

Identifying eastern Baltic cod nursery grounds using hydrodynamic modelling: knowledge for the design of Marine Protected Areas

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Knowledge of the spatial and temporal distribution of juvenile cod is essential to closing the life cycle in population dynamic models, and it is a prerequisite for the design of Marine Protected Areas (MPAs) aiming at the protection of juveniles. In this study, we use a hydrodynamic model to examine the spatial distribution of eastern Baltic cod larvae and early juveniles. The transport patterns of the larvae spawned at the three major spawning grounds in the central Baltic Sea were investigated by drift model simulations for the period 1979–2004. We analysed potential habitats for their suitability for juvenile settlement, i.e. the change from pelagic to demersal life. The results revealed a clear dependence of the probability for successful settling on wind-induced drift of larval cod, which is controlled by the local atmospheric conditions over the Baltic Sea. Furthermore, we found evidence that the final destinations of juvenile cod drift routes are affected by decadal climate variability. Application of the methodology to MPA design is discussed, e.g. identifying the overlap of areas with a high probability of successful juvenile cod settlement and regions of high fishing effort in small-meshed fisheries targeting sprat and herring.

Keywords: eastern Baltic cod, gadoid settlement, larval transport, nursery areas.

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Introduction

Eastern Baltic cod (*Gadus morhua*) has declined from a historical high stock size in the early 1980s to record low levels in the early 1990s as a result of adverse, climate-driven hydrographic conditions affecting reproductive success and overfishing, with no signs of recovery to date (Köster *et al.*, 2005). The reproductive success of the eastern Baltic cod stock is closely linked to hydrographic conditions in the deep Baltic basins (Bornholm and Gotland Basins, Gdańsk Deep). A minimum salinity of 11 psu is required for fertilization of eggs (Westin and Nissling, 1991) and is critical for attaining neutral buoyancy (Vallin and Nissling, 2000). Oxygen concentrations of at least 2 ml l⁻¹ are required for successful egg development (Wieland *et al.*, 1994). Since the mid-1980s, successful spawning has been generally restricted to the Bornholm Basin; the available depth strata with minimum conditions for egg development have declined, reaching their lowest point in 1989 (MacKenzie *et al.*, 2000). Hydrographic conditions allowing successful spawning depend on the frequency and magnitude of inflows of oxygen-rich, high-saline North Sea water, as well as on the temperature of the inflowing water, which influences oxygen solubility (Hinrichsen *et al.*, 2002a) and oxygen consumption rates by biological processes (MacKenzie *et al.*, 1996). Coupled biophysical model runs on drift and feeding indicate that Baltic larval cod change from a non-limited to a food-limited

stage, and reveal that retention and dispersion from the main spawning ground is a key influence on larval survival (Hinrichsen *et al.*, 2002b). When *Pseudocalanus acuspes* nauplii were available in the prey fields, cod survival was good in spring and early summer, if the larvae remained in the deep basins. In contrast, when *P. acuspes* nauplii were not available, hatched larvae had high survival probabilities only during dispersal periods later in the year, i.e. if they were transported into shallower coastal areas.

Although processes affecting developmental success of the egg and larval stages of eastern Baltic cod have been studied extensively and are understood rather well, this is not true for the juvenile stage, both in the demersal and especially in the pelagic phases (Bagge *et al.*, 1994). Processes during the pelagic and demersal juvenile stages of eastern Baltic cod represent a clear gap in available knowledge of the cod life cycle, resulting from the difficulty and cost of sampling juveniles during the pelagic stage because of broad dispersal and therefore low density. These sampling difficulties have hampered studies on the impact of variable food supply for pelagic and demersal juveniles on stock recruitment. Without a suitable settling habitat in a time frame that allows them to feed on larger, benthic organisms, juveniles might face starvation and possibly death during their first winter (Hüssy *et al.*, 1997). Sufficient benthic prey is found only in regions with relatively high oxygen concentration in bottom layers.

Hence, the spatial and temporal variability in oxygen concentration in bottom layers might affect the benthic food supply of demersal juvenile cod. Data-storage tags reveal that Baltic cod remain in less-oxygenated water masses (<40% oxygen saturation) for feeding purposes for only ~10% of their time (Neuenfeldt, pers. comm.). Laboratory experiments indicate that cod-settling habitat requires a minimum oxygen saturation of 40% (Chabot and Dutil, 1999). The residence times of the various water layers in the Baltic Sea, coupled with the sedimentation of organic matter from terrestrial sources and the surface euphotic layers, result in the accumulation of organic matter in the deep layer (Wulff *et al.*, 1990). The organic matter is degraded by bacteria, leading to the depletion of oxygen in the deep layers, and in periods of stagnation (between major inflows of oxygen-rich, saline waters from the North Sea; Matthäus and Franck, 1992), low oxygen concentrations limit the distribution of adult cod within this spawning habitat (Tomkiewicz *et al.*, 1998) as well as the survival of the offspring (Nissling *et al.*, 1994; Wieland *et al.*, 1994; MacKenzie, *et al.*, 2000).

Because traditional fishery management has largely failed to prevent overexploitation of the eastern Baltic cod stock effectively, a suite of different spatio-temporal fishing closures to protect the Baltic cod stock has been implemented to reduce fishing pressure on spawning individuals. The aim was to ensure undisturbed spawning and, as a consequence, enhancement of larval and juvenile production (Kraus *et al.*, 2009). However, as no signs of recovery have been observed yet, alternative closure, e.g. to protect juvenile cod, has been suggested.

Fishing closures might protect the juvenile cod population of this stock, e.g. from being caught in small-meshed sprat and herring fisheries, which operate in slope regions of the central basins and in shallow near-coast regions. However, as a prerequisite for establishing effective Marine Protected Areas (MPAs) for juvenile cod, the spatial and temporal dynamics of the juvenile cod distribution need to be resolved. Information on potential cod nursery areas may also be used to investigate and consider the impact of other anthropogenic activities on juvenile cod survival and overall stock dynamics, e.g. gravel extraction and offshore construction activity.

To investigate the drift of early life stages of Baltic cod with respect to variable atmospheric forcing conditions in space and time, Hinrichsen *et al.* (2003) calculated transport patterns, which allowed the identification of changes in the final destinations of juvenile cod, within and between spawning seasons. These transport patterns were obtained by the same hydrodynamic model being utilized to investigate the potential mixing of eggs and larvae between the western and the eastern Baltic cod stocks (Hinrichsen *et al.*, 2001). Besides theoretical identification of the Baltic cod nursery grounds, this study focuses on the description of the environment in which juveniles settle, i.e. where they change from pelagic to demersal life. Simulated sizes and locations of potential nursery areas have already been applied in a spatially explicit population model of eastern Baltic cod, used as a component of a fishery simulation model to design and evaluate spatial management measures (Kraus *et al.*, 2009).

Material and methods

Hydrodynamic circulation model

A comprehensive description of the hydrodynamic model and the Lagrangian particle-tracking technique was published by

Lehmann (1995). The hydrodynamic model used in this study is based on the free-surface Bryan–Cox–Semtner model (Killworth *et al.*, 1991). The model domain encompasses the entire Baltic Sea, including the Gulf of Bothnia, Gulf of Riga, the Belt Seas, the Kattegat, and the Skagerrak, with a realistic bottom topography. The horizontal resolution is 5 km, and 60 vertical levels were specified, with a thickness chosen that best represents the different sill depths in the Baltic Sea. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping). The data are provided on a 1°-by-1° grid (i.e. geostrophic wind, 2 m air temperature, 2 m relative humidity, surface pressure, cloudiness, and precipitation). River run-off was taken from a mean run-off database (Bergström and Carlsson, 1994). The model was run for a time-series of 26 years (1979–2004). Three-dimensional velocity fields, extracted from the circulation model, were used to predict the trajectories of passive Lagrangian drifters, using a fourth order Runge–Kutta scheme (Hinrichsen *et al.*, 1997), which allowed particles to be tracked independently from the resolution of the hydrodynamic circulation model. The positions of the drifter varied over time as a result of the three-dimensional velocities experienced. Furthermore, along the tracks, the temporal evolution of the corresponding bottom depths and the hydrographic property fields (temperature and salinity) were stored in 6-h intervals.

The particles are released within the historically important Baltic cod spawning grounds (Figure 1) as larvae. The larval drifter release areas represent the main spawning grounds, and altogether, 5150 Lagrangian drifters were released at depths between 25 and 35 m on a regularly spaced grid. Most feeding larvae are found after their initial ontogenetic vertical migration in this depth range (Grønkvær *et al.*, 1997), with weak diel vertical migration behaviour exhibited later. To consider seasonal variability in relation to spatial and temporal variations in larval transport, drifters, representing first-feeding larvae, were inserted into the modelled flowfields at 10-d intervals, between 1 April and 20 September, encompassing the historical as well as the current main spawning period of eastern Baltic cod (Wieland *et al.*, 2000).

Once the larvae reached the settlement age of ~70 d (Hüsey *et al.*, 2003), drift was stopped and larvae were assumed to settle at that position, regardless of the suitability of the substratum and other spatial characteristics (e.g. oxygen content, benthic food availability). The settlement probability was subsequently calculated with respect to habitat suitability. As demonstrated by a weight-over-length relationship for juvenile cod obtained from field-caught pelagic and demersal juvenile cod between 1993 and 1999, pelagic juveniles change to the demersal stage at a length of 5–15 cm (Figure 2). This range might cover a wider spread of ages of juveniles at settlement than the assumed settlement age of 70 d. Therefore, a potential settlement age of ~70 d is a simplified approach, but detailed knowledge of juvenile behaviour upon encountering unfavourable environmental oxygen while intending to settle is not available. Typically, adult cod have a minimum requirement of ~40% oxygen saturation for survival (Chabot and Dutil, 1999). As there is no specific information about oxygen tolerance or preference of eastern Baltic juvenile cod at the stage of settlement, it was assumed that the same threshold for oxygen saturation as described by Chabot and Dutil (1999) can be applied. However, most recent laboratory experiments on Atlantic cod have revealed that their level of activity (swimming, feeding, etc.) is proportional to dissolved

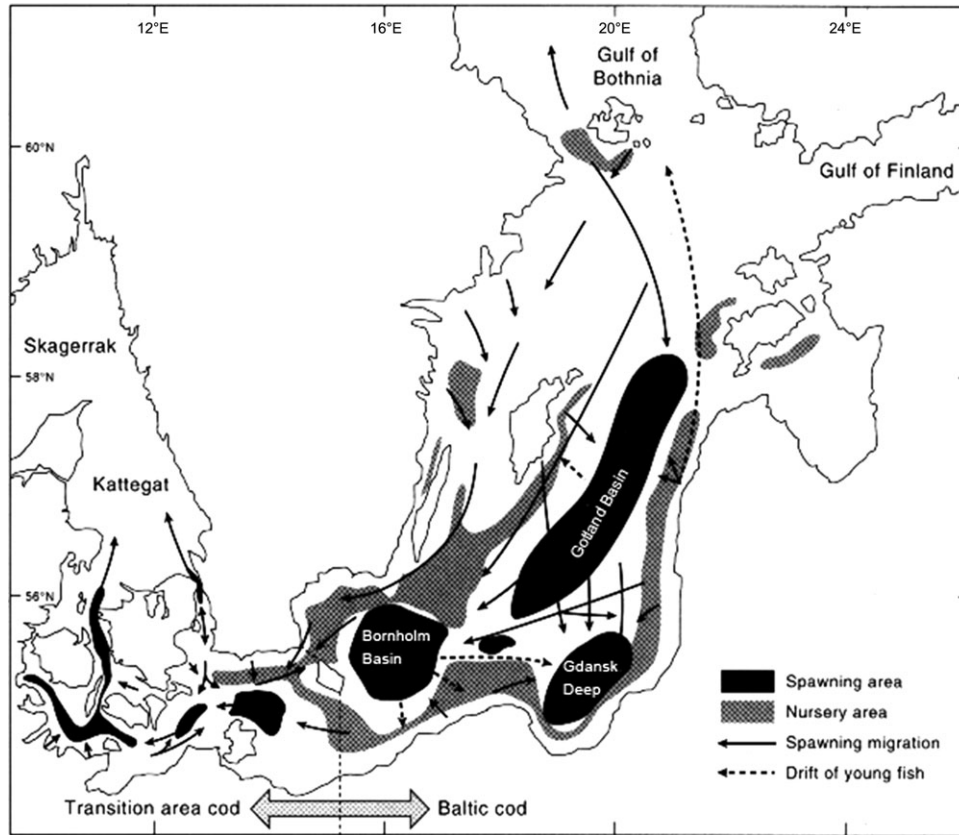


Figure 1. Baltic cod spawning and nursery areas and a schematic indication of spawning migration and larval/early juvenile drift, after Bagge *et al.* (1994).

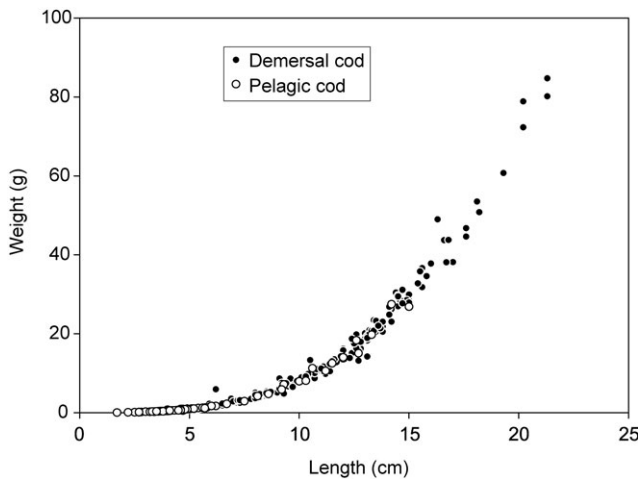


Figure 2. Weight–length relationship of Bornholm Basin field-caught pelagic and demersal juvenile cod (1993–1996); data from the Institute of Baltic Sea Fishery, Rostock, Germany.

oxygen, and becomes nil when oxygen saturation is $\sim 20\%$ (Chabot and Claireaux, 2008).

To obtain a proxy for the settlement habitat quality of juvenile cod in the different basins of the central Baltic Sea (Bornholm, Gdańsk, Gotland), we compiled monthly mean oxygen profiles from the International Council for the Exploration of the Sea (ICES) Oceanographic Database (<http://www.ices.dk/ocean>), containing two main datasets of depth-specific CTD and bottle

measurements. From the combined data, we selected all available oxygen concentrations between 1979 and 2004, within the major distribution area of the cod spawning stock.

The transport of Baltic cod larvae is primarily determined by windstress (Voss *et al.*, 1999). Windstress acting at the sea surface results in Ekman transport, but the surface currents are compensated for by a mainly topographically steered return flow in the interior of the basins (Krauß and Brüggge, 1991). This return flow is generally opposite in direction to the prevailing winds. To analyse the direct meteorological impacts on larval and juvenile transport, we related juvenile occurrence after the end of the simulated drift to the potential nursery areas in the central Baltic Sea to prevailing atmospheric conditions over the Baltic Sea during their drift. Relevant to the atmospheric forcing are the local meteorological conditions over the Baltic Sea, which are embedded in the large-scale atmospheric patterns. To characterize local forcing, Lehmann *et al.* (2002) defined a Baltic Sea index (BSI), which is the difference of normalized sea-level pressure anomalies between Oslo, Norway, and Szczecin, Poland. Daily mean sea-level pressures at each position obtained from the long-term meteorological NCEP/NCAR re-analysis data (Kalnay *et al.*, 1996) are normalized by dividing them by the long-term mean (1948–1999) standard deviation. For example, a positive BSI corresponds to an anomalous sea-level pressure difference associated with westerly winds over the Bornholm Basin. In near-surface layers, this results in transport towards the east. In contrast, a negative BSI corresponds to easterly winds, favouring currents towards the west near the sea surface.

Results

The long-term mean spatial distribution (1979–2004) of juvenile cod originating in the Bornholm spawning ground after 70 d of drift duration, represented by the drifter endpoints, is concentrated in the central part of the basin (Figure 3a). The Figure represents the relative abundances of drifter endpoints normalized by the abundance for the grid cell, yielding the maximum value. Most of the juveniles would have to settle in an unfavourable oxygen environment. Figure 3b represents the eastern Baltic cod nursery grounds for the same cohorts, when areas with <40% oxygen saturation for the juveniles are excluded. The spatial distribution of the drifter endpoints is based on the same larval cohorts, but the relative abundance of larval drifters has been normalized by the maximum abundance value obtained at reduced probability for successful settlement. Compared with Figure 3a, the environmental oxygen conditions at the bottom on average allow juveniles to settle at the edges of the basin where the halocline hits the bottom. The settlement probability in the deeper central parts of the basin is low and was only possible during inflow and post-

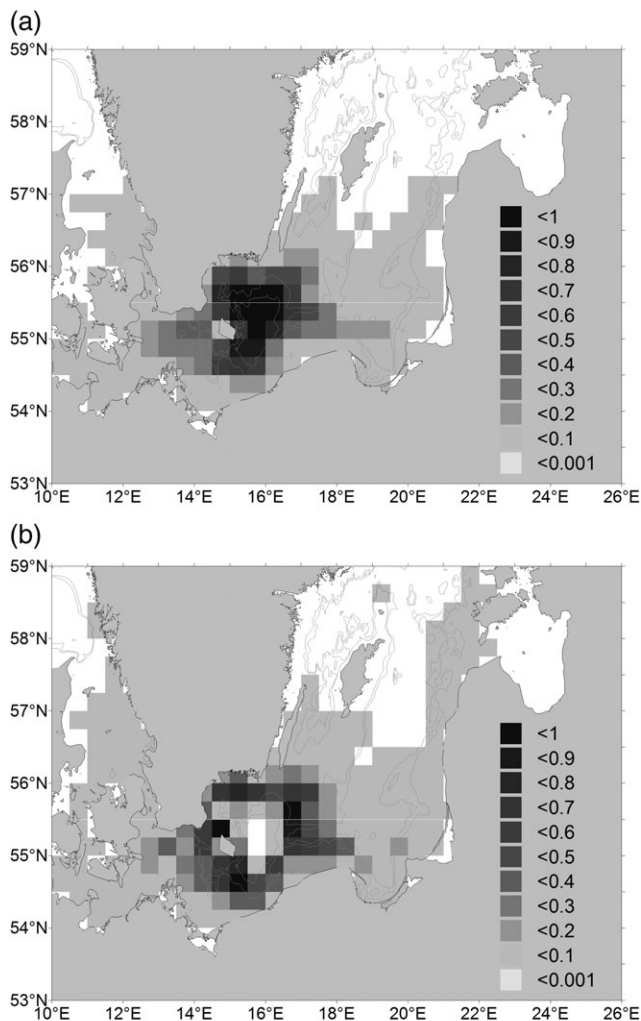


Figure 3. Mean final destination of larval/juvenile drifters, initially released in the Bornholm Basin for the period 1979–2004; (a) not accounting for minimum oxygen requirements of Baltic cod juveniles, and (b) accounting for minimum oxygen requirements of Baltic cod juveniles (lower panel).

inflow periods, when inflowing high-saline, well-oxygenated water masses from the North Sea and the western Baltic enlarged the suitable juvenile habitat size.

The overall changes in the transport towards potential nursery areas of juveniles initially released in the Bornholm Basin were clearly coupled with the local atmospheric conditions (Figure 4). The highest transport rates towards the southern as well as the eastern shallower water regions were related to strong easterly winds (BSI⁻). In contrast, northward transport was mainly caused by strong westerly winds (BSI⁺), although under these conditions, a significant portion of juveniles also drifted to southern shallow water areas. It is notable that high larval and juvenile transport rates towards the adjacent basins in the east were only possible by virtue of strong easterly winds.

The decadal variability (1979–1988 vs. 1989–1998) in potential nursery areas of juvenile Baltic cod originating in different spawning areas (Bornholm Basin, Gdańsk Deep, Gotland Basin) is shown in Figure 5. More drifters initially released in the Bornholm Basin were predicted to settle as juveniles within the basin in the 1980s than the 1990s (Figure 5a). On average, only a small number of larval drifters was transported eastwards out of the Bornholm Basin. Generally, potential nursery areas were located in the northern and southern shallower water regions

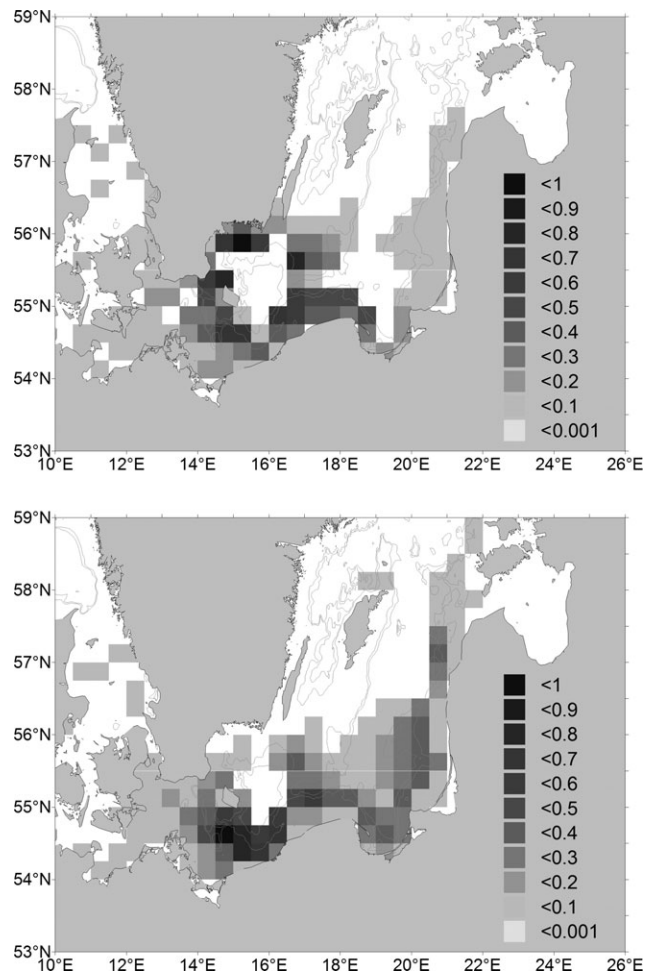


Figure 4. Wind-induced variability of potential nursery areas of Bornholm Basin spawners; upper panel: high BSI (high westerly winds); lower panel: low BSI (strong easterly winds).

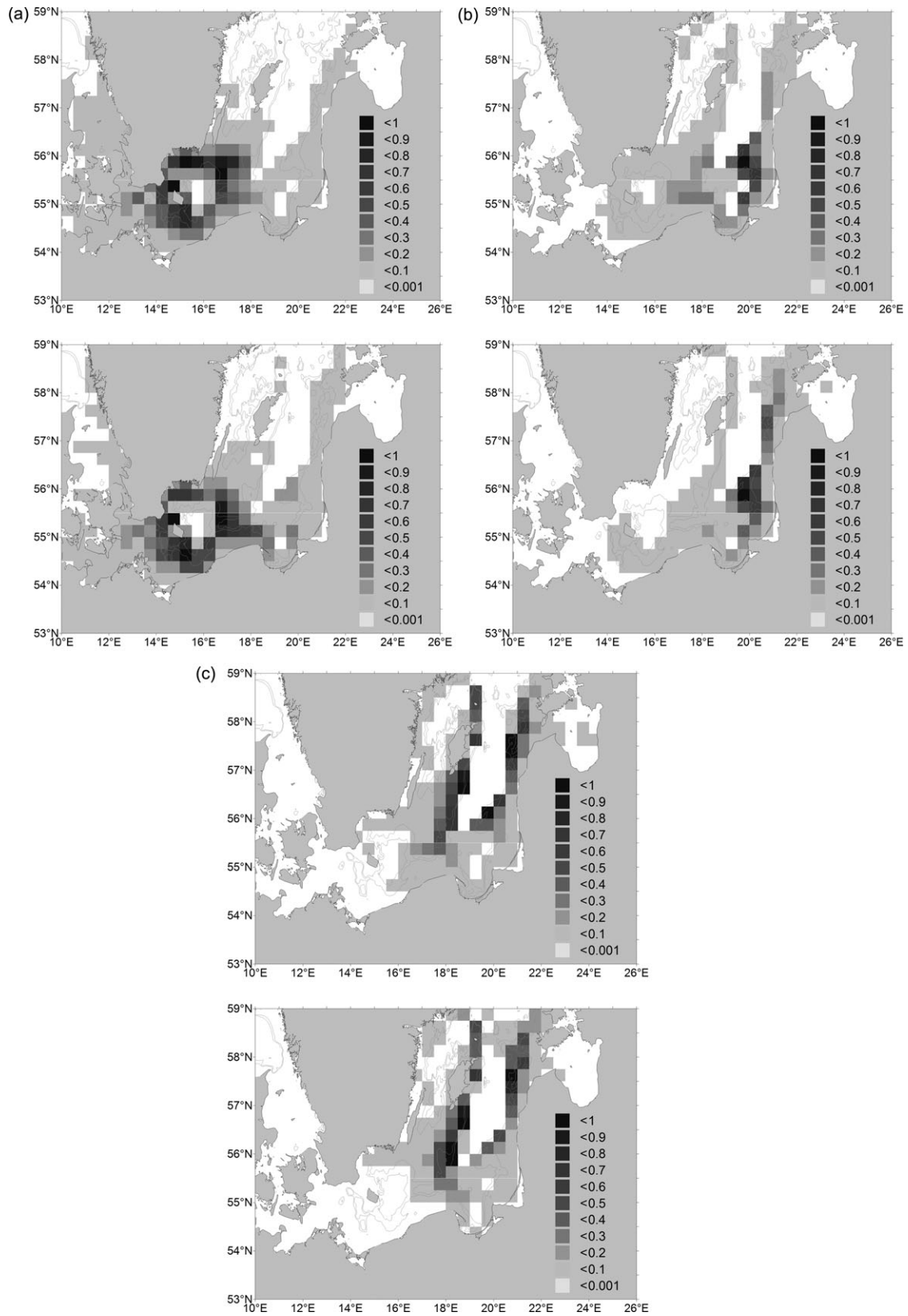


Figure 5. Decadal variability of potential nursery areas; upper panel: 1979–1988; lower panel: 1989–1998, for (a) Bornholm Basin spawners, (b) Gdańsk Deep spawners, and (c) Gotland Basin spawners.

around the Bornholm Basin. During the 1990s, there was evidence of stronger east- and southward transport than in the 1980s. This resulted in an increased probability of settlement of juveniles in the southern and eastern shallow water areas of the Gdańsk Deep and the Gotland Basin.

Generally, potential nursery areas for the drifters released to represent the Gdańsk Deep stock component were identified in the eastern part of the Gdańsk Deep and the southeastern Gotland Basin (Figure 5b). Areas predicted to have the highest average concentrations of settling juveniles were found along the Lithuanian and Latvian coasts. Increased northward transport along the east coasts during the 1990s was predicted to contribute considerably to the Gotland Basin population. Similar variations in the location of the potential nursery areas were not observed for the drifters representing Gotland Basin cohorts (Figure 5c). On average, nursery areas were located at both the western and eastern slopes of the basin, with indications of higher transport rates during 1990s than the 1980s.

The model runs provide estimates of the intra- and interannual variability of the number of individuals of a larval cohort that ended up in areas where they were able to settle successfully, based on variations in larval and juvenile drift. The seasonal averages of predicted successful settlers originating in different cod spawning grounds of the Baltic are shown in Figure 6. The highest settling probability (>50%) was predicted for the Bornholm Basin cohorts, whereas the settling probability of the Gotland Basin cohorts rarely exceeded 25%. The fate of drifters released to represent the Gdańsk Deep spawning area revealed the strongest variability. For all basins, simulations of early spawning generally yielded the highest successful settlement. Low wind-forcing during summer resulted in significantly fewer larval drifters being transported towards areas with suitable benthic habitat for settlement of juveniles. The drifters representing later spawned fish potentially contributed more to recruitment after

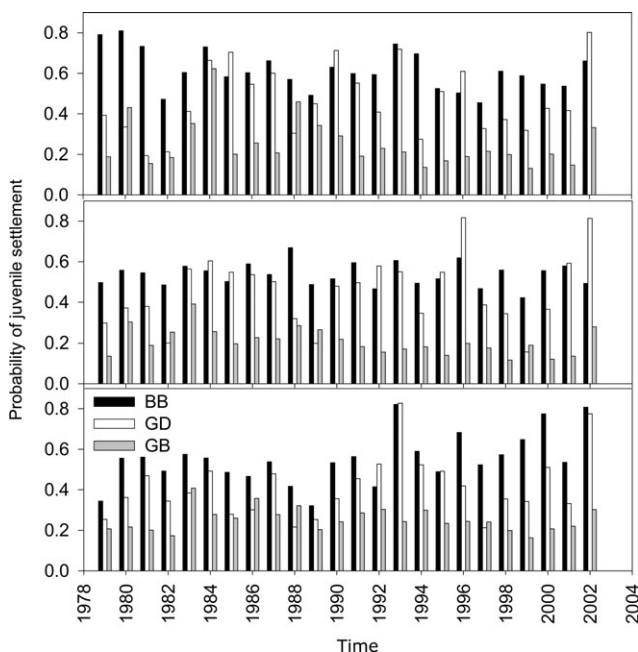


Figure 6. Time-series of simulated settlement probability of juvenile Baltic cod in potential nursery areas; upper panel, early; middle panel, summer; lower panel, late spawned cohorts; BB, Bornholm Basin; GD, Gdańsk Deep; GB, Gotland Basin.

the early 1990s, because the settling probability of Bornholm Basin and Gdańsk Deep spawners increased.

Discussion

In the present study, the transport of eastern Baltic cod larvae spawned within the historically important spawning grounds was investigated by detailed drift model simulations for the period 1979–2004. We analysed the spatial and temporal variability in the potential of juveniles to change from pelagic to suitable demersal habitat, i.e. where and when successful settlement is possible. Hence, the output of the simulations could be used to identify the potential eastern Baltic cod nursery grounds. Generally, the simulations confirmed the conceptual distributions of spawning and nursery areas as well as the drift patterns of larvae and juveniles (Figure 1) presented by Bagge *et al.* (1994). However, this schematic view could not explain any potential for variation in drift patterns and, perhaps most importantly, was not able to assign local nursery areas to different subpopulations spawning in the different deep basins of the Baltic Sea. The results of the drift scenarios demonstrated dependence of larval and juvenile drift on wind-induced current patterns, which were mainly controlled by the local atmospheric conditions over the Baltic Sea. The long-term drift simulations revealed decadal variability of the location of eastern Baltic cod nursery grounds. Until the early 2000s, the distribution of simulated juvenile cod locations was only partly consistent with observed distributions, because the catch rates of demersal juvenile cod in the Baltic international trawl survey during their first winter were normally too low to derive a general picture of the overall distribution pattern (CORE, 1998). However, a change in survey gear in 2001 may produce a time-series of age group 1 distribution from the first quarter survey, which can, in future, be used for a more detailed analysis. Pelagic juvenile cod caught by Isaacs–Kidd midwater trawl hauls (1993–1996), however, confirmed at least the modelled patterns for juveniles in the Bornholm Basin (Hinrichsen *et al.*, 2003). The distribution of simulated larval or juvenile cod locations was partly consistent with the observed distribution of juvenile cod. Few juveniles were caught by bottom trawls within the northern coastal environment and in the deep Bornholm Basin. Peaks in abundance of demersal juvenile cod encountered in the southern region from the beginning and the end of the spawning season confirmed the pattern obtained from drift modelling. This temporally resolved pattern agreed well with simulated distributions, predicting relatively high transport rates of larvae towards the southern coastal environment during the beginning and the end of the spawning season. On the other hand, the predicted appearance of juvenile cod along the north coast, resulting from drifters representing larvae hatched in summer, could not be validated by observations (Hinrichsen *et al.*, 2003).

In this modelling study, we examined the drift of virtual larval and juvenile cod released into simulated flowfields as first-feeding larvae. When studying living organisms, modelling exercises might be complicated by the individual behaviour of organisms. Therefore, a recurring point of criticism regarding these types of studies is the importance of swimming ability, especially as individuals grow over time. The onset of active movement can be used to demarcate the end of the period when individual-based drift models can be used reliably. Horizontal swimming is generally less important in the context of horizontal flow. Cod larvae, however, are actively able to change their vertical position in the water column, which might significantly alter their drift routes,

predominantly in wind-driven systems exhibiting a strong vertical current shear. Cod larvae do not appear to make large vertical movements, based on observations on the vertical distribution of larval cod in the Baltic (Grønckjær *et al.*, 1997).

In this modelling study, the larvae are seeded homogeneously on regular grids. It would be interesting to test the resulting distribution patterns if, for example, spatial variability in egg production, i.e. higher densities in central areas (Hinrichsen *et al.*, 2007), and larval survival, i.e. higher at basin slopes because of higher prey abundance (Hinrichsen *et al.*, 2002b), would be incorporated. Unfortunately, the latter could not be implemented in our modelling approach, because detailed spatially and temporally resolved information on egg production and larval survival are currently not available.

Finally, it is not yet clear how pelagic juveniles will behave when encountering low oxygen at the bottom while intending to settle. Will the juveniles simply continue to stay pelagic or will they move upslope to find more favourable oxygen concentrations? As a consequence, in our approach, we are only able to utilize simple behaviour: individual larval and juvenile fish will only conduct random, small-scale movements to catch prey, which does not have a significant influence on their overall drift patterns.

The results of our study have improved the understanding of the horizontal distribution of eastern Baltic cod early life stages in relation to environmental factors. This provided evidence that availability of suitable habitat for settling may be limited. However, as shown in the example for Bornholm Basin cohorts (Figure 3), potential settlement areas are concentrated in the central deep basin. Therefore, inflows of oxygen-rich, saline water masses from the North Sea lead not only to favourable spawning and favourable feeding conditions for early larvae (increase in *P. acuspes*), but in addition, probably facilitate better juvenile survival after settlement, as a result of more suitable habitat area size. Furthermore, the shift in spawning time from spring in the 1970–1980s to summer spawning today (Wieland *et al.*, 2000) could probably be linked to lower juvenile survival affecting year-class strength. On average, low windforcing in summer results in fewer juveniles settled in suitable habitat. It is generally questionable if there has been any juvenile production and successful settlement at all in the Gotland Basin and in the Gdańsk Deep in years with only less-favourable spawning conditions. Otherwise, for the last decade our study has demonstrated an increased potential for cod early life stages to drift from the Bornholm Basin into the Gdańsk Deep and the Gotland Basin to contribute there to the juvenile population.

The location of potential nursery areas in relation to fishing activities by small-meshed fisheries gives an indication of potential bycatches of juvenile cod in these fisheries. As a direct application, the results can be used to characterize the spatial and temporal variability of eastern Baltic cod settling habitats in light of implementing appropriate management measures to ensure survival of juveniles in high-density areas. However, the intra- and interannual variability in egg production and early life stage survival (Köster *et al.* 2005), as well as in the distribution pattern of cod juveniles driven by environmental variability makes it difficult to define such measures in the different Baltic basins.

Independently of the specific results obtained for eastern Baltic cod, the study demonstrates that hydrodynamic models provide an effective tool to account for the passive movements of early life stages of this species. Hence, they may also be helpful to respond dynamically to the establishment of spatially varying MPAs in relation to changes in transport patterns.

Despite the identified intra- and interannual variability in transport pattern, it is possible to identify overlapping areas of juvenile cod and high effort of small-meshed fisheries targeting sprat and herring, for example, in the southern shallow areas of the Baltic Sea, e.g. around Rügen. Systematic sampling of cod bycatch rates in the Rügen herring fishery were implemented recently, but the data have not been completely analysed yet.

In future, the presented methodology may be applied to the deployment of information on juvenile densities in monitoring programmes. This can be done by coupling larval and pelagic juvenile cod “online” transport patterns obtained from operationally running hydrodynamic models to simultaneous sample analyses on bycatch rates of juveniles in small-meshed fisheries within the predicted cod nursery areas.

Our modelling approach is quite simplistic and should be seen as a baseline exercise to be followed by more detailed and comprehensive investigation. On the other hand, an easier parameterization of transport processes potentially responsible for the location of the nursery grounds would be desirable. Potential Baltic cod nursery areas may be identified from simplified but online accessible physical forcing parameters, e.g. the BSI (Hinrichsen *et al.*, 2003).

Finally, as a starting point, the information on mean locations of potential eastern Baltic cod nursery grounds obtained from the model simulations provided by our study has already served as input to close the cod life cycle in a spatial population model of eastern Baltic cod within the ISIS-Fish fishery simulation tool (Kraus *et al.*, 2009). ISIS-Fish aims at assessing the impacts of spatial management measures on resources and fisheries (Pelletier *et al.*, 2005). In its present version, only the fleet dynamics of the Baltic cod fishery are mimicked in the model. Once a reliable parameterization of the different fishing fleets operating in the Baltic Sea becomes available, a comprehensive evaluation of different cod nursery area scenarios and interactions with the different fisheries will be possible with that model.

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