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The role of capelin (*Mallotus villosus*) in the foodweb of the Barents Sea

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Based on Barents Sea fish stomach content data for the years 1984–2000, the role of capelin, *Mallotus villosus* (Müller), as prey for various fish predators is evaluated. Capelin are consumed by more than 20 fish species, both commercial and non-target. Their importance to different length-classes of fish predator, and the interannual, seasonal, and spatial dynamics of predation, are discussed. The extent of predation by cod, haddock, Greenland halibut, long rough dab, and thorny skate is calculated. The main predator of capelin is Atlantic cod, which consumed 220 000–3 200 000 t annually, and the second most important, the harp seal.

Keywords: Barents Sea, capelin, cod, consumption, feeding.

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Introduction

The capelin, *Mallotus villosus* (Müller), is one of the most important prey items for many species of marine fish (e.g. cod, haddock, long rough dab, redfish) in the Barents Sea, a fact discovered long ago (Zenkevich and Brotskaya, 1931; Komarova, 1939; Zatsepin, 1939; Zatsepin and Petrova, 1939; Boldovsky, 1944). However, the importance of capelin in the foodweb, and as prey of cod in particular, varies from year to year as a result of fluctuations in capelin biomass and variability in hydrographic conditions (Zatsepin and Petrova, 1939; Grinkevich, 1957).

The capelin stock virtually crashed twice during recent decades, and changes in the trophic structure of the Barents Sea caused by such a reduction in biomass emphasized the necessity for more detailed study of the role of capelin in the foodweb. Therefore, the objectives of this paper are to determine the most important predators of capelin, and the sizes of predators and prey, to examine interannual, seasonal, and spatial trends in consumption of capelin, and to estimate the extent of consumption of capelin by the different predators.

Material and methods

Data on the food of cod and haddock in the Barents Sea for the period 1984–2000 were drawn from the joint Russian–Norwegian database. For other fish (long rough dab, Greenland halibut, skates, saithe, etc) for the period 1980–2000 and for non-target fish for the years 1998, 2000, and 2001, data were collected by the Polar Research Institute for Fisheries and Oceanography (PINRO). In all these data, the position of capture of predators and the total length (cm) of the capelin prey are given. To evaluate the importance of capelin as food, a percentage by weight of the food bolus (%w), and a percentage frequency of occurrence (%fo, calculated as the percentage of the total number of fish feeding) were calculated.

Information on capelin biomass was obtained from the proceedings of the ICES Northern Pelagic and Blue Whiting Fisheries Working Group (ICES, 2001a). Data on the abundance, mean weight, and natural and fishing mortality by age of cod, haddock, and Greenland halibut were derived from the ICES Arctic Fisheries Working Group (ICES, 2001b). Abundance, biomass, and mean weights of long rough dab and thorny skate were taken from the literature (Dolgov, 1997; Dolgova and Dolgov, 1997).

Food consumption by predator species was estimated separately by quarter, for the whole Barents Sea. For cod, haddock, and Greenland halibut, the mean weight and mean abundance of each predator age-class by quarter, taking natural and fishing mortality into account, were determined. Cod daily ration was

Table 1. Capelin importance in the food of the most abundant fish species in the Barents Sea during the 1980s and 1990s.

Predator species	Number of stomachs	Importance of capelin (%w)*	Size of capelin consumed (cm)	Investigation period
Cod, *Gadus morhua*	140 320	28.8	Eggs, larvae, 6–20.9	1984–2000
Haddock, *Melanogrammus aeglefinus*	22 267	9.6	Eggs, larvae, 6–20.9	1984–1999
Long rough dab, *Hippoglossoides platessoides*	5 691	21.0	8–18.9	1994–2000
Thorny skate, *Raja radiata*	1 947	5.1	6–17.9	1994–2000
Round skate, *Raja fyllae*	85	2.9	15–19.9	1996–2000
Arctic skate, *Raja hyperborea*	31	0		1989–1999
Sail ray, *Raja lintea*	6	0		1997–2000
Blue skate, *Raja batis*	39	0		1996–2000
Greenland halibut, *Reinhardtius hippoglossoides*	8 110	4.9	7–20.9	1990–2000
Deepwater redfish, *Sebastes mentella*	2 139	41.1		1991–2000
Golden redfish, *Sebastes marinus*	363	24.4	10–15.9	1988–2000
Saithe, *Pollachius virens*	323	57.3	9–18.9	1991–2000
Blue whiting, *Micromesistius poutassou*	912	20.1	6–16.9	1998–2000
Capelin, *Mallotus villosus*	3 557	0.23	4–4.9	1980–1999
Atlantic herring, *Clupea harengus*	1 903	0.3	5–6.9	1984–1998
Polar cod, *Boreogadus saida*	2 423	1.1	4–12.9	1986–1999

*%w = percentage by weight of the food bolus.

calculated using the model of dos Santos (Bogstad and Mehl, 1997) on the basis of water temperature, cod mean weight, mean weight of stomach contents and of some prey species, and evacuation rates of prey species. Data on the seasonal dynamics of daily ration for different age-classes of long rough dab were taken from Berestovsky (1995). The daily ration of haddock, Greenland halibut, and thorny skate was taken as 1% of the body weight, i.e. corresponding to data published on the maximum ration for those species (respectively Berestovsky, 1991; Podrazhanskaya and Chumakov, 1989; Berestovsky, 1989). For haddock, Greenland halibut, long rough dab, and thorny skate, the food composition by age (haddock) or 5-cm length-class (other species), expressed as a percentage by quarter, was determined.

Results

Predators

Capelin were recorded in the food of 13 of the most abundant and commercial fish species during the 1980s and 1990s (Table 1). It was seemingly an important prey item of saithe, Greenland halibut, redfish, haddock, blue whiting, and long rough dab, but it was extremely important (both %w and %fo) as food for cod. Pelagic fish species (capelin, herring, and polar cod) also preyed on capelin, but the percentages were low. Further, capelin were eaten by small, non-commercial fish. Overall, according to stomach content data collected by PINRO during a recent period of bottom fish surveys (autumn and winter of 1998, 2000, and 2001), capelin were preyed on by seven of 20–25 non-commercial fish species caught from the families Liparidae, Cottidae, Psychrolutidae, Zoarcidae, and others (Table 2). Of note is the fact that the maximum sizes of Atlantic hook-ear sculpin and mailed sculpin are smaller than that of capelin (13 and 17 cm respectively).

The body length by which predatory fish start to consume capelin is different for different species, and is connected with species-specific morphological features. Cod start feeding on capelin at a length of 5–10 cm. The importance of capelin as prey to cod 25–90 cm is virtually uniform across the length-classes, but it is less for fish of length <25 and >90 cm (Figure 1). Most other fish predators commenced feeding on capelin at a length of 20–25 cm, but capelin (cannibalism) and saithe started at a length of 13 cm. Capelin importance as prey tended overall to increase with increasing predator length for most of these fish predators, but as for cod, the importance decreased sharply at the top end of the predator size spectrum.

Size selectivity

The size of capelin in the stomachs of the different predators was similar (Figure 2), fish 10–17 cm long dominating the prey. There was no obvious change in capelin size composition with increasing predator length.

Spatial and temporal dynamics of fish preying on capelin

The fish species analysed displayed clear interannual, seasonal, and local trends in the importance of capelin as prey.

Table 2. Capelin importance in the food of non-target fish in 1998, 2000, and 2001.

Predator species	Number of stomachs			Importance of capelin (%w)*		
	1998	2000	2001	1998	2000	2001
Sea tadpole, *Careproctus reinhardtii*	151	145	28	3.08	4.74	0
Variegated snailfish, *Liparis gibbus*	67	15	8	19.78	0	0
Arctic eelpout, *Lycodes reticulatus*	55	4	4	2.24	0	0
Esmark's eelpout, *Lycodes esmarkii*	42	40	50	0	0	64.79
Arctic rockling, *Gaidropsarus argentatus*	8	5	3	62.50	0	0
Atlantic hook-ear sculpin, *Artediellus atlanticus*	138	293	41	0	24.30	0
Moustached sculpin, *Triglops murrayi*	153	157	42	0	39.59	0

*%w = percentage by weight of the food bolus.

For the years 1984–2000, the relationship between capelin stock size and their importance in the food of different fish species in the Barents Sea (Figure 3) was well defined. In periods of growth of the capelin stock (1989–1992 and 1998–2000), their role as prey increased. When the capelin biomass was diminishing (1985–1988 and 1993–1997), their role as prey dropped, even to the extent that no capelin were found in the stomachs of some fish species. However, even in such years of low abundance, capelin still contributed no less than 8–10% of bolus weight of cod.

There were also obvious seasonal trends in consumption of capelin by certain fish species (Figure 4). Predation by cod and long rough dab peaked in spring (February–April) and, less intensively, in autumn (August–October). Haddock fed on capelin almost exclusively in spring (March–May), and Greenland halibut in autumn and winter (October–December). However, there was no clear seasonal signal in the thorny skate/capelin trophic interaction.

Spatial variations in cod predation on capelin were pronounced (Figure 5). In February, capelin were consumed over a wide area from Norway to Murman, but in March and April, predation was concentrated along the coast, where the capelin were spawning. Throughout summer, capelin were preyed on by cod extensively throughout the Barents Sea, but by September/October, cod predation on capelin was apparently restricted to the Bear Island–Spitsbergen area. Haddock preyed on capelin primarily in spring and summer on the capelin spawning grounds along the Murman and Norwegian coasts, but capelin were found in haddock stomachs throughout the study area. Similar preferences for capelin were shown by saithe, but Greenland halibut consumed capelin mainly in the open water of the Barents Sea, where capelin congregated to feed.

Consumption of capelin

The calculated consumption of capelin by the abundant fish species is listed in Table 3. Cod were the biggest predators, annually (1984–2000) consuming 0.2–3.5×10^6 t (mean, 1.23×10^6 t). Other fish species consumed less capelin, on average between 9000 t (thorny skate) and 79 000 t (haddock) annually.

Analysis of capelin in cod stomachs revealed that capelin aged 2–4 years (up to 80% of the total biomass of capelin consumed) dominated, but that 1–3-year-old capelin (up to 85% of the total abundance) were targeted (Figure 6). Although cod aged 2–9 years consume capelin, most predation was effected by cod aged 3–6 years (Figure 7).

Discussion

Capelin are preyed upon by many species of marine organism in the Barents Sea, at least 21 species of fish alone. Previous investigations have shown the importance of capelin as food for those same fish species (Table 4). Practically all the most abundant fish consume capelin.

Of the 37 seabird species typical of the coastal and open Barents Sea that feed in coastal or open ocean waters (Anon., 2000b), capelin has been recorded in the prey of 18 (Table 5), including some that usually feed in freshwater reservoirs near the coast.

Of the seven species of pinniped in the Barents Sea (Anon., 1980), capelin are preyed upon by bearded *Erignathus barbatus* (Chapsky, 1938), ringed *Phoca hispida*, and harp seals *Phoca groenlandica* (Anon., 1980), but most intensively by harp seals (Nilssen *et al.*, 2000). Capelin are eaten by eight out of a total of 18 cetacean species found in the Barents Sea (Anon., 1980), namely white *Delphinapterus leucas*, minke *Balaenoptera acutorostrata*, sei *Balaenoptera borealis* (Anon., 1980), fin *Balaenoptera physalus* (Klumov, 1963), humpback *Megaptera novaeangliae* (Klumov, 1963; Anon., 1980), and killer whales *Orcinus orca* (Anon., 1980), and harbour porpoise *Phocoena phocoena* (Tomilin, 1962) and Atlantic white-sided dolphin *Lagenorhynchus albirostris* (Kondakov and Mishin, 1999). However,

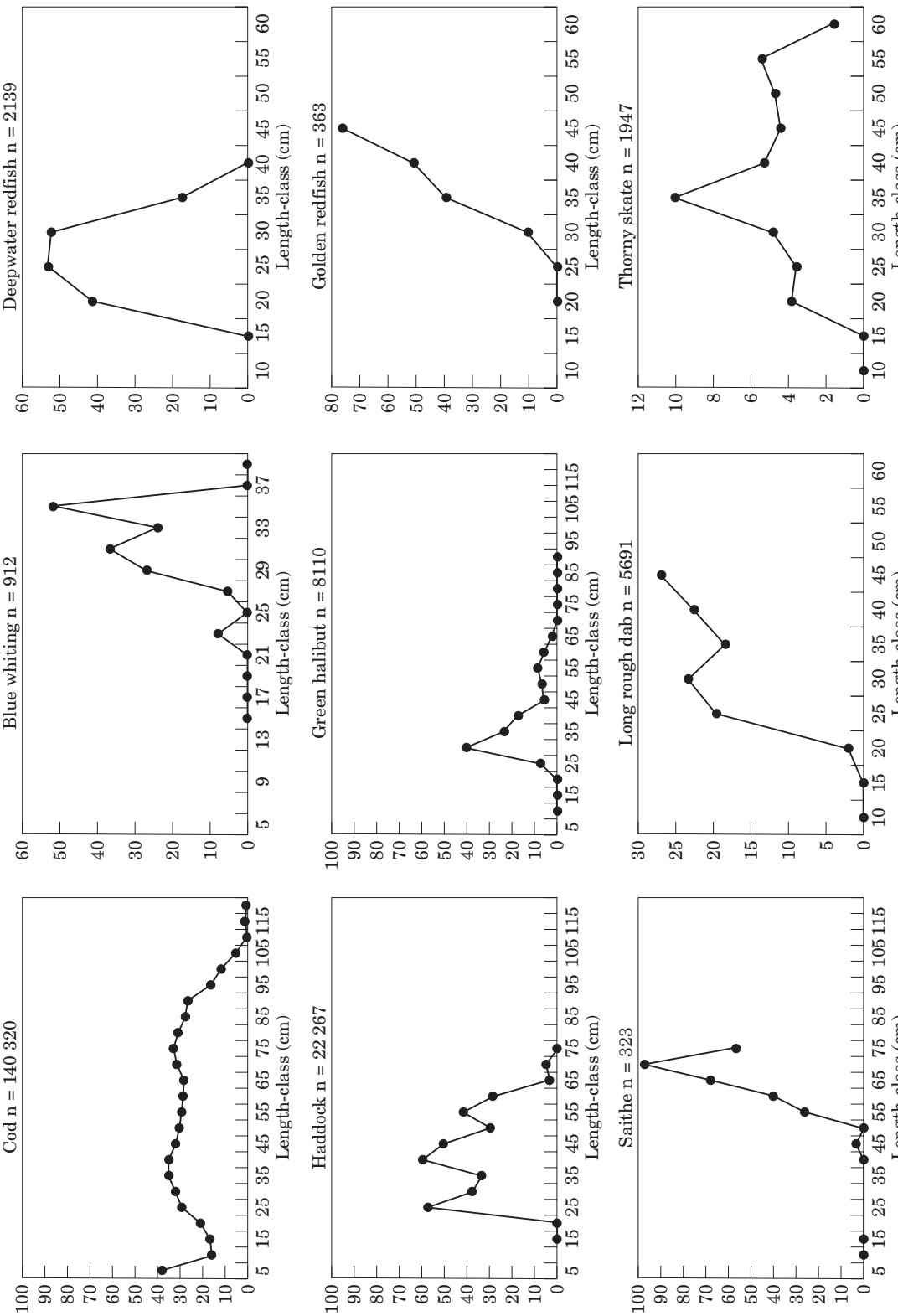

Figure 1. Capelin importance in the food of predatory fish of different length. Vertical axes are not to the same scale.

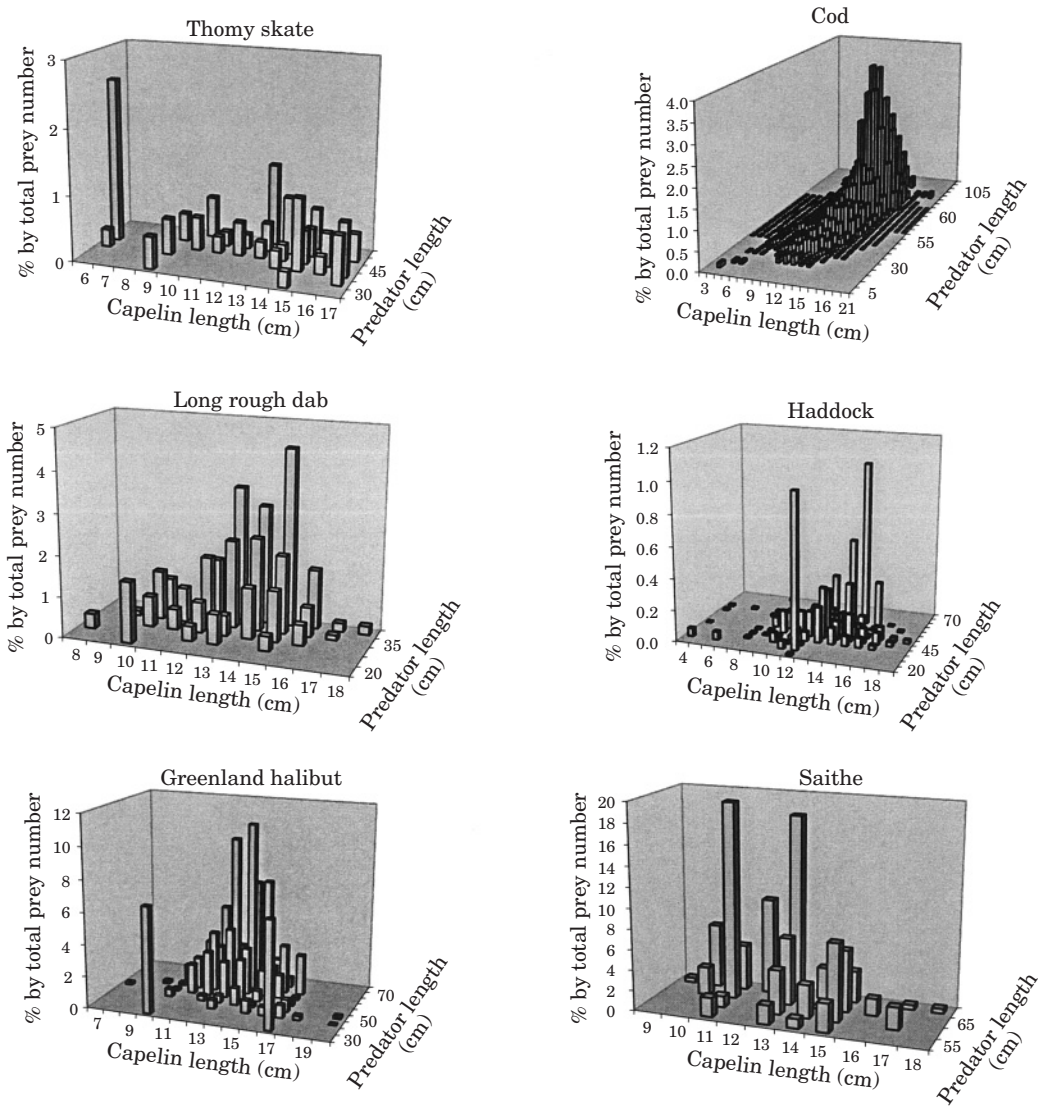

Figure 2. Length distribution of capelin in the stomachs of predatory fish.

with the exception of minke whale and harp seal, detailed quantitative data on feeding by marine mammals in the Barents Sea are not available.

Capelin are vulnerable to predation throughout their life. In the spawning areas, capelin eggs are actively consumed by haddock (Zatsepin, 1939) and other fish, as well as by birds (eider, spectacled eider, and long-tailed duck; Gjøsæter and Sætre, 1974; Anon., 2000b). Capelin larvae are eaten by herring (Huse and Toresen, 2000), cod, and haddock (Tables 1, 3). The small size of capelin, no more than 22 cm (Anon., 1991), makes all size-classes available to predators. Capelin taken by guillemot and puffin (the latter for their chicks) off Norway were between 10–14 cm (Barrett and Furness, 1990; Barrett and Krasnov, 1996) and 13–16 cm (Erikstad and Vader, 1989), and 8–12 cm long (Barrett *et al.*, 1987) respectively. Data on capelin size composition are not usually given in papers dealing with predation patterns of marine mammals in the Barents Sea, but Lindstrøm and Haug (2000) noted that minke whale were eating capelin 11–19 cm long. It may therefore be assumed that marine mammals feed primarily on capelin of that size.

Capelin are preyed on by many fish species once those fish have reached a length of 20–25 cm, but on the whole, capelin are targeted by few fish species throughout the year. Most fish species dwelling off the coasts of Norway and Murman (e.g. haddock, saithe) or on the continental slope (redfish), feed on capelin almost exclusively in spring (usually March–April), during the

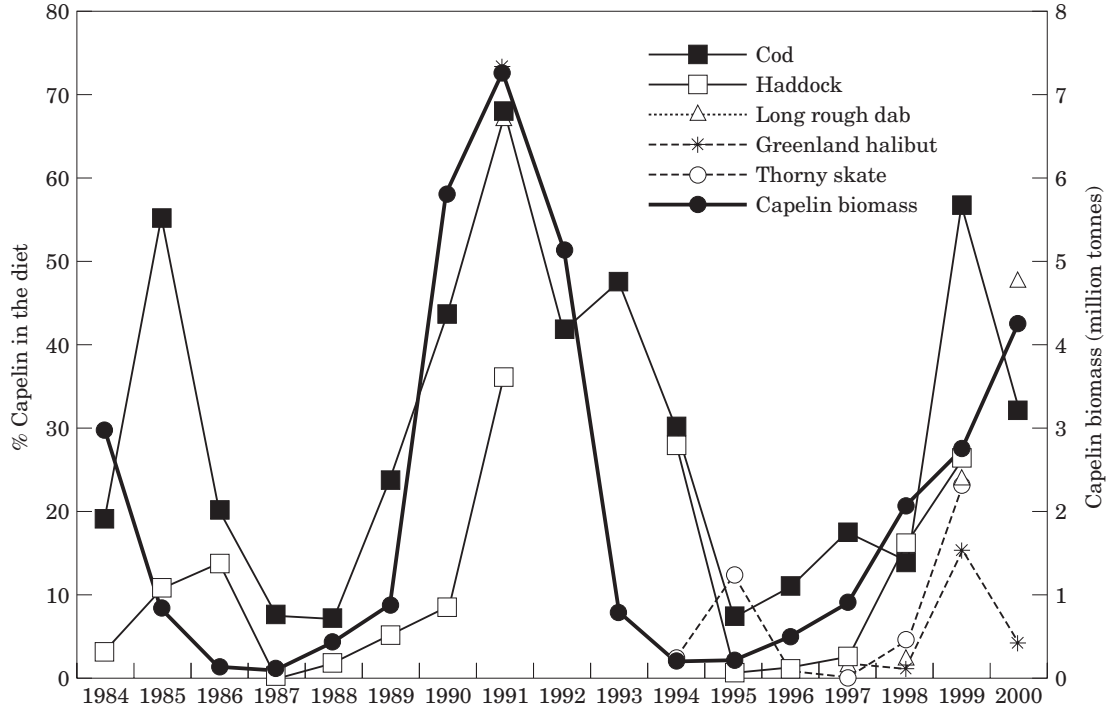

Figure 3. Capelin stock size and their importance in the food of predatory fish, 1984–2000.

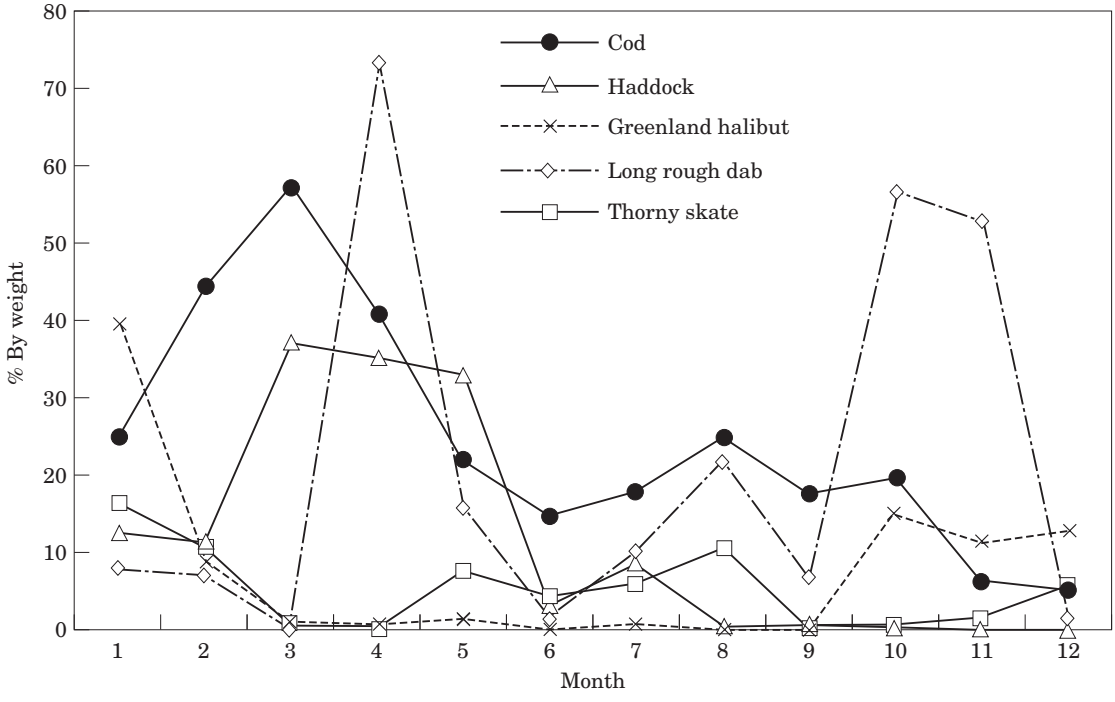

Figure 4. Seasonal dynamics of capelin importance in the food of predatory fish, 1984–2000.

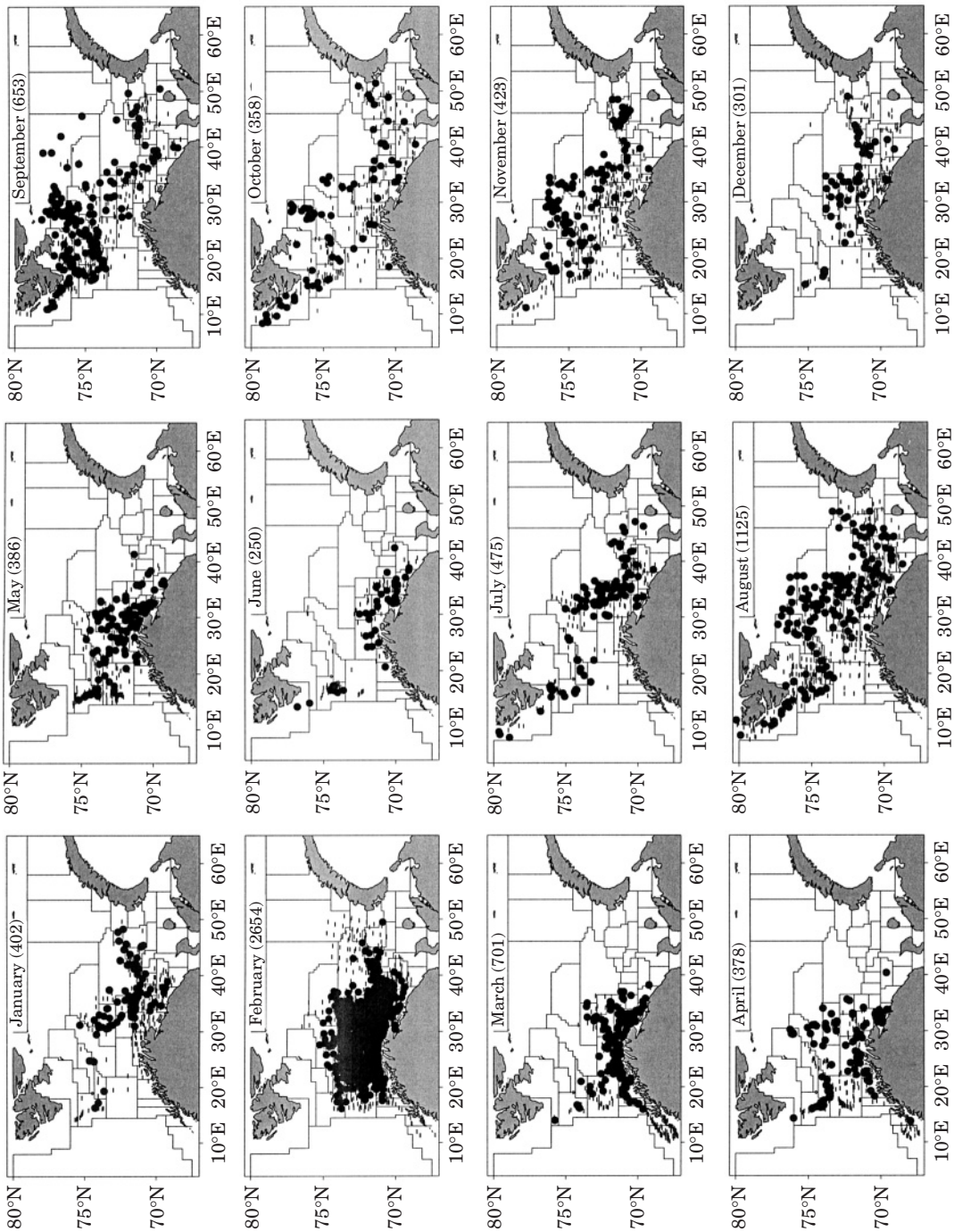

Figure 5. Monthly occurrence of capelin in cod stomachs, 1984–2000 (in parenthesis, the number of stations with cod stomach samples).

Table 3. Capelin biomass consumed by predatory fish, 1984–2000.

Year	Capelin biomass ('000 t) eaten by fish predators				
	Cod	Haddock	Greenland halibut	Long rough dab	Thorny skate
1984	627.9	—	—	—	—
1985	1329.4	—	—	—	—
1986	925.2	37.4	—	—	—
1987	243.4	0	—	—	—
1988	273.4	1.17	—	—	—
1989	726.1	57.8	—	—	—
1990	999.0	55.2	—	—	—
1991	3454.8	240.1	—	—	—
1992	1832.9	—	—	—	—
1993	2777.6	—	—	—	—
1994	1585.3	268.1	29.1	8.8	2.9
1995	755.1	19.1	29.1	8.8	2.9
1996	589.4	138.9	29.1	8.8	2.9
1997	695.7	24.3	3.3	11.1	6.2
1998	789.9	77.1	4.8	12.2	21.1
1999	1587.9	112.3	34.6	73.0	40.1
2000	1745.4	—	6.7	64.7	0
Mean	1231.7	80.0	17.1	23.4	9.5

— No data on food consumption.

capelin prespawning or spawning migrations (Zatsepin, 1939; Boldovsky, 1944; Antipova *et al.*, 1990). Other fish species in the open Barents Sea, populated by immature capelin, feed most intensively on capelin in winter (Greenland halibut; Nizovtsev, 1975; Shvagzhdis, 1990) or intermittently throughout the year (thorny skate, long rough dab; Komarova, 1939; Berestovsky, 1989, 1995; Antipova and Nikiforova, 1990).

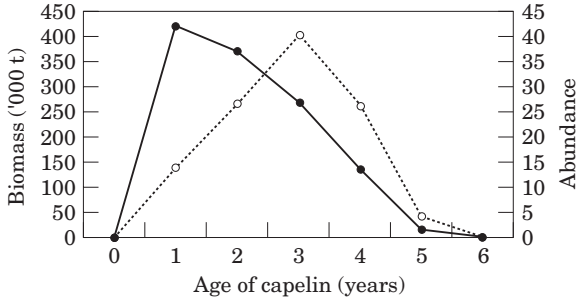

Figure 6. Mean abundance (10^9; solid curve) and biomass (broken curve) of capelin consumed by cod, 1984–2000.

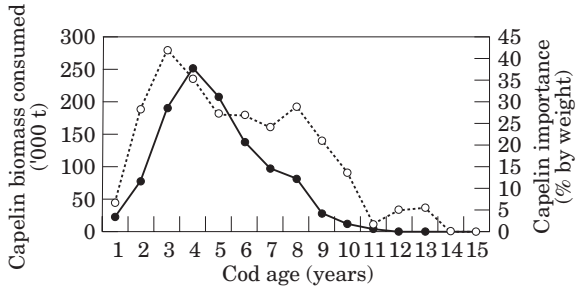

Figure 7. Capelin biomass consumed by (solid curve) and the importance of capelin in the food of (broken curve) different age-classes of cod, 1984–2000.

Overall, capelin are clearly most important as food for cod. The latter species preys on capelin during two separate periods that together encompass most of the year (Ponomarenko and Yaragina, 1990): in spring on the capelin spawning grounds, and in autumn, in areas where capelin congregate to feed. Capelin are also consumed by cod in other areas where cod and capelin overlap (Ponomarenko and Yaragina, 1996).

Seabirds generally dwell along the coast and, with few exceptions, travel no more than 150 km to forage (Anon., 2000b). Therefore, only when they approach the shore are capelin vulnerable to intense consumption by birds. In the vicinities of the Spitsbergen Archipelago and Bear and Hopen Islands, capelin may be very abundant and available to seabirds as prey the whole year round. However, polar cod are also preyed upon extensively by most of these birds (Mehlum and Gabrielsen, 1993), so overall, the quantity of capelin consumed by seabirds in the Barents Sea is not that high (maximum 200 000–300 000 t; Gjøsæter, 1998).

These estimates of consumption of capelin by different species of marine organism show that the greatest amount (about 49% of the total capelin mass consumed by fish, minke whales, and harp seals, on average, in the period 1992–2000) is consumed by cod (Figure 8). Of these cod, it is fish aged 3–6 that dominate in terms of the mass of capelin eaten. The second predator by

Table 4. Importance of capelin in the food of the most abundant fish species in the Barents Sea, 1934–1993.

Fish species	Number of stomachs examined	Importance of capelin*		Size of capelin consumed (cm)	Investigation period	Source
		%w	%fo			
Cod	8 541	18.7			1934–1938	Zatsepin and Petrova (1939)
	1 084 352		24		1947–1983	Ponomarenko and Yaragina (1990)
Haddock	1 683	13.2			1930–1931	Zenkevich and Brotskaya (1931)
	3 435	20.6			1930–1932	Zatsepin (1939)
	6 222	†			1953–1958	Tseeb (1964)
	235 136		8.9		1947–1977	Antipova *et al.* (1990)
Long rough dab	15 601		28.6		1969–1984	Simacheva and Glukhov (1990)
	6 878	0–100			1982–1991	Berestovsky (1995)
Thorny skate	2 947	†			1981–1984	Antipova and Nikiforova (1990)
	1 352	9–12	5.4–14.6		1983–1987	Berestovsky (1989)
Round skate	111	3.8	1.3		1983–1987	Berestovsky (1989)
Greenland halibut	5 363		33.7		1964–1969	Nizovtsev (1975)
	11 275		26.6		1980–1989	Shvagzhdis (1990)
Deepwater redfish	176	1.6–58.0		12	1982, 1985	Antonov *et al.* (1989)
	86 802		18.2		1968–1991	Dolgov and Drevetnyak (1993)
Atlantic wolffish, *Anarhichas lupus*	96	0			1984–1988	Orlova *et al.* (1989)
Spotted wolffish, *Anarhichas minor*	145	Up to 9			1984–1988	Orlova *et al.* (1989)
Blue wolffish, *Anarhichas denticulatus*	11	0			1984–1988	Orlova *et al.* (1989)
Atlantic herring	3 389		3.6	Larvae 0.8–2.5	1992–1993	Huse and Toresen (2000)

*Importance: %w, percentage by weight of the food bolus; %fo (%frequency of occurrence), percentage by number.
†Capelin in the food, but quantitative data are absent.

Table 5. Importance of capelin in the food of Barents Sea seabirds, 1935–1995.

Seabird species	Frequency of occurrence of capelin (%)	Capelin size (cm)	Investigation period	Source
Northern fulmar, *Fulmarus glacialis*	†		1988–1990	Camphuysen (1993)
Northern gannet, *Morus bassanus*	†			Krasnov and Barrett (1997)
Great cormorant, *Phalacrocorax carbo*	†		1985–1992	Krasnov *et al.* (1995)
	19.0		1989	Barrett *et al.* (1990)
European shag, *Phalacrocorax aristotelis*	†		1985–1992	Krasnov *et al.* (1995)
Common eider, *Somateria mollissima*	†	Eggs		Gjøsæter and Sætre (1974)
King eider, *Somateria spectabilis*	†	Eggs		Gjøsæter and Sætre (1974)
Long-tailed duck, *Clangula hyenalis*	†	Eggs		Anon. (2000b)
Arctic skua, *Stercorarius parasiticus*	18.1		1935–1949	Belopolsky (1971)
	36		1985–1992	Krasnov *et al.* (1995)
Mew gull, *Larus canus*	5.7		1935–1949	Belopolsky (1971)
Herring gull, *Larus argentatus*	9.3		1935–1949	Belopolsky (1971)
	†		1985–1992	Krasnov *et al.* (1995)
	†			Furness and Barrett (1985)
Great black-backed gull, *Larus marinus*	8.4		1935–1949	Belopolsky (1971)
	†		1985–1992	Krasnov *et al.* (1995)
	†		1966–1995	Anon. (2000b)
Black-legged kittiwake, *Rissa tridactyla*	20.8		1935–1949	Belopolsky (1971)
	Up to 60		1985–1992	Krasnov *et al.* (1995)
	50-90		1979–1994	Barrett and Krasnov (1996)
	90		1984	Barrett (1996)
Common guillemot, *Uria aalge*	18.7		1935–1949	Belopolsky (1971)
	†		1985–1992	Krasnov *et al.* (1995)
	99		1983	Vader *et al.* (1990)
	20–90		1980–1995	Barrett *et al.* (1997)
	60–100		1988–1995	Barrett *et al.* (1997)
Brunnich's guillemot, *Uria lomvia*	12.6		1935–1949	Belopolsky (1971)
	†		1992–1995	Krasnov *et al.* (1995); Barrett *et al.* (1997)
	Up to 33		1983–1993	Erikstad and Vader (1989); Vader *et al.* (1990); Barrett *et al.* (1997)
	1–4		1992–1995	Strøm *et al.* (1994, 1995); Krasnov (1995)
	†		1988–1995	Barrett *et al.* (1997)
Razorbill, *Alca torda*	21.7		1935–1949	Belopolsky (1971)
Black guillemot, *Cepphus grylle*	7.7		1935–1949	Belopolsky (1971)
	Up to 27		1985–1992	Krasnov *et al.* (1995)
Atlantic puffin, *Fratercula arctica*	15.5		1935–1949	Belopolsky (1971)
	20–76		1980–1994	Barrett and Furness (1990); Barrett and Krasnov (1996)

†Capelin occurred in the food but quantitative data are absent.

importance, consuming about 38% (up to 258 000 t when the capelin stock is abundant), is the harp seal (Nilssen *et al.*, 2000). Other fish species (our data) and marine mammals (Folkow *et al.*, 2000) take from 1 to 7% of the total mass of capelin consumed.

In summary, although capelin are eaten by many species of marine organism in the Barents Sea, their importance as prey of most predators is related to the size of the capelin stock. They are consumed mainly in spring, when they approach the spawning grounds along the coast of Norway and Murman. Two species, cod and, to a lesser extent, harp seal have the greatest influence on the dynamics of capelin abundance. It is therefore clear that, when regulating multispecies fisheries in the Barents Sea, the predatory needs of these

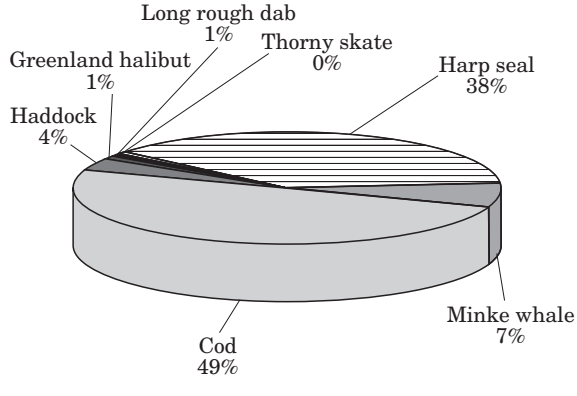

Figure 8. Mass of capelin eaten by various predators.

two species relative to capelin should be taken into consideration.

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References

Anon. 1980. Atlas of Marine Mammals of the USSR. Ed. by V. A. Zemsky. Pistchevaya promyshlennost Press, Moscow. 183 pp. (in Russian).

Anon. 1991. Recommendations on Rational Exploitation of the Barents Sea Capelin. Ed. by V. N. Shleinik. PINRO Press, Murmansk. 193 pp. (in Russian).

Anon. 2000b. The Status of Marine Birds Breeding in the Barents Sea Region. Ed. by T. Anker-Nilssen, V. Bakken, H. Strom, A. N. Golovkin, V. V. Bianki, and I. P. Tatarnikova. Norsk Polarinstitutt Rapportserie, 113. 213 pp.

Antipova, T. V., and Nikiforova, T. B. 1990. Peculiarities of thorny skate feeding in the Barents Sea. *In* Food Resources and Trophic Relations of Fish in the North Atlantic, pp. 167–172. Ed. by T. S. Rass, and S. S. Drobysheva. PINRO Press, Murmansk (in Russian).

Antipova, T. V., Ponomarenko, I. Ya., and Yaragina, N. A. 1990. Seasonal and annual variations in feeding of the Barents Sea haddock. *In* Food Resources and Trophic Relations of Fish in the North Atlantic, pp. 131–147. Ed. by T. S. Rass, and S. S. Drobysheva. PINRO Press, Murmansk (in Russian).

Antonov, S. G., Berestovsky, E. G., Orlova, E. L., and Shestova, L. M. 1989. A study on fishes of the genus *Sebastes*. *In* Diurnal Rhythms and Diets of Commercial Fish of the World Ocean, pp. 75–89. Ed. by S. G. Podrazhanskaya. VNIRO Press, Moscow (in Russian).

Barrett, R. T. 1996. Egg-laying, chick growth and food of kittiwakes *Rissa tridactyla* at Hopen, Svalbard. Polar Research, 15: 107–113.

Barrett, R. T., Anker-Nilssen, T., Rikardsen, F., Valde, K., Røv, N., and Vader, W. 1987. The food, growth and fledging success of Norwegian puffin chicks *Fratercula arctica* in 1980–1983. Ornis Scandinavica, 18: 73–83.

Barrett, R. T., Bakken, V., and Krasnov, Yu. V. 1997. The diets of common and Brunnich's guillemots *Uria aalge* and *U. lomvia* in the Barents Sea region. Polar Research, 16: 73–84.

Barrett, R. T., and Furness, R. W. 1990. The prey and diving depths of seabirds on Horny, northern Norway after a decrease in the Barents Sea capelin stock. Ornis Scandinavica, 21: 179–186.

Barrett, R. T., and Krasnov, Yu. V. 1996. Recent responses to changes in stocks of prey species by seabirds breeding in the southern Barents Sea. ICES Journal of Marine Science, 53: 713–722.

Barrett, R. T., Røv, N., Loen, J., and Montevecchi, W. A. 1990. Diets of shags *Phalacrocorax aristotelis* and cormorants *P. carbo* in Norway and possible implications for gadoid stock recruitment. Marine Ecology Progress Series, 66: 205–218.

Belopolsky, L. O. 1971. The food composition of seabirds in the Barents Sea. Scientific Reports of Kaliningrad State University. 47–67 (in Russian).

Berestovsky, E. G. 1989. Feeding of skates *Raja radiata* Donovan and *Raja fyllae* Lutken (Rajidae) in the Barents and Norwegian Seas. Journal of Ichthyology, 29: 994–1002 (in Russian).

Berestovsky, E. G. 1991. To the methods of calculating predatory fish daily rations. *In* Using Methods of Informatics and Statistics in Hydrobiological Investigations of the Barents Sea, pp. 85–90. Ed. by G. G. Matishov. MMBI Press, Apatity (in Russian).

Berestovsky, E. G. 1995. Feeding and feeding strategy of long rough dab in the Barents and Norwegian Seas. Journal of Ichthyology, 35: 94–104 (in Russian).

Bogstad, B., and Mehl, S. 1997. Interactions between cod (*Gadus morhua*) and its prey in the Barents Sea. *In* Proceedings of the International Symposium on the Role of Forage Fish in Marine Ecosystems, pp. 591–615. Alaska Sea Grant College Program Report No. 97–01. University of Alaska, Fairbanks.

Boldovsky, G. V. 1944. The food of Norwegian haddock in the Barents Sea. Trudy PINRO, 8: 307–330 (in Russian).

Camphuysen, C. J. 1993. Birds and mammals in Svalbard, 1985–1991. Sula, 7: 3–44.

Chapsky, K. K. 1938. Bearded seal *Erignatus barbatus* Fabr. of the Kara and Barents Sea. Trudy Arctic Institute, 123: 7–36 (in Russian).

Dolgov, A. V. 1997. Distribution, abundance, biomass and feeding of thorny skate *Raja radiata* in the Barents Sea. ICES CM 1997/GG: 04.

Dolgov, A. V., and Drevetnyak, K. V. 1993. Some peculiarities of feeding and feeding interactions of deepwater redfish *Sebastes mentella* in the Barents and Norwegian Seas. ICES CM 1993/G: 60.

Dolgova, N. V., and Dolgov, A. V. 1997. Stock status and predation of long rough dab *Hippoglossoides platessoides* in the Barents and Norwegian Seas. ICES CM 1997/HH: 05.

Erikstad, K. E., and Vader, W. 1989. Capelin selection by common and Brunnich's guillemots during the pre-laying season. Ornis Scandinavica, 20: 151–155.

Folkow, L. P., Haug, T., Nilssen, K. T., and Nordy, E. S. 2000. Estimated food consumption of minke whale *Balaenoptera acutorostrata* in Northeast Atlantic waters in 1992–1995. NAMMCO Scientific Publications, 2: 65–80.

Furness, R. W., and Barrett, R. T. 1985. The food requirements and ecological relationships of a seabird community in north Norway. Ornis Scandinavica, 16: 305–313.

Gjøsæter, H. 1998. The population biology and exploitation of capelin (*Mallotus villosus*) in the Barents Sea. Sarsia, 83: 453–496.

Gjøsæter, J., and Sætre, R. 1974. Predation of eggs of capelin (*Mallotus villosus*) by diving ducks. Astarte, 7: 83–89.

Grinkevich, N. S. 1957. Annual changes in the feeding of the cod of the Barents Sea. Trudy PINRO, 10: 88–105 (in Russian).

Huse, G., and Toresen, R. 2000. Juvenile herring prey on Barents Sea capelin larvae. Sarsia, 85: 385–391.

ICES. 2001a. Report of the Northern Pelagic and Blue Whiting Fisheries Working Group. ICES CM 2001/ACFM: 17.

ICES. 2001b. Report of the Arctic Fisheries Working Group. ICES CM 2001/ACFM: 19.

Klumov, S. K. 1963. Feeding and helminthofauna of baleen whale (Mystacoceti) in the main fishing areas of the World Ocean. Trudy Oceanology Institute, 71: 92–112 (in Russian).

Komarova, I. V. 1939. Feeding of long rough dab *Hippoglossoides platessoides* in the Barents Sea in connection with food resources. Trudy VNIRO, 4: 297–320 (in Russian).

Kondakov, A. A., and Mishin, V. L. 1999. The cetaceans of the West Arctic. Peculiarities of the biology, characteristics of the feeding spectrum. *In* Adaptation and Evolution in Biota of the Polar Seas under Oceanic Periglacial Conditions, pp. 315–322. Ed. by G. G. Matishov. MMBI Press, Apatity (in Russian).

Krasnov, Yu. V. 1995. Seabirds (retrospective analysis of population development). *In* The Environment and Ecosystems of Novaya Zemlya (the Archipelago and Shelf), pp. 138–147. Ed. by G. G. Matishov. MMBI Press, Apatity (in Russian).

Krasnov, Yu. V., and Barrett, R. T. 1997. The status and behaviour of the gannet *Sula bassana* in islands and along the Murman coast. Russian Journal of Ornithology, 12: 3–8 (in Russian).

Krasnov, Yu. V., Matishov, G. G., Galaktionov, K. V., and Savinova, T. N. 1995. The Colonial Seabirds of Murman. Ed. by V. V. Bianki. Nauka, St Petersburg. 228 pp (in Russian).

Lindstrøm, U., and Haug, T. 2000. Feeding strategy and prey selectivity in minke whale (*Balaenoptera acutorostrata*) foraging in the southern Barents Sea during early summer. International Whaling Commission, SC/52/E14. 35 pp.

Mehlum, F., and Gabrielsen, G. W. 1993. The diet of high-arctic seabirds in coastal and ice- covered pelagic areas near the Svalbard archipelago. Polar Research, 12: 1–20.

Nilssen, K. T., Pedersen, O. P., Folkow, L. P., and Haug, T. 2000. Food consumption estimates of the Barents Sea harp seals. NAMMCO Scientific Publications, 2: 9–27.

Nizovtsev, G. P. 1975. On feeding of Greenland halibut *Reinhardtius hippoglossoides* (Walbaum) in the Barents Sea. Deponent TSNIITEIRKH, 44: 1–44 (in Russian).

Orlova, E. L., Berestovsky, E. G., Karamushko, L. I., and Savelova, E. A. 1989. Age changes in feeding of the Barents Sea wolffish *Anarhichas lupus*, *A. minor* and *A. denticulatus*. *In* Trophic Interrelations of Benthos and Bottom Fish of the Barents Sea, pp. 4–13. Ed. by A. D. Chinarina. MMBI Press, Apatity (in Russian).

Podrazhanskaya, S. G., and Chumakov, A. K. 1989. Feeding, diets and food requirements of Greenland halibut in the Northwest Atlantic. *In* Diurnal Rhythms and Diets of Commercial Fish of the World Ocean, pp. 123–140. Ed. by S. G. Podrazhanskaya. VNIRO Press, Moscow (in Russian).

Ponomarenko, I. Ya., and Yaragina, N. A. 1990. Long-term dynamics of cod feeding on capelin, euphausiids, shrimp and annual consumption of these species in the Barents Sea. *In* Food Resources and Trophic Relations of Fish in the North Atlantic, pp. 109–130. Ed. by T. S. Rass, and S. S. Drobysheva. PINRO Press, Murmansk (in Russian).

Ponomarenko, I. Ya., and Yaragina, N. A. 1996. Feeding and food relations. Cod in the ecosystem of the Barents Sea. *In* The Barents Sea Cod (Biological and Fisheries Outline), pp. 56–104. Ed. by V. D. Boitsov, N. I. Lebed, V. P. Ponomarenko, V. V. Tereshchenko, V. L. Tretyak, M. S. Shevelev, and N. A. Yaragina. PINRO Press, Murmansk (in Russian).

Shvagzhdis, A. P. 1990. Feeding peculiarities of Greenland halibut from the Norwegian–Barents Sea stock in 1980–1989. ICES CM 1990/G: 12.

Simacheva, I. N., and Glukhov, A. A. 1990. Feeding of long rough dab in the Barents Sea. *In* Food Resources and Trophic Relations of Fish in the North Atlantic, pp. 160–166. Ed. by T. S. Rass, and S. S. Drobysheva. PINRO Press, Murmansk (in Russian).

Strøm, H., Øien, I. J., Opheim, J., Kuznetsov, E. A., and Khakhin, G. V. 1994. Seabird censuses on Novaya Zemlya 1994. Norwegian Ornithological Society. Report No. 2: 38 pp.

Strøm, H., Øien, I. J., Opheim, J., Kuznetsov, E. A., and Khakhin, G. V. 1995. Seabird censuses on Novaya Zemlya 1995. Norwegian Ornithological Society. Report No. 3: 24 pp.

Tomilin, A. G. 1962. Cetacea Fauna in the Seas of the USSR. Ed. by E. N. Pavlovsky. USSR Academy of Sciences Press, Moscow. 212 pp. (in Russian).

Tseeb, R. Ya. 1964. Feeding and Food Adaptations of Haddock. Ed. by Yu. I. Galkin. Nauka, Moscow, St Petersburg. 134 pp. (in Russian).

Vader, W., Barrett, R. T., and Erikstad, K. E. 1990. Differential responses of common and thick-billed murres to a crash in the capelin stock in the southern Barents Sea. Studies in Avian Biology, 14: 175–180.

Zatsepin, V. I. 1939. Feeding of haddock (*Melanogrammus aeglefinus* L.) in the area of the Murman coast relative to bottom fauna. Trudy PINRO, 3: 39–96 (in Russian).

Zatsepin, V. J., and Petrova, N. S. 1939. Feeding of cod in the south part of the Barents Sea (by observations in 1934–1938). Trudy PINRO, 5: 170 (in Russian).

Zenkevich, L. A., and Brotskaya, V. A. 1931. Data on feeding of fish from the Barents Sea. Reports of the First Session of the State Oceanographic Institute, 4: 1–35 (in Russian).