlap in the diet of these two species during summer, with *C. finmarchicus* and *Limacina* dominating, followed by Krill and Amphipods (Skjoldal et al. 2004; Prokopchuk and Sentyabov 2005). There were three likely explanations for the differences in diet between the species: 1) feeding motivation, 2) time of feeding, and 3) diet shift. The three explanations were not mutually exclusive, but did most likely affect the diet together. Foraging depth and fish length were also investigated as explanations for the differences in diet between the species, but were similar and did not explain the feeding pattern.

1) Higher stomach fullness of mackerel strongly indicates that the difference in diet could be caused by higher feeding motivation of mackerel than of herring. Herring's main feeding period in the Norwegian Sea is May-July (Holst et al. 2004), while mackerel's main feeding period in the Norwegian Sea is July-August/September (Iversen 2004). The most likely explanation was therefore that mackerel had stronger feeding motivation at the time of this study, while herring had almost stopped feeding unless presented with easy access to high nutritious prey. The next two explanations were probably a direct result of the different feeding motivations.

2) Low digestion and high stomach fullness at the stations taken close to dusk and dawn strongly indicated that herring fed on Euphausiids and Amphipods when they entered the surface layers to feed during their daily vertical migration, while mackerel was feeding throughout the day as indicated by low digestion also several hours after dawn. The main prey of mackerel was found in the top layers of the water column. Mackerel feeding seemed to change from particulate to filter during the dark hours, strongly indicating greedy continuous feeding throughout the day and night, while the diet of herring did not change, supporting feeding during dim hours, when Krill and Amphipods migrated to the upper 50 m of the water column. The same feeding patterns as in this study were also found for mackerel and herring based on preliminary analyses and results from the same research cruises performed in 2005 and 2006 in the same period and area. This strongly suggest that there exist a long-term consistent and predictable feeding pattern and limited feeding competition between mackerel and herring in late summer in the Norwegian Sea.

3) The significantly different diets between mackerel and herring could be due to a diet shift by one of the species in order to avoid competition for food. A diet shift in herring at this time of year from *C. finmarchicus* to Krill and Amphipods has previously been observed by Dalpadado et al. (2004), due to decreased Calanoidae population linked to the vertical migration of the Copepods towards deep water (Dalpadado et al. 2000).

The average weight of mackerel stomachs was higher than that of herring, even when comparing similar sized fish. These results are in accordance with previous studies (Maurer 1976), and could be explained by more greedy feeding behavior of mackerel, in agreement with the conclusions drawn by Maurer (1976). However, if herring only

fed during dusk and dawn some time may pass by between last feeding and the catch. During this time digestion progresses and the weight of stomach content should decrease. However, more greedy and active feeding behavior of mackerel was the most likely explanation for the higher stomach fullness of mackerel compared to herring.

Conclusion

Mackerel feeding ecology was dependent on prey availability, and therefore varied between water masses in July within the central part of the Norwegian Sea. Low importance of *Calanus finmarchicus* as prey species in Atlantic water masses strongly indicated that the Copepods had descended to overwintering areas in deeper waters. In the colder Arctic water a later zooplankton spring made *C. finmarchicus* still available near the surface and thus important in the mackerel diet. *C. finmarchicus* was important prey for mackerel when its abundance was high. However, when the abundance of *C. finmarchicus* decreased, Amphipods and Euphausiids were preferred prey species. Interestingly, large and mature *C. finmarchicus* were actively selected over the smaller copepodite stages as mackerel prey. High numbers of small (<1 mm) Copepods in all water masses were ignored, strongly suggesting particulate feeding and intentional selection of the most nutritious prey organisms. The diets of mackerel and herring were significantly different. The most likely explanation was a diet shift in herring caused by the underlying factor that the main feeding season was coming to an end and that the accumulated condition factor and fat content were high from previous months (May – June) of active and intensive feeding over large areas of the Norwegian Sea. Herring was thus likely to be moderate in its feeding behavior, with already high condition factor and fat content, and fed presumable only when high nutritious prey was easily available in the upper part of the water column. The descent of *C. finmarchicus* to deeper water could lower its abundance significantly, so that herring would not feed on it, while when Euphausiids and Amphipods entered the upper layers their abundance could be high enough to continue feeding. Mackerel was in the greedy middle part of their feeding migration, with feeding performed throughout the day, and the best feeding choice seemed to be *C. finmarchicus* compared to the dominating small copepods in shallow water. Approximately 20 – 24 hours of daylight in high latitudes in the Norwegian Sea should ensure more or less continuous visual feeding opportunities for the mackerel. These feeding patterns are supported by preliminary results on mackerel and herring feeding preferences from cruises in July 2005 and July 2006 in the Norwegian Sea.

Acknowledgement

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