

# Modelled dispersal of snow crab (*Chionoecetes opilio*) larvae and potential settlement areas in the western Barents Sea

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Since the mid-1990s, a snow crab (*Chionoecetes opilio*) population has established in the eastern Barents Sea. Spawning females and newly hatched larvae are now also found in the central Barents Sea, warranting speculations on a further westward colonization by pelagic larvae. Here, we model the potential for larval dispersal and settlement into uncolonized areas in the western Barents Sea. We used a biophysical model of ocean currents and hydrography, coupled with a Lagrangian dispersal algorithm and larval survival functions as response to temperature. The model predicts limited dispersal from the central Barents Sea to western areas, primarily due to a mismatch between prevailing temperature regimes and temperature tolerances for the different larval stages. In addition, there was limited westward transport of water masses with temperatures that would allow completion of the pelagic larval development. We speculate that for larvae to successfully supply benthic recruits to the remaining uncolonized areas in the western Barents Sea, adult crabs would first need to establish new spawning aggregations, for example along the western slopes of the Barents Sea shelf. Immediate implications are limited potential for expanding the fishery to the western areas of the Barents Sea.

**Keywords:** biophysical modelling, new fishery resource, non-indigenous species, pelagic larvae, survival, thermal habitat.

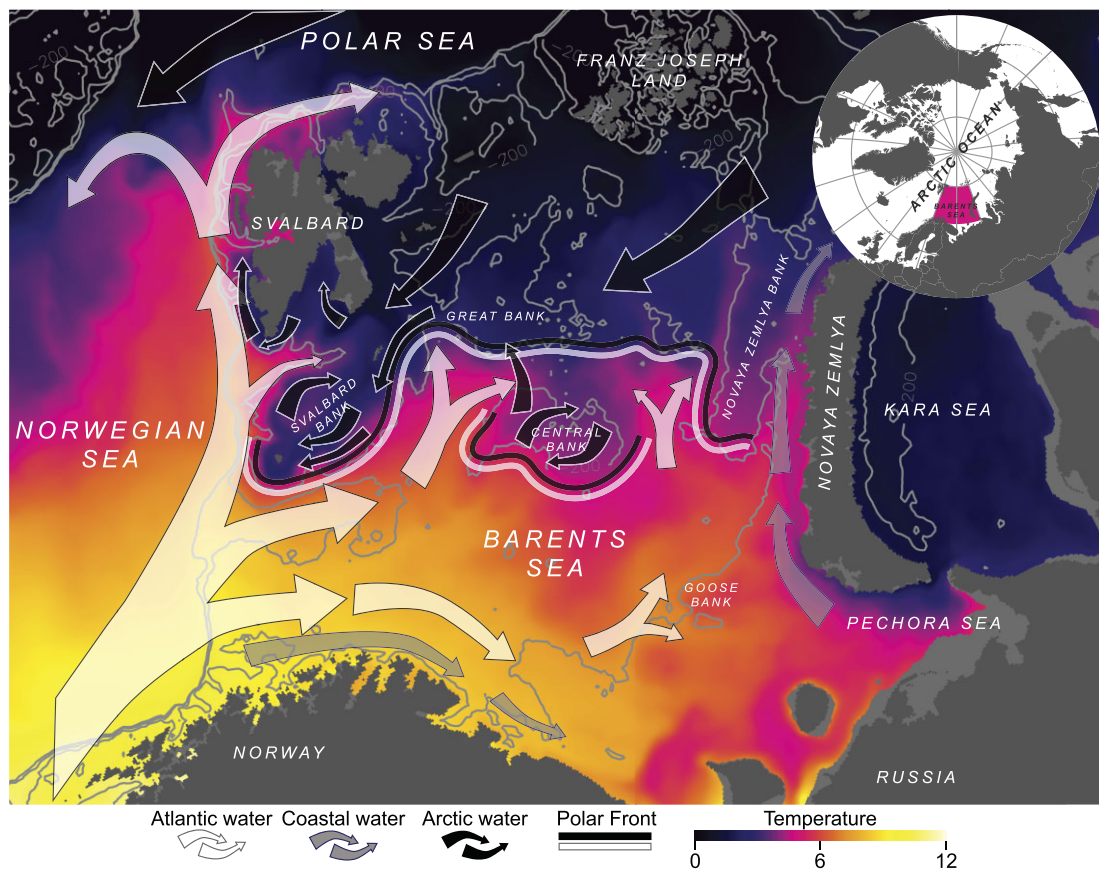
## Introduction

The snow crab (*Chionoecetes opilio*) is a newly established species in the Barents Sea, where the first adult specimens appeared near the Goose Bank in the early 1990s (Kuzmin *et al.*, 1998). About 30 years later, the snow crab has dispersed and colonized large parts of the eastern and central Barents Sea. A recent study on genetic analysis showed that the presence in the Barents Sea is the result of a recent natural range expansion from around Alaska (Dahle *et al.*, 2022). The recently established population now supports valuable commercial fisheries with total landings reaching 20000 tons in 2021. Although the life history characteristics driving the expanding distribution of snow crab in the Barents Sea are largely unresolved, the two main natural vectors of dispersal are active migration (or random movement) of benthic stages (juvenile to adult) and dispersal of larval stages with ocean currents. Benthic stages of snow crab are known to undertake both seasonal and ontogenetic migrations, and large male crabs tagged in the eastern Barents Sea have been shown to move up to 136 km (Mullowney *et al.*, 2018). However, only few snow crabs were captured during the joint Norwegian/Russian survey run from August to October 2019 in the western and north-western parts of the Barents Sea and around the Svalbard archipelago (Prozorkevich and van der Meer, 2020), areas otherwise thought to be a suitable habitat and hold the potential to support higher densities of snow crab in the future. The larval phase consists of three pelagic stages: zoea I, zoea II, and megalopa (Ouellet and Sainte-Marie, 2018). Long-distance dispersal with ocean currents is possible by at

least two of the three pelagic larval stages, zoea I and zoea II. Upon hatching, the larvae rise to the upper water masses, residing within and above the pycnocline (upper mixed layer) for the duration of the zoeal stages (Kon *et al.*, 2003; Ouellet and Sainte-Marie, 2018). Megalopa will migrate towards the bottom for settling (Kon *et al.*, 2003). The bottom currents on the Barents Sea shelf are generally weak (Loeng, 1991), and long-distance dispersal of megalopa is therefore less likely compared with zoea I and zoea II. The duration of each larval stage [intermoult duration (IMD)] is highly temperature dependent, meaning that the temperatures experienced in the water column will largely determine the duration of the larval phase. Ouellet and Sainte-Marie (2018) estimate the IMD at 7.8 and 2.8°C to be between 35 and 82 d for zoea I, 36 and 84 d for zoea II, and 42 and 80 d for the megalopa—in total giving a larval phase between 113 and 246 d (16–35 weeks). Optimal survival and growth of the pelagic larval stages is around 9°C, and survival is low to none at 3°C (Ouellet and Sainte-Marie, 2018). After settlement to the seabed, the snow crab metamorphoses into the first benthic instar, also having a narrow, yet colder temperature preference relative to the pelagic larvae (Lovrich *et al.*, 1995; Comeau *et al.*, 1998). Juvenile benthic stages prefer temperatures from <0 to 4.5°C (Brethes *et al.*, 1987; Dionne *et al.*, 2003), and adult stages are rarely found in temperatures above 3°C (Tremblay, 1997), thus suggesting a clear ontogenetic shift in selected and tolerated temperatures through life stages, from a warm water preference during the pelagic larval phase (at least by Arctic standards) to low temperatures during juvenile and adult stages.

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**Figure 1.** Major circulation patterns of upper water masses along and across the Barents Sea shelf (white, grey, and black arrows); bathymetric isolines at 200, 400, and 600 m (grey lines); and average temperature at 20 m in the summer/fall of 2019 (coloured gradient). Circulation patterns were adapted mainly from Pfirman *et al.* (1994), and references therein.

While holistic studies of snow crab larval distribution in the Barents Sea are lacking, recent scientific surveys have reported high concentrations of snow crab zoea on and around the Central Bank in early summer (Dvoretzky and Dvoretzky, 2019; Hjelset *et al.*, 2021). Oceanographically, the Central Bank is positioned in the interface between the two main water bodies found in the Barents Sea: the warm inflow region of Atlantic water from the southwest and the cold Arctic section to the north (as thoroughly reviewed by Ingvaldsen *et al.*, 2021), almost year-round divided by a sharply defined transition zone, with respect to temperature, salinity, and ice cover, termed the Polar Front (Figure 1). Given the differences in temperature tolerance and dispersal mechanisms among snow crab life stages, some stages might be more capable of traversing the distances and temperature gradients separating the Barents Sea ecosystem than others. A few studies exist that have modelled the dispersal of snow crab larvae, for example, Parada *et al.* (2010) used a circulation model to model crab larvae drift in the eastern Bering Sea, and Mao *et al.* (2019) have simulated larval drift in the Sea of Japan using a similar approach. However, due to the varying environmental conditions encountered across the pan-Arctic range of the snow crab, such studies may not necessarily be generalized to the dispersal and survival of snow crab larvae in the Barents Sea.

Here, we explore the potential dispersal of pelagic snow crab larvae from known geographic positions of high abundance of zoea I larvae on the Central Bank. Specifically, we

aim to (1) describe the main dispersal routes and settlement area of zoea I larvae found in water masses over the Central Bank; (2) quantify survival and developmental rates of these larvae; and (3) make first approximations of the suitability of the remaining, unoccupied areas in the western Barents Sea to colonization, with respect to larval, juvenile, and adult temperature tolerances. Larval dispersal was modelled by the coupling of a Lagrangian particle trajectory algorithm to a general circulation model, with particle initializations at previously sampled larval locations. The modelled larval dispersal kernels and settlement patterns were subsequently compared to the distribution of benthic stages (juvenile and adult) in scientific surveys. We contrasted the drift and survival trajectory of the most successful individuals ranked by average relative survival until settlement to a random sample of individuals that reflected a more representative drift/survival scenario of larvae spawned on and around the Central Bank. The modelled relative survival of zoea was defined as the predicted moulting success, as if larvae would stay at the *in silico* experienced temperature until next moulting, henceforth referred to as the relative stage-specific survival index (RSI). Finally, to map out the remaining suitable, yet uncolonized habitat to snow crab in the Barents Sea, we used the set of temperature-related RSI functions and benthic stage (i)juvenile and adult) temperature preferences by modelled long-term average temperature integrated over the water column, across the entire Barents Sea.

## Materials and methods

### Pelagic sampling of zoea and modelling the distribution of benthic stage crabs

As starting positions for particle dispersal scenarios, we used the locations where zoea I had been detected in a scientific survey between 22 June and 2 July 2019. In this survey, the larvae were sampled by vertical, depth-integrated net hauls from 5 m above bottom to surface, using a 1 mm WP3 plankton net (see Hjelset *et al.*, 2021 for further details).

The spatial probability of occurrence of benthic stage crab was modelled based on demersal trawl data from the Barents Sea Ecosystem Survey (BESS). Average trawling distance was 830 m taken at stations in a regular grid design ~65 km apart and covering the entire Barents Sea (see Eriksen *et al.*, 2018 for details on the annual survey). Only data between 2010 and 2019 were used, making up in total 3182 trawl hauls. A generalized additive model (GAM) was fitted to the presence/absence of snow crabs in each trawl haul, using the binomial distribution and geographical coordinates as covariates (assuming equal effect in all directions, i.e. isotropy), with all default settings in the R package “MGCV” (Wood, 2006).

### Modelling dispersal of pelagic stages

The hydrodynamic model used to represent the ocean currents, temperature, and salinity in the study area was supplied by the Norwegian Meteorology Institute (<https://ocean.met.no/models>), which was based on the Regional Ocean Modeling System (ROMS), a free-surface, hydrostatic, primitive equation, general ocean circulation model (Shchepetkin and McWilliams, 2005). ROMS was run with a horizontal resolution of 2.5 km × 2.5 km in an orthogonal, curvilinear grid covering the entire Barents Sea and with 42 vertical layers of depth-varying spacing (meaning tighter spacing/higher resolution at shallower depths). Hydrodynamic forcing on the model boundaries was applied from the larger TOPAZ4 model; tides from the TPXO tidal model; river runoff climatology from the Norwegian Water Resources and Energy Directorate (for mainland Norway) and AHYPE hydrological model (for Svalbard and Russia); bottom topography from the IBCAO v3 dataset; and wind forcing was applied from the 2.5-km AROME-MetCoOp atmospheric model—all assembled hereafter referred to as the Barents2.5-setup (Kristensen *et al.*, 2017, and see Fritzner *et al.*, 2018, 2019 for model performance). The output from the Barents2.5-setup contained velocity, salinity, and temperature fields with a temporal resolution of 1 h, thus adequately resolving the important tidal forces in the study area.

The advection of particles representing pelagic snow crab larvae was modelled by the Runge–Kutta fourth-order scheme “LADiM” (Ådlandsvik, 2020), using the velocity fields from the Barents2.5-setup (updated every hour), interpolated to an internal time step of 10 min with a random horizontal diffusion of up to 1.0 m<sup>2</sup> s<sup>-1</sup>. In LADiM, advection onto land is prohibited, ensured by explicitly evaluating whether particles hit the land mask at every step of the advection scheme. In effect, particles that are at risk of hitting land are stopped until currents at that particular place have changed direction. Note that land interaction is of minor importance since little to no land is found in the area of interest, as the large banks in the area are found at ≥200 m depth. Also note that particles hitting the model boundaries are taken out of the simulation.

One hundred particles were released from each of the WP3 stations at depth intervals of 1 m, from 1 to 20 m, initiated on the specific date of sampling (released between 22 June and 2 July 2019, in total 80000 particles). The 1–20 m depth interval was chosen based on the reported distribution of zoea stages (Ouellet and Sainte-Marie, 2018). Moreover, although data are scarce, there are suggestions in the literature that megalopa moves towards the bottom in its pre-moult stage (Kon *et al.*, 2003). However, due to the generally unknown vertical movement of snow crab zoea in the water column of the study area, particles drifted at the fixed depth assigned at model initiation until reaching megalopa stage, when larvae were considered to have settled. Individual, stage-specific, relative survival index (RSI), and IMD were modelled using quadratic functions of *in silico* temperature ( $T$ ), as shown in laboratory studies [Ouellet and Sainte-Marie, 2018, see Equations (1)–(6) below]. The incremental development function and instantaneous RSI function were updated every 10 min, based on average experienced temperature interpolated (using 3D interpolation) from the forcing field at the given position of the particle.

$$\text{IMD}_{\text{zoea I}} = 4903.33 \times [T - (-6.1)]^{-1.87}, \quad (1)$$

$$\text{IMD}_{\text{zoea II}} = 2461.31 \times [T - (-4.73)]^{-1.67}, \quad (2)$$

$$\text{IMD}_{\text{mega}} = 260.39 \times [T - (-1.37)]^{-0.82}, \quad (3)$$

$$\text{RSI}_{\text{zoea I}} = -0.011 T^2 + 0.237 T - 0.390, \quad (4)$$

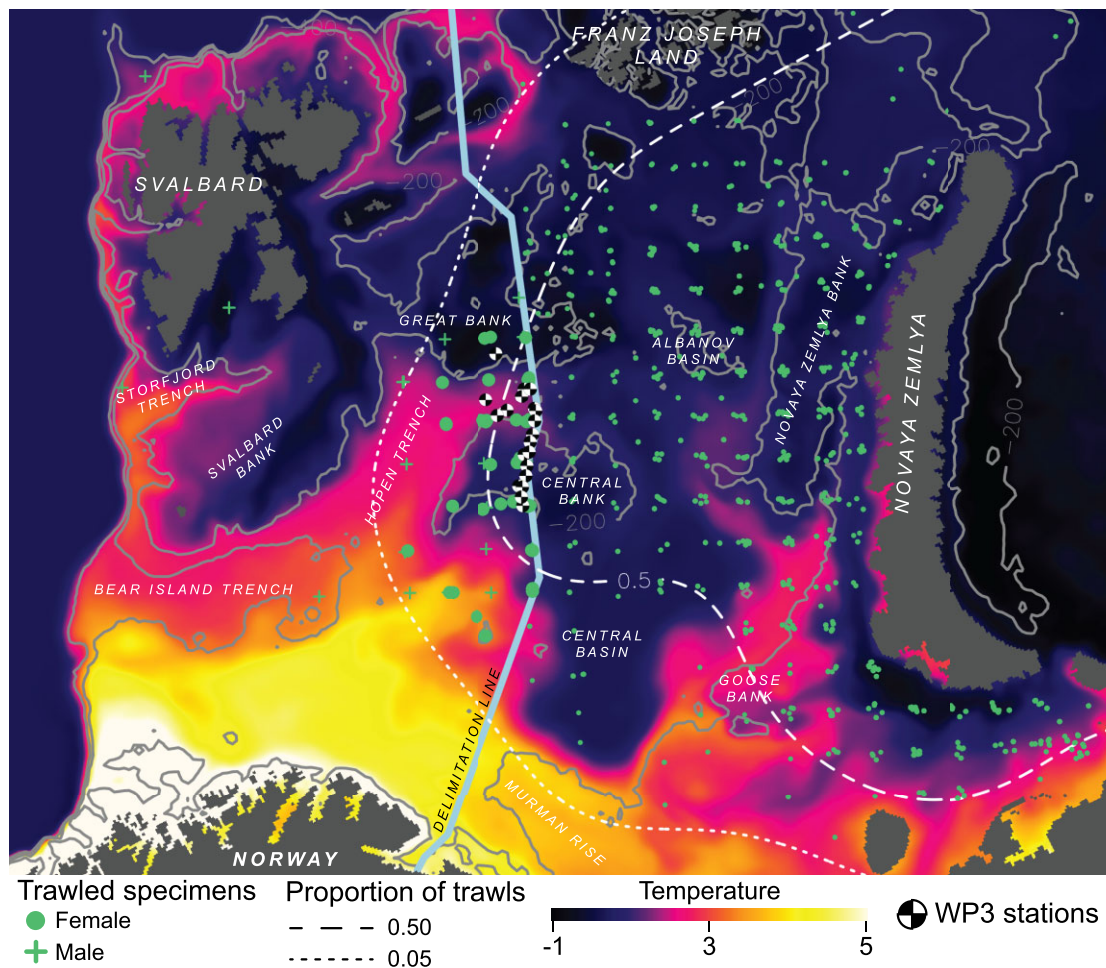
$$\text{RSI}_{\text{zoea II}} = -0.011 T^2 + 0.221 T - 0.037, \quad (5)$$

$$\text{RSI}_{\text{mega}} = -0.011 T^2 + 0.192 T + 0.105. \quad (6)$$

### Mapping thermal habitat availability and uncolonized area

Assuming temperature to be the main abiotic variable defining the survival of the pelagic stages of snow crab, we estimated suitable settlement areas by delineating stage-specific thermal habitats in the study area. These habitats were evaluated by the stage-specific RSI functions (same as used for the particle advection model), but with long-term (2010–2019) averages of modelled sea temperature as input at a given grid cell (i.e. the modelled climatology). For the initial two zoea stages, temperature at 20 m was used as input reflecting their modal vertical distribution in the wild. Modelled temperature at the bottom boundary layer was used for the megalopa stage function, and thermal limits for juveniles and adults were set at >3°C as suggested by field data from Atlantic Canada (Tremblay, 1997) and also supported by laboratory studies on Barents Sea wild caught crabs (Siikavuopio *et al.*, 2019). To highlight the sensitivity of modelled available habitat to different cut-off limits to the RSI functions of the different larval stages, we used set survival thresholds of 0.05, 0.1, 0.2, and 0.5. Uncolonized areas were defined as where snow crab was captured in <5% of the BESS trawl hauls, predicted by the GAM described in the first methods section. Areas deeper than 600 m were defined unsuitable for benthic settlement and adult/juvenile occupancy as well, largely excluding the deeper basins found in the Norwegian and Polar seas east and north of the Barents Sea shelf.





**Figure 2.** Observed and modelled distribution of snow crab in the Barents Sea. Observed data are from scientific survey (2010–2019). Green circles and green crosses represent captured female and male crabs, respectively; white dashed lines are the modelled probability of crab occurrence, where the dotted line is the 5% probability isocline and the dashed line is the 50% isocline. The white and black circles are the starting positions in drift experiment; bathymetric isolines at 200, 400, and 600 m (grey lines); light blue line is the delimitation line between Norwegian and Russian sectors; and modelled bottom temperature (coloured gradient) averaged over years 2010–2019.

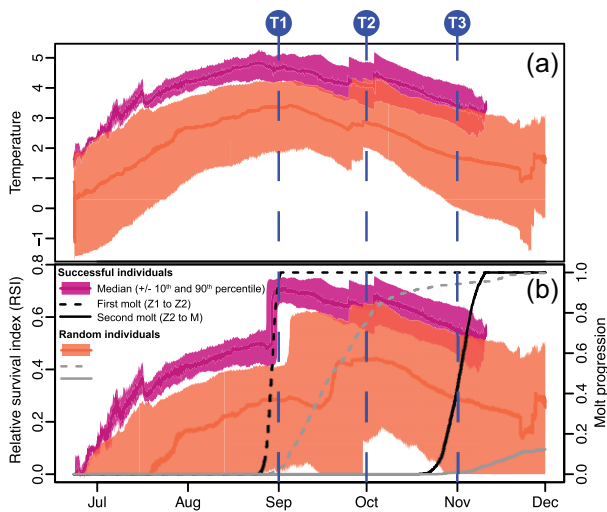
## Results

### Distribution of benthic stage crabs

The distribution of benthic stage crabs (juvenile and adult stages) over the period 2010–2019 was mainly concentrated on the Russian shelf of the Barents Sea, with a strongly decreasing gradient in probability of presence going west into the Norwegian zone (Figure 2). Specifically, the area where predicted occurrence in trawls was <50% (i.e. the 0.5 isocline of the GAM 2D probability surface) only covered about half of the Norwegian part of the Central Bank, including a narrow section between the Central Bank and the Great Bank and south of the Central Bank. The area where benthic stage crabs were sporadically present [ $5\% < p(\text{occurrence}) < 50\%$ ] covered the Central Basin, Hopen Trench, and the Great Bank (Figure 2). The deviance explained by the binomial GAM model was 58% ( $R^2_{\text{adj}} = 0.62$ ), using 21.28 effective degrees of freedom. Out of all 507 females caught at the Norwegian shelf, 447 (88%) carried eggs. Odd occurrences beyond the predicted 5% catch probability isocline were all male crabs. Few (five) benthic stage crabs have been caught beyond/above the 3°C isocline found south of the Bear Island Trench and west of the Murman Rise.

### RSI and dispersal of larvae

The *in silico* temperature experienced by modelled larva released on the Central Bank in June and July 2019 varied considerably through the drift period (July to December), from lowest temperatures at around 0°C to peak temperatures of 5°C in late August to September. The modelled RSI of zoea, here interpreted as the predicted moulting success if larvae would stay at the given temperature until next moulting, varied correspondingly: from close to zero at initiation on the Central Bank itself in June/July to up to >0.7 in September (Figure 3). The most successful larvae, ranked top 1000 by the average RSI along the entire drift phase, were generally advected in a southward direction, into the warmer Atlantic water masses found in the Central Basin south of the Central Bank. This is in contrast to the majority of larvae that were either retained on the Central Bank, advected northwards towards the Great Bank, and/or later advected eastwards along the Svalbard Bank that experienced significantly lower than preferred temperatures, leading to low expected RSI (Figure 4). Consequently, progression to the megalopa stage, and thus successful settlement (peak settlement rate 1 November), was only possible for zoea advected into the Atlantic waters to



**Figure 3.** Modelled temperature (a) and instantaneous RSI (b), interpreted as the expected moulting success if held at a given temperature) experienced by the 1000 larvae ranked highest by average RSI through drift period June to December (purple lines and polygons), and 1000 randomly chosen individuals (orange lines and polygons) selected from the 80000 particles released on and around the Central Bank representing “average” conditions. The proportion of the “cohort” progressing to next moult stage is indicated by grey and black, solid and perforated lines in (b). The blue perforated lines mark the timing at which larvae distribution snapshots are extracted as visualized in Figure 4 (T1 and T2) and Figure 5 (T3), on 1 September, 1 October, and 1 November, respectively.

the south and west of the Central Bank, while hardly any larvae that were advected to “the cold side” of the Polar Front reached settlement phase. In total, ~14% (11479 of 80000) of the larvae released were able to complete their development before simulation ended (31 December). Average RSI across all larvae having successfully settled (i.e. reached megalopa stage) varied between 0.26 and 0.56, with a median of 0.41. In general, the average RSI was highest for individuals released from the locations of the WP3 stations on the southern side of the Central Bank, towards the Central Basin (Figure 5).

### Habitat suitability mapping

Total uncolonized, yet suitable area to juvenile and adult stages given a bottom temperature  $<3^{\circ}\text{C}$  equaled 389000  $\text{km}^2$ , or ~27% of the Barents Sea total area (Figure 6). The subset of this uncolonized area that was suitable to all pelagic stages according to stage-specific, modelled temperature tolerance (zoea I, zoea II, and megalopa stages) decreased in a linear fashion with increasing cut-off value. For example, if loosely constricting the effect of temperature on RSI (e.g. at 0.05 mortality cut-off), a fairly large proportion (257474  $\text{km}^2$ ) of the hitherto uncolonized area was estimated as potential nursery area; at 0.1 mortality cut-off 234504  $\text{km}^2$  was available; at 0.2 195268  $\text{km}^2$ ; and at 0.5 cut-off only 24128  $\text{km}^2$  was available (for sensitivity to cut-off values, see Supplementary Figures S1 and S2). Thus only a few substantial uncolonized, yet habitable areas on the Norwegian continental shelf of the Barents Sea remains according to modelled climatology, namely (in a counterclockwise sequence around the Svalbard archipelago, with reference to Figure 6): the south-eastern facing slopes of the Svalbard Bank, the Bear Island Trench at large, the north-western facing slopes of the Svalbard Bank, the

Storfjord Trench, and the relatively narrow continental shelf along the western and northern coast of Svalbard.

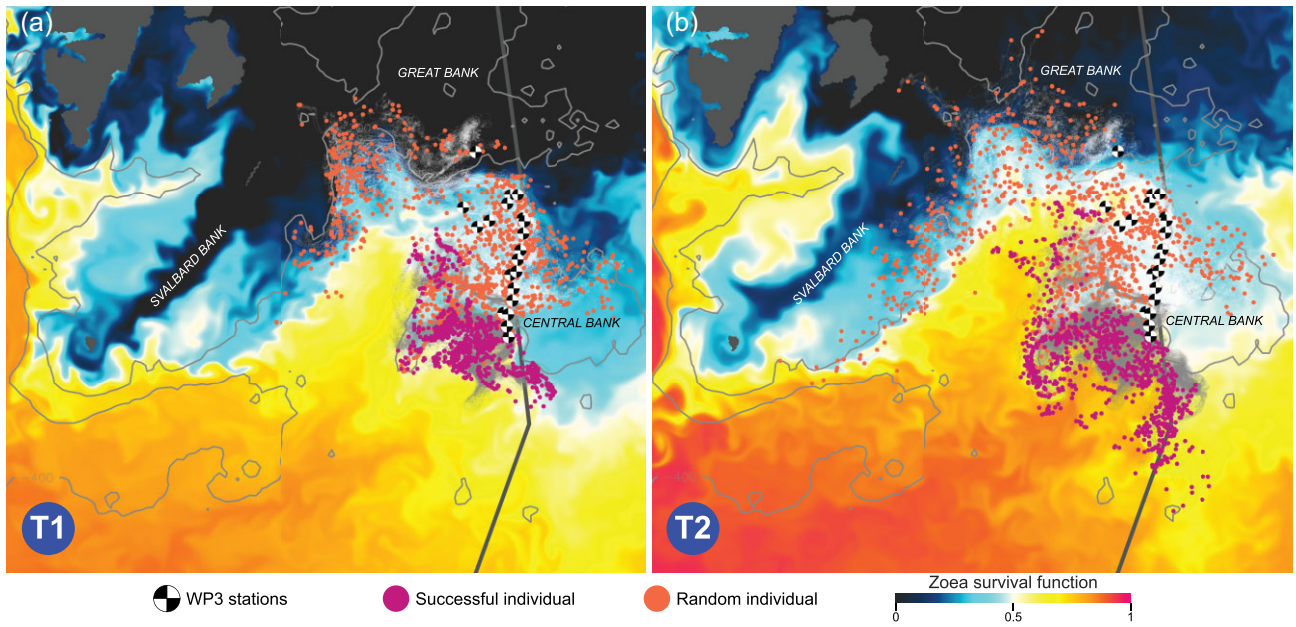
### Discussion

Here, we explore the dispersal and potential settlement areas for snow crab larvae in the Barents Sea. The snow crab has been expected to continue to expand its distribution westward on the Norwegian continental shelf in the Barents Sea—potentially having a large impact on the prospects of the newly established fishery for snow crab. However, our main findings suggest that dispersal and RSI of larvae from the Central Bank, being the westernmost area of high abundance of spawning females, will likely not support an extensive colonization of snow crab into the uncolonized, western part of the Barents Sea. We identify two large-scale abiotic factors that restrict the continued expansion by pelagic larvae dispersal: (1) the inherently sub-optimal or lethal temperatures for the development of pelagic larvae found on “the cold side” of the Polar Front, which constitutes most of the remaining uncolonized area; and (2) none of the large-scale ocean currents may carry water masses of suitable temperatures for larval survival flows westward (relative to the Central Bank).

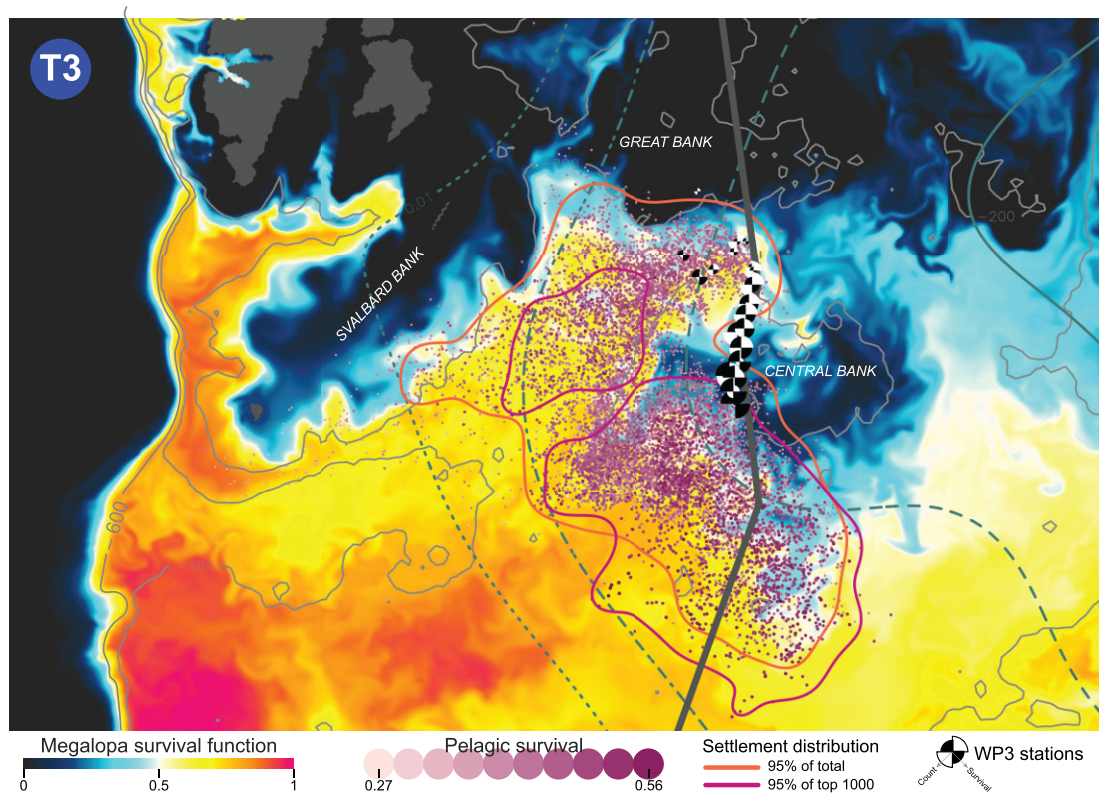
Although the main circulation system of water masses in the Barents Sea is well mapped by observational studies (e.g. Løeng, 1991; Pfirman *et al.*, 1994; Schauer *et al.*, 2002; Skagseth, 2008), the small-scale dynamics between Atlantic and Arctic water masses on and around the Central Bank, and along the Polar Front in general, is less studied. For example, short-term pockets of water masses with temperatures suitable for snow crab larvae can arise inside the long-term, average geographical position of the Polar Front, due to inherent instabilities of the front itself (Parsons *et al.*, 1996; Harris *et al.*, 1998; Fer and Drinkwater, 2014). While the ability of the ocean model to represent these small-scale dynamics is believed to be high (e.g. see Duarte *et al.*, 2022), due to lack of spatial and temporal coverage of dedicated planktonic surveys, it is currently hard to further validate our modelled dispersal patterns, RSI estimates, and settlement distribution. The few observations of snow crab larva available are concentrated along a transect across Central Bank in summer 2019 (22 June to 2 July), indicating abundances of up to 143 zoea  $\text{m}^{-2}$ , and all 601 individuals were zoea I (Hjelset *et al.*, 2021). The only other comparable study on snow crab larvae sampled stations along a wide swath across the central Barents Sea from the Russian coast to the Great Bank in summer 2013 (31 May to 16 June), and reported average concentrations of 4 zoea (2 SE)  $\text{m}^{-2}$  (Dvoretsky and Dvoretsky, 2019); however, only study-wide averages were reported and no stage-specific counts or size distributions were given.

Compiling and spatializing known temperature thresholds of adults and stage-specific larval survival functions (Tremblay, 1997; Ouellet and Sainte-Marie, 2018), only a few substantial areas seem habitable: The total habitable, yet uncolonized area was  $<250000 \text{ km}^2$ , excluding most of the areas on “the cold side” of the Polar Front. However, with regard to pelagic dispersal to these areas, only the south-eastern facing slopes of the Svalbard Bank appear available to be seeded from the concurrent spawning area on and around the Central Bank. It thus appears that for a continued western expansion to take place via larval dispersal, new spawning areas must be established, for example along the continental shelf/slope along the Norwegian Sea, potentially allowing newly hatched

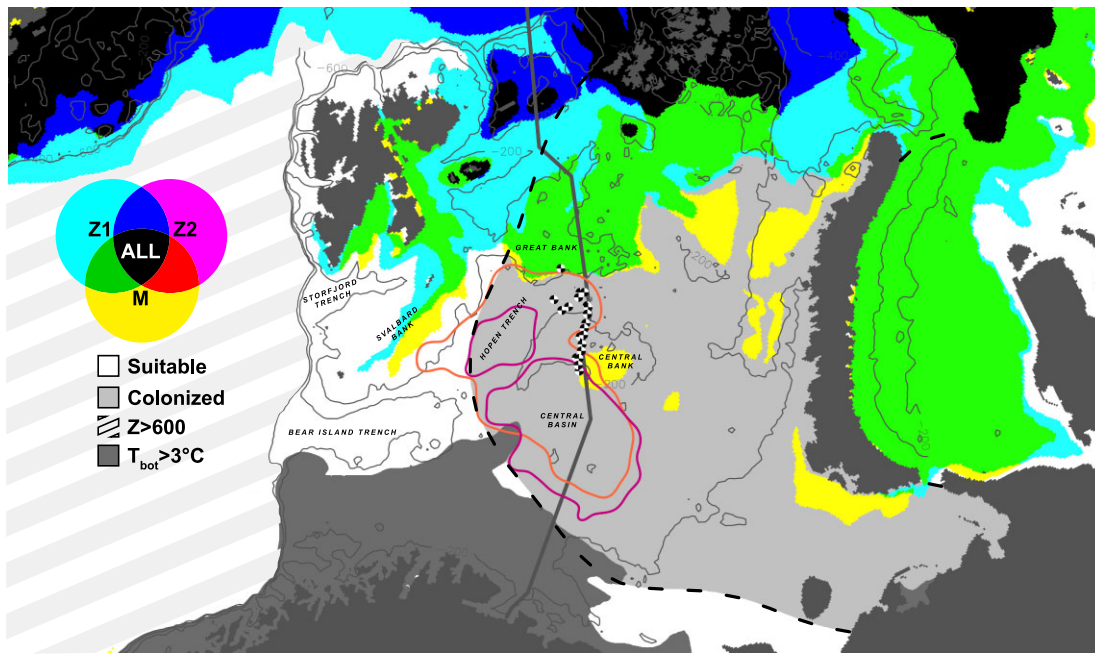




**Figure 4.** Pelagic drift patterns of the 1000 larvae with highest average RSI, integrated across their pelagic drift phase, on 1 September (a) and 1 October 2019 (b). The orange dots are 1000 individual particles randomly chosen to represent “average” drift trajectories. Here, coloured gradient represents the instantaneous stage-specific RSI (for Z1 and Z2 in (a) and (b), respectively), as a function of modelled temperature at 20 m.



**Figure 5.** Settlement locations of  $\approx 11,500$  successful larvae (coloured circles). The orange curve represents the 95% distribution of all successfully settled individuals; the purple curve the 95% distribution of the 1000 individuals with highest average RSI across pelagic drift; pie charts represent the locations of WP3 stations, where size of “pie slices” reflects counts of sampled zoea (white pie slice) and relative RSI of all particles released at the specific location integrated until settlement (black pie slice); dark green lines represent probability contours of modelled benthic stage occurrence based on scientific survey data, at 0.01, 0.05, and 0.5 level; all plotted over the instantaneous RSI surface of megalopa stage as response to bottom temperature (coloured gradient) at time of peak settlement rate (November 1<sup>st</sup> 2019).



**Figure 6.** Suitable, yet uncolonized habitat to entire life cycle of snow crab on the Barents Sea shelf (in white). Coloured areas represent RSI limits (at 0.1 cut-off) to different larval stages [Z1 (zoea I), Z2 (zoea II), and M (megalopa)] and the combination thereof, as indicated in the Venn's diagram; orange and purple curves represent the area seeded by larvae originating from the Central Bank area (see caption in Figure 5); light grey areas are already colonized (i.e. inside the 0.05 isoline of predicted adult/juvenile occurrence); dark grey areas are uninhabitable to juvenile and adult stages ( $T > 3^{\circ}\text{C}$ ); and shaded areas are deeper than 600 m.

larvae to be transported northwards by the warm Atlantic water masses of the West Spitsbergen Current. Such spawning areas could be established by an episodic inflow of larvae from central Barents Sea during abnormal oceanographic conditions, but most likely will have to originate from immigration of benthic stage crab.

Juvenile and adult crabs have shown a high adaptiveness and successfully prey on the available infaunal biomass of the Barents Sea (Zakharov *et al.*, 2020). A recent study on the benthic production unveils that food availability is not expected to be a limitation for further expansion (Holte *et al.*, 2022). A suite of biotic factors could potentially also impede colonization of the western areas (although not explicitly quantified here). For example, predation and competition will most likely intensify when the snow crab moves west, due to an increasing diversity of predators found there (Fossheim *et al.*, 2015; Kortsch *et al.*, 2015). Documented predators are Atlantic cod (*Gadus morhua*) and thorny skate (*Amblyraja radiata*) (Planque *et al.*, 2014; Holt *et al.*, 2021), and typical boreal, hyperbenthic predators more frequently encountered in the west include haddock (*Melanogrammus aeglefinus*), Atlantic and spotted wolffish (*Anarhichas lupus* and *A. minor*), and Greenland halibut (*Reinhardtius hippoglossoides*)—this list not including the many opportunistic marine mammals found in the area that also may prey on snow crab (e.g. Antonelis *et al.*, 1994). Although the predation pressure on pelagic snow crab larvae is largely unknown in the Barents Sea, a western expansion would also necessarily entail encountering a range of novel planktivores, including young saithe (*Pollachius virens*), polar cod (*Boreogadus saida*), and even Atlantic mackerel (*Scomber scombrus*) sometimes foraging in the warmer Atlantic water masses in summer and early autumn. However, further studies are needed on the potential

predators of snow crab (at least on pelagic stages) to further pinpoint specific impediments to western colonization by predation and competition.

It is expected that the snow crab will continue to expand its distribution westwards on the Norwegian continental shelf in the Barents Sea. However, the pace at which this will happen might be impeded by a mismatch between prevailing temperature regimes present in the Barents Sea and temperature tolerances for the larval stages. Especially the unfavourable temperature north of the Polar Front serves as a barrier to pelagic dispersal northwards and westwards. Although the Polar front does have some dynamical properties that generate short-term, warmer intrusions that can allow larvae to hatch and develop inside the front, we argue that the main spawning area in its western range (i.e. the Central Bank) is unlikely to serve as a springboard to areas further to the west and north. To increase our understanding of snow crab larval survival, development, and distribution in the Barents Sea, future studies should aim at increased spatial and temporal resolution in sampling and investigation into novel interactions with predators, competitors, and prey.

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## Supplementary data

Supplementary material is available at the ICESJMS online version of the manuscript.



## Conflict of interest

The authors declare no competing interests.

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## Author contributions

M.B.O.H. performed the simulations and analyses, and wrote the main manuscript. All authors participated in the development of the relevant research questions and helped revise the manuscript.

## Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

## References

- Ådlandsvik, B. 2020. Lagrangian advection and diffusion model (LADiM). <https://github.com/bjornaa/ladim> (last accessed 1 April 2022).
- Antonelis, G. A., Melin, S. R., and Bukhtiyarov, Y. A. 1994. Early spring feeding habits of bearded seals (*Erignathus barbatus*) in the Central Bering Sea, 1981. *Arctic*, 47: 74–79.
- Brethes, J.-C. F., Coulombe, F., Laffleur, P.-E., and Bouchard, R. 1987. Habitat and spatial distribution of early benthic stages of the snow crab *Chionoecetes opilio* O. Fabricius off the north shore of the Gulf of St. Lawrence. *Journal of Crustacean Biology*, 7: 667–681.
- Comeau, M., Conan, G. Y., Maynou, F., Robichaud, G., Therriault, J. C., and Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Canadian Journal of Fisheries and Aquatic Sciences*, 55: 262–279.
- Dahle, G., Sainte-Marie, B., Mincks, S.L., Farestveit, E., Jørstad, K.E., Hjelset, A.M., and Agnalt, A. 2022. Genetic analysis of the exploited snow crab (*Chionoecetes opilio*) in the Barents Sea—Possibilities of origin. *ICES Journal of Marine Science*, 79: 2389–2398.
- Dionne, M., Sainte-Marie, B., Bourget, E., and Gilbert, D. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. *Marine Ecology Progress Series*, 259: 117–128.
- Duarte, P., Brændshøj, J., Shcherbin, D., Barras, P., Albretsen, J., Gusdal, Y., Szapiro, N. *et al.* 2022. Implementation and evaluation of open boundary conditions for sea ice in a regional coupled ocean (ROMS) and sea ice (CICE) modeling system. *Geoscientific Model Development*, 15: 4373–4392.
- Dvoretzky, V. G., and Dvoretzky, A. G. 2019. Summer macrozooplankton assemblages of Arctic shelf: a latitudinal study. *Continental Shelf Research*, 188: 103967.
- Eriksen, E., Gjørseter, H., Prozorkevich, D., Shamray, E., Dolgov, A., Skern-Mauritzen, M., Stiansen, J. E. *et al.* 2018. From single species surveys towards monitoring of the Barents Sea ecosystem. *Prog Oceanogr*, 166: 4–14.
- Fer, I., and Drinkwater, K. 2014. Mixing in the Barents Sea Polar Front near Hopen in spring. *Journal of Marine Systems*, 130: 206–218.
- Fossheim, M., Primicerio, R., Johannesen, E., Ingvaldsen, R. B., Aschan, M. M., and Dolgov, A. V. 2015. Recent warming leads to a rapid borealization of fish communities in the Arctic. *Nature Climate Change*, 5: 673–677.
- Fritzner, S., Graversen, R., Christensen, K., Rostosky, P., and Wang, K. 2019. Impact of assimilating sea ice concentration, sea ice thickness and snow depth in a coupled ocean–sea ice modelling system. *The Cryosphere*, 13: 491–509.
- Fritzner, S.M., Graversen, R.G., Wang, K., and Christensen, K.H. 2018. Comparison between a multi-variate nudging method and the ensemble Kalman filter for sea-ice data assimilation. *Journal of Glaciology*, 64: 387–396.
- Harris, C. L., Plueddemann, A. J., and Gawarkiewicz, G. G. 1998. Water mass distribution and polar front structure in the western Barents Sea. *Journal of Geophysical Research: Oceans*, 103: 2905–2917.
- Hjelset, A. M., Danielsen, H. E. H., Westgaard, J.-I., and Agnalt, A.-L. 2021. Taxonomic and genetic confirmed findings of snow crab (*Chionoecetes opilio*) larvae in the Barents Sea. *Polar Biology*, 44: 2107–2115.
- Holt, R. E., Hvingel, C., Agnalt, A. L., Dolgov, A. V., Hjelset, A. M., and Bogstad, B. 2021. Snow crab (*Chionoecetes opilio*), a new food item for North-east Arctic cod (*Gadus morhua*) in the Barents Sea. *ICES Journal of Marine Science*, 78: 491–501.
- Holte, B., Fuhrmann, M. M., Tandberg, A. H.S., Hvingel, C., and Hjelset, A. M. 2022. Infaunal and epifaunal secondary production in the Barents Sea, with focus on snow crab (*Chionoecetes opilio*) prey resources and consumption. *ICES Journal of Marine Science*, 79: 2524–2539.
- Ingvaldsen, R. B., Assmann, K. M., Primicerio, R., Fossheim, M., Polyakov, I. V., and Dolgov, A. V. 2021. Physical manifestations and ecological implications of Arctic Atlantification. *Nature Reviews Earth & Environment*, 2: 874–889.
- Kon, T., Adachi, T., and Suzuki, Y. 2003. Distribution of snow crab, *Chionoecetes* spp., larvae off Wakasa Bay in the Sea of Japan. *Fisheries Science*, 69: 1109–1115.
- Kortsch, S., Primicerio, R., Fossheim, M., Dolgov, A. V., and Aschan, M. 2015. Climate change alters the structure of arctic marine food webs due to poleward shifts of boreal generalists. *Proceedings of the Royal Society B*, 282: 20151546.
- Kristensen, N., Debernard, J., Maartensson, S., Wang, K., and Hedstrom, K. 2017. metno/metroms: Version 0.3—before merge. <https://zenodo.org/record/1046114#.ZDPQVy8RqLd> DOI: 10.5281/zenodo.1046114 (last accessed 1 May 2022).
- Kuzmin, S. A., Akhtar, S. M., and Menis, D. T. 1998. The first findings of snow crab *Chionoecetes opilio* (Decapoda, Majidae) in the Barents Sea. *Зоологический журнал*, 77. <https://elibrary.ru/item.asp?id=14946207>.
- Loeng, H. 1991. Features of the physical oceanographic conditions of the Barents Sea. *Polar Research*, 10: 5–18.
- Lovrich, G. A., Sainte-Marie, B., and Smith, B. D. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. *Canadian Journal of Zoology*, 73: 1712–1726.
- Mao, X., Guo, X., Kubota, T., and Wang, Y. 2019. Numerical studies on snow crab (*Chionoecetes opilio*) larval survival and transport in the Sea of Japan. *Progress in Oceanography*, 179: 102204.
- Mullowney, D., Morris, C., Dawe, E., Zagorsky, I., and Goryanina, S. 2018. Dynamics of snow crab (*Chionoecetes opilio*) movement and migration along the Newfoundland and Labrador and Eastern Barents Sea continental shelves. *Reviews in Fish Biology and Fisheries*, 28: 435–459.
- Ouellet, P., and Sainte-Marie, B. 2018. Vertical distribution of snow crab (*Chionoecetes opilio*) pelagic stages in the Gulf of St. Lawrence (Canada) and effect of temperature on development and survival. *ICES Journal of Marine Science*, 75: 773–784.
- Parada, C., Armstrong, D. A., Ernst, B., Hinckley, S., and Orensanz, J. M. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—putting together the pieces of the puzzle. *Bulletin of Marine Science*, 86: 413–437.
- Parsons, A. R., Bourke, R. H., Muench, R. D., Chiu, C.-S., Lynch, J. F., Miller, J. H., Plueddemann, A. J. *et al.* 1996. The Barents Sea Polar Front in summer. *Journal of Geophysical Research: Oceans*, 101: 14201–14221.
- Pfirman, S. L., Bauch, D., and Gammelsrød, T. 1994. The northern Barents Sea: water mass distribution and modification. In *The Polar Oceans and Their Role in Shaping the Global Environment*, pp. 77–97. Ed. by O. M. Johannessen, R. D. Muench, and J. E. Overland. Wiley, New York.



- Planque, B., Primicerio, R., Michalsen, K., Aschan, M., Certain, G., Dalpadado, P., Gjørseter, H. *et al.* 2014. Who eats whom in the Barents Sea: a food web topology from plankton to whales. *Ecology*, 95: 1430–1430.
- Prozorkevich, D., and van der Meeren, G. I. 2020. Survey report from the joint Norwegian/Russian ecosystem survey in the Barents Sea and adjacent waters, August–October 2019. IMR/PINRO Jt Rep Ser, 2020: 1–93.
- Schauer, U., Loeng, H., Rudels, B., Ozhigin, V. K., and Dieck, W. 2002. Atlantic water flow through the Barents and Kara Seas. *Deep Sea Research Part I: Oceanographic Research Papers*, 49: 2281–2298.
- Shchepetkin, A. F., and McWilliams, J. C. 2005. The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. *Ocean Modelling*, 9: 347–404.
- Siikavuopio, S. I., Bakke, S., Sæther, B. S., Thesslund, T., and Christiansen, J. S. 2019. Temperature selection and the final thermal preference of snow crab (*Chionoecetes opilio*, Decapoda) from the Barents Sea. *Polar Biology*, 42: 1911–1914.
- Skagseth, Ø. 2008. Recirculation of Atlantic water in the western Barents Sea. *Geophysical Research Letters*, 35: 1–5.
- Tremblay, M. J. 1997. Snow crab (*Chionoecetes opilio*) distribution limits and abundance trends on the Scotian Shelf. *Journal of Northwest Atlantic Fishery Science*, 21: 7–22.
- Wood, S. N. 2006. Low-rank scale-invariant tensor product smooths for generalized additive mixed models. *Biometrics*, 62: 1025.
- Zakharov, D. V., Manushin, I. E., Nosova, T. B., Strelkova, N. A., and Pavlov, V. A. 2020. Diet of snow crab in the Barents Sea and macrozoobenthic communities in its area of distribution. *Ices Journal of Marine Science*, 78: 545–556.

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