



Polar cod egg and larval drift patterns in the Svalbard archipelago

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Abstract

Spawning of polar cod (*Boreogadus saida*) in the vicinity of the Svalbard archipelago has not been directly observed. From the distribution pattern of polar cod 0-group observed during annual monitoring of the Barents Sea, it has, however, been inferred that spawning occurs in Svalbard waters most years. We wanted to investigate the possibility of back-tracking the larvae from these observed distribution areas to the spawning areas from which they originated and applied a coupled ocean–sea ice and particle tracking model to simulate the drift of particles released at suggested spawning sites. The model was run for 1 year (December 2006–September 2007), and the results were compared to observations of polar cod larvae in the autumns of 2007 and 2004–2010. The particles released in the western fjords were mostly retained in the fjords. For the rest of the suggested spawning grounds, the released particles drifted mostly clockwise around the archipelago. Model runs mainly indicated a drift pattern with end points that qualitatively match the main features of the August–September distribution of the polar cod 0-group observed. We conclude that the suggested spawning sites on the southern, northern and eastern sides of Svalbard could have caused a distribution of 0-group polar cod similar to that observed during August–September 2007. From the environmental factors experienced during drift of eggs and larvae and assumptions about habitat suitability for survival and growth, we conclude that spawning in the Svalbard area probably occurs on the southern and eastern sides and later than the area in the southeastern Barents Sea.

Keywords *Boreogadus saida* · Particle tracking model · Spawning sites · Distribution · Habitat associations

Introduction

Sea ice in the Arctic is declining (Serreze et al. 2007) and this has sparked interest in utilizing natural resources in the high north. Understanding the impact of the changing climate and anthropogenic stressors on Arctic marine ecosystems requires detailed knowledge about the key species and the structure and functioning of these ecosystems. One fish species playing a key role in Arctic marine ecosystems is the polar cod (*Boreogadus saida*), a small and relatively short-lived (5–7 years) circumpolar species that is widely distributed in cold waters. Polar cod is assumed to play a key role in the Arctic marine food web (Bradstreet et al.

1986; Jensen et al. 1991; Gjøsæter 2009; Orlova et al. 2013; Ajjad et al. 2011; Renaud et al. 2012; Hop and Gjøsæter 2013). Maturity is reached at age 2 for males and age 3 for females (Craig et al. 1982). Polar cod is sometimes found in very dense shoals (Melnikov and Chernova 2013) and may undertake extensive migrations (Ponomarenko 1968; Hop and Gjøsæter 2013). Polar cod spawn from 9000 to 21,000 eggs (Gjøsæter 2009). The eggs of polar cod are buoyant (Graham and Hop 1995; Ponomarenko 2000) and are 1.6–1.8 mm in diameter (Andriyashev 1954; Graham and Hop 1995; Hop et al. 1995).

Over the last four decades, climatic conditions in the Barents Sea have changed from cold in the 1980s to variable and moderate in the 1990s to warm in the 2000s (ICES 2018). This recent warming has led to a larger area of Atlantic water and a smaller area of arctic water within the Barents Sea, which influences suitable habitats for arctic fish, such as the polar cod. Previous studies have shown that decreasing areas of arctic water are associated with a redistribution of the occupation area of both juveniles and adults (Hop and Gjøsæter 2013; ICES 2014).

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Polar cod feed over large parts of the Barents Sea, excluding the southwestern areas. The distribution of both adult fish and young-of-the-year (hereafter called the 0-group) in the summer–autumn season is well known from joint Russian–Norwegian surveys during August–October, but the spatial and temporal distributions of spawning are less understood (Anonymous 2004; Hop and Gjørseter 2013; Eriksen et al. 2015). The adult population often occupies a continuous area from the southeast to the northwest, but in some years is divided into a western and an eastern component. The 0-group is also often found in a continuous area over the northeastern to eastern Barents Sea, while in other years, there is a clear division between an area centred in the eastern Barents Sea and another around Svalbard. Spawning is known to occur in the southeastern Barents Sea during January–February (Ponomarenko 1968; Hop and Gjørseter 2013), and additional spawning areas may be found in the vicinity of Svalbard (Ponomarenko 1968; Boitsov et al. 2013), based on the observed distribution of the 0-group during annual surveys in autumn.

The polar cod stock has experienced large changes in abundance and geographical distribution over the last three decades. From 1986 to 1997, the stock was relatively small (0.1–0.5 million tonnes), which increased to nearly 2 million tonnes between 2001 and 2006, and decreased to 0.3 million tonnes in 2013 (Boitsov et al. 2013). The area occupied by adults of the eastern component shifted eastwards and southwards (ICES 2014). During most of the period when the distribution and abundance of 0-group polar cod was monitored, the eastern component was dominant, contributing an average of 81% to total 0-group polar cod abundance from 1980–2011. Since then, the western component has become more important (Eriksen et al. 2015; ICES 2016).

Ponomarenko (1968) suggested a Svalbard component of the Barents Sea polar cod population with spawning sites east of Svalbard. Persistent observations of disjoint 0-group distribution areas have led other authors to share this view (Gjørseter 1973; Boitsov et al. 2013). Russian literature reviewed by Boitsov et al. (2013) suggested that polar cod occurred in a spawning area close to Svalbard. Gjørseter (1973) concluded that, while the exact location of the western component is not known, the general current patterns suggest that it is probably found east of Svalbard. Although disjoint 0-group populations are not definite evidence of disjoint spawning areas, the distances between observations and circulation patterns in the area make this scenario highly likely. In addition to these two components, adult polar cod have been observed in fjords and coastal areas west and north of Svalbard. Korshunova (2012) collected polar cod by bottom trawling in the western fjords (Isfjord and Billefjord) of Svalbard from August to January and found mature polar cod that had spawned at least once or that were preparing for their first spawning in the coming winter. This study

has been supplemented by observations from other fjords (western: Adventsfjorden, Kongsfjorden and Bellsund and northern: Hinlopen and Rijpfjorden), where mature polar cod ages 1–3 were found (Nahrgang et al. 2016). However, no spawning has been observed in the area, most likely due to ice coverage and generally minimal survey effort.

While spawning areas have been inferred from knowledge of circulation patterns over the past several decades, recent improvements in computer technology have enabled the development of biophysical models with high temporal and spatial resolutions. In the present study, we applied a coupled ocean circulation and particle tracking model for Svalbard and the northwestern Barents Sea from December 2006 to September 2007 to evaluate possible spawning sites and egg/larval drift patterns in the northwestern Barents Sea, including the Svalbard archipelago. We initialized particle drift from potential spawning sites based on the existing literature as summarized above and supplemented with qualitatively similar spawning sites from the inner and outer coasts around Svalbard. Particle release times (late December–March) were based on known spawning times in other areas and gonad maturity stages of pre-spawners (Boitsov et al. 2013). Particle drift was tracked from these potential spawning sites, and environmental conditions (ice cover, water temperature and salinity) during egg and larval dispersal were recorded. We identified several environmental conditions considered to be favourable to the growth and survival of polar cod during their early life stages.

Materials and methods

Study area

The Barents Sea is a high latitude shelf sea located between approximately 70 and 80°N at the northwestern corner of the Eurasian continental plate. This area is a large and relatively deep shelf (approximately 1.5 million km², mean depth 230 m) bounded in the west and north by deep basins of the Norwegian Sea and the Nansen Basin of the Arctic Ocean, respectively. Atlantic water from the North Atlantic (partly as a continuation of the Gulf Stream) flows north through the eastern Norwegian Sea and splits into two main branches, one flowing into and through the Barents Sea from the southwest to the northeast and the other flowing north into the Fram Strait as the West Spitsbergen Current and continuing eastwards, north of Svalbard to the northern flanks of the Barents Sea (Lien et al. 2013). These two current branches meet at the opening of the St. Anna Trough in the northern Kara Sea before they continue further east along the Siberian shelf and into the Arctic Ocean, accounting for the biogeography and ecology of the Barents Sea. The heat content of the Atlantic water leads to relatively mild conditions in

the western and southern parts of this area, while more arctic conditions prevail in the northern and eastern parts of the Barents Sea, which is a biogeographical transition zone between boreal and Arctic provinces (Smedsrud et al. 2013). The northern part of the Barents Sea is covered with sea ice in winter. A phytoplankton bloom in arctic water follows retreating ice (i.e. induced by ice melting) (Melle and Skjoldal 1998; Loeng and Drinkwater 2007).

Spawning sites and timing

In the southeastern Barents Sea, polar cod spawning is associated with sea ice (Ponomarenko 1968). Detailed information about spawning areas and seasons is scarce due to the difficulty of sampling close to and under ice, but spawning is considered to occur from December–March (Boitsov et al. 2013). Possible spawning sites near the Svalbard archipelago, apart from those in fjords in West Spitsbergen, are even less studied than those in the southeastern Barents Sea. No definite information is available about spawning times in the proposed spawning areas near Svalbard, but Gjøsæter (1973) noted that 0-group polar cod near Svalbard were normally smaller than 0-group polar cod from the eastern Barents Sea, which might indicate either later spawning near Svalbard or slower growth. Boitsov et al. (2013) reviewed polar cod literature (since 1935) and concluded that polar cod probably spawn near Svalbard between February and March. Since

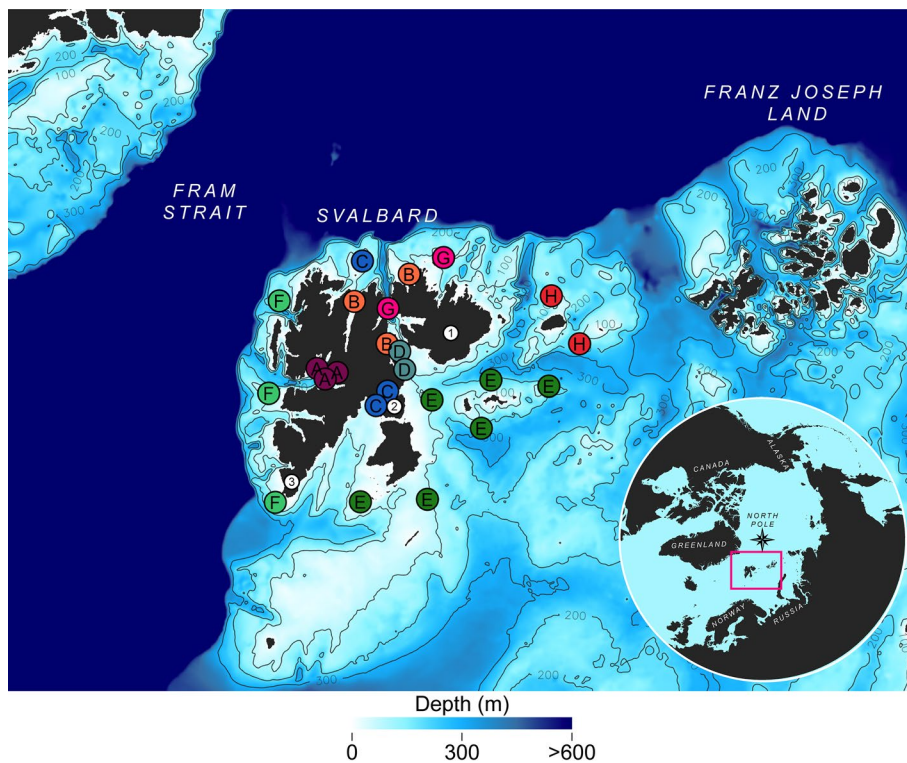
the spawning time in the Svalbard area has been estimated based on the gonad maturity stage of pre-spawners and not directly observed, we used particle tracking to identify potential spawning sites. We chose to release particles in late December, to test if environmental conditions around Svalbard are suitable at spawning times used in the Southeastern Barents Sea, and between February and March, based on the literature on gonad development reported in Svalbard area. In the western fjords of Svalbard, Korshunova (2012) found indications of spawning in February and March. In the present study, potential spawning sites were hypothesized to include fjords (four inner sites) and the Svalbard shelf (four outer sites) at a total of eight distinct locations around the Svalbard archipelago (Fig. 1).

An equal number of particles were released at each individual release point on five different dates on 20th December 2006, on 1st and 15th February 2007, and on 1st and 10th March 2007. In total, 5000 particles at each release location (Fig. 1), equally distributed over five release times (see hypothesized spawning times above).

Ocean model and particle drift simulations

The Regional Ocean Modelling System (ROMS, <https://myroms.org>) circulation model, a free-surface, hydrostatic, primitive equation ocean model (Shchepetkin and McWilliams 2005, 2009; Haidvogel et al. 2008), with an

Fig. 1 Svalbard archipelago and modelled spawning sites (to the right) showed by coloured dots: western-outer (A, purple), western-inner (B, orange), northern-outer (C, blue), northern-inner (D, grey), eastern-outer (E, green), eastern-inner (F, turquoise), southern-outer (G, pink), and southern-inner (H, red). Islands, which mentioned in the main text marked with number: Nordaustlandet (1), Barentsøya (2) and the South Cape (3)



ice component (Budgell 2005), was used. The circulation model was run with an 800 m resolution in the horizontal direction and 35 topography-following vertical levels, and it was run from 2nd September 2006 to 20th September 2007. The ROMS model had a temporal resolution of one hour, and contained velocity fields and hydrographical variables covering a total area of 1802×1352 grid points, giving a total model area of approximately 1440×1080 km. The atmospheric forcing (mean sea level pressure, winds, surface air temperature and humidity, cloud cover and precipitation) was provided by the Weather Research and Forecasting model (WRF model, Skamarock et al. 2008), developed by the National Center of Atmospheric Research, applying a 3 km resolution in the horizontal direction. Seasonal runoff was also applied to represent the main glaciers in Svalbard and was provided by a 1 km SnowModel grid for Svalbard (van Pelt et al. 2016) calculated by the SnowModel (Liston and Elder 2006). For further information on the model setup, see Hattermann et al. (2016) and Sundfjord et al. (2017). The ocean model has been extensively investigated and validated and we refer to Hattermann et al. (2016) for more details on model evaluation and performance.

Particle advection in the horizontal plane was modelled using a fourth-order Runge–Kutta scheme with the velocity field arrays from the hydrodynamic model. Individual particles were released uniformly at every metre between 1 and 30 m, keeping the particles at the fixed depth set at initialization throughout the simulation. The motivation for this approach was the lack of detailed observations of the pelagic vertical distribution during egg stage, and that 0-group polar cod were mainly captured in upper 30–50 m (Eriksen et al. 2015). By allowing dispersal at multiple depths, we could quantify the need and importance of obtaining such in situ measurements in the future. However, polar cod eggs have a lower density than the surrounding water (Boitsov et al. 2013) and occurrence of ice limits the level of turbulence that would otherwise mix buoyant eggs down in the water column (Sundby 1983). Hence, the eggs are expected to float immediately underneath the ice. On the other hand, larvae are expected to move vertically, possibly motivated by vertical distribution of prey and predators, but details of their vertical distribution are not known.

Criteria to define habitat suitability

Several studies have shown that environmental conditions during the first months after spawning could control the survival of eggs and fish larvae (Sætersdal and Loeng 1987; Loeng and Gjøsæter 1990; Ottersen and Loeng 2000). Therefore, we recorded environmental conditions (water temperature, salinity and ice coverage) during egg and larval

drift and simulated survival success along the various drift routes based on environmental preferences.

Polar cod produce large, floating eggs (1.6–1.8 mm, Rass 1949; Ponomarenko 1968). The floating eggs are covered by a thin, fragile membrane and can easily be damaged (Boitsov et al. 2013). Therefore, we hypothesize that during the egg stage, ice coverage may reduce water turbulence and thus mechanic damage to the eggs. We suggest that reduced sea ice concentrations during egg drift could be a critical factor indicating reduced egg survival.

The incubation period of the eggs may last for 1.5–3 months depending on ambient temperatures, and both eggs and small larvae are found in high concentrations below ice or in upper water layers after ice melting (Rass 1949; Ponomarenko 1968; Hop and Gjøsæter 2013). We estimated the possible incubation duration of individual eggs based on a linear relationship between the accumulated number of degree-days (evaluated at the egg's actual position in the ROMS output, at daily intervals) and incubation durations from laboratory studies (Kent et al. 2016). The summer feeding period in arctic waters is short, and the time allocated for feeding and growth for newly hatched larvae is therefore limited (Bouchard et al. 2017). We used estimated incubation duration (< 3 months or 90 days) as a criterion for sufficient time for summer feeding so that larvae can manage to survive the winter. Thus, we assumed that if eggs took longer than 90 days to hatch, then larvae would have insufficient time to grow and survive the overwintering period.

During winter and early spring (January–March), both phytoplankton biomass and productivity are relatively low in the Barents Sea (ICES 2018). The melting of sea ice increases light conditions and stabilizes the water column, thereby initiating a phytoplankton bloom and some weeks later a zooplankton bloom. Polar cod are visual predators that feed primarily on calanoid copepod nauplii (Bouchard et al. 2017; Michaud et al. 1996). Bloom duration is typically approximately 3–4 weeks and is followed by an increase in zooplankton biomass. In this study, the timing of the plankton bloom in melt water is linked to a strong reduction in ice coverage and salinity. The date when 50% of simulated larvae have hatched will be used to identify a match or mismatch with the plankton bloom. Yolk sacs are resorbed 3 weeks after hatching (Boitsov et al. 2013), and then, copepod eggs and nauplii are the major prey of first-feeding fish larvae (Fortier et al. 1995; Michaud et al. 1996; Bouchard et al. 2017). We suggest that icy and saline waters with temperatures close to or below 0 °C 3 weeks after hatching could indicate that the spring bloom has not yet occurred and thus this scenario could lead to death of the fish larvae. In addition, ice coverage may reduce visibility and the ability of first-feeding polar cod larvae to successfully detect and capture prey.

During August–September, most of the 0-group polar cods (80%) occupy a thermal habitat between 2.0 and 5.5 °C, and fish length increases with increasing temperature between 2.0 and 7.0 °C, which suggests favourable conditions for growth at these temperatures (Eriksen et al. 2015). Thus, we included the thermal habitat (temperatures between 2.0 and 5.5 °C) during August–September as an indicator of favourable conditions.

Four criteria, described above, were used to define life stage specific habitat suitability to more completely evaluate potential spawning areas and times (Table 1). Based on these criteria, we defined habitat suitability for three early life stages (eggs, larvae and juveniles), for larvae originating from eight different spawning areas at five different times, as (1) “most likely suitable habitat”, (2) “possibly suitable habitat” or (3) “unsuitable habitat”. If two or more criteria resulted in “unsuitable habitat”, then the overall assessment of spawning success at the site was characterized as “unsuitable habitat”.

Observed distribution of 0-group polar cod in autumn

The Norwegian–Russian ecosystem survey (BESS) monitors several ecosystem components, including the abundance and distribution of 0-group fish. The 0-group polar cod are sampled approximately 8–9 months after spawning by a small-mesh pelagic trawl (“Harstad”) with a 20 × 20 m mouth opening (Eriksen and Prozorkevich 2011). The trawl is used to cover the upper water column (0–60 m), and in each haul, the headline is towed at three knots and remains at depths of 0, 20 and 40 m for ten minutes (Anonymous 2004; Eriksen et al. 2009). Additional tows with the headline at 60 and 80 m are occasionally made when dense concentrations of 0-group fish are recorded deeper than 60 m on the echo-sounder. Based on trawl opening, towed distance, and depth covered, an estimate of the density of larvae (numbers per square nautical miles) can be obtained (Eriksen and Prozorkevich 2011). The coverage of areas where polar cod 0-group could potentially be found is not consistent between years. Unfortunately, the areas east of the Svalbard archipelago were not covered in 2007, which was the year

when the ocean-sea-ice model was available to run the drift model. Therefore, in addition to the observations in 2007, we also used observations averaged over 2004–2010 to obtain a general pattern of 0-group polar cod distribution in recent years to compare with particle output from the drift model in 2007.

Results

Modelled egg/larvae drift and environmental conditions

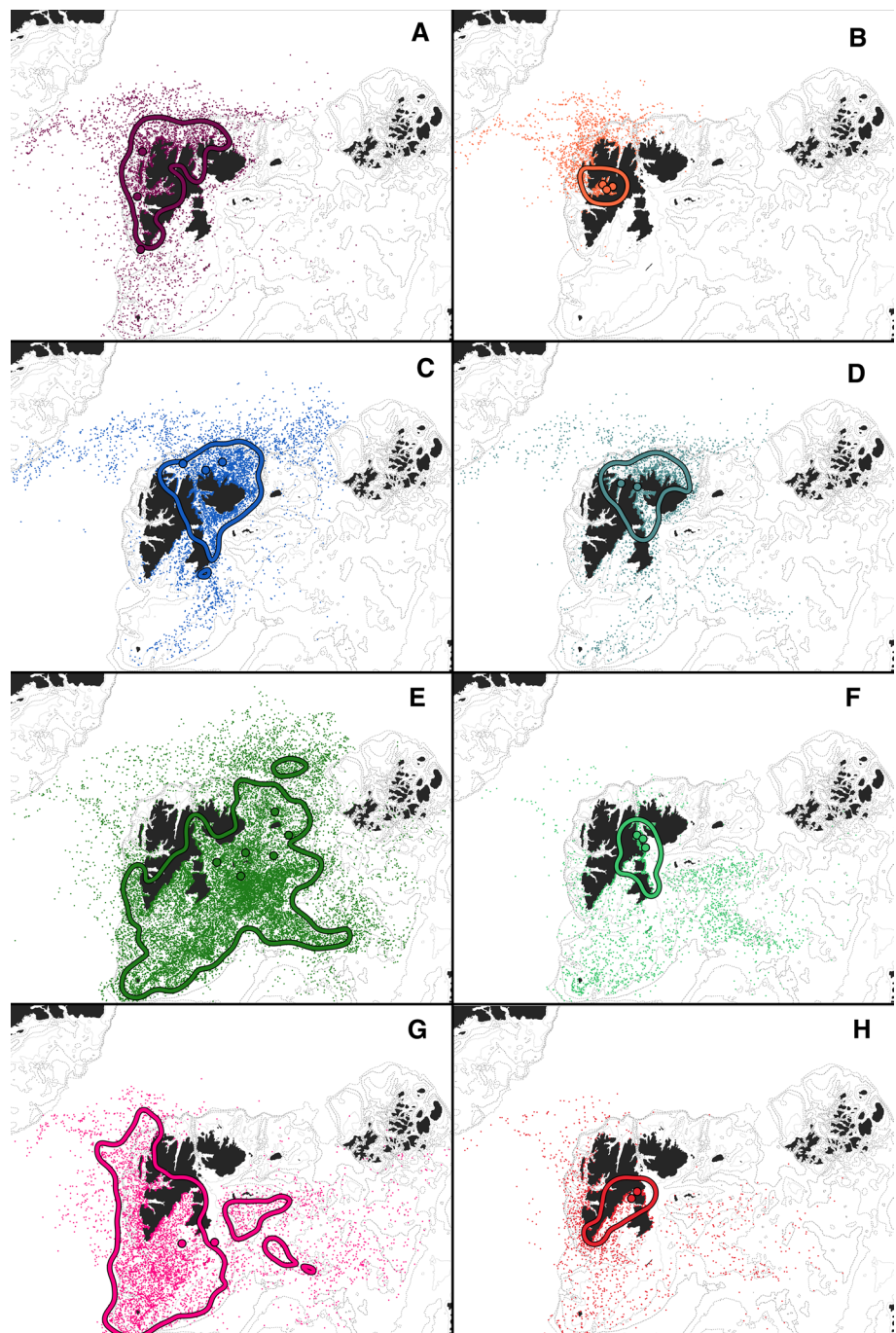
In general, the particles released from the inner spawning sites had shorter drift routes than the particles released from outer spawning sites (Figs. 2, 3). Most particles released from the western-inner (WI) sites were retained within their ‘native’ fjord, while the majority of particles released from the outer western (WO) sites drifted the third longest distance northwards and eastwards along the western and northern coasts of Svalbard. Most particles released from the inner northern (NI) sites drifted northwards, while particles from outer northern (NO) sites drifted northwards/north-eastwards along the shelf edge and southwards around Nordaustlandet but also southwards through the Hinlopen Strait between Nordaustlandet and Spitsbergen. The particles released to the west of Barentsøya (EI) had a tendency to drift southwards around the South Cape or farther north into the Hinlopen Strait (Figs. 1, 2, 3). Most particles released from the eastern outer (EO) sites had the longest drift trajectories and were distributed from 74°N south of Svalbard to 82°N northwest of Franz Josef Land. The particles released from the southern-inner (SI) sites were transported southwards along the southern coast of Spitsbergen and then northwards along western Svalbard. Most particles released from the outer southern (SO) part of Svalbard had the second longest drift trajectories and were distributed over a large area from 74°N south of Svalbard to 80°N west of Svalbard (Figs. 2, 3).

Incubation time (Fig. 4) was shortest (with an average of 46 days) for the eggs from the outer western-spawning (WO) sites in comparison to those from the other sites because these eggs drifted in the warmest water with temperatures

Table 1 Criteria used to define habitat suitability

Development stage	Factor	Effects
Egg	Ice cover	Protection from mechanic damage to eggs (+)
Larval feeding		Decreased light availability to detect prey (–)
Larval, 1st feeding	Plankton bloom	Overlap/match with prey resource (+)
Egg	Thermal habitat: (1–2 °C)	Appropriate time for development (+)
Juveniles, 6–8-month-old	(2–5.5 °C)	Temperatures within optimum range for growth (+)

Fig. 2 Individual drift trajectories of particles released at eight modelled spawning sites (coloured dots): **a** western-outer (WO, purple), **b** western-inner (WI, orange), **c** northern-outer (NO, blue), **d** northern-inner (NI, grey), **e** eastern-outer (EO, green), **f** eastern-inner (EI, turquoise), **g** southern-outer (SO, pink), and **h** southern-inner (SI, red). Here 80% of particles are located within the enclosed polygons (coloured solid lines)



of 1.5–2.5 °C (Figs. 4, 5). Half of the particles released in late December along the western shelf drifted in Atlantic water masses (temperature close to 2 °C and a salinity of 35 o/00) and hatched in early February. The particles released later hatched mainly between mid-March and late April. Early hatched larvae experienced icy and saline waters and most likely did not survive due to decreased light availability to detect prey and mismatch with the plankton bloom, while larvae hatched in April experienced melting sea ice and increasing light conditions and were more likely to

better match with the plankton bloom. Eggs from the western fjord (WI) and northern (NI and NO) spawning sites hatched after 60 days on average, and approximately half of them hatched between March (released in December) and late May (released in March). Particles from the eastern (EI and EO) and southern-inner (SI) spawning sites had the longest incubation time, with an average of 85 days, where approximately half of them hatched between mid-March (released in December) and the beginning of June (released in March) due to stable cold temperature conditions (close

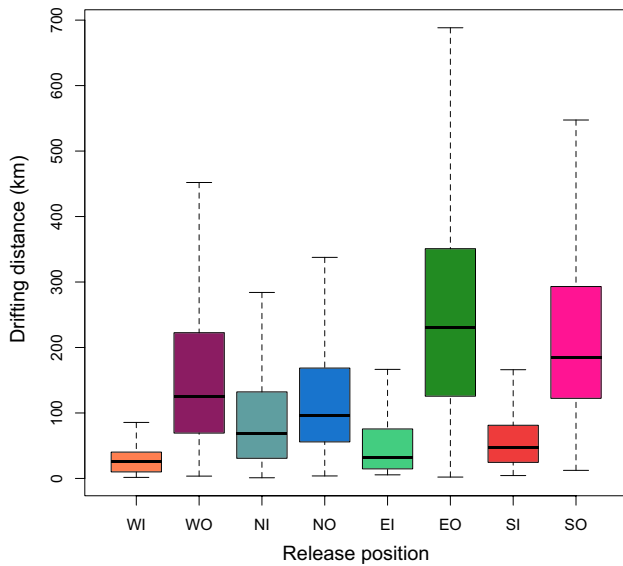


Fig. 3 Boxplots of drifting distances classified into the eight modelled spawning sites (coloured dots): western-outer (WO, purple), western-inner (WI, orange), northern-outer (NO, blue), northern-inner (NI, grey), eastern-outer (EO, green), eastern-inner (EI, turquoise), southern-outer (SO, pink) and southern-inner (SI, red)

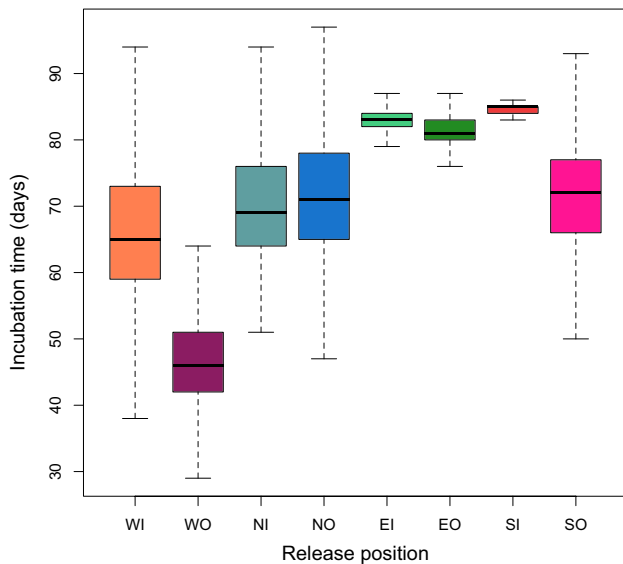


Fig. 4 Boxplots of incubation time (in days) classified into the eight spawning sites (coloured dots): western-outer (WO, purple), western-inner (WI, orange), northern-outer (NO, blue), northern-inner (NI, grey), eastern-outer (EO, green), eastern-inner (EI, turquoise), southern-outer (SO, pink), and southern-inner (SI, red)

to $-2\text{ }^{\circ}\text{C}$, Fig. 5) during egg drift. The particles from the SO experienced temperatures from $1\text{ }^{\circ}\text{C}$ to $-2\text{ }^{\circ}\text{C}$ (Fig. 5), most likely due to mixing of Atlantic water and arctic water masses. Thus, the estimated incubation duration varied from 30 to 95 days (Fig. 4).

The different spawning groups were exposed to widely different physical conditions during the drift simulations. The majority of eggs ($\approx 90\%$) that spawned on the eastern and southern side of Svalbard (i.e. EI, EO and SI) were covered by ice for most of their egg phase and experienced cold temperatures (between -1 and $-2\text{ }^{\circ}\text{C}$) until ice breakup at the end of June (Fig. 5). The timing of the ice breakup was approximately 3 weeks after hatching (corresponding to the time it took for the larvae to absorb the yolk sac) of the two latest-spawning egg groups in the east, and thus, these egg groups experienced increasing light conditions enabling them to detect prey more easily and be better matched with the plankton bloom. In contrast, the eggs from the western spawning sites, notably the western shelf (WO), experienced mainly Atlantic waters (lack of ice, high salinity and relatively warm temperatures) during the egg stage (Fig. 5). The particles released in the north experienced conditions between these two extremes, where particles were found only partly under ice for several months (March–June). The particles in the north experienced the most stable temperatures, with close to $0\text{ }^{\circ}\text{C}$ throughout the larval stage (Fig. 5). During August–September, most particles (90%) were found in water masses within the suitable/optimal temperature range for juvenile polar cod defined by Eriksen et al. (2015) (Fig. 5).

The ambient conditions of polar cod early life stages are summarized in Fig. 6. The fates of particles from eight spawning sites are briefly summarized in Table 1, where habitat is coarsely categorized as “most likely suitable”, “possibly suitable” and “unsuitable”. We included results from only three of the five spawning times (20th December, 15th February and 10th March) in the table because of table size and the lack of significant information provided by the additional spawning dates. Early spawning in December resulted in 4 out of 8 spawning grounds considered unsuitable due primarily to a mismatch with the plankton bloom and lack of ice during the egg stage (Figs. 5, 6). With later spawning (mid-February), eggs would most likely experience better living conditions (except for NO), although in this study, ice was still frequently missing at the spawning sites. Due to a reduction in ice cover after hatching, larvae experienced better light conditions, and first-feeders better matched with plankton blooms. Late spawning in early March provided suitable habitat for polar cod eggs/larvae/juveniles from all spawning sites. The thermal habitat during August–September seemed to be within the range we specified as suitable for almost all spawning sites and all spawning dates, except spawning in December at EI and in February at NO.

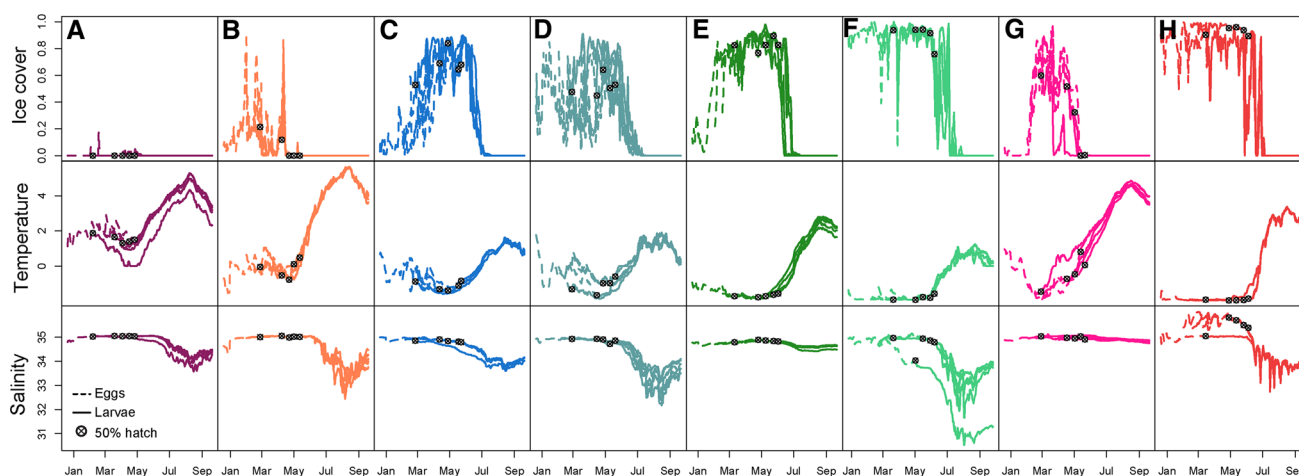


Fig. 5 Pelagic habitat experienced by polar cod eggs, larvae and juveniles. Here each line represents the median of the variable that a given ensemble of particles experienced (i.e. one line for each of the five release times and five spawning groups = 25 ensembles/lines). Proportion ice-covered particles (upper panel), salinity (middle panel) and temperature (lower panel). The broken lines represent

the egg phase, circles with cross represent day of 50% hatching, and solid lines represent the larval stage, distinguishing between the eight spawning groups by different colours; western-outer (purple), western-inner (orange), northern-outer (blue), northern-inner (grey), eastern-outer (green), eastern-inner (turquoise), southern-outer (pink), and southern-inner (red)

Observation of 0-group polar cod in 2004–2010

The observations of polar cod 0-group in the autumn of 2004–2010 demonstrate that these cod exhibited similar patterns to those described above, as the 0-group was found close to the coast west and north of the archipelago and much farther offshore to the east and south (Fig. 7). In 2007, the highest concentrations of the 0-group were found to the south (with an average of 0.5 million individuals per nm^2) and to the west (with an average of 0.2 million individuals per nm^2) of Svalbard, although lower concentrations were also detected to the north and in the Hinlopen Strait (Fig. 7). No survey was conducted east of Svalbard that year. While most years were characterized by a similar cod distribution to the west and north of the archipelago, the distribution of 0-group polar cod stretched much farther offshore on the eastern and southern coasts of Svalbard in some years (specifically, 2005, 2006 and 2010).

An 0-group polar cod with an average body length of 4.4 cm (3.2–6.8 cm) was observed in September 2007. Juveniles from the southern part of the distribution area (south of 78°N) were smaller, with an average body length of 3.8 cm (3.2–4.3 cm), than those from the northern part of the distribution area (north of 78°N), with an average body length of 4.9 cm (3.9–6.8 cm). Juveniles, which were found south of 78°N in September, could have been 150–250 days old (based on the regression line of fish length on age of Bouchard and Fortier 2008), corresponding to a spawning time between January and April, depending on the temperature they experienced. Polar cod found north of 78°N

in September could have been 170 days and older, corresponding to a spawning time between December and March, depending on the temperature they experienced.

The model runs indicated a clockwise drift around the archipelago, which kept particles close to the coast on the western and northern sides. End points from the drift simulation fit well with the observed distributions of polar cod 0-group during 2004–2010. Furthermore, the model runs also indicated that on the eastern and southern sides of Svalbard, the particles were transported farther from the coast. These results also fit well with the 0-group distribution observed during the autumn surveys in 2004–2010.

A comparison between modelled and observed distributions of 0-group polar cod revealed the following:

- (i) Both the modelled and observed distributions indicated that most eggs were spawned either within fjords or near the coast of Svalbard and remained close to the coast, except for some individuals advected off the coast and into the Fram Strait, east along the shelf edge of the polar basin or along the polar front in the Barents Sea.
- (ii) The 0-group polar cod observed in the northwestern Barents Sea most likely originated from spawning sites at Svalbard, as indicated by the retention of a significant number of particles.
- (iii) When several of the inner or outer spawning grounds were combined, the observed 0-group abundance surrounding Svalbard was approximately matched the simulated distribution based on visual comparisons.

Particles released December 20th 2006 and their habitat									
Habitat association	Development stage	WI	WO	NI	NO	EI	EO	SI	SO
Ice coverage	Egg	Red	Red	Yellow	Red	Yellow	Red	Yellow	Red
	Larval feeding	Green	Green	Yellow	Yellow	Red	Red	Yellow	Yellow
Plankton bloom	Larval, 1st feeding	Red	Yellow	Red	Red	Red	Red	Red	Yellow
Thermal habitat	Juveniles	Green	Green	Yellow	Yellow	Red	Green	Green	Green
Overall assessment	early life stage	Red	Yellow	Yellow	Red	Red	Red	Yellow	Yellow
Particles released February 15th 2007 and their habitat									
Habitat association	Development stage	WI	WO	NI	NO	EI	EO	SI	SO
Ice coverage	Egg	Red	Red	Yellow	Red	Green	Yellow	Green	Red
	Larval feeding	Green	Green	Yellow	Yellow	Yellow	Yellow	Yellow	Green
Plankton bloom	Larval, 1st feeding	Green	Yellow	Red	Red	Yellow	Yellow	Yellow	Yellow
Thermal habitat	Juveniles	Green	Green	Yellow	Red	Yellow	Green	Green	Green
Overall assessment	early life stage	Yellow	Yellow	Yellow	Red	Yellow	Yellow	Yellow	Yellow
Particles released March 10th 2007 and their habitat									
Habitat association	Development stage	WI	WO	NI	NO	EI	EO	SI	SO
Ice coverage	Egg	Red	Red	Yellow	Yellow	Green	Green	Green	Yellow
	Larval feeding	Green	Green	Yellow	Yellow	Yellow	Green	Green	Green
Plankton bloom	Larval, 1st feeding	Green	Green	Yellow	Yellow	Green	Green	Green	Green
Thermal habitat	Juveniles	Green	Green	Yellow	Yellow	Yellow	Green	Green	Green
Overall assessment	early life stage	Yellow	Yellow	Yellow	Yellow	Yellow	Green	Green	Green

Fig. 6 A coarse categorization of the habitat that egg/larvae/juveniles experienced during the first months: most likely suitable (green), possibly suitable (yellow) and unsuitable (red). The particles from eight spawning sites (western-outer (WO), western-inner (WI), northern-

outer (NO), northern-inner (NI), eastern-outer (EO), eastern-inner (EI), southern-outer (SO), and southern-inner (SI) were released in 20th December, 2006 (top), 15th February, 2007 (middle) and 10th March, 2007 (bottom)

- (iv) Only the northeastern spawning grounds (NI, NO and EO) resulted in a 0-group polar cod distribution northeast of Svalbard, while the southern and eastern spawning grounds (SO and EO) resulted in a 0-group polar cod distribution at the Svalbard Bank south of Svalbard.

Discussion

The polar cod stock in the Barents Sea, mainly inhabiting areas covered by arctic water masses or melting sea ice, declined from 1.8 million tonnes (age 1 +) in 2005 to

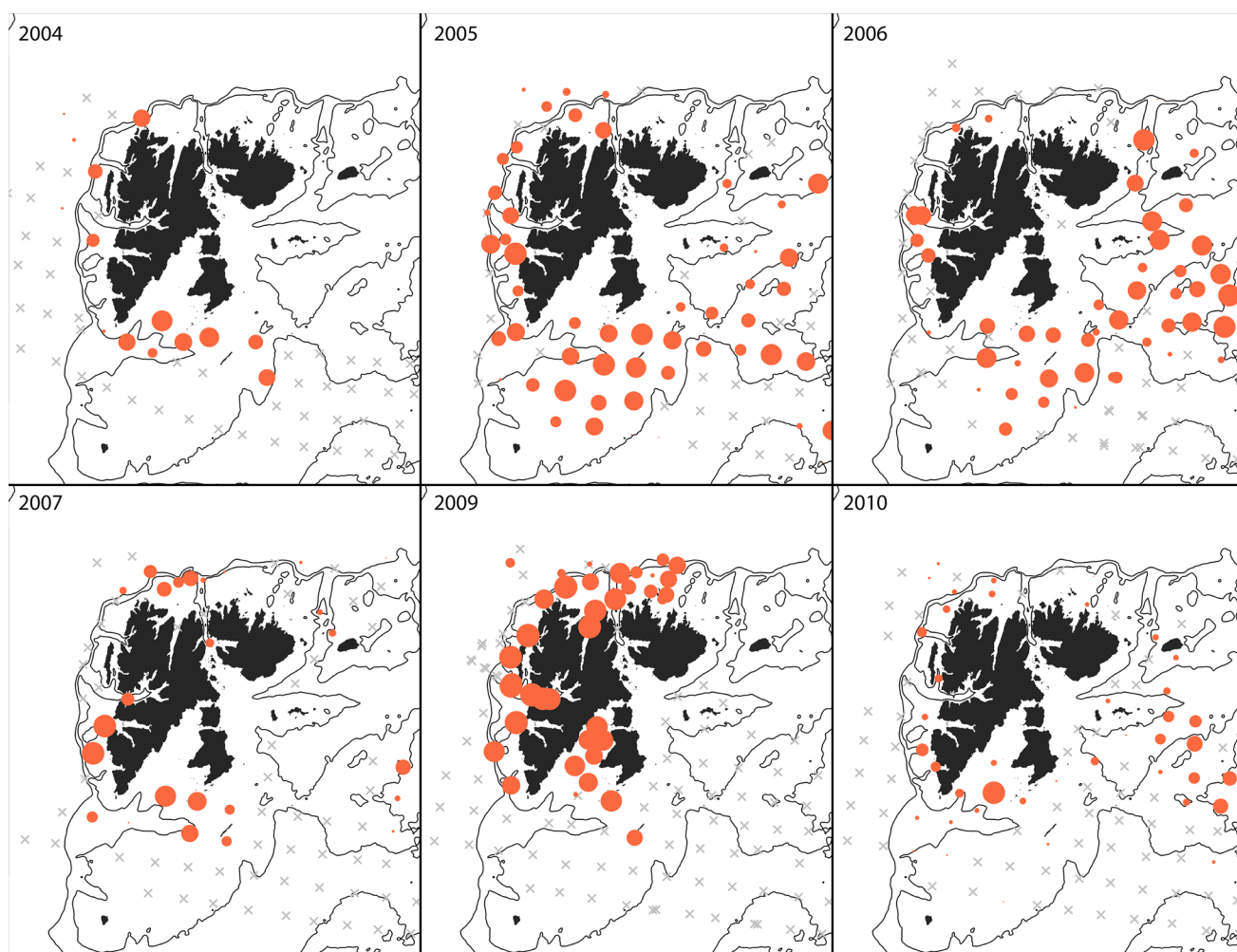


Fig. 7 Distribution of 0-group polar cod during August–September over the period 2004–2010. Coloured dots showed polar cod catches (abundance per square nautical miles). The 2008 observations were not shown due to few stations sampled

0.1 million tonnes in 2014 (ICES 2018). Traditionally, the spawning areas in the southeastern Barents Sea or Pechora Sea have produced the majority of polar cod offspring (an average of 80% from strong year classes and 52% for average and weak year classes, Eriksen et al. 2015). Since 2002, only four average year classes and no strong year classes were produced. The spawning areas around Svalbard have become more important due to the decline in the southeastern Barents Sea (Eriksen et al. 2015), but these spawning areas have not contributed significantly to the occurrence of strong or average year classes. Additionally, to date, we have not had details on which parts of the Svalbard coast and fjords contain spawning grounds. This lack of information has hampered our ability to consider the impacts of changes in the local marine environment due to climate change and long-term variability in key species such as polar cod.

The present study used the best available ocean circulation model fields for Svalbard and the northwestern Barents Sea to evaluate possible spawning sites at various distances from the coast around the Svalbard archipelago. Simulated distributions from these spawning sites were compared to observed 0-group abundances during early fall, which were observed in upper 30–50 m. The eggs, which are most likely associated with the underside of the ice due to their buoyancy, the release depth could be important. Thus, we tested differences between particles released at 10 and 30 m depths and no significant differences were found. We decided to release particle uniformly at every metre between 1 and 30 m, keeping the particles at the fixed depth, to link to 0-group polar cod vertical distribution. Most of the particles released drifted clockwise around the archipelago. However, northward drift of early life stages along Svalbard may also result in displacement into Fram Strait due to

mesoscale eddies (Hattermann et al. 2016). The same study also demonstrates the skill of the current ROMS application to replicate circulation features in the area of interest. Corresponding offshore transport also occurred elsewhere around Svalbard, resulting in distribution patterns of 0-group polar cod off the coast despite the fact that eggs were only initiated near the coast and within fjords. In particular, offshore transport led to modelled 0-group abundance along the shelf edge of the polar basin to the northeast of Svalbard and along the polar front in the Barents Sea. Notably, no single spawning ground resulted in a modelled 0-group distribution that corresponded to the observed distributions. However, in combination, the projected spawning grounds produced patterns that overlapped the in situ measurements. The suggested criteria for suitable egg and larval habitat, evaluated for all modelled individuals, further narrowed the search for the most likely spawning grounds.

Atlantic water masses influence the climate of the waters around Svalbard by releasing large heat fluxes into the atmosphere, especially during winter. This process significantly influences ice cover (Walczowski and Piechura 2011). Ambient conditions for the individual drift trajectories in terms of sea ice cover, temperature and food availability are highly variable, which suggests that survival conditions for eggs and larvae will also vary with where and when an egg is spawned. For example, we defined a lack of ice coverage as unsuitable habitat for eggs since harsh weather and increased water turbulence can lead to mechanical tears (Boitsov et al. 2013). The model runs indicated that eggs spawned at the western-outer spawning sites experienced open water during almost the entire winter, spring and summer seasons. Hence, according to these criteria, these spawning grounds were considered unsuitable. However, we defined unsuitable spawning grounds as those that resulted in individual drift trajectories violating at least two out of four criteria (ice was the key factor in three separate criteria) during the egg or larval stages. In brief, we found that late spawning resulted in more favourable conditions for the offspring because early spawning was often associated with a lack of ice during the egg stage, which can result in turbulent conditions for fragile eggs, and too much ice during the later larval period, which can limit visual feeding due to low light conditions and may be associated with minimal production as the productive season is initiated with the retreat of ice. This scenario is consistent with earlier findings, based on the maturity stage of pre-spawners, which suggests that polar cod from the Svalbard component mature and spawn later (February–April) than polar cod from the Pechora component (December–March, Boitsov et al. 2013).

Early ice breakup in spring was found to be favourable for early hatchers by allowing sufficient time to grow before the next winter. Large juveniles have better survival rates during the first winter due to increased lipid content, resistance to

starvation, and physiological tolerance (Fortier et al. 2006; Hunt et al. 2011; Bouchard and Fortier 2008; Fortier et al. 2015; Bouchard et al. 2017). Based on modelled ambient temperatures for all particles, we estimated the incubation duration from Kent et al. (2016) to evaluate whether larvae would have sufficient time to grow and accumulate sufficient lipid content. The incubation duration for polar cod eggs varied between 33 and 95 days, and 50% of the hatching occurred from March to late June, which is in agreement with results from earlier studies where newly hatched polar cod larvae were observed primarily from May to July in the Barents Sea (Baranenkova et al. 1966). In other areas, newly hatched larvae were observed from mid-May to mid-July (Northeast Water polynya of the Greenland Sea, Fortier et al. 2006) and from early January to early July (Laptev Sea, Bouchard and Fortier 2008). Observations from August–September in the Barents Sea showed that the average length of polar cod juveniles varied between 3.3 and 5.1 cm during the period 1980–2017 (Eriksen et al. 2017) and was 4.4 cm in 2007 (see results). These average values were all larger than the assumed minimum fish length for pre-winter juveniles of 3 cm (Bouchard et al. 2017). Thus, the incubation duration calculated from our study appears to provide sufficient time for larvae to grow and survive the next winter. Hence, we did not feel that the reduced feeding season resulting from the suggested spawning in March was a limitation to reaching a favourable size for surviving the next winter. However, a fully developed mechanistic bio-physical model enabling prey- and temperature-dependent growth is needed to reduce uncertainty in these conclusions.

Bouchard and Fortier (2008) suggest that open water in winter may provide polar cod larvae with necessary light conditions for prey perception and capture. In Arctic areas (75–82°N), the polar night prevails until the end of January, with some diffuse solar light. However, in our study, we considered early spawning in December at the western-inner, northern-outer and eastern (inner and outer)-spawning sites, which were still covered by ice 3 weeks after the potential hatching, to be unfavourable because polar cod larvae could have challenges with visual identification of prey after yolk sac resorption. A better understanding of survival when there is minimal food availability is needed to test this hypothesis.

The match/mismatch hypothesis suggests that early fish growth and survival depend on the synchronized development of larvae and their plankton food (Cushing and Horwood 1994). A phytoplankton bloom in arctic water follows retreating ice (i.e. induced by ice melting) and is followed by a zooplankton bloom with a time lag (Melle and Skjoldal 1998; Loeng and Drinkwater 2007). We defined zooplankton bloom production as starting 3 weeks after the ice breakup, but we acknowledge that this time frame is a crude approximation. We see that this criterion was most often violated

across the various spawning sites and was responsible for unfavourable conditions for larvae from almost all spawning grounds for spawning in December and mid-February due to a presumed lack of essential prey abundance (Fortier et al. 1995). Eggs from later spawning cod experienced significantly better feeding conditions if our assumption about zooplankton production is met.

During 30 years of observations, a majority of the 0-group polar cod (80%) was found in thermal habitat of 2.0–5.5 °C during August–September, which suggests that these temperatures provided favourable conditions for feeding, growth and survival (Eriksen et al. 2015). The model runs indicated that these favourable ambient conditions generally prevailed for juveniles spawned in the western, eastern and southern sites. In contrast, juveniles from the northern and eastern-inner spawning sites (NI, NO and EI) experienced unsuitable thermal conditions in the form of lower temperatures (below or close to 2 °C) during the whole drift period, including August–September. As a true arctic species, polar cod juveniles could also survive at temperatures below 2 °C if prey abundance is sufficient. However, low temperatures may still be unfavourable resulting in reduced growth and therefore prolonged exposure to numerous small predators. In the Canadian Arctic, the 0-group polar cod density and biomass were positively correlated with water temperature, and high densities were found in the thermal habitat of 4.0–6.5 °C during August–September (Bouchard et al. 2017).

Based on the comparison of observed and modelled 0-group distributions, specifically a comparison of environmental requirements with modelled ambient conditions in 2007, the southern and eastern spawning sites are most consistent with polar cod observations. Northern spawning grounds are clearly less suitable than the other spawning grounds independent of spawning time, and western spawning grounds often lack ice to reduce turbulence during the egg stage. Conditions for offspring from the eastern and southern spawning grounds overall seem to improve more than those for offspring from the other grounds with later spawning.

Through our combined in situ measurements and biophysical modelling, we narrowed down suitable spawning habitats around Svalbard. This process is an important first step towards assessing the impacts of human activities, including climate change, fisheries and petroleum activities, on a key arctic species. Understanding that the main spawning habitat of polar cod in the southeastern Barents Sea appears to have recently supported less reproduction than in previous years elevates the importance of obtaining more information on the northwestern Barents Sea polar cod. To reduce uncertainties and further enhance this work, we recommend the following activities: (i) more field work possibly introducing instrument platforms that can operate

under ice to ensure observation of spawning polar cod and eggs; (ii) development of mechanistic biophysical models that can utilize high-resolution general circulation models and outcomes of controlled laboratory efforts to allow parametrization of vital rates; and (iii) genetic studies to determine regional population structure that in combination with biophysical models may provide information on connectivity across the Barents Sea.

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Compliance with ethical standards

Conflict of interest All authors declare that they have no conflict of interest.

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