Marine Environmental Research 166 (2021) 105262

Contents lists available at ScienceDirect

Marine Environmental Research

journal homepage: http://www.elsevier.com/locate/marenvrev

Review

Distribution and ecology of polar cod (*Boreogadus saida*) in the eastern Barents Sea: A review of historical literature

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ARTICLE INFO

Keywords:
Polar cod
Eastern Barents Sea
Kara Sea
Spawning
Larvae
Ecology
Distribution
Boreogadus saida

ABSTRACT

The polar cod (*Boreogadus saida*) has a circumpolar distribution and is the most abundant planktivorous fish in the Arctic. Declining sea-ice coverage impacts polar cod directly and also facilitates expansion of human activities in the region leading to increasing anthropogenic pressures on biota. Here we summarize current data and knowledge on polar cod from the Russian sector of the Barents Sea and discuss knowledge needs for the management of polar cod under changing environmental conditions and anthropogenic impacts. We review 36 Russian historical (1935 - 2020) sources of data and knowledge largely unknown to western researchers, in addition to sources already published in the English language. This effort allowed for digitalization and visualization of 69 separate datasets on polar cod ecology, including maturation, fertility, feeding intensity, diet, lipid content, length-weight relationships and seasonal variation in larval size. Our review suggests that polar cod abundances are particularly large in the eastern Barents Sea and adjacent waters. Here, we identify and discuss key knowledge gaps. The review of polar cod in the eastern Barents Sea revealed 1) major variation in the timing and area of polar cod spawning, 2) uncertainty as to what degree the polar cod is dependent on sea ice, 3) deficient knowledge of juvenile (e.g., 0-group) distributions, particularly in the north-eastern Barents Sea, 4) deficient knowledge of the species' genetic structure and spatio-temporal distributions, and 5) insufficient understanding as to whether ongoing environmental change may induce phenological changes affecting the availability of potential food items for polar cod larvae and their match in space and time. Filling these knowledge gaps would provide an important step towards the reliable knowledge base needed in order to perform well-founded management and impact assessment under environmental changes and increasing anthropogenic impacts.

1. Introduction

Successful ecosystem management depends on contemporary, multifaceted knowledge to ensure the production, structure and function of ecosystems under dynamic environmental conditions, and accounting for the co-existence of resource exploitation (e.g., fisheries, oil and gas extraction) and other anthropogenic impacts (e.g., shipping, tourism; Olsen et al., 2007). Given the large number of species, habitats and other ecosystem elements that could occur within a management area, it is neither possible, nor particularly useful, to attempt to measure effects on all possible receptors. A common management approach is to define Valued Ecosystem Components; environmental elements that

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https://doi.org/10.1016/j.marenvres.2021.105262
Received 27 October 2020; Received in revised form 5 January 2021; Accepted 9 January 2021

have scientific, ecological, social, cultural, economic, historical, archaeological or aesthetic importance (Beanlands and Duinker 1983). The polar cod (*Boreogadus saida*) has a high lipid content and plays a central role in the transfer of energy from Arctic zooplankton to higher trophic levels including piscivorous fish, seabirds and marine mammals (Pechenik et al., 1973; Welch et al., 1992; Hop and Gjøsæter 2013). Also, the species is caught in subsistence fisheries of indigenous people (e.g., Zeller et al., 2011; Christiansen 2017). Thus, it is viewed as a key species in the Arctic ecosystem and is well-recognized by management authorities as a Valued Ecosystem Component (e.g., NMCE 2015). Yet knowledge of polar cod is lacking in several critical areas for successful management and protection from disturbances.

Management of fish species requires data on total and spawning stock biomass, abundance/biomass and weight at age of each year class, maturity, recruitment and fishery and natural mortality (e.g., ICES 2018). These parameters vary in space and time and with the frequency, nature, and intensity of human-induced disturbances. Developing a management strategy that integrates sensitivity to disturbance regimes, therefore, requires understanding of species distributions, spatial patterns in disturbance factors, and species' traits (Jennings et al., 1998; French-McCay 2004; Zacharias and Gregr 2005).

The polar cod is a circumpolar species, with several separate populations (e.g., Klumov 1937; Moskalenko 1964; Ponomarenko 1968; Chernova 2018; Nelson et al., 2020) and it is regularly observed in ice-covered waters (e.g., Gradinger and Bluhm 2004; Melnikov and Chernova 2013; David et al., 2016; Christiansen 2017; Gjøsæter et al., 2020). The species is regarded as the most abundant fish species in Arctic shelf seas (e.g., Craig et al., 1982; Dolgov et al., 2011; Antonov et al., 2017; Johannesen et al., 2017; Marsh et al., 2020), and its life history and behavior (e.g., spawning, juvenile period, feeding) are adapted to the Arctic environment (Rass 1968). Polar cod display spatial traits that vary in response to environmental conditions including feeding preferences (Lønne and Gulliksen 1989; Efimkin, 2013; Dalpadado et al., 2016; Majewski et al., 2016; Prokopchuk 2017; Kuznetsova 2018), hatching dates (Bouchard and Fortier 2011), age composition and growth rate (Fey and Węsławski 2017),and reproductive strategy (Nahrgang et al., 2014). Similarly, feeding patterns vary through the year (Ponomarenko 2000a; Cusa et al., 2019). Despite links to sea ice, polar cod are frequently observed in large numbers in ice-free Arctic waters during summer and winter (Wienerroither et al. 2011, 2013), suggesting weaker sea ice dependence than for ice-obligate species such as ice algae, ice amphipods, ringed seals and polar bears. Also, a particular species' fate in response to declining sea ice is challenging to predict (Fortier et al., 2006; Eamer et al., 2013; Hop and Gjøsæter 2013; Varpe et al., 2015). The above-discussed seasonal and spatial variation in biological and ecological characteristics (e.g., diet, reproduction, age composition and growth) reinforces that management and impact assessment of the polar cod should account for population-specific data. Furthermore, uncertainty related to the species' sea-ice dependency and response to environmental changes suggest that the management plans should be continuously updated with integration of new knowledge.

The Barents Sea, a sub-Arctic shelf sea off the northern coasts of Russia and Norway, hosts one of the largest stocks of polar cod in the entire Arctic (Ponomarenko 1968; Hop and Gjøsæter 2013, Fig. 1). Polar cod within the Barents Sea are currently monitored during joint Norwegian-Russian surveys (Michalsen et al., 2013). Most literature suggests that the species spawns in two separate areas of the Barents Sea: an area east of Svalbard/Spitsbergen and an area southwest of Novaya Zemlya (e.g., Boitsov et al., 2013; Huserbråten et al., 2019). In the Svalbard/Spitsbergen area, gonad maturation and, consequently, spawning, are reported to be 1.5 months later as compared to the south-eastern Barents Sea (Boitsov et al., 2013). Polar cod spawning southwest of Novaya Zemlya are thought to belong to a larger stock distributed across the Barents, Kara and White Seas, distinct from the polar cod spawning in the Svalbard area (Ponomarenko 1968; Pechenik

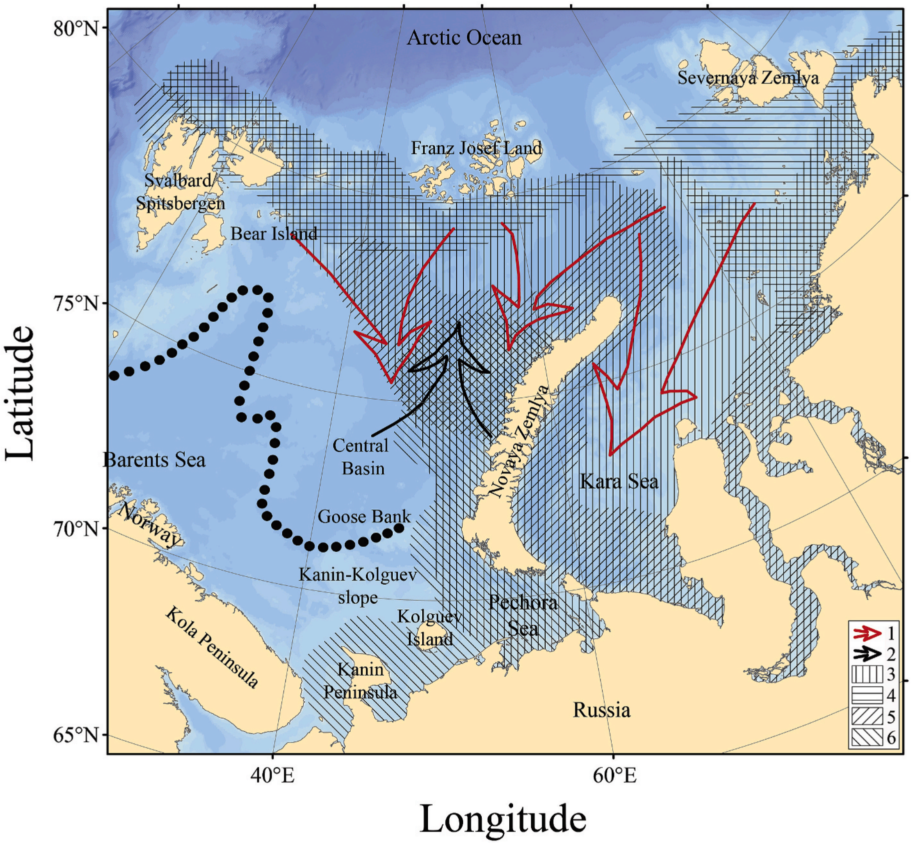

Fig. 1. Assumed distributions and migrations of polar cod in the Barents Sea and adjacent areas. 1: wintering and spawning migration (red arrows); 2: feeding migration, places of mass occurrence of polar cod (black arrows); 3: June to July; 4: August to September; 5: October; 6: from November–December to January–February. Occurrences near Svalbard/Spitsbergen possibly belong to a distinct population spawning in that area. Figure is modified from Ponomarenko (1968) in line with Matkovskiy (2006) and Mecklenburg et al. (2018). Dotted line indicates approximate position of the Polar Front. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

et al., 1973). Conclusive genetic studies have not been conducted, and the degree of mixing during feeding migrations outside of spawning periods is also unknown.

Our understanding of Arctic marine ecosystems is incomplete in many ways, not the least with respect to processes occurring during winter (Berge et al., 2015). Here we gather and interpret historical knowledge acquired by Russian scientists and interpret this knowledge in the context of contemporary investigations. We focus on results from the eastern Barents Sea, Kara Sea and White Sea, which we will refer to as the "eastern polar cod" stock. Publication traditions have resulted in a rich Russian literature on marine ecology being largely unknown by European and North American researchers. Current understanding, therefore, is missing this critical body of literature which can aid and inform the development of management procedures. We here review historic literature and data on eastern polar cod ecology, life history, distribution and exploitation. Finally, we identify key knowledge gaps, in order to effectively manage and assess impacts to the eastern polar cod.

2. Material and methods

Detailed studies of polar cod in the Russian sector of the Barents Sea were conducted from approximately 1930 to 1970, often based on fisheries data. We compiled information on species biology, ecology and fisheries across the Barents, White and Kara Seas. This was done by reviewing the results of multiple historical investigations and digitizing historical figures and tables to better visualize, assess, and synthesize the existing research and data. Sources of information include peer-reviewed articles and books that included data regarding distribution, size and age composition, reproduction, feeding habits, fishery and stock assessments of polar cod. Much of this information up until 1970s has been summarized by Pechenik et al. (1973). The later data on polar cod have been presented in the book of Boitsov et al. (2013), where a full list of Russian publications on polar cod was also presented. Data on 0-group (August–September) size composition in the eastern Barents Sea were obtained from reports of surveys conducted by the Norwegian Institute of Marine Research (IMR) and the Russian Knipovich Polar Research Institute of Marine Fisheries and Oceanography (PINRO) (since 2019 – Polar Branch of Russian Federal Research Institute of Fisheries and Oceanography) in the period 1966–1993 (Table 1). Selected life history data, including length, weight, age and fertility (i.e., the actual reproductive performance of an individual; Bradshaw and McMahon 2008) and data on feeding intensity, diet and lipid content were extracted from tables and figures available in the above-mentioned literature as well as other articles (Table 1). Data from tables were copied or digitized from original sources and cross-checked to correct for errors. Figures were scanned and uploaded to the program WebPlotDigitizer which allows extraction of numerical values (Rohatgi 2019). The datasets are provided as supplementary material.

Sampling of polar cod was carried out using a combination of gears, depending on requirements and availability, including horizontal, vertical and oblique towing gear, covering the whole water column. The data presented here are a compilation of data collected using these different sampling methods which might differ among areas and years. Eggs and larvae of polar cod were sampled with gear including IKS-80 ichthyoplankton nylon nets (0.57-mm mesh size), Nansen silk nets (50-cm diameter opening with 0.33-mm mesh size), ring trawl nylon nets (160-cm diameter opening with 3-mm and 5-mm mesh size), and a fine-meshed net, installed on top of a bottom trawl. Vertical sampling was carried out from the bottom or from 50 m to the surface. Horizontal sampling comprised 10-min tows at 0–15 m depth. At deeper stations, the ring trawl and the net installed on top of the bottom trawl were employed (Baranenkova et al. 1964, 1966; Ponomarenko 2000b). Juveniles and adult fishes were sampled by bottom and mid-water trawls with a 10-20-mm mesh size cod end.

Biological sampling included morphological measurements (total length and weight), reproductive parameters (maturity stage, gonadal mass, fertility), diet identification (stomach fullness and prey registration/weighting) and otolith sampling for age determination. To determine individual fertility, female gonads were weighed to the nearest 0.01 g and then fixed in a 4% formalin solution. From mature ovaries, 1 g of eggs was extracted and counted. Fertility was calculated by extrapolating the number of eggs in 1 g to the total gonad mass. For aging purposes, otoliths were extracted and age-determined under a microscope. Values representing fertility at age, length or weight were averaged for each class group (Shleinik 1978). As the polar cod accumulates lipids in the liver, the fat content was estimated as the ratio between liver mass and body mass, expressed as a hepato-somatic index (in %) (Pechenik et al., 1973).

Table 1
Biological parameters of polar cod from studies in the eastern Barents Sea.

Source	Area(s)	Years	Biological parameters
Baranekova et al. (1964)	Southeast, Northeast Barents Sea	1934, 1936, 1958, 1959, 1961	Post-larvae length distribution
ICES (1966, 1969–1971, 1974, 1977, 1978, 1980, 1981, 1984, 1985–1988, 1990–1992, 1994)	Eastern Barents Sea	1966, 1969–1971, 1974, 1977, 1978, 1980, 1981,1984–1988, 1990–1993	Post-larvae length distribution
Pechenik et al. (1973)	Eastern Barents Sea	1970	Adult length, weight, age, fecundity
	Eastern Barents Sea	1969	Diet
	Eastern Barents Sea	1969	Lipid content
	Eastern Barents Sea	1969	Stomach fullness
Shleinik (1978)	Eastern Barents Sea	1962–1976	Adult length, weight, age, fecundity
Ponomarenko (2000b)	Barents Sea	1956–1961 (averages over whole period)	Post-larvae length and weight relationship
Boitsov et al. (2013)	Barents Sea	1969–1988 (averages over whole period)	Adult length, weight, age, fecundity
	Novaya Zemlya	1969–1990, 1995–1997, 1999, 2001–2005	Adult length, age, fecundity
	Eastern Barents Sea	1977–1978, 1980–1986	Post-larvae length distribution and weight
	Eastern Barents Sea	1970–1998 (averages for the periods 1970–1980, 1981–1990, 1991–1998, 1995–1998)	Maturation (cumulative) as a function of length

3. Review of Russian data

3.1. General distribution

Research and fisheries data suggest that polar cod can be found in the entire northern, northeastern and eastern parts of the Barents Sea (Yudanov 1976; Wienerroither et al., 2011, 2013, Figs. 1 and 2). Most data suggest that adult fish from the eastern polar cod stock conduct two major seasonal migrations: one pre-spawning/spawning/winter migration (Quarters, Q4 [October–December] and Q1 [January–March]) and

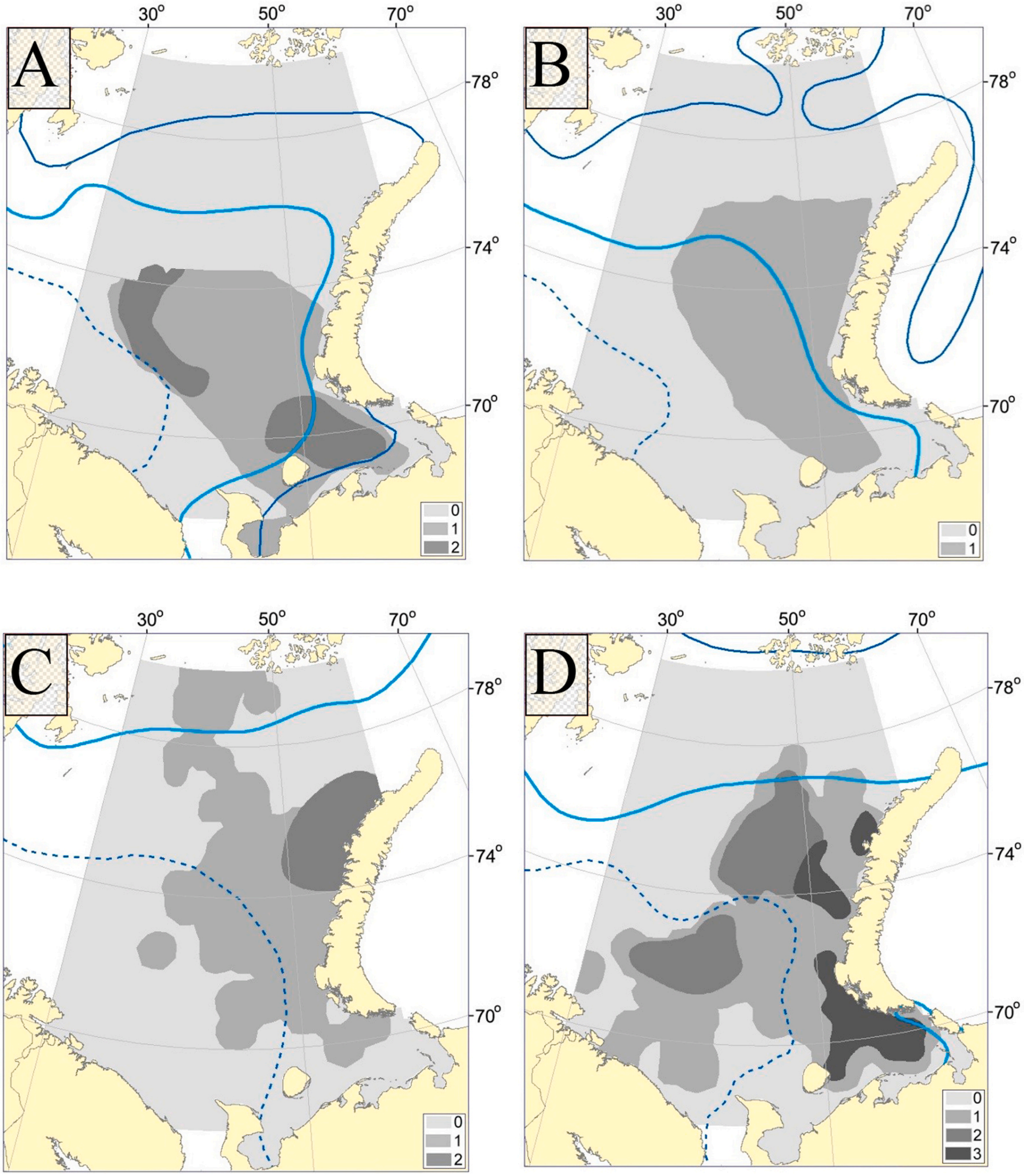

Fig. 2. Density maps of polar cod aggregation by quarters, based on fishery statistics data. 0: no catch; 1: <5 tons per hour of trawling; 2: 5–20 tons per hour of trawling; 3: >20 tons per hour of trawling. The dark blue line shows minimum sea ice extent, the dotted line shows the maximum sea ice extent, and the light blue line shows the average sea ice extent. A) January–March; B) April–June; C) July–September; D) October–December. In addition to catch data registered during the fisheries on polar cod, conducted in October–December, by-catch data of polar cod were registered during the year-round commercial fishing of Atlantic cod. The maps were generated based on seasonal ranked distributions of polar cod, i.e., summaries of long-term data for the observation period (1977–2001) based on fishing statistics with expert additions of MMBI and PINRO (PINRO 2006; Shavykin and Ilyin 2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

one post-spawning and feeding migration (Q2-3 [April–September]) (Pechenik et al., 1973; Boitsov et al., 2013, Fig. 1). These overall distribution patterns are supported by quarterly density maps of polar cod aggregations based on Russian commercial fisheries data (Fig. 2). These migrations lead to aggregations of polar cod during winter months, whereas the stock is more dispersed and evenly distributed across its range for the rest of the year. In general, the distributions of polar cod are thought to depend on environmental factors including water temperature (Boitsov et al., 2013).

The Russian reports highlight seawater temperatures, ocean currents, sea ice distribution and food availability as drivers of the reported spatio-temporal patterns (Rass 1968; Pechenik et al., 1973; Boitsov et al., 2013). Outside of the spawning period, polar cod are generally found where the water masses are coldest (i.e., temperatures below 0 °C; Hognestad 1968). The first scheme of seasonal migrations of polar cod in the Barents Sea was presented by Moskalenko (1964). Later, many Russian publications provided detailed descriptions of polar cod distributions and migration routes in Russian waters (e.g., Ponomarenko 1968; Pechenik et al., 1973). Interpretations of migrations routes are based on research surveys and reports from scientists and fishermen (e.g., Ponomarenko 1968; PINRO 2006; Shavykin and Ilyin 2010). Sampling and monitoring of pre-spawning polar cod, as well as eggs and larvae, have primarily been conducted in ice-free waters, thus potentially biasing conclusions.

3.2. Spawning migration

The spawning migration towards the southern distribution range is initiated in August–September, when polar cod are most widely distributed, close to the ice edge in the northwest, north and northeast (Ponomarenko 1968; Boitsov et al., 2013). At this time of year, the Barents Sea polar cod is found across the entire northern areas of the Barents and Kara Seas, possibly further to the east than Severnaya Zemlya (Ponomarenko 1968; Wienerroither et al., 2011; Boitsov et al., 2013).

In most years, spawning migration into the southern Kara Sea and southeast Barents Sea is observed. These are areas where sea ice has historically formed in wintertime, but recent years have been largely ice-free (Rass 1968; Ponomarenko 1968; Fetterer et al., 2002; Boitsov et al., 2013). From October–November, polar cod move from the Kara Sea, along Novaya Zemlya and into the Barents Sea (Pechenik et al., 1973; Boitsov et al., 2013). The highest annual densities are observed in the October–December period, sometimes resulting in catches of >20 tons of polar cod per hour of commercial trawling along the western coast of Novaya Zemlya and in the Pechora Sea (Fig. 2D). Based on observations of pre-spawning polar cod aggregations and recently hatched larvae, polar cod is assumed to use the shallow Kolguev Island - Pechora Sea area in the south-eastern Barents Sea as a key spawning ground in warm years (Pechenik et al., 1973; Boitsov et al., 2013), although several additional spawning grounds have been identified. In cold years, spawning shifts further to the west, near Kanin Peninsula and into the White Sea (Ponomarenko 1968; Boitsov et al., 2013), although spawning in the White Sea seems to result in low offspring survival (Altukhov 1981). For instance, in the relatively cold winter of 1967, spawning was observed as far west as the Central Basin and the north-central area, and in the winters of 1968 and 1969 spawning was limited to the slopes of the Goose Bank (Shleinik 1970). Spawning is also recorded in the brackish waters of river estuaries along the coast (Yudanov 1976), and polar cod regularly spawn along the east coast of Novaya Zemlya (i.e., within the Kara Sea; Boitsov et al., 2013). The first observations of spawning in the Barents Sea are often made in mid-December (Ponomarenko 2000b), but spawning is most intensive in January–February (Boitsov et al., 2013). Survey data from open waters along the east coast of Novaya Zemlya indicate that spawning in those areas may take place as early as October–December (Borkin 1990; Ponomarenko 1968; Boitsov et al., 2013). However, interannual variations in the timing of spawning are likely due to environmental variations (Borkin 1990). For instance, in the cold year 1971, the first spawning individuals were recorded in Kolguev area at the end of November, and it was estimated that 60% of spawning was completed by the end of the year (Shleinik 1973). In other years, spawning may extend until April (Ponomarenko 1968). Mass migrations to the spawning areas in the south-eastern Barents Sea and the White Sea did not occur every year (e.g., Yudanov 1976), and various sources indicate that also the abundance of polar cod influence the timing of the spawning. For instance, in years with low polar cod abundance, fish enter the spawning areas later than in years with high abundance (Boitsov et al., 2013). Furthermore, in years with particularly low abundance (e.g., in 1977–1980 and 1983–1991), dense aggregations of polar cod in the spawning areas have barely been observed (Boitsov et al., 2013). Therefore, fishing for the species in these areas was also carried out irregularly (Yudanov 1976).

High densities of polar cod in shallow coastal waters off the northern coast of Russia in wintertime sometimes lead to mass-strandings after storm events: in the Kara Sea, strandings of polar cod 50–100 cm wide, 30–50 cm high, extending over tens of kilometers have subsequently been observed (Ponomarenko 1968). This suggests that polar cod schools occur in surface waters close to the shore, or may be forced into shallow waters by predators, as has been observed in the Canadian Arctic (Hop et al., 1997; Welch et al., 1993). In the eastern Barents Sea, diurnal vertical migrations have been observed between shallow waters in nighttime and bottom layers in daytime during autumn and winter (Shleinik 1970).

3.3. Maturation and spawning

The data indicate that some individuals of polar cod in the eastern Barents Sea can become mature at a size of 8 cm, whereas 50% of the individuals of between 13 and 14 cm are mature and 100% of the individuals >22 cm are mature (Fig. 3), a finding that is supported by data from Arctic waters of the western Barents Sea (Nahrgang et al., 2014). No long-term trends in size-at-maturity have been recorded (Boitsov et al., 2013). Although spawning may occur in ice-free waters (i.e., in warm years; Boitsov et al., 2013), most spawning is assumed to be conducted under sea ice or close to the ice edge (Rass 1968; Shleinik 1973; Borkin 1990). Although direct observations are sparse, spawning is thought to occur at 20–60 m depth (Boitsov et al., 2013), at temperatures above 0 °C and <2 °C (Ponomarenko 1964). Spawning has been presumed to be initiated by the sea ice formation (which usually occurs in November) (Pechenik et al., 1973; Boitsov et al., 2013).

The large, transparent eggs are buoyant (Aronovich et al., 1975), and the fertilized eggs are therefore assumed to rise to the underside of the sea ice (Yudanov 1976). The stable physical conditions under the sea ice are thought to protect the fragile eggs from temperature changes, mechanical effects of waves, and predation by visual predators, thereby favoring egg development and survival (Pechenik et al., 1973; Boitsov et al., 2013). Surprisingly, offspring survival has been observed after the eggs have been frozen into sea ice (Yudanov 1976).

3.4. Post-spawning and feeding migration

In March–April, post-spawning polar cod have been reported to migrate north and northwest to return to the ice edge, which has been traditionally located at the northern Kanin-Kolguev slope and at the southern and western slopes of the Goose Bank (Pechenik et al., 1973). Yet, others report that post-spawning fish remain in the spawning area until April–May (Shleinik 1970). The subsequent post-spawning migration has been termed a “feeding migration” (e.g., Rass 1968), but stomach fullness data indicate low feeding intensity until June; in March–April about 67% of the stomachs analyzed were empty or weakly filled (Pechenik et al., 1973, Fig. 4). Polar cod continue migrating northwards in May–June, more or less following the ice edge, with the largest fish moving first, from the central regions to the east and northeast along the Polar Front where temperatures fluctuate from 0 to −1.5 °C (Shleinik 1970; Pechenik et al., 1973; Boitsov et al., 2013). In

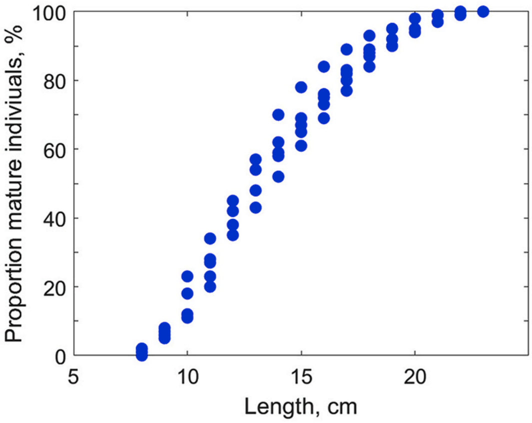

Fig. 3. Cumulative length at maturity of polar cod in the eastern Barents Sea. Averages for the time periods 1970–1980, 1981–1990, 1991–1998 and 1995–1998. Figure is based on data obtained from Boitsov et al. (2013).

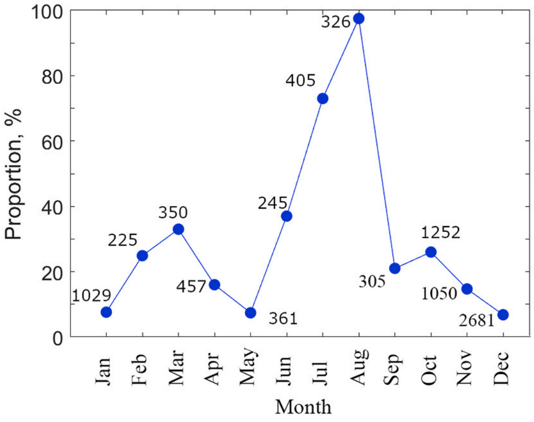

Fig. 4. Observed monthly variation in stomach fullness in adult polar cod (size range 11–36 cm, age range 2–7 years) in the eastern Barents Sea in 1969, expressed as the proportion of the stomachs being full or extended. Numbers in the plot corresponds to the number of stomachs sampled per month. Data were obtained from Pechenik et al. (1973).

this period (i.e., Q2), polar cod show little aggregation compared to other seasons (Fig. 2B), and small schools stay in the water column, without diurnal vertical migrations (Shleinik 1970). In July–August, feeding migrations continue to the north of Novaya Zemlya and the Kara Sea. From October–November, polar cod migrate southward from the Kara Sea to the spawning areas in the Barents Sea.

3.5. *Hatching and early life history*

Polar cod have the largest eggs and the lowest fertility among all species in the family Gadidae (Andriyashev 1954). Egg diameters range from 1.53 to 1.90 mm (Rass 1968). Russian data indicate a consistent, positive relationship between fertility and female age, body size and weight (Fig. 5; Shleinik 1978; Boitsov et al., 2013), typically ranging from ∼5000 eggs per fish of body size ∼12 cm to >60,000 eggs per fish of body size ∼30 cm.

After spawning, eggs and larvae drift with the ocean currents in the upper water layers in a north- and northwest direction. Egg development takes 1.5–3.5 months or longer (up to 5 months; Rass 1968; Borkin 1990, and references therein), and is temperature-dependent. Although hatching of polar cod has not been observed under natural conditions, it has been suggested that the event is timed to coincide with the break-up and melting of the sea-ice (Yudanov 1976; Ponomarenko 2000b). Moreover, high mortality of eggs and newly-hatched larvae, and subsequently low abundance of young polar cod, has been linked to early break-up of sea-ice during storms (e.g., Boitsov et al., 2013). Hatching normally occurs in May–June, which indeed is a period when sea-ice is often breaking up in the area (Borkin 2013; Boitsov et al., 2013). Laboratory experiments estimated incubation time in cold water (∼−1.5 °C) to 77–79 days (Altukhov 1981), whereas in temperatures of −0.3-2.5 °C (mean temperature: 0 °C) hatching occurred after 26–35 days (Aronovich et al., 1975). Hatching has been observed as early as March and as late as September (e.g., Baranenkova et al., 1966), likely as a result of variations in factors such as spawning time, seawater temperature, and sea-ice formation and breakup. Also, the presence of polynyas may promote earlier hatching, as observed in the Laptev Sea (Bouchard and Fortier 2008). Spawning in open water would normally imply egg development in warmer waters as compared to spawning below the sea-ice, and a shorter egg development time would therefore be expected. Eggs and larvae are also known to develop faster below sea ice in front of rivers, according to the freshwater winter refuge hypothesis (Bouchard and Fortier 2011). Larval size is highly variable and depends on factors including spawning and hatching date, water temperature and food availability (Kashkina 1962; Baranenkova et al., 1964; Boitsov et al., 2013), and spatial variability in these.

The larvae stay close to the surface (<10 m depth) the first days after hatching, until they undergo the transition to first-feeding larvae). Within 12–14 days (Aronovich et al., 1975; Borkin 1990). The farther larvae are from the ice edge, the greater their depth range (Borkin 1990). Eggs and nauplii of copepods are important food items for polar cod larvae, and their densities have been observed to be greater in the open water adjacent to the ice edge than in open water further away from the ice edge (Ponomarenko 1967; Borkin 2013). The underside of sea-ice presumably constitutes an appropriate predator refugium during early life stages. Larval and post-larval fish are found in the upper water layers until August–September, after which they gradually descend towards the seabed, where most individuals stay until March–April the following year (Ponomarenko 2000b).

In autumn the 0-group juveniles are normally observed in two separate areas of the Barents Sea: one area west of Novaya Zemlya and one area east of Svalbard/Spitsbergen (Eriksen et al. 2011, 2020; Boitsov et al., 2013). Most literature assumes that the 0-group juveniles found in the former area originate from spawning areas in the south-eastern Barents Sea, whereas those found around Svalbard/Spitsbergen largely originate from the spawning area east of Svalbard/Spitsbergen (e.g., Borkin and Oganin 2004; Ajiad et al., 2011; Gjøsæter et al., 2020). The spatial distribution of polar cod larvae varies among years depending on the interannual variation in water temperature (Boitsov et al., 2013), but even in normal and warm years larvae occurred far to the south in the area between Norwegian coast and Bear Island (Mukhina 2005). In cold years, the autumn distribution of 0-group juveniles extends westward from Novaya Zemlya and southwards from Svalbard/Spitsbergen, sometimes resulting in a continuous distribution of 0-group juveniles across the entire northern Barents Sea (Boitsov et al., 2013). In most years, the northern distribution limit of the 0-group juveniles is, not fully covered by the joint IMR-PINRO autumn survey, and, thus, the actual distribution of the 0-group larvae in Arctic waters of the Barents Sea is in many years not fully known (Joint IMR-PINRO survey reports 1966–2019, available from www.imr.no). However, in years when the ecosystem survey covers the entire northern Barents Sea (e.g., 2005–2006), a continuous distribution of 0-group polar cod between the two spawning areas is observed (Boitsov et al., 2013). As such, it is not

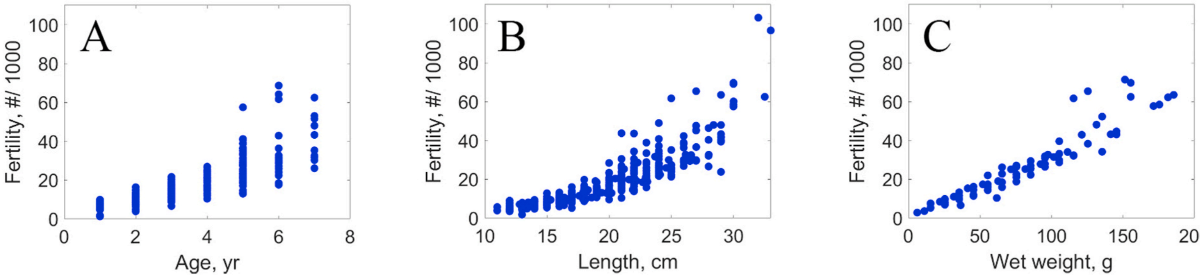

Fig. 5. Absolute individual fertility (number of eggs) of polar cod in Russian Barents Sea as function of age (A), length (B) and weight (C) of the spawning females. Sources: Figures are based on data obtained from Shleinik (1978) and Boitsov et al. (2013). Samples were collected during the pre-spawning period.

known whether the commonly observed non-continuous autumn distribution of 0-group polar cod in the northern Barents Sea is real or simply an artefact of incomplete survey coverage.

3.6. Development and growth

Laboratory studies of the development of juvenile polar cod showed that feeding started at 12–14 days after hatching, even though the yolk sac was not yet depleted (Aronovich et al., 1975). Until feeding started, the growth rate was 0.148 mm d^{-1}, after which it dropped to 0.065 mm d^{-1}. The absorption of the yolk sac was faster before than after the start of feeding; and after 22–24 days, the yolk sac was completely absorbed. Field data collected in the eastern Barents Sea from 1984 to 1986 indicate little variation in length-weight relationships for polar cod larvae and juveniles (Fig. 6; Ponomarenko 2000b; Boitsov et al., 2013). Polar cod metamorphosis from larvae to pelagic juveniles was completed at the size range between 27 and 35 mm (Ponomarenko 2000b).

Larval and post-larval data collected between June and January–February of the following year indicate large variations in the size of polar age-0 cod (Fig. 7; see figure caption for overview of sources). Also, there is apparently a strong interannual as well as spatial variation in larval size during summer. Whereas fish sampled in June and July were largely in the 5–14 mm range (most individuals were in the size range 6–8 mm and 7–9 mm, respectively), juveniles sampled in August–September varied greatly in size (15–70 mm), with a peak in abundance at approximately 40 mm. However, there were large variations among years. Higher (intra-annual and interannual) variation in size later in the year is not unexpected and is likely a consequence of different feeding and environmental conditions experienced by the fish.

The longevity of polar cod has previously been reported as being between 5 and 6 years (Andriyashev 1954; Falk-Petersen et al., 1986; Nahrgang et al., 2014); but 8–10-year-old fish are occasionally found (Pechenik et al., 1973; Boitsov et al., 2013, and citations therein). Age-1 polar cod are normally 8–9 cm long (Boitsov et al., 2013). During the next two or three years, annual growth is approximately 3–4 cm, but decreases with age (Boitsov et al., 2013). Polar cod can reach up to 40 cm, with a weight of about 430 g (Boitsov et al., 2013, and references therein). Based on the Norwegian-Russian demersal trawl survey data sampled in the Barents Sea in the autumns of 2004–2009, the mean length of polar cod was 11.5 cm (Wienerroither et al., 2011). The corresponding Norwegian-Russian winter survey data (February–March 2007–2012) indicates a mean length of 12.8 cm (Wienerroither et al., 2013). In the southeastern Barents Sea, the largest individuals are often caught in October (Ponomarenko 1977). No long-term trends in body size have been recorded (Boitsov et al., 2013).

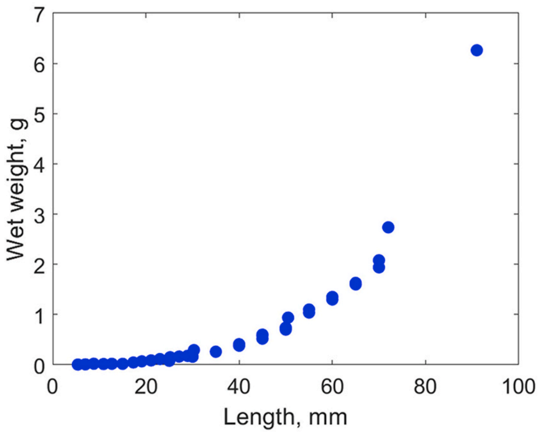

Fig. 6. Length-weight relationships for polar cod larvae and post-larvae in the eastern Barents Sea for the years 1956–1986. Figure is based on data obtained from Ponomarenko (2000) and Boitsov et al. (2013). Averages based on 2527 individual fish.

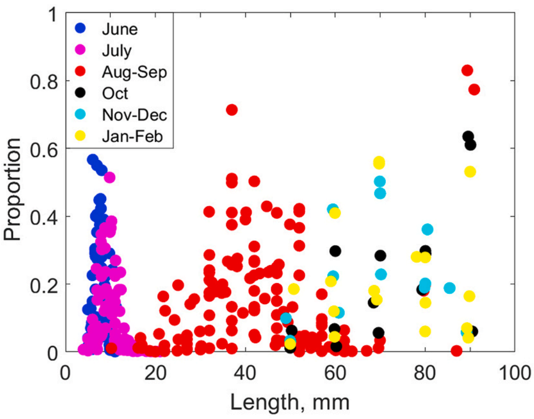

Fig. 7. Size distribution (mm) of polar cod larvae and post-larvae in various months of the year. Data are presented as proportions. For each period, multiple datasets are presented. Figure is based on data obtained from ICES (1966, 1969, 1970, 1971, 1974, 1977, 1978, 1980, 1981, 1984, 1985, 1986, 1987, 1988, 1990, 1991, 1992, 1994), Baranenkova et al. (1964) and Boitsov et al. (2013).

3.7. Feeding

3.7.1. Larvae feeding

Polar cod larvae display a period of mixed nutrition (yolk sac and external feeding) (Borkin 1990; Ponomarenko 2000b), a common feature among Arctic fish larvae, which is likely an adaptation to Arctic conditions characterized by high seasonal variability in food availability (e.g., Ottesen et al., 2011; Aune et al., 2018). They have a generalist diet, but prey items must be abundant and in close proximity to larvae due to their poor swimming ability. Graham and Hop (1995) reported that potential food items were eaten after the larvae had collided with them. Polar cod larvae have been reported to prey on pelagic larvae of bottom-dwelling molluscs and early stages of copepods (e.g., *Pseudocalanus* sp., *Limnocalanus* sp. [Zalesskikh 1987]). A field study from 1983 to 1984 showed that larvae in the size range 5.0–5.9 mm mostly prey on pelagic larvae of bottom-dwelling molluscs (57.1%), but also on copepod eggs and nauplii (Borkin 2013). These prey items were in the size range 0.15–0.60 mm. Later, when the larvae were in the size range 6.0–11.0 mm, they continued to prey mainly on mollusc larvae, but broadened their diet to include other items in the size range 0.15–0.90 mm, including *Pseudocalanus elongatus*, *Oithona similis*, cirriped nauplii, euphausiid eggs and polychaete larvae. This implies that larvae of size <11 mm can prey on many of the smaller mesozooplankton species present in the Arctic, which makes starvation less likely. Mollusc larvae have been proposed to be less mobile and therefore easier to catch than the more mobile copepod larvae (Borkin and Nesterova 1990; Borkin 2013). The polar cod diet becomes more diverse as the larvae grow to become juveniles and adults (Ponomarenko 2008; Borkin 2013).

3.7.2. Juvenile and adult feeding

The stomach fullness data for adult polar cod reflect seasonal and spatial variation in feeding intensity related to prey availability (Pechenik et al., 1973, Fig. 4). In Arctic marine waters, primary production in particular (Ji et al., 2013) and food availability for polar cod are highly seasonal (Pechenik et al., 1973). In 1969, during the months from September through May, >40% of stomachs were empty or weakly filled (range: ~41%–93%). In the summer months (June, July and August) the proportion of full or extended stomachs ranged from 37.0% (in June) to 97.5% (in August).

Stomach content data sampled in the eastern Barents Sea in 1969 also revealed a strong seasonal variation in feeding patterns (Pechenik et al., 1973, Fig. 8), largely indicating seasonal differences in prey availability. The juveniles (size range 50–70 mm) mainly prey on zooplankton, including *Themisto* spp. and adult *Calanus* spp. (Pechenik et al., 1973). For larger fish (>11 cm), lipid-rich *Calanus* spp., the biomass-dominant mesozooplankton during summer, constituted a key food source in the period from March through November (ranging 26.5–92.0% of the stomach content during these months). In May and June, euphausiids constituted 63.1% and 27.5% of the diet, respectively. Together, *Calanus* spp. and euphausiids dominated in the diet (>50% of the stomach content) from March through November (Fig. 8). From October–November, the diet of *Calanus* spp. and krill was gradually replaced by alternative prey items including bottom-dwelling organisms (Pechenik et al., 1973, Fig. 8). Indeed, benthic crustaceans (including shrimps), as well as polar cod (cannibalism) and capelin were important food sources in December (13.3%, 10.8% and 51.6%, respectively) and January (26.5%, 20% and 49.0%, respectively). Other prey categories included amphipods (*Themisto* spp.), arrow worms (*Parasagitta* sp.), comb jellies (Ctenophora) and molluscs (probably pelagic pteropods). For adult polar cod (2+ years), phytoplankton (most likely ice algae) made up 40.5% of the diet in February and 9.2% in March (Pechenik et al., 1973). Such phytoplankton consumption is thought to occur in association with sea-ice, and the importance of phytoplankton in the diet is reported to decrease with increasing distance from the ice edge (Pechenik et al., 1973). Yet, as most stomachs were either empty or weakly filled in February–March (Fig. 4), the amount of algae consumed by polar cod was likely limited. During 1956–1961 copepods (mainly *Calanus finmarchicus*; 41.7% by weight), fish (mainly polar cod juveniles; 26.8%), shrimps (10.2%) and hyperiids (9.7%) were the most important groups in the polar cod diet (Ponomarenko 2008). In summer-autumn 1980–1987 copepods (mainly *Pareuchaeta norvegica*), hyperiids (mainly *Themisto libellula*) and euphausiids (mainly *Thysanoessa raschii*) dominated in diet of polar cod (6–27 cm) by weight – 32.5, 32.3 and 21.1% respectively (Tarverdieva et al., 1996). More recent data on polar cod diet (2004–2005) in the eastern Barents Sea showed that hyperiid amphipods constituted important prey, together with *Calanus* sp., but also krill *Meganyctiphanes norvegica* for large fish (13–17 cm) (Orlova et al., 2009). The diet of small (9–13 cm) and larger polar cod also included juvenile pteropods, jellyfish, chaetognaths, gammarid amphipods and young fish (polar cod) of size 4–10 cm.

Both feeding intensity (Fig. 4) and diet composition (Fig. 8) were reflected in seasonal patterns in lipid content of polar cod adults (Pechenik et al., 1973). In 1969, the hepato-somatic index (i.e., the lipid content) in January to July was relatively low (median values of 6.7–9.1%), whereas values nearly doubled in August and remained elevated through December (median values 13.1 and 9.9%, respectively) (Pechenik et al., 1973, Fig. 9).

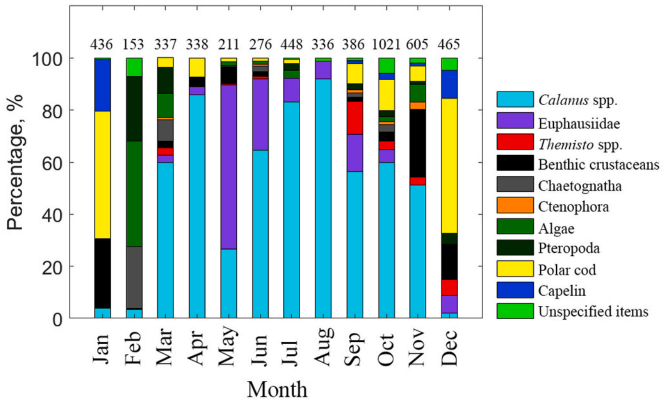

Fig. 8. Observed monthly variation in diet composition of adult polar cod (size range 11–36 cm, age range 2–7 years) in the eastern Barents Sea in 1969 (% of prey items registered). Numbers in the plot corresponds to the number of stomachs sampled per month. Data were obtained from Pechenik et al. (1973).

3.8. *Fisheries and biomass*

Polar cod has been fished throughout the last century, but with considerable variability in fishing intensity. A small-scale subsistence fishery was carried out by the Soviet Union from the beginning of the 1930s (Klumov 1935; Manteifel 1943), and intensive industrial fishing was initiated in 1969 (Pechenik et al., 1973). The species was exploited commercially by both Norway and the USSR from 1969 until 1973, peaking in 1971, reaching 331,000 tons caught by Russian vessels and 16,000 tons caught by Norwegian vessels (Pechenik et al., 1973). Harvesting combined with weak recruitment to the stock resulted in a diminished polar cod biomass during the second half of the 1970s (Borkin et al., 1987; Monstad and Gjøsæter 1987; Belikov et al., 1991). In 1982–1983, the stock recovered to some extent due to strong year classes in 1979 and 1980, but intensive fishery on juveniles of these year classes as well as the absence of new strong year classes, led to another period of low polar cod biomass from 1984 to 1997 (Borkin et al., 1987; Monstad and Gjøsæter 1987; Belikov et al., 1991). From 1998 to 2011, polar cod biomass was generally high despite large variation (Boitsov et al., 2013; McBride et al., 2016). A combination of low demand, high fuel prices and the introduction of a Russian resource fee in 2004 has largely led to a lack of commercial exploitation of the eastern polar cod in the last 15 years (Boitsov et al., 2013). In addition to variation in recruitment success and fisheries exploitation, factors including predation and incomplete monitoring survey coverage have been proposed as key drivers of the major fluctuations in observed stock biomass (Boitsov et al., 2013).

Both polar cod seasonal distributions and the extent and variability in sea-ice coverage in the Barents Sea impact which areas are accessible to fishing fleets, and hence the choice of polar cod fishing grounds (Fig. 10). For example, in the cold year 1998, the sea-ice coverage of the Arctic Ocean in November was 10.8 million km^2 (Fetterer et al., 2002) and included a significant portion of the Barents Sea (blue line in Fig. 10). Consequently, Russian fisheries in November were predominantly carried out close to the ice edge around Goose Bank and further south (Fig. 10). In contrast, in the warmer year 2007, sea-ice covered only 10.1 million km^2 of the Arctic Ocean in November (Fetterer et al., 2002) and the Barents Sea was nearly ice-free in November (red line in Fig. 10). That year, the Russian November fisheries on polar cod were

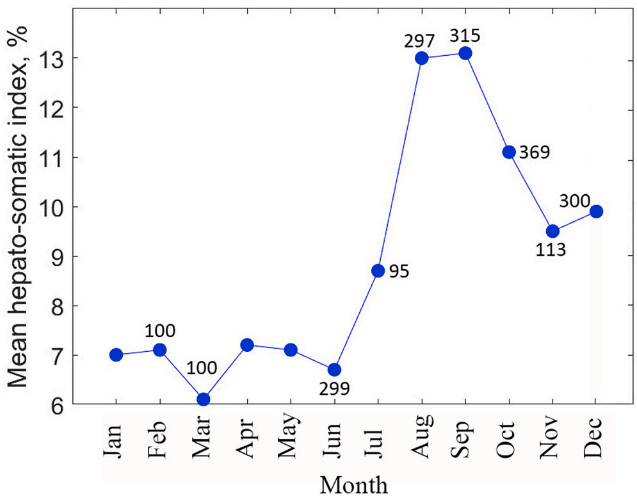

Fig. 9. Observed mean monthly variation in hepato-somatic index (i.e., lipid content) in eastern Barents Sea polar cod (size range 12-40 cm, age range 3-7 years). Numbers in the plot corresponds to the number of samples per month. The number of samples taken in January, April and May is not known. Data were obtained from Pechenik et al. (1973).

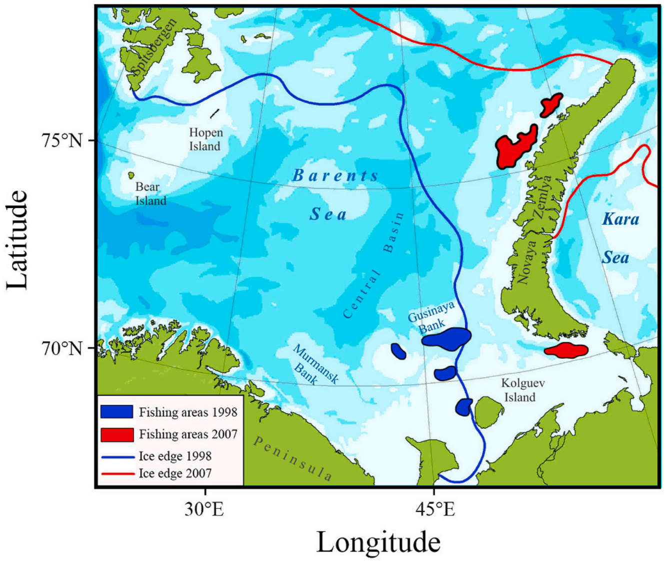

Fig. 10. Sites of the polar cod (*Boreogadus saida*) commercial fishery in November–December of 1998 (cold year) and 2007 (warm year), with lines showing the location of the ice edge in November in the two years.

carried out along the northwestern coast of Novaya Zemlya as well as close to the Kara Strait south of Novaya Zemlya. In warm years with limited ice coverage, the Russian fisheries were also conducted further to the north and east of Novaya Zemlya (Fig. 10). More details on seasonal and spatial distribution of Russian fishery on polar cod in 1972–2002 are presented in the Calendar of Fishery of polar cod (Akhtarina and Guzenko 2004).

4. Discussion

4.1. *Distributions and migrations*

The tendency to conduct seasonal migrations is a fundamental property of numerous high-latitude Arctic and boreal planktivores, including fishes, seabirds and marine mammals (e.g., Nøttestad et al., 1999; Varpe et al., 2005; Skern-Mauritzen et al., 2011; Aune et al., 2018). In the summer, these species migrate northwards, with some of them benefiting from elevated biological production along the retreating ice edge (e.g., Gjøsæter 1998). The extent of these migrations may also be related to population size and hence form density-dependent migratory waves, as suggested for capelin (Fauchald et al., 2006). Such waves, which may be caused by food depletion, involves increased aggregation and a longer and faster migratory movement (Fauchald et al., 2006). In autumn, when biological production and planktonic biomass in surface waters decline, predators return to more southern areas. Early studies that summarized the migration patterns of the eastern polar cod across the borders of the Barents, Kara and White Seas suggested an eastwards extension throughout the Kara Sea and possibly into the Laptev Sea (Moskalenko 1964; Ponomarenko 1968; Pechenik et al., 1973). Dense aggregations of polar cod near the northern border of the Barents Sea are regularly observed (e.g., Prozorkevich et al., 2018). Also, dense aggregations in the Kara Sea area near the border to the Barents Sea have been reported (Borkin et al., 2008). Indeed, the polar cod is found to be an important food source for seabirds found at Franz Josef Land, located at the northern border of the Barents Sea (Węsławski et al., 1994). In wintertime, when the eastern polar cod stock is assumed to conduct a migration towards the south-eastern Barents Sea (Ponomarenko 1968), they are commonly observed along the ice edge in the central Barents Sea (e.g., Wienerroither et al., 2013). Although commercial fishing is not necessarily conducted in the areas where target species show their densest concentrations, fishery data presumably inform about spatio-temporal variation in density, which in turn is indictive of seasonal distribution and migration patterns. Indeed, polar cod fishery data reveal that in quarters 4 and 1 (October–March), the densest aggregations have been found in the south-east, with lower yet considerable occurrences in the central and north-eastern Barents Sea. Likewise, in Q3 (July–September), the largest catches were made in the north-east, but substantial catches in more southern areas have also been registered. Thus, although seasonal migrations are well established, distributional maps shown here also indicate that polar cod are present throughout the year in the eastern Barents Sea.

While seasonal migrations of polar cod within the Barents Sea have been described, many of these observations were made approximately half a century ago (e.g., Ponomarenko 1968; Pechenik et al., 1973), and should be revisited given the extensive recent environmental changes. Also, in the eastern Barents Sea, descriptions of migrations are to some degree based on fisheries data, which are biased since fisheries tend to take place where catches are most profitable. Unbiased sampling schemes have therefore not always been applied, and stock components of commercial value (i.e., adult polar cod) may have received more attention than larvae and juveniles. To ensure proper management, the ongoing joint Norwegian-Russian survey programs (e.g., Michalsen et al., 2013) are therefore crucial.

Although ice-covered waters of the Barents Sea are rarely surveyed, sporadic studies and observations suggest that polar cod can be found under the sea-ice throughout the year. In summertime, under-ice observations of individuals and small schools in ridged sea-ice and water wedges in the ice have been made in the western Barents Sea and north of Svalbard (e.g., Lønne and Gulliksen 1989; Renaud et al., 2012, H. Hop unpublished data) as well as in the Central Arctic ocean (Melnikov and Chernova 2013). Overwintering aggregations of polar cod below sea-ice have mostly been recorded in the Canadian Arctic (Benoit et al. 2008, 2010; Geoffroy et al., 2011). For instance, a wintertime study conducted in the Amundsen Gulf (Beaufort Sea) documented the formation of dense polar cod aggregations co-occurring with the formation of sea-ice (i.e., in December), and that the aggregations disappeared by the time the sea-ice broke up, in April (Geoffroy et al., 2011). Clearly, studies of under-ice occurrences of eastern polar cod may modify our understanding of the species' abundance and distribution.

4.2. *Spawning stocks and sea-ice dependency*

Polar cod spawn during winter. High densities of polar cod spawning in the southeast Barents Sea are thought to be restricted to the areas east of 40° E, suggesting that fish spawning in the southeast are part of a separate Barents Sea/Kara Sea/White Sea stock (Pechenik et al., 1973; Boitsov et al., 2013), possibly differing from fish in the western Barents Sea. For instance, there are observations of delayed gonadal development and spawning in the Svalbard area compared to the Pechora Sea area (Borkin and Oganin 2004; Boitsov et al., 2013). Although the existence of two separate spawning stocks in the Barents Sea (i.e., in the Svalbard/Spitsbergen and in the Pechora Sea areas; Ponomarenko 1968) has been supported by autumn observations of elevated 0-group densities in the two areas (Borkin and Oganin 2004; Eriksen et al., 2011; Boitsov et al., 2013; Gjøsæter et al., 2020), survey coverage is incomplete in the northeastern corner of the Barents Sea and, therefore, this premise may be invalid. Although recent back-trajectory modelling experiments strengthen the premise that two distinct spawning areas exist in the Barents Sea (Huserbråten et al., 2019), the degree of genetic exchange between these two areas is unknown. Polar cod residing in the fjords of Svalbard/Spitsbergen were found to be genetically distinct from conspecifics in northeast Greenland waters (Madsen et al., 2016), but genetic methods have not yet been applied to assess genetic separation among polar cod residing within the Barents Sea. However, for comparison, little genetic differentiation was detected for specimens from the Greenland Sea, Iceland and the Laptev Sea (Nelson et al., 2020).

Recent methodological developments using otoliths may be applied to shed light on polar cod stocks and migrations in the Barents Sea. By analyzing the chemical composition of polar cod otoliths collected from different locations, natal sources of polar cod could be identified, together with the species' broad-scale migration patterns, revealing for example, whether mature fish or larvae share a common environment, or whether distinct populations of mature fish spawn in the same area (Bouchard et al., 2015; Gleason et al., 2016). In the Barents Sea, otolith chemical composition was recently employed to study possible spawning locations of Atlantic cod (*Gadus morhua*) as well as migration and residency patterns in northern Norway and Svalbard (Andrade et al., 2020). Such techniques could be applied to determine whether the eastern polar cod stock should be split into a Kara Sea and eastern Barents Sea stocks. If they are not two separate stocks, it implies long seasonal migrations to the Kara Sea from the eastern Barents Sea (Dolgov et al., 2011). Indeed, some migration of polar cod from the Kara Sea to the Barents Sea through the Kara Strait is thought to occur in January–March (Boitsov et al., 2013). Conversely, observations suggest that the mean length and growth rates of polar cod in the Kara Sea are lower than for same age individuals in the Barents Sea, and that different size and age compositions are found in the two stocks (Moskalenko 1964; Shepel 1971; Pechenik et al., 1973; Antonov et al., 2017). It is therefore possible that there is a local stock of polar cod in the Kara Sea and that only a fraction of this stock migrates to the Barents Sea for spawning. This hypothesis is supported by the fact that there are separate spawning grounds in the Kara Sea (Moskalenko, 1964; Antonov et al., 2017; Bolshakova and Bolshakov 2018). Alternatively, small and juvenile fish may reside in the Kara Sea whereas mature fish migrate to the Barents Sea to conduct spawning (e.g., Antonov et al., 2017). For instance, in 2007, dense concentrations of polar cod were observed near the Kara Strait the south-western Kara Sea, while the 0-group was distributed throughout the entire sea (Borkin 2008; Antonov et al., 2017). Thus, it is possible to deduce that recruitment to the polar cod stock in the Kara Sea may result from a drift of eggs and larvae from the Barents Sea. Clearly, the origins of the Kara Sea stock, and links with stocks in the Barents Sea, still need to be resolved.

Another explanation for the absence of polar cod in the southeast Barents Sea in some years could be due to environmentally-driven displacement of spawning to other areas. Recent research suggests that spawning of polar cod in the northwestern Barents Sea had been displaced over the time period 1990–2017, possibly due to changes in environmental conditions (Huserbråten et al., 2019). According to that study, the spawning was first displaced eastwards towards the central Barents Sea and later towards the north, ending up occurring >150 km further north than the most likely spawning site in 1990. Assuming the species depends on sea-ice for successful recruitment (e.g., Eriksen et al., 2015), a displacement of spawning may be associated with declining sea-ice coverage in the Barents Sea. Indeed, inter-annual variation in sea-ice coverage between "cold" and "warm" years can be significant and has been shown to impact the distribution of polar cod in the pre-spawning period (November–December), which in turn likely influence their choice of spawning ground in the eastern Barents Sea (Fig. 10). These are interesting possible scenarios, but it is important to remember that spawning has never been observed in the northwestern Barents Sea, and thus, locations of spawning sites past or present are largely speculative.

Similarly, the Barents Sea capelin (*Mallotus villosus*), a local arcto-boreal forage fish that shares many life history and functional traits with the polar cod (Hop and Gjøsæter 2013), displays significant inter-annual variation in spawning grounds along the northern coast of Norway and Russia (Gjøsæter 1998). Environmental changes are predicted to cause the establishment of new capelin spawning grounds in the Novaya Zemlya area (Huse and Ellingsen 2008). Further investigations on polar cod under-ice spawning and the strength of its sea-ice dependency would be valuable given the desire to predict future habitat and spawning grounds, and ultimately the species' fate under changing environmental conditions.

It is often assumed that the polar cod is obligately associated with sea-ice. First, the polar cod has antifreeze proteins, which allows the species to enter the sea-ice habitat during spawning and early life stages (Rass 1968; Osuga and Feeney 1978; Christiansen 2017). Second, as polar cod spawning has been proposed to occur under ice in wintertime (December–April; Ponomarenko, 2000), Geoffroy et al. (2011) assumed that the observed under-ice aggregations were related to reproduction. On the other hand, the proposed spawning area in the southeastern Barents Sea has in recent decades been virtually ice-free during the entire spawning season of polar cod (Fetterer et al., 2002). Little information on spawning below sea-ice or in open water exists for the Barents Sea. Likewise, since the Barents Sea is normally ice-free in the autumn when the annual monitoring surveys of polar cod are conducted, the distribution of polar cod in ice-covered waters is not regularly assessed. Other recordings of dense under-ice aggregations of polar cod have included mostly immature fish, such as near the North Pole during winter (mostly age-2; Melnikov and Chernova 2013) and in Arctic pack ice during autumn (mostly age-1; David et al., 2016). Hence, central research questions related to sea-ice dependency of the eastern polar cod remain to be answered, including: to what degree do the eastern polar cod reside under sea-ice, and how strong is its sea-ice dependency for different life stages and seasons?

4.3. Traits and associated implications

The polar cod is an atypical gadid with traits typical for other Arctic fishes, including small body size, presumed under-ice spawning, large eggs and newly-hatched larvae, early development in cold ice-associated water masses with a water temperature of less than 0–2 °C, and a relatively long duration of egg and larval stages (Rass 1968). On the one hand, the present review has shown that studies conducted on polar cod in the Barents Sea have provided a good understanding of several of its characteristics, including length-weight relationships, egg size, fertility and length at maturation. Yet, a better understanding of the plasticity of these characteristics under various types of natural and anthropogenic impacts would be helpful in order to improve management and impact assessments. On the other hand, the monthly data on larval size provided here reveal that there are important gaps of knowledge with respect to the timing of spawning, the length of the incubation period, and the growth of the larvae under natural conditions. For instance, the large variation in larval and post-larval size from hatching and at least until February the following winter suggest either a very long spawning period or highly variable growth conditions. Although numerous laboratory studies of larval growth have been performed (e.g., Graham and Hop 1995; Sakurai et al., 1998; Laurel et al., 2019), there is a lack of high-resolution data on eggs and larval development under natural conditions. This can also be related to considerable geographic variability in the size of post-larvae and juveniles due to local conditions in various Arctic seas (Mishin et al., 2018). Further investigation of the growth and survival of the early life stages under natural conditions should be performed. For instance, even if less sea-ice and warmer temperatures could enhance feeding and growth during early larval development during the dark season (Bouchard and Fortier 2008), survival could be negatively affected by UV exposure during early spring and also increased predation (e.g., from surface-feeding seabirds). It should also be noted that recent research has shown that the early life stages of polar cod are sensitive to oil exposure (Nahrgang et al., 2016; Laurel et al., 2019). This is of particular importance since a declining sea-ice coverage facilitates increased levels of anthropogenic activities in the Arctic, which in turn may lead to an elevated risk of accidental oil spills there (e.g., Eamer et al., 2013). In general, anthropogenic activities in the remote Arctic and in bordering shelf seas have historically been limited by notoriously challenging environmental conditions (AMAP 2010). However, the current loss of sea ice facilitates a higher anthropogenic footprint with increasing tourism, shipping, fisheries, and petroleum exploration (e.g., ACIA 2005; AMAP, 2007; Eamer et al., 2013; Glickson et al., 2014). In addition to the increased risk of oil pollution in Arctic waters, these developing activities are associated with rising levels of noise pollution (e.g., AMAP, 2007). Indeed, a recent study conducted in Canadian Arctic waters showed that shipping-induced noise may alter the movement and behavior of polar cod (Ivanova et al., 2020). These factors call for a corresponding rise in the knowledge level of Arctic key species and their fate under changing environmental and anthropogenic regimes.

While the Russian diet data (Pechenik et al., 1973; Tarverdieva et al., 1996; Ponomarenko 2000a, b, 2008) largely supports previous studies suggesting that the polar cod is a generalist planktivore (see Renaud et al., 2012; Hop and Gjøsæter 2013), the monthly resolution of eastern polar cod diet, stomach fullness and hepato-somatic index here presented reveal an extreme seasonality in the species' feeding cycle and lipid content. Furthermore, data from 1996 to 2010 showed that copepods were the most important food items for polar cod in the size range 5–19 cm, but decreased in relative contribution to the diet from 95-99% to 35–40% by weight during this period (Dolgov 2016). Hyperiid amphipods (15–20%) and euphausiids (5–15%) were important food for polar cod in the size range 9–20 cm whereas smaller fish were important as prey for polar cod >19–20 cm (Dolgov 2016). In the Barents Sea and Svalbard/Spitsbergen area, polar cod feeding occurs both in summer and wintertime, and the diet is dominated by various pelagic crustaceans including *Calanus* spp., euphausiids and *Themisto* spp. (e.g., Borkin and Oganin 2004; Renaud et al., 2012; Berge et al., 2015; Cusa et al., 2019). *Calanus* spp. are highly energy-rich zooplankton and the biomass-dominant herbivores in the Arctic (e.g., Falk-Petersen et al., 2009). In wintertime, a shift to a diet that to a larger degree is characterized by fish have been observed (Cusa et al., 2019). Here, we show that fish (including polar cod juveniles) and benthic crustaceans may dominate the diet in the winter months (e.g., December and January; Fig. 8), a finding that corresponds well with the observation that the eastern polar cod are more strongly associated with the bottom layers at this time of the year (Shleinik 1970). Indeed, the polar cod is cannibalistic, but studies from the Canadian Arctic suggest that a vertical segregation by size prevents larger individuals (e.g., age-1+) from feeding on smaller ones (e.g., age- 0), the latter being found in shallower waters than the former (Geoffroy et al., 2016). Yet, when age-0 polar cod descend to deeper water masses in the autumn, the risk of cannibalism increases (e.g., Bouchard and Fortier 2011), which may explain the winter cannibalism observed. Furthermore, whereas a diet dominated by *Themisto libellula* has been observed in Arctic waters of Svalbard/Spitsbergen (Dalpadado et al., 2016; Cusa et al., 2019), we show that mainly *Calanus* spp., but also euphausiids, may completely dominate the diet of eastern polar cod from March to November (Fig. 8).

Our data confirm a high degree of stomach fullness and a corresponding peak in lipid content in the summer and early autumn (Pechenik et al., 1973), which is likely a reflection of high food availability (zooplankton in particular) at this time of the year. In contrast, levels of stomach fullness and lipid content are lower the rest of the year (Pechenik et al., 1973). Access to high densities of *Calanus* spp. during the short summertime feeding season is likely decisive in fueling reproduction and survival of the eastern polar cod during the winter and spring months.

Under-ice sampling of polar cod in the Svalbard/Spitsbergen area in the summer season revealed that ice fauna is common but not dominant in the diet of polar cod (Lønne and Gulliksen 1989; Renaud et al., 2012). Development of Barents Sea zooplankton communities, and the timing and spatial distribution of polar cod and capelin feeding grounds, exhibit strong interannual variability (Orlova et al., 2010; Dalpadado et al., 2014). Thus, it will be important to document distributional patterns of both polar cod, capelin, and their prey under the changing environmental conditions now being experienced. Because capelin as well as other pelagic species and predators may move into the areas occupied by polar cod, competition and predation may become more important to consider for population dynamics and survival (e.g., Renaud et al., 2012).

5. Conclusions

This review has synthesized and evaluated knowledge on polar cod in the eastern Barents Sea and adjacent areas, highlighting information available in Russian literature that, to a large extent, has not previously been available for understanding the ecology of polar cod in the Barents Sea. The review has documented large variation in key traits and properties of this species, including larval demography, distributions and location and timing of life history events (e.g., spawning and migrations), and highlighted the existence of key gaps of knowledge necessary to fill for effective management of an ecosystem where the species plays such an important role. Furthermore, much of our knowledge on polar cod is based on data gathered several decades ago from the western Barents Sea and in other Arctic areas, and new studies should be performed for comparison. In our opinion, five categories of knowledge gaps need to be filled:

1. Early life stages of polar cod (i.e., eggs and larvae) are sensitive to anthropogenic disturbance and environmental variation (e.g., oil spills and changes in food availability). Currently, it is not known whether spawning will be displaced in time and space in response to interannual variations in sea-ice distribution. If the spawning areas or periods used as input data in impact assessment models are inaccurate, sensitive areas or periods may not be protected. Thus, better knowledge about the location and timing of spawning events, as well as subsequent distributions of the earliest life stages, is needed.
2. There is uncertainty as to what degree the eastern Barents Sea polar cod is dependent on sea-ice (including drifting sea-ice or landfast ice, particularly near river deltas on the Russian coast) during different life stages and seasons (if such a dependency exists). While it is generally assumed that polar cod spawn in association with sea-ice, it is not known whether spawning in ice-free waters can be successful. While it is challenging to conduct comparative monitoring studies of polar cod larval development and survival in ice-free vs. ice-covered waters, model studies can provide new insight if realistic input values are used (e.g., Gjøsæter et al., 2020). Another alternative is to use commercial catch data to shed light on distributions of mature individuals in the spawning seasons. Although the polar cod currently is not directly commercially exploited, the species is taken as by-catch in the shrimp fishery (e.g., Jacques et al., 2019), which is conducted in the Barents Sea (including ice-covered areas) throughout the year. Coupled with data on sea ice coverage, systematic registration and analyses of polar cod by-catch data, including biomass, gonadal development and spatial coordinates of catches, could inform about the extent to which spawning is conducted in ice-free waters. Associated recruitment success may in turn be assessed by correlations with conventional measures of recruitment (e.g., abundance of age-0 and age-1 individuals).
3. In order to have the best possible input data for management and impact assessment, better knowledge about the spatial and seasonal distributions of all life stages is needed. Indeed, seasonal information outside of the autumn surveys can provide information about habitats that might be important to spawning and early life stages. Furthermore, although the annual autumn surveys do not always fully cover the northeastern-most corner of the Barents Sea, resulting distribution maps may indicate a continuous distribution of 0-group polar cod larvae from the northwest towards the northeast. A determination of the full 0-group distribution would therefore grant enhanced precision of the impact assessment in these northern areas. New survey technology including autonomous underwater vehicles (AUV's) may be used to gather new data from ice-covered waters, which combined with data gathered during dedicated

ichthyoplankton (eggs and larvae) surveys would help establish reliable information about spawning grounds and 0-group distributions of polar cod.

4. The population in the Barents Sea is managed as one stock through the joint Russian-Norwegian fisheries surveys, with biomass estimates conducted during the autumn. Yet, the relation between Barents and Kara Seas groups of polar cod is not well known, and there is considerable uncertainty as to where and when polar cod spawning occurs in these two seas, if they exhibit genetic differentiation, display different life history traits, or if their distributions overlap in time and/or space. Provided that distinct populations of polar cod in the Barents and Kara Seas exist, environmental (warming) and ecological (e.g., altered competition and predation regimes) could affect the connectivity and biomass distribution among these populations and even further east along the Siberian coast and north into the Arctic Ocean. Therefore, a better knowledge of the population structure of polar cod in the Barents Sea and adjacent waters could help understand the species' response to future environmental changes, which in turn would inform the management about the species.
5. Field and experimental studies have shown that polar cod larvae may feed on various types of food items, but that they have certain diet preferences. However, successful feeding requires a strong match in time and space between the larvae and the food items. Therefore, it is unknown whether ongoing environmental change may induce phenological changes affecting the availability and potential food items for polar cod larvae and their match in time and space.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to thank Equinor for funding the work with this manuscript. We also acknowledge support from the Research Council of Norway through 'The Nansen Legacy project' (RCN no. 276730) and Akvaplan-niva. The work includes previously unpublished results of recent studies of Murmansk Marine Biological Institute. We are grateful to Georgy Dukhno for preparation of maps. We thank the four anonymous reviewers for their valuable comments on the manuscript.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2021.105262.

References

ACIA, 2005. Arctic Climate Impact Assessment. Cambridge University Press, p. 1042.

Ajiad, A., Oganin, I.A., Gjøsæter, H., 2011. Polar cod. In: Jacobsen, T., Ozhigin, V.K. (Eds.), The Barents Sea. Ecosystem, Resources, Management. Half a Century of Russian-Norwegian Cooperation. Tapir Academic Press, Trondheim, pp. 315–328.

Akhtarina, T.A., Guzenko, V.V., 2004. Calendar of Fishery of Polar Cod in the Barents Sea in 1972-2002. Murmansk. PINRO Press, p. 138 pp. (In Russian).

Altukhov, K.A., 1981. The reproduction and development of the Arctic cod, *Boreogadus saida,* in the White Sea. J. Ichthyol. 19, 93–101.

AMAP, 2010. Assessment 2007: Oil and Gas Activities in the Arctic - Effects and Potential Effects, vol. 1. AMAP, Oslo, Norway, p. 2010.

Andrade, H., van der Sleen, P., Black, B.A., Godiksen, J.A., Locke, W.L., Carroll, M.L., Ambrose, W.G., Geffen, A., 2020. Ontogenetic movements of cod in Arctic fjords and the Barents Sea as revealed by otolith microchemistry. Polar Biol. 43, 409–421. https://doi.org/10.1007/s00300-020-02642-1.

Andriyashev, A.P., 1954. Fishes of Northern Seas of the U.S.S.R. Academy of Science Press. Translated from Russian by the Israel Program for Scientific Translations, Jerusalem, Moscow-Leningrad, p. 1964.

Antonov, N.P., Kuznetsov, V.V., Kuznetsova, E.N., Tatarnikov, V.A., Belorustseva, S.A., Mitenkova, L.V., 2017. Ecology of polar cod *Boreogadus saida* (Gadiformes, Gadidae) and its fishery potential in Kara sea. J. Ichthyol. 57, 721–729.

Aronovich, T.M., Doroshev, S.I., Spectorova, L.V., Makhotin, V.M., 1975. Egg incubation and larval rearing of navaga (*Eleginus navaga* Pall.), polar cod (*Boreogadus saida* Lepechin) and Arctic flounder (*Liopsetta glacialis* Pall.) in the Laboratory. Aquaculture 6, 233–242.

Aune, M., Aniceto, A.S., Biuw, M., Daase, M., Falk-Petersen, S., Leu, E., Ottesen, C.A.M., Sagerup, K., Camus, L., 2018. Seasonal ecology in ice-covered Arctic seas – considerations for spill response decision making. Mar. Environ. Res. 141, 275–288.

Baranenkova, A.S., Ponomarenko, V.P., Khokhlina, N.S., 1964. Distribution, sizes and growth of larvae and fry of polar cod *Boreogadus saida* (Lepechin) in the Barents Sea. Coun Meet Int Coun Explor Sea 1964 Gadoid Fish Committee (Mimeo) 96, 1–15.

Baranenkova, A.S., Ponomarenko, V.P., Khokhlina, N.S., 1966. Distribution, size, and growth of larvae and fry of the polar cod in the Barents Sea. Vopr. Ikhtiol. 3, 498–518 (In Russian).

Beanlands, G.E., Duinker, P.N., 1983. An Ecological Framework for Environmental Impact Assessment in Canada. Institute for Resource and Environmental Studies, Dalhousie University, Nova Scotia, Canada.

Belikov, S.V., Borkin, I.V., Krysov, A.I., Seliverstova, E.I., Ushakov, N.G., 1991. State of stocks of pelagic fishes and prospects for their recovery in the seas of the European North. In: Kompleksnye Rybokhozyaistvennye Issledovania PINRO Na Severnom Basseine: Rezultaty I Perspektivy Integrated Fisheries Research of PINRO in the Northern Basin: Results and Perspectives. PINRO, Murmansk. Polar Nauchno-Issled Inst Rybn Khoz Okeanogr, pp. 130–144 (In Russian).

Benoit, D., Simard, Y., Fortier, L., 2008. Hydroacoustic detection of large winter aggregations of Arctic cod (*Boreogadus saida*) at depth in ice-covered Franklin Bay (Beaufort Sea). J Geophys Res Ocean 113, C06S90.

Benoit, D., Simard, Y., Gagné, J., Geoffroy, M., Fortier, L., 2010. From polar night to midnight sun: photoperiod, seal predation, and the diel vertical migrations of polar cod (*Boreogadus saida*) under landfast ice in the Arctic Ocean. Polar Biol. 33, 1505–1520.

Berge, J., Daase, M., Renaud, P.E., Ambrose, W.G., Darnis, G., Last, K.S., Leu, E., Cohen, J.H., Johnsen, G., Moline, M.A., Cottier, F.C., Varpe, Ø., Shunatova, N., Balazy, P., Morata, N., Massabuau, J.-C., Falk-Petersen, S., Kosobokova, K., Hoppe, C.J.M., Wesławski, J.M., Kuklinski, P., Legezynska, J., Nikishina, D., Cusa, M., Kedra, M., Włodarska-Kowalczuk, M., Vogedes, D., Camus, L., Tran, D., Michaud, E., Gabrielsen, T.M., Granovitch, A., Gonchar, A., Krapp, R., Callesen, T.A., 2015. Unexpected levels of biological activity during the polar night offer new perspectives on a warming Arctic. Curr. Biol. 25, 1–7.

Boitsov, V.D., Dolgov, A.V., Krysov, A.I., Seliverstova, E.I., Shevelev, M.S. (Eds.), 2013. Polar cod of the Barents Sea. PINRO Press, Murmansk (In Russian).

Bolshakova, Y.Y., Bolshakov, D.V., 2018. Ichthyofauna of the eastern coast bays of the Novaya Zemlya archipelago. Oceanology 58, 228–232.

Borkin, I.V., 1990. Reproduction and early ontogenesis in *Boreogadus saida* (Lepechin) from the Barents Sea. In: Extended Abstract of Cand. Sci. (Biol.) Dissertation. VNIRO, Moscow, p. 21 pp. (In Russian).

Borkin, I.V., 2008. Ichthyoplankton. In: The Ecosystem of the Kara Sea. Murmansk. PINRO Press, pp. 124–129 (In Russian).

Borkin, I.V., 2013. The value of forage nutritional conditions and the distribution of larvae of Polar cod *Boreogadus saida* Lepechin Barents Sea. Vestnik. Kamch. Gos. Tekhnic. Univer. 25, 35–41 (In Russian).

Borkin, I.V., Nesterova, V.N., 1990. Distribution of polar cod larvae and its food objects in the Barents Sea in the summers of 1983–1984. In: *Kormovye Resursy I Pishchevye Vzaimootnosheniya Ryb Severnoi Atlantiki* (Food Resources and Feeding Interactions of Fish in the North Atlantic). Polar Nauchno-Issled Inst. Rybn. Khoz. Okeanogr., Murmansk, pp. 99–108 (In Russian).

Borkin, I.V., Oganin, I.A., 2004. Polar cod. In: Shevelev, M.S. (Ed.), Investigations by PINRO in the Spitsbergen Archipelago Area. PINRO Press, Murmansk, pp. 129–139 (In Russian).

Borkin, I.V., Ponomarenko, V.P., Tret'yak, V.L., Shleinik, V.N., 1987. The polar cod *Boreogadus saida* (Lepechin)—a fish of the polar seas: reserves and use. In: *Biologicheskie Resursy Arktiki I Antarktiki* (Biological Resources of the Arctic and Antarctic). Nauka, Moscow, pp. 183–207 (In Russian).

Borkin, I.V., Vasiliev, A.V., Chetyrkina, O.Yu., 2008. Ichthyofauna. In: The Ecosystem of the Kara Sea. Murmansk. PINRO Press, pp. 130–206 (In Russian).

Bouchard, C., Fortier, L., 2008. Effects of polynyas on the hatching season, early growth and survival of polar cod *Boreogadus saida* in the Laptev Sea. Mar. Ecol. Prog. Ser. 355, 247–256. https://doi.org/10.3354/meps07335.

Bouchard, C., Fortier, L., 2011. Circum-arctic comparison of the hatching season of polar cod *Boreogadus saida*: a test of the freshwater winter refuge hypothesis. Prog. Oceanogr. 90, 105–116.

Bouchard, C., Thorrold, S.R., Fortier, L., 2015. Spatial segregation, dispersion and migration in early stages of polar cod *Boreogadus saida* revealed by otolith chemistry. Mar. Biol. 162, 855–868. https://doi.org/10.1007/s00227-015-2629-5.

Bradshaw, C.J.A., McMahon, C.R., 2008. Fecundity. In: Jørgensen, S.E., Fath, B.D. (Eds.), Encyclopedia of Ecology. Academic Press, Oxford, pp. 1535–1543.

Chernova, N., 2018. Arctic cod in the Russian Arctic: new data, with notes on intraspecific forms. J. Aquac. Mar. Biol. 7 (1), 00180.

Christiansen, J.S., 2017. No future for Euro-Arctic ocean fishes? Mar. Ecol. Prog. Ser. 575, 217–227.

Craig, P.C., Griffiths, W.B., Haldorson, L., McElderry, H., 1982. Ecological studies of Arctic cod (*Boreogadus saida*) in Beaufort Sea coastal waters, Alaska. Can. J. Fish. Aquat. Sci. 39, 395–406.

Cusa, M., Berge, J., Varpe, Ø., 2019. Seasonal shifts in feeding patterns: individual and population realized specialization in a high Arctic fish. Ecol. Evol. 9, 11112–11121.

Dalpadado, P., Arrigo, K.R., Hjøllo, S.S., Rey, F., Ingvaldsen, R.B., Sperfeld, E., van Dijken, G.L., Stige, L.C., Olsen, A., Ottersen, G., 2014. Productivity in the Barents Sea - response to recent climate variability. PloS One 9 (5), e95273.

Dalpadado, P., Hop, H., Rønning, J., Pavlov, V., Sperfeld, E., Buchholz, F., Rey, A., Wold, A., 2016. Distribution and abundance of euphausiids and pelagic amphipods in Kongsfjorden, Isfjorden and Rijpfjorden (Svalbard) and changes in their importance as key prey in a warming marine ecosystem. Polar Biol. 39, 1765–1784.

David, C., Lange, B., Krumpen, T., Schaafsma, F., van Franeker, J.A., Flores, H., 2016. Under-ice distribution of polar cod *Boreogadus saida* in the central Arctic Ocean and their association with sea-ice habitat properties. Polar Biol. 39, 981–994.

Dolgov, A.V., 2016. Composition, Formation and Trophic Structure of the Barents Sea Fish Communities. PINRO Press, Murmansk, p. 336 (In Russian).

Dolgov, A.V., Smirnov, O.V., Sentyabrov, E.V., Drevetnyk, K.V., Chetyrkina, O.Yu., 2011. New data on the ichthyofauna of the Kara Sea (based on the results of the PINRO investigations in 2007–2008). In: Matishov, G.G., Tishkov, A.A. (Eds.), *Nazemnye I Morskie Ekosistemy* (Terrestrial and Marine Ecosystems). Paulsen, Moscow, pp. 112–128 (In Russian).

Eamer, J., Donaldson, G.M., Gaston, A.J., Kosobokova, K.N., Lárusson, K.F., Melnikov, I. A., Reist, J.D., Richardson, E., Staples, L., von Quillfeldt, C.H., 2013. Life linked to ice: a guide to sea-ice-associated biodiversity in this time of rapid change. In: CAFF Assessment Series No. 10. Conservation of Arctic Flora and Fauna, Iceland, ISBN 978-9935-431-25-7.

Efimkin, A.Ya., 2013. Feeding of Arctic cod *Boreogadus saida* in the Bering and Chukchi seas. Izvestuya TINRO 173, 184–192 (In Russian).

Eriksen, E., Bogstad, B., Nakken, O., 2011. Ecological significance of 0-group fish in the Barents Sea ecosystem. Polar Biol. 34, 647–657.

Eriksen, E., Huserbråten, M., Gjøsæter, H., Vikebø, F., Albretsen, J., 2020. Polar cod egg and larval drift patterns in the Svalbard archipelago. Polar Biol. 43, 1029–1042.

Eriksen, E., Ingvaldsen, R.B., Nedreaas, K., Prozorkevich, D., 2015. The effect of recent warming on polar cod and beaked redfish juveniles in the Barents Sea. Reg. Stud. Mar. Sci. 2, 105–112.

Falk-Petersen, I.B., Frivoll, V., Gulliksen, B., Haug, T., 1986. Occurrence and size/age relations of polar cod, *Boreogadus saida* (Lepechin 1773), in Spitsbergen coastal waters. Sarsia 71, 235–245.

Falk-Petersen, S., Mayzaud, P., Kattner, G., Sargent, J., 2009. Lipids and life strategy of Arctic *Calanus*. Mar. Biol. Res. 5, 18–39.

Fauchald, P., Mauritzen, M., Gjøsæter, H., 2006. Density-dependent migratory waves in the marine pelagic ecosystem. Ecology 87, 2915–2924.

Fetterer, F., Knowles, K., Meier, W., Savoie, M., 2002. Sea Ice Index. National Snow and Ice Data Center, Boulder, Colorado, USA. Available online at: http://nsidc.org/data/g02135.html.

Fey, D.P., Węsławski, J.M., 2017. Age, growth rate, and otolith growth of polar cod (*Boreogadus saida*) in two fjords of Svalbard, Kongsfjord and Rijpfjorden. Oceanologia 59, 576–584.

Fortier, L., Sirois, P., Michaud, J., Barber, D., 2006. Survival of Arctic cod larvae (*Boreogadus saida*) in relation to sea ice and temperature in the Northeast Water Polynya (Greenland Sea). Can. J. Fish. Aquat. Sci. 63, 1608–1616.

French-McCay, D.P., 2004. Oil spill impact modeling: development and validation. Environ. Toxicol. Chem. 23, 2441–2456.

Geoffroy, M., Robert, D., Darnis, G., Fortier, L., 2011. The aggregation of polar cod (*Boreogadus saida*) in the deep Atlantic layer of ice-covered Amundsen Gulf (Beaufort Sea) in winter. Polar Biol. 34, 1959–1971. https://doi.org/10.1007/s00300-011-1019-9.

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

Gjøsæter, H., Huserbråten, M.B.O., Vikebø, F., Eriksen, E., 2020. Key processes regulating the early life history of Barents Sea polar cod. Polar Biol. 43, 1015–1027. https://doi.org/10.1007/s00300-020-02656-9.

Gleason, C.M., Norcross, B.L., Spaleta, K.J., 2016. Otolith chemistry discriminates water mass occupancy of Arctic fish in the Chukchi Sea. Mar. Freshw. Res. 67, 967–979. https://doi.org/10.1071/MF15084.

Glickson, D., Grabowski, M., Coolbaugh, T., Dickins, D., Glenn, R., Lee, K., Majors, L., Myers, M., Norcross, B., Reed, M., Suydam, R., Tiedje, J., Timmermans, M.-L., Wadhams, P., 2014. Responding to oil spills in the U.S. Arctic marine environment. In: International Oil Spill Conference Proceedings: May 2014. American Petroleum Institute, pp. 283–740.

Gradinger, R.R., Bluhm, B.A., 2004. In situ observations on the distribution and behavior of amphipods and Arctic cod (*Boreogadus saida*) under the sea ice of the high Arctic Canadian Basin. Polar Biol. 27, 595–603.

Graham, M., Hop, H., 1995. Aspects of reproduction and larval biology of Arctic cod (*Boreogadus saida*). Arctic 48, 130–135.

Hognestad, P.T., 1968. Observations on polar cod in the Barents Sea. Rapp. P.-ver. Reun. Cons. Internat. l'Explor. Mer. 158, 126–130.

Hop, H., Gjøsæter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species in marine food webs of the Arctic and the Barents Sea. Mar. Biol. Res. 9, 878–894. https://doi.org/10.1080/17451000.2013.775458.

Hop, H., Welch, H.E., Crawford, R.E., 1997. Population structure and feeding ecology of Arctic cod schools in the Canadian High Arctic. In: Reynolds, J. (Ed.), Fish Ecology in Arctic North America, vol. 19. Am Fish Soc Symp, Bethesda, Maryland, pp. 68–80.

Huse, G., Ellingsen, I., 2008. Capelin migrations and climate change – a modelling analysis. Climatic Change 87, 177–197.

Huserbråten, M.B.O., Eriksen, E., Gjøsæter, H., Vikebø, F., 2019. Polar cod in jeopardy under the retreating Arctic sea ice. Commun. Biol. 2, 407. https://doi.org/10.1038/s42003-019-0649-2.

ICES, 1966. Preliminary Report of the Joint International 0-group Fish Survey in the Barents Sea and Adjacent Waters August-September 1966. ICES C.M. 1966/H:23.

ICES, 1969. Report of the 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1969. ICES C.M. 1969/F:34.

ICES, 1970. Preliminary Report of Joint Soviet-Norwegian 0-group Fish Survey in Barents Sea and Adjacent Waters in August-September 1970. ICES C.M. 1970/H:34.

ICES, 1971. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1971. ICES C.M. 1971/H:32.

ICES, 1974. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1974. ICES C.M. 1974/H:33.

ICES, 1977. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1977. ICES CM 1977/H:45.

ICES, 1978. Report of the International 0-gruup Fish Survey in the Barents Sea and Adjacent Waters in August-September 1978. ICES C.M. 1978/H:33.

ICES, 1980. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1980. ICES CM 1980/G:53.

ICES, 1981. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1981. ICES CM 1981/G:78.

ICES, 1984. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1984. ICES C.M. 1984/H.-36.

ICES, 1985. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1985. ICES C.M. 1985/G:7.

ICES, 1986. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1986. ICES C.M. 1986/0:78.

ICES, 1987. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1987. ICES C.M.1987/G:38.

ICES, 1988. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1988. ICES C.M. 1988/G:45.

ICES, 1990. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1990. ICES C.M. 1990/G:46.

ICES, 1991. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1991. ICES C.M. 1991/G:50 Ref. H.

ICES, 1992. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1992. ICES C.M. 1992/G: 82 Ref. H.

ICES, 1994. Preliminary Report of the International 0-group Fish Survey in the Barents Sea and Adjacent Waters in August-September 1993. ICES C.M. 1994/G:3.

ICES, 2018. Report of the Arctic Fisheries Working Group (AFWG), 18–24 April 2018. ICES CM 2018/ACOM:06, Ispra, Italy, p. 859.

Ivanova, S.V., Kessel, S.T., Espinoza, M., McLean, M.F., O'Neill, C.O., Landry, J., Hussey, N.E., Williams, R., Vagle, S., Fisk, A.T., 2020. Shipping alters the movement and behavior of Arctic cod (*Boreogadus saida*), a keystone fish in Arctic marine ecosystems. Ecol Appl, e02050.

Jennings, S., Reynolds, J.D., Mills, S.C., 1998. Life history correlates of responses to fisheries exploitation. Proc. R. Soc. B. 265, 333–339.

Ji, R., Jin, M., Varpe, Ø., 2013. Sea ice phenology and timing of primary production pulses in the Arctic Ocean. Global Change Biol. 19, 734–741.

Johannesen, E., Mørk, H.L., Korsbrekke, K., Wienerroither, R., Eriksen, E., Fossheim, M., Wenneck, T.L., Dolgov, A., Prokhorova, T., Prozorkevich, D., 2017. Arctic Fishes in the Barents Sea 2004-2015: Changes in Abundance and Distribution. IMR-PINRO Joint Report Series No. 1/2017, p. 50.

Kashkina, A.A., 1962. Ichthyoplankton of the southeastern part of the Barents Sea. Tr. Murm. Morsk. Biol. Inst. 4 (8), 97–131 (In Russian.).

Klumov, S.K., 1935. Problems of polar cod in Arctic. Rybnoe Khozyaystvo 11, 95–96 (In Russian).

Klumov, S.K., 1937. Saika i ee znachenie dlya nekotorykh zhiznennykh prozessov v Arktike (Polar cod and their importance for some life processes in the Arctic). Proc. Acad. Sci. USSR, serie "Biol." 1, 175–195 (In Russian).

Kuznetsova, N.A., 2018. New data on the diet of juvenile fishes in the eastern Chukchi Sea. Izvestiya TINRO 194, 139–152 (In Russian).

Laurel, B.J., Copeman, L.A., Iseri, P., Spencer, M.L., Hutchinson, G., Nordtug, T., Donald, C.E., Meier, S., Allan, S.E., Boyd, D.T., Ylitalo, G.M., Cameron, J.R., French, B.L., Linbo, T.L., Scholz, N.L., Incardona, J.P., 2019. Embryonic crude oil exposure impairs growth and lipid allocation in a keystone Arctic forage fish. iScience 19, 1101–1113.

Lønne, O.J., Gulliksen, B., 1989. Size, age and diet of polar cod, *Boreogadus saida* (Lepechin 1773), in ice covered waters. Polar Biol. 9, 187–191.

Madsen, M.L., Nelson, R.J., Fevolden, S.-E., Christiansen, J.S., Præbel, K., 2016. Population genetic analysis of Euro-Arctic polar cod *Boreogadus saida* suggests fjord and oceanic structuring. Polar Biol. 39, 969–980.

Majewski, A.R., Walkusz, W., Lynn, B.R., Atchison, S., Eert, J., Reist, J.D., 2016. Distribution and diet of demersal Arctic cod, (*Boreogadus saida*), in relation to habitat characteristics in the Canadian Beaufort Sea. Polar Biol. 39, 1087–1098. https://doi.org/10.1007/s00300-015-1857-y.

Manteifel, B.P., 1943. Polar Cod and Their Fishery. OGIZ, Arkhangelsk, p. 32 (In Russian).

Marsh, J.M., Mueter, F.J., Quinn II, T.J., 2020. Environmental and biological influences on the distribution and population dynamics of polar cod (*Boreogadus saida*) in the US Chukchi Sea. Polar Biol. 43, 1055–1072.

Matkovskiy, A.K., 2006. Ryby Obskoy i Tazovskoy gub Karskogo morya (fish of the Obskaya and Tazovskaya bays of the Kara Sea). In: Ecologia Ryb Ob'Irtyshskogo Basseina (Ecology of Fish from the Ob-Irtysh Basin), vol. 2006. Moscow: Tov. Nauch. Izd. KMK, pp. 311–325.

McBride, M.M., Hansen, J.R., Korneev, O., Titov, O., Stiansen, J.E., Tchernova, J., Filin, A., Ovsyannikov, A., 2016. Joint Norwegian - Russian environmental status 2013. Report on the Barents Sea ecosystem. Part II - complete report. IMR/PINRO Joint Report Series 2016 (2), 359 pp.

Mecklenburg, C.W., Lynghammar, A., Johannesen, E., Byrkjedal, I., Christiansen, J.S., Dolgov, A.V., Karamushko, O.V., Mecklenburg, T.A., Møller, P.R., Steinke, D., Wienerroither, R.M., 2018. Marine fishes of the Arctic Region. In: Conservation of Arctic Flora and Fauna, Akureyri, Iceland.

Melnikov, I.A., Chernova, N.V., 2013. Characteristics of under-ice spawning of polar cod *Boreogadus saida* (Gadidae) in the central Arctic Ocean. J. Ichthyol. 53, 7–15.

Michalsen, K., Dalpadado, P., Eriksen, E., Gjøsæter, H., Ingvaldsen, R.B., Johannesen, E., Jørgensen, L.L., Knutsen, T., Prozorkevich, D., Skern-Mauritzen, M., 2013. Marine living resources of the Barents Sea – ecosystem understanding and monitoring in a climate change perspective. Mar. Biol. Res. 9, 932–947.

Mishin, A.V., Evseenko, S.A., Bolshakov, D.V., Bolshakova, Ya.Yu., 2018. Ichthyoplankton of Russian Arctic seas: 1. Polar cod *Boreogadus saida*. J. Ichthyol. 58 (5), 710–716.

Monstad, T., Gjøsæter, H., 1987. Observations on polar cod (*Boreogadus saida*) in the Barents Sea 1973 to 1986. ICES CM 1987/G, p. 13.

Moskalenko, B.F., 1964. O biologii polyarnoi treski (saiki) *Boreogadus saida* (Lepechin). (On the biology of Polar cod *Boreogadus saida* (Lepechin. Vopr. Ikhtiol. 4, 433–443 (Translated by Alaska Dept. of Fish and Game).

Mukhina, N.V., 2005. Distribution of Eggs and Fish Larvae in the Norwegian and Barents Sea/Murmansk. PINRO Press, p. 419 (In Russian).

Nahrgang, J., Varpe, Ø., Korshunova, E., Murzina, S., Hallanger, I.G., Vieweg, I., Berge, J., 2014. Gender specific reproductive strategies of an Arctic key species (*Boreogadus saida*) and implications of climate change. PloS One 9, e98452.

Nahrgang, J., Dubourg, P., Frantzen, M., Storch, D., Dahlke, F., Meador, J.P., 2016. Early life stages of an arctic keystone species (*Boreogadus saida*) show high sensitivity to a water-soluble fraction of crude oil. Environ. Pollut. 218, 605–614.

Nelson, R.J., Bouchard, C., Fortier, L., Majewski, A., Reist, J., Præbel, K., Madsen, M.L., Rose, G., Kesselh, S., Divoky, G., 2020. Circumpolar genetic population structure of polar cod, *Boreogadus saida*. Polar Biol. 43, 951–961, 10.1007/s0030 0-020-02660-z.

NMCE (Norwegian Ministry of the Climate and Environment), 2015. Meld. St. 20 (2014-2015). Report to the Storting (White Paper).

Nøttestad, L., Giske, J., Holst, J.C., Huse, G., 1999. A length-based hypothesis for feeding migrations in pelagic fish. Can. J. Fish. Aquat. Sci. 56, 26–34.

Olsen, E., Gjøsæter, H., Røttingen, I., Dommasnes, A., Fossum, P., Sandberg, P., 2007. The Norwegian ecosystem-based management plan for the Barents Sea. ICES J. Mar. Sci. 64, 599–602.

Orlova, E.L., Rudneva, G.B., Renaud, P.E., Eiane, K., Savinov, V., Yurko, A.S., 2010. Climate impacts on feeding and condition of capelin *Mallotus villosus* in the Barents Sea: evidence and mechanisms from a 30 year data set. Aquat. Biol. 10, 105–118.

Orlova, E.L., Dolgov, A.V., Rudneva, G.B., Oganin, I.A., Konstantinova, L.L., 2009. Trophic relations of capelin *Mallotus villosus* and polar cod *Boreogadus saida* in the Barents Sea as a factor of impact on the ecosystem. Deep Sea Res II 56, 2054–2067.

Osuga, D.T., Feeney, R.E., 1978. Antifreeze glycoproteins from Arctic fish. J. Biol. Chem. 253, 5338–5343.

Ottesen, C.A.M., Hop, H., Christiansen, J.S., Falk-Petersen, S., 2011. Early life history of the daubed shanny (Teleostei: *Leptoclinus maculatus*) in Svalbard waters. Mar. Biodivers. 41, 383–394.

Pechenik, L.N., Ponomarenko, V.P., Shepel, L.I., 1973. Biologia i promysel saiki v Barentsevom more (Biology and fishery of the Barents Sea polar cod). Pishchevay promyshlennostʹ, Moscow, p. 68 (In Russian).

PINRO, 2006. Implement calculation of integrated estimation of area in Russian economic zone in the Barents Sea vulnerability to oil pollution. In: Scientific Report by Agreement 22/2006. PINRO-WWF-Russia, Murmansk, p. 113 p. (In Russian).

Ponomarenko, V.P., 1964. Regions and conditions of polar cod spawning in the Barents Sea. In: Materialy Sessii Uchenogo Soveta PINRO Po Rezulʹtatam Issledovanii 1962–1963 Gg. (Materials of the PINRO Scientific Council Based on the Results of PINRO Research in 1962-1963), vol. 3, pp. 220–226 (In Russian).

Ponomarenko, V.P., 1967. Feeding of the larvae and fry of the polar cod (*Boreogadus saida* Lepechin) in the Barents and Kara seas. In: Materialy Rybokhozyaistvennykh Issledovanii Severnogo Basseina (Materials of Fishery Investigation in the Northern Basin). Tr Polar Nauchno-Issled Inst Rybn Khoz Okeanogr, vol. 10. Tr. Polar Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., pp. 20–27 (In Russian).

Ponomarenko, V.P., 1968. Some data on the distribution and migrations of polar cod in the seas of the Soviet Arctic. Rapp RV Rèun Cons Perm Int Explor Mer 158, 131–135.

Ponomarenko, V.P., 1977. Polar cod. In: Promyslovye Biologicheskie Resursy Severnoy Atlantiki I Prilegayuschikh Morey Severnogo Ledovitogo Okeana (Commercial Biological Resources of the North Atlantic and Adjacent Seas of the Arctic Ocean. Part 1). Pishchevay promyshlennostʹ, Moscow, pp. 309–313 (In Russian).

Ponomarenko, V.P., 2000a. Sezonnye izmenenia v pitanii saiki *Boreogadus saida* (Lepechin) Barenzeva morya (po materialam 1956-1964 gg.) (Seasonal changes in feeding of the Barents Sea polar cod *Boreogadus saida* (Lepechin) (based on materials of 1956-1964.). In: Marine Hydrobiological Investigations. VNIRO Publishing, Moscow, pp. 151–157 (In Russian).

Ponomarenko, V.P., 2000b. Eggs, larvae, and juveniles of the polar cod *Boreogadus saida* in the Barents, Kara, and White seas. Vopr. Ikhtiol. 40, 203–211 (In Russian).

Ponomarenko, 2008. Characteristics of feedings of polar cod (*Boreogadus saida*) in the Barents Sea. Voprosi Rybolovstva 9 (2), 330–343 (In Russian).

Prokopchuk, I.P., 2017. Feeding of polar cod in the Kara sea. J. Ichthyol. 57, 591–602.

Prozorkevich, D., Johansen, G.O., van der Meeren, G.I., 2018. Survey Report from the Joint Norwegian/Russian Ecosystem Survey in the Barents Sea and Adjacent Waters, August-October 2017. IMR/PINRO Joint Report Series, p. 97. No. 2/2018.

Rass, T., 1968. Spawning and development of polar cod. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer 158, 135–137.

Renaud, P.E., Berge, J., Varpe, Ø., Lønne, O.J., Nahrgang, J., Ottesen, C., Hallanger, I., 2012. Is the poleward expansion by Atlantic cod and haddock threatening native polar cod, *Boreogadus saida*? Polar Biol. 35, 401–412.

Rohatgi, A., 2019. WebPlotDigitizer, Ver 4.2. https://automeris.io/WebPlotDigitizer/.

Sakurai, Y., Ishii, K., Nakatani, R., Yamaguchi, H., Anma, G., Jin, M., 1998. Reproductive characteristics and effects of temperature and salinity on the development and survival of eggs and larvae of Arctic cod (*Boreogadus saida*). Mem. Fac. Fish. Hokkaido Univ. 44, 77–89.

Shavykin, A.A., Ilyin, G.V., 2010. An Assessment of the Integral Vulnerability of the Barents Sea from Oil Contamination. MMBI KSC RAS, Murmansk, p. 110 pp. (In Russian).

Shepel, L.I., 1971. Size and age composition of polar cod in the southwestern part of the Kara Sea in the fall of 1969. Vopr. Ikhtiol. 11 (1), 161–164 (In Russian).

Shleinik, V.N., 1970. Distribution and migration of polar cod in the eastern Barents Sea. ICES CM F 20, 5.

Shleinik, V.N., 1973. The state of stock and perspectives of polar cod (*Boreogadus saida*) fishery in the Barents Sea. Formirovanie godovykch klassov I ekspluatatsiya zapasov promyslovykch ryb Barentseva I Norvezhskogo morei (Formation year-classes and exploitation of commercial fish stocks in the Barents and Norwegian Seas). Tr. Polar. Nauchno-Issled. Inst. Rybn Khoz Okeanogr 33, 225–236 (In Russian).

Shleinik, V.N., 1978. Fecundity of polar cod in the Barents Sea, in *Biologiya i promysel pelagicheskikch ryb Severnogo basseina* (Biology and fishing of pelagic fish in the Northern Basin). Tr. Polar Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr. 41, 156–166 (In Russian).

Skern-Mauritzen, M., Johannesen, E., Bjørge, A., Øien, N., 2011. Baleen whale distributions and prey associations in the Barents Sea. Mar. Ecol. Prog. Ser. 426, 289–301.

Tarverdieva, M.I., Panasenko, L.D., Nesterova, V.N., 1996. Feeding of polar cod in the Barents Sea. In: Hydrobiological Studies in Marine and Oceanic Fishing Grounds. Moscow VNIRO Publishing, pp. 98–109 (In Russian).

Varpe, Ø., Fiksen, Ø., Slotte, A., 2005. Meta-ecosystems and biological energy transport from ocean to coast: the ecological importance of herring migration. Oecologia 146, 443–451.

Varpe, Ø., Daase, M., Kristiansen, T., 2015. A fish-eye view on the new Arctic lightscape. ICES J. Mar. Sci. 72, 2532–2538.

Welch, H.E., Crawford, R.E., Hop, H., 1993. Occurrence of Arctic cod (*Boreogadus saida*) schools and their vulnerability to predation in the Canadian high Arctic. Arctic 46, 331–339.

Welch, H.E., Bergmann, M.A., Siferd, T.D., Martin, K.A., Curtis, M.F., Crawford, R.E., Conover, R.J., Hop, H., 1992. Energy flow through the marine ecosystem of the Lancaster Sound region, Arctic Canada. Arctic 45, 343–357.

Węsławski, J.M., Stempniewicz, L., Galaktionov, K., 1994. Summer diet of seabirds from the Franz-Josef-Land archipelago, Russian Arctic. Polar Res. 13, 173–181.

Wienerroither, R., Johannesen, E., Dolgov, A., Byrkjedal, I., Bjelland, I., Drevetnyak, K., Eriksen, K.B., Høines, Å., Langhelle, G., Langøy, H., Prokhorova, T., Prozorkevich, D., Wenneck, T., 2011. Atlas of the Barents Sea fishes. IMR/PINRO Joint Rep Ser 1, 272.

Wienerroither, R., Johannesen, E., Dolgov, A., Byrkjedal, I., Aglen, A., Bjelland, O., Drevetnyak, K., Eriksen, K.B., Høines, Å., Langhelle, G., Langøy, H., Murashko, P., Prokhorova, T., Prozorkevich, D., Smirnov, O., Wenneck, T., 2013. Atlas of the Barents Sea fishes based on the winter survey. IMR-PINRO Joint Rep. Ser. 2–2013, 220.

Yudanov, I.G., 1976. Zoogeography of polar cod in the Arctic ocean. Priroda i khoziaistvo severa (nature and economy of the north). Murmansk: Murm. Knizhn. Izd. 4, 111–113 (In Russian).

Zacharias, M.A., Gregr, E.J., 2005. Sensitivity and vulnerability in marine environments: an approach to identifying vulnerable marine areas. Conserv. Biol. 19, 86–97.

Zalesskikh, L.M., 1987. Feeding of larvae and juveniles of polar cod in the Barents Sea. In Problemy issledovaniy, ratsionalʹnogo ispolzovaniya I okchrany prirodnykch resursov Belogo moray (Problems of investigations, rational using and conservation of nature resources of the White Sea). Kandalaksha. Book 2, 300–302 (in Russian).

Zeller, D., Booth, S., Pakhomov, E., Swartz, W., Pauly, D., 2011. Arctic fisheries catches in Russia, USA, and Canada: baselines for neglected ecosystems. Polar Biol. 34, 955–973.