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Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics

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To disentangle the effects of different drivers on recruitment variability of marine fish, a spatially and temporally explicit understanding of both the spawning stock size and the early life stage dynamics is required. The objectives of this study are to assess the transport of western Baltic cod early life stages as well as the variability in environmentally-mediated survival along drift routes in relation to both spatial (within and between different spawning areas) and temporal (interannual and seasonal) dynamics. A spatially and temporally highly-resolved biophysical model of the Baltic Sea was used to describe mortalities and survival success of eggs and yolk-sac larvae—represented by individual, virtual drifters—as predicted proportions of drifters that either died due to bottom contact or lethal temperatures, or that survived up to the end of the yolk-sac larval stage. The environmental conditions allowing survival of cod and yolk-sac larvae indicate that favourable conditions predominately occurred during the late spawning season, while minimum survival rates could be expected from January to March. The spatial analysis of different spawning areas revealed highest survival chances in the Kattegat, intermediate survival in the Great Belt, and only low survival in the Sound, Kiel Bay and Mecklenburg Bay.

Keywords: advective transport, biophysical model, cod eggs, dispersal, *Gadus morhua*, mortality, recruitment, retention, yolk-sac larvae.

Introduction

Recruitment variability of marine fish requires a spatially and temporally explicit understanding of both the spawning stock size and the early life stage dynamics. Hence, the development of environmentally-mediated mortality and survival success of early life stages of fish stocks has to be analysed.

In the area under consideration (Figure 1), cod spawning takes place in the deeper, saline waters of the Kattegat, the Sound, the Little and Great Belt, the Kiel Bay, the Fehmarn Belt, and to a limited degree in the Mecklenburg Bay (Vitale *et al.*, 2008; Bleil *et al.*, 2009). The timing of spawning (including peak spawning) is progressively directed from early spawning in the north to later spawning in the south (Bleil and Oeberst, 1997; Bleil *et al.*, 2009) and may last up to 6–7 months, while peak spawning is limited to March and April (Thurow, 1970; Bleil and Oeberst, 1997, 2004; Vitale *et al.*, 2008; Bleil *et al.*, 2009). Environmental factors affect an area's suitability as a spawning area through their power to limit fertilization of eggs as well as development and survival of early life stages. In the hydrographically very dynamic western Baltic Sea, the impact of environmental factors results in strong seasonal and interannual variability in suitable cod spawning habitat size (Hüssy *et al.*, this issue). Hussy *et al.* (this issue) showed the impact of spawning habitat suitability on recruitment to be surprisingly limited, suggesting that other processes during the early life stages are bottlenecks for their survival.

Eggs, and probably also yolk-sac larvae, are particularly vulnerable due to their non-existent, or at least very limited, ability to avoid water masses with adverse conditions.

Previous studies separated cod juveniles caught during trawl surveys in the more eastern Baltic (Arkona and Bornholm Basin) into origins from the western and eastern stock, based on their different total body lengths (Bleil and Oeberst, 1997), as well as on

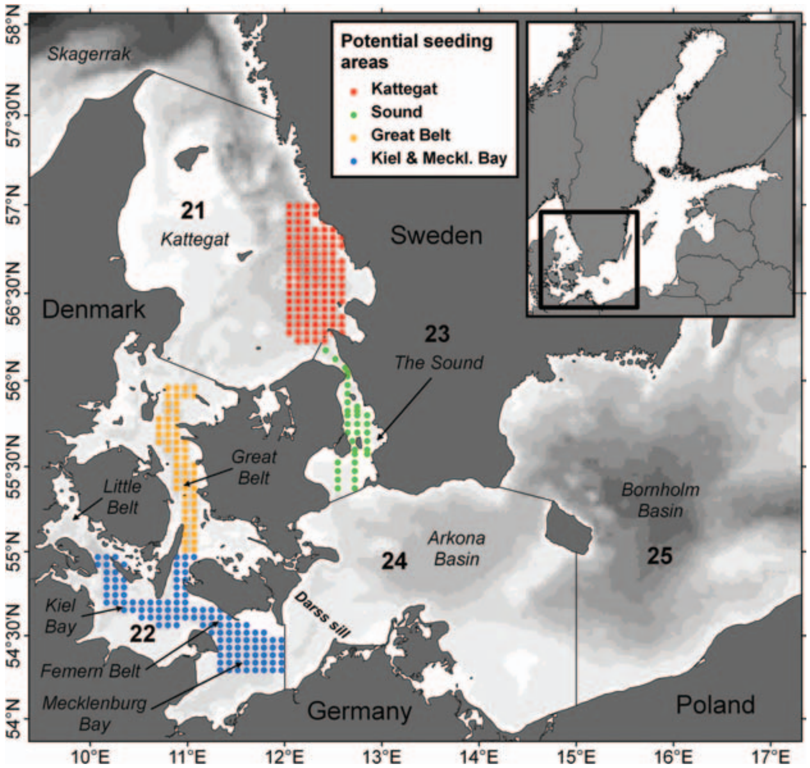

Figure 1. Study area of western Baltic cod: Coloured dots represent areas of historical spawning activity and grid of cod egg drifter release positions in the Kattegat, the Sound, the Great Belt, and the western Baltic, numbers indicate ICES-subdivisions.

their different spawning dates derived from otolith age readings (Hinrichsen *et al.*, 2001). There were several different reasons given as to why juveniles of the two different stocks were found in the eastern Baltic Sea. First, but presently non-verified, adult cod of the western stock in spawning condition may have actively migrated eastwards and their offspring remained in these nursery areas. This is not very likely as spawning cod were never caught during trawl fishing carried out between February and April in the eastern Baltic Sea (Bleil and Oeberst, 1997). Second, eastward directed water mass transport suggests the probability of an advective exchange of early life stages of the western stock towards the deep eastern basins of the Baltic Sea (Hinrichsen *et al.*, 2001).

The Belt Sea, as part of the western Baltic, is the transition area between the Kattegat and the Arkona Basin as well as the Bornholm Basin to the east (Figure1). The Belt Sea consists of the Sound, the Little and Great Belt as well as the Kiel Bay, the Fehmarn Belt and the Mecklenburg Bay region. This area is of fundamental importance for water mass exchange and hence for the transport and exchange of e.g. planktonic organisms, including fish eggs and larvae, between the Skagerrak/Kattegat area and the central Baltic Sea (Figure 1). This region includes the Darss Sill which is one of the shallowest obstacles the water masses and particles have to pass in order to enter the central Baltic (Fennel and Sturm, 1992). The Darss Sill (18 m deep) separates the easterly Belt Sea from the Arkona Basin, an area with maximum depths of about 45 m. The Kattegat is a shallow area with a mean depth of only 23 m, which is directly connected to the Skagerrak. In the upper layers, the water mass distribution is strongly affected by water masses of Baltic origin. The Belt Sea is on average 13 m deep. However, there are deep and narrow channels in this area, e.g. the Great Belt and the Fehmarnbelt, through which most of the water mass exchange and planktonic organisms transport occurs between the Kattegat and the Arkona Basin (Fennel and Sturm, 1992; Schincke and Matthäus, 1998). Another connection between the Kattegat and the Arkona Basin is the Sound. As it contains two sills east of Copenhagen with depths of only about 8 m, usually only a minor part of the exchange is happening through this area. A third connection between the Kattegat and the Arkona Basin is the Little Belt, which is situated between Jutland and the island of Fyn. Because of its small cross section, this channel only plays a minor role for water mass exchange and transport processes.

The water balance of the Baltic Sea is controlled by in- and outflows through the Belt Sea, river runoff and net precipitation (Lehmann *et al.*, 2002). River runoff and precipitation are causing a freshwater surplus, which forces a general outflow of brackish Baltic Sea water in the upper layer that may be compensated by deep inflows of saline water from the Kattegat. Dietrich (1951) relates the surface currents in the Belt Sea to the local wind conditions.

Baltic inflows are mainly caused by persistent, i.e. of a longer-term duration, strong westerly winds over the eastern North Atlantic and northern Europe (Schinke and Matthäus, 1998). For the long-term mean, it is reasonable to assume that the volume change of the Baltic is zero, and the freshwater surplus is balanced by the outflow. Thus, the highly fluctuating in- and outflow is forced by the sea level inclination between the Kattegat and the western Baltic Sea, and is mainly responsible for the volume change on a weekly timescale (Lehmann *et al.*, 2002). A review of the current knowledge of the dynamics of the water exchange between the Baltic Sea and the North Sea has been given by Gustafsson (1997).

Management and conservation efforts could benefit from considering explicitly how environmental factors influence the survival success of early life stages and the connectivity of fish stocks. In the past, attempts have been made to analyse how bio-physical modelling can support management efforts in protecting and rebuilding fish stocks (Hinrichsen *et al.*, 2011). Hinrichsen *et al.* (2001) already used hydrodynamic modelling approaches to evaluate possible impacts of different atmospheric conditions on western Baltic egg and larval spatial distribution patterns within and between spawning seasons. Two years with different atmospheric situations (inflow vs. stagnation) were selected. The major focus of Hinrichsen *et al.* 2001 was on the transport potential of passively drifting early live stages of western Baltic cod and their ability to contribute to the eastern areas of the Baltic Sea, especially the Arkona Sea and the Bornholm Basin.

The present study is based on such a modelling approach, aiming to examine the spatial (within and between different spawning areas) and temporal (seasonal and interannual) variability in the survival of western Baltic cod eggs and yolk-sac larvae in relation to the ambient hydrography and the hydrodynamics of the main spawning areas. In particular, the objectives of this study are to perform long-term assessments of (i) the transport of western Baltic cod early life stages from spawning to hatching areas and their survival success along drift routes, (ii) the retention and dispersal of early life stages originating from different spawning grounds, (iii) the contribution of different spawning grounds for early life stage survival in relation to the variability in environmental conditions, and (iv) the impact of the timing of spawning on early life stage survival.

Material and Methods

The approach used in this study was based on a hydrodynamic model, coupled with an Individual Based Model (IBM) considering western Baltic cod egg stages as well as the yolk-sac larval stage. The model was used to provide predictions of the survival success of proportions of eggs and yolk-sac larvae, characterized by losses due to bottom contact or by ambient water temperatures falling below a critical survival threshold. In order to calculate the temperature-dependent stage-specific developmental times for western Baltic cod eggs and yolk-sac larvae, a functional relationship established by Petereit (2004) was utilized.

Hydrodynamic model

The hydrodynamic model is based on the free surface Bryan-Cox-Semtner model (Killworth *et al.*, 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and modifications made in order to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). A detailed analysis of Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b), and by Lehmann *et al.* (2002). The model domain comprises the entire Baltic Sea. The horizontal resolution is 5 km, with 60 vertical levels specified. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a monthly mean runoff database (Bergström and Carlsson, 1994). Prognostic variables of the model are the baroclinic current field, the three-dimensional temperature, salinity and oxygen distributions, the two-dimensional surface elevations and the barotropic transport, all of them available at six-hourly intervals. Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen *et al.*, 1997; Lehmann and Hinrichsen, 2000a).

Individual Based Model

This IBM tracks individuals through the different life stages. Along the drift trajectories within the coupled model, the temporal development of eggs and yolk-sac larvae depended on ambient temperatures, while their survival success until the end of the yolk-sac stage depended on a threshold value in ambient temperature (>2°C) and on contact with the sea floor. Developmental times of egg and yolk-sac larvae stages are based on relationships for Baltic cod provided by Petereit (2004).

Drifter release locations

In order to consider the seasonal variability of the spawning environment in relation to its spatial and temporal variability, locations were extracted at the hydrodynamic model 5 × 5 km grid within the well-known spawning areas. Based on threshold values for egg buoyancy from von Westernhagen (1970), suitable spawning habitat was defined as the water body exhibiting salinities between 18 and 33 psu, temperatures >2°C and oxygen concentrations >2 ml/l. This revealed a broad range of neutral buoyancy levels (18–33 psu) at which western Baltic cod eggs and yolk-sac larvae can float. These locations were taken for the initial releases of the drifting particles representing newly spawned and fertilized cod eggs. In the vertical domain, particles were released at 1-psu intervals, where the required salinities between 18 and 33 psu were available. Initial release locations fulfilling these requirements were extracted from a time series of simulated hydrographic data lasting from 1979–2005. The maximal possible aggregated suitable habitat size for spawning is represented by 5424 particles (Hüssy et al., this issue). Based on the duration of the spawning season from December to May, particles were seeded at the centre of the grid cells every 10 days from December 1 to May 30, resulting in 19 different release dates throughout each spawning season, corresponding to the "spawning dates" in Hüssy *et al.* (this issue). A total of 494 (26 years × 19 release dates) drift model runs were performed. The seeding positions were located in the four sub-regions representing the main spawning areas, i.e. the Kattegat, the Sound, the Great Belt, the Little Belt, Kiel Bay, Fehmarn Belt and Mecklenburg Bay (Figure 1). A detailed evaluation of seasonal and interannual patterns for possible release locations is given by Hüssy *et al.* (this issue).

Particle tracking and model scenarios

Simulated three-dimensional velocity fields were extracted (at 1 h intervals) from the hydrodynamic model in order to develop a database for particle tracking. This dataset offers the possibility of deriving Lagrangian drift routes by calculating the advection of "marked" water particles. Based on the egg buoyancy measurements performed by von Westernhagen (1970), for their whole drift periods the particles did not change the buoyancy (density) levels at which they initially were launched. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen *et al.*, 1997). Particles representing cod eggs at developmental egg stage Ia were released into the simulated flow fields and tracked through the different egg stages as well as the yolk-sac larval stage. During their drift, eggs and yolk-sac larvae floated at the initially-assigned density levels, but died due to bottom contact if their initially-assigned density levels were found to be higher than those available at the bottom along the positions of the drift route, or due to lethal temperature conditions (<2°C). For individuals that died during the simulations, the positions where the death occurred were recorded, while for the surviving individuals the final positions reached at the end of the yolk-sac stage were recorded.

Duration of the egg and yolk-sac larval drift depended on temperatures provided by the hydrodynamic model. For each of the one-hourly time steps of the drift model, these temperatures were recorded to calculate the corresponding temperature-dependent development times from stage Ia eggs to first-feeding larvae (Petereit, 2004) along the drift paths of each individual egg/larva. The simulations were stopped when yolk-sac larvae started to become first feeding larvae (mouth opening).

Baltic Sea Index (BSI)

To analyse the effect of wind forcing conditions over the Baltic Sea on survival of early life stages, the Baltic Sea Index (BSI) (Hinrichsen *et al.*, 2001; Lehmann *et al.*, 2002) was used, which represents the normalized sea level pressure differences between Oslo (Norway) and Szczecin (Poland) as proxy for the general wind forcing conditions. The BSI is available at 3-hourly intervals. Generally, for this study the BSI was forward-averaged over 15-day periods (i) to present a mean of the developmental time from first egg to the yolk-sac larval stage, and (ii) to provide a first approximation of wind-induced transport measures for the whole coverage of western Baltic cod spawning events (December to May). Furthermore, these averages might be an opportunity for a better inter-comparison of environmental influences on western Baltic cod early life stage survival rates. Positive indices correspond to anomalous sea level pressures associated with westerly winds, whereas negative values indicate predominately easterly winds over the Baltic Sea.

Results

For drifters initially released in the spawning areas of western Baltic cod, the relative survival probability of cod eggs until the end of the yolk-sac stage clearly shows highest values at the end of the spawning period (Figure 2a, release dates March 31 to May 30). Egg releases in December (release dates December 1 to December 31) showed highly variable survival rates. Lowest survival was observed for release events from January to the beginning of March. This corresponds to time periods which were mainly characterized by high proportions of eggs dying due to bottom contact (Figure 2b). Relatively low survival rates during the spawning periods 1979/80 to 1986/1987 were attributable to temperature-related mortality due to extremely cold water temperatures during severe winters (Figure 2c), and were only to a minor degree related to bottom contact. During the yolk-sac stage, larval mortality due to bottom contact appeared to be much lower (0–20%) compared to the egg stages and revealed no significant time trend (Figure 2d).

The interannually averaged BSI, indicating wind-induced particle transport towards suitable or unsuitable habitats for the survival of eggs and yolk-sac larvae, was found to be significantly and negatively correlated to the interannually averaged survival rates of the yolk-sac larval stage. This correlation was obtained for the combination of all four spawning grounds ($r^2 = 0.67$). For survivors initially released as drifters in the Kattegat, the BSI explains 66%, for the Sound 59%, the Great Belt 58%, and the western Baltic 41% of the variability. Generally, the relationships indicated

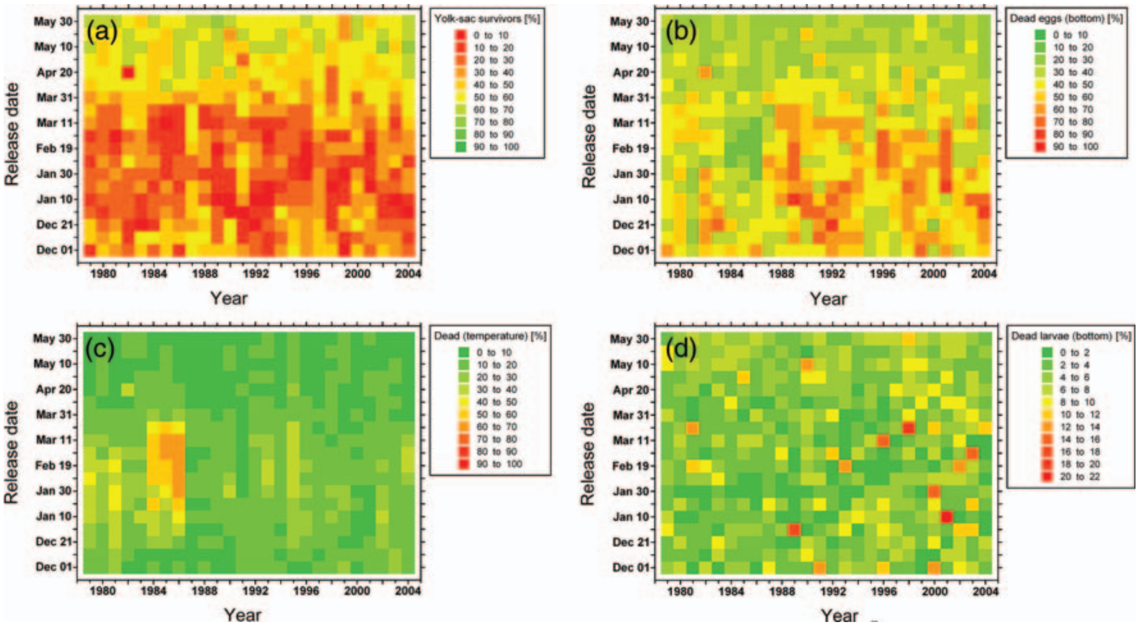

Figure 2. Long-term development of western Baltic cod early life stages: a) mean relative cohort survival probability from egg stage IA to the end of the yolk-sac stage, b) mean relative cohort mortality probability of cod eggs due to bottom contact, c) mean cohort temperature-related mortality probability, and d) mean relative cohort mortality probability of the larval yolk-sac stage due to bottom contact.

that differences in sea level pressure associated with westerly winds lead to relatively low survival rates, while negative BSIs, representing easterly winds, are more beneficial for survival.

For drifters initially released in the Kattegat area, horizontal distribution maps of mean end positions clearly showed high concentrations of bottom- and temperature-related dead eggs and dead yolk-sac larvae in the vicinity of the release area (Figure 3a–c). In contrast, the surviving fraction of the released particles was transported to areas north of the spawning site, with particles released during the early and mid spawning season being more widely dispersed than those released during the late spawning season (Figure 3d). The dead egg and larval fraction (only low buoyancy levels) of the Sound spawners on average peaked in their corresponding spawning area (Figure 4a, b), while a relatively high proportion of eggs which died due to unfavourable temperature conditions finally ended up in the southern Kattegat (Figure 4c). As for the Kattegat population, most of the surviving yolk-sac larvae were widely distributed over the whole Kattegat area, with particles released during the early and mid spawning season also more widely dispersed than those released during the late spawning season (Figure 4d). The non-surviving parts of the Great Belt stock component were located in the close vicinity of the initial spawning area (Figure 5a–c). The major part of the surviving fraction of the late spawners was retained close to the spawning area (Figure 5d), although some cohorts, mainly spawned early or in the middle of the spawning period, were advected towards the Kattegat region. The highest connectivity of the stock components was found for the most southern subpopulation (Kiel Bay, Fehmarn Belt and Mecklenburg Bay). All sources of mortality predominately acted south of 55°N (Figure 6a–c) and only a minor fraction of the survivors were transported into the southern part of the Kattegat (Figure 6d).

The average relative probabilities of successful particle releases according to the ambient hydrographic conditions (see Hüssy *et al.*, this issue), the relative mortalities of eggs and larvae due to bottom contact and temperature, as well as the relative probabilities of survival until the yolk-sac larval stage of western Baltic cod, are shown in Table 1. The average probabilities of habitat suitability at spawning (particle release) as well as survival until the end of the yolk-sac larval stage decreased from the north (Kattegat) to the south (Kiel and Mecklenburg Bay). Egg mortality due to bottom contact was observed to lie within the range of 0.17

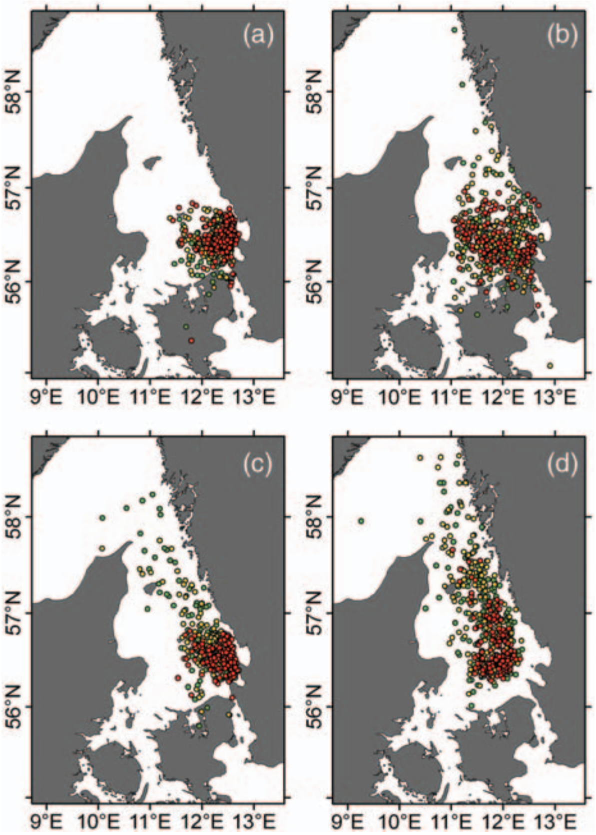

Figure 3. Kattegat cod early life stage mortality/survival during drift phase: drifter end points of a) mean cohort mortality due to bottom contact,b) mean cohort temperature-related egg mortality, c) mean cohort mortality of yolk-sac larvae due to bottom contact, and d) mean cohort survival of eggs from stage IA to the end of the larval yolk-sac stage. Green dots – early spawning period: release dates Dec 01 to Jan 20; yellow dots – middle of spawning period: release dates Jan 30 to Mar 30; and red dots –late spawning period: release dates Apr 10 to May 30.

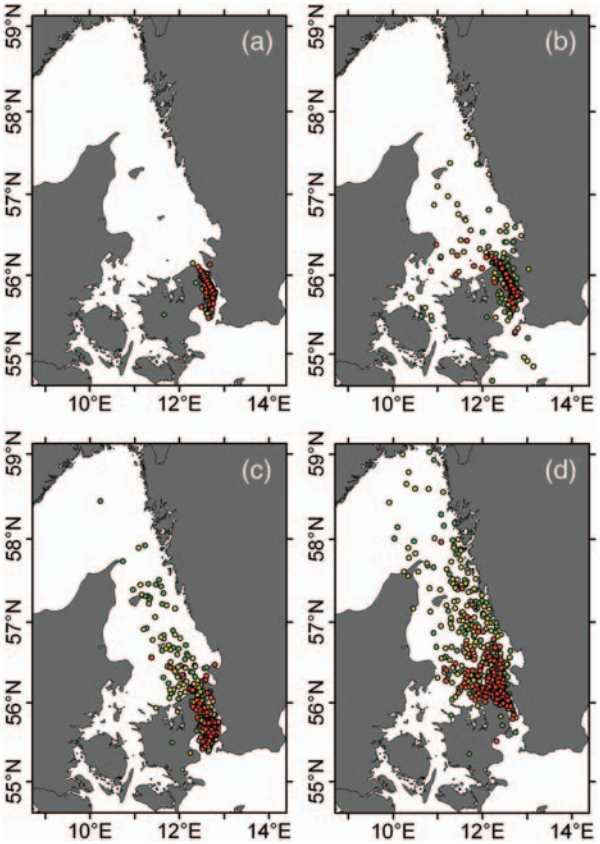

Figure 4. Sound cod early life stage mortality/survival during drift phase: drifter end points of a) mean cohort mortality due to bottom contact, b) mean cohort temperature-related egg mortality, c) mean cohort mortality of yolk-sac larvae due to bottom contact, and d) mean cohort survival of eggs from stage IA to the end of the larval yolk-sac stage. Green dots – early spawning period: release dates Dec 01 to Jan 20; yellow dots – middle of spawning period: release dates Jan 30 to Mar 30; and red dots –late spawning period: release dates Apr 10 to May 30.

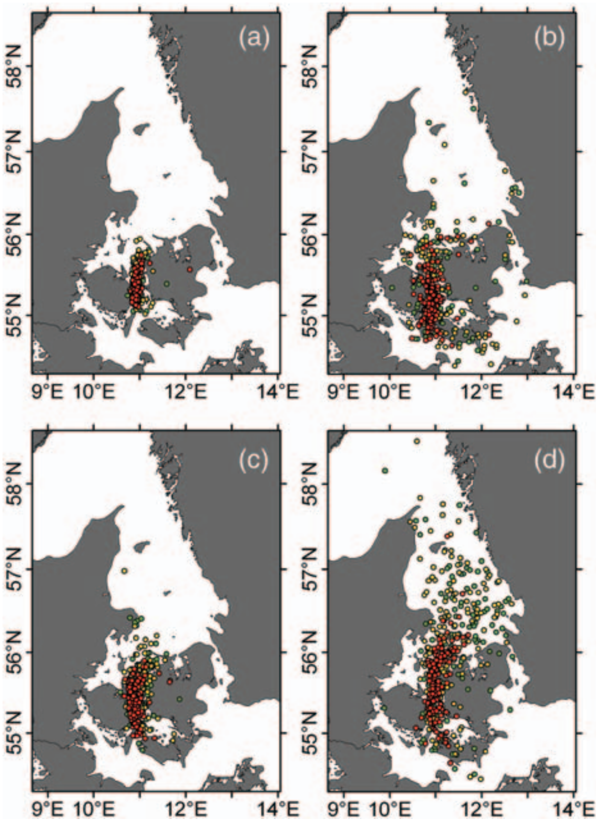

Figure 5. Great Belt cod early life stage mortality/survival during drift phase: drifter end points of a) mean cohort mortality due to bottom contact, b) mean cohort temperature-related egg mortality, c) mean cohort mortality of yolk-sac larvae due to bottom contact, and d) mean cohort survival of eggs from stage IA to the end of the larval yolk-sac stage. Green dots – early spawning period: release dates Dec 01 to Jan 20; yellow dots – middle of spawning period: release dates Jan 30 to Mar 30; and red dots – late spawning period: release dates Apr 10 to May 30.

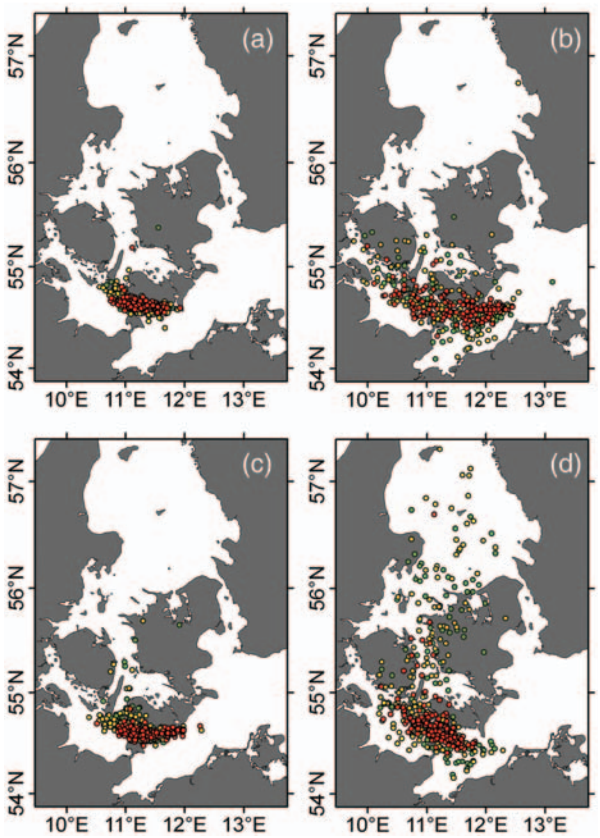

Figure 6. Kiel Bay and Mecklenburg Bay cod early life stage mortality/survival during drift phase: drifter end points of a) mean cohort mortality due to bottom contact, b) mean cohort temperature-related egg mortality, c) mean cohort mortality of yolk-sac larvae due to bottom contact, and d) mean cohort survival of eggs from stage IA to the end of the larval yolk-sac stage. Green dots – early spawning period: release dates Dec 01 to Jan 20; yellow dots – middle of spawning period: release dates Jan 30 to Mar 30; and red dots – late spawning period: release dates Apr 10 to May 30.

to 0.32, and mortality due to temperature from 0.04 to 0.11. Larval mortality due to bottom contact played only a very minor role (0.02 to 0.04). For most of the areas, the means of the estimated parameters revealed strong standard deviations.

Relative probabilities are also presented for retention of survivors within the release areas, dispersal of survivors between areas, as well as total losses of survivors out of the investigated areas (Table 2). The model runs indicated only a low probability of the survivors being retained in the investigated area. Highest retention was observed for the Kiel and Mecklenburg Bay area. Highest exchange rates between subareas were obtained between the Sound and the Kattegat, and between the Great Belt and the Kiel and Mecklenburg Bay. However, due to strong intraannual and interannual variations in wind forcing conditions over the western Baltic area, all these patterns appear to be completely unstable over time.

Discussion

In the present study, the development and the environmentally-mediated mortality and survival success of western Baltic cod eggs and yolk-sac larvae spawned within their historically important spawning grounds was investigated by detailed biophysical model simulations for the period 1979–2005. The processes affecting mortality or survival of western Baltic cod eggs and yolk-sac larvae were predominantly buoyancy, ambient temperatures and transport of early life stages towards suitable or unsuitable habitats. We analysed the influence of variations in the above-mentioned forcing mechanisms on cod egg and yolk-sac larval mortality or survival.

Variability in ocean circulation results in spatio-temporal differences of transport patterns of fish early life stages, which may have consequences for their survival and hence recruitment. Retention or dispersion during their development from early egg stage Ia until the end of the yolk-sac larval stage has been identified as one of the key processes determining the survival of western Baltic cod early life stages. In the western Baltic Sea, the highly dynamic hydrographic conditions result in a complex environmental scenario, which limits the survival success of cod early life stages.

Generally, mortality of the eggs and yolk-sac larvae result to a limited degree from exposure to low temperature regimes, but predominately from transport into areas, where buoyancy levels are not sufficient to avoid mortality of individual eggs and yolk-sac larvae due to contact with the bottom.

Table 1. Relative probabilities (mean + standard deviation) of (1) successful release according to hydrography (see Hüssy *et al.*, this issue), (2–4) mortality of eggs and larvae due to bottom contact and temperature, and (5) survival to the yolk-sac larval stage of western Baltic cod.

Category	Kattegat	Sound	Great Belt	K. & M. Bay	Total
Released eggs	0.79 ± 0.16	0.36 ± 0.08	0.57 ± 0.29	0.35 ± 0.18	0.54 ± 0.17
Dead eggs (bottom)	0.17 ± 0.11	0.22 ± 0.08	0.32 ± 0.16	0.21 ± 0.11	0.22 ± 0.08
Dead (temperature)	0.11 ± 0.11	0.04 ± 0.05	0.09 ± 0.09	0.07 ± 0.06	0.08 ± 0.07
Dead larvae (bottom)	0.04 ± 0.03	0.02 ± 0.02	0.02 ± 0.03	0.02 ± 0.02	0.02 ± 0.02
Yolk-sac survivors	0.48 ± 0.25	0.08 ± 0.08	0.15 ± 0.17	0.05 ± 0.07	0.21 ± 0.13

K. & M. Bay = Kiel & Mecklenburg Bay

Table 2. Relative probabilities (mean ± standard deviation) for retention of surviving yolk-sac larvae within the release areas (bold values on diagonal from upper left to lower right), dispersal of survivors between areas (above and below bold values on diagonal) as well as total loss of survivors out of the investigated areas.

Release area	Destination Kattegat	Destination Sound	Destination Great Belt	Destination K. & M. Bay	Loss
Kattegat	**0.26 ± 0.16**	0.02 ± 0.03	0.01 ± 0.03	0.00 ± 0.00	0.70 ± 0.17
Sound	0.21 ± 0.27	**0.23 ± 0.30**	0.01 ± 0.04	0.00 ± 0.01	0.45 ± 0.35
Great Belt	0.08 ± 0.19	0.01 ± 0.07	**0.26 ± 0.26**	0.13 ± 0.20	0.42 ± 0.33
K. & M. Bay	0.02 ± 0.09	0.00 ± 0.03	0.07 ± 0.16	**0.40 ± 0.32**	0.31 ± 0.28

K. & M. Bay – Kiel & Mecklenburg Bay

This study indicated the importance of timing of cod spawning associated with high sea level pressure (low BSI) over the Baltic Sea for the survival success of western Baltic cod up to the yolk-sac larval stage. Drift patterns and survival success differed over the spawning season. Lower ambient temperatures and the correspondingly longer developmental times of eggs and yolk-sac larvae during early and mid spawning season were associated with longer drift durations, larger drift distances and a relatively smaller fraction of survivors remaining in their spawning areas. During the early and mid spawning periods when the probability of survival was extremely low, most of the eggs tended to be transported to coastal environments or towards the southeast, where they met insufficient salinity conditions to remain buoyant. Temperature-dependent mortality of eggs and yolk-sac larvae showed only little variation over the spawning period, except during the cold years of the mid 1980s, when temperature-related egg mortality increased drastically. At the end of the spawning period survival rates were generally relatively high. This was mainly associated with wind-induced westerly particle transport, preventing eggs and yolk-sac larvae from being transported into regions farther east where the salinity is generally low; egg and yolk-sac larvae in the more eastern and central parts of the Baltic are likely to suffer death due to bottom contact. Higher survival at the end of the spawning season was also slightly associated with higher ambient temperatures and the resulting shorter drift durations and distances, which in turn caused the eggs and yolk-sac larvae to be subjected to potential mortality causes for shorter periods of time.

The possibility of an advective exchange between western and eastern Baltic stocks only exists for feeding larvae and/or juveniles, because the majority of eggs and yolk-sac larvae were dying due to bottom contact before entering the eastern Baltic Sea. On average there is a narrower salinity range predominant in the eastern Baltic (11 to 18 psu), so passively drifting particles such as cod eggs and yolk-sac larvae will not meet the required neutral buoyancy levels for survival there.

The locations and extension of western Baltic cod spawning grounds were taken from (Vitale *et al.*, 2008; Bleil *et al.*, 2009), while egg buoyancy data were based on field experiments performed by von Westernhagen (1970). As these experiments gave no indication that the buoyancy levels of eggs and yolk-sac larvae changed during their development, they remained fixed after initializing. Unfortunately, spatial distribution data of eggs and yolk-sac larvae are not available in order to evaluate the model results for early life stage survival of western Baltic cod. Our simulations provide a baseline for quantifying and understanding corresponding variations in buoyancy levels and the final spatial distribution of early life stages originating from different spawning areas in the western Baltic Sea. However, in order to correctly predict egg and larval survival success based on transport processes, a relatively high level of complexity in initial conditions is required (Gallego *et al.*, 2007). For example, for a model that predicts spatial and temporal patterns in absolute numbers of surviving eggs and larvae, input in the form of spatially- and temporally-resolved egg production is needed (Heath and Gallego, 1998). Unfortunately, this information is not available for western Baltic cod. Thus, our investigations were only able to estimate relative survival rates.

To our knowledge, this study is the first one to investigate temporal and spatial differences in advective transport patterns of particles and survival success up to the yolk-sac larval stage of the western Baltic cod stock based on biophysical modelling. Because of the observed strong variations in the egg and yolk-sac larval drift patterns of western Baltic cod between areas, as well as the high loss rates of particles from their initial spawning grounds, the model results can hardly be quantitatively employed in short- and medium-term stock projections. Moreover, our modelling exercise indicates that if one wants to incorporate such information into stock projections, extensive sampling programs with small-scale spatial resolution are required to obtain data on egg production as well as on stock structure, especially spatially- and temporally-resolved information on age and sex diversity. However, without that data and without detailed knowledge of the reproduction biology of western Baltic cod, this approach provides a guideline for the potential spatial distributions and the identification of the temporal windows needed. Usually, processes operating at relatively small scales are poorly resolved (Irigoien *et al.*, 2008). Many conclusions about the physical environmental conditions in the Baltic Sea depend largely on long-term time series data analyses, which are not able to resolve environment-dependent processes on smaller temporal and spatial scales. Hence, the present approach appears to be able to more effectively support fisheries stock assessment by condensing, summarizing and visualizing the highly-resolved information obtained from the biophysical model to scales presently used in fisheries management models (Gallego *et al.*, 2007; deYoung *et al.*, 2010). An approach that combines observations, process knowledge, and numerical modelling, seems to be a promising tool for simulating the dynamics of the western Baltic cod stock. Despite the lack of necessary information about the western Baltic cod (such as stock demography, egg production rates, etc.) the application of a biophysical model can be seen as a direct attempt to characterize the spatial and temporal variability of transport processes and their impact on the subsequent survival success of early life stages. From a management perspective, these analyses can provide valuable information with respect to the design and implementation of closed areas or seasons to ensure undisturbed spawning. Furthermore, our case study exemplifies the effects of climate variability for the understanding of the dynamics of fish stocks. Hence, long-term fisheries management has to consider climate forcing on recruitment in order to achieve sustainable resource utilization and conservation (Köster *et al.*, 2005).

Generally, the initially distinct horizontal distribution patterns of eggs and yolk-sac larvae, as well as the temporal variability of circulation patterns during the spawning season indicate a high probability for the occurrence of regionally self-sustaining yolk-sac larvae populations in the western Baltic Sea. Furthermore, the Kattegat and the eastern Skagerrak are areas of relatively high mixing probability between the different subpopulations. Higher probabilities for a relatively strong connectivity of stock components were found during late spawning, especially in the Kiel and Mecklenburg Bay. It is possible that the cod spawning population may have developed with limited connectivity between subpopulations of cod spawning in distinct areas of the western Baltic Sea. Thus, investigating possible genetic differences within or between spawning populations remains an interesting topic.

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