Survival and dispersal variability of pelagic eggs and yolk-sac larvae of central and eastern baltic flounder (Platichthys flesus): application of biophysical models

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A hydrodynamic model coupled with a Lagrangian particle tracking technique was utilized to simulate spatially and temporally resolved long-term environmentally related (i) size of habitat suitable for reproduction, (ii) egg/yolk-sac larval survival, (iii) separation of causes of mortality, and (iv) connectivity between spawning areas of Baltic flounder with pelagic eggs. Information on reproduction habitat requirements and mortality sources were obtained from field or laboratory studies. In our modelling study we only quantified physical processes generating heterogeneity in spatial distribution of eggs and yolk-sac larvae, as e.g. predation is not accounted for. The spatial extent of eggs and larvae represented as modelled particles is primarily determined by oxygen and salinity conditions. The reproduction habitat most suitable was determined for the Gdansk Deep, followed by the Bornholm Basin. Relatively low habitat suitability was obtained for the Arkona Basin and the Gotland Basin. The model runs also showed yolk-sac larval survival to be to a large extent affected by sedimentation. Eggs initially released in the Arkona Basin and Bornholm Basin are strongly affected by sedimentation compared with those released in the Gdansk Deep and Gotland Basin. Highest relative survival of eggs occurred in the Gdansk Deep and in the Bornholm Basin. Relatively low survival rates in the Gotland Basin were attributable to oxygen-dependent mortality. Oxygen content had almost no impact on survival in the Arkona Basin. For all spawning areas mortality caused by lethally low temperatures was only evident after severe winters. Buoyancy of eggs and yolk-sac larvae in relation to topographic features appear as a barrier for the transport of eggs and yolk-sac larvae and potentially limits the connectivity of early life stages between the different spawning areas.

Keywords: connectivity, Egg buoyancy, environmental variability, Individual-Based modelling, mortality, retention vs. dispersal.

Introduction

The Baltic Sea is the largest brackish water area in the world, with a restricted water exchange through the Sound and the Belt Sea [ICES Subdivision (SD) 22 and 23, Figure 1], resulting in a gradient in salinity in the surface water from 9 in the western Baltic Sea (SD 24) to 3 in the far north (SD 31, Voipio, 1981). In the deep basins of the Baltic proper, SD 24–28, there is also a vertical gradient with higher salinity (10–22) below the halocline (Voipio, 1981). Renewal of the bottom water is mainly driven by major inflows of saline, oxygenated water occurring under certain
meteorological conditions (Schinke and Matthäus, 1998). Stagnant conditions, accompanied by a decrease in salinity and oxygen concentration, may prevail for years (Franck et al., 1987; Matthäus and Lass, 1995). Although major Baltic inflows may not occur for longer time periods, minor inflow events affecting only upper halocline water masses are recorded regularly (Lehmann et al., 2014). The Baltic Sea is heavily affected by human activities including eutrophication which have led to large part of the deeper areas in the Baltic Sea being oxygen depleted (Conley et al., 2000; Diaz and Rosenberg, 2008). This has been further aggravated by less frequent inflow events during the last decades, potentially an effect of climate change (Meier et al., 2014).

The low salinity is a limiting factor for successful reproduction for most marine teleosts, directly by reducing fertilisation success and diminishing egg survival and indirectly by reduced buoyancy for most marine teleosts, directly by reducing fertilisation success potentially an effect of climate change (Meier et al., 2014). After the larval stage in the pelagic zone above the halocline larvae undergo a metamorphosis, become flat, and settle in suitable nursery areas (<1 m depth sandy beaches) and feed on benthic fauna (Ustups et al., 2007; Florin et al., 2009; Martinsson and Nissling, 2011). Passive drift during the larval stage may affect recruitment by failure to transport larvae to suitable nursery areas (Riley et al., 1981; van der Veer et al., 2000).

The flounder is a commercially exploited species and advice for management is given yearly by ICES (e.g. ICES, 2015). In the last years there has been an extensive debate about stock structure of this species with a current suggestion of one stock with demersal eggs in SD 27, 29–32, and three different stocks of flounder with pelagic eggs: one in SD 22–23, one in SD 24–25 and one in SD 26 and 28 (ICES, 2015). There are major knowledge gaps related to whether connectivity of the flounder stock in the central and eastern Baltic Sea (ICES, 2014) is an important process (e.g. by dispersal of eggs and yolk-sac larvae).

Spatial and temporal distribution patterns of early life stages could be obtained by simulating survival and drift of eggs and yolk-sac larvae. Drift modelling studies have already been used for eastern Baltic cod (Gadus morhua) spawning in the Bornholm basin (SD 25) to investigate the dispersal dynamics of early life stages (Hinrichsen et al., 2003a, 2016), the impact of dispersal on the survival of larvae (Hinrichsen et al., 2001a, 2003b), and the influence of copepod species composition on the growth and survival of larvae (Hinrichsen et al., 2002a). These studies also suggested the potential for considerable connectivity between areas through dispersal of early life stages (Hinrichsen et al., 2001b; 2009).

In the western Baltic Sea (SD 22–23), dispersal patterns of flounder eggs and yolk-sac larvae have been recently modelled (Peteiret et al., 2014). Generally, the results suggest retention of early life stages as an important process, both under hydrodynamic inflow events and stagnant conditions. However, considerable variation in egg specific gravity among experimentally derived flounder egg batches was obvious, which could mirror a much more complex population structure than currently assumed. Mortality of modelled western Baltic flounder eggs was mainly caused by sedimentation (bottom contact) and/or lethal temperatures, while oxygen content was not expected to be a major cause of egg mortality, because model results suggested that eggs were exposed to a generally high saturation level (Peteiret et al., 2014). On the contrary for fish spawning in the central and eastern deep basin oxygen conditions are crucial

![Figure 1. ICES SDs in the Baltic Sea and Baltic flounder spawning areas: BS, Belt Sea; AB, Arkona Basin; BB, Bornholm Basin; GD, Gdansk Deep; lines indicate 60 m depth contour.](https://academic.oup.com/icesjms/article-abstract/74/1/41/2444572)
Application of biophysical models

(Bagge, 1981; Grauman, 1981; MacKenzie et al., 2000). One of today’s major challenges for modelling the central and eastern Baltic Sea ecosystem, i.e. the simulation of deep water dissolved oxygen distribution with its seasonal and quasi-permanent extended areas of oxygen deficiency, has been successfully performed by Lehmann et al. (2014). Since mortality of eastern Baltic cod early life stages was shown to be severely affected by oxygen content (Hinrichsen et al., 2016), the oxygen content as a major contributor to egg mortality for the central and eastern Baltic flounder stock should be taken into consideration.

The objectives of this manuscript are to analyse the effects of environmental variability on the spatial and temporal distribution of early life stages of one of the most widely distributed, and commercially important, marine fish species in the Baltic Sea, the European flounder. We aim to reveal egg survival probabilities and drift/dispersal of flounder of the pelagic egg ecotype in the eastern and central Baltic Sea (SD 24–26 and 28) with similar spawning strategy/spawning areas as cod but with somewhat different threshold levels for egg survival due to egg specific gravity and different vertical egg distribution patterns. We simulate spatio-temporal differences in egg survival rates within the main spawning areas of the stock in relation to season and year and use drift modelling to test, whether along the drift routes of simulated eggs and yolk-sac larvae the experienced environmental conditions in the different spawning areas are (i) suitable for reproduction, (ii) suitable for egg and yolk-sac larval survival, and (iii) estimate the population connectivity of central and eastern Baltic flounder early life stages between the different spawning areas.

Material and methods

Hydrodynamic modelling

The basis of the Lagrangian particle tracking is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM, Lehmann and Hinrichsen, 2000; Lehmann et al. 2002). The 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). Prognostic variables are the baroclinic current field, the 3D temperature, salinity and oxygen distributions, the 2D surface elevations and the barotropic transport. The horizontal resolution of the coupled sea-ice ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat, and Skagerrak. The oxygen conditions in the entire Baltic Sea are described by an oxygen consumption sub-model coupled to BSIOM (Lehmann et al., 2014). At the western boundary, a simplified North Sea is connected to the model domain to represent characteristic North Sea water masses in terms of characteristic temperature and salinity profiles resulting from the different forcing conditions. The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of 1° x 1° with a temporal increment of 3 h. The database consists of synoptic measurements (including geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness, and precipitation) that were interpolated on the regular grid with a two-dimensional optimum interpolation scheme. This database, which for modelling purposes was further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and geostrophic wind. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kromsoll and Andersson, 2012). The model is also forced by low frequency sea level variations in the North Sea/Skagerrak (Baltic Sea Index, Lehmann et al., 2002; Novotny et al., 2006). The numerical model BSIOM has been run for the period 1971–2010. This time series was used for the subsequent analysis of habitat suitability and early life stage survival in the Baltic.

Environmental threshold levels

Simulated habitat suitable for reproduction is exclusively based on the required environmental threshold limits of particles released as spawned eggs, i.e. the stage Ia. Other additional information which might be of relevance for the determination of habitats such as adult behaviour or fecundity could not be considered due to the lack of stock specific flounder data. The environmental threshold levels for egg survival were based on field and laboratory experiment-based minimum requirements for temperature and oxygen. At oxygen levels < 1.0 ml O2 l−1, or temperatures < 2.0°C development fails and the eggs die or result in inferior larvae (Vitinsh, 1980; Grauman, 1981; Bagge 1981). More than 90% survival occurred at 4–10°C but significantly lower at 2°C with a higher fraction of inferior larvae. Although high temperatures become increasingly detrimental to egg development, this effect could be disregarded, since temperatures >10°C are not expected. Moreover, egg development and consumption of yolk sac is strongly temperature dependent, with development times decreasing exponentially from around 45 to 15 days with increasing temperature (Figure 2; data source and method are described in Appendix 1). A salinity of ~10 is needed for spermatozoa activation and fertilisation (Nisling et al., 2002). However, based on egg specific gravity measurements, successful reproduction of flounder with pelagic eggs is restricted by the ability to obtain neutral egg buoyancy. Observed minimum egg specific gravity, 1.0079 g/cm3 (calculated as average egg specific gravity in SD 28, subtracted 2.326 standard deviations, corresponding to the 1 and 99% percentiles of a normal distribution, verified by observations in situ in the main spawning areas) corresponds to a salinity of 10.2 (Nisling et al., own data), i.e. 98% of all egg batches are included. Since some discrepancies between areas have been observed (Nisling et al., 2002) we used a salinity of 12.0 for SD 24, 10.8 for SD 25 and 10.2 in SD 26 and 28 as minimum salinity for neutral egg buoyancy in the respective spawning area (Table 1; data source and method are described in Appendix 1). Eggs being neutrally buoyant at salinity levels exceeding those at the bottom presumably die due to sedimentation, while eggs displaying neutral buoyancy at lower salinities ensure them to be buoyant and to float in the water column (e.g. Nisling et al., 1994).
Particle tracking, drift model and reproduction habitat suitability

Simulated three-dimensional velocity fields were extracted (at 3 h intervals) from the hydrodynamic model in order to develop a database for a particle tracking method. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated particles were computed using a fourth order Runge-Kutta scheme (Hinrichsen et al., 1997). Particles representing flounder eggs at developmental egg stage Ia (Thompson and Riley, 1981) were released into the simulated flow fields in each of the respective spawning areas (ICES subdivisions) and were tracked through the different egg stages as well as the yolk-sac larval stage. If the released eggs at spawning survived in response to the required environmental condition, their area and volume extensions determined the habitat suitability for reproduction. As a second step particles were exposed to hydrographic property fields along the drift routes with high temporal and spatial resolution provided by the hydrodynamic model (temperature, salinity and oxygen). The hydrographic information was used to calculate the development time of the eggs/yolk-sac larvae as well as the environmentally-related mortalities. For individual particles that died during the simulations, the positions where death occurred were recorded, while for the surviving particles the final positions reached at the end of the yolk-sac stage were noted.

Table 1. Egg specific gravity/buoyancy of pelagic flounder eggs, based on average ± 2.326*SD (corresponding to 98% of egg batches).

<table>
<thead>
<tr>
<th>SD</th>
<th>N</th>
<th>Density g/cm³</th>
<th>Salinity (psu)</th>
<th>Range (psu)</th>
</tr>
</thead>
<tbody>
<tr>
<td>26 ± 28</td>
<td>69</td>
<td>1.00791–1.01119</td>
<td>10.2–14.3</td>
<td>4.1</td>
</tr>
<tr>
<td>25</td>
<td>29</td>
<td>1.00842–1.01416</td>
<td>10.8–18.1</td>
<td>7.3</td>
</tr>
<tr>
<td>24</td>
<td>13</td>
<td>1.00936–1.01504</td>
<td>12.0–19.3</td>
<td>7.3</td>
</tr>
</tbody>
</table>

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Estimation of survival and mortality and model experiment design

Duration of the drift period until the end of the yolk-sac larval stage was based on the temperature-dependent developmental time (Figure 2, see Appendix 1) and was provided by the hydrodynamic model, i.e. temperature-dependent development from stage Ia eggs to the yolk-sac larval stage was calculated along the
drift paths of individual particles. The simulations were stopped when yolk-sac larvae reached the first feeding larval stage (mouth opening), because for feeding purposes the larvae migrate into the near surface layers. Drift simulations of the later larval and juvenile stages were not subject of this manuscript, because other processes (e.g., swimming ability, ontogenetic shift and subsequent settlement) have to be taken into account. However, this will be included in future studies on the drift of these later early life stages of Baltic flounder.

**Spawnning time and spawning areas**

The focus of this study is on the central and eastern Baltic flounder’s general reproduction potential for the whole spawning season. These stocks are known to generally spawn from March to June, with the main spawning season differing between different parts of the Baltic Sea (SD 24 March–April, SD 25 March–May, SD 26–28 March–June; Bagge 1981).

**Results**

**Spatially disaggregated patterns of habitat suitability for reproduction**

The probabilities of successful particle release (habitat suitability for reproduction) of central and eastern Baltic flounder eggs is shown in Figures 3–6 (long-term trends are presented in Appendix 2). Generally, the spatial patterns showed almost constant habitat suitability throughout the time period in the Arkona Basin (ICES SD 24, Figure 3a) while for the Bornholm Basin (ICES SD 25, Figure 4a) stronger inter- and intra-annual variability occurred. Best habitat suitability was revealed for the first half of the time series in the Gdansk Deep (ICES SD 26, Figure 5a) with lower levels and higher intra- and inter-annual variability during the most recent decades. Similar conditions, but with strong inter- and intra-annual variability were observed in the Gotland Basin (ICES SD 28, Figure 6a), however, for some years in the 1990s and 2000s the habitat was not suitability for egg and yolk-sac larval survival.

**Spatially disaggregated patterns of mortality**

Differences in survival probability are caused by spatial and temporal variations of different mortality sources. Generally, predicted temperature-related mortality was low as released particles were not subject to sub-lethal temperatures and could be noticed only in the Arkona and Bornholm Basin (ICES SDs 24 and 25) due to cold water temperatures after severe winters. On the contrary, an expected relatively high impact on survival rates in the Gdansk Deep (ICES SD 26, Figure 5b) and especially in the Gotland Basin (ICES SD 28, Figure 6b) was attributable to predicted oxygen-dependent mortality. Oxygen-related mortality was more important in the Gdansk Deep, but highest temporal variability of predicted oxygen-dependent mortality was observed in the Gotland Basin. Low oxygen content had almost no impact on survival in the Arkona Basin (ICES SD 24, Figure 3b) and in the Bornholm Basin (ICES SD 25, Figure 4b). In these areas the majority of eggs (on average >50%) died due to sedimentation (Figures 3c and 4c). Bottom contact of the flounder eggs also played a significant role in the Gdansk Deep (Figure 5c), while it was almost negligible in the Gotland Basin (Figure 6c).

**Spatially disaggregated patterns of survival probability**

When compared with the habitat suitable for reproduction (released particles within the environmental thresholds limits), only relatively low survival of central and eastern Baltic flounder eggs up to the yolk-sac larval period was observed in the Arkona Basin (ICES SD 24, Figure 3d) and in the Gotland Basin (ICES SD 28, Figure 6d), while higher survival was obtained for the Bornholm Basin (ICES SD 25, Figure 4d) and in the Gdansk Deep (ICES SD 26, Figure 5d). For the two analysed westernmost spawning areas (Arkona and Bornholm Basin) relatively constant levels of survival probability occurred. Contrary, for the Gdansk Deep and the Gotland Basin the modelled egg survival was relatively high during the first half of the time series but with lower values for the second half. Especially in the Gotland Basin egg survival was on a low level since the 1990s.

**Geographic patterns of egg survival probability**

The long-term spatial distribution (1971–2010) of surviving eggs (stage Ia) originating in the spawning areas of the different SDs, represented by the particle release positions, is illustrated in Figure 7. For particles released in the SDs 24, 25, and 28, the horizontal distribution maps clearly show highest concentrations of survivors originating from the central areas. In contrast, survivors of SD 26 originated from a more widely distributed spawning area over almost the entire areas of this SD. The spatial distribution of the particle endpoints (Figure 8) is based on the same egg cohorts. Generally, the particle distributions revealed retention of surviving eggs and yolk-sac larvae in their SDs; however, there indication for dispersal (transport to neighbouring SDs) was shown. Eggs spawned in the SD 24 were mainly transported towards the SD 25 area, while a relatively small fraction of survivors from SD 25 was advected to SD 26. Strongest dispersal was observed from SD 26 towards 28 as well as northward into SD 29. From SD 28 a minor fraction dispersing towards SD 26 as well as northward into SD 29 occurred.

**Connectivity patterns of eggs and yolk-sac larvae**

To quantify the connectivity patterns of central and eastern Baltic flounder early life stages, we calculated retention within and advective transport rates of eggs and yolk-sac larvae between ICES subdivisions (Table 2). The long-term mean survival probability of eggs and yolk-sac larvae calculated for the whole simulation period (1971–2010) were dominated by retention of particles in the ICES SDs 25, 26, and 28. However, in total SD 25 contributed on average to 39% and SD 26 around 42% of survivors to the overall production of yolk-sac larvae. This can be compared with 16% from SD 28 and merely around a 3% contribution from SD 24. For particles initially released at the spawning ground in SD 26 a relatively high probability of transport towards SD 28 (8%) was estimated and for particles released in SD 24 2% were transported to SD 25. In contrast, westward transport is in general of only minor importance.

**Intra- and interannual reproduction potential of central and eastern Baltic flounder spawning grounds**

The numerical simulations showed remarkable inter- and intra-annual differences in survival of flounder yolk-sac larvae. Relative survival of flounder yolk-sac larvae in their different spawning grounds are presented in Figure 9. From our modelling exercise it...
becomes evident that reproduction in terms of survival was highest in the Bornholm Basin. Here, for many years since the end of the late 1980s, relative survival reached a maximum of 75%, while before the late 1980s, the same survival was also obtained for the Gdansk Deep and occasionally on a similar level in the Gotland Basin. Throughout the entire time period relative survival was lowest in the Arkona Basin.

**Discussion and conclusions**

**Survival probabilities related to abiotic factors**

For the first time survival probabilities and dispersal of flounder eggs and early larvae in the central and eastern Baltic have been considered and show that survival probabilities vary greatly, both spatially and temporally with causes of mortality differing

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**Figure 3.** Number of particles representing the Arkona Basin (ICES SD 24) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.
between basins. The highest survival probabilities occurred in SD 26 (Gdansk Deep) with a decrease since the beginning of the 1990s. Estimated survival probabilities were of the same level in SD 25 compared with SD 26, but with no decreasing trend, low in SD 24 and highly variable in SD 28 with a minor decreasing trend. The importance of favourable salinity and oxygen conditions for the reproductive success (Nissling et al. 2002; Casini et al., 2011; Ustups et al. 2013) of eastern Baltic flounder is clearly visible, e.g. the dependency of saline water inflows from the North Sea, but additionally sedimentation is an important source of mortality, especially in SD 24, 25 and 26.

**Sedimentation and temperature-related mortality**

Similar to previous research on early life stage processes on eastern Baltic cod (Pacariz et al., 2013; Hinrichsen et al. 2016), the
finding of sedimentation derived mortality is rather new. If the assumption of egg mortality upon bottom contact is true, then this source of mortality is predicted to be relatively high compared with mortality affected by sub-lethal temperature and oxygen conditions. However, for any field-based validation of sedimentation-related mortality, no functional sampling gear which reliably samples the boundary layer between substrate and water column and would allow the determination of the condition of the egg exists. It remains a challenge to collect eggs from soft bottom, which constitutes by far the largest area of substrate where eggs are lost due to sedimentation. To the authors knowledge the direct evidence (either derived by observations or experiments) of our assumption that eggs do not survive if hitting the bottom (sedimentation) has not yet been published in the

Figure 5. Number of particles representing the Gdansk Deep (ICES SD 26) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounder eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.
literature. The likelihood for fragile pelagic eggs to survive these conditions, like potential predation pressure or exposure to benthic fungi, is at least largely reduced. A large body of recently published studies shares this assumption (Hinrichsen et al., 2012; Hüssy et al., 2012; Pacariz et al., 2013; Petereit et al., 2014).

Although temperature was shown not to be an important source of mortality, temperature directly affects developmental time and thus the probabilities for sedimentation and dispersal, e.g. the simulations provided temperature-dependent egg and yolk-sac larval stage durations of 45 days at low and only 15 days at high temperatures. Hence, not only sedimentation mortality can be expected but also strong intra-annual variability of predation mortality (see below), with the highest impact of predation potentially occurring during the early spawning season of Baltic flounder. Furthermore, spatial differences in temperature among spawning grounds (increasing from west to east) as well as

**Figure 6.** Number of particles representing the Gotland Basin (ICES SD 28) Baltic flounder spawning ground (a) reproduction habitat suitability (released as initially successfully spawned flounder eggs), (b) relative oxygen-related mortality of flounder eggs during drift, (c) relative mortality of flounder eggs caused by sedimentation during drift, and (d) relative survival of flounders eggs until the first-feeding yolk-sac larval stage. Bars represent the range of single release events.
differences in spawning time (early in the west and later in the east), might explain why the SD 24 (Arkona Basin) appears to be a highly used spawning ground despite low egg and yolk-sac larval survival.

Additional mortality sources during drift period

The here presented abiotic environment-dependent mortality sources could only partly contribute to the determination of the overall absolute survival of the flounder early life stages from the egg stage Ia to the end of the yolk-sac stage (mouth opening). First of all, it is presently impossible to specifically quantify these mortality sources, because no field based or laboratory-based experiments describing environmentally driven relationships, as e.g. for eastern Baltic cod (Köster et al., 2005), are available. For example, we lack relationships between oxygen/temperature and egg survival for flounder derived from laboratory experiments or field studies. Due to the lack of field data on the vertical distribution of flounder eggs, as a simplification particles representing successfully spawned eggs were distributed only evenly every 3 m. When compared with in situ conditions, vertical egg distributions vary in accordance with variability in egg specific gravity (assuming normal distribution), i.e. most eggs will obtain neutral buoyancy at water densities corresponding to average egg specific gravity and fewer at water densities corresponding to the lower and upper range. Second, mortality attributed to abiotic factors interacts with key biotic factors, such as encounter with predators (Bailey and Houde, 1989). Based on estimates for Baltic cod and sprat (Voss et al., 2011; Neumann et al., 2014), it is evident that our modelled environment-driven abiotic mortality rates accounted for only a part of the total mortality. Usually, estimates of field-based total mortality rates rely on daily egg production of different egg stages (Voss et al., 2011), which could be compared with independent estimates obtained from cohort analyses.

To our knowledge, calculations of any kind of field-based total mortality rates have never been performed for Baltic flounder. Consequently, we have to consider the results of our mortality calculations to be an underestimate of the total mortality.

Drift related dispersal patterns vs. Current ICES stock management units

Concerning dispersal the results revealed dominance for retention (although an east-northward dispersal was observed from SD 26 to 28) apart from SD 24 where the majority of eggs/larvae were transported into SD 25.

The current stock unit of western Baltic flounder (SD24 + 25) seems to be justified by the relatively strong drift from SD 24 into SD 25 and the retention of larvae in SD 25. Furthermore SD 24 by itself has very little contribution of larvae surviving to the end of the yolk-sac stage, hence it could be questioned to what extent it could be a self-sustaining population. Although there is some drift from SD 25 into SD 26 it is minor compared with the number of surviving larvae spawned in SD 26 and retained in SD 26. From SD 26 there is however a contribution to SD 28 and also some larvae in SD 26 originating from SD 28. Hence the stock units of SD 26 and 28 also seem to be justified from an egg and larval connectivity perspective.

Temporal and spatial survival probabilities in relation to other stock measures and critical periods

Looking at the trends in environment-related survival probabilities of eggs and yolk-sac larvae in the respective spawning area (Figures 3–6), an increasing trend is shown for SD 25 while decreasing over time in SD 26 and 28 with a notable change in the late 1980s/early 1990s. Interestingly, despite the stable egg to yolk-sac larval survival of flounder in SD 24 and 25 the stock has
increased significantly during the last decade as assessed in trawl surveys (ICES, 2015; Figure 10) suggesting that what happens after the yolk-sac larval stage has a significant impact on recruitment and thus stock development. This is evident also for SD 26 and 28 where egg to yolk-sac larval survival decreased significantly, especially in SD 28, while at the same time the adult stock size (flounders above 20 cm in length with a majority of 3–8 years age) increased in the late 1990s and has since then fluctuated up to recently, when it declined in SD 28 (Figure 10). This means that the production of surviving larvae was, at least until 2010, still high enough to sustain a viable population. However, results of our study are covering a relatively short time period of early life stage of flounder eggs and yolk-sac larvae (ca. 20–40 days depending on temperature) while flounder larval development until metamorphosis is remarkable longer (Grauman, 1981).

Interestingly, the survival probabilities of flounder early life stages is highest in SD 25 but the density of flounder is much higher in the eastern Baltic SD 28 compared with the central Baltic (SD 24 and 25) when comparing catch per unit effort in the Baltic International Trawl Survey (Figure 10).

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**Table 2.** Overall means and standard deviations of dispersal/retention patterns (percentages) of particles representing surviving of central and eastern Baltic flounder eggs until the yolk-sac larval stage.

<table>
<thead>
<tr>
<th>Spawning area</th>
<th>West</th>
<th>SD 24</th>
<th>SD 25</th>
<th>SD 26</th>
<th>SD 28</th>
<th>Total contribution</th>
</tr>
</thead>
<tbody>
<tr>
<td>SD 24</td>
<td>0.1±0.4</td>
<td>0.8±1.4</td>
<td>1.9±2.1</td>
<td>0.0±0.1</td>
<td>0.0</td>
<td>2.8±1.7</td>
</tr>
<tr>
<td>SD 25</td>
<td>0.0</td>
<td>0.1±0.2</td>
<td><strong>37.8±16.</strong></td>
<td>0.1±1.3</td>
<td>0.0±0.0</td>
<td>39.0±13.6</td>
</tr>
<tr>
<td>SD 26</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0±0.1</td>
<td><strong>33.9±24.2</strong></td>
<td>8.2±8.7</td>
<td>42.1±21.1</td>
</tr>
<tr>
<td>SD 28</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>1.3±2.8</td>
<td><strong>16.8±24.2</strong></td>
<td>16.1±22.4</td>
</tr>
</tbody>
</table>

Bold numbers represent retention patterns within ICES subdivisions. West means ICES SDs further west than ICES SD 24.
Apparently food availability following the yolk-sac period, predation on eggs, larvae or juveniles (Bailey and Houde, 1989), transportation of early stages to suitable nursery areas along the coast (see van der Veer et al., 2000) or availability/quality of nursery areas (Florin and Lavados 2010; Martinsson, 2011) may be regulating factors. Alternatively, stock development might reflect mortality in the adult stage such as fishing mortality, but unfortunately no estimates of fishing mortality are available for flounder in the Baltic Sea. Moreover, stock development, especially in SD 26 and 28 may be blurred due to mixing between the ecotypes. Recent findings (EU BONUS project INSPIRE) show that the distribution of the ecotype with demersal eggs is wider than previously assumed. As both ecotypes share the same feeding and wintering areas, and are separated only during spawning in March to May (e.g. Nissling et al., 2014), surveys (BITS carried out by trawling at 10–120 m depth in Q 1 January–March and Q 4 November–December) may target both ecotypes.

**Figure 9.** Fraction of particles representing intra- and inter-annual reproduction potential of Baltic flounder spawning grounds, (a) Arkona Basin, (b) Bornholm Basin, (c) Gdansk Deep, and (d) Gotland Basin. Bars represent the range of single release events.
Application of biophysical models

**Figure 10.** Trends in abundance of flounder stocks in ICES SD 24, 25, 26, and 28, measured as kg per hour in the Baltic International Trawl survey. Geometric mean for Quarter 1 and 4. Data from ICES (2015).

**Methodological considerations: probabilities of processes and parameters**

This article presents results of a numerical drift modelling exercise on central and eastern Baltic Sea flounder eggs originating from different spawning areas. The applicability of coupled biophysical models in fisheries management includes estimation of connectivity within fish stocks through transport of egg, larval and early juvenile stages, and spatio-temporal differences in potential survival (Hinrichsen et al., 2011). Habitat suitable for reproduction, mortality, survival and transport patterns of central and eastern Baltic flounder eggs and yolk-sac larvae were quantified by detailed model simulations for the years 1971–2010. The data were derived from highly spatially and temporally resolved hydrographic Eulerian property fields obtained from hydrodynamic model runs performed by Lehmann et al. (2014).

Here we examined the transport of particles initially released into these simulated flow fields as successfully spawned and fertilised eggs. However, this exercise only provides probabilities of different processes and parameters, and does not take into account how many eggs are actually spawned, e.g. factors affecting female fecundity. The estimation of habitat suitability as well as mortality and survival probabilities during drift are based on abiotic tolerance levels in terms of threshold values and egg specific gravity measurements, selected for egg survival at the spawning location as well as during drift duration.

**Recommendations for managers and scientific needs considering environmental change**

To reveal the population structure of flounder in the whole Baltic Sea (as a tool in management to obtain a sustainable stock development), connectivity and population mixing in all life stages should be considered. Dispersal may occur during the egg and early larval stage (this study) and during the pelagic larval stage until settlement (different cohorts with settling from early July to early September share the same nursery areas; Martinsson and Nissling, 2011), and furthermore, the two ecotypes share feeding and wintering areas (e.g. Bagge, 1981; Nissling et al., 2014). Hence, apart from genetic discrepancies (Hemmer-Hansen et al., 2007; Florin and Högland, 2008) throughout the distribution area, drift patterns during the larval phase (see van der Veer et al., 2000) and migration patterns (Aro, 1989), e.g. occurrence of natal homing (e.g. Svedäng et al., 2007) and changes in distribution due to poor oxygen conditions in deeper areas, remain topics for future studies.

With respect to the ongoing climate change, presumably resulting in less frequent saline water inflows (MacKenzie et al., 2007), with potentially lower oxygen concentrations due to elevated water temperatures (Hinrichsen et al., 2002b), egg and early larval survival of flounder with pelagic eggs can be expected to decrease in the future as salinity and oxygen conditions (major sources of mortality according to the model, particularly in SD 26 and 28) will deteriorate. However, mortality caused by low water temperatures after severe winters (identified as a source of mortality in SD 24 and 25) probably will decrease. Hence, potentially poorer conditions in SD 26 and 28 but less so in SD 24 and 25 may cause a shift in the distribution of flounder with pelagic eggs (especially as drift from SD 24–25 to SD 26 and 28 seem to be insignificant). Egg and early larval survival probabilities and the connectivity between areas may also be affected by the age/size structure of the stock determined by fishing mortality. In several species, larger (older) females have been shown to produce more buoyant eggs (Vallin and Nissling, 2000) affecting the vertical egg distribution (buoyant at lower salinities, i.e. less deep) and thus both survival probabilities and connectivity patterns by drift. Although this has not been studied for Baltic flounder so far, it might be expected to be valid also for the flounder ecotype with pelagic eggs. Thus, an important topic for management may be to counterbalance a truncation of the length/age distribution to maintain a sustainable stock development and increase the resilience of climate change.

**Supplementary data**

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

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**References**


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