



Floating along buoyancy levels: Dispersal and survival of western Baltic fish eggs



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ABSTRACT

Vertical distribution is an important feature of pelagic fish eggs and yolk sac larvae impacting their survival and dispersal, especially in heterogeneous and highly variable estuarine environments like the Baltic Sea. Egg densities determining the vertical distribution pattern were experimentally ascertained for cod (*Gadus morhua*), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) from the western Baltic Sea. Plaice eggs floated at lower mean (\pm standard deviation) density range ($1.0136 \pm 0.0007 \text{ g cm}^{-3}$) compared to cod ($1.0146 \pm 0.0009 \text{ g cm}^{-3}$) and flounder eggs ($1.0160 \pm 0.0015 \text{ g cm}^{-3}$), which floated on the highest density level. In flounder egg diameter was significantly related to egg density and in cod a weak correlation could be found between egg dry weight and density. All other relationships between female size, egg size, egg dry weight and egg density were not significant for any of the species. Available egg density data for Baltic Sea cod, plaice and flounder are summarized considering ICES subdivisions and stock management units. A hydrodynamic drift modeling approach was applied releasing drifters in the Belt Sea continuously from December to May, covering the species' spawning seasons. The model implemented experimentally derived egg density ranges and included ontogenetic egg density modifications for cod eggs, increasing egg density from a late egg development stage to first hatch. A drifter was removed from the model, i.e. considered dead, when its initially prescribed density value exceeded the density range available at the temporally resolved geographical positions along the drift trajectories. Highest survival occurred during releases in April and May but no cohorts survived if they were drifted east into the central Arkona Basin or the central Baltic Sea, irrespective of whether a major Baltic Inflow (1992/1993) or a stagnation-year (1987/1988) was simulated. The dispersal characteristics of the surviving yolk sac larvae of all three species reflected retention within the Belt Sea or northwards transport through the Great Belt into the Kattegat and partly into the Skagerrak. There was no successful transport to more eastern Baltic areas past a hypothetical line from the island of Moen (Denmark) to Kap Arkona on Rügen Island (Germany).

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1. Introduction

Fish eggs and larvae are important life stages to a large extent determining the recruitment strength in marine fish (Cowan and Shaw, 2002; Houde, 2002). The survival success of these stages can vary significantly both between years and within a spawning season due to a variety of factors (e.g. occurrence of unfavorable temperature and salinity conditions or hypoxia, Cushing, 1990; Bunn et al., 2000). Moreover, adequate neutral buoyancy of pelagic early life stages plays a major role in survival, distribution and dispersal, which can shape population structure (Ciannelli et al., 2010; Myksovoll et al., 2013). In addition, specific adaptations of egg buoyancy, fertilization and development of marine fish populations spawning in estuarine areas became evident in a meta-analysis

of egg buoyancy data of 16 fish species (MacKenzie and Mariani, 2012).

A review on buoyancy patterns of eggs, yolk sac larvae and later larval stages of fish is given by Govoni and Forward (2008). They summarized the general assumptions and mechanisms on how egg density (buoyancy) is derived and controlled in marine fish eggs. It is achieved through passive physiological mechanisms due to the eggs' constituent compounds and through developmental events within the ovary of the female fish (Cerdà et al., 2007; Goarant et al., 2007; Govoni and Forward, 2008 and references therein). It is known that brackish water eggs have relatively higher water content (e.g. cod 97%) compared to marine cod eggs (93%), due to the increased water uptake during final oocyte maturation which is aquaporin-mediated (Thorsen et al., 1996; Craik and Harvey, 1987; Fabra et al., 2005). Recent studies on cod (Jung et al., 2012a,b; Guðmundsdóttir, 2013) and anchovy (Ospina-Álvarez et al., 2012) found egg buoyancy increasing and decreasing

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towards the end of the ontogenetic development, respectively. Changes in biochemical components are likely to be the main cause that accounts for decreased specific gravity towards hatching (Jung et al., 2012b). Several studies recommended incorporating such detailed density changes into the modeling of potential drift routes (Myksovoll et al., 2011; Jung et al., 2012a,b; Ospina-Álvarez et al., 2012). For Norwegian coastal cod, such density adjustment was applied using linear models considering development time and temperature (Myksovoll et al., 2013). For anchovy eggs a polynomial model estimating egg density as a function of temperature dependent time from fertilization was suggested (Ospina-Álvarez et al., 2012).

It is uncertain whether these models developed for full marine salinity conditions can be applied for the pelagic eggs of fish species adapted to the brackish water of the Baltic Sea. The western Baltic Sea is part of the world's largest brackish sea with specific, highly variable hydrographic conditions in respect to time and space. All water flowing in and out of the Baltic Sea has to pass through the Belt Sea, the Sound or the Femern Belt (Matthäus and Franck, 1992). Through the Danish Straits (e.g. Belt Sea) on average, outflow is prevailing overlaid by highly fluctuating in- and outflow periods of a few days reaching occasionally volume changes of 100–200 km³ (Lehmann and Hinrichsen, 2000a,b). Thus, volume changes during in and outflow situations are in the same order of magnitude as the river runoff and an averaged outflow rate of 1.24 km³ day⁻¹ (~453 km³ year⁻¹) representing the mean Baltic Sea water discharge including river runoff and the net effect of precipitation minus evaporation (Lehmann and Hinrichsen, 2000a,b). Due to the strong current fluctuations in the Danish Straits the stability of the barotropic flow [0 = no stable current flow; 1 = high stable current flow] hardly reached values over 0.3 (Lehmann and Hinrichsen, 2000a,b). Characterized by an inhomogeneous bottom morphology and separated by small trenches and channels, the western Baltic acts as a shallow connection (<40 m) between the North Sea (high salinity) and the brackish central Baltic Sea which is characterized by deep basins with stratified water layers. The International Council for Exploration of the Sea (ICES) has partitioned the Baltic Sea into Subdivisions (SD's) according to prevailing hydrological and geographic conditions, wherein the Belt Sea (SD 22), the Sound (SD 23) and the Arkona Sea (SD 24) constitute the western Baltic Sea management unit for cod, *Gadus morhua* L. (Fig. 1).

The Belt Sea (SD 22, Fig. 1) is the main fishing area for plaice (*Pleuronectes platessa* L.) in the Baltic Sea and ~830 t were landed in 2009 (ICES, 2010). Slightly higher landings were reported for flounder (*Platichthys flesus* L.; ~1020 t) and cod (~3450 t) (ICES, 2010, 2011). To a high degree, these fish species form the basis for the local fisheries. They have their reproductive season during winter and early spring in the western Baltic Sea spawning pelagic eggs. The spawning season extends for cod from January to April (Bagge et al., 1994; Muus and Nielsen, 1999; ICES, 2011), for plaice from November to March (Muus and Nielsen, 1999) and for flounder from February to April (Saeger, 1974). To date, it is not well known at which depths, or corresponding density layers, the eggs from these three species are developing and where they get passively transported to. A first estimate has been given by Westernhagen von et al. (1988). They reported the highest proportions of eggs of all three species to occur in the salinity range from 17.5 to 21 psu [this calculates to densities of 1.0139–1.0168 g cm⁻³ at 1 °C (Fofonoff and Millard, 1983)].

The precise density layers for each species are of major interest since the existing transport mechanisms can be detrimental to the survival of the eggs. If the eggs are transported to areas with insufficient density levels, they sink to the bottom and die most probably. In addition, this information helps to disentangle small scale population structure of the species (Ciannelli et al., 2010; Myksovoll

et al., 2013). For example, the degree and proportion of exchange between the two Baltic cod stocks (western Baltic versus eastern Baltic cod) are insufficiently understood (ICES, 2011; Hüsey, 2011). The existence of two separate cod stocks has been postulated and shown by various analytical methods such as different morphometric characteristics (for references see Aro, 1989 and Hüsey, 2011), otolith microchemistry (Heidemann et al., 2012), hemoglobin characteristics (Sick, 1961; Andersen et al., 2009) or population genetics (Nielsen et al., 2003, 2009). A hydrodynamic drift model study suggested that eggs or early larval stages of the western cod stock could have the potential to contribute under certain strong westerly wind conditions to the juvenile proportion of the eastern stock east of Bornholm Basin (Hinrichsen et al., 2001). However, at that time the authors had no neutral egg buoyancy data available which are mandatory to determine the initial depth of the released eggs in the water column.

In the present study, we measured neutral egg buoyancy of stage IA eggs obtained by strip spawning running ripe individuals of cod, plaice and flounder during participation in commercial fishing trips to the Northern Kiel Bight (SD 22), an area described historically as the main spawning ground for western Baltic cod (Kändler, 1944; Thurow, 1970; Westernhagen von et al., 1988). This study uses experimentally derived neutral egg densities (neutral buoyancies ranged from 1.011 to 1.018 g cm⁻³) and ontogenetic egg density development (8–15 days duration) of three species in combination with literature-based temperature dependent development rates (7–31 days duration), to model survival rates and dispersal routes from newly fertilized egg stages until the start of mixed feeding larval stage, which was defined to start at the time of mouth gap opening (MGO).

The main focus of our experimental work was to answer the questions: (i) where (at which density layers) do the early egg stages of western Baltic cod, plaice and flounder float? (ii) do different salinity conditions during the fertilization process influence the final eggs' density? (iii) do ontogenetic (egg stage specific) differences exist?

In a subsequent step, we used hydrodynamic modeling approaches to evaluate possible consequences of different hydrographical and hydrodynamic conditions on egg survival and spatial horizontal distribution patterns within, and between spawning seasons. Two years with different hydrographical situations were selected. We used the same years as Hinrichsen et al. (2001) to achieve comparability of the improved model. Our major focus was on the transport potential of the passively drifting eggs and yolk sac larvae until these were able to start mixed feeding (MGO), and their possibility to contribute to recruitment in the central Arkona Basin (SD 24) or Bornholm Sea (SD 25).

2. Materials and methods

2.1. Gametes acquisition and processing

Starting early January, individuals of cod, plaice and flounder were acquired on 12 commercial fishing day-cruises every 7–10 days in the Northern Kiel Bight, western Baltic Sea (ICES SD 22; Fig. 1, Table 1). The sampling intervals covered largely the natural spawning seasons of the species in the western Baltic Sea and matched specifically well for cod and plaice as previously described (Strodtmann, 1906; Thurow, 1970; Westernhagen von et al., 1988). Trawling was performed but the specific gear type (shape, mesh size of the cod-end, haul duration) was changed during all trips depending on the captains' daily strategy and target fish species (flatfish/whiting/cod). Since the use of ship based oceanographic measurement systems (CTD) on commercial fishing boats was impossible, a small scale solution was applied instead.

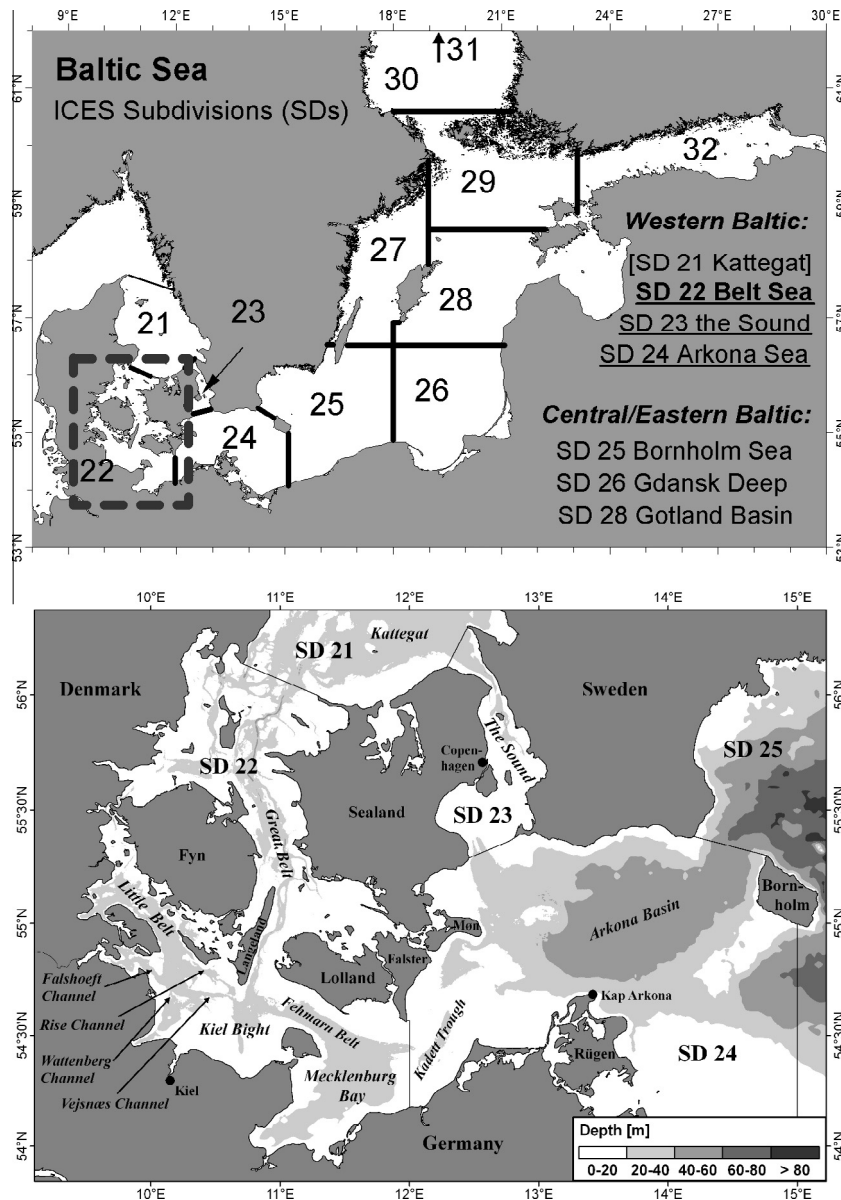


Fig. 1. (Top) Map of selected International Council for Exploration of the Sea (ICES) subdivisions (SDs) of the Baltic Sea. The dark dashed square visualizes the Belt Sea (SD 22), the focus area of the present study. (Below) Depth resolved map of SD 22. Arrows indicate specific trawling channels in Kiel Bight.

Two simultaneously recording data loggers (DST logic CTD from StarOddi©) measuring oceanographic data (pressure, temperature, salinity – later converted into density values) at a rate of 1 s^{-1} were attached to the fishing line on a fishing rod. The line was slowly and as steadily as possible released to the bottom and subsequently lifted in the same manner by fishing reel. Three casts were made during the hauling procedure of the net on the first haul of the day and results of the measurements were finally averaged (Table 1).

The catches were screened for male and female fish in spawning condition and fertilization was performed within 1 h after the net came on board. Total length (TL, cm) of each selected male and female fish was measured. Eggs of every selected female were strip spawned into separate cone-shaped transparent 1 l PVC containers filled with 20 psu artificial seawater (demineralized water with SEQUASAL©) at 2–6 °C. Sperm from three males (1–2 drops per male) were pooled in 200 ml Kautex containers, activated at 20 psu and subsequently poured onto the eggs. After 30 min, the

outlet on the bottom of the cones was opened to discard dead or unfertilized eggs, and the fraction of fertilized eggs was gently inserted into new 20 psu water in 1 l PVC containers. On board, ambient temperature was dependent on the weather conditions and ranged between 1 and 8 °C over the sampling period. Eggs were stored at 6–9 °C overnight until measurements were conducted the next day in the laboratory. The diameters of 30 eggs per batch were measured at 240-fold magnification under a stereomicroscope (Wild M3Z) using an ocular micrometer scale and egg development stages were determined according the staging schemes of [Westernhagen von \(1970\)](#) and [Thompson and Riley \(1981\)](#). Subsequently, eggs (stage 1A) with regular cell divisions were inserted into the salinity gradient to assure optimal egg quality. After a settling time of 60 min, the position of every single egg in the salinity gradient column was recorded to calculate the respective density value. This general method has been regularly applied to measure fish egg density (neutral egg buoyancy) for various Baltic fish species including cod, sprat and flatfish from other

Table 1
Catch dates, positions and numbers of acquired batches from cod, plaice and flounder in relation to each stations temperature, salinity and density characteristics measured with CTD-DST loggers. For details on channel (Ch.) and depth structure of the trawling areas see Fig. 1. Hydrographic data and exact positions were not determined (n.d.) during the experimental campaign in 2010.

ID #	Date			Area SD 22 (DST/CTD-measurement)		Measured batches (n)			Temperature (°C)		Salinity (psu)		Density (g cm ⁻³)		Depth (m)
	Year-month-day	Trawling	Coordinates	Cod	Plaice	Flounder	Min	Max	Min	Max	Min	Max	Min	Max	
A	2010 2 09	Vejsnaes West	n.d.	1	1	0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
B	2010 3 09	Vejsnaes West	n.d.	1	1	1	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
C	2010 3 11	Vejsnaes West	n.d.	4	0	0	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
1	2011 1 10	Vejsnaes West	54.685N 10.506E	0	10	0	0.5	2.2	14.4	18.6	1.0116	1.0151	28		
2	2011 1 17	Vejsnaes West	54.705N 10.219E	0	7	0	0.6	1.1	15.2	18.9	1.0123	1.0152	24		
3	2011 1 24	Vejsnaes West	54.710N 10.279E	0	4	0	0.7	1.1	15.0	18.6	1.0121	1.0149	21		
4	2011 1 31	Wattenberg Ch.	54.649N 10.142E	0	0	0	0.3	1.2	15.1	17.8	1.0121	1.0148	23		
5	2011 2 1	Falshoef Ch.	54.766N 10.051E	0	13	0	0.5	1.3	15.4	18.2	1.0124	1.0147	29		
6	2011 2 9	Falshoef Ch.	54.759N 10.051E	3	16	1	1.5	2.2	16.5	20.5	1.0132	1.0165	29		
7	2011 2 17	Vejsnaes West	54.684N 10.160E	5	3	2	1.3	2.5	17.0	21.0	1.0137	1.0168	32		
8	2011 2 28	Rise Ch. L. Belt	54.832N 10.174E	1	7	7	0.4	0.5	16.1	18.3	1.0130	1.0147	31		
9	2011 3 3	Vejsnaes East	54.681N 10.574E	20	0	5	0.3	1.2	17.1	19.5	1.0137	1.0157	27		
10	2011 3 14	Vejsnaes West	54.692N 10.134E	12	4	1	1.2	1.9	14.3	17.8	1.0114	1.0143	18		
11	2011 3 21	Wattenberg Ch.	54.677N 10.137E	5	0	0	1.0	1.8	14.8	18.5	1.0119	1.0149	24		
12	2011 3 30	Vejsnaes West	54.706N 10.293E	11	4	5	2.2	3.2	15.0	18.4	1.0120	1.0147	26		
I	2012 3 13	Vejsnaes West	54.684N 10.160E	0	2	3	2.1	3.5	15.9	18.9	1.0126	1.0151	29		
II	2012 3 14	Vejsnaes East	54.683N 10.494E	0	1	1	2.3	3.1	14.7	18.7	1.0117	1.0149	29		
III	2012 3 29	Vejsnaes East	54.679N 10.590E	0	4	0	4.1	5.3	14.9	22.7	1.0117	1.0179	31		

areas of the Baltic Sea (Nissling et al., 1994, 2002; Petereit et al., 2009). We used density gradient columns similar to the setup described by Coombs (1981) and Coombs et al. (1985). A minimum of 3–4 calibrated glass floats (Spartel, UK) assured the determination of accurate linear calibration curves ($r^2 > 0.99$) for each salinity gradient, which were used to convert the measured heights of the inserted eggs in the column into the respective density values. As density relations are known to be highly temperature sensitive, all measurements were conducted in a temperature controlled climate cabinet at 7.3 ± 0.5 °C with temperature being controlled in addition at the surface of each column after each measurement. The applied temperature range was chosen according to the normal tolerable temperature range of the eggs for all three species (Westernhagen von, 1970).

For the following analyses the mean density values of each egg batch were grouped into 0.0005 g cm^{-3} density classes and absolute and relative frequency distributions were calculated. One subsample of eggs ($n = 6$ –8) per batch was washed with demineralized water to eliminate remaining salt particles, collected in pre-weighed aluminum vials for freeze drying (Christ Alpha 1–4 freeze-drier at -51 °C for 16 h) and finally weighed to the nearest $0.1 \mu\text{g}$ (Sartorius microbalance SC2) the next day. Successful pilot experiments in February and March 2010 delivered first egg density data of a few cod, plaice and flounder individuals (Table 1). However, the sample sizes were not sufficient for a comparative approach between years, but have been included in the 2011 series data since the identical method and sampling area had been chosen. To approve previous years results some density measurements of flounder and plaice egg batches from 2012 have been added in addition (Table 1).

Linear regressions (Sigma Plot 8.02 SPSS Inc.) were used to analyze the effects of egg diameter and dry weight on egg density as well as female size on egg diameter, dry weight and density for all three species. The seasonal development of the mean egg batch density, diameter and dry weight was analyzed by linear regressions over a time period of 49 days in cod and flounder, whereas the investigated period was 79 days for plaice.

2.2. Effect of fertilization salinity on egg density

Three independent salinity trials were performed for each species to assess the impact of different salinity conditions on egg

density during fertilization and short term incubation processes. Artificial seawater of 16, 18, 20 and 22 psu was prepared with sea salt (SEQUASAL®) and demineralized water and applied during the fertilization and sperm activation process. Each of the salinity solutions contained several fractions of the egg batch, thus homogeneous egg quality should be expected. Egg density values were compared among the 4 salinity treatments by single factor ANOVA ($\alpha = 0.05$) followed by Tukey's HSD post hoc test.

2.3. Effect of ontogeny on egg density

Within the salinity gradient columns changes in egg density were observed daily over the course of ontogenetic development from egg stage IA to hatch. Three egg batches for flounder, four batches for plaice (two subsamples of one egg batch were tested to evaluate the density variation within a batch) and five egg batches in cod were analyzed ($n > 30$ eggs per batch). Subsamples of remaining eggs in the identical batches were kept under similar temperature conditions (7.3 ± 0.5 °C) at 20 psu and development stages were determined daily (Westernhagen von, 1970; Thompson and Riley, 1981). It was carefully checked that dead eggs, which sunk to the bottom of the column, were not measured. We used only 3 of the 5 batches of cod for further calculations since the beginning of egg stage IV was missed in two trials due to logistic difficulties during observations. The total egg development time until first hatch was observed and the thermal sum calculated (thermal sum in day degrees [dd°] = time [days] * temperature [°C]) using 7.3 °C as the mean incubation temperature. When consistent density change patterns in all batches of a species were observed, specific linear regression models (Sigma Plot 8.02 SPSS Inc.) were developed for each batch which described the direction of density change. Subsequently, the overall batch mean slope was calculated and this slope factor was used and multiplied by the duration term until first hatch to parameterize the observed density change. For details see Appendix A1.

2.4. Modeling egg and yolk sac larval survival and horizontal distribution

The applied model is a combination of a three-dimensional eddy-resolving hydrodynamic model (see below) of the Baltic Sea (Lehmann, 1995) with Individual Based Models (IBM) considering

western Baltic cod, plaice and flounder egg stages as well as the yolk sac larval stage until MGO. These IBMs track individuals through the aforementioned life stages. Along the drift trajectories within the coupled model, the temporal egg and yolk sac larval development depended on ambient temperature. Based on experimental work of [Westernhagen von \(1970\)](#) egg development time and duration to MGO were parameterized for each species ([Table 2](#)). A drifter was removed from the model (considered “dead”) when its initially prescribed density value exceeded the density range available at the temporally resolved geographical positions along the drift trajectories. Thus, the survival success of the egg until MGO was determined by absence of contact with the seafloor. The field validation of this assumption requires high resolving bottom egg sampling devices (need still to be developed) including the possibility to judge, if detected eggs have died slightly before (died within the water column) or as a consequence of accumulation at the bottom. Even the production of demersal eggs by a conspecific population, as realized e.g. by the sympatric Baltic Sea flounder population, results in a higher egg mortality rate compared to the sympatric population spawning pelagic eggs ([Nissling and Dahlman, 2010](#)). Potential causes for the increased mortality could be predation, infestation of bacteria ([Nissling and Dahlman, 2010](#)) or marine fungi. Accordingly, the circumstance that species have evolutionary adapted by e.g. thickening their egg shell to be able to spawn demersal instead of pelagic eggs, make it highly unlikely that the survival of purely pelagic eggs is not severely reduced by bottom contact. No temperature dependent mortality term was included in our model because water temperatures during the two analyzed scenario years were above critical values ($>2\text{ }^{\circ}\text{C}$; [Westernhagen von, 1970](#)) for the three analyzed species. More details on the relevance of temperature dependent egg mortality in the Western Baltic Sea can be found in [Hinrichsen et al. \(2012\)](#).

2.4.1. 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, necessary to adapt the model to the Baltic Sea can be found in [Lehmann \(1995\)](#) and [Lehmann and Hinrichsen \(2000a\)](#). A detailed analysis of the Baltic Sea circulation has been performed by [Lehmann and Hinrichsen \(2000b\)](#) and by [Lehmann et al. \(2002\)](#). An explicit validation for one of the study periods, the inflow situation in 1992/1993, can be found in [Lehmann \(1995\)](#). 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 mean runoff database ([Bergström and Carlsson, 1994](#)). Prognostic variables of the model are the baroclinic current field, the 3-D temperature, salinity and oxygen distributions, the 2-D surface elevations and the barotropic transport. 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](#)).

2.4.2. Drifter release locations

Drifters were released into the model in areas exceeding 20 m depth in the Kiel Bight, Femern Belt and western parts of the Mecklenburg Bight (all SD 22). These areas cover known major spawning grounds of the western Baltic cod ([Thurow, 1970](#); [Westernhagen von et al., 1988](#); [Hüssy, 2011](#)). No peer reviewed information is available for the specific spawning areas of plaice and flounder in this region, therefore areas identical to cod spawning were assumed. This assumption was supported by the detection of large proportions of plaice and flounder individuals in spawning conditions during the commercial fishing cruises and through personal communications with local fishermen. In order to consider the seasonal variability of the spawning environment in relation to its spatial and temporal variability, locations were extracted at a 5×5 km grid within the spawning areas. These locations were taken for the initial releases of the drifting particles representing newly spawned and fertilized eggs of cod, plaice or flounder. In the vertical domain particles were released at every 1 psu step between 15 and 25 (representing $\sim 1.0116\text{ g cm}^{-3}$ and $\sim 1.0195\text{ g cm}^{-3}$ at $7\text{ }^{\circ}\text{C}$, respectively), where available in the water column. These density layers covered the range of the results from the vertical distribution of the density experiments. Survival rates of drifters released at each density layer were calculated separately. In a consecutive step, each survival rate at each density layer was then weighted by the species specific relative frequency occurrence of the egg densities derived from the experiments. With this approach, we were able to use the experimentally derived information of egg densities to construct the initial vertical distribution of drifting particles during the species specific spawning seasons.

2.4.3. Particle tracking

Simulated three-dimensional velocity fields were extracted at 1 h intervals in order to develop databases for the particle tracking exercises of the eggs and yolk-sac larvae from the three species. These data sets offer the possibility to derive Lagrangian drift routes from Eulerian flow fields by calculating the advection of “marked” water particles. If definite patterns in egg density change were observed during the ontogenetic trials, a term of ontogenetic

Table 2

Parameters of exponential equations fitted to the temperature derived egg development times in days from fertilization to hatch and fertilization to mouth gap opening (MGO) at 20 psu for cod, flounder and plaice eggs and early larvae ([Westernhagen von, 1970](#)). Experiments were conducted with individuals caught in Femern Belt, western Baltic Sea (ICES SD 22) and development times were extracted from presented figures (# 17, #32 and #42) by [Westernhagen von \(1970\)](#).

Species	Exponential function	Coefficient	St. error	<i>t</i>	<i>p</i>	<i>r</i> ² _{adjusted}
Cod Egg development MGO	Time [days] = $a * \exp(-b * \text{TEMP})$	<i>a</i> : 45.4465	1.5626	29.084	<0.001	0.99
		<i>b</i> : 0.1609	0.0078	20.6124	<0.001	
		<i>a</i> : 49.2852	2.1898	22.5067	<0.001	
		<i>b</i> : 0.1613	0.0101	15.9700	<0.001	
Plaice Egg development MGO	Time [days] = $a * \exp(-b * \text{TEMP})$	<i>a</i> : 44.431	2.2126	20.0807	<0.001	0.98
		<i>b</i> : 0.1478	0.0109	13.5294	<0.001	
		<i>a</i> : 45.9746	1.2506	36.7635	<0.001	
		<i>b</i> : 0.1424	0.0059	24.2105	<0.001	
Flounder Egg development MGO	Time [days] = $a * \exp(-b * \text{TEMP})$	<i>a</i> : 30.3288	1.9149	15.8386	<0.001	0.79
		<i>b</i> : 0.1754	0.0149	11.7808	<0.01	
		<i>a</i> : 56.809	2.6436	21.4891	<0.001	
		<i>b</i> : 0.1849	0.0112	16.4462	<0.001	

density changes over development time was included in the model (see Section 2.3 for details). If not, the particles were allowed to stay at the buoyancy (density) levels at which they initially were launched for their whole drift periods. This means that due to temporal variations in the vertical water mass characteristics the particles must not necessarily persist at the same water depth levels where they originally had been released at the beginning.

The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge–Kutta scheme (Hinrichsen et al., 1997). In this modeling study, we examined the drift and development of eggs and yolk sac larvae released into simulated flow fields at developmental egg stage IA by 1 hourly time steps. We stopped the simulations when yolk sac larvae started to become mixed feeding larvae (MGO). We showed final drift positions

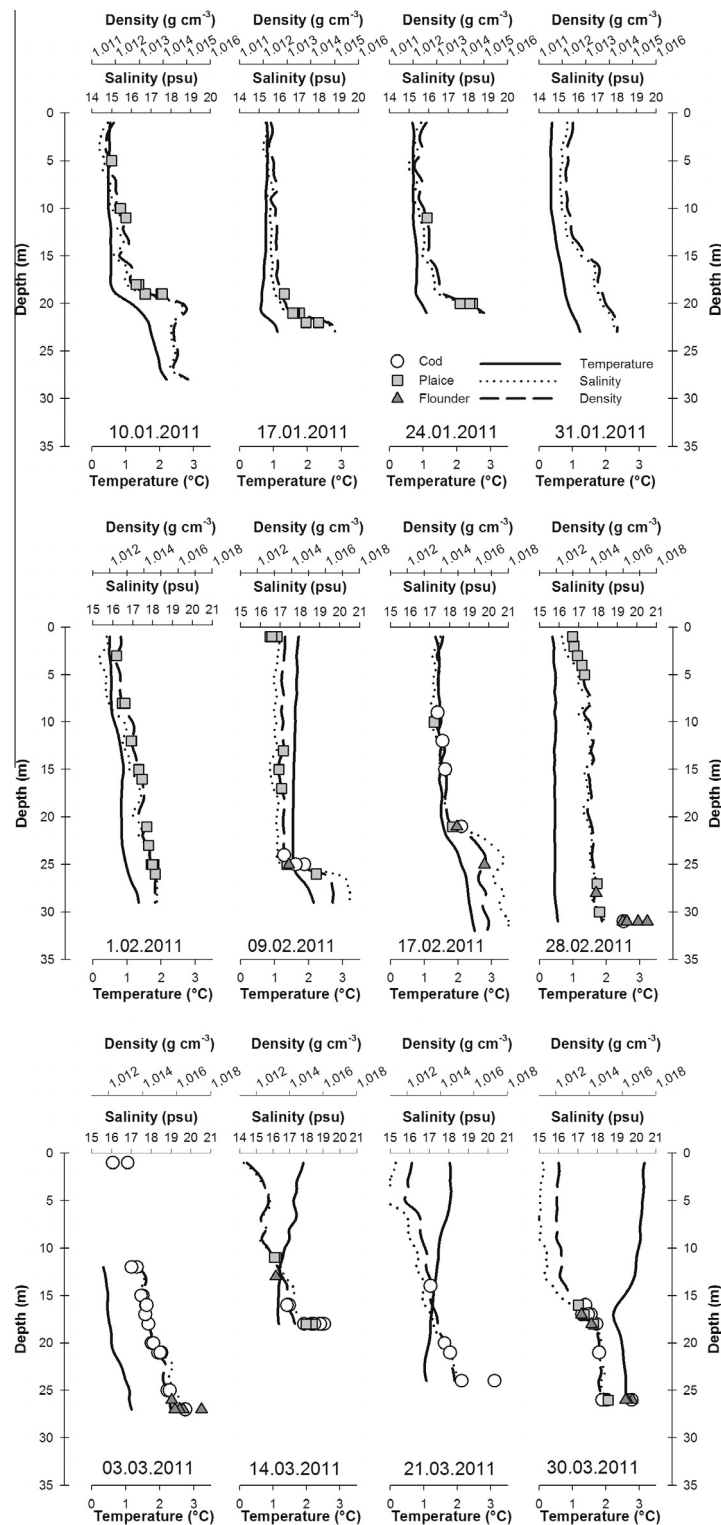


Fig. 2. Depth distribution of egg batches as derived by experimental egg density measurements in 2011. Hydrographic profiles were measured with DST-CTD (temperature and salinity averaged from 3 casts) following the first haul of the fisheries day (respective date). For the geographic areas see Table 1, but note that no real station grid with identical positions has been sampled.

of all surviving drifters of each cohort, differentiating between early, mid and late spawning season.

2.4.4. Model experiments

The main purpose of our modeling study was to analyze the spatial and temporal distributions of cod, plaice and flounder early life

stages and the changes in seasonal survival proportions. In a first experiment, we treated eggs and yolk sac larvae as absolutely passive drifters, i.e. they remain at the initially prescribed buoyancy levels. Their final spatial distribution was exclusively determined by their survival success along the drift routes. In a second experiment solely for cod, we compared this output with the results of

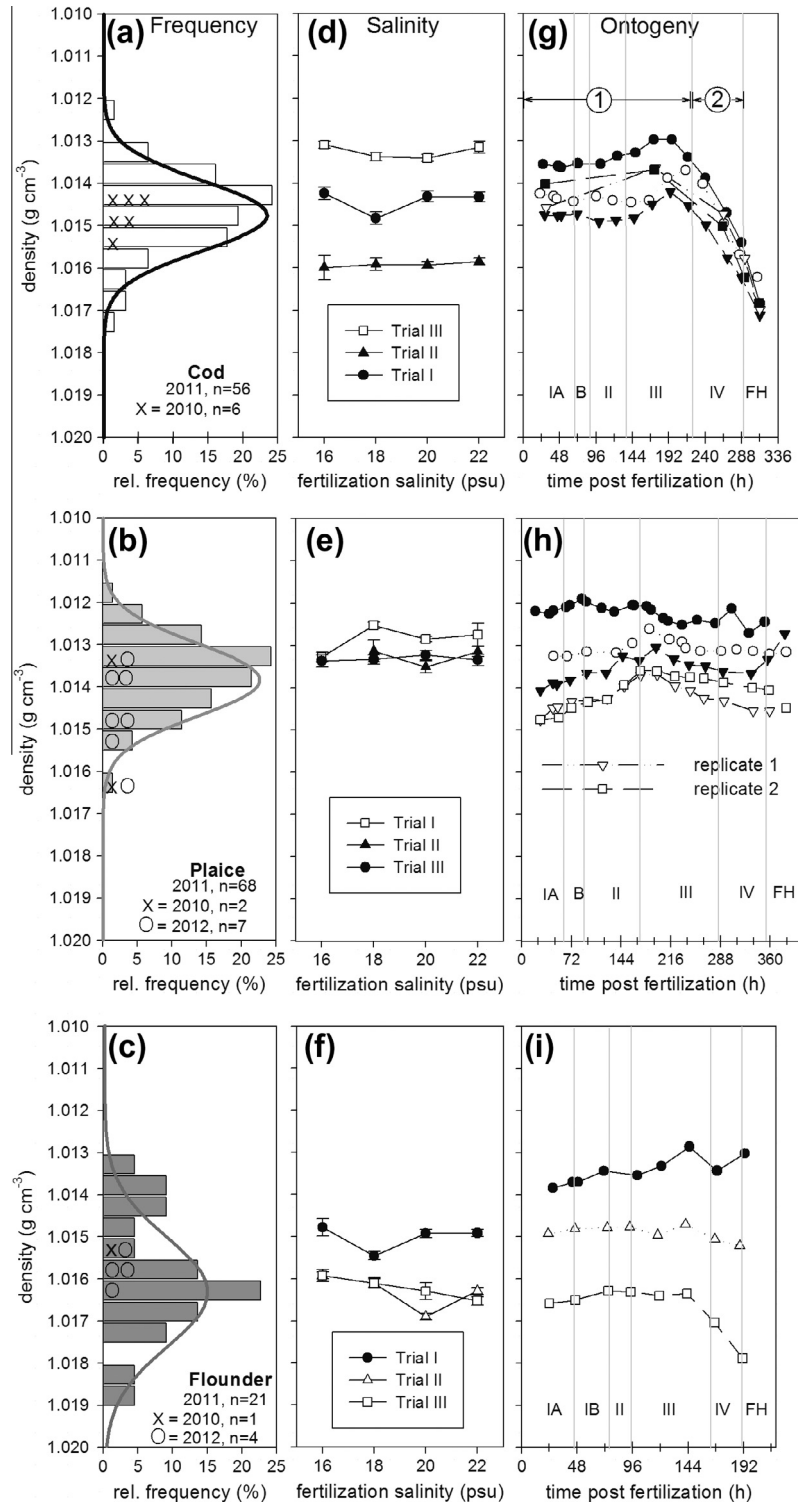


Fig. 3. (a–c) Relative frequency distributions of measured mean batch density values of cod, plaice and flounder eggs grouped into 0.0005 g cm⁻³ classes. Bars indicate results of 2011 experimental campaign, results from the 2010 pilot study are signed by crosses and were included in the calculations of the normal distribution models (for details see Table 4). (d–f) Three trials, each with different individuals per species, were used for the salinity fertilization experiment. Shown are mean \pm standard deviation of $n > 25$ eggs per salinity treatment (for details refer to Table 6). (g–i) Means of egg density values in relation to development time (IA–IV) until first hatch (FH). Please note that time axes differ between species. (g) Numbers in circles refer to different time periods for the drift modeling process.

observed ontogenetically related density modification during late egg stages. Variability in the duration of the egg and yolk sac larval drift depended on temperature (Westernhagen von, 1970) which in this study converted to the amount of time taken for stage IA eggs to develop to mixed feeding larvae. Changes in temperature may result from several mechanisms including up- and down-welling events, advection of anomalously cold or warm water masses as well as seasonal warming and cooling. Drifters representing cod, plaice or flounder eggs were released at the aforementioned release locations at 10 day intervals. In order to cover the entire spawning period of the three species, the simulations commenced on December 1st and lasted until May 30th. The particle tracking model was utilized for two selected years with different hydrographical conditions to obtain intra- and inter-annual variability in distribution and transport patterns. In 1988, relatively low and variable wind forcing prevailed, whereas, due to sustained strong, mainly westerly, winds, in January 1993, a major inflow to the Baltic Sea occurred. In addition, these two years have already been compared by Hinrichsen et al. (2001) with a different approach to follow the potential advective exchange of cod early life stages between the western and eastern Baltic cod stocks. Thus, the outcome of the present study can be directly compared.

3. Results

3.1. Vertical egg distribution following hydrographic profiles

According to the measured mean batch densities, specific depth distributions have been calculated for each individual on the respective date (Fig. 2). Some profiles show pronounced density stratifications (e.g. 10.01., 09.02., 17.02., 30.03.2011) at about 20–25 m depth and the associated accumulation of plaice and cod egg batches. Alternatively, batches from plaice or cod eggs

were assigned to almost all depth layers at a station at some dates (01.02. or 03.03.2011) including even the top layers (28.02.2011). On the contrary, flounder egg batches were found in general close to the bottom layer or theoretically even deeper according to density measurements (18.02. or 03.03.2011) and also directly in the halocline (09.02 or 30.03.2011).

3.2. Egg density distributions, diameters and dry weights

3.2.1. Cod

In 56 egg batches of cod (size range of females 30–101 cm), the egg density ranged from 1.012 to 1.017 g cm⁻³ with a mean of 1.0146 g cm⁻³ (Fig. 3a and Table 3). A normal distribution function was fitted to the relative frequency distribution (Fig. 3a); all parameters were highly significant (Table 4; $p < 0.001$; $r^2_{\text{adj}} = 0.96$) with the calculated egg density peak of 1.0148 g cm⁻³ from all measured batches (2010 and 2011 combined). Egg diameters ranged from 1.23 to 1.57 mm with an overall mean of 1.43 mm and an overall mean egg dry weight of 0.082 mg, respectively (Table 3). No significant linear relationship could be found for cod egg density and egg diameter (Fig. 4; $p = 0.59$) but a weak correlation was detected between egg density and egg dry weight ($p < 0.05$). Female size of cod had no significant effect on egg diameter (Fig. 5; $p = 0.15$), egg dry weight ($p = 0.33$) or egg density ($p = 0.75$).

3.2.2. Plaice

In total, 68 plaice batches (size range of females 28–52 cm) were analyzed and the egg densities ranged from 1.011 to 1.015 g cm⁻³ with a mean density of 1.0136 g cm⁻³ (Fig. 3b and Table 3). The fitted normal distribution model (Fig. 3b) resulted in a peak at 1.0138 g cm⁻³ with all parameters being highly significant (Table 4; $p < 0.001$; $r^2_{\text{adj}} = 0.97$). Egg diameters ranged from 1.49 to 1.98 mm (mean 1.80 mm) and the mean egg dry weight was

Table 3

Size ranges, means of total lengths and numbers of analyzed cod, plaice and flounder females caught in the Kiel Bight, western Baltic Sea (Belt Sea; ICES SD 22) from January 10th to March 30th 2011. Shown are measured numbers of batches and eggs respectively and the ranges and means with standard deviations (std) of the traits egg diameter, egg dry weight and egg density.

Species	Female length (cm)			Egg (stage IA) – diameter; dry weight; density			
	Range	Mean	<i>n</i>	Trait	Range	Mean ± std	#Batch (eggs)
Cod	30–101	46	57	Diameter (mm)	1.23–1.57	1.43 ± 0.07	57 (1838)
				Dry weight (mg)	0.053–0.117	0.082 ± 0.012	57 (399)
				Density (g cm ⁻³)	1.0122–1.0172	1.0146 ± 0.0009	56 (1769)
Plaice	28–52	35	68	Diameter (mm)	1.49–1.98	1.80 ± 0.09	68 (2433)
				Dry weight (mg)	0.079–0.225	0.156 ± 0.024	64 (469)
				Density (g cm ⁻³)	1.0118–1.0154	1.0136 ± 0.0007	68 (2009)
Flounder	31–49	38	23	Diameter (mm)	0.92–1.15	1.06 ± 0.06	23 (733)
				Dry weight (mg)	0.031–0.052	0.039 ± 0.005	22 (155)
				Density (g cm ⁻³)	1.0132–1.0189	1.0160 ± 0.0015	21 (566)

Table 4

Parameters and statistics of normal distribution functions fitted to the relative frequency data of egg batch mean density values of western Baltic Sea cod, plaice and flounder eggs from experiments performed during January to March in 2010 and 2011.

Species	Normal distribution $f =$	Coefficient	St. error	<i>t</i>	<i>p</i>	r^2_{adjusted}
Cod	$a * \exp(-0.5 * ((x - x_0)/b)^2)$	<i>a</i> : 23.4469	1.0262	22.8488	<0.0001	0.96
		<i>b</i> : 0.0008	0.00004	19.735	<0.0001	
		<i>x</i> ₀ : 1.0148	0.00004	24237.4234	<0.0001	
Plaice	$a * \exp(-0.5 * ((x - x_0)/b)^2)$	<i>a</i> : 23.4486	0.7825	29.9672	<0.0001	0.97
		<i>b</i> : 0.0009	0.00003	25.939	<0.0001	
		<i>x</i> ₀ : 1.0138	0.00003	30757.1807	<0.0001	
Flounder	$a * \exp(-0.5 * ((x - x_0)/b)^2)$	<i>a</i> : 14.6542	2.1428	6.8389	<0.0001	0.63
		<i>b</i> : 0.0013	0.0002	5.9207	<0.0001	
		<i>x</i> ₀ : 1.0163	0.0002	4638.5651	<0.0001	

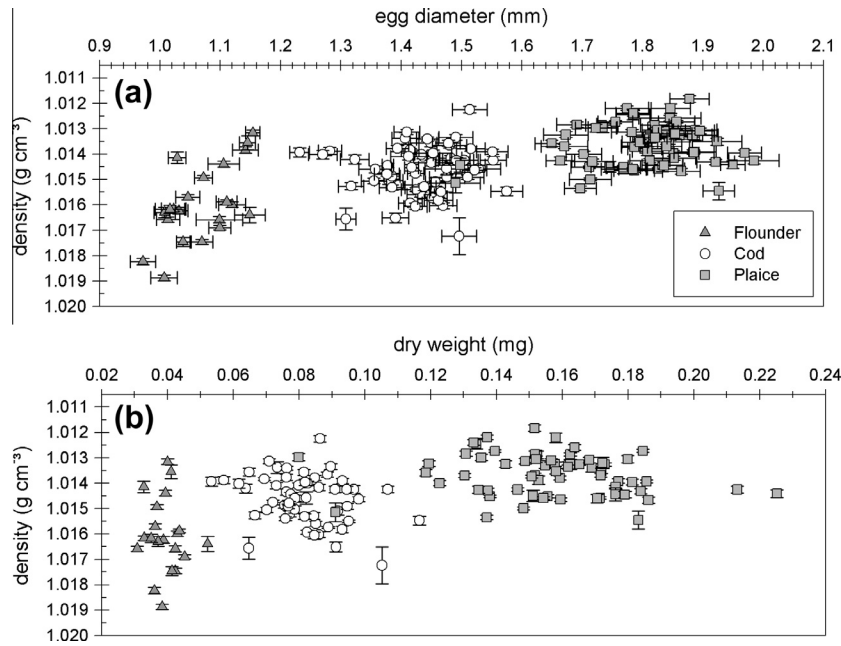


Fig. 4. (a) Means \pm standard deviations (std) of egg density versus egg diameter means (\pm std) of cod, plaice and flounder egg batches ($n \sim 30$ eggs) from SD 22 (Belt Sea). (b) Mean (\pm std) egg density versus mean egg dry weight (pooled samples of $n = 6$ –8 eggs per batch).

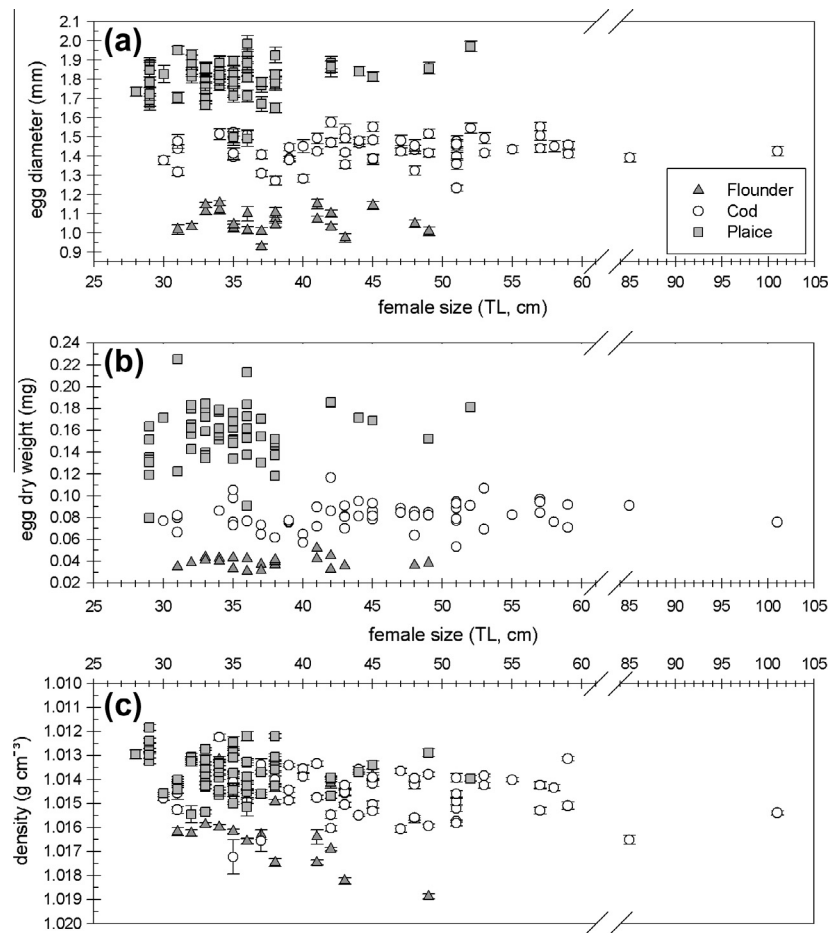


Fig. 5. Female sizes of cod, plaice and flounder caught in SD 22 (Belt Sea) versus (a) means \pm standard deviation (std) of egg batch diameter, (b) egg batch dry weight and (c) mean (\pm std) egg batch density.

0.156 mg (Table 3). Egg density was not significantly related to egg diameter or egg dry weight (Fig. 4; $p = 0.15$; $p = 0.17$). Female size in plaice was not significantly related to egg diameter, egg dry weight or egg density (Fig. 5; $p = 0.21$; $p = 0.08$; $p = 0.13$).

3.2.3. Flounder

Twenty-three flounder batches (female size range 31–49 cm) were analyzed during the 2011 campaign (Table 3). The egg density range was the broadest of all species and ranged from 1.013 to 1.018 g cm⁻³ with a mean value of 1.016 g cm⁻³ (Fig. 3c and Table 3). Egg densities of two batches could not be calculated since density exceeded the prepared density range in the salinity gradient column and eggs hit the bottom. The normal distribution model was significant but the correlation coefficient explained less variability compared to the results of cod and plaice (Table 4; $p < 0.001$; $r^2_{\text{adj}} = 0.63$). Egg diameters ranged between 0.92 and 1.15 mm (mean 1.06 mm) with measured dry weights ranging

from 0.031 to 0.052 mg (Fig. 4 and Table 3). Mean egg density was significantly related to mean egg diameter (Fig. 4; $p < 0.01$; $r^2_{\text{adj}} = 0.33$) with larger eggs displaying a lower density (increased buoyancy), but not related to mean egg dry weight ($p = 0.74$). Female size (Fig. 5) did not show any significant relation either to mean egg diameter ($p = 0.19$), mean egg dry weight ($p = 0.99$) or mean egg density ($p = 0.62$).

3.3. Seasonality (spawning season)

3.3.1. Cod

Even though a significant egg diameter decrease (Fig. 6b; Table 5; $p < 0.001$; $r^2_{\text{adj}} = 0.19$) could be observed over the course of the spawning season no significant trend in egg density was found ($p = 0.28$; Fig. 6a). The mean dry weight of the eggs decreased significantly ($p < 0.05$), but with low explanatory power ($r^2_{\text{adj}} = 0.09$; Fig. 6c).

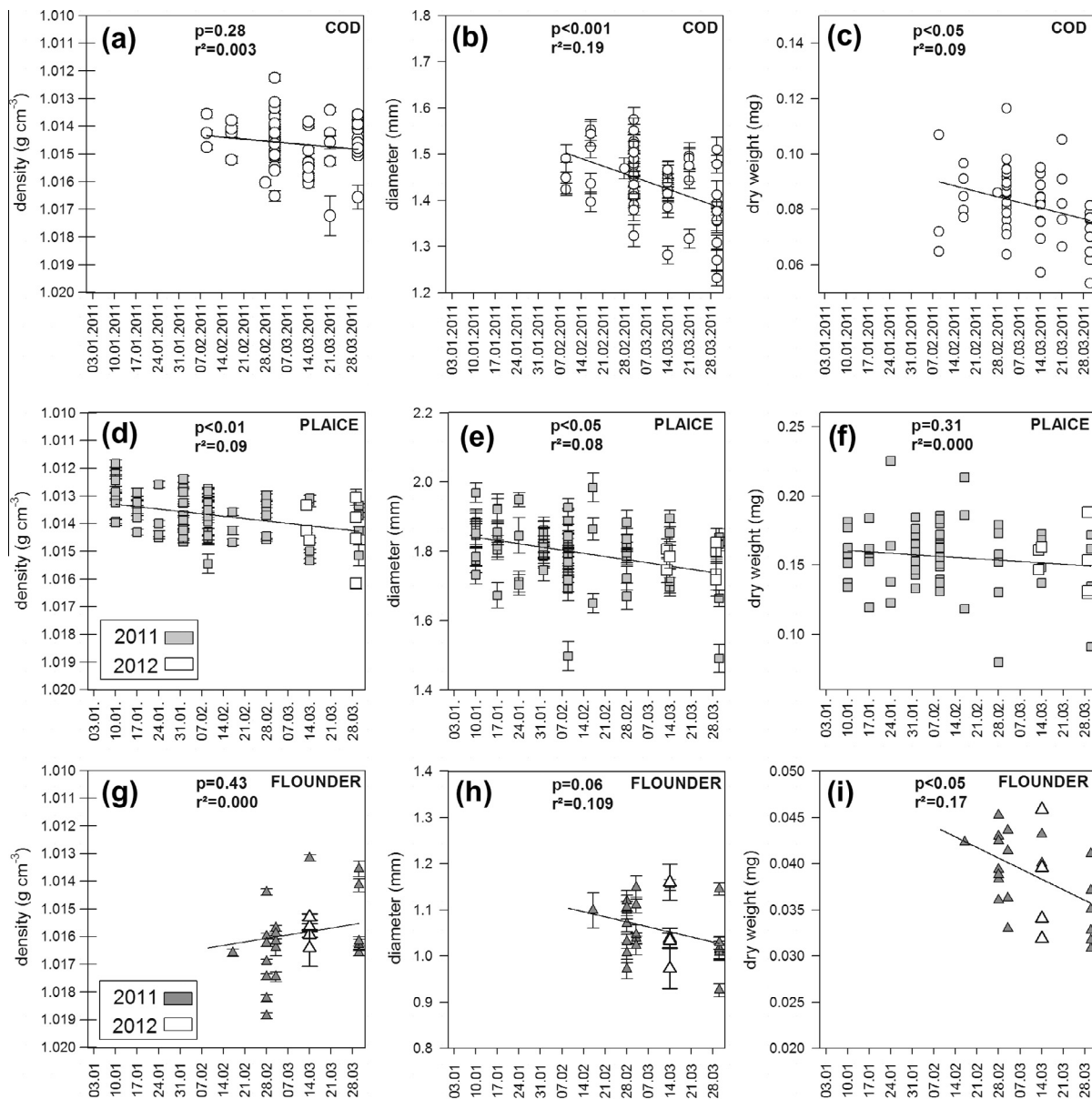


Fig. 6. Seasonal development of egg batches: density (a, d and g), diameter (b, e and h) and dry weight (c, f and i). Data from 2011 experiments were used for the linear regression analyses in cod (a–c), plaice (d–f) and flounder (g–i). Data from 2012 experiments are shown as additional, independent results from single egg batches from only plaice and flounder.

Table 5

Statistical results of linear regression analyses of the seasonal development of egg density, egg diameter and egg dry weight of cod, plaice and flounder eggs over 49 (cod and flounder) and 79 days (plaice), respectively.

Species	Linear regression $f =$	Coefficient	St. error	t	p	r^2_{adjusted}
Cod	$y_0 + a * x$	$a: -23.776$	22.785	-1.043	0.301	0.003
Density		$b: 0.00001$	0.000009	1.088	0.281	
Diameter		$a: 5806.24$	2527.74	3.800	<0.001	0.19
		$b: -0.0024$	0.0006	-3.799	<0.001	
Dry weight		$a: 700.251$	268.513	2.6079	<0.05	0.09
		$b: 0.0003$	0.0001	-2.607	<0.05	
Plaice	$y_0 + a * x$	$a: -29.311$	10.6058	-2.763	<0.01	0.09
Density		$b: 0.000012$	0.000004	2.8593	<0.01	
Diameter		$a: 3235.53$	1232.14	2.6259	<0.05	0.08
		$b: -0.0013$	0.0005	-2.6245	<0.05	
Dry weight		$a: 351.2133$	343.349	1.0229	0.310	<0.00
		$b: -0.0001$	0.0001	-1.0224	0.310	
Flounder	$y_0 + a * x$	$a: 44.879$	55.992	0.8015	0.432	<0.00
Density		$b: 0.0000$	0.0000	-0.7834	0.443	
Diameter		$a: 3839.66$	1993.498	1.9261	0.067	0.109
		$b: -0.0016$	0.0008	1.9256	0.067	
Dry weight		$a: 400.864$	173.7980	2.3065	<0.05	0.17
		$b: -0.0002$	0.0001	-2.3063	<0.05	

3.3.2. Plaice

Plaice egg diameter decreased ($p < 0.05$; $r^2_{\text{adj}} = 0.08$; Fig. 6e) and egg density increased ($p < 0.01$; $r^2_{\text{adj}} = 0.09$; Fig. 6d) significantly over the observation period of 79 days. However, eggs showed no change in dry weight (Table 5; $p = 0.31$; Fig. 6f) over the spawning season.

3.3.3. Flounder

Flounder eggs did not exhibit clear coherent seasonal trends but high variability between the different egg batches was detected. Non-significant trends towards decrease in egg diameter (Fig. 6h; Table 5; $p = 0.07$) and egg density (Fig. 6g) were found during the course of the analyzed season. Mean egg dry weight decreased significantly over the season ($p < 0.05$; $r^2_{\text{adj}} = 0.17$).

3.4. Salinity

3.4.1. Cod

Statistically significant differences in mean egg densities due to different fertilization and short term incubation salinities (16, 18, 20 or 22 psu) were found (Fig. 3d and Table 6). Both, the intensity of change and the trend of an increase or decrease in salinity differed among the trials, however, they did not show any coherent patterns (Fig. 3d). Consequently, the vertical distribution was modeled without a salinity dependent term modifying the vertical distribution in dependence of the salinity at the release position.

3.4.2. Plaice

The different fertilization and incubation salinities did not show consistent trends affecting egg buoyancy levels (Fig. 3e and Table 6). The differences of egg densities between the salinities varied among the trials between 0.0003 and 0.0009 g cm^{-3} (Table 6). As a consequence, similar to cod no salinity dependent function was applied in the modeling exercise.

3.4.3. Flounder

Results of all three trials attested significant influences of fertilization and short term incubation salinity on the mean egg density (Table 6). The differences of the egg densities between the salinities ranged among the trials between 0.0007 and 0.0011 g cm^{-3} (Fig. 3f, Table 6). The lowest salinity of 16 psu led in all three trials to the lowest density values. Results from trial III exhibited a continuous trend of density increase with increasing salinity, which however was not obvious for the other trials. Therefore, similar to the other species, no salinity dependent function was included in the modeling exercise.

3.5. Ontogeny

3.5.1. Cod

Cod eggs developed at mean temperature of 7.3 °C on average for 312 h post-fertilization (hpf) to first hatch which equaled a thermal sum of about 95 dd°. The survival rates of the 5 batches within the column until 288 hpf ranged from 75% to 100%. The continuous

Table 6

Statistical parameters of single-factor ANOVA of egg density measurements from different salinity treatments (16, 18, 20, 22 psu) during fertilization and short term incubation of cod, plaice and flounder eggs. Different superscript letters indicate significant differences ($\alpha = 0.05$) between salinity levels. Density ranges with resulting density differences (delta) as well as the general trend from low to high incubation salinity are given. Eggs could not be fertilized in the plaice trial II at 16 psu (n.f.).

Species	Trial	F	p	Tukey HSD post hoc	Density range at 16–22 psu	Delta density	Visual trend
Cod	I	$F_{3,108} = 3.66$	<0.05	16 ^a , 18 ^b , 20 ^a , 22 ^a	1.0158–1.0160 (g cm^{-3})	0.0003	Divergent
	II	$F_{3,113} = 122.15$	<0.001	16 ^a , 18 ^b , 20 ^a , 22 ^a	1.0142–1.0148 (g cm^{-3})	0.0007	Divergent
	III	$F_{3,124} = 69.69$	<0.001	16 ^{ad} , 18 ^{bc} , 20 ^{bd} , 22 ^{ae}	1.0131–1.0134 (g cm^{-3})	0.0004	Dome shaped
Plaice	I	$F_{3,126} = 133.71$	<0.001	16 ^a , 18 ^b , 20 ^c , 22 ^d	1.0125–1.0133 (g cm^{-3})	0.0009	Divergent
	II	$F_{2,71} = 33.85$	<0.001	16 n.f., 18 ^a , 20 ^b , 22 ^a	1.0131–1.0135 (g cm^{-3})	0.0005	Dome shaped
	III	$F_{3,120} = 7.59$	<0.001	16 ^a , 18 ^a , 20 ^b , 22 ^a	1.0132–1.0134 (g cm^{-3})	0.0003	Divergent
Flounder	I	$F_{3,110} = 135.37$	<0.001	16 ^a , 18 ^b , 20 ^c , 22 ^c	1.0148–1.0155 (g cm^{-3})	0.0008	Divergent
	II	$F_{3,120} = 753.22$	<0.001	16 ^a , 18 ^b , 20 ^c , 22 ^d	1.0159–1.0169 (g cm^{-3})	0.0011	Divergent
	III	$F_{3,122} = 91.77$	<0.001	16 ^a , 18 ^b , 20 ^c , 22 ^d	1.0159–1.0165 (g cm^{-3})	0.0007	Density increase

monitoring revealed similar density characteristics for 5 egg batches (Fig. 3g). The mean density level of stage IA to early stage III eggs exhibited only minor variations within each batch. Subsequently, slight egg density decreases could be observed until about mid stage III followed by continuous density increases to late stage III/early stage IV (Fig. 3g). At beginning of stage IV, the approximate initial density level of stage IA eggs was reached again, followed by a continuous increase in density throughout stage IV. Therefore, we applied a two step approach for the egg phase in our model. At first, a level of stable conditions in egg density development from stage IA to end of stage III was used (Fig. 3g, labeled with encircled 1). The duration of this phase is about 77% (~ 73 dd°) of the total development time from fertilization to first hatch. The second step included a linear density increase term from the beginning of egg stage IV to first hatch (Fig. 3g, termed with encircled 2). The duration of this phase is about 23% of the total egg development time (~ 22 dd°, rounded up from 21.4 ± 0.06 dd°). A slope value of 0.00011 ± 0.00002 g cm⁻³ dd°⁻¹ (mean \pm standard deviation) was calculated based on the analyses of three batches. We used the presented slope value in combination with the observed duration of 22 dd° in our modeling approach. Details per trial and alternative expressions for the density increase (slope coefficients h⁻¹ or day⁻¹) are summarized in Table A.1.

3.5.2. Plaice

The analyses of the continuous mean density development of the 4 egg batches (one batch in duplicate) from stage IA to first hatch revealed no clear trends of density change in plaice (Fig. 3h). Three out of four trials exhibited a small decreasing trend with a magnitude of approximately 0.001 g cm⁻³ from stage IA to the end of stage II,

subsequently declining until the end of stage IV. At first hatch, egg density decreased in one batch and remained similar to the last egg stage in the other batches. The differences in the duplicated batch were small, a slight reduced density trend was observed for replicate 2 compared to replicate 1. Since the overall egg density changes from early stage IA to first hatch in at least 3 of 4 trials remained below a magnitude of 0.0005 g cm⁻³, which corresponds to the size of the selected grouping interval, no term of ontogenetic density changes has been included in our modeling process.

3.5.3. Flounder

The egg survival until 167 hpf, which was the last measurement before hatching started, ranged from 82% to 100% between replicates. During the first half of the total development time (egg stage IA to II) only very minor density modifications were recorded in all three batches (Fig. 3i). The latter half (late stage III to first hatch) was inhomogeneous since egg density decreased (~ 0.001 g cm⁻³), increased (>0.001 g cm⁻³) or remained constant depending on batch (Fig. 3i). Therefore, no specific term of density change during ontogeny was included in the model.

3.6. Modeled horizontal distribution and seasonal survival rates

3.6.1. Transport potentials from newly spawned egg stage to the mixed feeding yolk sac larval stage (MGO)

Cod, plaice and flounder early life stages survived until the beginning of the mixed feeding period almost exclusively if they remained in the deeper parts of the Great Belt, in the Kiel Bight, in and around the Femern Belt or in the Mecklenburg Bight (Figs. 7 and 8). With the exceptions of single released drifters, no final drift

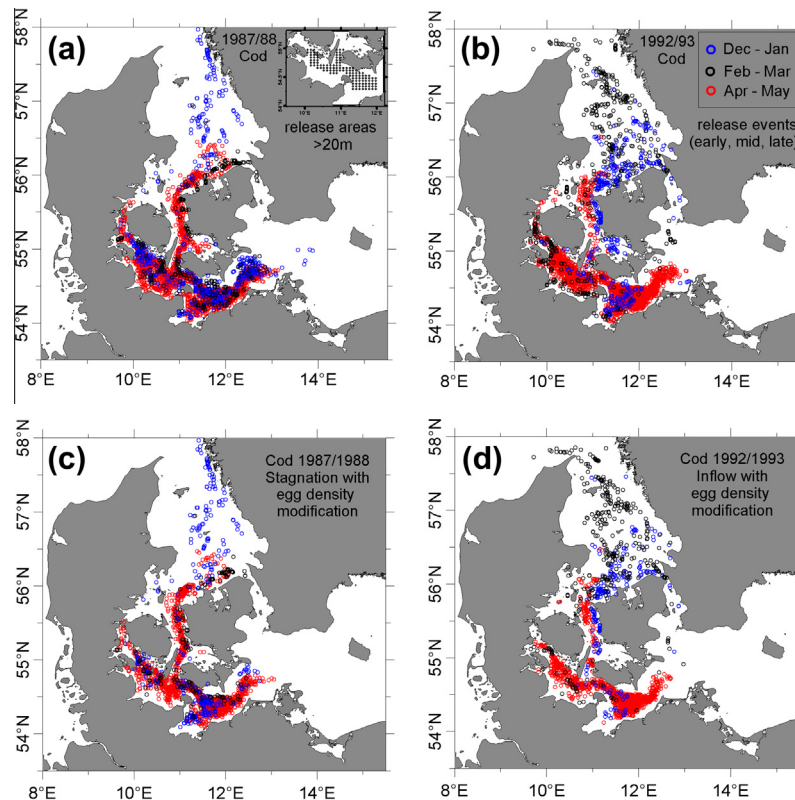


Fig. 7. Final position of drifters representing identical density levels as cod eggs after accomplishing the passive drift phase. This phase covered the duration from egg stage IA lasting until the mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO). Individual drifters were released on 19 events every 10 days from December 1st to May 30th covering the spawning season of cod. According to the species' natural spawning season the release events were separated by color code [early (blue), mid and peak (black) or late (red) season]. (a) Small insert: Grid of drifter release positions in Kiel Bight, Femern Belt and western Mecklenburg Bight in areas > 20 m. Two divergent hydrographic situations have been simulated, the 'stagnation' period 1987/1988 and the major Baltic inflow event 1992/1993. (a) and (b) Final drift positions without ontogenetically derived egg density increase. (c) and (d) Final drift positions including ontogenetically derived egg density increase.

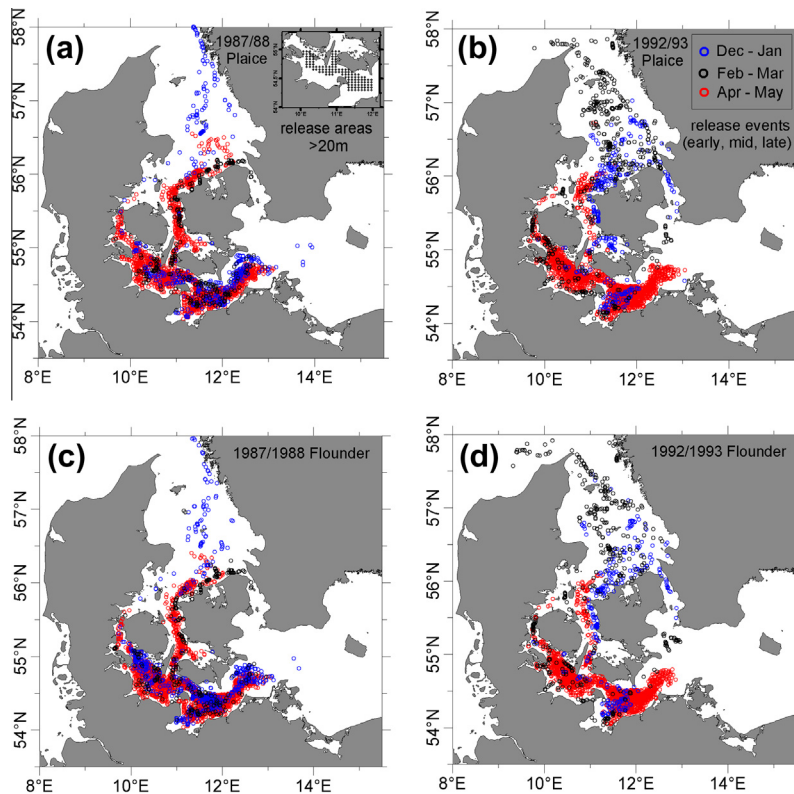


Fig. 8. Final positions of drifters representing identical density levels as plaice (a and b) or flounder (c and d) eggs after accomplishing the passive drift phase. This phase covered the duration from egg stage IA lasting until the mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO). Individual drifters were released on 19 events every 10 days from December 1st to May 30th covering the spawning season of the two species. According to the species natural spawning seasons the release events were separated by color code [early (blue), mid (black) or late (red) season]. (a) Small insert: Grid of drifter release positions in Kiel Bight, Femern Belt and western Mecklenburg Bight in areas >20 m. Two divergent hydrographic situations have been simulated, the 'stagnation' period 1987/1988 and the major Baltic inflow event 1992/1993. No ontogenetically derived changes in egg density have been applied in the modeling.

position was found east of a line from the island of Moen (Denmark) to Kap Arkona on Rügen (Germany). This area is still outside of the central deep Arkona Basin. The general drift patterns were observed irrespective of different large scale hydrographic conditions like stagnation periods or a major Baltic inflow situation. Regularly, some yolk sac larval cohorts (in both years released in January) drifted out of the western Baltic into the Kattegat (SD 21). Especially during the inflow scenario, released particles in February and March reached both the Kattegat and even areas further north or drifted towards the German and Danish mainland coast and the Little Belt. Drift routes of particles released in April and May terminated in the Little Belt, Kiel Bight, Mecklenburg Bight and the Great Belt, but much less in the Kattegat. The final locations were never found in SD 25 or other areas within the central Baltic Sea, independent of species and hydrographic conditions, i.e. inflow or stagnation scenario.

3.6.2. Seasonal survival variability within and between species

3.6.2.1. Seasonal mean survival rates per salinity class. Plaice early life stages experienced higher survival rates compared to cod (Fig. 9a), while the survival rate of flounder was lowest (Fig. 9c). Early in December, released cohorts showed survival rates between 30% and 40% in all three species during the stagnation year 1987/1988 but <5% in 1992/1993 shortly before the Baltic inflow (Fig. 9a–c). Cohorts released during the period January, February and March produced mostly low proportions of surviving larvae, <10% during the stagnation year and <20% during the inflow year. Only two survival peaks occurred mid January (~20% cod; ~30% plaice; ~15% flounder) and mid March (in about the same magnitude) during the stagnation year. In contrast, the February

release events produced the highest survival peak (~15% cod; ~20% plaice; ~10% flounder) during the first three month of the inflow year (Fig. 9a–c). Survival rates increased for all three species from April to end of May, with a moderate reduction from mid April to early May. Over 50% survival rates were only found late in the season (Fig. 9a–c).

3.6.2.2. Weighted mean survival rates per salinity class. The implementation of the experimentally derived egg density distributions instead of the balanced numbers of drifters in each salinity class resulted in a significant reduction in the survival until the end of the drift period (Fig. 9d–f). The seasonal patterns were kept in both hydrodynamic scenarios for all three species (Fig. 9d–f). Reasons for the considerable reductions are the depletion of salinity classes with very high modeled survival probabilities. For example, in cod only a small proportion of egg batches were detected below salinities of 17, whereas the highest survival probability was predicted for the salinity classes 15 and 16. In cod, maximum weighted survival hardly exceeds 5–8% (Fig. 9d) during inflow conditions with maximum mean survival of ~8% during stagnation and ~6% during inflow situation. The modeled maximum survival rates for plaice were ~13% (inflow) and ~11% (stagnation) and for flounder ~4% and ~6% under stagnation and inflow conditions, respectively. Detailed information about each mean survival rate per salinity class are presented in Figs. 10 and 11, without (a, c, e and f) and including (b, d, f and g) the weighted density frequency distributions for each species.

3.6.3. Impact of ontogenetic density increase term on cod egg survival

The implementation of the proposed density increase function (see Section 3.5.1) resulted in a decrease in cod survival rates

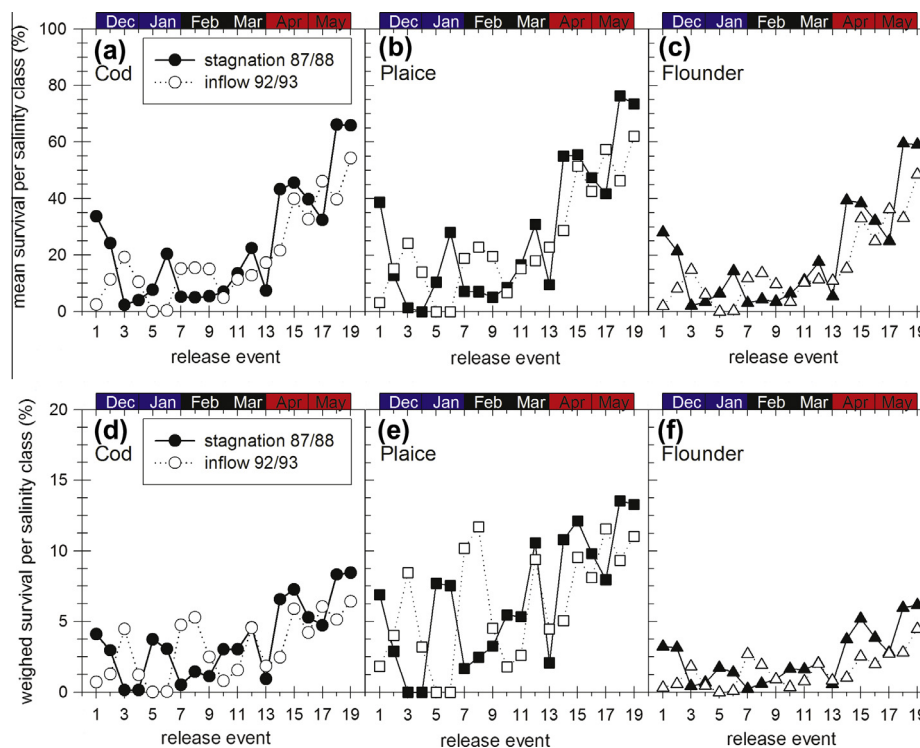


Fig. 9. Mean cohort survival of drifters released at salinity classes from 15 to 25 psu representing the developing early life stages of cod, plaice and flounder from egg stage 1A until the beginning of mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO). (a) cod (b) plaice (c) flounder. Weighted survival per salinity class according to the relative frequencies of the experimentally derived egg batch densities (compare to Fig. 3) of cod (d), plaice (e) and flounder (f) cohorts. Drifter cohorts were released every 10 days from December 1st to May 30th simulating two divergent hydrographical situations, during a stagnation period (1987/1988, black dots) and during a major Baltic inflow event (1992/1993, transparent dots). Color codes for early, mid and late release events are similar as in Fig. 7.

(Fig. 12a versus b). The seasonal trends and the differences both between and within the two hydrographic conditions were only marginally modified (Fig. 12a versus b). However, density modifications resulted in a seasonal (including all 19 release events) mean survival reduction of 43% in the stagnation year 1987/1988 compared to the modeled survival rate without density change (Fig. 12c). During the inflow year 1992/1993, the survival rate was reduced by 41% compared to the scenario without density change (Fig. 12c). During the cod peak spawning season, the reduction was largest with 60% compared to the early release (December–January; 35%) and late release (April–May; 36%) events (Fig. 12c). The maximum survival rate in May during stagnation was reduced by 23% and during the inflow situation by 24%. There was a high variability in the reduction of survival between the release events which followed no obvious temporal pattern (Fig. 12c).

4. Discussions

This study provides the first comprehensive data set on egg densities of western Baltic Sea cod, plaice and flounder. Our results contribute fundamentally to the current scientific knowledge considering that so far no certain information on the depths, where spawning of these species takes place in the western Baltic Sea, is available.

Westernhagen von et al. (1988) found highest abundances of cod, plaice and flounder eggs in the salinity layers between 17.5 and 21 psu (which corresponds at 1 °C to densities of 1.0139–1.0168 g cm⁻³ [Fofonoff and Millard, 1983]). The egg densities measured in our study match well with these results. Our study addresses factors potentially modifying or influencing the vertical distribution characteristics of cod, plaice and flounder eggs and early yolk sac larvae, like the abiotic factor salinity and the biotic, or more specifically, intrinsic factor of ontogenetic density change.

This combination provides unique input parameters for drift modeling applications of early life stages, which are relevant for several reasons. Our study improves: (i) the understanding of important processes affecting early life stages survival such as the effect of oxygen deficiency and low temperatures, (ii) the so far insufficiently analyzed drift of early life stages to adjacent Baltic areas (e.g. in cod: Hüsey, 2011), and (iii) the assessment of impacts due to anthropogenic activities caused by e.g. increased sediment loads by providing necessary baseline data on egg vertical distribution (Petereit et al., unpublished data).

4.1. Salinity effect on egg density distribution

In central Baltic cod, ambient salinity conditions during gonad maturation and spawning have been suggested to affect the eggs' buoyancy and a pronounced shift of the vertical egg distribution towards higher mean egg densities was observed when high saline water was present in the Bornholm Sea (Wieland and Jarre-Teichmann, 1997; Hinrichsen et al., 2011a). Due to the use of field-caught fish, we had no control on oocyte hydration and spawning status of the single females. In our study it remains unknown if salinity, temperature or oxygen conditions during gonad maturation of cod were exceptional in the analyzed year 2011 or cluster within the seasonal range. The comparison with the egg density results of three species from 2010 and two species in 2012, however, did not indicate pronounced differences. Whether the 20 psu salinity treatment, which was used for fertilization and short term exposure in this study, had a significant impact on egg density distributions cannot be answered. But from the conducted salinity trials it appears that the potential impact was low since the variation was higher among different individuals compared to the different salinity treatments within an individual. To perfectly address the effects of salinity on the egg density, brood stock rearing at different salinity regimes

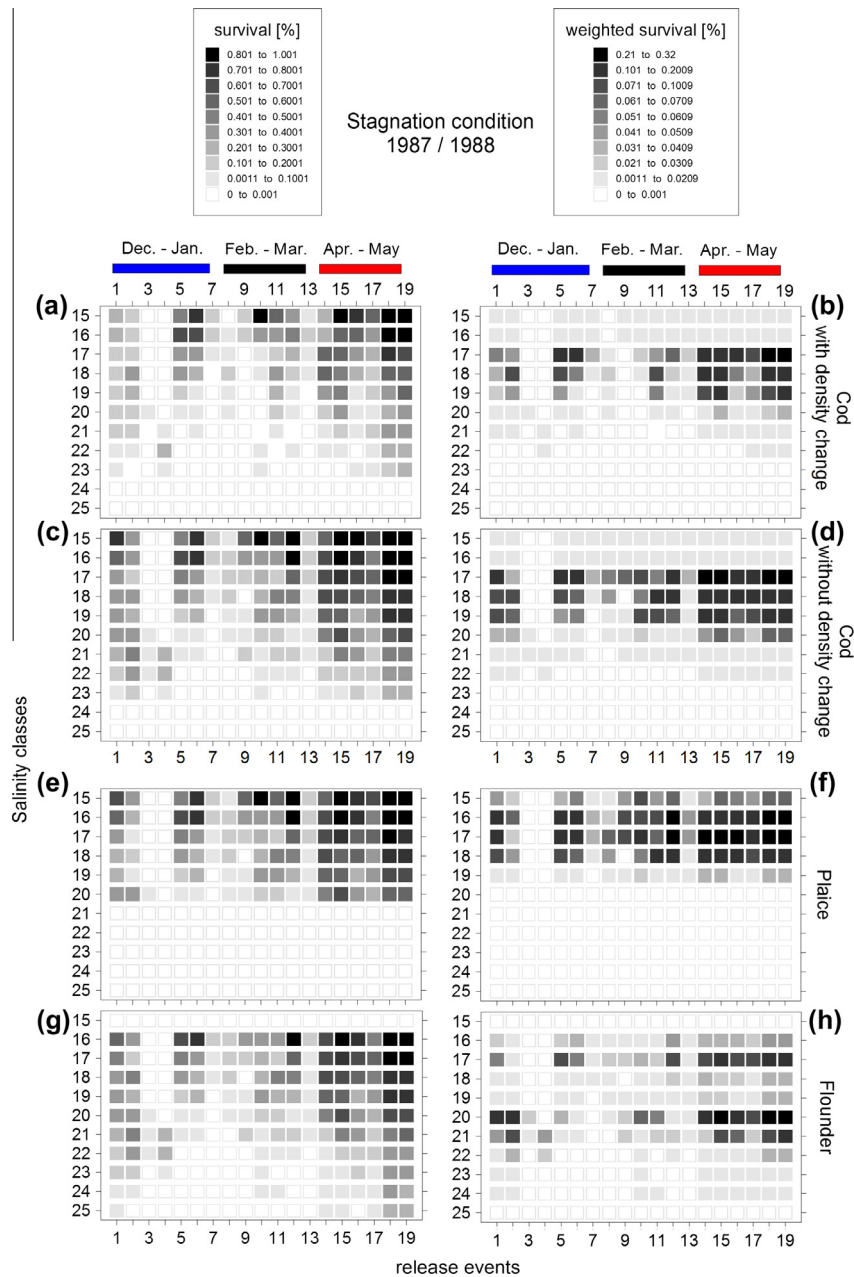


Fig. 10. Survival rates of drifters released every 10 days from December 1st to May 30th representing the developing early life stages of cod, plaice and flounder from egg stage IA until the beginning of mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO) during the stagnation phase 1987/1988. The identical color code for release periods was used as in Fig. 7. Survival rates per salinity class without modeled density change for cod (c), plaice (e) and flounder (g) and including ontogenetic density increase in cod (a). Weighted survival rates according to the relative frequencies of the experimentally derived egg batch densities (compare to Fig. 3) of cod (d), plaice (f) and flounder (h) without modeled density change and including density change for cod (b).

would be necessary. Spawning of cod occurs below 20 m depth (Bleil and Oeberst, 2000, 2002), and water depth does in general not exceed 30 m in Kiel Bight. Some areas below 20 m depth in the western Baltic Sea are characterized by vertical density stratification near the bottom. Accordingly, different salinity conditions during the egg fertilization process are possible and might partially modify egg density since it was altered even due to small changes in salinity (2 units) in our study. Therefore, further research is needed.

4.2. Relationship between female size, spawning state and experience, egg characteristics and egg density

Several other studies found positive relationships of female size to egg size (at least at comparable batch numbers; Kjesbu, 1989;

Marteinsdottir and Steinarrsson, 1998; Vallin and Nissling, 2000) or significant relations of egg size to egg density (Nissling and Westin, 1991; Kjesbu et al., 1992; Nissling et al., 1994). The vast majority of our results do not show such relationships, with the exception of cod egg dry weight being positively related to egg density. In flounder, egg diameter was positively related to egg density. Applying an age-length key for the western Baltic cod stock (Bagge et al., 1994) revealed that the ages of the majority of cod used in this study were of 2–4 years. This indicates that a substantial proportion of our analyzed batches might have come from first spawning individuals (Tomkiewicz et al., 1997). First spawners show stable egg diameters being significantly smaller throughout the spawning season than eggs produced by second year repeat spawners in general (Kjesbu et al., 1992) but also the opposite may occur on individual basis (Jung

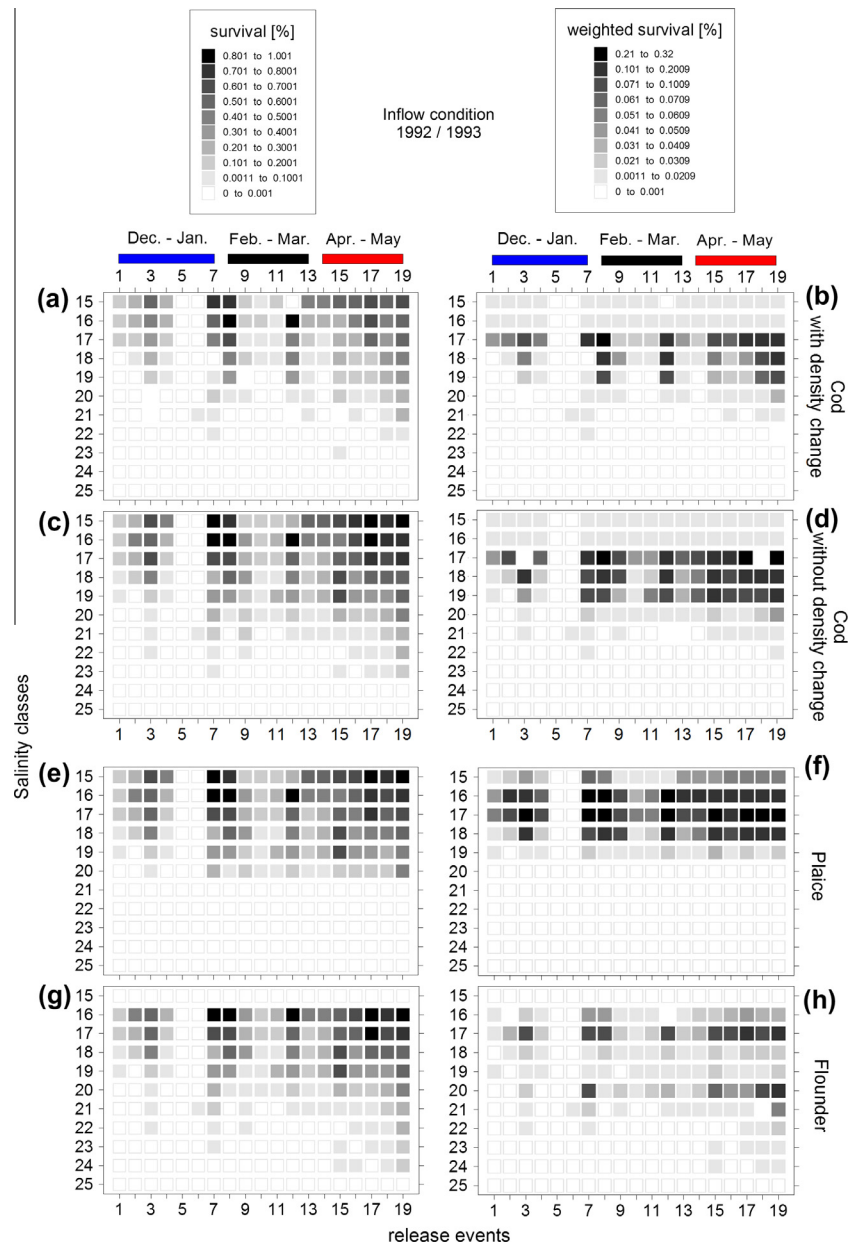


Fig. 11. Survival rates of drifters released every 10 days from December 1st to May 30th representing the developing early life stages of cod, plaice and flounder from egg stage IA until the beginning of mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO) during the inflow phase 1992/1993. The identical color code for release periods was used as in Fig. 7. Survival rates per salinity class without modeled density change for cod (c), plaice (e) and flounder (g) and including ontogenetic density increase in cod (a). Weighted survival rates according the relative frequencies of the experimentally derived egg batch densities (compare to Fig. 3) of cod (d), plaice (f) and flounder (h) without modeled density change and including density change for cod (b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2012b). In first spawners egg densities did not vary over the spawning season, being independent of the batch number. However, in the second spawning season, egg density increased with batch number as well as egg size decreased towards the end of the spawning season (Kjesbu et al., 1992). In central Baltic cod, Nissling et al. (1994) found a weak correlation of egg buoyancy with egg size in 3–5 years old fish from the Gotland Basin (SD 28). Nissling and Westin (1991) found a density decrease from the 1st to the 5th batch of the same female of 0.0012 g cm^{-3} (from 15.0 to 13.3 psu). This change is outside the standard deviation of the mean cod egg density found in our study and could either exemplify a high degree of variability in egg density on an individual level (Jung et al., 2012a) or, indicate that the variability of egg density is higher in the eastern Baltic cod stock.

After three quarters of the cod egg development time, egg density increased confirming earlier field and experimental observations made for central Baltic and Atlantic cod eggs (e.g. Mangor-Jensen, 1987; Nissling and Westin, 1991; Włodarczyk and Horbowa, 1997; Ouellet, 1997). Mangor-Jensen (1987) explained this density increase with an increase in the perivitelline space as a result of water loss in late egg stages until shortly before hatch. Guðmundsdóttir (2013) found in the two Icelandic “coastal” and “frontal” cod behavioral types of the same stock no difference in egg density development during the first third of the egg development phase; however during the last third of development the eggs of coastal cod females tended to have higher specific densities than those of frontal females. This difference in the life-history of the two behavior groups was considered to be attributed to

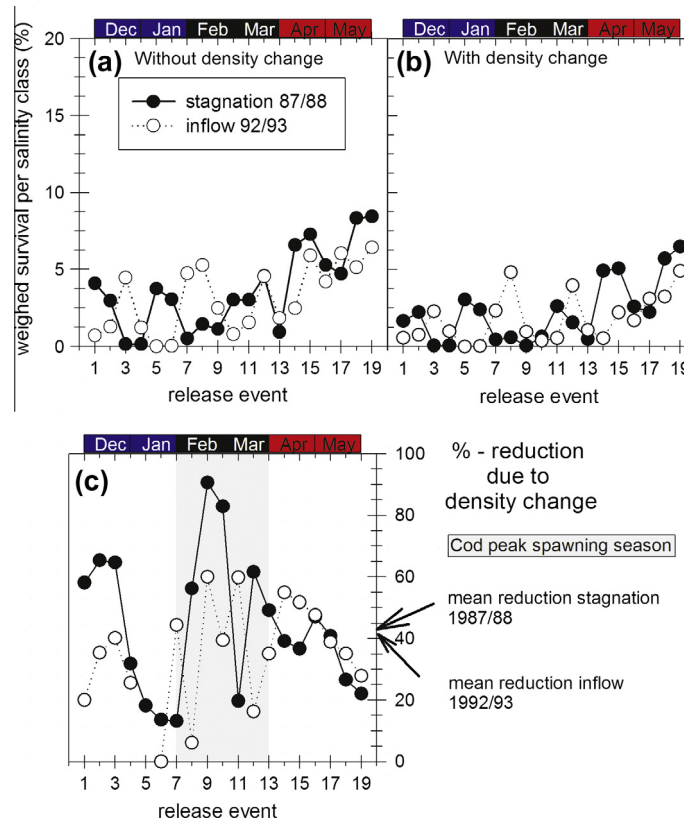


Fig. 12. Weighted mean survival per salinity class of drifters representing the developing early life stages of cod from egg stage IA until the beginning of mixed feeding yolk sac larval stage indicated by mouth gap opening (MGO). (a) Without density change, (b) including density increase from egg stage IV to first hatch. Drifter cohorts were released every 10 days from December 1st to May 30th simulating two divergent hydrographical situations, during a stagnation period (1987/1988, black dots) and during a major Baltic inflow event (1992/1993, transparent dots) and (c) magnitude of reduction in reduced survival (in percent) due to implemented density change compared to the modeled survival without density change. Gray area highlights peak spawning season of western Baltic cod. Arrows indicate overall seasonal mean percent reductions for each hydrographic scenario.

environmental factors or genetics (Guðmundsdóttir, 2013). But also the opposite that the egg density significantly decreased from gastrulation to before hatching accompanied by increased contents of ATP and ADP has been discussed for North East Arctic cod from the Barents Sea, recently (Jung et al., 2012b). Jung et al. (2012b) mentioned concerns about potential artifacts due to husbandry management of brood stocks, experimental conditions or potential restrictions in the interpretation of egg density development caused by e.g. low egg quality in earlier studies. But they also argued that stock-specific trends in the specific gravity should not be ruled out in the concept of metapopulations (Jung et al., 2012b). If the rate of decrease in neutral buoyancy for the western Baltic cod stock is implemented into the drift modeling, the relevance for the resulting survival rates is high. During peak spawning season in February and March, the calculated survival from early egg stage to the mixed feeding yolk sac larval stage was reduced by 60%. The quantification of correct egg mortality rates is crucial to identify and understand processes impacting the cod recruitment and is furthermore a prerequisite for egg production-based, fisheries independent stock assessment methods suggested to be applied for Baltic cod (Kraus et al., 2012).

4.3. Special considerations on model details: turbulence and horizontal diffusion

It might be that eggs with higher or lower density than the surrounding water stay afloat due to turbulence. Vertical turbulent diffusion might be an important characteristic of the water mass distribution in the Baltic. Therefore, it is considered in the hydrodynamic model which provides the flow fields for “off-line”

particle tracking. Eggs heavier or lighter than sea water could (at least partly) occur in the water column because of diffusion due to wind or vertical shear, etc., but primarily the vertical distribution of eggs and yolk-sac larvae depends on their neutral buoyancy. Unfortunately, we were not able to perform ichthyoplankton surveys and accompanied hydrographic/hydrodynamic measurements in this respect. Thus, our input to the model approach (vertical distribution of fertilized eggs) is exclusively based on experimental work with eggs obtained from field-caught fish. Secondly, eggs experiencing vertical changes by turbulence to levels representing positive or negative buoyancy levels will not remain there for longer time periods, because their neutral buoyancy will cause them to ascend/descend to their equilibrium state of water density. Thus, and because of a time step of 1 h for our drift model we have not directly considered any re-distribution of eggs and yolk-sac larvae.

Another methodological problem in our model experiments was that small-scale variations of current velocities (e.g. horizontal diffusion), which could not be resolved by our hydrodynamic modeling approach, may contribute to further variability in cod egg survival and distribution. Generally, in the Baltic Sea mean circulation patterns exist, however the stability of these patterns is relatively low (Lehmann and Hinrichsen, 2000b), i.e., in case of the western Baltic Sea the variability of horizontal current velocities is one magnitude larger compared to their means. On the other hand, small-scale fluctuation velocities are assumed to be very small and principally difficult or impossible to be directly measured in the field. Model sensitivity experiments (see Appendix A2) to evaluate the impact of horizontal diffusion on egg mortality and distribution have not revealed any significant deviations from the results of the reference run (particle transport without any addition of fluctuating velocity components).

4.4. Population structure, egg buoyancy, transport and early life stage survival

Neutral egg buoyancy is important and crucial for survival of pelagic eggs and can be a major factor impacting recruitment success in heterogeneous, highly variable estuarine environments that are found in the Baltic Sea. A summary of published but also unpublished data (C. Petereit, unpublished data) on egg densities of cod, plaice and flounder from different ICES Baltic SDs is compiled in Table 7. It provides Baltic Sea specific, species-specific and regional differences in egg densities e.g. information for pelagic spawning flounder from SD 28 showing the difference to the egg density values of benthic spawning flounder in the same SD (Nissling et al., 2002). The degree, to which these differences have already led to distinguishable populations, needs still to be

investigated. However, specific adaptations of egg buoyancy, fertilization and development of local populations of marine fish spawning in estuarine areas are common (MacKenzie and Mariani, 2012).

4.4.1. Cod

Lower mean egg density values were found for the Belt Sea cod (SD 22) compared to Skagerrak cod or cod from the Sound (SD 23) (Table 7). However, individual batches with the highest densities corresponded to individual cod from the Skagerrak or the Sound. Only few data are available for the Arkona Sea (SD 24), however, the timing of measurements during the spawning season is very important. Early batches measured in March ranged from 1.0134 to 1.0166 g cm⁻³ and are similar to the presented values for SD 22 (M. Bleil and R. Oeberst, Thünen Institute for Baltic Sea

Table 7

Compilation of available egg density potentials (g cm⁻³) of Baltic cod, plaice and flounder separated (i) by their regional ICES management subdivision (SDs, columns) and (ii) according their current pre-defined stock origin (assigned by different shading colors; ICES, 2010, 2011). Note that plaice from the western part (W) of the Arkona Sea is apportioned to the western stock component (SD 22) and plaice from the eastern part (E) is allocated to the central, eastern plaice stock (ICES, 2010). Numbers of measured batches (in brackets), mean and standard deviation (std) are provided and, if available, also the range.

Species	SD 23	SD 22	SD 24	SD 25	SD 26	SD 28	
	Skagerrak	The Sound	Belt Sea	Arkona Sea (W/E)	Bornholm Sea	Gdansk Deep	Gotland Basin
Cod	(10) ^a	(3) ^a	(56) ^{b1}	(4) ^a	(14) ^a	(2) ^{c1}	(53) ^d
mean ± std	1.0167 ± 0.0009	1.0162 ± 0.0004	1.0146 ± 0.0009	1.0106 ± 0.0012	1.0111 ± 0.0011	1.0101 ± 0.0010	1.0113 ± 0.0008
range			1.0122 - 1.0172				1.0095 - 1.0142
		Field samples ^e	(6) ^{b2}	(1) ^{c1}	(21) ^{c1}	Field samples ^j	(2) ^{c1}
		density ≈	1.0146 ± 0.0006	1.01023	1.0096 ± 0.001	1.0093 ± 0.0003	1.0096 ± 0.0005
		18-20 psu	1.0142 - 1.0150		1.0076 - 1.0123	1.0090 – 1.0097	
				(6) ^{g1}			Field samples ^j
				1.0134 - 1.0166			1.0083 ± 0.0002
			Field samples ^f	(17) ^{g2}	(3) ^{c2}		1.0080 – 1.0086
			density ≤5 °C 21 psu	1.00879 - 1.01339	1.0112 ± 0.001		
			≈1.0165 [*]		1.0100 - 1.0120		
Plaice			(68) ^{b1}	(3) ^h	(11) ^h		(3) ^h
mean ± std			1.0136 ± 0.0007	1.0119 ± 0.0002	1.0122 ± 0.0006		1.0130 ± 0.0009
range			1.0118 - 1.0154	1.0117 - 1.0122	1.0109 - 1.0138		1.0127 - 1.0142
			(7) ^{b3}				
			1.0142 ± 0.001				
			1.0130 – 1.0161				
			Experiment ⁱ				
			density ≤8 °C 20 psu				
			≈1.0152 [*]				
Flounder		(4) ^h	(21) ^{b1}	(20) ^h	(10) ^h	(3) ^{c1}	(10) ^h - demersal eggs ⁱ
mean ± std		1.0204 ± 0.0005	1.0160 ± 0.0015	1.0118 ± 0.0014	1.0108 ± 0.0010	1.0089 ± 0.0005	1.0158 ± 0.0007
range		1.0195 - 1.0208	1.0132 - 1.0189	1.0102 - 1.0138	1.0091 - 1.0130	1.0082 - 1.0092	1.0140 - 1.0168
			(4) ^{b3}	(5) ^k	(3) ^{c1}	(7) ^{c2}	(10) ^{c2}
			1.0158 ± 0.0004	1.0128 ± 0.004	1.0101 ± 0.0006	1.0090 ± 0.0004	1.0091 ± 0.0006
			1.0152 – 1.0164	1.0124 – 1.0134	1.0094 - 1.0106	1.0084 – 1.0096	1.0079 – 1.0099
			Experiment ⁱ				
			density ≥10 °C 25 psu				
			≈1.0191 [*]				

^{*} If authors provided salinity and temperature data from experiments or field samples, the density values of the eggs have been calculated according Fofonoff and Millard (1983).

^a Nissling and Westin (1997) – no dates given.

^{b1} This study, January to March 2011.

^{b2} This study, February and March 2010.

^{b3} This study, March 2012.

^{c1} Petereit, unpublished data from April and May 2011.

^{c2} Petereit, unpublished data from April 2012.

^d Nissling et al. (1994).

^e Westerberg (1994) – no temperature data.

^f Westernhagen von et al. (1988).

^{g1} Bleil and Oeberst, unpublished data from March.

^{g2} Bleil and Oeberst, unpublished data from May and June.

^h Nissling et al. (2002).

ⁱ Westernhagen von (1970).

^j Makarchouk and Hinrichsen (1998) – field samplings – values at maximum cod egg abundance May, June, July, August 1996.

^k Solemdal (1973) 14 und 16 PSU combined.

Fisheries, Rostock, Germany, unpublished data from the central Arkona Basin). Mean batch densities later in spring (April) or in early summer (May and June) were lower, and coincide more with values found for cod from the central Baltic in eastern areas like the Bornholm Sea (SD 25), the Gdansk Deep (SD 26) or the Gotland Basin (SD 28) (Table 7). The seasonal differences in egg density match with the general evaluation that western Baltic cod spawn in early spring, whereas the central Baltic cod stock spawns in late spring and summer (Hüssy, 2011). The observation of seasonally divergent egg density potentials supports the assumption that the Arkona Sea functions as a spawning area for both, the western and the eastern cod stock (Nissling and Westin, 1997; Bleil et al., 2009). In fact, the question arises if neutral egg buoyancy should be considered as a new discriminative parameter to separate the two cod stocks as previously suggested by Nissling and Westin (1997)? Selected individual cod with anomalous egg densities for their spawning locations were genetically analyzed and first results showed reasonable evidence for a more complex stock structure matching with egg neutral buoyancy characteristics (Petereit et al., unpublished data). This needs, however, to be further investigated and ideally coupled to another independent method like otolith microchemistry (Heidemann et al., 2012).

Knowledge on egg density can be used in combination with a hydrodynamic drift model as a powerful tool to locate important areas for early life stage survival. Results from our study indicate retention within the Belt Sea for two characteristic hydrographical scenarios, a stagnation phase and an inflow event. This retention pattern is strongest during the late spawning season in April and May, generating highest survival. During this time the majority of surviving larvae were found in Kiel Bight, Little Belt, Great Belt, Femern Belt and the Mecklenburg Bay. The late spring/early summer survival is supported by the analyses of juvenile cod from the Kiel Bight: Rehberg-Haas et al. (2012) used otolith microstructure analyses of juvenile cod (2008, 2009) and back-calculated their hatch dates. The majority of individuals hatched in May and June (Rehberg-Haas et al., 2012). Early spawning season drift simulations (December to January) revealed the highest spatial variability in final positions, especially under stagnation conditions (1987/1988). Drifters released in February and March reached the Kattegat under inflow conditions and to a lesser extent left the Great Belt in northeast direction during stagnation. Considering the heterogeneous and highly variable system of the Belt Sea, this rather homogeneous distribution over parts of the season and divergent hydrographical states is remarkable and may favor small-scale genetic structuring. In Belt Sea cod, retention is higher if the eggs float in deeper water layers, compared to water layers near to the surface. The higher densities of the eggs prevent the eastward transport over shallow sills with low bottom water density. Knutsen et al. (2007) observed in Norwegian fjords with shallow sills an abrupt reduction of cod egg abundance towards the open sea. This observation was interpreted as support for an offspring retention hypothesis helping to explain the maintenance of local population structure in pelagic marine systems (Knutsen et al., 2007).

The presented results partly deviate from the conclusion of Westerberg (1994) that cod egg import through the Sound (SD 23) and the Great Belt (SD 22) could be a significant process for maintaining the cod egg population in the Southern Baltic Sea during periods of strong inflows. At least for the egg transport via the Great Belt into the Central Arkona Basin, our modeling results show for the vast majority of released drifters no survival during the major Baltic inflow event in 1993. The different conclusion drawn by Westerberg (1994) is at least partly based on the assumption that turbulent mixing keeps eggs in suspension even if they become negatively buoyant during drift. Our drift model results are contrary to previous findings of Hinrichsen et al. (2001) who suggested that strong west wind forcing conditions (shown

for 1992/1993) allow egg and early larval stage transport up east into the Bornholm Sea. Presumably, their assumption was triggered by (i) the lack of data on the vertical distribution of the eggs and (ii) the missing information on changes in buoyancy during egg development. In this study we provide data on vertical distribution and ontogenetic density increase for cod eggs. Therefore, we could show that almost no survival during eastward transport of cod eggs and early larvae occurs. Accordingly, the Eastern Baltic cod stock is most likely not supported through eggs and larvae produced by the western cod stock spawning in the Belt Sea.

4.4.2. Plaice

The range in density of the egg batches measured in this study encompasses almost all published egg densities from other Baltic areas like SD 24, SD 25 and SD 28 (Nissling et al., 2002; Table 7). Based on the salinity requirement for successful reproduction Nissling et al. (2002) supposed that only a single stock in the Baltic exists. ICES (2010) distinguish three different plaice stocks in the Baltic Sea. One stock is located in the Öresund (SD 23), one stock covers SD 22 including the western parts of SD 24 and one stock comprises the SDs 24, 25, 26 and 28. No major difference in mean egg density between SDs is obvious (Table 7). Tagging experiments have shown that no migration of adult plaice from SD 22 to SD 24 occurs but there is some migration into the Kattegat (Bagge and Steffensen, 1989). Our modeling results confirm retention of early life stages in the Belt Sea (SD 22), transport to the western part of the Arkona Sea (SD 24) and regular northward transport through the Great Belt into the Kattegat and occasionally further north with highest survival very late in the spawning season. Compared to cod and flounder, plaice benefit from the lowest mortality rate during the drift phase. It is unknown, however, if the advantage in egg size (larger eggs are more buoyant compared to smaller eggs of cod or flounder) is negatively compensated by longer development time, resulting e.g. in longer exposure and better visibility to ichthyoplankton predators, such as sprat and herring (Köster and Möllmann, 2000).

4.4.3. Flounder

This study provides the first data on flounder egg density for the Belt Sea (SD 22) complementing substantially previous work of Nissling et al. (2002) (Table 7). In 3 out of 6 sampling sites, approximately 60% of the egg batches had a higher mean egg density compared to the ambient hydrographic condition of the respective stations. Consequently, the eggs would have sunk to the sea floor if they were spawned naturally. Westernhagen von et al. (1988) described a very similar phenomenon. They successfully fertilized and incubated 67 pairs of flounder caught in the Kiel Bight in 1984 and all batches showed normal egg development. However, only 65% (44 batches) produced eggs that floated at a salinity of 25 psu, a value which from previous investigations should have been adequate for neutral buoyancy. According to Westernhagen von et al. (1988), different former studies had shown that eggs could be in general found lying at the bottom when salinity was not sufficient to support neutral buoyancy. No information was given, if these eggs survived or not.

An explanation for the frequent occurrence of individuals which likely produce non-buoyant eggs could be the divergent population structure of Baltic Sea flounder. The specific density of the eggs is assumed to be a fixed population characteristic (Sølemdal, 1973). Our findings of a comparatively broad range in flounder egg density in SD 22 could indicate a mixture of individual females from SD 24 (low egg density) and SD 23 (high egg density). The high density values could be related to small egg size since a negative relationship between egg diameter and egg density has been found.

It might also be possible that we have measured egg densities from the second ecotype of Baltic flounder spawning demersal eggs. Mielck (1926) and Mielck and Künne (1932) found female flounders with either large, presumably “pelagic-type” eggs or with small “benthic-type” eggs, spawning at the same time on the Oderbank (SD 24; 54°15.20N, 14°25.49E). They were uncertain if individuals might be able to change their annual spawning mode and type of eggs or if they were genetically different. Egg diameters in our study were near or within the range (0.93–1.14 mm) given for benthic eggs (Mielck, 1926; Nissling et al., 2002). A clear population separation between demersal and pelagic spawners has been supported by microsatellite genetic markers (Florin and Höglund, 2008). However, no samples were taken in that particular study from the Belt Sea (SD 22) and all samples from the Oderbank (SD 24), which is a historical and well-known spawning spot for “Bank-flounders” (Mielck, 1926; Mielck and Künne, 1932), were derived from a single sampling event. That individual fish from SD 24 have the potential to migrate to the Belt Sea was shown by tagging experiments (Bagge and Steffensen, 1989). The existence of hybridization between the two genetically different populations is unknown (Nissling and Dahlman, 2010).

Our modeling results showed retention of flounder eggs within the Belt Sea and transport to the Kattegat but did not show any contribution to the eastern and central parts of the Arkona Basin or further east Baltic SDs. This pattern favors a closer genetic relation of SD 22 flounder to the Kattegat, Skagerrak and North Sea area, which represent the north-western management unit as suggested by Florin and Höglund (2008). Further research aiming at the early life stages and spawning characteristics of flounder in the western Baltic Sea is mandatory for clarifying the population structure before establishing analytical assessments for the different stocks. At least 35% of the egg batches apparently have buoyancy deficits compared to ambient conditions and the consequences for the egg survival and the population development are unknown.

5. Outlook and perspectives

The western Baltic is the southernmost part of the transition between the North Sea and the Baltic Proper. The relatively narrow, shallow, and strongly stratified area is subject to different external forces: (i) local winds, (ii) barotropic pressure gradients due to sea level differences between Baltic and North Sea and (iii) baroclinic pressure gradients caused by freshwater outflow at the sea surface and inflow of saline water near the bottom (Fennel and Sturm, 1992). Due to the complicated coast lines, the complex topography, the strong density gradients, and the variable wind conditions in the western Baltic, it is ultimately required to employ highly temporally and spatially resolving hydrodynamic models to describe the flow dynamics as well as the resulting transport and exchange processes of water masses and pelagically floating individual particles. Our study serves as an example how to combine observations, process knowledge and modeling in such a bio-physical framework to elucidate the fate of pelagic eggs and larvae of abundant fish species in the western Baltic, both throughout their spawning season and under contrasting hydrographic conditions. Furthermore, determining the contribution of spawning events of Western Baltic fish stocks to stocks inhabiting neighboring areas is possible, which is of fundamental importance for fisheries management approaching a sustainable reproductive potential of fish stocks. It is evident that a multitude of effects influence the stock development of resident western Baltic fish species. Adequate long-term fisheries management, for example has to consider the impact of climate forcing on recruitment processes in order to achieve optimal resource utilization and conservation. Our modeling framework is a

promising tool that allows the simulation and assessment of the dynamics of marine fish populations under different climatic and hydrographic forcing scenarios and is at the same time a test bed for improving our process understanding (Hinrichsen et al., 2011b).

A rigorous approach for model validation should force modelers to accept that observations and experiments are an integral part of the overall modeling process (Hannah, 2007). As a final step, models and model results could be made accessible to managers and other stakeholders, but only in close collaboration with scientists to ensure that model results are interpreted and applied appropriately (Gallego et al., 2007).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.pocean.2014.01.001>.

References

- Andersen, Ø., Frang Wetten, O., De Rosa, M.C., Andre, C., Carelli Alinovi, C., Colafranceschi, M., Brix, O., Colosimo, A., 2009. Haemoglobin polymorphisms affect the oxygen-binding properties in Atlantic cod populations. *Proceedings of the Royal Society B: Biological Sciences* 276, 833–841.
- Aro, E., 1989. A review of fish migration patterns in the Baltic Sea. *Rapports et Procès – Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 190, 72–96.
- Bagge, O., Steffensen, E., 1989. Stock identification of demersal fish in the Baltic. *Rapports et Procès – Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 190, 3–16.
- Bagge, O., Thurow, F., Steffensen, E., Bay, J., 1994. The Baltic cod. *Dana* 10, 1–28.
- Bergström, S., Carlsson, B., 1994. River runoff to the Baltic Sea: 1950–1990. *Ambio* 23, 280–287.
- Bleil, M., Oeberst, R., 2000. Reproduction Areas of the Cod Stock in the Western Baltic Sea. *ICES CM* 2000/N: 02.
- Bleil, M., Oeberst, R., 2002. Spawning areas of the cod stock of the western Baltic Sea and minimum length at maturity. *Archive of Fishery and Marine Research* 49, 243–258.
- Bleil, M., Oeberst, R., Urrutia, P., 2009. Seasonal maturity development of Baltic cod in different spawning areas: importance of the Arkona Sea for the summer spawning stock. *Journal of Applied Ichthyology* 25, 10–17.
- Bryan, K., 1969. A numerical method for the study of the circulation of the world ocean. *Journal of Physical Oceanography* 15, 1312–1324.
- Bunn, N.A., Fox, C.J., Webb, T., 2000. A literature Review on Studies on Fish Egg Mortality: Implications for the Estimation of Spawning Stock Biomass by the

- Annual Egg Production Methods. Science Series Technical Report, CEFAS, Lowestoft, No. 111, pp. 1–37.
- Cerdà, J., Fabra, M., Raldúa, D., 2007. Physiological and molecular basis of fish oocyte hydration. In: Babin, J.F., Cerdà, J., Lubzens, E. (Eds.), *The Fish Oocyte: From Basic Studies to Biotechnological Applications*. Springer, The Netherlands, pp. 349–396.
- Ciannelli, L., Knutsen, H., Olsen, E.M., Espeland, S.H., Asplin, L., Jølmert, A., Knutsen, J.A., Stenseth, N.C., 2010. Small scale genetic structure in a marine population in relation to water circulation and egg characteristics. *Ecology* 91, 2918–2930.
- Coombs, S.H., 1981. A density-gradient column for determining the specific gravity of fish eggs, with particular reference to eggs from the mackerel *Scomber scombrus*. *Marine Biology* 63, 101–106.
- Coombs, S.H., Fosh, C.A., Keen, M.A., 1985. The buoyancy and vertical distribution of eggs of sprat (*Sprattus sprattus*) and pilchard (*Sardina pilchardus*). *Journal of the Marine Biological Association of the United Kingdom* 65, 461–474.
- Cowan, J.H., Shaw, R.F., 2002. Recruitment. In: Fuiman, L.E., Werner, R.G. (Eds.), *Fishery Science: The Unique Contribution of Early Life Stages*. Blackwell Science, Oxford, pp. 88–111.
- Cox, M.D., 1984. A primitive Equation 3-Dimensional Model of the Ocean. GFDL Ocean Group Technical Report No. 1, Geophysical Fluid Dynamics Laboratory, Princeton, NJ, 75 pp.
- Craik, J.C.A., Harvey, S.M., 1987. The causes of buoyancy in eggs of marine teleosts. *Journal of the Marine Biological Association of the United Kingdom* 67, 169–182.
- Cushing, D.H., 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in Marine Biology* 26, 250–293.
- Fabra, M., Raldúa, D., Power, D.M., Deen, P.M., Cerdà, J., 2005. Marine fish egg hydration is aquaporine-mediated. *Science* 307, 545.
- Fennel, W., Sturm, M., 1992. Dynamics of the western Baltic. *Journal of Marine Systems* 3, 183–205.
- Florin, A.-B., Höglund, J., 2008. Population structure of flounder (*Platichthys flesus*) in the Baltic Sea: differences among demersal and pelagic spawners. *Heredity* 101, 27–38.
- Fofonoff, P., Millard Jr. R.C., 1983. Algorithms for Computation of Fundamental Properties of Seawater. UNESCO Technical Paper in Marine, Science, No. 44, 53 pp.
- Gallego, A., North, E.W., Petitgas, P., 2007. Introduction: status and future of modeling physical-biological interactions during the early life of fishes. *Marine Ecology Progress Series* 347, 121–126.
- Goarant, A., Petitgas, P., Bourriau, P., 2007. Anchovy (*Engraulis encrasicolus*) egg density measurements in the Bay of Biscay: evidence for the spatial variation in egg density with sea surface salinity. *Marine Biology* 151, 1907–1915.
- Govoni, J.J., Forward Jr., R.B., 2008. Buoyancy. In: Finn, R.N., Kapoor, B.G. (Eds.), *Fish Larval Physiology*. Science Publishers, Enfield, USA, pp. 495–521.
- Guðmundsdóttir, L.O., 2013. Intra-stock Diversity in Egg Specific Gravity of Atlantic Cod in Icelandic Waters. Master's Thesis, Faculty of Life and Environmental Sciences, Univ. of Iceland, Iceland. <http://www.skemman.is/en/stream/get/1946/15316/37186/1/Lov%C3%ADsa%C3%93%C3%B6f_Gu%C3%B0mundsd%C3%B3ttir.pdf>.
- Hannah, C.G., 2007. Future directions in modeling physical-biological interactions. *Marine Ecology Progress Series* 347, 301–306.
- Heidemann, F., Marohn, L., Hinrichsen, H.-H., Huwer, B., Hüsey, K., Klügel, A., Böttcher, U., Hanel, R., 2012. Suitability of otolith microchemistry for stock separation of Baltic cod. *Marine Ecology Progress Series* 465, 217–226.
- Hinrichsen, H.-H., Lehmann, A., StJohn, M.S., Brügge, B., 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. *Continental Shelf Research* 17, 1765–1784.
- Hinrichsen, H.-H., Boettcher, U., Oeberst, R., Voss, R., Lehmann, A., 2001. The potential for advective exchange of the early life stages between the western and eastern Baltic cod (*Gadus morhua* L.) stocks. *Fisheries Oceanography* 10, 249–258.
- Hinrichsen, H.-H., Huwer, B., Makarchouk, A., Petereit, C., Schaber, M., Voss, R., 2011a. Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*). *ICES Journal of Marine Science* 68, 2019–2028.
- Hinrichsen, H.-H., Dickey-Collas, M., Huret, M., Peck, M.A., Vikebo, F.B., 2011b. Evaluating the suitability of coupled biophysical models for fishery management. *ICES Journal of Marine Science* 68, 1478–1487.
- Hinrichsen, H.-H., Hüsey, K., Huwer, B., 2012. Spatio-temporal variability in western Baltic cod early life stage survival mediated by egg buoyancy, hydrography and hydrodynamics. *ICES Journal of Marine Science* 69, 1744–1752.
- Houde, E.D., 2002. Mortality. In: Fuiman, L.E., Werner, R.G. (Eds.), *Fishery Science: The Unique Contribution of Early Life Stages*. Blackwell Science, Oxford, pp. 64–87.
- Hüsey, K., 2011. Review of western Baltic cod (*Gadus morhua*) recruitment dynamics. *ICES Journal of Marine Science* 68, 1459–1471.
- ICES, 2010. Report of the ICES/HELCOM Workshop on Flatfish in the Baltic Sea (WKFLABA). Öregrund, 8–11 November, 2010. *ICES CM 2010/ACOM:68*, 85 pp.
- ICES, 2011. Report of the Baltic Fisheries Assessment Working Group (WGBFAS). Copenhagen, 12–19 April, 2011. *ICES CM 2011/ACOM:10*, 824 pp.
- Jung, K.-M., Folkvord, A., Kjesbu, O.S., Agnalt, A.L., Thorsen, A., Sundby, S., 2012a. Egg buoyancy variability in local populations of Atlantic cod (*Gadus morhua*). *Marine Biology* 159, 1969–1980.
- Jung, K.-M., Svardal, A.M., Eide, T., Thorsen, A., Kjesbu, O.S., 2012b. Seasonal trends in adenylate nucleotide content in eggs of recruit and repeat spawning Atlantic cod (*Gadus morhua* L.) and implications for egg quality and buoyancy. *Journal of Sea Research* 73, 63–73.
- Kändler, O., 1944. Untersuchungen über den Ostseefisch während der Forschungsfahrten mit dem R.F.D. "Poseidon" in den Jahren 1925–1938. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 11, 137–245 (in German).
- Killworth, P.D., Stainforth, D., Webb, D.J., Paterson, S.M., 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. *Journal of Physical Oceanography* 21, 1333–1348.
- Kjesbu, O.S., 1989. The spawning activity of cod, *Gadus morhua* L. *Journal of Fish Biology* 34, 195–206.
- Kjesbu, O.S., Kryvi, H., Sundby, S., Solemdal, P., 1992. Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. *Journal of Fish Biology* 41, 581–599.
- Knutsen, H., Olsen, E.M., Ciannelli, L., Espeland, S., Knutsen, J.A., Simonsen, J.H., Skreslet, S., Stenseth, N.C., 2007. Egg distribution, bottom topography and small-scale population structure in a coastal marine system. *Marine Ecology Progress Series* 333, 249–255.
- Köster, F.W., Möllmann, C., 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? *ICES Journal of Marine Science* 57, 310–323.
- Kraus, G., Hinrichsen, H.-H., Voss, R., Teschner, E., Tomkiewicz, J., Köster, F.W., 2012. Robustness of egg production methods as a fishery independent alternative to assess the Eastern Baltic cod stock (*Gadus morhua callarias* L.). *Fisheries Research* 117–118, 75–85.
- Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. *Tellus* 47A, 1013–1031.
- Lehmann, A., Hinrichsen, H.-H., 2000a. On the thermohaline variability of the Baltic Sea. *Journal of Marine Systems* 25, 333–357.
- Lehmann, A., Hinrichsen, H.-H., 2000b. On the wind driven and thermohaline circulation of the Baltic Sea. *Physics and Chemistry of the Earth (B)* 25, 183–189.
- Lehmann, A., Krauß, W., Hinrichsen, H.-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. *Tellus* 54A, 299–316.
- MacKenzie, B.R., Mariani, P., 2012. Spawning of Bluefin Tuna in the Black Sea: historical evidence, environmental constraints and population plasticity. *PLoS One* 7, e39998. <http://dx.doi.org/10.1371/journal.pone.0039998>.
- Makarchouk, A., Hinrichsen, H.-H., 1998. The Vertical Distribution of Ichthyoplankton in Relation to the Hydrographic Conditions in the Eastern Baltic. *ICES CM 1998/R:11*, pp. 1–14.
- Mangor-Jensen, A., 1987. Water balance in developing eggs of the cod *Gadus morhua*. *Fish Physiology and Biochemistry* 3, 17–24.
- Marteinsdóttir, G., Steinarrson, A., 1998. Maternal influences on the size and viability of Icelandic cod *Gadus morhua* eggs and larvae. *Journal of Fish Biology* 52, 1241–1258.
- Matthäus, W., Franck, H., 1992. Characteristics of Major Baltic inflows – a statistical analysis. *Continental Shelf Research* 12, 1375–1400.
- Mielck, W., 1926. Untersuchungen über die pelagische Fischbrut (Eier und Larven) in der Ostsee im April 1925. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 2, 311–318 (in German).
- Mielck, W., Künne, C., 1932. Fischbrut und Plankton-Untersuchungen auf dem Reichsforschungsdampfer "Poseidon" in der Ostsee, Mai-Juni 1931. *Wissenschaftliche Meeresuntersuchungen Abteilung Helgoland* 19, 1–120 (in German).
- Muus, B.J., Nielsen, J.G., 1999. *Sea Fish. Scandinavian Fishing Year Book*, Hedehusene, Denmark, 340 pp.
- Mykssvoll, M.S., Sundby, S., Ådlandsvik, B., Vikebø, F.B., 2011. Retention of Coastal cod eggs in a Fjord caused by interactions between egg buoyancy and circulation pattern. *Marine and Coastal Fisheries: Dynamics, Management and Ecosystem Science* 3, 279–294.
- Mykssvoll, M.S., Jung, K.-M., Albretsen, J., Sundby, S., 2013. Modeling dispersal of eggs and quantifying connectivity among Norwegian coastal cod subpopulations. *ICES Journal of Marine Sciences*. <http://dx.doi.org/10.1093/icesjms/fst022>.
- Nielsen, E.E., Hansen, M.M., Ruzzante, D.E., Meldrup, D., Grønkjær, P., 2003. Evidence of a hybrid-zone in Atlantic cod (*Gadus morhua*) in the Baltic and the Danish Belt Sea revealed by individual admixture analysis. *Molecular Ecology* 12, 1497–1508.
- Nielsen, E.E., Hemmer-Hansen, J., Poulsen, N.A., Loeschcke, V., Moen, T., Johansen, T., Mittelholzer, C., Taranger, G.-L., Ogden, R., Carvalho, G.R., 2009. Genomic signatures of local directional selection in a high gene flow marine organism: the Atlantic cod (*Gadus morhua*). *BMC Evolutionary Biology* 9, 276.
- Nissling, A., Dahlman, G., 2010. Fecundity of flounder, *Pleuronectes flesus*, in the Baltic Sea – reproductive strategies in sympatric populations. *Journal of Sea Research* 64, 190–198.
- Nissling, A., Westin, L., 1991. Egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for cod stock fluctuations in the Baltic. *Marine Biology* 111, 33–35.
- Nissling, A., Westin, L., 1997. Salinity requirements for successful spawning of Baltic and Belt Sea cod and the potential for cod stock interaction in the Baltic Sea. *Marine Ecology Progress Series* 152, 261–271.
- Nissling, A., Kryvi, H., Vallin, L., 1994. Variation in egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for egg survival in prevailing conditions in the Baltic Sea. *Marine Ecology Progress Series* 110, 67–74.
- Nissling, A., Westin, L., Hjerne, O., 2002. Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*) and flounder (*Pleuronectes flesus*), in the brackish water Baltic Sea. *ICES Journal of Marine Science* 59, 93–108.

- Ospina-Álvarez, A., Palomera, I., Parada, C., 2012. Changes in egg buoyancy during development and its effect on the vertical distribution of anchovy eggs. *Fisheries Research* 117–118, 86–95.
- Ouellet, P., 1997. Characteristics and vertical distribution of Atlantic cod (*Gadus morhua*) eggs in the northern Gulf of St. Lawrence, and the possible effect of cold water temperature on recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 54, 211–223.
- Petereit, C., Hinrichsen, H.-H., Voss, R., Clemmesen, C., Haslob, H., Freese, M., Kraus, G., 2009. The influence of different salinity conditions on egg buoyancy and development and yolk sac larval survival and morphometric traits of Baltic Sea sprat (*Sprattus sprattus balticus* Schneider). In: Clemmesen, C., Malzahn, A.M., Peck, M.A., Schnack, D. (Eds.), *Advances in Early Life History Study of Fish*. Scientia Marina 73(S1), 59–72.
- Rehberg-Haas, S., Hammer, C., Hillgruber, N., Hüsey, K., Temming, A., 2012. Otolith microstructure analysis to resolve seasonal patterns of hatching and settlement in western Baltic cod. *ICES Journal of Marine Science* 69, 1347–1356.
- Saeger, J., 1974. Der Befischungszustand der Flunderpopulation in der Kieler Bucht. Dissertation, Christian-Albrechts University Kiel, Germany (in German).
- Semtner, A.J., 1974. A General Circulation Model for the World Ocean. UCLA Department of Meteorology Technical, Report, No. 8, 99 pp.
- Sick, K., 1961. Haemoglobin polymorphism in fishes. *Nature* 192, 894–896.
- Solemdal, P., 1973. Transfer of Baltic flatfish to a marine environment and the long term effects on reproduction. *Oikos* 15, 268–276.
- Strodtmann, S., 1906. Laichen und Wandern der Ostseefische. *Wissenschaftliche Meeresuntersuchungen Abteilung Helgoland* 7, 133–216 (in German).
- Thompson, B.M., Riley, J.D., 1981. Egg and larval studies in the North Sea cod (*Gadus morhua* L.). *Rapports et Procès – Verbaux des Réunions du Conseil International pour l'Exploration de la Mer* 178, 553–559.
- Thorsen, A., Kjesbu, O.S., Fyhn, H.J., Solemdal, P., 1996. Physiological mechanisms of buoyancy in eggs from brackish water cod. *Journal of Fish Biology* 48, 457–477.
- Thurrow, F., 1970. Über die Fortpflanzung des Dorsches (*Gadus morhua* L.) in der Kieler Bucht. *Berichte der Deutschen Wissenschaftlichen Kommission für Meeresforschung* 21, 170–192 (in German, with English Abstract and Summary).
- Tomkiewicz, J., Eriksson, M., Baranova, T., Feldman, V., Müller, H., 1997. Maturity Ogives and Sex Ratios for Baltic Cod: Establishment of a Database and Time Series. *ICES CM* 1997/CC:20.
- Vallin, L., Nissling, A., 2000. Maternal effects on egg size and egg buoyancy of Baltic cod, *Gadus morhua*: implications for stock structure effects on recruitment. *Fisheries Research* 49, 21–37.
- Westerberg, H., 1994. The Transport of Cod Eggs and Larvae through Öresund. *ICES CM* 1994/Q:4.
- Westernhagen von, H., 1970. Erbrütung der Eier von Dorsch (*Gadus morhua*), Flunder (*Pleuronectes flesus*) und Scholle (*Pleuronectes platessa*) unter kombinierten Temperatur- und Salzgehaltsbedingungen. *Helgoländer Wissenschaftliche Meeresuntersuchungen* 21, 21–102 (in German, with English Abstract).
- Westernhagen von, H., Dethlefsen, V., Cameron, P., Berg, J., Fürstenberg, G., 1988. Developmental defects in pelagic fish embryos from the western Baltic. *Helgoländer Meeresuntersuchungen* 42, 13–36.
- Wieland, K., Jarre-Teichmann, A., 1997. Prediction of vertical distribution and ambient development temperature of Baltic cod, *Gadus morhua* L., eggs. *Fisheries Oceanography* 6, 172–187.
- Włodarczyk, E., Horbowa, K., 1997. Size-specific vertical distribution of Baltic cod (*Gadus morhua* L.) eggs in the Bornholm Basin in 1993 and 1994. *ICES Journal of Marine Science* 54, 206–212.