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THEMATIC REVIEW

Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea

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Abstract

Polar cod and capelin are key species in Arctic and sub-Arctic marine food webs, respectively, and the objective of this study is to compare and contrast the two species. Their distributions are dependent on water masses, with polar cod being associated with cold, sub-zero Arctic water, whereas capelin is distributed further south into Atlantic water masses. The distribution of polar cod is more static than that of capelin, whose distribution extends further north in warm years and fluctuates greatly based on predator–prey relationships. The species occur sympatrically in the Barents Sea, with large standing biomasses ($0.5\text{--}1.5 \times 10^6$ t polar cod versus $3\text{--}4 \times 10^6$ t capelin). They overlap in distribution in the southern and eastern Barents Sea, whereas polar cod are most abundant in the icy waters of the Arctic. Both species aggregate in large schools and utilize zooplankton food sources, such as calanoid copepods. Polar cod also feed to a larger extent on amphipods, whereas capelin feed predominately on krill. Both species represent high-energy prey (lipids) for upper trophic levels. Global warming, with reduction in sea ice and increase in temperature, is expected to affect these two species differently. Polar cod will likely lose the sympagic (ice-associated) part of its life cycle and become more restricted in pelagic distribution during summer, whereas the capelin stock may expand to the north and east, although with considerable interannual fluctuations.

Key words: Arctic fish distribution, stock size, Barents Sea, environmental change, marine food web

Introduction

Polar cod (*Boreogadus saida* (Lepechin, 1774)) and capelin (*Mallotus villosus* (Müller, 1776)) are abundant pelagic fishes that are considered key species in Arctic and sub-Arctic ecosystems, respectively (Welch et al. 1992; Sakshaug et al. 1994; Dolgov 2002; Wassmann et al. 2006; Orlova et al. 2009). Both species have large standing biomasses in the Barents Sea, with some overlap in distributions, where they may compete for the same zooplankton resources (Orlova et al. 2009). Due to their main distributions in Arctic versus sub-Arctic water masses, as well as differences in life-history aspects, they are expected to respond very differently to climate warming. Because of their important functions in the marine ecosystem, changes in their abundance, distribution and competition for food resources will have consequences for the energy flow in marine food webs leading up to predatory fishes, marine mammals and seabirds. The objective of this study is to compare and

contrast polar cod and capelin with regard to their relationship to water masses, sea ice conditions, life histories, feeding ecology with potential competition, and predation. For this purpose we review the function of polar cod and capelin as key species in Arctic and sub-Arctic marine food webs. Our focal area for comparisons of population development and temperature-related distribution is the Barents Sea, where we provide long-term population and catch data as well as recent (2011) information on the distribution of the two species relative to prevailing water masses. Polar cod and capelin have very different relationships to sea ice, and we provide information on this from studies of physiological properties (i.e. antifreeze) and distributions around the Arctic. Their life histories and feeding ecology are compared and there is also some evidence for competition in the eastern Barents Sea. Finally, we indicate likely effects of increased temperature and reductions in sea ice on the two species with consequences for the marine food web.

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Polar cod and capelin: their distribution and function in marine food webs

The polar cod is the only member of its genus *Boreogadus* (Günther, 1862) in the family Gadidae (Rafinesque, 1810) (Cohen et al. 1990). It is a small fish, generally with lengths up to 300 mm (Scott & Scott 1988), although extreme sizes up to 460 mm have been recorded (Pethon 1994). It is relatively short-lived, with maximum age of 7 years (Hop et al. 1997b), but rarely >5 years (Bradstreet et al. 1986; Ajiad et al. 2011), with early maturation (males at age 2, females at age 3; Craig et al. 1982; Table I). The polar cod has a circumpolar distribution mainly above the Arctic Circle (Svetovidov 1948; Andriashev et al. 1980; Cohen et al. 1990) and is probably one of the most abundant fishes in the Arctic (Moskalenko 1964; Ponomarenko 1968). The species is abundant in the Barents Sea (Ajiad et al. 2011), in fjords in Svalbard (Falk-Petersen et al. 1986; Renaud et al. 2012) and Greenland (Christiansen et al. 2012) and there is a relict population in Porsangerfjorden, northern Norway (Hognestad 1968; Christiansen & Fevolden 2000). On the western side of the North Atlantic, its southern distribution is generally limited to cold waters off Northern Labrador and Newfoundland (Templeman 1948; Lear 1979; Scott & Scott 1988), but it may be found further south, in the Gulf of St. Lawrence and in the Saguenay fjord, Quebec (Lesage et al. 2001). In the North American Arctic, surveys of polar cod have indicated large abundances

in the Canadian Arctic archipelago and in the Beaufort and Chuckchi seas (Crawford & Jorgenson 1993, 1996; Benoit et al. 2008; Geoffroy et al. 2011; Crawford et al. 2012). There are probably several stocks distributed around the Arctic Ocean (Bouchard & Fortier 2011), and two possible spawning areas that exist in the Barents Sea region, one east of Svalbard (inferred from egg and larval drift) and one in the Pechora Sea (Rass 1968; Aglen et al. 2012). In the Barents Sea, polar cod occur both in the areas of drifting sea ice in the northern Barents Sea and north of Svalbard (Lønne & Gulliksen 1989) and in the open water masses of the central and southern Barents Sea (Ajiad et al. 2011). In the Arctic, polar cod are often in areas with ice cover, but only part of the population is usually directly associated with ice (i.e. sympagic), primarily as larvae and juveniles (Andriashev 1954; Bradstreet 1982; Bouchard & Fortier 2011), whereas the larger fish (sub-adults and adults) often occur pelagically in deeper water below the ice (Geoffroy et al. 2011) or in open water (Hop et al. 1997b). They may also occur close to the bottom, associated with the benthic habitat (Falk-Petersen et al. 1986; Hop et al. 1997b; Christiansen et al. 2012; Renaud et al. 2012). Thus, the polar cod utilizes a range of habitats throughout its life cycle, and part of the population is sympagic, also in the northern Barents Sea, where individuals are frequently observed and sampled in drifting sea ice by divers (Lønne & Gulliksen 1989; Søreide et al. 2006).

Table I. Comparative morphometrics and life-history aspects of polar cod* and capelin**.

Life-history aspect	Polar cod	Capelin	Reference
Life mode	Pelagic/sympagic	Pelagic	Lønne & Gulliksen (1989)*, Gjøsæter (1998)*
Distribution	Arctic	Subarctic	Andriashev et al. (1980)*, Carscadden et al. (2013)**
Antifreeze	Glycoproteins	None known	Osuga & Feeney (1978)*
Feeding	Amphipods/ copepods	Krill/ copepods	Orlova et al. (2009, 2010)**, Renaud et al. (2012)*, Dalpadado & Mowbray (2013)**
Spawning strategy	Iteroparous	Semelparous	Moskalenko (1964)*, Scott & Scott (1988)**
Spawning habitat	Pelagic/sympagic	Demersal	Rass (1968)*, Scott & Scott (1988)**
Spawning time	Nov–March	March–April	Moskalenko (1964)*, Craig et al. (1982)*, Aglen et al. (2012)**
Fecundity (1000 eggs)	10–30 (–70)	5–50	Andriashev (1954)*, Scott & Scott (1988)**, Hop et al. (1995)*, Hedeholm et al. (2011)**
Egg size (mm)	1.5–1.9	0.65–1.0	Rass (1968)*, Forberg (1982)**, Hop et al. (1995)*
Incubation time (days)	45–90	15–50	Rass (1968)*, Frank & Leggett (1981)**, Pethon (1994)**, Graham & Hop (1995)*
Sexual maturity (years)	2–3	2–5	Craig et al. (1982)*, Pethon (1994)**, Hop et al. (1995)*
Maximum age (years)	6–7	5–7	Hansen (1943)**, Hop et al. (1997b)*
Adult size (cm)	15–30	20	Falk-Petersen et al. (1986), Hop et al. (1997b)*, Aglen et al. (2012)**
Maximum size (cm)	46	25	Winters (1970)**, Pethon (1994)*
Liver lipids (% ww)	60–65	6–9	Henderson et al. (1984)**, Hop et al. (1995, 1997a)*
Muscle lipids (% ww)	3	3–23	Winters (1969)**, Montevecchi & Piatt (1984)**, Hop et al. (1997a)*
Female gonad lipids (% ww)	5–14	4–7	Henderson et al. (1984)**, Montevecchi & Piatt (1984)**, Hop et al. (1995, 1997a)*
Male gonad lipids (% ww)	3–14	2	Henderson et al. (1984)**, Hop et al. (1995, 1997a)*
Energy content (kJ g ⁻¹ ww)	5–7	4–5	Montevecchi & Piatt (1984)**, Brekke & Gabrielsen (1994)**, Hedeholm et al. (2011)**

The capelin is a small pelagic fish belonging to the smelt family (Osmeridae). It is somewhat smaller than polar cod (maximum length 250 mm; Scott & Scott 1988), and males grow faster than females until they reach maturity at 130–200 mm, generally at age 3 (Table I). The maximum life span is similar to polar cod, 7 years in cold waters (Hansen 1943). The capelin is also considered an Arctic species, with circumpolar distribution in the Northern Hemisphere, but has a more sub-Arctic distribution. Its feeding distribution overlaps with the polar cod, but its southward distribution with regard to spawning areas extends further south than the polar cod on both sides of the Atlantic. In the eastern and central North Atlantic it extends to Nord-Trøndelag, Norway (Pethon 1994) and southwest Iceland (Vilhjalmsson 2002), whereas in the western part it has been recorded in the Bay of Fundy (Tibbo & Humphreys 1966) and may extend as far south as Cape Cod (Scott & Scott 1988). On the Pacific side, this species occurs in the Bering Sea as well as in the Sea of Okhotsk (Naumenko 1996; Velikanov 2002). Its northward distribution extends into the marginal ice zone on the Atlantic side (Gjøsæter et al. 2011) and to Cape Barrow in the Beaufort Sea (Scott & Scott 1988). Capelin is rarely encountered in high Arctic waters (Stergiou 1989), whereas polar cod have been recorded in different parts of the Arctic Ocean up to the North Pole (Andriashev et al. 1980). Genetically, the circumpolar capelin can be divided into four regional groups: (1) west Pacific, (2) east Pacific, (3) Newfoundland, and (4) northeast Atlantic and west Greenland (Præbel et al. 2008), although the stocks in the North Atlantic may be further discriminated genetically or based on their spawning ecology (e.g. stocks in Newfoundland, western Greenland, Iceland, Barents Sea: Sørensen & Simonsen 1988; Dodson et al. 1991; Friis-Rødel & Kannevorff 2002; Carscadden et al. in press).

The Barents Sea stock, which is the largest of these, spawns along the Norwegian coast from Vesterålen northeastwards to and including the Murman coast of Russia. Its main feeding area is in central and northern parts of the Barents Sea (Gjøsæter et al. 2011). Capelin may also be found in the White Sea, Pechora Sea, and the fjords of Svalbard (e.g. Isfjorden) at various times of the year. Spawning did occur near Novaya Zemlya during the 1920s (Rass 1933) and spawning was observed near Dolgiy Island, eastern Pechora Sea, in August 1992 (S. Dahle, Akvaplan-niva, pers. comm.). Rass (1933) divided the Barents Sea capelin into three local stocks: the Finnmark stock, the Murman stock and the Novaya Zemlya stock, spawning in winter, summer and autumn, respectively. However, Prokhorov (1965) and Luka (1978) suggested that

spring and summer–autumn spawning capelin were not ecologically isolated groups. This was supported by electrophoretic enzyme investigations by Dushchenko (1985). Today, Barents Sea capelin are considered to be one large oceanic stock (Aglen et al. 2012), and several populations are additionally present year-round in fjords of Northern Norway, such as Balsfjorden, Porsangerfjorden and Varangerfjorden (e.g. Kennedy 1979; Nyholmen & Hopkins 1988). However, these are not genetically isolated from the oceanic stock (Mork & Friis-Sørensen 1983).

Both polar cod and capelin are key species in the Arctic marine food web, although the polar cod is more important in the high-Arctic systems and capelin more important in sub-Arctic systems. These species typically occupy the third trophic level (Hop et al. 2002), and large schools are formed by both species (Crawford & Jorgenson 1993; Welch et al. 1993; Gjøsæter 1998). Large schools of polar cod have frequently been observed in shallow waters (< 4 m depth) of the Canadian Arctic (Welch et al. 1993; Hop et al. 1997b), but aggregations have also been recorded acoustically deeper (200–500 m depth) during winter in the Amundsen Gulf (Benoit et al. 2008; Geoffroy et al. 2011), and aggregations have been recorded in coastal areas and fjords in Svalbard at 100–385 m depth (Falk-Petersen et al. 1986). Schooling fish represent aggregated prey energy (lipids) for predatory fishes, marine mammals and seabirds (Welch et al. 1993; Crawford & Jorgenson 1996; Benoit et al. 2010). Large polar cod schools are sustained by ubiquitous zooplankton, such as *Calanus* sp., and their feeding may deplete zooplankton locally (Hop et al. 1997b). Capelin form large schools in open water masses (Rose 1993; Gjøsæter 1998), and when capelin biomass in the Barents Sea is high, the zooplankton density tends to be low (Dalpadado & Skjoldal 1996; Dalpadado et al. 2001).

The key function of the polar cod in the Arctic marine food web is related to the large standing biomass of fish coupled with efficient transformation of the energy in small invertebrates (particularly *Calanus* spp. and *Themisto* spp.) into growth, and the fish constitutes a large enough body size to be exploited by animals at higher trophic levels. A considerable fraction of the annual energy flow of the food web passes through polar cod in the marginal ice zone, in fjords and coastal waters of Svalbard as well as other areas of the Arctic (Welch et al. 1992). The polar cod is very efficient in transforming the energy of ingested prey into growth, with gross growth efficiency (GGE) of 50% and assimilation efficiency (AE) of 80%, as determined in laboratory experiments (Hop et al. 1997a). The AE for polar cod is about 10% higher than general values for carnivorous

fishes (Brett & Groves 1979), and more similar to that for the Antarctic *Notothenia neglecta* Nybelin, 1951 (Everson 1970). The GGE for polar cod was much higher than for the generalized budget (29%) and that of Antarctic fish (6%; Everson 1970). However, its daily consumption and growth rate are very low at sub-zero temperatures, and the annual production to sustain predators mainly reflects the large standing biomass of polar cod in the Arctic (Hop et al. 1997b; Benoit et al. 2008; Geoffroy et al. 2011). Polar cod is a very important food source for ice-associated marine mammals, such as ringed seals (*Pusa hispida* Schreber, 1775), narwhal (*Monodon monoceros* Linnaeus, 1758) and white whale (*Delphinapterus leucas* Pallas, 1776) as well as fish-eating Arctic seabirds such as Brünnich's guillemot (*Uria lomvia* L.), Black guillemot (*Cepphus grylle* L.) and Northern fulmar (*Fulmarus glacialis* L.) (e.g. Bradstreet & Cross 1982; Lønne & Gabrielsen 1992; Welch et al. 1992).

The capelin is a key species in the Barents Sea ecosystem, utilizing the zooplankton production in the central and northern parts of the Barents Sea during the Arctic summer (Sakshaug et al. 1994; Gjøsæter 1998; Bogstad et al. 2000; Dolgov 2002). During extensive migrations, the capelin carries energy from north to south in the Barents Seas, and through its function as forage fish it funnels energy to higher trophic levels such as Atlantic cod (*Gadus morhua* L.), seabirds and marine mammals (Sakshaug et al. 1994; Gjøsæter 1998; Wassmann et al. 2006). The upper food web's dependence on capelin was clearly demonstrated during the first capelin stock collapse in the mid 1980s, when survival and growth of Atlantic cod, seals and seabirds were negatively affected (Vader et al. 1990; Hamre 1994; Barrett & Krasnov 1996; Gjøsæter et al. 2009).

Both species are energetically valuable prey mainly because they contain large amounts of lipids (as % wet weight; Table I). The polar cod stores most of the lipids, as triacylglycerols, in its relatively large liver (Hop et al. 1995). Juvenile polar cod may only contain 3–5% lipids, whereas adults with larger livers typically contain 10% lipids and 15% protein (Brekke & Gabrielsen 1994). The large livers in polar cod may contain as much as 60–65% lipids in August (Hop et al. 1995). The capelin has large amounts of this lipid class in muscle, varying from lows of 3–8% in summer to as high as 18–23% in late autumn/winter, whereas protein levels are relatively constant at 13–14% throughout the year (Winters 1969; Montevecchi & Piatt 1984). The lipids, which originate from phytoplankton and *Calanus*, are transferred as energy up through the food chains and end up as subcutaneous fat and blubber in seabirds and marine mammals in <6 months (Falk-Petersen et al. 1990, 2007).

Population development and temperature-related distribution in the Barents Sea

Polar cod and capelin in the Barents Sea are surveyed annually during August–September as part of the Joint Norwegian/Russian Ecosystem Survey, which includes acoustic surveys for pelagic fish (Anon. 2011). The polar cod population in the Barents sea has been relatively stable at about 0.5×10^6 t or less during the period 1986–1997, but then increased to a higher and more variable level from 1998 (Figure 1a). There are some indications that the low abundance value in 2003 is not representative (Ajiad et al. 2011), and the polar cod population has probably been about $1\text{--}2 \times 10^6$ t in recent years. Apart from the period prior to the early 1980s, when the exploitation rate may have been substantial, the exploitation of polar cod has been low relative to stock size. The Russians have fished polar cod in the Barents Sea since 1966, with peak catches (332,000 tonnes) in 1971. Norway also fished for polar cod during 1969–1971, but to a much lesser extent (16,000 tonnes in 1971) and declined to zero since the early 1980s (Ajiad et al. 2011; Figure 1a). The reason for the increased stock size from the late 1990s is unknown, but may be due to better conditions for growth and survival, which is likely related to higher temperature but still within their optimal thermal range for growth.

The population of capelin in the Barents Sea has been highly variable during the last 40 years with population estimates starting in the early 1970s (Figure 1b). The capelin population follows a typical boom and crash in abundance, with very high biomass in the 1970s to early 1980s, in the early 1990s and around 2000, and dramatic crashes in the mid 1980s, mid 1990s and from 2003 to 2006. The capelin fishery generally follows the peaks in abundance (Figure 1b). The quota for the winter 2011 was 380,000 t, and it decreased to 320,000 t in 2012. The crashes in the capelin stock have been associated with cascading effects in the marine food web, resulting in reproductive failure in fish-eating seabirds (Vader et al. 1990; Barrett & Krasnov 1996). While the first capelin collapse turned out to be a 'crisis' for the Barents Sea ecosystem, the two following population crashes had fewer ecological effects, mainly because the availability of alternative prey, such as herring (*Clupea harengus* L.), polar cod and blue whiting (*Micromesistius poutassou* Risso, 1827), was better (Gjøsæter et al. 2009).

In the Barents Sea, polar cod are associated with cold (<0°C) water masses (Figure 2a). These Arctic water masses are also less saline (34.4–34.8) than Atlantic water (>34.9) and generally extend down to >100 m depth in the Northern Barents Sea (Figure 2b; Loeng 1991). To the south, the Arctic

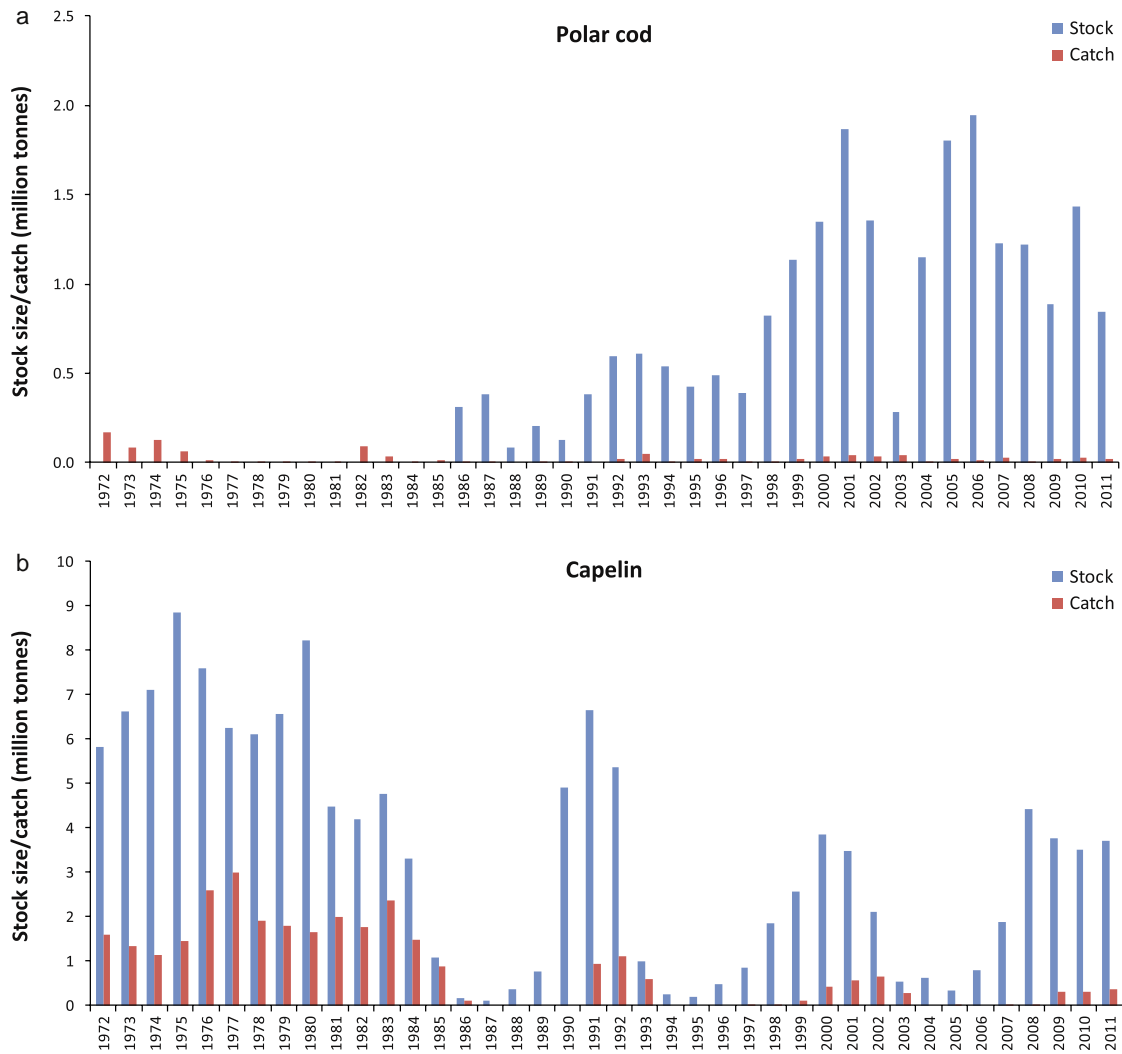


Figure 1. Acoustic stock size estimates and commercial catches of polar cod (a) and capelin (b) in the Barents Sea during the period 1972–2011. For polar cod, stock size estimates started in 1986. Note that their stock estimate from 2003 is considered to be a gross underestimate due to lack of coverage that year. Stock size from Anon (2011) and catch data from Aglen et al. (2012).

water masses are limited by the Polar Front, where Arctic and Atlantic water masses meet. The southern distribution of polar cod reflects the extent of these cold and relatively fresh water masses. The distribution area for polar cod seems to be more static than that of the capelin. Thus, the areal distribution of polar cod in 2011 (Figure 3a) is not very different from its general distribution pattern (Ajiad et al. 2011). However, in cold years it can be distributed further south on both sides of the Atlantic (Lilly et al. 1994). Even though polar cod are associated with cold water, this species can tolerate higher temperatures (Bain & Sekerak 1978), and its final temperature preference has been determined experimentally to be in the 3–4°C range (Christiansen et al. 1996). Thus, its growth and survival may be better in slightly warmer water, and polar cod on the west coast of Spitsbergen typically grow faster than polar cod in the colder

Canadian high Arctic (Falk-Petersen et al. 1986; Hop et al. 1997b). This species most likely occupies waters below its preferred temperature due to its special adaptations (antifreeze proteins) and reduced competition.

The distribution of capelin in the Barents Sea is more variable (Figure 3b), as they are less dependent on specific water masses (Figure 2a, b). During autumn, adult capelin are found in both Atlantic and Arctic waters, with ambient temperature from -1°C to 2°C (Gjøsæter & Loeng 1987; Ingvaldsen & Gjøsæter 2013). The distribution in August–September 2011 adhered to this pattern, but indicated some larger aggregations in the NW parts of the Barents Sea, particularly NW of Hopen Island, around Storbanken, Kvitøya and in the Franz-Viktoria Trough (Figure 3b). The younger stages are normally found in warmer water ($> 2^{\circ}\text{C}$) than larger fish, because they are distributed closer to the

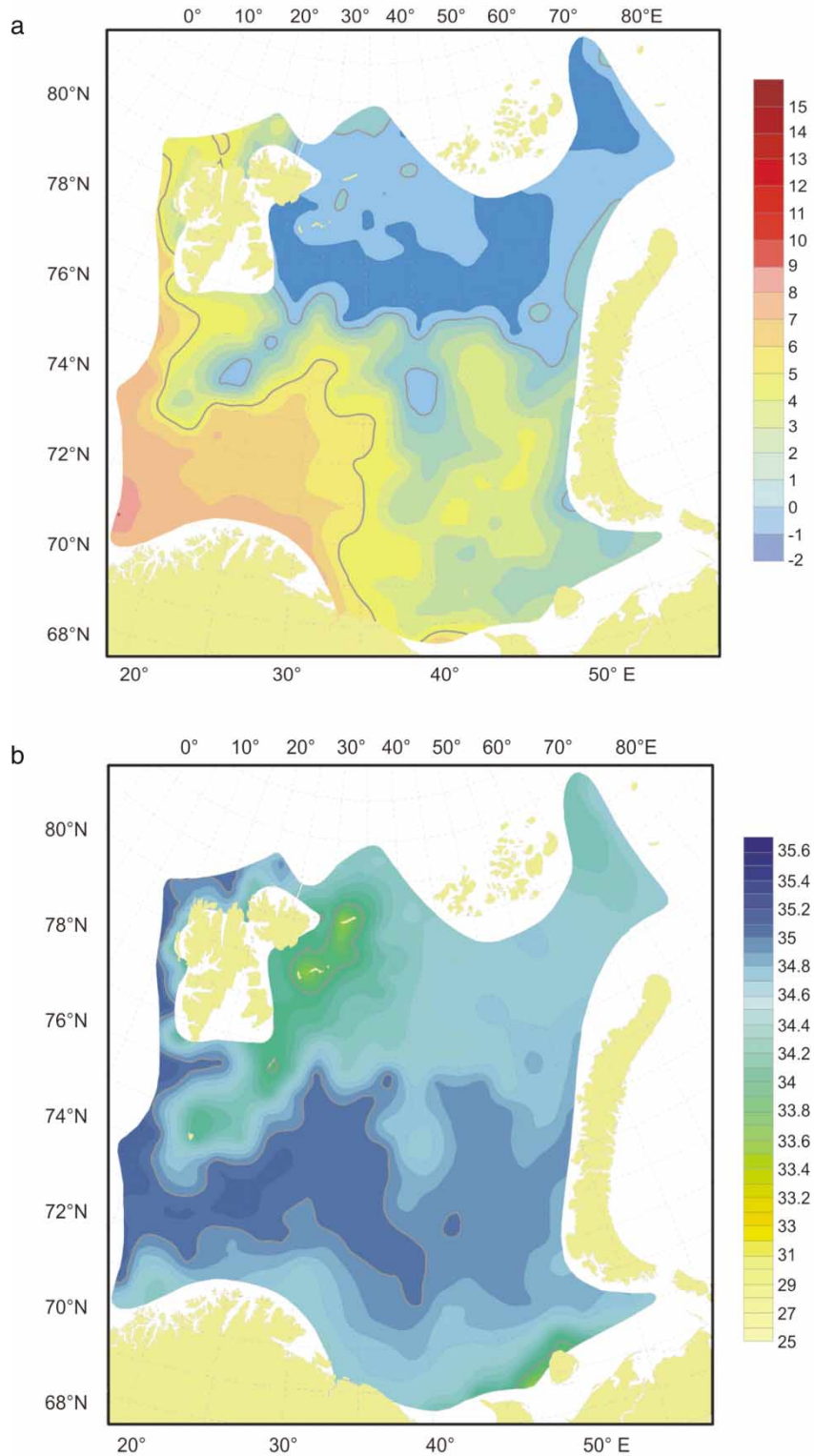


Figure 2. Distribution of temperature (°C) and salinity (psu) at 50 m depth in the Barents Sea during August–September 2011. Redrawn from Anon (2011).

spawning areas in the southern Barents Sea. Changes in the distribution of capelin are related to changes in sea temperature, with general expansion during warm periods and contraction during cold years (Loeng

1981, 1989a, b; Ozhigin & Luka 1985; Ozhigin & Ushakov 1985; Gjøsæter & Loeng 1987; Ushakov & Ozhigin 1987; Gjøsæter 1998, 1999). However, Gjøsæter (1999) and Ingvaldsen & Gjøsæter (2013)

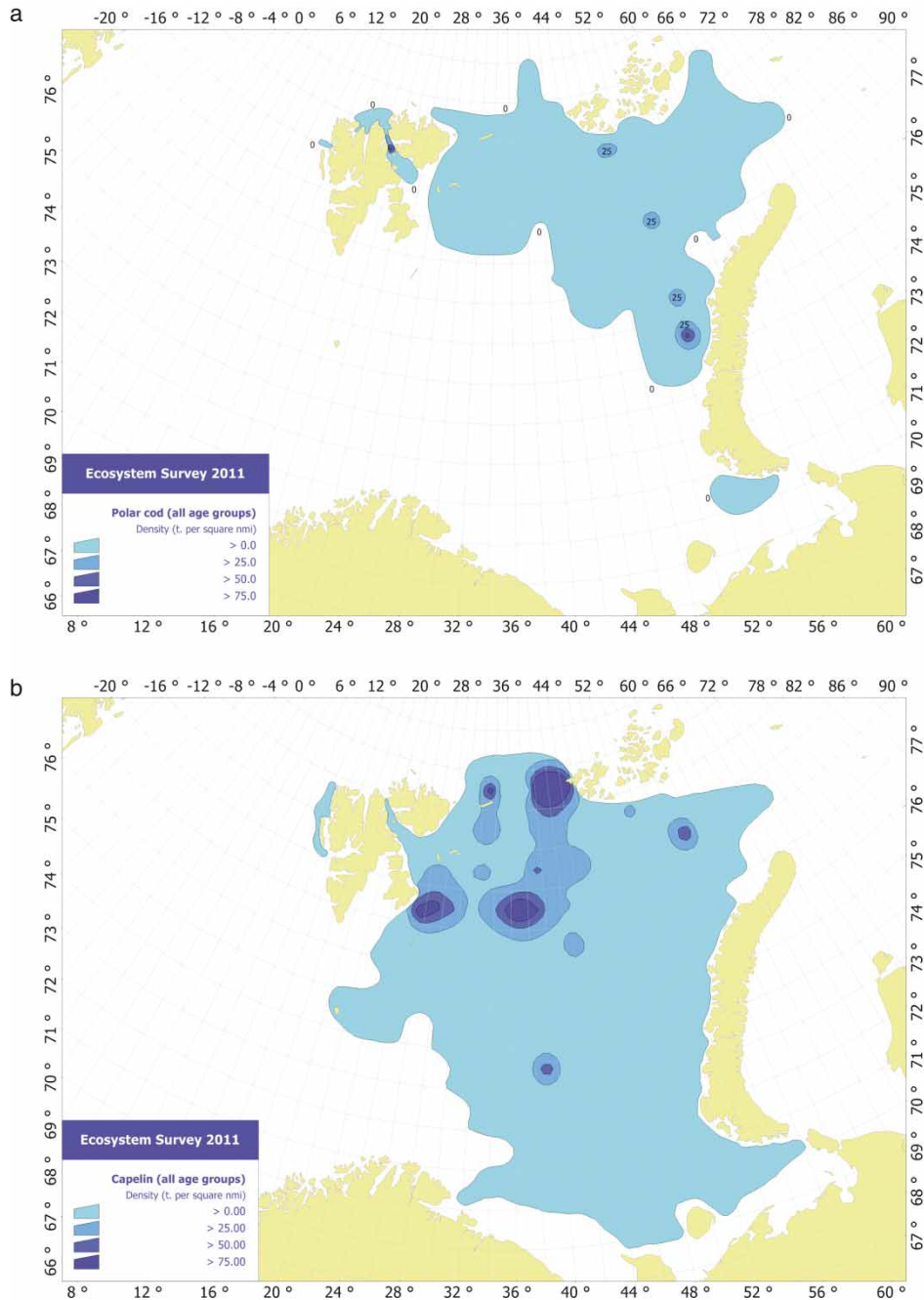


Figure 3. Distribution of biomass (t nm^{-2}) for polar cod (a) and capelin (b) in the Barents Sea during August–September 2011 (Anon 2011). Maps are drawn based on acoustic stock size estimates made during the Joint Norwegian-Russian ecosystem surveys. The contour plot of fish biomass is made from estimated fish density in 1° latitude \times 2° longitude grid cells, from acoustic estimates of fish numbers combined with length–weight keys based on trawl catches in each grid cell.

also found a good correlation between the north-eastern extension of the feeding distribution during autumn and stock size, which may be caused by the need to spread out northeastwards when the stock expands and the zooplankton production of larger areas needs to be utilized.

In recent years, the capelin stock has been rather large, in the range of 3–4 million tonnes. Together with the fact that the temperature has been above

normal, this might explain why the main concentration was found very far north, e.g. in 2011 (Figure 3b), when the main concentration was located between 77° and 81°N , which is farther north compared to most years in the period 1972–2011 (Gjøsæter et al. 2011). In the period 2007–2011, capelin were also detected north and northwest of Svalbard, which is less typical. The amount of capelin found there, however, was small (i.e. present in trawl catches).

Relationships of polar cod and capelin to sea ice

The retraction of the ice edge during summer likely plays an important role in the feeding of both polar cod and capelin. The so-called ice-edge effect (Sakshaug & Skjoldal 1989), with enhanced primary and secondary production, is based on the physical and biological processes that occur during the seasonal melting of the marginal ice zone (Falk-Petersen et al. 2000). During winter, no production takes place under the ice, while brine rejection during freezing and breakdown of the summer pycnocline will cause turbulence and replenishment of nutrients. When the ice melts, this has the double effect of stabilizing the upper, nutrient-rich water layers, and allowing light to penetrate into the water. Consequently, intense algal blooms will take place in the marginal ice zone (Engelsen et al. 2002, 2004), and secondary producers will follow behind (Wassmann et al. 2006; Søreide et al. 2010). Ice algae, which start to bloom on the underside of the ice about 2 months before the phytoplankton blooms, may constitute 20% of the primary production in the northern Barents Sea (Hegseth 1998). Ice algae represent an early food source for some zooplankton species (e.g. *Calanus glacialis* Jaschnov, 1955) after their winter diapause (Søreide et al. 2010). Even though the blooms are limited in time and space, they will generally follow the receding ice edge northwards, and for this reason the ice edge effect is thought to be of special importance for planktivorous fishes.

Polar cod use the ice as habitat for feeding on ice-associated fauna as well as allochthonous zooplankton (Lønne & Gulliksen 1989; Søreide et al. 2006). Thus, the ice-algal stable isotope signal can be traced to polar cod in the sympagic food web (Søreide et al. 2006). In the marginal ice zone, the two species may occur sympatrically in the pelagic system, but polar cod is the only fish species that also resides inside the pack ice (Lønne & Gulliksen 1989; Gradinger & Bluhm 2004). This is made possible by the possession of antifreeze components (glycoproteins) in its blood (Osuga & Feeney 1978), which prevents freezing at sub-zero temperatures. The ice ridges and cracks in the ice provide refuge for polar cod from predators (Gradinger & Bluhm 2004). Drifting sea ice mostly serves as a habitat for juvenile polar cod (ages 1 and 2; Lønne & Gulliksen 1989; Hop et al. 1997b), and they become part of the pelagic stock when the ice melts. Large schools are found below sea ice during winter (Benoit et al. 2008; Geoffroy et al. 2011) and also during summer–autumn (Crawford & Jorgenson 1990, 1993, 1996). In the Canadian high-Arctic, the landfast ice may persist until early August (Hop et al. 1997b) and, after the break-up, drifting sea ice moves in and out for the

bays depending on the wind conditions. Adult polar cod schools have been observed below sea ice as well as in open water from June to September (Crawford & Jorgenson 1990; Hop et al. 1997b). Schools have been persistently present in Allen Bay, Cornwallis Island, for up to two months (Welch et al. 1993). When landfast ice is present, white whales and narwhals typically travel along the ice edge, but may also dive below it (Bradstreet 1982; Asselin et al. 2011). Access to polar cod schools by white whales is limited by their swimming speed (about 2 m s^{-1}) and duration of dives (about 10 min; Martin & Smith 1992). If a cod school resides 200 m below fast ice, it will be inaccessible to whales > 600 m from the ice edge. Ringed seals can maintain dive holes in the ice, but their densities are typically low in landfast ice ($0.5\text{--}1.0 \text{ ind. km}^{-2}$; Smith 1987), with highest abundance close to ice edges (Bradstreet 1982). Seabirds can also dive below the ice, but their diving range is generally limited to < 100 m and they only have access to schools right below the ice from leads or in shallow waters. As polar cod are often recorded below sea ice throughout the summer and autumn, as well as during the winter, the ice cover obviously offers protection against marine mammal and seabird predators (Welch et al. 1993).

The development of eggs takes place below sea ice but may end in open water. Polar cod eggs have been found in the southeastern Barents Sea and coastal areas of the Pechora Sea from January to June (Rass 1968). Larvae of polar cod are often found under ice cover near river plumes, which they may use as a thermal refuge during winter (Bouchard & Fortier 2011) and as feeding habitat during spring (Fortier et al. 1996). They utilize the nauplii of *Calanus glacialis* and *Pseudocalanus* sp., which are fuelled by the early production of ice algae (Tourangeau & Runge 1991).

The position of the ice edge varies greatly over years (Falk-Petersen et al. 2000), and it is much further north in warm years towards the end of the summer (September). The Polar Front is rather stable in the western Barents Sea, but is pushed further north in warm years in central and eastern areas. The primary production in the Barents Sea is greater in warm years than in cold years (Wassmann et al. 2005), and this presumably also enhances secondary production. Whether capelin extends its distribution to the ice edge during September–October, when the ice coverage is at its minimum in the Barents Sea, varies from year to year. During the early 1980s, when the capelin stock was large and the ice typically extended down to $76\text{--}77^\circ\text{N}$ during these months, the northernmost parts of the capelin distribution normally reached the ice. In

periods when the capelin stock has been smaller or the ice edge has been found further north, the northernmost capelin observations have been quite far south of the ice.

Comparison of life history and feeding ecology in polar cod and capelin

The polar cod spawns in winter beneath the ice, with peak spawning between January and February in Russian waters (Andriashev 1954), whereas the capelin spawns on the bottom along the north Norwegian and Murman coasts in sub-tidal areas during spring and summer (Table I). The oceanic capelin stock is rather flexible with regard to where and when it spawns. While the main spawning season is in March–April, spawning in July–August occurs some years, mainly in eastern spawning areas (Gjøsæter 1998).

The eggs of polar cod (1.5–1.9 mm), which are the largest among gadoids, are larger than those of capelin (0.65–1.0 mm; Table I). The polar cod generally produces about 9000–21,000 eggs (Andriashev 1954; Rass 1968), although higher numbers of 26,500 eggs have also been determined for 25-cm spawners (Hop et al. 1995) and even higher (30–60,000 range) in Russian waters (Rass 1941). The fecundity of capelin from the Barents Sea has been found to vary with the length of the fish (Pozdnyakov 1957; Gjøsæter & Monstad 1973; Galkin & Kovalev 1975; Huse & Gjøsæter 1997). For a large female capelin of about 18 cm length, the fecundity ranged from 10,000 to 20,000 eggs.

Since polar cod is a winter spawner (November–March), whereas capelin is a late-winter-spring spawner (March–April), the incubation times and hatching for the two species are different (Table I). The incubation time for polar cod eggs in the Barents Sea is 45–60 days at 1°C (Rass 1968), implying that eggs spawned in December–February could hatch from February to April. Around the Arctic, the mean hatching date varies from April in the Laptev and Beaufort Sea to early June in the Canadian high-Arctic (Bouchard & Fortier 2011). In the Barents Sea, the polar cod larvae are initially below the ice, but are subsequently found in open water masses as a result of oceanic drift by surface currents from spawning areas, e.g. northwest of the Pechora Sea (Ponomarenko 1967). Due to a shorter incubation time for capelin (15–50 days), the larvae appear in the upper pelagic zone from April to June, but they can also appear later for summer–autumn spawners. Hatched capelin larvae are carried into the central and eastern Barents Sea by the prevailing currents (Gjøsæter et al. 2011).

The larvae of both species are pelagic, feeding on eggs, nauplii and juvenile stages of copepods (Ponomarenko 1967; Fossheim et al. 2006; Godiksen et al. 2006). In the Barents and Kara Seas, the timing of hatching of polar cod seems to be closely tied to the development of *Pseudocalanus* sp. generations (Ponomarenko 1967). Small polar cod (13–17 cm) in the Barents Sea feed mainly (50%) on large Arctic *Calanus* spp. and other copepods (e.g. *Metridia longa* Lubbock, 1854; Figure 4a), whereas larger adults (> 21 cm) prey less on copepods (32%), but to a greater extent on amphipods (21%), such as *Themisto* spp. and *Onisimus* spp., and also on krill (4.5%) and juvenile polar cod (Bain & Sekerak 1978; Figure 4b). In ice-covered waters, polar cod also prey to some extent on ice-associated amphipods (Lønne & Gulliksen 1989; Renaud et al. 2012). Small capelin (< 12 cm) feed mainly on copepods (57%) and also on krill (19%) in the Barents Sea (Figure 4c). Larger capelin (> 12 cm) feed mostly on krill (52%) and on copepods (26%), but also on amphipods (2.9%) and other crustaceans (8.6%; Figure 4d).

Competition and predation

The extensive migrations of capelin towards northern areas, when the sea ice retracts during summer, allow capelin to utilize the secondary production in areas where few other planktivorous fish feed. The only species that likely is a competitor is the polar cod, since there seems to be a considerable overlap in zooplankton diets (Panassenko & Soboleva 1980; Orlova et al. 2009; Figure 4). When both species co-occur in the northern Barents Sea, capelin tend to have less body condition (up to 40% reduction in fat content; Orlova et al. 2009). There was less overlap in diets of polar cod vs. juvenile Atlantic cod and haddock (*Melanogrammus aeglefinus* L.) in Svalbard waters (Renaud et al. 2012), although herring could be a competitor to both species and also a predator on capelin larvae (Huse & Toresen 2000). In fjords in Greenland, polar cod show considerable dietary overlap (Schoener's Index 0.6–0.7) with the Arctic gadoid *Arctogadus glacialis* Peters, 1872 (Christiansen et al. 2012). However, there was some spatial segregation in feeding habitat, with polar cod being more associated with the pelagic food web, feeding on *Metridia longa* and other pelagic prey.

The northward summer feeding migration of capelin may be an adaptation to avoid predators, mainly the Atlantic cod, which is a main predator of capelin (Mehl & Yaragina 1992; Lilly 1994; Bogstad & Mehl 1997). However, while Atlantic cod will normally avoid water <0°C, such as the Arctic waters masses in the northern Barents Sea,

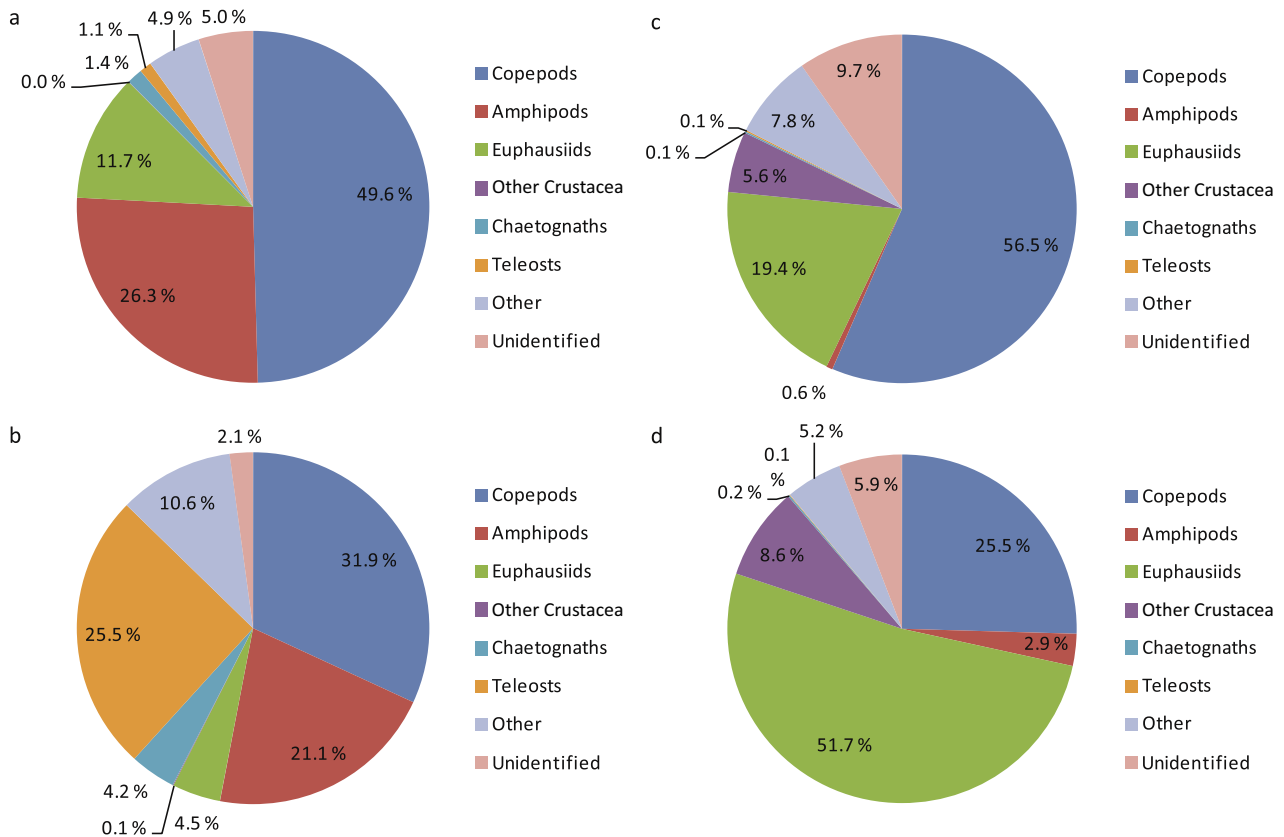


Figure 4. Relative dietary composition for polar cod length groups 13–15 cm (a) and 21–27 cm (b) and capelin < 12 cm (c) and > 12 cm (d) in the Barents Sea. Stomach data are based on Partial Fullness Index (PFI), pooled for years 2006–2009, for polar cod (Bogstad et al. 2011) and capelin (Dalpadado & Mowbray 2013).

they have been observed feeding on capelin in waters at least down to -1.0°C . Capelin may constitute >50% of the diet of Atlantic cod, when the capelin has high abundance in the Barents Sea (Bogstad & Mehl 1997; Link et al. 2009). The polar cod is also preyed upon by Atlantic cod, but generally constitutes only a small fraction (<10%) of their diet (Bogstad & Mehl 1997). The main reason for this is that the population of capelin normally is several times larger than polar cod, e.g. $3\text{--}4 \times 10^6$ t capelin versus $0.5\text{--}1.5 \times 10^6$ t polar cod in the Barents Sea. Also, the Atlantic cod has no access to a large part of the polar cod population in sub-zero water masses and inside the pack ice, whereas capelin can be pursued almost through their entire distribution range, except when they are in the vicinity of the ice edge. However, in periods when the capelin stock is small, such as during the mid 1980s and mid 1990s, the consumption of polar cod by Atlantic cod reached $4\text{--}6 \times 10^5$ t or about half the consumption of capelin during those years (Gjøsæter et al. 2009). Larval capelin are heavily preyed upon by herring during their drift into the southern Barents Sea (Hamre 1991; Huse & Toresen 2000; Hallfredsson 2006). Thus, when the biomass of young herring is

high in the Barents Sea, the capelin biomass is generally low.

Potential food web effects of sea ice reduction and temperature increase

The sea ice has been reduced substantially, about 9% per decade for the ice minimum in September, and about 2% per decade for winter maximum (Comiso 2006; Serreze et al. 2007). The seasonal decline in 2012 led to a record-low sea ice extent in September (National Snow and Ice Data Centre, Boulder, Colorado). The consequence is a drastic reduction in the sympagic habitat available for juvenile polar cod as well as its ice-associated prey and predators (Søreide et al. 2006; Hop & Pavlova 2008). Declining trends in Arctic sea-ice cover, with increased sea surface temperature and freshwater discharge, will potentially alter the timing and success of the reproduction and larval development of polar cod. Newly hatched polar cod often occur in freshwater plumes, in turbid waters with reduced light conditions below the ice (Bouchard & Fortier 2011). Earlier removal of the ice cover, or increased temperature, could result in earlier hatching and better survival of winter hatchlings (Bouchard &

Fortier 2011). On the other hand, the availability of suitable zooplankton prey may be reduced in the upper part of the water column if their early food sources fuelled by ice algae disappear. The polar cod larvae would also be more vulnerable to predation by visual predators while feeding in open water. Both direct and indirect effects of reduced ice cover also apply to juveniles, which are partly sympagic in the high-Arctic, and this could alter the subsequent recruitment to the stocks. In the Amundsen Gulf of the Canadian Arctic, the polar stock has been estimated as 257,400 tonnes during the freeze-up period (Benoit 2011), and because other parts of the Canadian Arctic Archipelago also host high biomass of polar cod (Crawford & Jorgenson 1990, 1993, 1996), the total stock of polar cod in the Canadian Arctic is likely comparable to the pelagic biomass in the Barents Sea (Benoit 2011). Loss of the ice habitat and its protective coverage to schooling fish will likely increase their vulnerability to predation and ultimately cause reductions in polar cod populations in the high-Arctic. This will mainly affect polar cod in shallow waters through increased accessibility to avian predators, but also the deep aggregations below landfast ice (e.g. Benoit et al. 2008), since they will become more accessible by deep-diving predators, such as ringed seals and white whales, with recorded diving depths of 230 m (Benoit et al. 2010) and 350 m (Martin & Smith 1992), respectively.

With warming scenarios in the 6°C increase range for an ice-free Arctic Ocean and the Barents Sea by the end of this century (Christensen et al. 2007; Slagstad et al. 2011), increased competition with other pelagic species, such as capelin, herring and juvenile haddock, is expected (Orlova et al. 2009; Renaud et al. 2012). These three species were caught in Kongsfjorden, Svalbard, in 2006 (H. Hop, unpubl. data), which was the first of a series of warm years (2006–2008) with warm water (3–4°C) and little ice in this fjord. The main water masses of some of the fjords in Spitsbergen may eventually become too warm for polar cod. In late July 2006, the water temperature in Kongsfjorden rose to 7.5°C at 80 m depth outside Ny-Ålesund (H. Hop, unpubl. data).

Both capelin and Atlantic cod, as well as herring, have expanded their distributions northeastwards in response to warmer temperatures (Drinkwater 2005; Stenevik & Sundby 2007), and this trend will likely continue as temperatures are expected to remain elevated. However, demersal fishes, such as Atlantic cod, are not likely to migrate north of the shelf edge. Pelagic fishes like capelin, herring and polar cod, on the other hand, could migrate into the Arctic Ocean. Location of spawning areas in the southern Barents Sea or further south along the Norwegian coast may

set limitations for expansion northwards because of higher energy expenditure during longer spawning and feeding migrations. Thus, the response to warmer temperatures will likely depend on whether spawning areas also can be displaced northwards. Capelin spawning along the Novaya Zemlya coast during the 1920s was described by Rass (1933). The extent of this spawning is unclear, but it shows that capelin were able to find suitable spawning beds in that area.

Another limitation for capelin may be lack of antifreeze production (Eastman et al. 1987), which may limit this species to water masses $> -0.5^{\circ}\text{C}$, or they have to stay away from ice at sub-zero temperatures in a supercooled state (Raymond & Hassel 2000). In Arctic waters around Svalbard, capelin would need to move out of cold water masses before the winter and into Atlantic water, which flows into the Barents Sea and also along the continental margins into the Arctic Ocean (Beszczynska-Möller et al. 2012). Mass mortalities of capelin have been observed after exposure to sub-zero water masses (Templeman 1965). However, their eggs are highly resistant to freezing (Davenport 1989), which could facilitate new spawning areas in the Arctic. Given a continued warming of Arctic seas and rapid decline in sea ice thickness and extent in the Arctic Ocean (Comiso et al. 2008; Polyakov et al. 2010), the capelin may become a year-round resident of the Arctic Ocean in a few decades. During the winter, it may avoid the upper water masses, as currently seen in the marginal ice zone where capelin distribution extends beyond the ice cover.

The pelagic production in the Barents Sea will likely increase when the ice-free season becomes longer or permanent (Wassmann et al. 2006), and there will probably also be substantial changes in the structure and energy flow of the marine food web as the oceanic environment becomes warmer (Falk-Petersen et al. 2007; Figure 5). Predators feeding on capelin, such as harp seal (*Pagophilus groenlandicus* Erxleben, 1777) and minke whale (*Balaenoptera acutorostrata* Lacepede, 1804), will follow. The food web in the northern Barents Sea and areas around Svalbard will probably develop towards the current situation in the central and southern Barents Sea. Capelin and herring may then alternately replace polar cod as the important key species in a revised Arctic marine food web. This, however, may not greatly influence the energy flow through the ecosystem, given that polar cod and capelin are of similar size and energy content (Table I).

Fish predators, such as seabirds, can shift prey species based on their availability (Gaston et al. 2003, 2009). In Hudson Bay (low Arctic), polar cod as forage fish delivered to Brünnich's guillemot

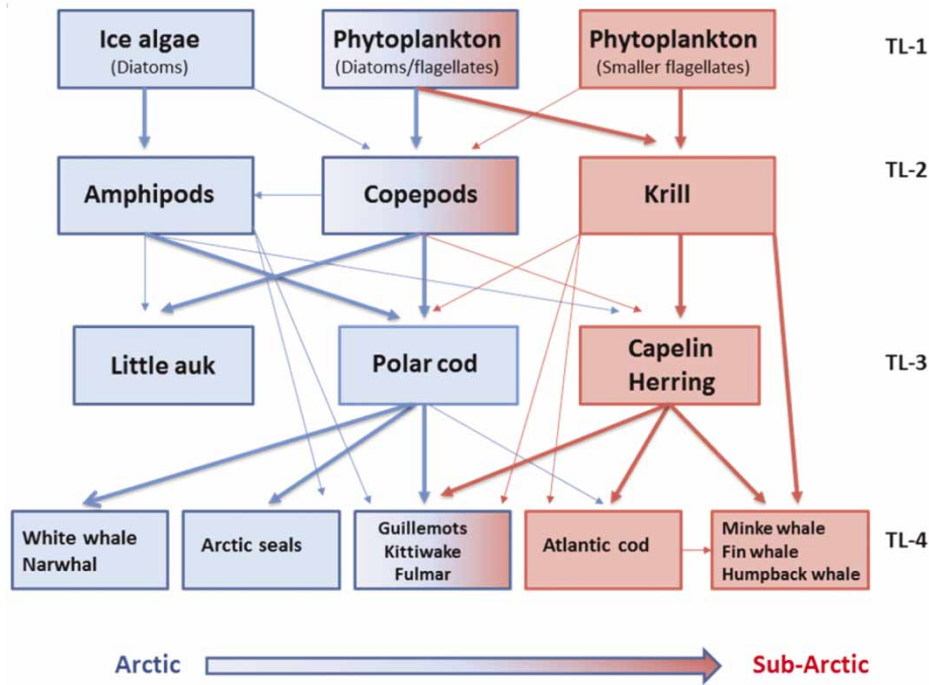


Figure 5. Polar cod and capelin in Arctic to sub-Arctic marine food webs, with indicated links and trophic levels (TL-1 to -4). Thickness of arrows indicates relative importance of energy flow based on known stomach content of predators. The system is expected to shift from Arctic (blue) to sub-Arctic (red) as the polar cod is being replaced by capelin and/or herring as a key forage species.

chicks was reduced from 43% to 15% of deliveries from the mid-1980s to the late 1990s, while capelin increased from 15% to 50% during the same period. Similar changes were observed for Kongsfjorden in 2007, when they came into the fjord and the diet of the black-legged kittiwake (*Rissa tridactyla* L.) shifted from 58% polar cod to 75% capelin (J. Welcker, Norwegian Polar Institute, pers. comm.). As long as fish prey of suitable size and energy content is available during the chick rearing period, it may not matter much if these are polar cod or capelin. Increased abundance of capelin in the Hudson Bay caused the Brünnich's guillemot to direct their foraging efforts preferentially towards this species (Gaston et al. 2003). However, when they switched from polar cod to capelin for feeding their young, nestlings had reduced growth rates, indicating that this change was not beneficial to the young (Gaston et al. 2005). If the existing Arctic predators on polar cod become reduced in abundance, such as reductions in several Brünnich's guillemot populations in the North Atlantic and the Arctic (Tanner & Varty 2009), their predation pressure will also be reduced. However, because fluctuations in seabird populations often are linked to climate oscillations as well as the underlying food webs (Irons et al. 2008), positive effects on prey species are difficult to show. Top-down effects with negative outcomes have been detected,

such as depletions of polar cod schools after intense feeding events (Welch et al. 1993).

Plankton feeders, such as polar cod, capelin and herring, all feed on abundant zooplankton. Even though there is some evidence of dietary preferences (e.g. more krill for capelin), there is also a dietary overlap as well as variations in diet based on relative zooplankton abundance (Figure 4). Thus, top-down effects from changes in plankton feeding fishes would most likely not result in major changes in zooplankton abundance. However, the fluctuating capelin population in the Barents Sea may cause opposite variations in the abundance of their zooplankton prey (Gjøsæter et al. 2009). Zooplankton distribution and composition may also change in response to increased advection of Atlantic water or warmer temperatures, with an estimated 3-fold increase in secondary production of *Calanus finmarchicus* (Gunnerus, 1770) but a 10-fold decrease in the Arctic *Calanus glacialis* (Slagstad et al. 2011). Such changes are already evident in the West Spitsbergen Current and fjords in Spitsbergen, where the boreal *Calanus finmarchicus* is advected with Atlantic water masses and has become increasingly dominant (Willis et al. 2008; Carstensen et al. 2012). Smaller *Calanus* prey, with less energy content, could then favour capelin over polar cod, based on their food preferences. On the other hand, greatly

fluctuating population numbers in capelin (Figure 1) may result in a more unpredictable food supply for fish-eating predators and lower ecosystem resilience, with potentially large bottom-up effects on seabirds (Erikstad 1990; Gjøsæter et al. 2009). Capelin may also be less available prey during critical times of the year in the Arctic, such as spring, unless the spawning areas move northward to the Arctic islands.

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