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Interannual variability in the transport of fish eggs in the Kattegat and Öresund

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The dispersal and retention of early life stages are essential factors for the recruitment of fish stocks, and often depend on local meteorological and hydrographical conditions. A BAltic sea Long-Term large Scale Eutrophication Model (BALTSEM) was used to examine interannual variation in the retention and dispersal of fish eggs, Atlantic cod (Gadus morhua) at spawning areas in the Kattegat and Öresund and to investigate the mechanisms responsible for this variation. Model simulations over period 1971–2006 showed that years with high retention were related to variable weak winds and a strong outflow of water from the Baltic Sea, while years with low retention were related to strong westerly winds. Low egg retention was associated with enhanced southward transport from the Kattegat towards the Great Belt and from the Öresund towards the Baltic Sea. This southward transport of eggs was highly correlated with the local westerly wind component. The southbound egg transport and the westerly wind component both increased after 1989, and were connected with a change in the large-scale atmospheric circulation pattern, as represented by the NAO index. Results of this study provide information about the connectivity between neighboring areas and suggest that sedimentation is an important mortality factor.

Keywords: atlantic cod, buoyancy, dispersal, fish egg, kattegat, retention, transport, windforcing.

Introduction

The Kattegat and Öresund, next to the Baltic Sea (Figure 1), are important spawning and nursery areas for Atlantic cod (*Gadus morhua*) and other broadcast spawning fish, such as plaice (*Pleuronectes platessa*), sole (*Solea solea*), sprat (*Sprattus sprattus*) and herring (*Clupea harengus*). Historically, cod spawning has occurred at several locations in the Kattegat (Pihl and Ulmestrand, 1988; Svedäng and Bardon, 2003); however, results from a combined study using both commercial logbooks and data on cod maturity from the International Bottom Trawl Survey (IBTS) clearly indicate that the number of spawning aggregations in the Kattegat have declined since the 1980s (Vitale *et al.*, 2008). Today, the Kattegat cod stock is classified as suffering from reduced reproductive capacity (ICES, 2010), as the spawning-stock biomass has decreased to only a fraction of its former level in the 1970s, mainly due to overfishing (Cardinale and Svedäng, 2004). In contrast to the Kattegat cod, the cod stock in the Öresund is still considered highly productive (e.g. Svedäng *et al.*, 2010a).

The geographical proximity and hydrographical exchange between the Kattegat and Öresund point towards high connectivity and gene exchange, raising questions about the separation of cod populations and spawning. Svedäng *et al.* (2010b) found no genetic differences, based on microsatellite DNA analysis, between cod caught on spawning grounds in the middle of the Kattegat, at the entrance to the Öresund, or in the middle of the Öresund. On the other hand, their tagging results, in combination with analyses of element contents of otolith cores, suggest that cod in the southern Kattegat and the Öresund are indeed separated to some extent, as they indicate philopatric behaviour by dispersing from mixed feeding areas and returning to their natal spawning grounds. In other words, connectivity between neighbouring basins is related to the magnitude of transport of early life stages from the spawning area, although it is not the sole process that affects the stock structure (e.g. Pawson and Jennings, 1996). Therefore, to define and understand marine fish population dynamics, effectively manage fish stocks and design marine reserves, it is essential to study the dispersal of early life stages.
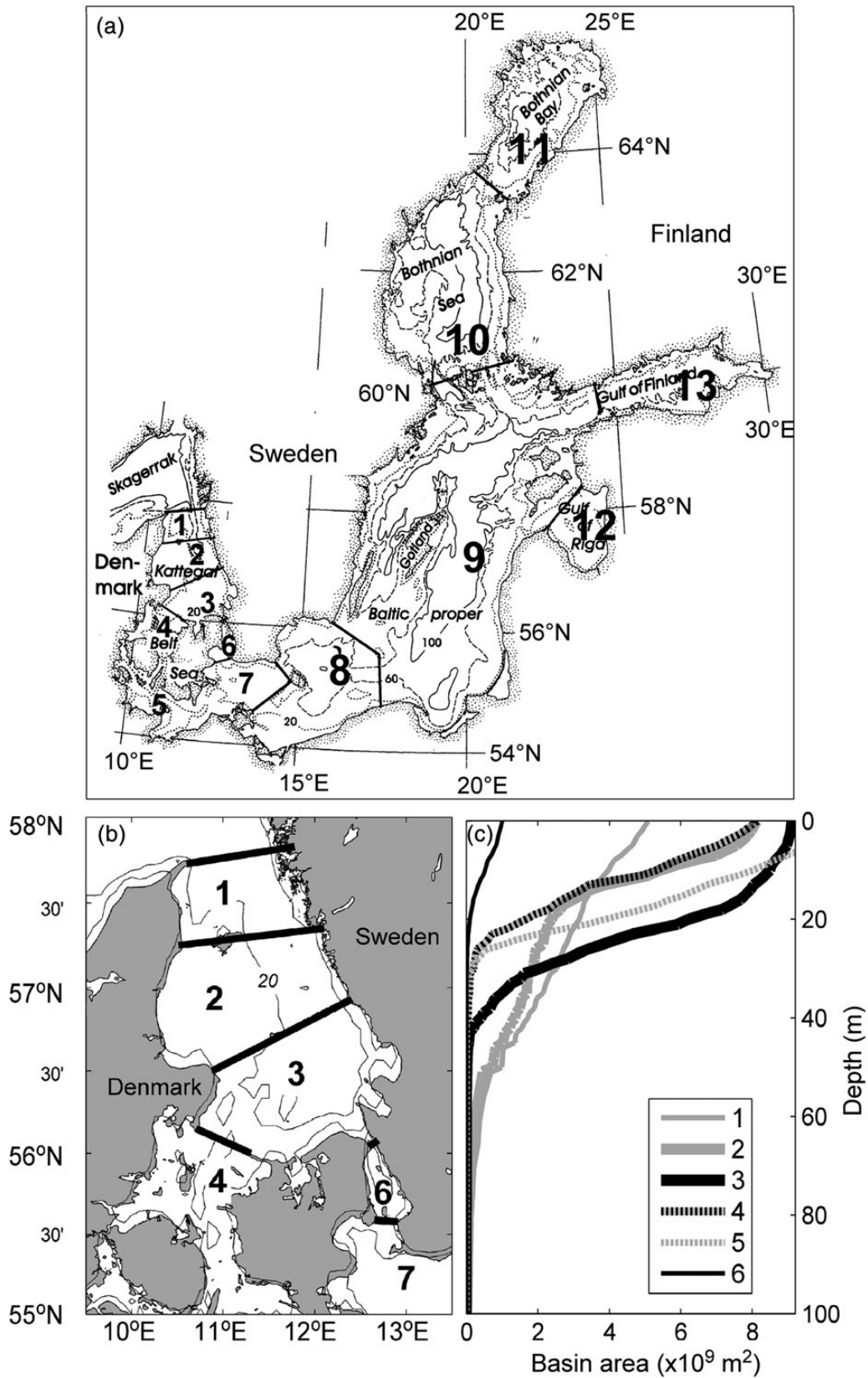
Figure 1. (a) Map of the Kattegat and the Baltic Sea with model sub-basins marked with numbers (1, northern Kattegat; 2, central Kattegat; 3, southern Kattegat; 4, Great Belt; 5, Little Belt; 6, Öresund; 7, Arkona; 8, Bornholm; 9, Baltic Proper; 10, Bothnian Sea; 11, Bothnian Bay; 12, Gulf of Riga; 13, Gulf of Finland) (Gustafsson, 2003). (b) Enlargement of the map of the Kattegat and the Belt Sea with marked model sub-basins. (c) Hypsographic curves (area distribution with depth) of sub-basins 1–6.

Dispersal and retention of early life stages of fish are important factors for the recruitment of fish stocks, as they affect the survival of young propagules and possibly stock integrity (Allain *et al.*, 2007; Hüssy, 2011). The transport of early life stages is highly influenced by hydrographical conditions and meteorological forcing, as well as by the timing and location of spawning and the vertical distribution of eggs in the water column (Sundby, 1991; Hinrichsen *et al.*, 2001a). In general, eggs and early larval stages follow ocean currents, and their vertical distribution thus becomes important for transport patterns in areas where the current varies with depth. The vertical egg distribution is, in turn, dependent on the density and size of the eggs, the density stratification of the water column, and vertical mixing (Sundby, 1983, 1991).

The Kattegat is a shallow transition area with a mean depth of 24 m (Figure 1b) located between the brackish environment of the Baltic Sea and the oceanic salinity conditions of the North Sea (Gustafsson, 2000a; Figure 1a). Between the Kattegat and the Skagerrak, the Kattegat-Skagerrak front forms a hydrographical border with a large horizontal salinity gradient, roughly going eastwards from the northernmost cape of Denmark to the Swedish coast (Rodhe, 1996). In the south, the water exchange between the Kattegat and the Baltic Sea is restricted through the narrow and shallow straits of the Great and Little Belt with a mean depth of 13 m and a sill depth of 18 m, and the Öresund with a mean depth of 11 m and a sill depth of only 8 m (Gustafsson, 1997). The instantaneous water exchange between the Baltic Sea and the Kattegat is mainly driven by the sea level difference across the straits (Stigebrandt, 1992; Gustafsson, 2000a). The freshwater supply of ~15 000 m^3 s^{-1} generates a mean outflow through the straits, but it is superposed by much larger fluctuations driven by sea level differences between the Baltic Sea and Kattegat, which oscillate from 0 to 100 000 m^3 s^{-1} (Gustafsson, 1997; Omstedt *et al.*, 2004). The sea level in the Kattegat responds almost instantaneously to the windforcing on a short time scale (days), while the sea level in the Baltic Sea varies over longer time scales (weeks to months) in response to the freshwater supply and long-period sea level changes in the Kattegat. Sea level variations in the Kattegat are mainly generated by large-scale zonal winds over the Skagerrak and the North Sea, which raise the sea level for westerly winds. The large outflow of brackish water from the Baltic Sea forms a low-salinity surface layer in the Kattegat (from 15 in the south to 20 in the north), which generally streams in a northerly direction. The bottom water, originating in the Skagerrak, has a salinity of ~33–34 and flows predominantly southwards. A strong halocline, typically found at a depth of ~15 m, is present throughout the year, with a salinity difference of ~10 (Svansson, 1975). This density structure is mainly determined by salinity, while temperature is of minor importance.

The flow in the Öresund is controlled by the sea level difference between the Kattegat and the Baltic Sea (Mattsson, 1996). The surface flow is usually directed northwards, but during strong winds that induce inflow towards the Baltic Sea, the low-salinity surface water is replaced by the higher-salinity Kattegat water masses. Salinity conditions in the northern part of Öresund are similar to those in the southern Kattegat, and the main halocline in the Kattegat extends into Öresund. In the southern Öresund, surface salinity drops to about 10, as the surface layer is influenced by surface outflow from the Baltic Sea. The shallow sill, at just 8 m depth, strongly limits the inflow of high-salinity deep water from the Öresund into the Baltic Sea (Mattsson, 1996).

Egg density can be expected to play a vital role for the dispersal of the early life stages of fish in the Kattegat and Öresund due to the

generally large variations of the vertical density structure in time and space, in combination with the typically different circulation patterns of the deep and surface water masses (Gustafsson, 2000a; Nielsen, 2005). Eggs and larvae can easily be dispersed over long distances if they become affected by the strong surface currents in the Kattegat. However, the extent of dispersal is essentially determined by the vertical distribution of the eggs, which in turn is determined by the density of the eggs and stratification of the surrounding water. The typical density range for cod eggs in the Kattegat is not well known due to the lack of direct density measurements. However, an egg density range of 1017–1022 kg m^{-3} has been estimated based on data from egg collection in the area using repeated net hauls over different depth intervals (Pacariz *et al.*, 2014). The reported density measurements of cod eggs in the Öresund are within the range of 1015–1018 kg m^{-3} (Westerberg, 1994; Nissling and Westin, 1997).

Previous research in the Baltic and Belt Sea has shown that the egg and larval transport from the spawning area in the central Bornholm Basin to coastal nursery areas is connected to different wind conditions during the spawning period (Hinrichsen *et al.*, 2001b). Weak winds, especially northerly and easterly, were found to retain early life stages within the Bornholm Basin (Hinrichsen *et al.*, 2001b). Hinrichsen *et al.* (2012) further examined the retention and survival of western Baltic cod eggs and larvae, including the southern Kattegat cod, by using particle tracking in a three-dimensional biophysical model. In their study, retention and dispersion were defined as one of the key factors influencing the survival rate of early life stages, as eggs can be transported to shallow areas where mortality is high owing to contact with the seabed, i.e. due to sedimentation.

The aim of the present study is to explore the interannual variability of the retention and dispersion of the early life stages of cod in the Kattegat and Öresund and to determine how these processes are related to egg density and meteorological forcing. A process-oriented numerical model BALTSEM is used for this purpose. Detailed analysis is given for years representing high and low retention of eggs in the three spawning areas (the central and southern Kattegat and the Öresund). Also, the local windforcing is compared with changes in the large-scale atmospheric circulation patterns over the North Atlantic and Europe, as expressed by the North Atlantic Oscillation (NAO) index (Hurrell, 1995).

Material and methods
The Kattegat and Baltic Sea model

To resolve the strong stratification typical of the study area, a model with fine vertical resolution is required. For the present study, horizontal resolution is less critical, because the focus is not on the detailed, small-scale variability. The BALTSEM model computes highly resolved vertical salinity and temperature profiles in relatively large horizontal sub-basins (Gustafsson, 2000a, b) and was considered to be a suitable tool for this task. This model has been shown to be successful compared with two three-dimensional models, and it has been used in studies of biogeochemical cycles in the Baltic Sea (Eilola *et al.*, 2011; Gustafsson *et al.*, 2012; Meier *et al.*, 2012). In a detailed verification study, making use of observations from extensive surveys in the Kattegat from 2005 and 2006, it was confirmed that the model also gives an adequate representation of the short-term variability of the hydrographical structure in the Kattegat (Pacariz *et al.*, 2014).

The model is process-oriented and includes mixed-layer dynamics, controlled by wind-driven entrainment and buoyancy fluxes

through the sea surface. The flows through the straits are set by sea level and density differences across the straits. The flows across wide, internal boundaries, such as in the southern Kattegat, are given by the Ekman transport. The outflow from the northern Kattegat towards the Skagerrak is controlled by the baroclinic geostrophic transport. Vertical mixing below the mixed surface layer is given by a turbulent diffusivity coefficient inversely dependent on buoyancy frequency.

The model domain covers the Kattegat, which is divided into three sub-basins (sub-basins 1–3 in Figure 1a and b) and the Baltic Sea, Belt Sea and Öresund, divided into a total of 10 sub-basins that are, in most cases, joined at well-defined straits (sub-basins 4–13 in Figure 1a and b). The variation of the basin area with depth (hypsography) is accounted for in each sub-basin, meaning that surface grid cells have a larger area than the deeper layers. The fine vertical grid is built by dynamic density layers with thicknesses down to centimetre scales. New layers are created when an inflow of water occurs from adjacent boxes. The inflowing water is supplied at the level of neutral density, and the total number of layers is kept below the prescribed maximum for each sub-basin by a merging procedure of the layers.

The model was forced using daily-averaged meteorological data from weather stations across the model domain (Gustafsson, 2000b). The freshwater supply to each sub-basin was provided by river run-off plus precipitation. A full technical description of the model is given in Gustafsson (2003).

In the model, particles are treated as a concentration (number per m^3) distributed uniformly over each layer and sub-basin. The egg concentrations are carried passively by the water flow between basins, but depending on whether the eggs are positively or negatively buoyant, they either sink or rise towards the level of neutral buoyancy within each sub-basin. A routine for treating passively drifting buoyant particles was implemented in the model. The vertical velocity of eggs relative to the ambient water is calculated using Stokes' equation, including an adjustment due to non-laminar flows at moderately large Reynolds numbers (Dalla Valle, 1943; Sundby, 1983). The effect of temperature variations on the egg density was not included in the simulation, which is a valid approximation, as the temperature effect gives a density variation of only 0.01–0.05%, corresponding to a variation in the vertical velocity of ~1–2%. Eggs that sink to the bottom were classified as sedimented and removed from the model. Thus there is no re-suspension of eggs in the model, as predation at the bottom is considered high (Westerberg, 1994; Westerberg et al., 1996), and eggs are unlikely to return to the water column.

Model setup for egg simulations
The model was run for the period 1971–2006 with the release of eggs in three spawning sub-basins (2, 3 and 6). For each spawning sub-basin, three egg densities were used. For the southern and central Kattegat, egg densities of 1017 and 1021 kg m^{-3} were chosen to represent the lowest and highest estimated egg densities according to haul data from the Kattegat in 2005 and 2006 (Börjesson et al., 2013; Pacariz et al., 2014), whereas 1025 kg m^{-3} is the density of maximum retention based on earlier simulation results (Pacariz et al., 2014). For the Öresund, low, medium, and high egg densities (1015, 1016.5, and 1018 kg m^{-3}) were chosen to match an experimentally estimated egg density range for this region (Westerberg, 1994; Nissling and Westin, 1997). A constant egg diameter of 1.4 mm was used in all simulations, as a test run with minimum and maximum diameters of 1.2 and 1.6 mm of the range for cod

eggs in the Kattegat showed no significant influence on the results. Four egg batches with durations of 15 days were released in each of the three spawning sub-basins. The first batch was released Julian day 15–29, the second batch day 30–44, the third batch day 45–59, and the fourth batch day 60–74. The eggs were completely removed from the system before initiating new spawning batches the following year. The egg source, given as the number of eggs m^{-3} s^{-1}, was evenly distributed over the depth interval 25–35 m to mimic what is generally known about cod-spawning behaviour in this area (Henrik Svedäng, pers. comm.). The absolute source strength was arbitrarily chosen; thus, only relative values are presented. The only source of mortality included in the simulation was sedimentation. At typical spring temperatures in the Kattegat (1–5°C), cod eggs develop into larvae after ~20–30 days (Thompson and Riley, 1981).

The egg abundance is presented as an average of the four batches, where the abundance for each batch was taken after 28 days from the start day of each batch, representing 13- to 28-day-old eggs/passive larvae, roughly corresponding to the last period of the passive life stages. At this time, most of the eggs are not yet hatched, and very young larvae are considered to have a very weak (if any) swimming or vertical migration ability and thus can also be considered passive (Hinrichsen et al., 2001a). For the first 10 days after hatching, the larvae can be considered passive, but even active larvae and young juveniles are to some extent sensitive to drift.

Egg abundance and environmental indices
The results are given in terms of a total budget; the amount of eggs in each sub-basin represents the fraction of the total eggs released in the spawning sub-basin. The relative abundance of eggs is divided into eggs remaining in the water column (light-colour shades in Figure 2) and eggs that have settled in the sediment (dark-colour shades in Figure 2). The amount of eggs lost to the Skagerrak is determined by the accumulated net flux of eggs across the northern border of the model (given only as grey). Eggs transported to the Little Belt (4) and the sub-basins from the Bornholm basin to the Bothnian Bay (8–13) are summed and marked other. Eggs retained in the Little Belt amounted to 91% of the summed value, on average, while there were only trace amounts of eggs transported into sub-basins 8–13. For the presented results, the retention in each spawning sub-basin and transport to the other receiving sub-basins refers to the total amount of eggs, i.e. eggs in the water column together with sedimented eggs. However, the sedimented eggs and the amount of eggs in the water column are also treated separately when relevant.

Years with high and low egg retention were analysed in further detail to clarify their relationships with various physical processes. Low-retention years are exemplified in 1990 and 2002 for all three sub-basins, while high-retention years in the central and southern Kattegat are represented in 1982 and 2006 and in the Öresund in 1975 and 1988.

Meteorological data used in this study were winter index (i.e. averaged January–April) from NAO Index data provided by the Climate Analysis Section, NCAR, Boulder, USA, Hurrell (1995) and mean west-east component of the local wind (January–April) extracted from daily observations at local weather stations in the Kattegat. Pearson's product–moment correlation was calculated between observed local wind and relative egg abundance of eggs (low, medium, and high densities) in the water column as well as local wind and relative abundance of sedimented eggs (low, medium, and high densities) in three spawning sub-basins and eight receiving sub-basins. The same correlation analysis was used
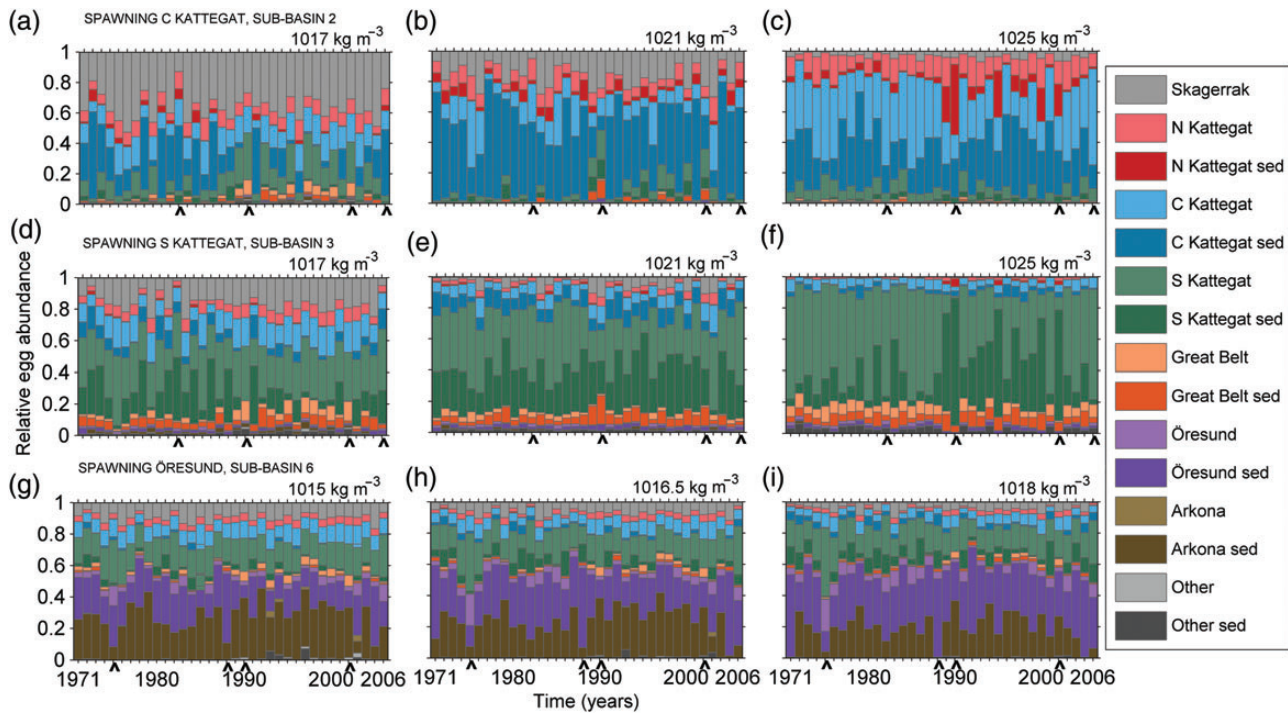
Figure 2. Time series of relative egg abundance (averaged over four batches each year) in the sub-basins of the model domain. Sub-basins are represented by different colours. Light-colour shades represent the amount of eggs in the water column, while dark-colour shades represent the amount of sedimented eggs. (a – c) Eggs spawned in the central Kattegat (sub-basin 2) with three egg densities (1017, 1021, and 1025 kg m^{-3}). (d – f) Eggs spawned in the southern Kattegat (sub-basin 3) with three egg densities (1017, 1021, and 1025 kg m^{-3}). (g – i) Eggs spawned in the Öresund (sub-basin 6) with three egg densities (1015, 1016.5, and 1018 kg m^{-3}). "Skagerrak" represents the amount of eggs that have passed the model's northern border out of the Kattegat. "Other" represents the egg content summed over sub-basins 5 and 8 – 13. Arrows mark the high and low retention years discussed in the text.

when the winter NAO index was used instead of local wind to examine influence between large-scale winds and egg abundance.

Results

The modelled annual concentrations of eggs (yearly averages of four batches) were calculated for three specific egg densities released from spawning sites in three sub-basins: the central Kattegat (2), the southern Kattegat (3), and the Öresund (6). The resulting egg abundances are shown in Figure 2.

Interannual variation of egg abundance

In general, low-density eggs were easily transported with the northward-directed surface flow into the Skagerrak. In particular, eggs spawned in the central Kattegat were more frequently transported to the Skagerrak, due to its geographical proximity. The high-density eggs were located deeper in the water column, typically in the lower part of the pycnocline, and were thus less exposed to mixing and transport with the swifter surface flow. This led to a high retention of high-density eggs, more than 80%, in the southern

Kattegat (Figure 2f). The southward transport (i.e. into the Great Belt, Öresund and Arkona basin) of eggs released in the southern Kattegat was limited because of the generally northward-directed net flow of the surface layer. For eggs released in the central Kattegat, the southward transport was even lower. The supply of eggs from the southern Kattegat into the Arkona basin was found to be extremely small, <5%. Eggs released in the Öresund (Figure 2g–i) were transported northwards and southwards in approximately equal amounts. The southward transport into the Arkona basin was >40% for the low-density eggs during some years, such as 1992 (Figure 2g). A detailed description of the average transport of eggs in this area is given by Pacariz *et al.* (2014).

The interannual variations of the retention and transport of eggs were greater for the low-density eggs in all three spawning areas. The low-density eggs were generally located in the surface layer, where the transport fluctuates more than in the bottom layer. For low-density eggs released in the central Kattegat, the retention ranged between 17 and 64% in 1990 and 1972, respectively (Figure 2a), while for high-density eggs it oscillated between 41 and 82% in
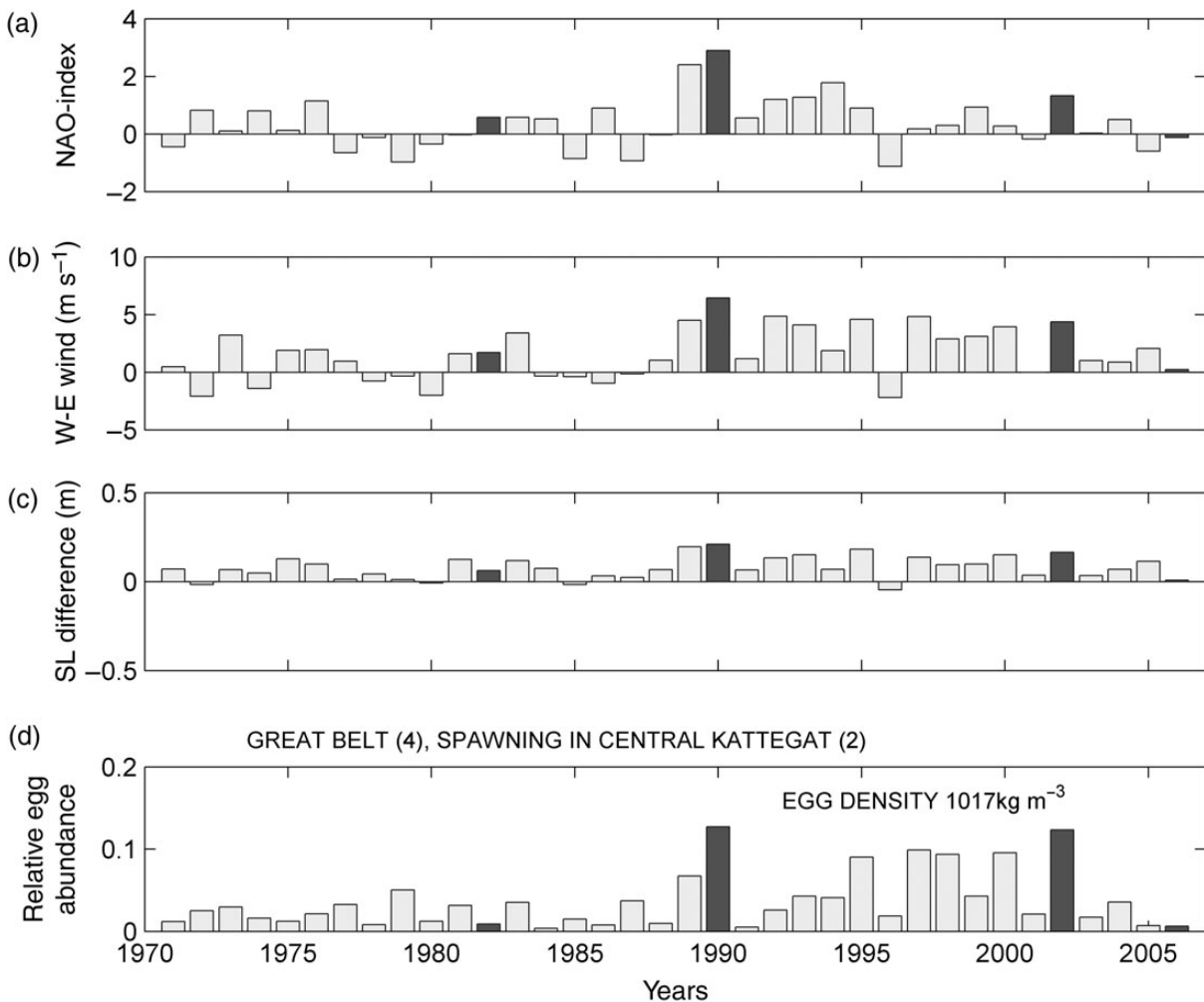
Figure 3. Interannual variation during the period 1971–2006 of (a) NAO index (January–April); (b) Mean west-east component of the local wind (January–April) from daily observations at local weather stations in the Kattegat (positive bars indicate west-wind component); (c) Mean (January–April) sea level difference between the model sea level in the Baltic Proper and observed sea level in the southern Kattegat; (d) Relative egg abundance in the Great Belt in fraction of total release of eggs in the southern Kattegat, (same as orange bars in Figure 2b, total of water column and sediment). Dark-grey bars mark years that exemplify low retention in all three spawning basins (1990, 2002) and high retention in the central and southern Kattegat (1982, 2006). NAO Index data were provided by the Climate Analysis Section, NCAR, Boulder, USA (Hurrell, 1995).

1990 and 2001, respectively (Figure 2c). For eggs released in the southern Kattegat, the corresponding minimum and maximum retention for low-density eggs was 29 and 68% in 1979 and 1982, respectively (Figure 2d), while for high-density eggs, it was 64 and 82% in 1979 and 1990, respectively (Figure 2f). For eggs released in the Öresund, the variability was found to be high and similar for all densities, but it should be noted that all tested egg densities were below or equal to 1018 kg m^{-3} (Figure 2g−i), meaning that the eggs were typically located in and above the upper part of the halocline, where the flow fluctuates considerably. In the Öresund, the minimum and maximum retention of low density eggs was ∼11, and 46% respectively, compared with high-density eggs 22 and 57%, respectively.

The sedimentation varied significantly in all sub-basins and for all egg densities. The sedimentation of eggs at the intermediate densities ranged from 9 to 78% in the central Kattegat (average 46.6%), 3−51% in the southern Kattegat (average 28.1%), and 11−54% in the Öresund (average 26.4%), (Figure 2b, e, and h). During some years, more than 90% of the eggs that were retained in the spawning sub-basin were sedimented (e.g. in 1990 in the southern Kattegat) in contrast to only a few per cent at the opposite extreme (e.g. in 1985) (Figure 2f).

Winds and egg abundance

During the simulation period, there was a change in transport patterns and distribution of eggs between the water column and the sediment around 1989. After 1989, low- and medium-density eggs spawned in the central Kattegat and low-density eggs in the southern Kattegat exhibited increased southward transport, while northward transport increased for high-density eggs released in the central

Kattegat. For all egg densities, the transport from the Öresund to the Great Belt (sub-basin 4, orange bars in Figure 2g−i) was significantly higher after 1989, whereas the transport from the Öresund to the Arkona basin (sub-basin 7, brown bars in Figure 2) was also slightly higher and more consistent. This period coincides with a change in the large-scale wind pattern over the North Atlantic, with more intensified westerly winds after 1989. The NAO index had a clear dominance of positive values averaged over the spawning period (January−April) between 1989 and 1995 (Figure 3a). The local winds had an even stronger westerly dominance and for a longer period after 1989, corresponding to the period of high egg transport (Figure 3b).

While the relationship between egg transport and physical forcing in this region is complex, results still showed some remarkable strong bivariate correlations between windforcing and egg abundance. One such example is the abundance of low-density eggs in the Great Belt that were released in the southern Kattegat (Figure 3d), which had a strong correlation to the west-east local wind component (correlation coefficient, $r = 0.76$, $p < 0.01$). This correlation suggests that during years with strong westerly winds, the inflows towards the Baltic Sea can transport more than 10% of the eggs spawned in the Kattegat into the Great Belt which, because of high surface salinity, can remain in the water column beyond 28 days.

A more systematic analysis of the correlations between the local windforcing and egg abundance, as shown in Tables 1 and 2, indicated some clear patterns. For low-density eggs remaining in the water column in the spawning sub-basin, the correlations were generally low (Table 1). For transport to other basins, in particular, the correlation between the local wind and southward transport of

Table 1. Pearson's product-moment correlation coefficients between observed local wind (mean west-east component January−April) and relative egg abundance (low, medium, and high densities) in the water column in three spawning sub-basins and eight receiving sub-basins.

Spawning sub-basin	Central Kattegat (2)			Southern Kattegat (3)			Öresund (6)		
Egg density (kg m^{-3})	1017	1021	1025	1017	1021	1025	1015	1016.5	1018
Receiving sub-basin									
Skagerrak	−0.05	0.41	0.31	0.36	0.61	0.51	−0.15	0.20	0.40
N Kattegat (1)	−0.01	−0.29	0.34	0.47	0.51	0.56	0.32	0.49	0.47
C Kattegat (2)	0.38	−0.22	−0.58	0.48	0.22	−0.35	0.20	0.48	0.46
S Kattegat (3)	**0.75**	0.67	−0.46	0.04	−0.62	−**0.81**	−0.06	−0.06	−0.17
Great Belt (4)	**0.76**	0.56	−0.43	**0.71**	−0.40	−**0.77**	**0.76**	**0.72**	**0.75**
Öresund (6)	0.61	0.49	−0.55	−0.08	−0.61	−**0.73**	−0.11	−0.15	−0.22
Arkona (7)	0.19	−0.19	−0.19	0.05	−0.13	−0.19	0.16	0.01	−0.06
Other (5, 8−13)	0.53	−0.17	−0.53	0.41	−0.52	−0.61	0.35	0.46	0.40

High correlations (>0.7) are marked in bold.

Table 2. Pearson's product-moment correlation coefficients between observed local wind (mean west-east component January−April) and relative abundance of sedimented eggs (low, medium, and high densities) for three spawning sub-basins and eight receiving sub-basins.

| Spawning sub-basin	Central Kattegat (2)			Southern Kattegat (3)			Öresund (6)		
Egg density (kg m^{-3})	1017	1021	1025	1017	1021	1025	1015	1016.5	1018
Receiving sub-basin									
N Kattegat (1)	−0.51	−0.24	**0.72**	−0.51	−0.01	0.68	−0.05	−0.45	−0.65
C Kattegat (2)	−0.63	−0.39	−0.06	−0.63	0.15	0.10	−0.26	−0.59	−0.56
S Kattegat (3)	0.03	0.60	0.61	−0.46	0.16	**0.83**	−0.15	−0.47	−0.54
Great Belt (4)	0.42	0.69	0.11	−0.03	0.62	0.52	0.00	0.09	0.36
Öresund (6)	0.52	0.63	0.01	−0.21	0.54	0.12	−0.32	−0.26	0.14
Arkona (7)	0.61	0.35	−0.39	0.11	−0.37	−0.46	0.15	0.29	0.12
Other (5, 8−13)	**0.78**	0.66	−0.44	**0.72**	−0.06	−**0.77**	0.40	0.36	0.54

High correlations (>0.7) are marked in bold.

low-density eggs into the Great Belt was high for spawning in the central and southern Kattegat, with a positive correlation of $r = 0.76$ ($p < 0.01$) and $r = 0.71$ ($p < 0.01$), respectively. The shallow 8 m sill between the Öresund and Baltic Sea normally prevents eggs from being transported further southwards. However, during long-lasting inflows into the Baltic Sea, typically on the scale of 4 days or longer (Mattsson, 1996), the near-surface salinity of the Öresund increases enough to allow eggs to be carried over the sill. This delay in transport most likely makes the wind response less direct, resulting in a low correlation between wind and egg abundance in the Arkona basin (for spawning both in the Öresund and in the southern Kattegat).

Other strong correlations can be noted, such as between the sedimentation of the high-density eggs released in the southern Kattegat and local winds (Table 2). As shown in Figure 2, the sedimentation can reach extremely high levels in years with strong westerly winds, such as 2002, when nearly 100% of the eggs retained in the spawning sub-basin were sedimented. The correlation coefficient between local wind and sedimentation in the southern Kattegat was $r = 0.83$ ($p < 0.01$) for the highest density eggs, showing a strong link between high surface salinity and a deep halocline during years with strong westerly winds resulting from reduced outflow of low-

salinity water from the Baltic Sea. Years with weaker and more easterly winds were characterized by a strong outflow from the Baltic Sea, low surface salinity, and a shallow halocline. Running the same correlation analysis as presented in Tables 1 and 2, but using the NAO index instead of local wind information, gave generally much lower correlations although the connection between the NAO index and the local west-east wind component was relatively strong as seen in Figure 3 with $r = 0.6$ ($p < 0.01$).

Low egg retention years

The low egg retention of eggs in 1990 and 2002 stands out in all basins and for all egg densities (Figure 2). It is noteworthy that there was a significant, increased southward transport and a negligible sedimentation for low-density eggs in the Kattegat. The surface salinity was high in those years ($\sim$25) and corresponds to density of $\sim$1020 kg m^{-3} (Figure 4), which means that low-density eggs (1017 kg m^{-3}) were positively buoyant in the surface layer. There was an increased transport northwards of the high-density eggs released in the central Kattegat that followed the compensation deep flow caused by the strong southward Ekman transport. The sedimentation was high for high-density eggs released in the southern Kattegat. For these years with high surface salinity, the halocline
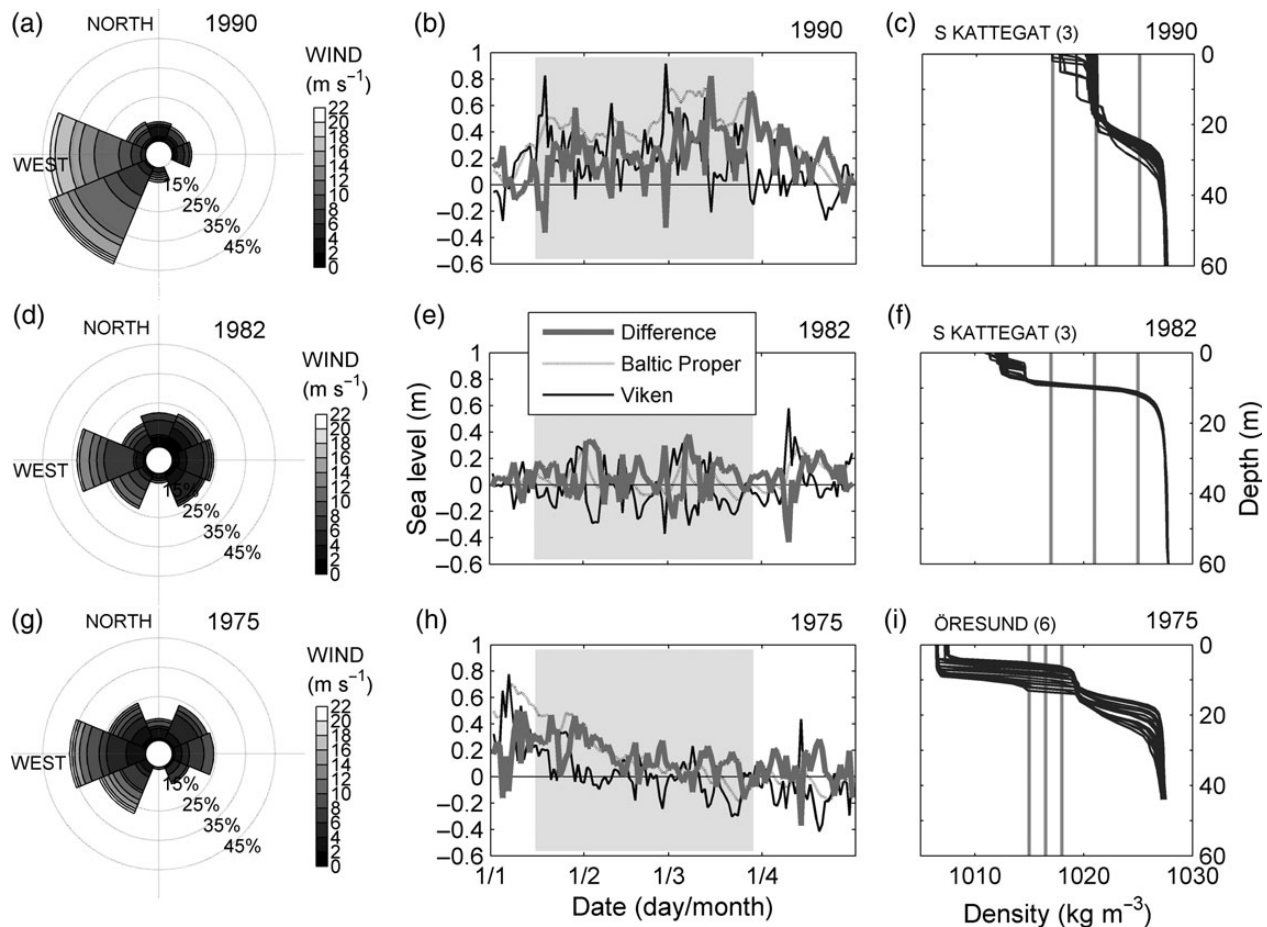
Figure 4. (a) Wind rose based on daily wind observations at local weather stations in the Kattegat for the period of January–April 1990. (b) Observed sea level at the Viken in the southern Kattegat, model sea level in the Baltic Proper, and sea level difference during the period of January–April 1990. Shaded area represents modelled spawning period. (c) Modelled salinity profiles in the southern Kattegat during January–April 1990. The vertical lines represent modelled egg densities in the area. (d–f) Same as a–b but for the year 1982. (g–i) Same as a–b but for the year 1975; model salinity profiles from the Öresund.

was located at 20–30 m depths, which is much deeper than the typical location at a 15 m depth (Figure 4). The isopycnals, corresponding to the densities of high-density eggs, were thus located at depths where the area of the sub-basins is only 10–20% of the surface area (Figure 1c); as a result, the high-density eggs were more likely to sediment to a larger extent. The signal was similar but less prominent in the Öresund (Figure 2g–i). Transport to the Great Belt (orange) and Arkona (brown) increased somewhat, and sedimentation in the Öresund was high (dark shade of violet). High transport and low retention in 1990 and 2002 were most likely related to an increased frequency of strong winds in the westerly sector (Figures 3b, dark grey bars, and 4a). Approximately 10–15% of the windspeed observations were above 12 m s^{-1} during the spawning season in 1990. During this period, the sea level difference between the Baltic Proper and southern Kattegat was generally positive (Figures 3c, dark grey bars, and 4b). Westerly winds elevate the sea level in the Kattegat and generate short-term inflows into the Baltic Sea (e.g. around January 15, February 10 and February 28) bringing eggs from the southern Kattegat. During repeated inflow events, the sea level in the Baltic Proper gradually rises higher than normal (for a detailed sea level series, see Figure 4b, e and h).

High egg retention years

The years 1982 and 2006 were chosen because they were characterized by high egg abundance in the central and southern Kattegat spawning sub-basins. Egg retention was enhanced at the expense of both southward and northward egg transport. For these years, the winds during the spawning period were weak (below 6–8 m s^{-1}) and with no dominant direction (Figure 4d). The sea level difference between the Baltic Proper and the Kattegat was generally small (Figures 3c, dark grey bars, and 4e), indicating a steady outflow of brackish water from the Baltic Sea, resulting in low surface salinity (13–21) in the Kattegat during the spawning period. These salinities correspond to densities below 1017 kg m^{-3}, which is low compared with surface water density around 1020 kg m^{-3} in 1990 and 2002 (Figure 4f). The halocline was shallow and thin in the model, located at 10 m depth, with a density range spanning more than 10 kg m^{-3}. Thus, high-density eggs were located in the halocline, while sedimentation was largely low. However, low-density eggs sedimented to a somewhat greater degree in this situation, as they were located in the upper part of the halocline and, because of mixing, were transported to shallower parts of the Kattegat where they sedimented.

In the Öresund, 1975 and 1988 represent high-retention years. It must be emphasized that although total retention was not exceptionally high in 1975 the amount of eggs in the water column was extremely high. During the spawning period, winds were generally of variable strength and direction (Figure 4g). Winds were predominantly westerly at the beginning of the spawning season, which induced water inflow into the Baltic Sea, raised the sea surface and resulted in a positive sea level difference (Figure 4h). Later in the season, when the westerly winds ceased, the outflow from the Baltic Sea formed a new low-salinity surface layer in the Öresund, and the halocline moved slightly downwards. Both these years were characterized by low surface salinity in the model and a halocline deep enough to retain eggs below the 8 m sill that limits outflows to the Baltic Sea. The model results also indicate that rather small differences in the depth of the halocline resulted in a large difference in the amount of eggs retained in the water column between the two studied years. The average halocline depth of 16 m in 1988 resulted in a higher egg sedimentation rate than that of 1975 when

average halocline depth of was 13 m. The basin area at 13 m depth is ∼40% of the surface area, while it is only 20% at 16 m depth leading to an increased likelihood of sedimentation.

Discussion

The results of our study clearly showed how variation in physical forcing affects the retention and transport of early life stages. Years with extremely low retention of eggs (e.g. 1990, 2002) were generally associated with strong winds with a dominant westerly component, while years with extremely high retention (e.g. 1982, 2006) were a result of weak, variable winds. Further analyses showed relatively strong bivariate correlations among local winds, egg transport, and sedimentation. Water exchange between sub-basins and egg transport in the area were indeed influenced by large-scale atmospheric circulation, as characterized by the NAO index. During positive phase of winter NAO index, dominant strong westerly winds were related to low retention and generally southward transport of eggs. However, the local wind index gave more relevant information on the direct forcing of the system. The change in egg abundance after 1989 was reflected by local wind variations for some features (such as the egg transport towards the Great Belt, Figure 3), but many of the circulation and sedimentation patterns had a weak (if any) correlation with the mean local wind over the spawning season, as shown in Tables 1 and 2. This result reflects the hydrographical complexity in this area as a transition zone between the Baltic Sea and the Skagerrak, with large differences in salinity and a large, intermittent water exchange between years, influenced by mechanisms other than the local windstress. In comparison, drift studies in the Bornholm basin (Hinrichsen *et al.*, 2001b), having relatively stable hydrographic conditions, showed a strong relationship between windforcing and egg retention and dispersal. Larval transport from the Bornholm Basin to coastal areas intensified during persistent westerly winds, and retention was higher during weak variable winds (Hinrichsen *et al.*, 2001b). In a modelling study on the influence of wind-induced upwelling and downwelling on the gene exchange and retention of fish eggs in the Norwegian fjords (Masfjorden), a strong relation between the non-local windforcing, as well as local fjord water mass dynamics were found, which were both important for the retention and gene exchange of the early life stages of fish (Asplin *et al.*, 1999), similar to what is indicated in this study for the Kattegat. In open oceanic areas, such as on the Newfoundland Shelf, significant but rather weak correlations among recruitment, retention, and windstress have been found (Deyoung and Davidson, 1994).

Throughout the simulation period, the correlation between local wind and egg abundance in the water column in the spawning area in the southern Kattegat and Öresund was generally low, while sedimentation rates and transport to other basins were strongly correlated. This result implies that there may be a fairly continuous supply of eggs in the water column of the spawning basins from year to year, while the dispersal of eggs to other areas and the mortality rate due to sedimentation are highly affected by changes in the physical environment. In an analysis of the mortality of western Baltic cod eggs caused by unfavourable temperature conditions and sedimentation, Hinrichsen *et al.* (2012) noted that transport had a significant effect on the survival rate. Unfavourable environmental conditions can have a considerable impact on recruitment, and this impact, as well as the impact of fishing, should be accounted for in fishery management (Larkin, 1996; Hinrichsen *et al.*, 2012). If survival of eggs dispersed towards the northern Kattegat and Skagerrak and thereby the return to the native spawning grounds is low, it

could to some extend explain the low productivity of Atlantic cod stock in the Kattegat. The results of our study indicate that transport and sedimentation are highly dependent on the egg density, which is likely an important factor in determining the amount of sedimentation and local retention. For example, in a year such as 1990, low-density eggs remained in the water column while high-density eggs were exposed to the risk of high mortality via sedimentation. Low-survival probabilities for high-density eggs during the extremely unfavourable conditions (e.g. strong westerly winds, high sea level differences, and deep surface layers with high salinity) indicated a selection towards slightly lower cod egg density in the Kattegat. Indications of such an adaptation were obtained from vertical egg haul data from the area (Pacariz *et al.*, 2014).

Compared with a three-dimensional particle-tracking simulation (Hinrichsen *et al.*, 2012), the BALTSEM model yielded similar results for basic quantities, such as retention and sedimentation. Average retention over all densities in the southern Kattegat was 33.5%, which corresponds well with 26% ($\pm$16%) in the three-dimensional-model study. The estimated average sedimentation over all densities in the southern Kattegat in this study was 19.6%, compared with the 17% ($\pm$11%) mortality of eggs due to sedimentation in the three-dimensional-model study. The use of egg concentration in relatively large boxes seems to corroborate with the more detailed particle-tracking modelling concept. The model differences can be explained partly by the dynamic egg buoyancy routine used in the BALTSEM, vs. eggs being located at constant density levels throughout the simulation in the particle-tracking model (Hinrichsen *et al.*, 2012). The process of mixing eggs instantaneously over each layer and the entire sub-basin in the BALTSEM may somewhat overestimate egg sedimentation by a too rapid transport to shallow areas, where sinking eggs can reach the bottom. The main advantage of BALTSEM model is high vertical resolution down to centimetre scale and active egg mixing which should be more realistic description of vertical egg distribution and thereby large-scale horizontal transport in this highly sheared system. Since the instantaneous horizontal mixing does not allow any horizontal variations within each sub-basin, it may give a too direct exchange of eggs between sub-basins since in reality it will take some time for the eggs in a concentrated spawning area to reach the border to the next sub-basin. It is thus likely that this type of model somewhat overestimates egg fluxes caused by short-term flow variability, but it should give realistic results on longer time scales. Consider for example a strong flow towards the Baltic for several days. Such a flow will bring large amounts of eggs from the southern Kattegat towards the Öresund and the Belt Sea irrespectively of the horizontal mixing in the model.

This study suggests a high connectivity between the central and southern Kattegat, as the exchange between these sub-basins is direct and unrestricted by bottom topography. According to our modelling study, the southward transport of eggs towards the Great Belt was significantly increased after 1989. There were regular exchanges between the Öresund and the southern Kattegat as well as the Öresund and the Arkona sub-basins. The outflow of eggs from the Öresund could seemingly affect recruitment in the Arkona basins. It has been suggested that such exchanges between the basins may lead to gene flow between the stocks, i.e. may affect their connectivity (Nielsen *et al.*, 2005). The exchange of eggs and larvae among the Baltic Sea, the Belt Sea, and the Kattegat and the possibility of enhanced transport eastwards resulting from different physical forcing have been discussed in Hinrichsen (2001a, 2012) and Westerberg (1994). Genetic isolation and divergence, as noted by Cowen *et al.* (2000), is supported by physical environmental conditions that ensure the retention of eggs, such as estuarine circulation causing high retention and low connectivity between Norwegian fjords (Myksvoll *et al.*, 2011). However, behavioural factors, such as natal homing, may also counteract the effects of larval dispersal (e.g. Svedäng *et al.*, 2007). Comparing the Öresund and Kattegat it appears that transport of early life stages is not the main factor describing the decrease of the fish stock and that fishing regulations play important role for the management. To correctly study the relationship between egg abundance and recruitment success, a number of parameters must be accurately estimated. The effect of egg and larval transport on recruitment success can be limited by, for example, a lack of a suitable recruitment time series, information on spawning grounds and spawning periods, or accurate quantifications of the reproductive effort (Hinrichsen *et al.*, 2001a), including the origin of the recruits (Svedäng, 2003). Furthermore, the period of the larval stages is influenced by a number of factors and processes (e.g. food availability, swimming ability development) that are not well documented. To improve results, future efforts should consider factors discussed above. There is also a need to use detailed three-dimensional hydrodynamic modelling that allows vertical mixing of eggs to further study, e.g. the sedimentation which was elucidated as an important mortality factor.

In conclusion, this type of modelling study can give indications about recruitment success and stock connectivity issues between neighbouring areas in this hydrodynamically, fairly complex area and how these are related to ocean circulation due to shifting atmospheric forcing conditions. It can also indicate important nursery areas for stocks in the Kattegat and western Baltic region.

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