# Trophic ecology of blue whiting in the Barents Sea

Andrey V. Dolgov, Edda Johannesen, Mikko Heino, and Erik Olsen

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Blue whiting (*Micromesistius poutassou*) are distributed throughout the North Atlantic, including the Norwegian and Barents Seas. In recent years, both abundance and distribution of blue whiting in the Barents Sea have increased dramatically. Therefore, to evaluate the trophic impact of this increase, we analysed the diet of the species. In all, 54 prey species or taxa were identified, the main prey being krill. However, the diet varied geographically and ontogenetically: the proportion of fish in the diet was higher in large blue whiting and in the north of the range. Blue whiting overlap geographically with other pelagic species at the edge of their distribution in the Barents Sea, with juvenile herring in the south, with polar cod in the north, and with capelin in the northeast. The overlap in diet between blue whiting and these other pelagic species ranged from 6 to 86% and was greatest with capelin in areas where both species feed on hyperiids and krill. The importance of blue whiting as prey for predatory fish was highest in the areas of greatest abundance, but overall, blue whiting were seemingly unimportant as prey of piscivorous fish in the Barents Sea.

**Keywords:** blue whiting, competition, diet, ecosystem survey, predation, trophic interactions.

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*A. V. Dolgov: Polar Research Institute of Marine Fisheries and Oceanography (PINRO), Knipovich Street 6, Murmansk 183038, Russia. E. Johannesen, M. Heino, and E. Olsen: Institute of Marine Research, PO Box 1870 Nordnes, NO-5817 Bergen, Norway. M. Heino: Department of Biology, University of Bergen, PO Box 7800, NO-5020 Bergen, Norway, and Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria. Correspondence to A. V. Dolgov: tel: +7 8152 472469; fax: +7 8152 473331; e-mail: dolgov@pinro.ru.*

## Introduction

The blue whiting (*Micromesistius poutassou*) supports one of the largest fisheries in the Atlantic, with annual catches of more than 2 million tonnes from 2003 to 2006 (ICES, 2007a). In the Northeast Atlantic, the species is treated as a single stock for assessment purposes (ICES, 2007a), but the stock is regarded as consisting of two main components: the southern component in the Bay of Biscay, and the northern component that extends north from the Porcupine Bank west of Ireland (Zilanov, 1984; Monstad, 2004). The northern component makes long-distance migrations from its main feeding areas in the Norwegian Sea to its spawning area west of the British Isles. The Barents Sea is at the northeastern limit of the distribution of the northern component of blue whiting, but data from standardized annual surveys of the Barents Sea since 1981 show a marked increase in its abundance since about 2000 (Belikov *et al*., 2004; Heino *et al*., 2008). Concurrently, the distribution has extended towards the east and north within the Barents Sea. The greater abundance in the Barents Sea in recent years is probably the result of an expansion of the northern main oceanic component of the stock, which feeds mainly in the Norwegian Sea (Varne and Mork, 2004; Heino *et al*., 2008). Heino *et al*. (2008) showed that the greater abundance and wider distribution of Barents Sea blue whiting are indirectly related to climate through a correlation with strong year classes of blue whiting spawned west of the British Isles and, to a lesser extent, directly related to climate through a positive correlation with inflows of Atlantic water into the Barents Sea.

Climate-mediated changes in the distribution and abundance of species can influence other species in the foodweb through ecological interactions (e.g. Hamre, 1994). To date, the greater abundance of blue whiting has had no obvious effect on the abundance of other Barents Sea species. However, the consumption of blue whiting by cod (*Gadus morhua*) has increased in proportion to the increase in blue whiting abundance (ICES, 2007b). Blue whiting therefore appear to have become an important component of the foodweb as prey for cod. However, little is known about the diet of blue whiting themselves in the Barents Sea in recent years and hence on which species blue whiting prey. The average biomass of blue whiting in the Barents Sea from 2004 to 2006 was 1.1 million tonnes (Anon., 2004, 2005, 2006a, 2007, 2009), making it the second most abundant pelagic fish species in the Barents Sea in those years, after juvenile herring (*Clupea harengus*). Besides juvenile herring, polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*), other pelagic species are present and potential competitors of blue whiting, but no studies have been made of diet overlap between blue whiting and those species.

The diet of blue whiting has been studied throughout its geographic range in the Atlantic (Timokhina, 1974; Bailey, 1982; Zilanov, 1984; Bergstad, 1991; Cabral and Murta, 2002; Monstad, 2004; Prokopchuk and Sentyabov, 2006), particularly in the Norwegian Sea, its most important feeding area. Although diet analyses and trophic interactions of blue whiting in the Norwegian Sea have been documented recently (Monstad, 2004; Skjoldal, 2004; Prokopchuk and Sentyabov, 2006; see also Bergstad, 1991), the only English-language publications on blue whiting diet from the Barents Sea are by Zilanov (1968, 1982) and are based on data from the 1960s and 1970s. However, the Barents Sea has undergone significant ecological change since then. Moreover, although the Barents and Norwegian Seas share some species, they differ in many key characteristics (Yaragina and Dolgov, 2009) that might influence the trophic ecology of blue whiting. Therefore, diet information obtained in the Norwegian Sea does not necessarily apply to the Barents Sea, and updated information on the trophic ecology of blue whiting in the Barents Sea is needed.

Here, the diet and distribution of blue whiting in the Barents Sea from 1998 to 2006 is described. We also examine spatial and dietary overlap between blue whiting and its potential competitors, i.e. juvenile herring, capelin, and polar cod. Finally, we evaluate the importance of blue whiting as prey for cod, the most important fish predator in the Barents Sea (Bogstad *et al.*, 2000), and other piscivorous fish.

## Material and methods

### Data acquisition and diet analysis

Blue whiting are caught with demersal trawls in the Barents Sea, and most of the stomach samples (>95%) utilized in this study were taken from fish so trawled. The stomachs were collected on Russian and Norwegian routine research surveys in the Barents Sea (Table 1). Data from the first quarter were from the Joint IMR–PINRO demersal winter survey (hereafter winter survey), run every February/March since 1981. This survey covers most of the ice-free Barents Sea (Jakobsen *et al.*, 1997). Data from the second quarter were from a Russian survey that targets redfish and haddock and that covers only a part of the Barents Sea in May/June (Anon., 2006b). Data from the third quarter were from the Joint IMR–PINRO ecosystem survey (hereafter ecosystem survey) that covers the whole of the Barents Sea and has been run every August/September since 2003 (Anon., 2005). Data from the fourth quarter are from the Russian demersal survey (hereafter Russian demersal survey) covering most of the Barents Sea between October and December (Lepesevich and Shevelev, 1997; Anon., 2006b).

Trawl gear and towing time differed between surveys. On the winter survey, the towing time was 30 min and all vessels were equipped with a standard research bottom trawl, a Campelen 1800 shrimp trawl with 80 mm (stretched) mesh size in front, and a codend with 16–22 mm meshes. The horizontal opening of this trawl is 20 m, and the vertical opening 4–5 m. On the ecosystem survey, the same gear was used, but towing time was 15 min. The standard towing time in PINRO surveys is 60 min. Surveys in May/June used a standard 125-mm Russian research demersal trawl with a mesh size in the codend of 22 mm. The surveys from October to December used a standard 125-mm Russian research demersal trawl with a mesh size in the codend of 16 mm. The opening of the standard Russian research trawl was 24.5–25 m, and the vertical opening 6.5–7 m.

On IMR surveys, blue whiting stomachs were removed from the fish and frozen individually on board. Stomach contents were later analysed ashore, after thawing. On PINRO vessels, diet composition was analysed from fresh stomachs on board ship. Stomachs suffering clear regurgitation, e.g. when the stomachs were everted into the throat of the fish, were rejected for analysis. All stomach contents were studied under a binocular microscope. Prey were counted and identified to the lowest taxon possible, prey groups weighed to the nearest milligramme (wet weight), and prey length measured where feasible.

Analyses in which different surveys are compared may be confounded by differences in survey gear, procedures, and spatial coverage. However, we believe that this is not a problem for our analyses. In analyses of the catch rates of blue whiting (Heino *et al.*, 2008), changes in mesh size and tow duration did not have significant effects. The availability of blue whiting to bottom gear may vary with season, through seasonal differences in vertical distribution, but we are not aware of any studies or confirmed observations of seasonal variation in catchability.

Differences in towing time of 30–45 min should have a negligible effect on stomach content, because it takes 2–3 d for the Barents Sea cod to digest gammarids and 3–5 d to digest fish (Orlova and Matishov, 1993). Towing-induced regurgitation is only a minor problem in gadoids, but because we removed regurgitated stomachs from our analysis, this will not affect the diet data.

**Table 1.** The number of blue whiting stomachs analysed by year, quarter, and institution (IMR/PINRO).

| Year | First quarter | Second quarter | Third quarter | Fourth quarter |
|---|---|---|---|---|
| 1998 | – | – | – | 0/425 |
| 2000 | – | 0/127 | – | 0/360 |
| 2001 | – | 0/100 | – | 0/180 |
| 2002 | 33/0 | – | – | 0/50 |
| 2003 | – | – | – | 0/400 |
| 2004 | – | – | 0/219 | 0/301 |
| 2005 | 0/100 | 0/1 | 266/205 | 0/350 |
| 2006 | 46/0 | – | 0/771 | 0/205 |
| All years | 179 | 228 | 1 451 | 2 271 |

### Data analysis

We compared seasonal blue whiting distribution by mapping catch data from demersal trawl hauls from the winter surveys, the ecosystem surveys, and the Russian demersal surveys of 2003–2006. For these analyses, we excluded the survey data from the second quarter because of poor spatial coverage. We calculated catch rates from these surveys (fish per nautical mile towed) from a subarea covered by all surveys in all years. Additionally, we used acoustic data from the ecosystem survey to map spatial overlap among blue whiting, polar cod, capelin, and juvenile herring.

We characterized blue whiting diet using three indices. First, the total fullness index (TFI, in $10^4$ g cm$^{-3}$) was defined as $\text{TFI} = 10^4 \times W/L^3$, where $W$ is the total wet weight (g) of prey in the stomach and $L$ the blue whiting length (cm). Second, the proportion of total weight (PW) was defined as $\text{PW}_i = w_i/W$, where $w_i$ is the total wet weight (g) of the prey *i*. Finally, frequency of occurrence (FO) was defined as $\text{FO}_i = n_i/N$, where $n_i$ is the number of stomachs containing prey $i$ and $N$ the total number of stomachs. Logistic regression was applied when analysing FO.

Stomach samples from blue whiting were compared with similar samples from polar cod, juvenile herring, and capelin. We compared samples taken at the same time of year and from the same main Russian fishing areas, but not necessarily from the same trawling stations. Diet overlap between blue whiting and capelin, polar cod, and herring was calculated using the coefficient of diet similarity (CDS; Shorygin, 1952), defined as $\text{CDS} = 100 \times \Sigma_i \min(\text{PW}_{i,m}, \text{PW}_{i,n})/\Sigma_i \max(\text{PW}_{i,m}, \text{PW}_{i,n})$, where $\text{PW}_{i,m}$ and $\text{PW}_{i,n}$ are the average percentages by weight of prey $i$ in the diet of predators $m$ and $n$, respectively, in the samples being compared. Here, area-specific averages were used. CDS can vary between 0% (no similarity) and 100% (full similarity).

We also analysed diet data from potential predators of blue whiting. Dietary data for cod were obtained from the Joint IMR–PINRO stomach sampling programme on the same Norwegian and Russian survey listed above, and also on board Russian commercial fishing vessels (see Mehl and Yaragina, 1992, for detail of the sampling procedures). Data on other predatory fish were obtained from PINRO surveys as well as from commercial fishing vessels throughout the year and analysed on board using standard quantitative methods (as described above for stomachs of blue whiting). Thanks to the availability of a more comprehensive dataset for cod, we were able to test for the effects of season and cod length on the FO of blue whiting in cod stomachs, using data from the winter and ecosystem surveys of 2003–2006. We also tested for spatial overlap between small and large cod by correlating the log of the catch rate of blue whiting with that for cod from bottom trawls taken in the course of the winter and ecosystem surveys.

## Results

### Abundance and distribution of blue whiting

Annual mean catch rates (fish per nautical mile towed) for the winter survey (1984–2006), the ecosystem survey (2003–2006), and the Russian demersal survey (2003–2006) are depicted in Figure 1. The catch rates are not directly comparable across surveys because of differences in gear, tow duration, and possibly also seasonal availability of blue whiting to the bottom trawl (see above). With these caveats in mind, the data suggest that there are more blue whiting in the central Barents Sea in the third quarter of the year than in the first and fourth quarters. The data also show that blue whiting are most concentrated in the southwestern Barents Sea during the first quarter, then spread out and reach their broadest and most even distribution during the fourth quarter (Figure 2).

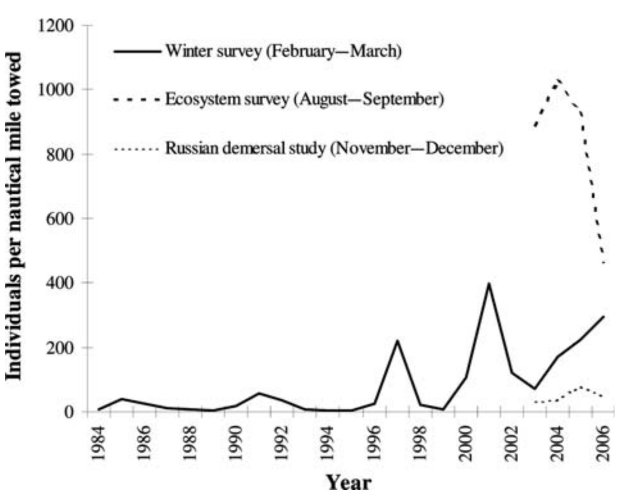


**Figure 1.** Blue whiting catch rate for the area 16.6–37.2°E and 70.2–73.9°N (see Figure 2) for the winter survey (solid line, years 1984–2006), the ecosystem survey (dashed line, years 2003–2006), and the Russian demersal survey (dotted line, years 2003–2006).

### Blue whiting diet

In all, 4165 non-everted stomachs of blue whiting were analysed, of which 1591 (38%) were empty. The diet is plotted on quarterly maps in Figure 3. The average size of the blue whiting analysed was 27 cm (range 13.7–45 cm), somewhat larger than the average size from the surveys (Figure 4). On average, stomach content made up 1.5% of the total body weight of the fish, and average TFI was 0.88 (all stomachs).

Prey from 54 species (or higher taxa) were found in the stomachs (Table 2). Crustaceans were found in 95% of the non-empty stomachs and constituted 39% of the total stomach weight (all stomachs pooled). Euphausiids (krill) were the most common crustaceans in the stomachs, found in 60% of stomachs that contained food, making up 27% of total stomach content. Only a small proportion of the euphausiids found in the stomachs was classified to species; two species were identified, *Thysanoessa inermis* and *Meganyctiphanes norvegica*, with the latter, larger species being more common (Table 2). Amphipods, mostly pelagic hyperiids, were the second most important group of crustaceans, and were found in 22% of the stomachs containing food, accounting for 7% of stomach content by weight. Copepods made up just 1% of stomach content weight and were found in <8% of the stomachs containing food. Other invertebrates accounted for <1% of total stomach content weight. Fish accounted for 60% of total stomach content weight, and fish prey were found in 24% of the non-empty stomachs. Gadoids were found in 9% of the stomachs containing food and made up 35% by weight. Surprisingly, polar cod, a cold-water species, was the most frequent fish prey in the stomachs. Blue whiting (cannibalism) were found in four stomachs.

Diet varied with location (Figure 3). In the central Barents Sea, smaller blue whiting fed mainly on zooplankton, in particular krill. Large blue whiting farther north and east preyed also on abundant pelagic fish (capelin, polar cod), as well as juveniles of other species. Polar cod was mostly found in the blue whiting caught west of Svalbard in the fourth quarter of the year (Figure 3). The intensity of feeding (measured as stomach fullness) also varied spatially and was highest at the limit of blue whiting distribution in the Barents Sea, in areas where the species fed on fish (Figure 3). In the areas with the greatest concentration of blue whiting, stomachs were less full and krill was the main prey (Figures 2 and 3).

The proportion of empty stomachs varied significantly by quarter (Table 3), being very high in the second quarter when 287 of the 456 stomachs examined were empty (63%). The proportion of empty stomachs was lowest in the third quarter (26%), whereas the proportion in the first and fourth quarters was intermediate (42 and 43%, respectively). The proportion of stomachs of blue whiting-containing fish varied significantly by season (Table 3, Figure 4) and was highest in the third and fourth quarters (10 and 18%, respectively), and lowest in the first and second quarters (3 and 2%, respectively).

The importance of fish prey increased with the size of blue whiting, but there was no obvious size threshold at which prey preference switched from invertebrates to fish (Table 3, Figure 5). Blue whiting 24 cm long (the average size caught in the surveys) included 42% fish and 41% krill in the diet by weight, whereas krill were more important in terms of FO. Blue whiting >30 cm had more than half their stomach weight of fish. TFI also increased with predator length (Table 3) and was positively correlated with

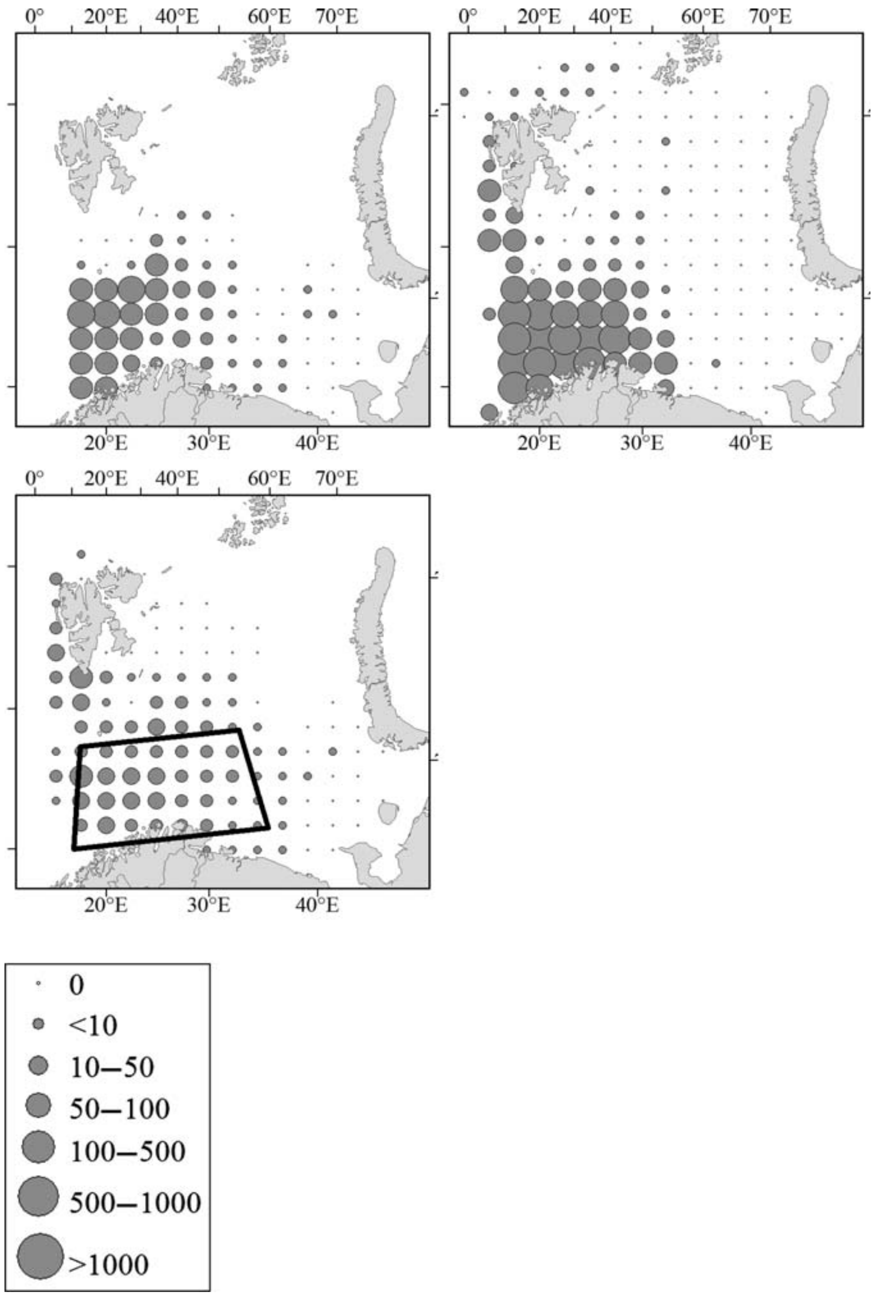


**Figure 2.** The number of individual blue whiting per nautical mile towed for the first quarter (winter survey: top left), the third quarter (ecosystem: top right), and the fourth quarter (Russian demersal survey: bottom left). The symbol size is proportional to the average values for grid cells of 100 × 100 nautical miles, based on the survey data from 2003 to 2006. The rectangle between 16.6° – 37.2°E and 70.2 – 73.9°N on the map for the first quarter shows the area used to calculate the catch rate in Figure 1.

FO ($r = 0.66$); stomachs containing the items of fish prey were fuller, so that larger blue whiting had fuller stomachs containing more fish prey (Table 3). There was no effect of fish length on the proportion of empty stomachs (Table 3).

## Diet and spatial overlap between blue whiting and other planktivorous fish

Several planktivorous fish species potentially compete with blue whiting for similar prey in the Barents Sea. The most abundant species are capelin, polar cod, and juvenile herring. Data from the joint Russian–Norwegian ecosystem surveys of 2003–2006 revealed spatial overlap with herring, capelin, and polar cod at the edge of the distribution of blue whiting (Figure 6), but in general, the distributions of these species were fairly distinct. Blue whiting overlapped with capelin and polar cod at the northern and eastern limits of the former's distribution in the Barents Sea, as well as along the west coast of Svalbard. Blue whiting and herring overlapped mainly in the southwestern Barents Sea (Figure 6).

Diet similarity between blue whiting and herring, capelin, and polar cod was greatest for blue whiting and capelin, with values of

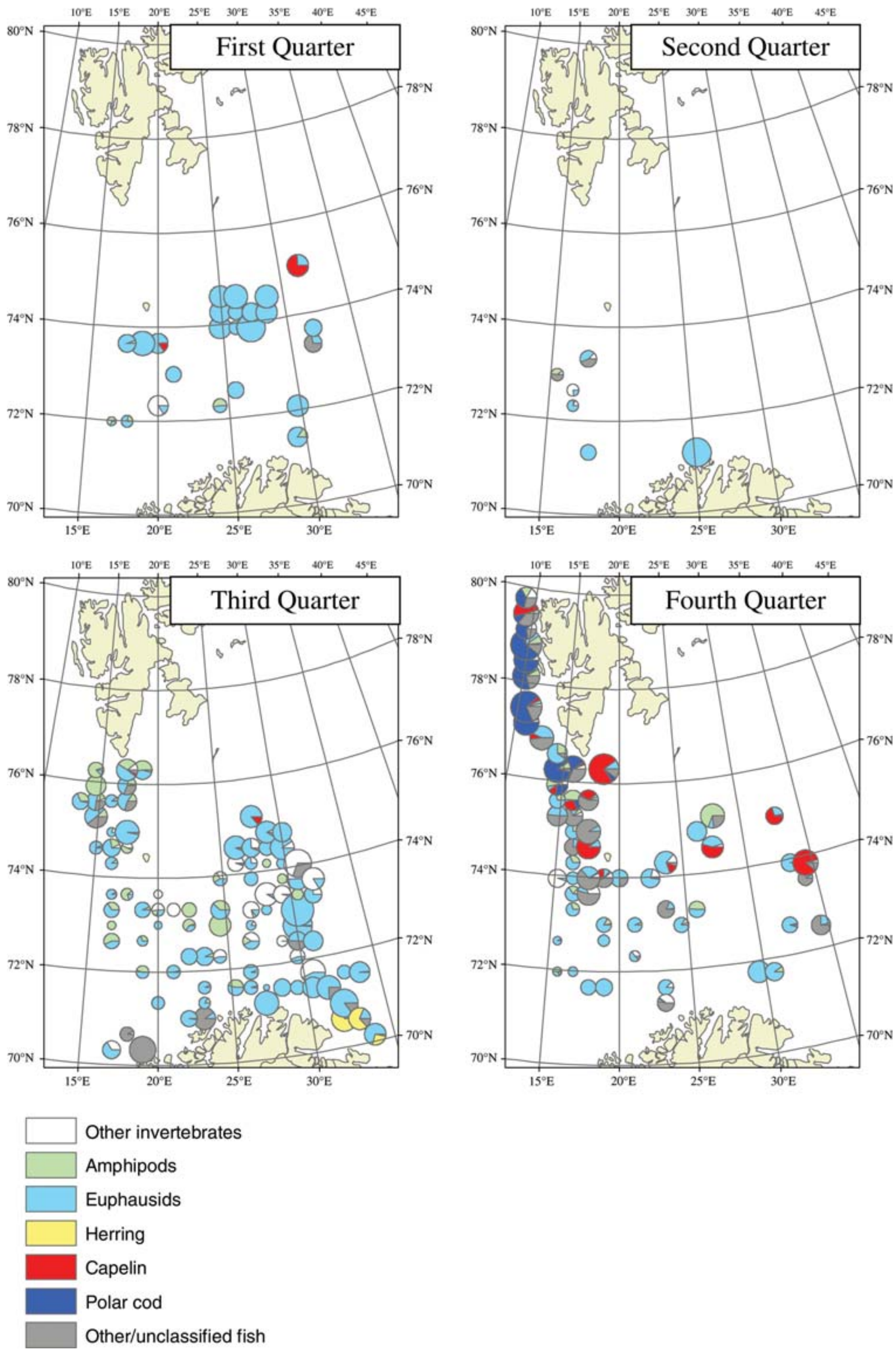


**Figure 3.** Blue whiting diet composition by quarter. Each pie represents the diet composition by weight in grid cells of 20 × 20 nautical miles. The size of the pie is proportional to the average TFI in the grid cell.

CDS reaching 65–86% in the Western Deep and on the eastern slope of Bear Island Bank (Figure 6, Table 4). Diet similarity was greatest where there was a large proportion of krill and smaller hyperiids in the diet of both species. The diets of blue whiting and of herring and polar cod were generally different, the values of CDS ranging from 8 to 27%.

## Blue whiting in the diets of predatory fish

Blue whiting were found in the stomachs of 9 of 15 predatory fish species analysed (Table 5). FO was highest in Arctic skate (*Amblyraja hyperborea*; 6.1%) and was ∼1% or more in five other species. Blue whiting contributed most to the diet of Greenland halibut (*Reinhardtius hippoglossoides*; 6.8% by

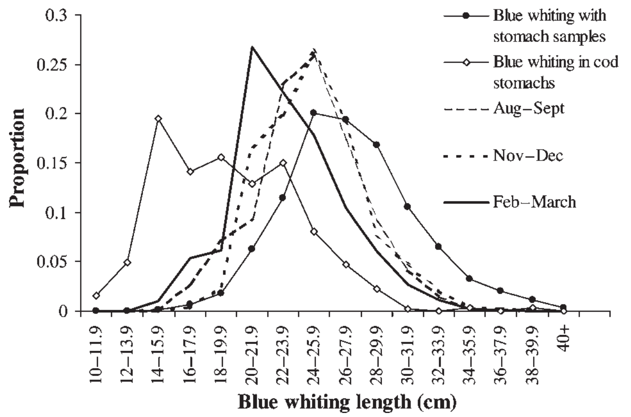


**Figure 4.** Length distribution of blue whiting with stomach samples, blue whiting in cod stomachs, and blue whiting in bottom-trawl catches in the winter, ecosystem, and Russian demersal surveys for 2003–2006.

weight), and the contribution exceeded 1% by weight in six other species. Feeding on blue whiting was spatially concentrated: blue whiting were mainly found in the stomachs of other species along the shelf edge (Figure 7).

Of the potential predators of blue whiting in the Barents Sea, cod are by far the most abundant. The blue whiting eaten by cod were on average smaller than those caught during the surveys (Figure 4). Blue whiting were only found in 0.6% of the stomachs of cod <50 cm (winter and ecosystem surveys of 2003–2006), but in larger cod (>50 cm), the percentage of stomachs containing blue whiting varied with season, and was 1.5% in the first quarter and 4% in the third quarter. In the areas with the greatest concentration of blue whiting, that species may constitute a large part of the diet of cod (Figure 7). However, blue whiting and cod have limited spatial overlap: there was no correlation between the catches of large cod (>50 cm) and blue whiting at a station level ($r = -0.05$, $p = 0.1$, $n = 4015$, winter and ecosystem surveys pooled). Moreover, small cod are found in



**Table 2.** FO and percentage by weight of total stomach contents of different blue whiting prey in the Barents Sea.

| Prey taxon | | | | |
|---|---|---|---|---|
| **Main group** | **Lowest available taxonomic level** | **Proportion of total weight (%)** | **FO (%)** | **Prey length (cm)** |
| Jellyfish | Scyphozoa | 0.01 | 0.05 | |
| Comb jellies | Ctenophora | 0.01 | 0.14 | |
| Gastropods | Limacinidae | 0.01 | 0.02 | |
| Cephalopods | Cephalopoda | 0.00 | 0.02 | |
| | Coleoida | 0.00 | 0.02 | |
| | Theutida | 0.32 | 0.07 | 7.0–7.9 |
| | Oegopsida | 0.37 | 0.14 | 5–5.9 |
| | *Gonatus fabricii* | 0.16 | 0.05 | |
| Crustaceans | Crustacea | 0.06 | 0.48 | |
| | Copepoda | 0.01 | 0.14 | |
| | Calanoida | 0.71 | 1.27 | |
| | *Calanus* sp. | 0.49 | 2.45 | |
| | *Calanus finmarchicus* | 0.00 | 0.05 | |
| | *Gaidius tenuispinus* | 0.00 | 0.02 | |
| | *Euchaeta* sp. | 0.00 | 0.07 | |
| | *Pareuchaeta norvegica* | 0.05 | 0.91 | |
| | Mysidae unidentified | 0.03 | 0.17 | |
| | Amphipoda | 0.01 | 0.07 | |
| | Gammaridea | 0.01 | 0.07 | |
| | Hyperiidea | 1.40 | 1.85 | |
| | *Parathemisto* sp. | 2.50 | 6.99 | 0.4–0.49 |
| | *Parathemisto libellula* | 1.74 | 2.83 | 2.5–2.9 |
| | *Parathemisto abyssorum* | 0.17 | 1.22 | 0.5–0.99 |
| | *Parathemisto gaudichaudi* | 0.00 | 0.02 | |
| | Euphausiidae unidentified | 28.1 | 36.3 | 3.0–3.9 |
| | *Meganyctiphanes norvegica* | 0.87 | 1.27 | 3.0–5.9 |
| | *Thysanoessa* sp. | 0.09 | 0.10 | 2.5–2.9 |
| | *Thysanoessa inermis* | 0.00 | 0.07 | |
| | Caridea | 0.81 | 1.13 | 2.0–7.9 |
| | *Pasiphaea* sp. | 0.10 | 0.02 | |
| | Pandalidae unidentified | 0.09 | 0.05 | |
| | *Pandalus* sp. | 0.24 | 0.14 | 5.0–10.9 |
| | *Pandalus borealis* | 1.98 | 1.63 | 3.0–10.9 |
| Arrow worms | Chaetognatha | 0.05 | 0.10 | |
| | *Sagitta* sp. | 0.00 | 0.05 | |
| Fish | Teleostei unidentified | 7.50 | 3.51 | |
| | *Clupea harengus* | 5.17 | 2.02 | |
| | *Mallotus villosus* | 10.3 | 2.09 | 6.0–16.9 |
| | *Maurolicus muelleri* | 0.01 | 0.02 | |

Continued

**Table 2.** *Continued*

| Prey taxon | | | | |
|---|---|---|---|---|
| **Main group** | **Lowest available taxonomic level** | **Proportion of total weight (%)** | **FO (%)** | **Prey length (cm)** |
| | Gadidae unidentified | 0.00 | 0.02 | |
| | *Boreogadus saida* | 30.3 | 4.80 | 3.0–13.9 |
| | *Gadus morhua* | 0.98 | 0.24 | 7.0–11.9 |
| | *Pollachius virens* | 0.13 | 0.02 | 10.0–10.9 |
| | *Melanogrammus aeglefinus* | 2.75 | 0.29 | 10.0–13.9 |
| | *Trisopterus esmarkii* | 0.62 | 0.12 | 11.0–11.9 |
| | *Micromesistius poutassou* | 0.42 | 0.10 | 7.0–8.9 |
| | *Sebastes* sp. | 0.44 | 0.31 | 4.0–5.9 |
| | Cottidae unidentified | 0.04 | 0.02 | 3.0–3.9 |
| | *Liparis* sp. | 0.01 | 0.02 | |
| | *Anarhichas* sp. | 0.01 | 0.02 | |
| | Stichaeidae unidentified | 0.15 | 0.12 | 6.0–7.9 |
| | *Lumpenus* sp. | 0.24 | 0.17 | |
| | *Leptoclinus maculatus* | 0.14 | 0.07 | 6–13.9 |
| | *Hippoglossoides platessoides* | 0.11 | 0.05 | |
| Indeterminate | n.a. | 0.33 | 1.49 | |

**Table 3.** Test statistics of the effect of blue whiting length and sampling quarter on TFI, FO of fish prey, and proportion of empty stomachs.

| | Length of blue whiting | | | | Quarter | |
|---|---|---|---|---|---|---|
| **Parameter** | ***F*-value** | ***p*-value** | **$\beta$-value** | **s.e.** | ***F*-value** | ***p*-value** |
| TFI | 18.6 | $<0.001$ | 0.03 | 0.01 | 1.96 | 0.12 |
| FO of fish prey | 108 | $<0.001$ | 0.14 | 0.01 | 4.07 | 0.01 |
| Proportion of empty stomachs | 0.04 | 0.84 | 0.00 | 0.01 | 15.0 | $<0.001$ |

Station and year are modelled as random factors. Estimated coefficients ($\beta$, with standard errors) for the effect of blue whiting length on TFI, FO of fish prey, and proportion of empty stomachs are also listed.

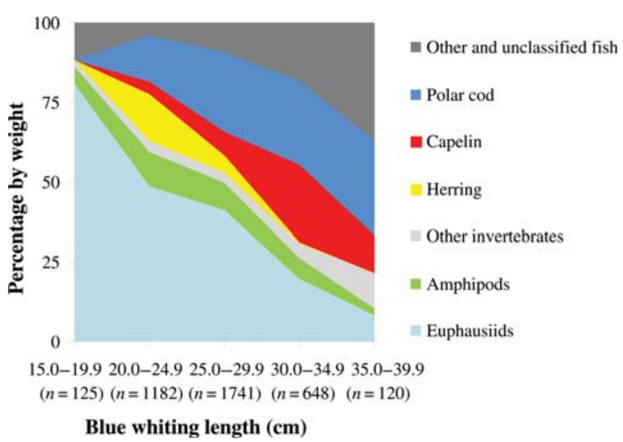


**Figure 5.** Percentage by weight of prey in the diet of blue whiting by 5-cm length group, with sample sizes on the *x*-axis.

the more shallow eastern parts of the Barents Sea, and catches of cod ($<$50 cm) correlated negatively with catches of blue whiting ($r = -0.2$, $p < 0.0001$, $n = 4015$).

## Discussion

Our work was motivated by the recent dramatic increase in the abundance of blue whiting in the Barents Sea (Heino *et al*., 2008), although the latest observations (Anon., 2007, 2009) seem to indicate that the abundance is now declining. Blue whiting have periodically been common in the Barents Sea before the recent increase (e.g. in the 1930s: Boldovsky, 1939; Zatsepin and Petrova, 1939). The increased abundance seen from around 2000 seems to have been caused primarily by the presence of enhanced numbers of juveniles (aged 1–4 years) migrating from the Norwegian Sea (Varne and Mork, 2004; Heino *et al*., 2008). After reaching maturity (at 2–4 years old), most Atlantic blue whiting probably migrate back out of the Barents Sea to spawn and do not return. Therefore, blue whiting are ecologically more similar to Norwegian spring-spawning herring, another highly migratory pelagic fish, than to the resident capelin and polar cod. One consequence of the increased abundance of juvenile blue whiting may then be an increased net transportation of production out of the Barents Sea when they mature. Population genetic studies suggest that there is also a local resident population in the Barents Sea (Giæver and Stien, 1998; Varne and Mork, 2004; Ryan *et al*., 2005), but this population is and probably always has been relatively small.

Our results suggest that krill are the most regular prey of blue whiting in the Barents Sea, agreeing with the results of earlier studies (Zilanov, 1968, 1982). Krill are the main prey of blue whiting throughout its range: in the Norwegian Sea, in the areas around Iceland, Greenland, and Ireland, and on the Porcupine and Rockall Banks and the Flemish Cap (Zilanov, 1968, 1982; Dumke, 1983), as well as in the Skagerrak (Degnbol and Munch-Petersen, 1985), in the Norwegian Deep (Bergstad, 1991), and off Portugal (Cabral and Murta, 2002). Zilanov (1968, 1982) compared the diets of blue whiting in the Barents and the Norwegian Seas, and found that pelagic hyperiids and krill were equally important prey in both areas, but that fish were more important in the Barents Sea and copepods in the Norwegian Sea. This finding agrees with our results. However, we found copepods in just 0.05% of the stomachs, whereas studies from the Norwegian Sea have reported

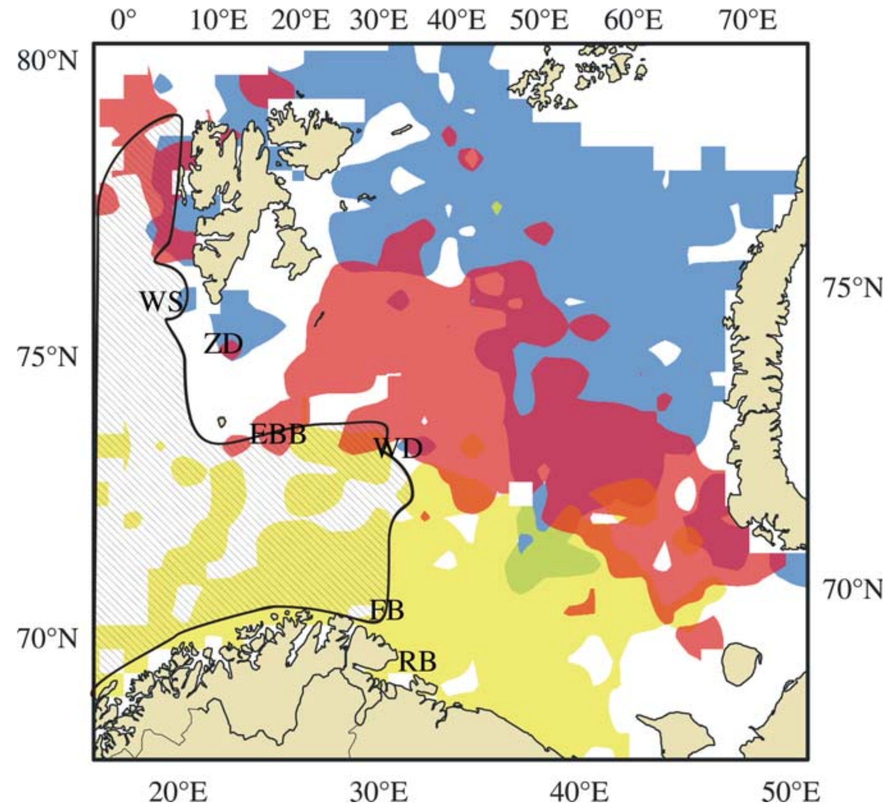


**Figure 6.** Interpolated acoustic registrations from the joint IMR–PINRO ecosystem surveys of 2003–2006. Acoustic densities ($s_A > 10$ m$^2$ nautical mile$^{-2}$) of blue whiting (hatched), capelin (red), polar cod (blue), and herring (yellow). The areas where stomach samples for diet overlap were taken (Table 4) are noted: Western Spitsbergen (WS), Zuidkap Deep (ZD), eastern slope of the Bear Island Bank (EBB), Western Deep (WD), Finmarken Bank (FB), and Rybachya Bank (RB).

**Table 4.** CDS between blue whiting and herring, capelin, and polar cod.

| Area and date | Stomach numbers (bw/h/c/pc) | Coefficient of diet similarity (%) | | |
|---|---|---|---|---|
| | | Herring | Capelin | Polar cod |
| Finmarken Bank (FB, August 2006) | 178/44/0/0 | 7.6 | – | – |
| Rybachya Bank (RB, August 2006) | 50/87/0/0 | 16.1 | – | – |
| Western Spitsbergen (WS, November 2003) | 50/0/0/25 | – | – | 7.7 |
| Zuidkap Deep (ZD, September 2005) | 150/0/50/50 | – | 14.8 | 16.9 |
| Zuidkap Deep (ZD, November 2005) | 50/0/50/0 | – | 44.4 | – |
| Zuidkap Deep (ZD, September 2006) | 50/0/74/150 | – | 20.3 | 27.5 |
| Western Deep (WD, August 2006) | 44/0/66/0 | – | 77.5 | – |
| Western Deep (WD, September 2006) | 161/0/132/0 | – | 65.1 | – |
| Eastern slope of the Bear Island Bank (EBB, August 2006) | 100/0/100/0 | – | 6.4 | – |
| Eastern slope of the Bear Island Bank (EBB, September 2006) | 11/0/119/0 | – | 86.3 | – |

The areas sampled are shown in Figure 6. Sample sizes are given in the second column for each species; bw, blue whiting; h, herring; c, capelin; pc, polar cod.

*C. finmarchicus* in up to 97% of stomachs (Prokopchuk and Sentyabov, 2006). We also found that blue whiting fed to a large extent on fish, the most important species being polar cod. Blue whiting also took a large proportion of mesopelagic and demersal fish. The latter is perhaps surprising, given that blue whiting are usually regarded as mesopelagic. However, the Barents Sea is a shallow shelf sea, where blue whiting can best be described as bentho-pelagic. It is known from other areas of the North Atlantic that blue whiting are mainly found at depths beyond 200–300 m (Monstad, 2004), which corresponds to the bottom depths in the areas where blue whiting are found in the Barents Sea.

There are large seasonal differences in the catch rates of blue whiting in the Barents Sea, with more taken in summer/autumn than winter. This must reflect a seasonal difference either in catchability or in the abundance of the species (see above). The wider and more even distribution in the second half than in the first half of the year suggests that a large proportion of the Barents Sea stock of blue whiting is continuous with the Norwegian Sea stock and that the stock contracts and expands into the Barents

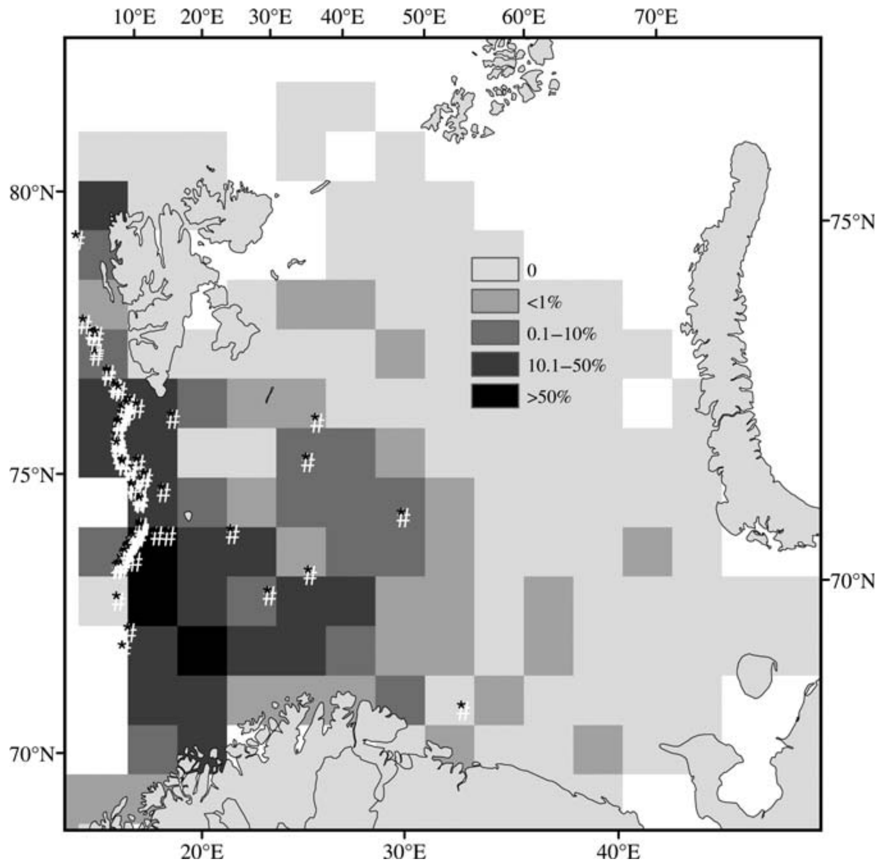


**Figure 7.** Percentage by weight of blue whiting in cod diet by 100 × 100 km grid cells. Data are from the winter and ecosystem surveys of 2003–2006. The white symbols represent the observations of blue whiting in the diet of other predatory fish from 2003 to 2006.

**Table 5.** Blue whiting in the diet of predatory fish in the Barents Sea, 2003–2006.

| | Importance of blue whiting | | |
|---|---|---|---|
| **Predator fish species** | **Proportion of total weight (%)** | **FO (%)** | **Number of stomachs investigated** |
| Greenland halibut (*Reinhardtius hippoglossoides*) | 6.8 | 1.5 | 14 142 |
| Arctic skate (*Amblyraja hyperborea*) | 6.6 | 6.1 | 197 |
| Thorny skate (*Amblyraja radiata*) | 6.0 | 2.0 | 1 860 |
| Saithe (*Pollachius virens*) | 4.5 | 0.8 | 3 328 |
| Cod (*Gadus morhua*) | 2.9 | 1.0 | 58 439 |
| Blue skate (*Dipturus batis*) | 1.4 | 5.0 | 20 |
| Northern wolffish (*Anarhichas denticulatus*) | 0.09 | 0.2 | 531 |
| Spotted wolffish (*Anarhichas minor*) | 0.06 | 0.1 | 1 638 |
| Haddock (*Melanogrammus aeglefinus*) | 0.02 | 0.1 | 27 627 |
| Long rough dab (*Hippoglossoides platessoides*) | 0 | 0 | 8 854 |
| Deepwater redfish (*Sebastes mentella*) | 0 | 0 | 4 691 |
| Striped wolffish (*Anarhichas lupus*) | 0 | 0 | 828 |
| Golden redfish (*Sebastes marinus*) | 0 | 0 | 801 |
| Round skate (*Rajella fyllae*) | 0 | 0 | 37 |
| Spinetail skate (*Bathyraja spinicauda*) | 0 | 0 | 26 |

Sea as part of its seasonal feeding migration, or in response to seasonal changes in ocean climate. The Barents Sea can therefore be regarded as part of the oceanic feeding grounds of blue whiting (Zilanov, 1984). We also found seasonal differences in diet, some of which can be attributed to differences in the spatial survey coverage between seasons. For instance, we found more fish in the diet in the fourth quarter, which was due to the high prevalence of polar cod in the stomachs of blue whiting along the west coast of Svalbard, an area only surveyed at that time of year. The large proportion of empty stomachs in the second quarter might be an artefact of the limited spatial coverage then. The lowest proportion of empty stomachs was in the third quarter. The stomachs also appeared to be full in this quarter, especially along the Polar Front. This seasonal pattern is also typical of capelin and polar cod in the Barents Sea (Shleinik and Borkin, 1986; Orlova *et al.*, 2004). High feeding intensity and an aggregation of predators feeding on zooplankton and pelagic fish along the Polar Front are well-known phenomena in the Barents Sea in summer (Belopolskii, 1979; Mehlum *et al*., 1998) and in other areas (Franks, 1992). Interestingly, the period with the greatest proportion of empty stomachs in the Barents Sea (spring) corresponds to the time when blue whiting in the Norwegian Sea feed most intensely on copepods (Monstad, 2004; Prokopchuk and Sentyabov, 2006). There is a seasonal difference in the availability of *C. finmarchicus* between the two areas. The Norwegian Sea is the main spawning area of *C. finmarchicus*, whereas most of the *C. finmarchicus* in the Barents Sea are advected into the area (Dalpadado *et al*., 2003). Feeding migrations of blue whiting, extending further into the Barents Sea in late summer/autumn and retracting in late winter/spring, might be a response to the seasonal dynamics of copepod blooms in spring in the Norwegian Sea and the high productivity along the front in the Barents Sea in late summer.

Despite the limited overlap between blue whiting and the other pelagic species in the Barents Sea, food competition from blue whiting may still be important. Krill being transported into the Barents Sea from the Norwegian Sea have to pass through the "filter" of blue whiting feeding on them in the southwestern Barents Sea, so the quantity of krill available to other krill-feeders in the central and eastern Barents Sea could be reduced. Limited krill availability could in turn influence the energetic condition of pelagic species in the Barents Sea. However, we have no data to support this suggestion.

Cod are the main predator in the Barents Sea and the only fish predator whose consumption of prey is estimated annually (ICES, 2007a). However, although the estimated consumption of blue whiting by cod has increased in proportion to the increase in abundance of blue whiting in the Barents Sea, from 2004 to 2006 blue whiting made up on average just 3% of the total biomass consumed by cod (B. Bogstad, pers. comm.). In some local areas (especially in the southwestern Barents Sea), blue whiting are an important constituent of cod diet, contributing up to half the diet (by weight) during short periods. In general, however, the average contribution of blue whiting to the diet of cod is small owing to the restricted overlap in distribution of the two species, and size-dependence in predation limiting the consumption of blue whiting to larger cod only. Blue whiting were found in the stomachs of other predatory fish, mainly along the edge of the continental shelf, as previously observed by Zatsepin and Petrova (1939). Blue whiting have been documented in the diet of many species of fish in the Barents Sea in the Russian literature (Zenkevich and Brotskaya, 1931; Komarova, 1939; Zatsepin and Petrova, 1939; Boldovsky, 1944; Antipova and Kovtsova, 1982; Berestovsky, 1989; Antipova and Nikiforova, 1990; Shvagzhdis, 1990; Dolgov, 2000). All these studies suggested that, in general, blue whiting play a minor role in the diet of various predators, agreeing with our results here. Both our study and all those mentioned above indicate that blue whiting is not a major prey species in the Barents Sea, even when its abundance is high. Limited spatial overlap between blue whiting and potential predators might be an important explanatory factor. Blue whiting might also be a less preferred prey than species such as herring and capelin. Blue whiting is a lean fish, with a low fat content (2–6% in wet tissue; Björnsson, 2001), especially compared with herring (10–15%; Björnsson, 2001) and capelin (8–17%, L. Konstantinova, PINRO, unpublished data). Size may also play a role because the average blue whiting sampled was 24 cm, implying that a cod (or similar predator) would have to be >50 cm long to eat it (Bogstad *et al*., 1994). Cod preyed on blue whiting below the average size found in surveys. We believe that this pattern arises from the constraints that prey size set on predator size because we are not aware of spatial patterns in blue whiting and cod sizes that could explain it. Indeed, large cod fed on both small and large blue whiting, whereas smaller cod only fed on smaller blue whiting (Norvillo, 1989). Therefore, the predation pressure on blue whiting of average size or larger appears to be relatively low.

In conclusion, krill are the most important prey of blue whiting in the Barents Sea. Our results agree well with findings on blue whiting diet in the Barents Sea in the 1960s and 1970s, and corroborate these findings when it comes to the difference in blue whiting diet in the Norwegian and Barents Sea, with less copepods and more fish in the diet in the Barents Sea. The ecological significance of blue whiting seems to be moderate in the Barents Sea. The increased abundance of blue whiting in the Barents Sea in the early 2000s was probably the result of an increase in the northern component of the oceanic stock, which migrates out of the Barents Sea to spawn west of the British Isles, probably never to return. There is limited predation on blue whiting in the Barents Sea. Our results therefore suggest a scenario in which the increased abundance of blue whiting of Atlantic origin channels more of the production in the Barents away from that ecosystem, with less production being channelled up the local food chain.

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