

Recruitment mechanisms of Atlantic cod (*Gadus morhua*) living in an extreme low-salinity environment

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Abstract

A better understanding of recruitment mechanisms in fishes is a high priority for operational management, as it can improve both stock assessment models and impact assessments, given that early life stages are particularly sensitive to changes in the environment. The impacts from anthropogenic pressures, including climate change, can be especially severe in extreme environments, where fish are already living close to their physiological limits. In the brackish Baltic Sea, Atlantic cod (*Gadus morhua* L.) exhibits unique adaptations to the low salinity, but suffers from long-term overexploitation and a loss of spawning areas due to climate change and eutrophication. At the northern edge of its distribution range, in the Åland Sea (ICES subdivision (SD) 29N), a healthy stock component continues to thrive, despite living in an extreme low-salinity environment. Here, we study recruitment mechanisms of this stock component, to understand where cod in the area reproduces. Cod collected by commercial gillnet fishers at 220–250 m depth in May–June 2019 had a mean weight of 2.6 kg and were all in spawning condition. Laboratory experiments showed that fertilisation and egg development was not successful at a salinity corresponding to the Åland Sea (7.5 psu), but to some extent at 9 and 10 psu. Hydrographical modelling suggests that, in addition to known spawning areas further south, conditions in the northern Baltic Proper (SD 27, 29S and 32) may occasionally be suitable for reproduction. Larval drift models show that these areas are highly connected to the Åland Sea and may be important for recruitment, although larvae can also drift in from known spawning areas in the Gdansk and Gotland Basins (SD 26 and 28). To fully understand the recruitment mechanisms, further studies on the migratory behaviour, genetic population structure, and occurrence of eggs and larvae are needed.

Keywords: gadidae; brackish water; fertilisation; salinity adaptation; source-sink; fisheries management

Introduction

Understanding the processes that drive fish recruitment is critical for sustainable marine management, particularly for identifying and protecting spawning and nursery habitats, delineating population structures and conducting reliable stock assessments. While recruitment mechanisms are reasonably well understood for some stocks (Kjesbu et al. 2023, Ma et al. 2024), there are still considerable gaps in knowledge, even for many ecologically and economically important species. This is largely due to the biological complexity of early life stages, their high natural mortality, the influence of variable environmental conditions, and the inherent difficulties in collecting field data on early life stages (Houde 2008, 2016). Among human pressures, habitat alteration and loss are having major effects on fish recruitment, whereas the effects of climate change are expected to increase over time (Pankhurst and Munday 2011, Macura et al. 2019, Alix et al. 2020). While research on climate change impacts has mainly focused on the effects of warming and acidification, the effects of shifts in salinity on marine species is an overlooked area (Rijnsdorp et al. 2009, Röthig et al. 2023, Agarwal et al. 2024). For fishes already living close to their physiological salinity limits, even minor changes in salinity may have strong effects on their reproductive success, and ultimately on population sizes and ranges (Westin and Nissling 1991). Understanding recruitment mechanisms

of fish populations in these marginal environments may thus provide broadly applicable lessons on how fishes may be affected by environmental changes.

One such extreme environment, where many marine species live close to their physiological limits, is the Baltic Sea. Here, local adaptation and genetic differentiation is widespread, and this large semi-enclosed, brackish sea therefore offers a test case of how marine species may adapt to the impacts of climate change (Reusch et al. 2018, Johannesson et al. 2020). A key species of the Baltic ecosystem is the Atlantic cod (*Gadus morhua* L.), which is divided into two stocks, a Western and an Eastern. The larger Eastern Baltic stock was very abundant in the major part of the Baltic in the 1970s and 1980s (ICES subdivisions (SD) 25–30 and 32; Fig. 1), whereafter the stock has declined dramatically. The stock size is now at a historical low, exhibiting a stunted individual growth rate and a severe lack of large fish, and no targeted fishing is currently allowed (Mion et al. 2021, Bryhn et al. 2022, ICES 2025). At the same time, a contraction in the geographical distribution of the stock towards the southern Baltic Proper has been observed, partly driven by a loss of spawning areas due to climate change and eutrophication (Hinrichsen et al. 2016, Orto et al. 2019).

The Eastern Baltic cod is reproductively isolated and genetically differentiated from populations in fully marine

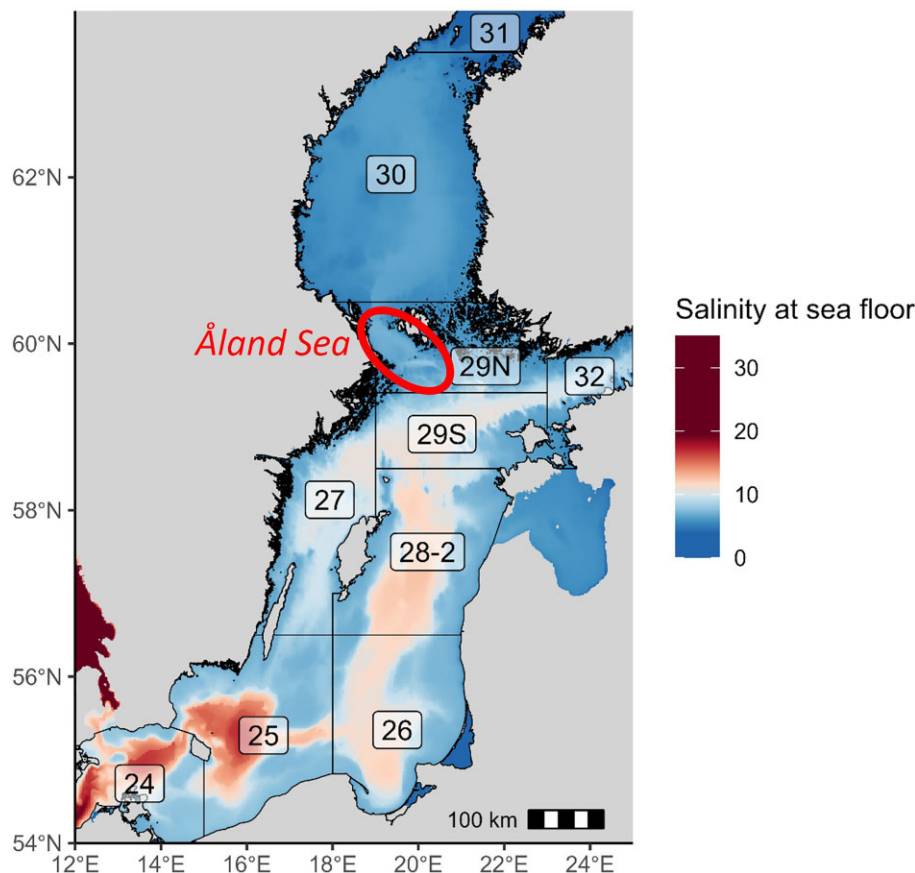


Figure 1. Map of the Baltic Sea, with the connection to the Atlantic through narrow straits in southwest. The ICES subdivisions included in the study are indicated with numbers, where the Åland Sea is found in SD 29N (encircled), while SD 30 corresponds to the Bothnian Sea, SD 28 to the Gotland Basin, SD 26 to the Gdansk Basin, and SD 25 to the Bornholm Basin. The salinity at the seafloor, representing mean values for 1999–2018, is shown across the Baltic Sea.

environments (Larsen et al. 2012, Berg et al. 2015), and here pushes the limits of salinity adaptation of the species. The adaptation to the low-salinity conditions of the Baltic Sea involves more buoyant eggs, with buoyancy increasing with maternal size, and sperms with a higher ability to swim in low salinity (Nissling and Westin 1997, Berg et al. 2015). Fertilisation and egg development may be successful in salinities down to 10–11 psu for large individuals (Westin and Nissling 1991, Vallin and Nissling 2000). Reproduction of Eastern Baltic cod is therefore considered to be restricted to the deep basins of the southern and eastern Baltic Proper, i.e. the Bornholm Basin (SD 25), the Gdansk Deep (SD 26) and the Gotland Basin (SD 28) (Bagge 1994). The last decades, however, a loss of spawning areas has occurred. Decreasing salinities interact with an elevated oxygen consumption, caused by excessive primary production in combination with higher temperatures, to decrease the availability of suitable spawning habitats especially in the eastern parts of the Baltic Proper (Hinrichsen et al. 2011, 2016, Köster et al. 2017, Bryhn et al. 2022).

Further north, in the Åland Sea (SD 29N) and Bothnian Sea (SD 30), cod has been fished continuously despite the considerable geographical distance from the known spawning areas (300–600 km). Documented periods of higher catches in these areas occurred in e.g. 1550–1610 (MacKenzie et al. 2007), in the 1940s–1950s and in the 1980s (Segerstråle 1969, Eero 2008). Here, the bottom salinity is only 7–7.5 psu, raising the

question of how cod is recruited to the area. Cod has been reported to spawn also in these northern areas, but this spawning has been considered not to result in successful reproduction due to the low salinity (Hessle 1923, Modin 1987). Studies investigating the recruitment mechanisms for this northern stock component are, however, lacking.

Following the decline of the Eastern Baltic cod stock from the peak abundances in the 1980s, intense studies on the reproduction mechanisms and the effects on recruitment and stock development were initiated (e.g. Plikshs et al. 1993, Wieland et al. 1994, MacKenzie et al. 1996, 2000, Hinrichsen et al. 2003, Köster et al. 2005). Experimental studies of fertilisation, egg development and egg buoyancy at different salinities have been confined to cod from SD 25 and 28 (e.g. Westin and Nissling 1991, Nissling et al. 1994, Vallin and Nissling 2000). Modelling of egg and larval drift patterns from the major spawning areas has been conducted to understand survival and dispersal in nursery areas in SD 25–26 and 28 (Hinrichsen et al. 2009, 2016, 2017), but these studies have not included potential drift to the northern parts of the distribution of cod, i.e. the Åland Sea and Bothnian Sea (SD 29–30). Aiming to increase the understanding of cod recruitment in this extraordinarily low-salinity environment, we approached the described knowledge gaps through:

- (i) Performing laboratory experiments on Åland Sea cod to study spermatozoa motility, fertilisation success and egg development at different salinities, as well as to

estimate egg specific gravity, to assess if cod from this stock component is capable of reproducing in lower salinities than previously reported for Eastern Baltic cod more generally

- (ii) Compiling long-term commercial landings statistics for the Åland Sea and Bothnian Sea compared to the recruitment of the Eastern Baltic cod stock, to investigate potential covariation in development
- (iii) Spatiotemporal analysis of hydrographic conditions, focusing on salinity, temperature and oxygen, to map potential spawning areas of the Eastern Baltic cod, including the Åland Sea stock component
- (iv) Spatial modelling of larval drift from the known spawning areas in the southern and eastern Baltic Sea, as well as from potential reproduction areas in the northern Baltic Sea, to assess opportunities for larval transport to the Åland Sea and the Bothnian Sea.

Material and methods

The study area

The Baltic Sea (Fig. 1) is characterised by brackish water conditions with salinities decreasing from the shallow entrance at the Sound, the Danish Belts and the Arkona Basin (ICES SD 22–24) towards the deeper eastern and northern basins. Accordingly, salinity in the surface layer decreases from ~8–9 psu in SD 24 to merely ~3 psu in the north (SD 31). In the deep areas of SD 25–28 salinities range between 10–20 psu below the permanent halocline at 50–70 m depth. Exchange between the surface and bottom water is restricted and renewal of the bottom water occurs mainly following sporadic major inflows of saline water from the North Sea. Stagnant conditions in the bottom water accompanied by decreasing salinity and oxygen conditions may last for years (Mohrholz et al. 2015). During the last two decades severe oxygen conditions have prevailed, with a historically high distribution of hypoxic and anoxic areas covering most deep areas in SD 25–28 (Köuts et al. 2021). The irregular major inflow events to a large extent determine salinity and oxygen conditions, and thus the reproductive success of cod spawning in the Bornholm Basin, the Gdansk Deep and the Gotland Basin (MacKenzie et al. 2000, Plikshs 2015, Wikström et al. 2016).

The major distribution area of cod in the northern Baltic Sea, i.e. the Åland Sea (SD 29N) and the Bothnian Sea (SD 30; Fig. 1), is separated from the Baltic Proper by sills with channels at ca 60 m depth (Jakobsson et al. 2019), which partly prevent inflows of saline bottom water. As a result, only a weak halocline occurs in the main basin of the Åland Sea, with a salinity of 5–6 psu in the surface water and 7–7.5 psu at the bottom. In the southern Bothnian Sea, bottom salinities drop to below 6 psu. Strong mixing across the halocline in the Åland Sea makes it oxygenated all the way down to the deepest parts, at more than 200 m depth (Westerlund et al. 2022, Muchowski et al. 2023). In the southern part of the Åland Sea there is a smaller sub-basin, the Lågskär Deep, where bottom salinities are higher, 8–9 psu, due to a stronger halocline and inflow of bottom water from the Baltic Proper (Westerlund et al. 2022).

The Åland Sea and the Bothnian Sea have been regarded as feeding areas for cod (Otterlind 1984, Aro 1989), with adults undertaking southward migrations to the spawning areas in

the Baltic Proper (Aro 1989, 2002, Mion et al. 2022). Despite this, frequent spawning in the Åland Sea and Bothnian Sea deep areas has been observed, with periodically dense spawning aggregations (Modin 1987). In the Åland Sea, a small-scale commercial gillnet fishery involving some 20 boats from Sweden and Finland was active, with low (compared to catches in the main fishing areas in SD 25 and 26) but sustained catches up to the emergency closure of fisheries on Eastern Baltic cod in 2019. This fishery took place in the deep trench between the northern Baltic Proper and the Bothnian Sea, at around 100–260 m depth. Similarly, the cod fishery that occurred previously in the Bothnian Sea was concentrated to the deeper areas and their slopes (Hessle 1923, Modin 1987, Fig. 1).

Covariation of fisheries landings and recruitment

The regularly performed Baltic International Trawl Survey, coordinated by the ICES and the basis for stock assessment of cod in the Baltic Sea, does not cover the northern Baltic Sea, as cod in the area has been of minor commercial importance the last decades (Eero et al. 2019). Hence, to provide an indication of long-term stock size fluctuations in the Åland Sea and the Bothnian Sea, we compiled data of Swedish landings for the period 1914–2020. Landings representing SD 28, SD 29 and northern SD 27, and SD 30 (Fig. 1) were compiled from Hentati-Sundberg (2017) and ICES catch statistics (<https://ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx>). To investigate potential covariation in stock development, we collated data on recruitment (age-0 cod) for the entire Eastern Baltic cod stock (SD 25–32) in 1946–2019, based on an analytical stock assessment for recent years (ICES 2022) and a reconstruction of the historical development (Eero et al. 2007).

Salinity effects on fertilisation and egg development

Cod for experimental work on egg and spermatozoan performance and fertilisation at different salinities were caught by a commercial fisher using trammel nets (140–160 mm stretched mesh size, soak time 20–24 h) at 220–250 m depth at ca 60.2°N, 19.1°E, in the Åland Sea (Fig. 1) on May 27–29 and June 9–11 2019. Fish in spawning condition were killed, females stripped for eggs, and semen sampled using a dry Pasteur pipette. After the collection of eggs and sperm, fish were measured for total length and weight, and gonad status was estimated according to the 8-stage scale used in international fish surveys in the Baltic Sea (Tomkiewicz et al. 2002). A total of 89 individuals were sampled, but only individuals with healthy germ cells were used in the fertilisation experiments (see details below). Thus, for females, only individuals with freshly ovulated oocytes were selected, where the resulting eggs past fertilization showed regular cell cleavage (McEvoy and McEvoy 1992, Vallin and Nissling 1998), while for males only individuals with spermatozoa exhibiting normal swimming behaviour in 15 psu were included (Nissling and Westin 1997). The fish was not genetically analysed to check if they belonged to the Eastern Baltic cod stock, but available tagging and larval dispersal modelling studies indicate that the chance of catching Western Baltic cod in the area should be minimal (Hinrichsen et al. 2017, Mion et al. 2022). All samples were collected in compliance with the EU Directive 2010/63/EU and national legislation, under permits C 139/13 and 5.8.18–10 169/2019, issued to the Swedish University of Agricultural Sciences by the Ethical Committee on Animal Experiments.

Spermatozoa motility was assessed under a microscope at 250x magnification at a salinity of 15.0, 10.0, 9.0 and 7.5 psu at 7°C in a climate room. These salinities correspond roughly to the deep waters of the Bornholm Basin, the Gotland Basin, SD 29S and SD 29N (the Åland Sea) according to the data from Copernicus Marine Service used for hydrographic analysis (see below). For each salinity tested, a droplet of semen was diluted in ca 1 ml water, prepared from Baltic Sea water (6.5–7.0 psu) and synthetic sea salt. The time from mixing to observation was approximately 5 s and the initial motility of spermatozoa was assessed as swimming, vibrating (i.e. without progressive movement) or immobile. In total 18 males were investigated. Salinity was determined using a WTW MultiLine 3410 meter with a conductivity cell (TetraCon), with a resolution 0.1 psu and accuracy $\pm 0.5\%$ of reading.

Fertilisation success was assessed by mixing eggs and semen in water of 15.0, 10.0, 9.0 and 7.5 psu. 27 different males and 11 females were used in the experiment, resulting in a total of 27 series, each including all four different salinities, with eggs from one female and semen from one male. For each salinity tested, two droplets of semen (ca 0.1 ml) were mixed with 100 ml water at ca 7°C in a climate room and a spoonful (ca 5 ml) of eggs was then added immediately. After completing the series, the eggs were incubated for ca 2 h in 300 ml water, rinsed in water of the same salinity and incubated further at ca 7°C in a refrigerator until egg development reached stage 1A (Thompson and Riley 1981), i.e. with 4–64 cells. A sub-sample of 150–200 eggs in each incubation was examined and the proportion of fertilised eggs assessed. Only clear/transparent eggs were considered, with eggs displaying cell cleavages considered fertilised as opposed to activated cells (eggs with merely one germinal cell; Howell et al., 1991) and eggs without cells.

In series where fertilisation was successful at < 15 psu, fertilised eggs were incubated further up to hatching. Fifty 1-day-old eggs from each treatment were incubated in 500 ml water of the same salinity, prepared as described above, and treated with antibiotics (Ampicillin 0.1 g/l, Streptomycin 0.05 g/l and Nystatin 2500 IU/l). In treatments where less than 50 fertilised eggs were found, all developing eggs were used. The incubations were kept at ca 7°C in a refrigerator. Two thirds of the water was changed every second day. When hatching was completed (all eggs either were hatched or dead), the viable hatch was assessed as the percentage of larvae with normal swimming functions as opposed to larvae unable to swim or displaying an erratic swimming behaviour (Nissling et al. 1998). In total, four series were incubated up to hatching (20–21 days), with incubation at 15 psu as control.

Egg specific gravity

Egg specific gravity was determined using a density gradient column (Coombs 1981, Nissling and Westin 1997) at ca 7°C using 15–30 eggs in stage IA (Thompson and Riley 1981) in each trial. The eggs were inserted in the column and, after a settling time of ca 60 min, the vertical positions were recorded and compared with the positions of five density floats (Spartel, UK; Martin Instruments Co, UK) of known specific gravity; the correlation coefficient of the density floats was > 0.99 in all measurements. Egg diameter, assessed as the diameter set by the chorion, was measured by cross diagonal measurement at stage IA under a stereo microscope at 50x magnification using an ocular micrometer scale, with 20–30 eggs in each

determination. In total, 17 determinations of egg batches from different females were used.

Hydrographic analysis for mapping of potential spawning areas

The potential spawning areas in the Baltic Sea theoretically available for cod, referred to as the reproduction volume (Plikshs et al. 1993), was estimated by spatiotemporal analysis of oceanographic data from Copernicus Marine Service on oxygen (<https://doi.org/10.48670/moi-00012>), salinity and temperature (<https://doi.org/10.48670/moi-00013>), mainly based on the oceanographic circulation model Nemo-Nordic (see below for further description). A set of potential salinity threshold levels (≥ 11.0 , 10.5 and 9.0 psu) was combined with an oxygen concentration threshold of ≥ 2 ml/l, and a temperature threshold of $\geq 1.5^\circ\text{C}$ (Hinrichsen et al. 2016). The 11 psu level refers to the level commonly used to define the lower limit for successful spawning of Eastern Baltic cod (Plikshs et al. 1993, MacKenzie et al. 2000, Hinrichsen et al. 2016). The 10.5 psu level was set based on the lowest salinity for observed neutral egg buoyancy (10.4 psu; Grauman 1963), and measurements of egg specific gravity of newly fertilised eggs (corresponding to 10.5 psu; Vallin and Nissling 2000), while the 9 psu level was based on the minimum salinity for fertilisation and egg survival in the present study. Note that the > 9 psu level is expressed as reproduction volume although egg development is supposed to occur at the bottom (due to negative buoyancy). Thus, this estimate is not fully comparable with the ones for ≥ 11 or ≥ 10.5 psu, where eggs develop in the water column. All data represented the period April–September, which includes the major part of the extended spawning season of Eastern Baltic cod (Hinrichsen et al. 2017).

Larval drift modelling

Passive dispersal of Baltic cod occurs mainly during the larval stage, while egg dispersal is much more limited due to their deeper position in the water column (Hinrichsen et al. 2016, 2017). To study potential larval dispersal to the Åland Sea from known spawning areas, as well as from identified areas with suitable habitat for successful reproduction in SD 29–32 (this study), we used data from a connectivity database for the Baltic Sea region (Jonsson et al. 2020). The connectivity data has been generated using a Lagrangian biophysical particle-tracking model with flow fields generated from a 3D ocean circulation model (TRACMASS; Vries and Döös 2001). The database consists of matrices describing the dispersal probability due to passive dispersal of eggs and planktonic larvae for six years (1995, 1996, 1998, 2000, 2001, 2002) covering the variation in the North Atlantic Oscillation Index, which has been shown to correlate well with the variation in hydrography and circulation in the North Sea–Baltic Sea region (Hänninen et al. 2000).

Dispersal simulations are based on the oceanographic circulation model Nemo-Nordic (Hordoir et al. 2019) and is a regional Baltic/North Sea configuration of the NEMO ocean model, with a horizontal resolution of 2 nautical miles (3.7 km), and a vertical resolution ranging from 3 m at the surface and 22 m in the deepest parts. The model is forced with tidal surface variations on the three open boundaries and with atmospheric forcing based on wind and precipitation (see Hordoir et al. 2019, for details and validation). The Lagrangian particle-tracking model calculates



In series with fertilised eggs at salinities < 15 psu, egg development ceased during the early blastula stage in three incubations at 9 and 10 psu and in one at 7.5 psu (but continued at 15 psu). Egg development up to hatching was assessed in the four remaining series. $58 \pm 9\%$ (mean $\pm$ sd), $43 \pm 15\%$ and $27 \pm 5\%$ of incubated eggs resulted in viable larvae at 15, 10 and 9 psu, respectively, while no viable larvae were registered at 7.5 psu ($n = 2$; Fig. 3C). Thus, fertilised eggs developed

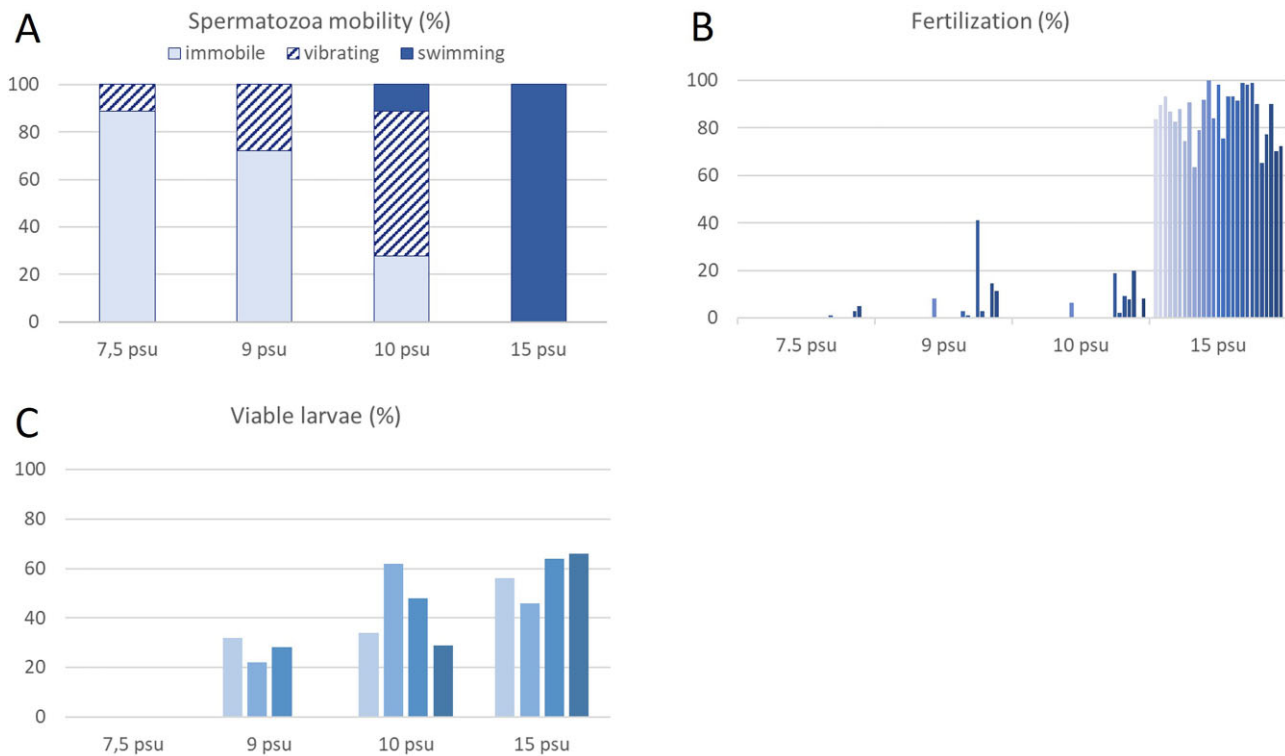


Figure 3. Results of experimental fertilisation of cod from the Åland Sea (SD 29N) at different salinities, showing the level of (A) initial spermatozoa activity (18 series, all with different males), (B) fertilised eggs (27 series with one female and one male) and (C) viable hatch (four series with one female and one male for 9–15 psu, and two series at 7.5 psu). Colours in (B) and (C) denote different pairs of males and females.

successfully and resulted in viable larvae at salinities ≥ 9 psu, although at rates decreasing with salinity.

Egg specific gravity

Egg specific gravity, expressed as salinity of neutral buoyancy (Table 1), of cod in the Åland Sea averaged 15.4 ± 2.1 (mean $\pm$ sd) psu, and did not differ from cod in the Gotland Basin (SD 28; $df = 20$, $t = 1.49$, $p = 0.15$) determined using the same methodology (Nissling and Westin 1997).

Hydrographic analysis for mapping of potential spawning areas

Suitable habitat, as characterized by salinity, oxygen concentrations and temperature, for successful fertilisation and egg survival decreased with the distance from the Danish Straits in the southwestern Baltic Sea towards the inner parts of this inland sea. At the 11 psu threshold, the highest habitat suitability for the Eastern Baltic cod stock occurred in the Bornholm Basin (SD 25), followed by the Gdansk Deep (SD 26) and, with considerably lower suitability, the Gotland Basin (SD 28) (Fig. 4A). Habitat suitability varied considerably over time in the Gdansk Deep, with favourable conditions occurring in 2003–2010 and in 2014–2017 following major inflow events (Fig. 5A). In the Gotland Basin substantial volumes of water suitable for reproduction occurred only in 2003–2007 and 2014–2017. No or very small reproduction volumes occurred in $> 50\%$ of the months during the period 1999–2018 (Fig. 5A). In SD 29S and the western part of SD 32, i.e. in the deep areas just south of the sill separating the Baltic Proper from the Åland Sea, no or very small volumes with suitable habitat occurred (Fig. 5A).

Using 10.5 psu as a threshold for reproduction, i.e. a level where only the most buoyant eggs may survive, revealed that suitable hydrological conditions occur periodically in most of the deeper parts of SD 29S, extending to SD 27 in the west and to SD 32 in the east (Fig. 4B). At this salinity level, conditions allowing for egg survival occurred in $< 20\%$ of the months during the period in these three northern SDs together, even though the volumes were small (on average 5 km^3) (Fig. 5B). In the Gdansk Deep and the Gotland Basin, hydrological conditions suitable for spawning occurred in all years, but with a high variability in volumes; similar to the situation for 11 psu, the most favourable conditions occurred in 2003–2010 and in 2014–2017 in the Gdansk Deep, and in 2003–2007 and 2015–2017 in the Gotland Basin (Fig. 4B and 5B).

According to our results (Fig. 3), eggs may to some extent be fertilised and develop successfully up to hatching at ≥ 9 psu. Spawning at 9–10 psu would however imply that eggs are negatively buoyant, i.e. will sink to the bottom. Using a salinity threshold of 9 psu, in SD 27, 29 and 32, on average 100 km^3 of suitable habitat (including oxic conditions down to the bottom, potentially allowing egg survival on the sediment surface) occurred every year during the period 1999–2018 (Fig. 5C). Thus, large areas in the northern Baltic Proper may function as a suitable habitat for reproduction, with the exception of the deepest parts due to oxygen deficiency (Fig. 4C). However, no suitable area for reproduction occurred in the Åland Sea or the Bothnian Sea at the 9 psu level, although the areas are well-oxygenated down to the deepest areas.

Larval drift modelling

The outcome from the larval drift model revealed that the probability for drifters to have end points in the Åland Sea and

Table 1. Salinity of neutral egg buoyancy at 7°C, and egg size of cod from SD 29N (present study), SD 28 (Nissling and Westin 1997) and SD 25 (Per Solemdal, Institute of Marine Research, Bergen, Norway, personal communication. Data received 1990; published in Nissling and Westin 1991, 1997)

	Åland Sea (SD 29N)	Gotland Basin (SD 28)	Bornholm Basin (SD 25)
Neutral buoyancy (psu)			
mean ± sd	15.4 ± 2.1	14.5 ± 1.2	14.3 ± 1.9
range	11.6–19.6	11.8–18.3	10.1–17.2
n	17	44	14
Egg diameter (mm)			
mean ± sd	1.57 ± 0.10	1.66 ± 0.07	1.64 ± 0.08
range	1.47–1.81	1.49–1.79	1.47–1.76
n	12	29	14

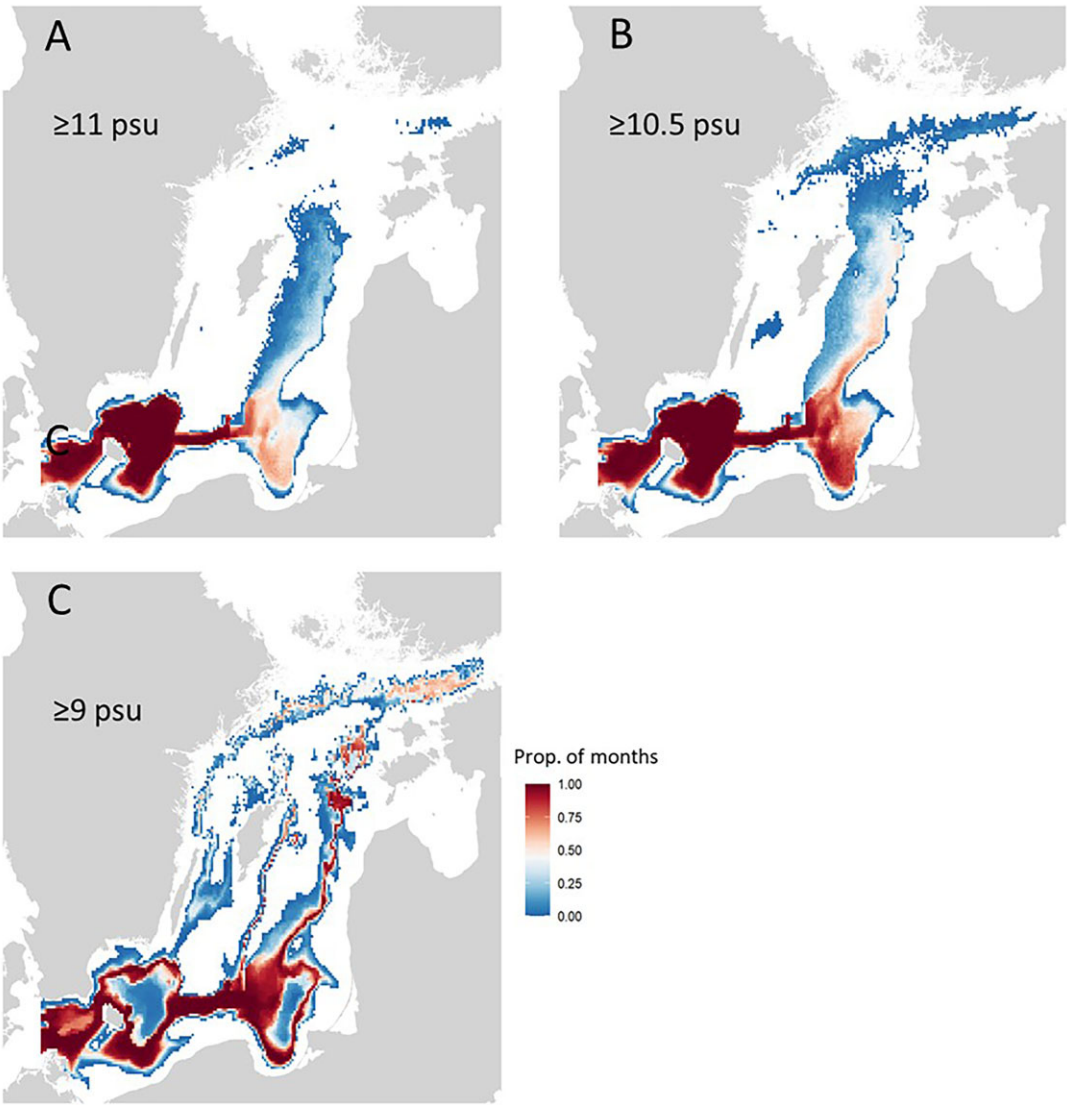


Figure 4A-C. Habitat suitability for egg survival at a salinity threshold level of A) ≥ 11 , B) ≥ 10.5 and C) ≥ 9 psu, showing the proportion of months during the spawning seasons (April–September) of 1999–2018 when salinity, oxygen and temperature conditions exceeded threshold levels. For the 9 psu level, where the eggs may sink to the bottom, only areas with oxygenated bottom water (>2 ml/l) were included in the calculations.

Bothnian Sea area (SD 29N–30) is close to zero when originating from the Bornholm Basin (SD 25; Fig. 6A), i.e. the main spawning area of the Eastern Baltic cod. The majority of these drifters remain in SD 25 and 26. From the Gdansk Deep (SD 26; Fig. 6B) drifters dispersed mostly in SD 26 and 28, but also

to SD 27 and SD 29S. However, a minor part, 0.11% (mean of the two dispersal depths and larval duration periods) of the drifters ended in the Åland Sea (SD 29N). Dispersal of drifters from the Gotland Basin (SD 28; Fig. 6C) yielded end points in mainly SD 26 and 28 but also in SD 27 and SD 29S. Only a

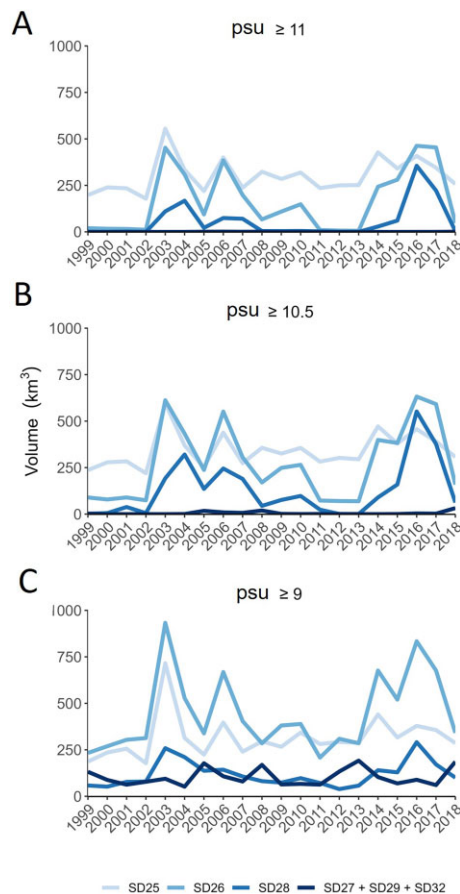


Figure 5. Volume of water suitable for reproduction of cod in 1999–2018 for three different potential salinity thresholds (A) ≥ 11 psu, (B) ≥ 10.5 psu and (C) ≥ 9 psu. The reproduction volumes were estimated from hydrographical modelling data, as volumes of water with an oxygen concentration > 2 ml/l and temperature $> 1.5^\circ\text{C}$ in April–September. For 9 psu, only areas that were oxygenated down to the bottom were included in the calculations. The curves show volumes for SD 25 (Bornholm Deep), SD 26 (Gdansk Deep), SD 28 (Gotland Basin), and SD 27, 29 and 32 (the potential spawning area in the northern Baltic Sea).

small fraction, 0.0056%, ended in the Åland Sea. The highest probability of drifters to disperse to the Åland Sea and the Bothnian Sea occurred from dispersal in the nearby deep areas in SD 29S-western SD 32 (Fig. 6D). Here most drifters stayed within the area (SD 27, SD 29S and SD 32), but 2.2% had end points in the Åland Sea and the Bothnian Sea.

Discussion

In the deep, well-oxygenated Åland Sea, large cod are still abundant, and display spawning activity during summer. However, the fertilisation experiments indicate that spawning in the area is not successful due to the low salinity. The local stock component in the Åland Sea may instead be upheld by northward larval transport from the Baltic Proper, as shown by the larval drift models, or by active migration of juveniles and adults. The high covariation in catches and stock development between the Åland Sea, as well as the Bothnian Sea further north, and the stock component in SD 28 suggests that cod recruitment in these areas is governed by the same mechanisms. The tight connection between the areas is also supported by that peaks in landings in the northern areas co-

incide with periods of high egg abundance in SD 28 (Karaseva 2018). The combined results of the fertilisation experiments, analyses of hydrographical time series data and larval dispersal models suggest that likely source areas for cod in the Åland Sea are the known spawning areas in the Gdansk and Gotland Basins, while also the deep areas just south of the Åland Sea in the northern Baltic Proper (SD 27, 29S and 32) may occasionally provide suitable habitat for cod reproduction.

Fertilisation experiments

Full activation of spermatozoa and fertilisation in cod from the Åland Sea required a salinity of ≥ 11 psu in the majority of the trials, which is in accordance with previous investigations of cod in SD 28 by Westin and Nissling (1991). However, some swimming or vibrating spermatozoa were noted at 10 psu, and in a few cases at 9 psu and even at 7.5 psu. This pattern was mirrored by the degree of fertilisation of eggs. Evidently, fertilisation and egg development is possible down to 9 psu in some individuals at least under experimental conditions, which involve dense concentration of spermatozoa, with the possibility that ovarian fluid may promote the spermatozoa activation and fertilization process (Litvak and Trippel 1998). Hyperosmotic condition is considered a prerequisite for spermatozoa motility and thus fertilization, i.e. a minimum salinity of ≥ 10 –11 psu is required (Nissling and Westin 1997, Alavi et al. 2021). Osmolality in seminal plasma varies to some extent with ambient salinity conditions: 12.6 ± 0.6 psu in cod at marine environment vs 10.9 ± 0.4 (range 10.3–11.2) psu in brackish conditions. This affects opportunities for fertilisation as shown in a transplant experiment (Nissling and Westin 1997). As salinity in the Åland Sea (around 7.5 psu in deep areas, and up to 9 psu in the Långskär Deep in the southern part) is substantially lower than in SD 28 (10–13 psu), osmolality in seminal plasma may also be somewhat lower and hence potentially allow successful fertilisation at a lower salinity; see discussion in Westin and Nissling (1991). Thus, the results are in agreement with earlier experimental studies of cod at low salinities (Westin and Nissling 1991, Nissling & Westin 1997). However, it cannot be ruled out that fertilisation and egg development resulting in viable larvae may still occur at salinities found in the Åland Sea. The number of individuals tested experimentally was quite low, and there is still a chance that some genotypes do display adaptation to these low salinities. To further explore whether some reproduction can occur, experiments on more individuals and from other parts of the Åland Sea may be desirable, and ultimately, field sampling for occurrence of eggs and newly hatched larvae.

The salinity of neutral egg buoyancy was in agreement with corresponding measurements of cod eggs in SD 25 and 28 (Nissling & Westin 1997), suggesting that the lowest salinity for neutral egg buoyancy is ca 10.5 psu (Vallin and Nissling 2000). This likely means that for successful reproduction at 9–10 psu, successful fertilisation is not enough. The eggs also need to be able to survive and develop on the sediment surface as they will sink to the bottom in these salinities. This issue was pointed out already by Hessle (1923), but we have not been able to find any reports of viable cod eggs found in bottom sampling (see e.g. Hessle 1923, Hinrichsen et al. 2016). Accordingly, benthic cod egg survival has been considered to be zero (Hinrichsen et al. 2016 and references therein). An interesting parallel is the Baltic flounder (*Platichthys sole-*

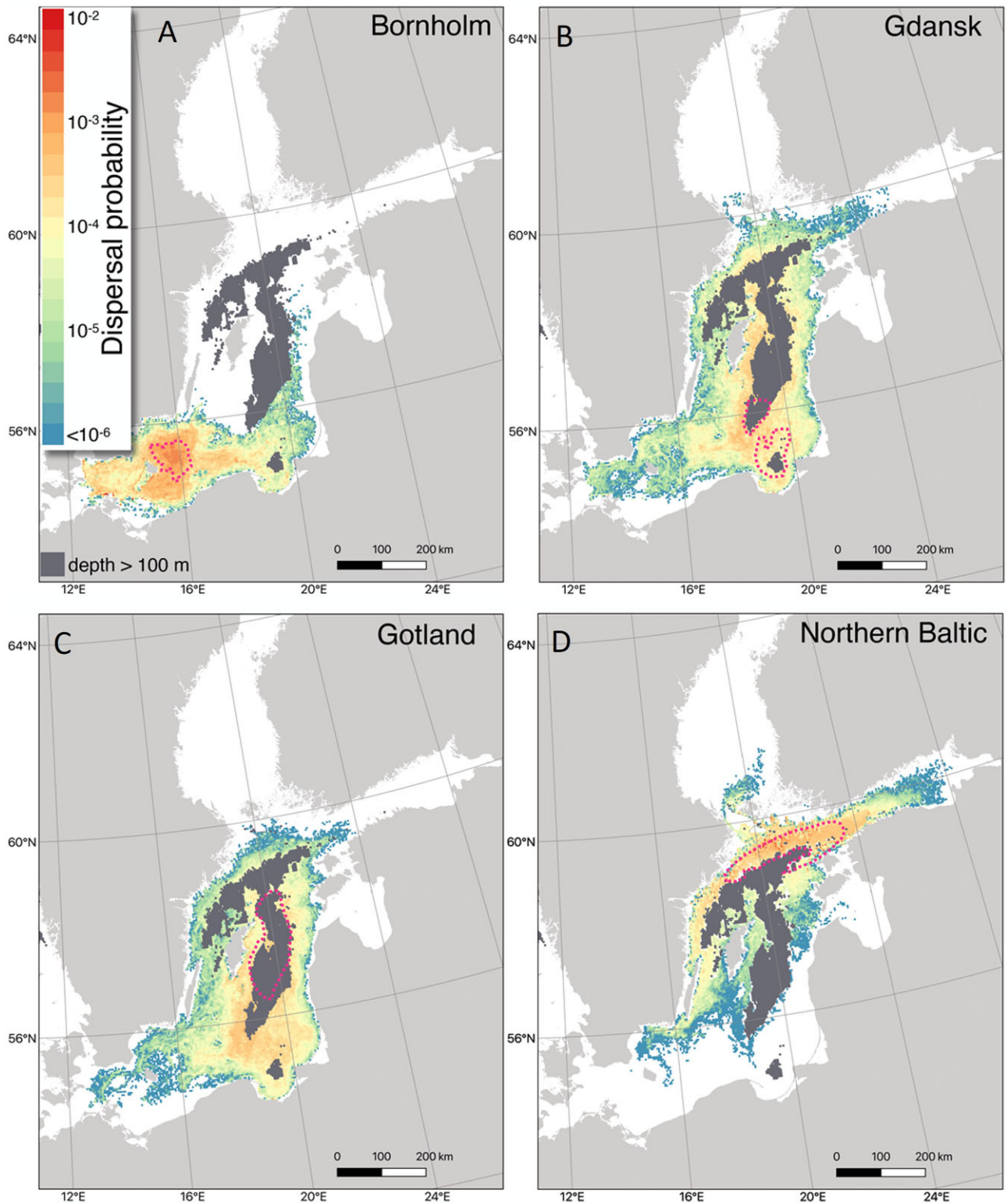


Figure 6. Estimated dispersal probabilities for cod larvae hatched in the known spawning areas in (A) the Bornholm Deep (SD 25), (B) the Gdansk Deep (SD 26), (C) the Gotland Basin (SD 28), and the potential spawning area in (D) the northern Baltic Sea (SD 27, 29 and 32). The dispersal maps are based on biophysical modelling of particles released from the spawning areas shown as dashed black polygons. Dark grey areas are deeper than 100 m for which there are no connectivity estimates from the model applied. These deep areas are assumed to have no successful settlement of larvae.

dali), an endemic species for the Baltic Sea recently described by Momigliano et al. (2018). While its close relative, the European flounder (*Platichthys flesus*), is a pelagic spawner with environmental requirements for successful reproduction sim-

ilar to those of cod (Ustups et al. 2013), the Baltic flounder has developed a demersal spawning strategy as an adaptation to the low-salinity conditions of the Baltic Sea (Sølem-dal 1973, Nissling et al. 2017). Additional experiments are

required to assess whether a similar adaptation for cod may have occurred, enabling survival of non-buoyant cod eggs at the bottom in salinities below 10 psu, corresponding to salinities with favourable oxygen conditions in the northern Baltic Proper (SD 27–29 and 32). While no eggs with neutral buoyancy at ≤ 10.4 psu have been found in field sampling (Hessle 1923, Grauman 1963, Lindblom 1973), it may still be worth considering the potential for eggs from some individuals having neutral buoyancy at the slightly lower salinities prevailing in the area. Large females usually display neutral buoyancy at low salinities, and individuals over 10 kg are still relatively common in the Åland Sea, likely because of good oxygen conditions and food availability (Heimbrand et al. 2023, Heimbrand and Limburg 2025).

Potential spawning areas

The hydrographic analyses for the period 1999–2018 showed that conditions suitable for reproduction of Eastern Baltic cod are common in the Bornholm and Gdansk Basins, while only occasionally in the Gotland Basin. Additionally, small water volumes with potentially suitable conditions occur also in the northern Baltic Proper (SD 27, 29 and 32) according to the model results. The estimates are highly dependent on the threshold limit for reproduction applied, with 12 years out of 20 at ≥ 10.5 psu and four years at ≥ 11 psu (Fig. 5). However, this only applies to the most buoyant eggs. If reproduction in these areas is successful today is unknown, but occurrence of cod eggs in the late 1910s–early 1920s (Hessle 1923) and in the late 1960s–early 1970s (Lindblom 1973, Grauman 1974) in SD 27, 29 and northern part of 28 indicate that reproduction may have taken place also in the northern Baltic Proper in the past. No egg surveys or monitoring has to our knowledge been performed in these areas during the last decades.

Water volumes suitable for cod reproduction, based on ≥ 11 psu, have been reported by for example Hinrichsen et al. (2016) and Svedäng et al. (2022). The present study represents an update mainly by applying salinity thresholds of ≥ 10.5 (lowest salinity for neutral egg buoyancy) and ≥ 9 psu (with the additional condition of oxygenated water at the sea floor), as suggested by the fertilisation experiments. In all areas, opportunities for egg survival vary greatly over time depending on salinity and oxygen conditions in the deep basins, mainly as a result of the magnitude and frequency of irregular saline water inflows (Köster et al. 2017, Svedäng et al. 2022). Even areas in the southern Åland Sea may occasionally have salinities ≥ 9 psu and oxygen ≥ 2 ml/l (Westerlund et al. 2022). Periods following inflows result in favourable conditions with higher egg survival and increased larval production, i.e. with higher opportunities for larval drift to the Åland Sea and Bothnian Sea. Otterlind (1984) studied historical reports of Swedish landings from the Åland Sea and northern Baltic Proper, and concluded that the cod stock component in these areas has varied greatly at least since the 1450s and onwards. Currently, periods with favourable conditions occur in the Gdansk Deep and occasionally in the Gotland Basin, in addition to the more stable conditions in the Bornholm Deep, and potentially for shorter periods in SD 27, 29 and 32.

The ongoing and projected decrease in salinity and oxygen conditions in deep basins as a result of climate change (Gröger et al. 2019, Saraiva et al. 2019) suggests that conditions for cod reproduction in the eastern and northern Baltic Proper are deteriorating, and may have negative effects on cod

in the Åland Sea and Bothnian Sea. Such a decline, presumably caused by the same mechanisms, has already been shown for the European flounder in SD 29 and 32 (Momigliano et al. 2019), a species with habitat requirements for spawning that are very similar to those of cod. In fact, a contraction in the distribution of the Eastern Baltic cod towards the southern areas of the Baltic Sea, as a consequence of a loss of spawning habitats, can already be seen (e.g. Orio et al. 2019). Importantly, the deterioration of spawning areas due to climate change may, however, be counteracted by eutrophication abatement measures that are projected to improve oxygen conditions in the eastern and northern Baltic Proper (Meier et al. 2021).

Connectivity mechanisms

The Åland Sea may be connected to the main stock component of the Eastern Baltic cod through larval dispersal and active migration by juveniles and adults. The larval drift models showed that there is a high level of connectivity through passive dispersal from the nearby potential spawning areas in northern Baltic Proper (SD 27, 29 and 32) to the Åland Sea, and a lower but still considerable connectivity from the Gdansk Deep and the Gotland Basin (SD 26 and 28), showing that these areas may contribute to the recruitment of cod to SD 29N and 30. For the main spawning area of Eastern Baltic cod, the Bornholm Basin (SD 25), the model results show very low levels of connectivity, which in accordance with previous modelling (Hinrichsen et al. 2017) indicates that this area is not an important source area for larvae settling in the Åland Sea, unless connectivity is dependent on active migration by juveniles or adults.

Results from tagging experiments show substantial southward spawning migrations from the Åland Sea and Bothnian Sea to the major spawning areas in the central Baltic Sea, including the Gotland, Gdansk and Bornholm Basins (Otterlind 1984, Aro 1989, Mion et al. 2022), indicating connectivity through active migration between the areas. Otterlind (1984) reports that a large proportion of the tagged young fish migrated to spawning areas in the south. However, spawning in the deeper areas in the Åland Sea and Bothnian Sea has also been reported (Hessle 1923, Modin 1987), and is supported by the fish in spawning condition found in this study. Whether these individuals represent a sink, not contributing to recruitment, or if they may change spawning areas between seasons is not known. Knowledge about homing behaviour of cod in the Baltic Sea is limited, but tagging experiments have shown that cod may shift between the major spawning areas (Bagge 1983, Otterlind 1984). To increase our knowledge of the migratory behaviour of cod in the area, tagging of fish with data storage tags (Hüssy et al. 2020) and otolith microchemistry utilizing a suite of trace elements may be applied (Heimbrand et al. 2020). In fact, recent otolith chemistry analysis of cod in the Åland Sea has revealed intriguing trace element patterns that may enhance understanding of differences in migration strategies and recruitment in this region. Some Åland Sea cod exhibit markedly elevated boron concentrations in otoliths compared to cod from the same and other areas of the Baltic Sea (Heimbrand and Limburg 2025), suggesting that these cod might not originate from the established southern Baltic spawning areas. Further otolith chemical analysis using higher resolution techniques could provide more precise information about the larval stages to assess provenance in detail.

To summarise, our study suggests that recruitment of cod to the Åland Sea is a result of larval drift and potentially active migration of juvenile and adult fish from spawning areas in SD 26 and 28, but also possibly the deep areas of the northern Baltic Proper (SD 27, 29 and 32). Local adaptation may enable reproduction in these northern areas, as indicated by the partly successful fertilisation and egg development down to 9–10 psu. To fully understand the recruitment mechanisms, further studies on the migratory behaviour (through tagging and otolith chemistry), genetic population structure, and occurrence of eggs and larvae are needed. While the role of the Åland Sea cod for the Eastern Baltic cod stock as a whole remains unknown, maintaining this unique stock component of large cod is still important for the local ecosystem from a conservation perspective.

Author contributions

Ulf Bergström (Conceptualization [lead], Data curation [lead], Formal analysis [lead], Funding acquisition [lead], Investigation [equal], Methodology [equal], Project administration [lead], Visualization [equal], Writing – original draft [lead], Writing – review & editing [lead]), Isa Wallin (Investigation [equal], Writing – review & editing [equal]), Carl André (Writing – review & editing [equal]), Jonsson Per (Formal analysis [equal], Investigation [equal], Writing – original draft [equal], Writing – review & editing [equal]), Mårten Erlandsson (Data curation [equal], Formal analysis [equal], Investigation [equal], Visualization [equal], Writing – review & editing [equal]), Yvette Heimbrand (Investigation [equal], Writing – review & editing [equal]), and Anders Nissling (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Methodology [lead], Writing – original draft [equal], Writing – review & editing [equal]).

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Data availability

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

References

Agarwal D, Shanmugam SA, Kathirvelpandian A *et al.* Unraveling the Impact of Climate Change on Fish Physiology: a Focus on Temperature and Salinity Dynamics. *Journal of Applied Ichthyology*, 2024;2024:5782274. <https://doi.org/10.1155/2024/5782274>

Alavi SMH, Hatf A, Butts IA *et al.* Some recent data on sperm morphology and motility kinetics in Atlantic cod (*Gadus morhua* L.).

Fish Physiol Biochem, 2021;47:327–38. <https://doi.org/10.1007/s10695-020-00915-4>

Alix M, Kjesbu OS, Anderson KC. From gametogenesis to spawning: how climate-driven warming affects teleost reproductive biology. *J Fish Biol*, 2020;97:607–32. <https://doi.org/10.1111/jfb.14439>

Aro E. A review of fish migration patterns in the Baltic. *ICES Rapports et Procès-verbaux*, 1989;190:72–96.

Aro E. Fish migration studies in the Baltic Sea—a historical review. *ICES Marine Science Symposia*, 2002;215:361–370. <https://doi.org/10.17895/ices.pub.8875>

Bagge O. Migrations of transplanted cod. *ICES Committee Meeting Papers*, 1983;1983.12.

Bagge O. The Baltic cod stock, fluctuations and the possible causes. *ICES Marine Science Symposia*, 1994;198:254–268. <https://doi.org/10.17895/ices.pub.19271216>

Berg PR, Jentoft S, Star B *et al.* Adaptation to Low Salinity Promotes Genomic Divergence in Atlantic Cod (*Gadus morhua* L.). *Genome Biol Evolut*, 2015;7:1644–63. <https://doi.org/10.1093/gbe/evv093>

Bryhn AC, Bergek S, Bergström U *et al.* Which factors can affect the productivity and dynamics of cod stocks in the Baltic Sea, Kattegat and Skagerrak? *Ocean & Coastal Management*, 2022;223:106154. <https://doi.org/10.1016/j.ocecoaman.2022.106154>

Coombs S. A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs of the mackerel *Scomber scombrus*. *Mar Biol*, 1981;63:101–6. <https://doi.org/10.1007/BF00394667>

Eero M, Carlshamre S, Stepputtis D *et al.* Report on eastern Baltic cod bycatch in non-targeted fisheries, mixing with western Baltic cod in SD24, and stock situation in SDs 27–32. *ICES Scientific Reports*, 2019;1:69. <http://doi.org/10.17895/ices.pub.5635>

Eero M, Köster FW, Plikshs M *et al.* Eastern Baltic cod (*Gadus morhua* callarias) stock dynamics: extending the analytical assessment back to the mid-1940s. *ICES J Mar Sci*, 2007;64:1257–71. <https://doi.org/10.1093/icesjms/fsm114>

Eero M. Reconstructing historical stock development of Atlantic cod (*Gadus morhua*) in the eastern Baltic Sea before the beginning of intensive exploitation. *Can J Fish Aquat Sci*, 2008;65:2728–41. <http://doi.org/10.1139/F08-176>

Grauman G. Features of the cod spawning in the Baltic in 1961. *Annales Biologiques*, 1963;18:128–9.

Grauman G. Investigations on the spawning of Baltic cod in 1968 to 1970. *ICES Rapports et Procès-verbaux*, 1974;166:7–9.

Gröger M, Arneborg L, Dieterich C *et al.* Summer hydrographic changes in the Baltic Sea, Kattegat and Skagerrak projected in an ensemble of climate scenarios downscaled with a coupled regional ocean–sea ice–atmosphere model. *Clim Dyn*, 2019;53:5945–66. <https://doi.org/10.1007/s00382-019-04908-9>

Grønkjær P, Wieland K. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. *Marine Ecology Progress Series*, 1997;154:91–105. <https://doi.org/10.3354/meps154091>

Hänninen J, Vuorinen I, Hjelt P. Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol Oceanogr*, 2000;45:703–10. <https://doi.org/10.4319/lo.2000.45.3.0703>

Heimbrand Y, Larsson S, Landfors F, *et al.* 2023 Beståndstatus för torsk i Ålands hav 2022. Report. <https://res.slu.se/id/publ/123802>

Heimbrand Y, Limburg KE, Hüsey K *et al.* Seeking the true time: exploring otolith chemistry as an age-determination tool. *J Fish Biol*, 2020;97:552–65. <https://doi.org/10.1111/jfb.14422>

Heimbrand Y, Limburg KE. Elevated boron in cod otoliths from the low-salinity Åland Sea: a unique marker for a new population in the Baltic Sea? *Marine and Coastal Fisheries*, 2025;17:vtaf022. <https://doi.org/10.1093/mcfafs/vtaf022>

Hentati-Sundberg J. *Svenskt fiske i historiens ljus—en historisk fiskeriatlas*. Lysekil: Swedish University of Agricultural Sciences, Department of Aquatic Resources, 2017.

- Hessle C. Undersökningar rörande torsken (*Gadus callarias* L.) i mellersta Östersjön och Bottenhavet (Research on cod (*Gadus callarias* L.) in the Baltic Main Basin and in the Bothnian Sea). *Meddelande från Kungliga Lantbruksstyrelsen (Communications from the Royal Agricultural Administration)*, 1923;243:19–74.
- Hinrichsen H-H, Böttcher U, Köster FW *et al.* Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift. *J Sea Res*, 2003;49:187–201. [https://doi.org/10.1016/S1385-1101\(03\)00006-6](https://doi.org/10.1016/S1385-1101(03)00006-6)
- Hinrichsen H-H, Huwer B, Makarchouk A *et al.* Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). *ICES J Mar Sci*, 2011;68:2019–28. <https://doi.org/10.1093/icesjms/fsr145>
- Hinrichsen H-H, Kraus G, Böttcher U *et al.* Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas. *ICES J Mar Sci*, 2009;66:101–8. <https://doi.org/10.1093/icesjms/fsn207>
- Hinrichsen H-H, Lehmann A, Peterreit C *et al.* Spawning areas of eastern Baltic cod revisited: using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability, and connectivity patterns. *Prog Oceanogr*, 2016;143:13–25. <https://doi.org/10.1016/j.pocean.2016.02.004>
- Hinrichsen H-H, von Dewitz B, Lehmann A *et al.* Spatio-temporal dynamics of cod nursery areas in the Baltic Sea. *Prog Oceanogr*, 2017;155:28–40. <https://doi.org/10.1016/j.pocean.2017.05.007>
- Hordoir B, Axell L, Höglund A *et al.* Nemo-Nordic 1.0: a NEMO-based ocean model for the Baltic and North seas—research and operational applications. *Geosci Model Dev*, 2019;12:363–86. <https://doi.org/10.5194/gmd-12-363-2019>
- Houde E. Emerging from Hjort's Shadow. *Journal of Northwest Atlantic Fishery Science*, 2008;41:53–70. <https://doi.org/10.2960/J.v41.m634>
- Houde E. Recruitment Variability. In *Fish Reproductive Biology*, pp.98–187. John Wiley & Sons, Ltd. 2016. <https://doi.org/10.1002/9781118752739>
- Howell B. R., Child A. R., Houghton R. G. Fertilization rate in a natural population of the common sole (*Solea solea* L.). *ICES Journal of Marine Science* 1991;48:53–59.
- Hüssy K, Casini M, Haase S *et al.* Tagging Baltic Cod—TABACOD. *Eastern Baltic cod: solving the ageing and stock assessment problems with combined state-of-the-art tagging methods*. 2020:64. DTU Aqua report368-2020. <https://www.aqua.dtu.dk/-/media/Institutter/Aqua/Publicationer/Rapporter-352-400/368-2020-TABACOD-Final-Report.ashx>
- ICES. Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). *Replacing advice provided in May 2024*. Report of the ICES Advisory Committee. 2025. <https://doi.org/10.17895/ices.advice.27202563.v1>
- ICES. Cod (*Gadus morhua*) in subdivisions 24–32, eastern Baltic stock (eastern Baltic Sea). *Report of the ICES Advisory Committee*. 2022. <https://doi.org/10.17895/ices.advice.19447874>
- Jakobsson M, Stranne C, O'keefe;Regan M *et al.* Bathymetric properties of the Baltic Sea. *Ocean Sci*, 2019;15:905–24. <https://doi.org/10.5194/os-15-905-2019>
- Johannesson K, Le Moan A, Perini S *et al.* A Darwinian Laboratory of Multiple Contact Zones. *Trends Ecol Evol*. 2020;35:1021–36. <https://doi.org/10.1016/j.tree.2020.07.015>
- Jonsson PR, Corell H, André C *et al.* Recent decline in cod stocks in the North Sea-Skagerrak-Kattegat shifts the sources of larval supply. *Fisheries Oceanography*, 2016;25:210–28. <https://doi.org/10.1111/fog.12146>
- Jonsson PR, Moksnes P, Corell H *et al.* Ecological coherence of Marine Protected Areas: new tools applied to the Baltic Sea network. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 2020;30:743–60. <https://doi.org/10.1002/aqc.3286>
- Karaseva EM. The Egg Abundance of Eastern Baltic Cod *Gadus morhua* callarias (Gadidae) in the 20th Century as a Population Status Indicator. *Journal of Ichthyology*, 2018;58:878–88. <https://doi.org/10.1134/S0032945218060061>
- Kjesbu OS, Tiedemann I, Alix M *et al.* Half a century of high-latitude fisheries oceanography research on the “recruitment problem” in Northeast Arctic cod (*Gadus morhua*). *ICES J Mar Sci*, 2023;80:1179–201. <https://doi.org/10.1093/icesjms/fsad073>
- Köster FW, Huwer B, Hinrichsen H-H *et al.* Eastern Baltic cod recruitment revisited—dynamics and impacting factors. *ICES J Mar Sci*, 2017;74:3–19. <https://doi.org/10.1093/icesjms/fsw172>
- Köster FW, Möllmann C, Hinrichsen H-H *et al.* Baltic cod recruitment—the impact of climate variability on key processes. *ICES J Mar Sci*, 2005;62:1408–25.
- Köuts M, Maljutenko I, Elken J *et al.* Recent regime of persistent hypoxia in the Baltic Sea. *Environmental Research Communications*, 2021;3:075004. <https://doi.org/10.1088/2515-7620/ac0cc4>
- Larsen PF, Nielsen EE, Meier K *et al.* Differences in Salinity Tolerance and Gene Expression Between Two Populations of Atlantic Cod (*Gadus morhua*) in Response to Salinity Stress. *Biochem Genet*, 2012;50:454–66. <https://doi.org/10.1007/s10528-011-9490-0>
- Lindblom R. Abundance and horizontal distribution of pelagic fish eggs and larvae in the Baltic Sea in 1967–1971, *Medd. Havsfiskelaboratoriet, Lysekil*, 1973;140:9–28.
- Litvak MK, Trippel EA. Sperm motility patterns of Atlantic cod (*Gadus morhua*) in relation to salinity: effects of ovarian fluid and egg presence. *Can J Fish Aquat Sci*, 1998;55:1871–7. <https://doi.org/10.1139/f98-093>
- Ma S, Huse G, Ono K *et al.* Recruitment regime shifts and nonstationarity are widespread phenomena in harvestable stocks experiencing pronounced climate fluctuations. *Fish and Fisheries*, 2024;25:320–48. <https://doi.org/10.1111/faf.12810>
- MacKenzie B, St John M, Plikshs M *et al.* Oceanographic processes influencing seasonal and interannual variability in cod spawning habitat in the eastern Baltic Sea. *ICES Council Meeting Papers*. 1996; C+J:4.
- MacKenzie BR, Bager M, Ojaveer H *et al.* Multi-decadal scale variability in the eastern Baltic cod fishery 1550–1860—Evidence and causes. *Fish Res*, 2007;87:106–19. <https://doi.org/10.1016/j.fishres.2007.07.003>
- MacKenzie BR, Hinrichsen H-H, Plikshs M *et al.* Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. *Marine Ecology Progress Series*, 2000;193:143–56. <https://doi.org/10.3354/meps193143>
- Macura B, Byström P, Airolidi L *et al.* Impact of structural habitat modifications in coastal temperate systems on fish recruitment: a systematic review. *Environmental Evidence*, 2019;8:14. <https://doi.org/10.1186/s13750-019-0157-3>
- McEvoy L, McEvoy J. Multiple spawning in several commercial fish species and its consequences for fisheries management, cultivation and experimentation. *J Fish Biol*, 1992;41:125–36. <https://doi.org/10.1111/j.1095-8649.1992.tb03874.x>
- Meier HEM, Dieterich C, Gröger M. Natural variability is a large source of uncertainty in future projections of hypoxia in the Baltic Sea. *Communications Earth & Environment*, 2021;2:1–13. <https://doi.org/10.1038/s43247-021-00115-9>
- Mion M, Griffiths CA, Bartolino V *et al.* New perspectives on Eastern Baltic cod movement patterns from historical and contemporary tagging data. *Marine Ecology Progress Series*, 2022;689:109–26. <https://doi.org/10.3354/meps14047>
- Mion M, Haase S, Hemmer-Hansen J *et al.* Multidecadal changes in fish growth rates estimated from tagging data: a case study from the Eastern Baltic cod (*Gadus morhua*, Gadidae). *Fish and Fisheries*, 2021;22:413–27. <https://doi.org/10.1111/faf.12527>
- Modin J. A note on large catches of cod, *Gadus morhua*, in the Bothnian Sea during spring 1987. *ICES Committee Meeting*, 1987;26:1–4.
- Mohrholz V, Naumann M, Nausch G *et al.* Fresh oxygen for the Baltic Sea—An exceptional saline inflow after a decade of stagnation. *J Mar Syst*, 2015;148:152–66. <https://doi.org/10.1016/j.jmarsys.2015.03.005>

- Momigliano P, Denys GPJ, Jokinen H *et al.* *Platichthys solemdali* sp. nov. (Actinopterygii, Pleuronectiformes): a New Flounder Species From the Baltic Sea. *Frontiers in Marine Science*, 2018;5:1–21. <https://doi.org/10.3389/fmars.2018.00225>
- Momigliano P, Jokinen H, Calboli F *et al.* Cryptic temporal changes in stock composition explain the decline of a flounder (*Platichthys* spp.) assemblage. *Evolutionary Applications*, 2019;12:549–59. <http://doi.org/10.1111/eva.12738>
- Muchowski J, Jakobsson M, Umlauf L *et al.* Observations of strong turbulence and mixing impacting water exchange between two basins in the Baltic Sea. *Ocean Sci*, 2023;19:1809–25. <https://doi.org/10.5194/os-19-1809-2023>
- Nissling A, Kryvi H, Vallin L. Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. *Marine Ecology Progress Series*, 1994;110:67–74. <https://doi.org/10.3354/meps110067>
- Nissling A, Larsson R, Vallin L *et al.* Assessment of egg and larval viability in cod, *Gadus morhua*: methods and results from an experimental study. *Fish Res*, 1998;38:169–86. [https://doi.org/10.1016/S0165-7836\(98\)00121-0](https://doi.org/10.1016/S0165-7836(98)00121-0)
- Nissling A, Nyberg S, Peterreit C. Egg buoyancy of flounder, *Platichthys flesus*, in the Baltic Sea—adaptation to salinity and implications for egg survival. *Fish Res*, 2017;191:179–89. <https://doi.org/10.1016/j.fishres.2017.02.020>
- Nissling A, Westin L. Egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for cod stock fluctuations in the Baltic. *Mar Biol*, 1991;111:33–5. <https://doi.org/10.1007/BF01986342>
- Nissling A, Westin L. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interactions in the Baltic Sea. *Marine Ecology Progress Series*, 1997;152:261–71. <https://doi.org/10.3354/meps152261>
- Orio A, Bergström U, Florin A *et al.* Spatial contraction of demersal fish populations in a large marine ecosystem. *J Biogeogr*, 2019;46:633–45. <https://doi.org/10.1111/jbi.13510>
- Otterlind G. On fluctuations of the Baltic cod stock. *ICES 1984;CM*:1–10.
- Pankhurst NW, Munday PL. Effects of climate change on fish reproduction and early life history stages. *Mar Freshwater Res*, 2011;62:1015–26. <https://doi.org/10.1071/MF10269>
- Plikshs M, Kalejs M, Grauman G. The influence of environmental conditions and spawning stock size on the year-class strength of the eastern Baltic cod. *Ices Cm*, 1993;1:22.
- Plikshs M. Reproduction of Baltic cod, *Gadus morhua* (Actinopterygii: gadiformes: gadidae), in the Gotland Basin: causes of annual variability. *Acta Ichthyologica et Piscatoria*, 2015;45:247–58. <https://doi.org/10.3750/AIP2015.45.3.04>
- Reusch TBH, Dierking J, Andersson HC *et al.* The Baltic Sea as a time machine for the future coastal ocean. *Sci Adv*, 2018;4:eaar8195. <https://doi.org/10.1126/sciadv.aar8195>
- Rijnsdorp AD, Peck MA, Engelhard GH *et al.* Resolving the effect of climate change on fish populations. *ICES J Mar Sci*, 2009;66:1570–83. <https://doi.org/10.1093/icesjms/fsp056>
- Röthig T, Trevathan-Tackett SM, Voolstra CR *et al.* Human-induced salinity changes impact marine organisms and ecosystems. *Global Change Biol*, 2023;29:4731–49. <https://doi.org/10.1111/gcb.16859>
- Saraiva S, Meier HEM, Andersson H *et al.* Uncertainties in Projections of the Baltic Sea Ecosystem Driven by an Ensemble of Global Climate Models. *Frontiers in Earth Science*, 2019;6:244. <https://www.frontiersin.org/articles/10.3389/feart.2018.00244/full> (1 April 2021, date last accessed).
- Segerstråle SG. Biological fluctuations in the Baltic Sea. *Prog Oceanogr*, 1969;5:169–84. [https://doi.org/10.1016/0079-6611\(69\)90039-1](https://doi.org/10.1016/0079-6611(69)90039-1)
- Solemdal P. Transfer of Baltic flatfish to a marine environment and the long term effects on reproduction. *Oikos Suppl*. 1973;15:268–76.
- Svedäng H, Savchuk O, Villnäs A *et al.* Re-thinking the “ecological envelope” of Eastern Baltic cod (*Gadus morhua*): conditions for productivity, reproduction, and feeding over time. *ICES J Mar Sci* 2022;fsac017. <https://doi.org/10.1093/icesjms/fsac017>
- Thompson B, Riley JD. Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). *ICES Rapports et Procès-verbaux*, 1981;178:553–9.
- Tomkiewicz J, Tybjerg L, Holm N *et al.* Manual to determine gonadal maturity of Baltic cod. *Danmarks Fiskeriundersøgelser*. 2002:49. DFU-rapport No. 116-02.
- Ustups D, Müller-Karulis B, Bergstrom U *et al.* The influence of environmental conditions on early life stages of flounder (*Platichthys flesus*) in the central Baltic Sea. *J Sea Res*, 2013;75:77–84. <https://doi.org/10.1016/j.seares.2012.05.001>
- Vallin L, Nissling A. Cell morphology as an indicator of viability of cod eggs—results from an experimental study. *Fish Res*, 1998;38:247–55. [https://doi.org/10.1016/S0165-7836\(98\)00157-X](https://doi.org/10.1016/S0165-7836(98)00157-X)
- Vallin L, Nissling A. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*. *Fish Res*, 2000;49:21–37. [https://doi.org/10.1016/S0165-7836\(00\)00194-6](https://doi.org/10.1016/S0165-7836(00)00194-6)
- Vries P, Döös K. Calculating Lagrangian trajectories using time-dependent velocity fields. *J Atmos Oceanic Technol*, 2001;18:1092–101. [https://doi.org/10.1175/1520-0426\(2001\)018%3c1092:CLTUTD%3e2.0.CO;2](https://doi.org/10.1175/1520-0426(2001)018%3c1092:CLTUTD%3e2.0.CO;2)
- Westerlund A, Miettunen E, Tuomi L *et al.* Refined estimates of water transport through the Åland Sea in the Baltic Sea. *Ocean Sci*, 2022;18:89–108. <https://doi.org/10.5194/os-18-89-2022>
- Westin L, Nissling A. Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod (*Gadus morhua*), and implications for cod stock fluctuations in the Baltic. *Mar Biol*, 1991;108:5–9. <https://doi.org/10.1007/BF01313465>
- Wieland K, Waller U, Schnack D. *Development of Baltic cod eggs at different levels of temperature and oxygen content*. 1994, 10, 163–77. Dana: Danish Institute for Fisheries Research.
- Wikström A, Knape J, Casini M *et al.* Fishing, reproductive volume and regulation: population dynamics and exploitation of the eastern Baltic cod. *Population Ecology*, 2016;58:199–211. <https://doi.org/10.1007/s10144-015-0520-3>

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