Diets of herring, mackerel, and blue whiting in the Norwegian Sea in relation to Calanus finmarchicus distribution and temperature conditions

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Diets of Norwegian spring-spawning herring, mackerel, and blue whiting in the Norwegian Sea are investigated in relation to the distribution of plankton and hydrographic conditions. Fish stomachs and zooplankton samples were collected during summer (June and July) cruises in 2001 and 2002. Calanus finmarchicus was the principal prey of mackerel, accounting for 53–98% of total stomach content by weight. The diet composition of herring varied depending on feeding area and availability of food under various environmental conditions. C. finmarchicus was important prey for herring only in July 2001 (about 77% by weight) in the central part of the sea and in June 2002 (about 82% by weight) near the Lofots. In July 2002 appendicularians (Oikopleura spp.), amphipods (mainly Parathemisto abissorum), and euphausiids were important in the diet of herring, and at some stations cannibalism was observed. The main prey of blue whiting were amphipods (10–34% by weight), appendicularians (11–34%), and euphausiids (8–47%), as they usually feed deep in the water column, though C. finmarchicus was important, particularly in June 2002, when blue whiting were caught in the upper layers of the sea. Higher water temperatures indirectly affect pelagic fish through accelerated development of their prey and favourable conditions for migration farther north.

Introduction

Copepods dominate the zooplankton community of the Norwegian Sea, with Calanus finmarchicus (Gunnerus) being the most important species with regard to both abundance and biomass (Wiborg, 1955; Gruzov, 1963; Marshall and Orr, 1972; Aksnes and Blindheim, 1996; Gislason and Astthorsson, 1996; Hirche et al., 2001). C. finmarchicus is prey for such pelagic fish as Norwegian spring-spawning herring (Clupea harengus Linne), Atlantic mackerel (Scomberus scomberus Linne), and blue whiting (Micromesistius poutassou Norman). All three species undergo summer feeding migrations into the Norwegian Sea, with herring and mackerel feeding near the sea surface, and blue whiting generally feeding deeper in the water column. Herring have been hypothesized to adapt their feeding migrations according to the temporal development of C. finmarchicus (Østvedt, 1965; Corten, 2000; Kaartvedt, 2000), but it has also been suggested that herring distributions influence the timing and duration of the C. finmarchicus migrations, as well as their annual descent and ascent, and the number of generations per year (Kaartvedt, 1996, 2000).

Hydrographic conditions are thought to influence the initiation of feeding of pelagic fish species and their feeding duration, intensity, and area preferences. Temperature impacts fish directly by changing digestion rates, and indirectly by influencing prey development rates and distribution. Also, extremely high temperature anomalies can decrease zooplankton productivity, which leads to poor feeding conditions for fish (Wyszynski, 1989).

The purpose of this study is to identify the diet of herring, mackerel, and blue whiting in the Norwegian Sea, and to estimate the effects on diet of temperature conditions and prey availability, with special focus on C. finmarchicus.
Material and methods

Data were collected during Russian surveys in the Norwegian Sea in June-July of 2001 and 2002. Hydrographic data were obtained using a CTD along standard sections and at trawl stations. Temperature anomalies were identified by comparing with the long-term (1951-2000) mean (Sentyabov et al., 2003).

Zooplankton data, collected by vertical hauls from 50 m to the sea surface using a Juday net (entrance diameter of 37 cm, mesh size of 180 μm), were taken simultaneously with hydrographic observations. Plankton samples were preserved in a 4% formaldehyde-seawater solution for later analysis. The total numbers of samples analysed were 159 in 2001 and 142 in 2002. Species composition of plankton and stage structure of C. finmarchicus were analysed at sea. Relative abundance indices of plankton organisms and different copepodid stages of C. finmarchicus were estimated (1 — single individuals in the sample, 2 — dozens, 3 — hundreds, 4 — thousands). The total biomass of plankton was also determined (wet weight ± 0.1 g).

Herring, mackerel, and blue whiting were sampled simultaneously with pelagic trawls in the Norwegian Sea. Sampling of fish by trawl was generally once per day, but herring were sampled twice on 14 June 2001 and blue whiting twice on 6 July 2002. The trawl had a vertical opening of 45 m and the vessel speed was approximately 4.3 knots. The trawling time varied from 30 to 75 min and the trawling depth from 0 to 310 m. Occasionally, several depths were trawled at the same site. The number of fish stomachs removed for diet analysis per trawl ranged from 19 to 30. In total, 172 herring stomachs, 181 mackerel stomachs, and 478 blue whiting stomachs were analysed. The stomachs were preserved in 10% formaldehyde-seawater solution immediately following removal from the fish. At the PINRO laboratory, stomach contents were analysed using a binocular microscope. The consumed organisms were identified to species level if possible, then counted, measured, and weighed with an accuracy of 0.1 mg. C. finmarchicus were staged and the abundance of each stage was estimated. In order to characterize the fish diet, mean stomach fullness, average fat content, and the percentage of prey species in the bolus (by weight) were calculated. Mean stomach fullness was determined visually using the following scale: 0 — empty; 1 — very little content; 2 — some content; 3 — full, but not bloated; 4 — bloated; 5 — everted.

The stage structure and abundances of C. finmarchicus in the plankton samples taken at the same locations as the trawl stations during July 2002 were identified and counted, respectively, for comparison with the fish stomach data. At all other times, only the relative abundance index was determined for the plankton samples.

Results

Hydrographic conditions

In 2001, temperatures in the Norwegian Sea in both the warm Norwegian Atlantic Current (NwAC) waters and the more offshore admixture of NwAC and East Icelandic Current (EIC) waters, hereafter called Mixed Waters, were close to their long-term means. Average temperatures of the upper 50 m layer in the NwAC were 8—9°C (Figure 1). In 2002, water temperatures in the Norwegian Sea were abnormally high, attaining more than 10°C in the NwAC (Figure 1), 1.5—2.0°C higher than the average throughout the region (Figure 2).

Plankton

Copepods were the most abundant prey with C. finmarchicus, the dominant species, making up to 60—95% of the total number of zooplankton organisms. The spatial patterns of C. finmarchicus of different stages varied between 2001 and 2002. In 2001, C. finmarchicus nauplii were concentrated in the central Norwegian Sea (Figure 3A). Copepodid stages CI—III occurred in considerable quantities throughout much of the area (Figure 3B), while stages CIV—V were distributed mostly in the south and between 68°N and 70°N (Figure 3C). In 2002, highest concentrations of C. finmarchicus nauplii were in the south and off

Figure 1. Temperature in the upper 50 m layer of the Norwegian Sea in June and July of (A) 2001, and (B) 2002.
Lofoten (68°–70°N 5°–15°E; Figure 3E). The highest concentrations of stages CI–III were observed near the zero meridian and in the northeast, while stages CIV–V were most abundant in the northwest and southeast (Figure 3F, G). The relative abundance of *C. finmarchicus* CIV–V in 2002 was somewhat higher than in 2001. This was also true for *C. finmarchicus* females (Figure 3D, H).

In 2001, zooplankton biomass concentrations ≥500 mg m⁻³ were observed in a large area, whereas in 2002 they were more limited to the northwest and southeast (Figure 4). Mean plankton biomass in 2001 and 2002 was 765 mg m⁻³ and 832 mg m⁻³, respectively. Plankton biomass in both years was dominated by *C. finmarchicus* stages CIV–V and to a lesser extent by mature individuals.

### The diet of pelagic fish

#### Herring

Food was found in 93% of the 172 herring stomachs analysed. Mean stomach fullness varied from 1.2 to 3.7 and the herring diet differed depending on area, month, and year (Table 1). *C. finmarchicus*, *C. hyperboreus*, and *Paracopea norvegica* were identified among the various copepods in the herring stomachs. *C. finmarchicus* constituted ~78% of the total prey by weight in the central Norwegian Sea in July 2001 and ~82% in June 2002 near the Lofotens (Figure 5). Note that the following percentages are also by weight unless otherwise indicated. The amount of *C. hyperboreus* and *P. norvegica* in the diet was insignificant (~0.3%).

In July 2001, herring fed mostly on *C. finmarchicus* stage CV (~45%) and females (stage CVI; ~33%) (Figure 6A). In June 2002, *C. finmarchicus* CIV–V dominated the stomach contents (~31% and 55%, respectively), but in July it was copepodid stages CIII–IV (~55% and 23%; Figure 6B). While *C. finmarchicus* females were found in herring stomachs in both years, they were relatively more abundant in 2001 (~33%) than in 2002 (~3%; Figure 6A, B). Based on the 2002 data when stage abundances from both the stomach and plankton data were available, herring strongly select larger *C. finmarchicus* (Figure 6C).

Appendicularians *Oikopleura* sp. (~21–41%), amphipods (~9–28%), and euphausiids (~6–59%) were also important prey for herring in July 2002 (Figure 5). Amphipods were *Parathemisto abyssorum* and *P. libellula*, of which the first species contributed an important proportion to the diet of herring but the second was found only very rarely and in insignificant proportions. Among euphausiids, two species were identified in the herring stomachs, *Meganyctiphanes norvegica* and *Thysanoessa longicaudata*, but the latter were rare.

In July 2002, cannibalism was observed, with herring juveniles constituting 100% of total stomach content in one sample (Figure 5). *Sebastes* spp. dominated (80.9%) herring stomachs at another trawl site (Figure 5).

#### Mackerel

Of the 181 mackerel stomachs analysed, only one was empty. The mean stomach fullness was quite high (~2.6), indicative of active feeding (Table 1). The average number of *C. finmarchicus* per mackerel stomach in 2001 was ~6000 individuals during June but <1000 in July, while in 2002 the average number was ~5000 individuals during June and ~30 000 in July, (Figure 7). *C. finmarchicus* was the principal prey species accounting...
Figure 3. Distribution of *Calanus finmarchicus* of different development stages (relative numbers) in the Norwegian Sea in 2001–2002. 1 — single individual in the sample, 2 — dozens, 3 — hundreds, 4 — thousands. A–D, 2001; E–H, 2002; n — nauplii; I–III and IV–V — copepodite stages; VI — females.
for \( \sim 52-\sim 98\% \) by weight of the stomach contents in 2001 and more in 2002 (Figure 8).

In June 2001, in the southern Norwegian Sea near the Faroe Islands, the diet of mackerel also consisted of small copepods (Pseudocalanus elongatus, Oithona similis, Temora longicornis, Acartia clausi, juveniles of Metridia spp.), Cladocera (Evadne nordmanni and Podon leucarti) (\( \sim 21\% \)), and euphausiids (\( \sim 31\% \)) (Figure 8). In 2002, mackerel fed almost exclusively on C. finmarchicus (Figure 8).

Stages CIV–V and CIII–IV of C. finmarchicus occurred in the diet of mackerel in the middle and at the end of June 2001 (Figure 6D). In July 2001, the diet of mackerel consisted mainly of C. finmarchicus CIV–V and females (CVF, Figure 6D). In June 2002, stages CV and females formed the highest percentage of the mackerel diet, while in July C. finmarchicus CIII–IV dominated (Figure 6E). In both June and July 2002, the percentage of older stages of C. finmarchicus was higher in the mackerel diet than in the plankton samples (Figure 6F, G).

The average fat content of mackerel in 2001 increased from 0.8 in June to 2.1 in July, but the mean stomach fullness decreased from 3.0 to 2.5, respectively. In 2002, the

Table 1. Results of the stomach content analysis for herring, mackerel, and blue whiting in the Norwegian Sea in June and July of 2001 and 2002. The mean and their standard deviations are shown.

<table>
<thead>
<tr>
<th></th>
<th>2001</th>
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<th>2002</th>
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<tr>
<td></td>
<td>June</td>
<td>July</td>
<td>June</td>
<td>July</td>
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<tr>
<td>Herring</td>
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<td>Stomach fullness</td>
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<td>3.2 ± 0.8</td>
<td>1.5 ± 0.5</td>
<td>2.1 ± 1.2</td>
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<td>Fat content</td>
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<td>2.7 ± 0.6</td>
<td>2.8 ± 0.4</td>
<td>2.3 ± 1.0</td>
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<tr>
<td>Number of stomachs</td>
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<td>19</td>
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<td>Empty stomachs (%)</td>
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<td>0</td>
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<td>Mean length of fish (mm)</td>
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<td>353.1 ± 9.8</td>
<td>277.7 ± 14.5</td>
<td>310.4 ± 37.8</td>
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<tr>
<td>Mean weight of fish (g)</td>
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<td>368.7 ± 36.7</td>
<td>188.4 ± 30.8</td>
<td>272.0 ± 88.8</td>
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<td>Mackerel</td>
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<tr>
<td>Stomach fullness</td>
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<td>2.5 ± 0.9</td>
<td>2.4 ± 0.9</td>
<td>2.8 ± 1.0</td>
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<tr>
<td>Fat content</td>
<td>0.8 ± 0.8</td>
<td>2.1 ± 0.4</td>
<td>1.9 ± 1.1</td>
<td>2.2 ± 0.5</td>
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<tr>
<td>Number of stomachs</td>
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<td>43</td>
<td>63</td>
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<td>Empty stomachs (%)</td>
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<td>Mean length of fish (mm)</td>
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<td>383.6 ± 21.4</td>
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<td>Mean weight of fish (g)</td>
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<td>557.1 ± 112.5</td>
<td>573.0 ± 138.3</td>
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<td>Blue whiting</td>
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<td>Stomach fullness</td>
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<td>2.3 ± 0.7</td>
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<td>Number of stomachs</td>
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<td>100</td>
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<td>Empty stomachs (%)</td>
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<td>Mean length of fish (mm)</td>
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<td>244.1 ± 20.9</td>
<td>262.3 ± 19.3</td>
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<td>Mean weight of fish (g)</td>
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<td>89.4 ± 40.7</td>
<td>88.2 ± 21.4</td>
<td>111.7 ± 22.3</td>
</tr>
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</table>
general proportion of *C. finmarchicus* in the mackerel diet increased from June to July, as respectively did the mean stomach fullness (from 2.3 to 2.8) and the fat content (from 1.9 to 2.2).

**Blue whiting**

Of the 478 blue whiting stomachs analysed, 92% contained food. The largest number of fish with empty stomachs was registered in 2001, increasing from June (8%) to July (~25%) (Table 1). The mean stomach fullness varied from 2.1 to 2.5, respectively.

In June 2001, blue whiting fed mostly on *C. finmarchicus* (~41%), euphausiids (25%), and juveniles of *Parathemisto* spp. (~20%), but in July, appendicularians *Oikopleura* spp. (~45%) were the most important diet component (Figure 9A). Large cold-water *C. hyperboreus* made up to 67% of

![Figure 5. Diet of herring (% of total stomach content weight) in the Norwegian Sea in 2001–2002 combined. The diameter of the circles reflects mean stomach fullness. Undt. — unidentified units.](image-url)
Deepwater copepods of the genus *Pareuchaeta* in the Norwegian Sea in 2001 constituted 35% of the total food weight at one station in the northwestern Norwegian Sea in July, although generally its importance in the diet was insignificant (Figure 9A).

In June 2002, *C. finmarchicus* constituted 97% of the stomach contents of the blue whiting caught in the upper 10 m layer. At depths of 200−240 m, blue whiting fed on adult euphausiids (46%), *Parathemisto* spp. (34%), and deepwater copepods of the genus *Pareuchaeta* (10%) (Figure 9B). In July *C. finmarchicus* constituted only ~17% of the blue whiting diet, with juveniles of *Parathemisto* spp. (~47%) and adults of euphausiids (~35%) the principal prey species (Figure 9B).

Only *C. finmarchicus* stage CV and females occurred in blue whiting stomachs (Figure 6H) although earlier stages were observed (Figure 6I). In 2001, the average number of *C. finmarchicus* per blue whiting stomach in June was nearly five times larger than in July.

**Discussion**

The period from the end of the 1990s to the beginning of the 2000s was characterized by continuous intensification of the advection of warm Atlantic waters into the Norwegian Sea and increasing water temperatures, with a maximum in 2002 (Figure 2). Summer temperatures in the central Norwegian Sea in 2001 and 2002 differed (Holst et al., 2001; ICES, 2002b), with the Atlantic water temperature in the upper 50 m in the central regions being 1 °C higher in 2002 than in 2001, and in the east higher by more than 2 °C (Figure 1).

The high abundances of nauplii and early copepodid stages of *C. finmarchicus* in both 2001 and 2002 suggest...
that the population was actively reproducing. Mature individuals were also numerous. Spawning times and the development rate of *C. finmarchicus* varied spatially in response to differences in hydrographic conditions. For example, spawning in the warmer southeast Norwegian Sea was over by June even though it was only just beginning in the colder waters in the northwest. Higher than normal temperatures during 2002 are thought to have led to the higher abundances of both nauplii and copepodid stages CIV—V. The higher abundance of older copepodid stages of *C. finmarchicus* during the survey 2002 is thought to be due to early spring spawning coupled with a faster developmental rate, which together resulted in better survival, perhaps due to reduced stage durations and hence lower predation. A second generation may also have contributed to the higher number of nauplii.

Figure 8. Food composition of mackerel (% of total stomach content weight) in the Norwegian Sea in 2001 (A) and 2002 (B). The diameter of the circles shows mean stomach fullness (see the legend in Figure 5).

Figure 9. Food composition of blue whiting (% of total stomach content weight) in the Norwegian Sea in 2001 (A) and 2002 (B). The diameter of the circles shows mean stomach fullness (see the legend in Figure 5). In 2002, samples for 15, 17, and 23 June were taken in the upper 10 m layer, and the sample for 12 June at a depth of 200—240 m.
Different stage compositions of *C. finmarchicus* in plankton samples compared with that in the stomachs of herring, mackerel, and blue whiting suggests prey selectivity (Figure 6C, F, I). For instance, herring fed mainly on large over-wintered *C. finmarchicus*, consistent with earlier studies (Pavshitskii, 1956; Shaposhnikova, 1964; Melle et al., 1994; Dalpadado et al., 2000; Gislason and Astthorsson, 2002). Dalpadado et al. (1996, 2000), who also found that herring stomachs contained larger *C. finmarchicus*, assumed that the absence of small copepodes in the herring diet was caused by faster digestion. However, the absence of early copepodid stages of *C. finmarchicus* in the herring stomachs even during early stages of digestion in our study indicates that herring probably did not feed on these small individuals.

Shaposhnikova (1964) states that most of the herring population leaves the spawning grounds to feed, migrating gradually northwards from one prespawning *C. finmarchicus* concentration to another. This behaviour may explain the high percentage of larger *C. finmarchicus* in the diet of herring compared with mackerel, and gives herring a competitive advantage over mackerel and blue whiting through its earlier arrival in the feeding areas.

Higher water temperatures resulted in a very strong year class of herring in 2002, and their larvae and 0-group were distributed over vast areas of the Norwegian Sea. The large year class is believed to have contributed to the cannibalism. Herring are active predators that feed on their own larvae (Dalpadado et al., 2000), and when the *C. finmarchicus* population is reduced, consumption of herring juveniles will increase (Rudakova, 1966). Holst (1992) found that cannibalism can act as a major factor regulating the abundance of herring year classes in some coastal areas in north Norway, where the distribution of the 0-group overlaps with that of adult herring.

Mackerel typically feed on copepods, euphausiids, pteropods, arrow-worms, and fish during summer (Vinogradov, 1982; Mehl and Westgård, 1983). In our studies, *C. finmarchicus* was the principal prey species for mackerel. While there was feeding selectivity for older stages of *C. finmarchicus* in the mackerel diet, the stage structure was more similar to the distribution pattern observed in the plankton samples than for either herring or blue whiting (Figure 6C, F, I). In contrast to our results, Vinogradov (1981), in comparing the diet of pelagic fish species with the composition of prey species in the zooplankton, found that in most cases they were similar, but that the composition varied according to area and season. Differences in the composition of *C. finmarchicus* copepodid stages in plankton samples and in the mackerel stomachs may be caused by the feeding selectivity of mackerel and the patchiness of *C. finmarchicus* as well (Boldovskiy, 1941).

The decrease in the number of individuals in the mackerel stomachs from June to July 2001 was due to fewer early copepodid stages of *C. finmarchicus* in July. The general proportion by weight of *C. finmarchicus* in the mackerel diet in 2002 increased greatly from June to July. The increase in the fat content and a decrease in the mean stomach fullness suggest that mackerel feeding activity might decline with a higher condition level, as observed in 2001. In 2002 mackerel condition level was not high and, therefore, the fish continued feeding intensively.

*C. finmarchicus* is of less importance for blue whiting than herring and mackerel. Generally inhabiting deeper waters, blue whiting feed mostly on Euphausiacea, Hyperiidae, Appendicularia, Chaetognatha, and juvenile fish (Zilanov, 1964). Nevertheless, blue whiting can actively feed on *C. finmarchicus* especially if they are in large concentrations and feeding near the surface. Blue whiting feed on large *C. finmarchicus* only. There were more *C. finmarchicus* consumed in 2002 than in 2001, perhaps due to increased time in the surface layer during 2002. The maximum intensity of blue whiting feeding most often occurs in June and depends on the plankton organisms' development rate, which in turn is connected to hydrographic conditions (Plekanova and Soboleva, 1986; Plekanova, 1990). Gersinsimova and Plekanova (1994) distinguished the areas where blue whiting feed on copepods in May–June. When feeding schools migrate farther north, copepods in the diet are replaced by hyperiids (in the west and northwest) and euphausiids (in the east).

The initiation of feeding migration of pelagic fish species and its duration is influenced by hydrographic conditions. The increased advection of warm Atlantic water by the Norwegian Current and high positive temperature anomalies in 2002 caused an early spring onset of *C. finmarchicus* development. As a consequence, the second generation of *C. finmarchicus* appeared earlier, and the number of young copepodid stages was high, resulting in poorer feeding conditions for herring, which prefer larger *C. finmarchicus*. In order for fish to find suitable food, e.g. large prespawning specimens of *C. finmarchicus*, they have to migrate farther north, outside the survey area. The regional difference in the seasonal development of the phytoplankton is reflected in the spawning time and the development of *C. finmarchicus*. The increased temperatures speed up the onset of the phytoplankton bloom and the development rates of *C. finmarchicus*, so fish can find appropriate food even in northern areas, where prespawning concentrations of *C. finmarchicus* form according to the rate of warming of the water.

In 2002 with abnormally warm conditions, mackerel were caught farther north than in previous years (ICES, 2003a, 2004). In June 2001, herring were rare, and in July only one trawl had sufficient herring for diet analysis. The sample was taken in the area of low concentration of *C. finmarchicus* in plankton samples compared with that in the stomachs of herring, and gives herring a competitive advantage over mackerel and blue whiting through its earlier arrival in the feeding areas.

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the recovery of the herring stock after its major stock collapse in the late 1960s (ICES, 2002a, 2003b; Morozova and Sentyabayov, 2003). Analysing the different factors influencing the migration pattern of fish will be the aim of future investigations.

Conclusion

Herring, mackerel, and blue whiting undertake feeding migrations to the Norwegian Sea. Predation by these fish species on Calanus finmarchicus varied by month (June to July) and by year (2001–2002) depending on fish behaviour, their feeding preferences, and environmental conditions. Herring migrate gradually northwards from one prespawning Calanus finmarchicus concentration to another, and their early start gives them a competitive feeding advantage over the later migrating mackerel and blue whiting. Herring mostly select large and mature Calanus finmarchicus, so may affect the reproductive potential of Calanus finmarchicus. Mackerel feed in the upper layers of the ocean. The stage structure of Calanus finmarchicus in the mackerel diet was more similar to the distribution pattern of Calanus finmarchicus stages, but still showed some selectivity for older stages. Blue whiting reside in deeper water and Calanus finmarchicus are less important in their diet than in that of herring and mackerel. Blue whiting mainly feed on euphausiids, hyperiids, and other prey. However, blue whiting consumption on the deep overwintering stock of Calanus finmarchicus may influence zooplankton population abundance in the following year. Higher water temperatures indirectly affect pelagic fish through accelerated development of their prey, and favourable conditions for migration farther north.

Acknowledgements

We thank Olga Gerasimova for help in processing the fish stomachs and useful advice.

References