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# Hydrographic influence on the spawning habitat suitability of western Baltic cod (*Gadus morhua*)

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Recruitment variability of marine fish is influenced by the reproductive potential of the stock (i.e. stock characteristics and abundance) and the survival of early life stages, mediated by environmental conditions of both a physical (water temperature, salinity and oxygen conditions, ocean currents) and a biological nature (i.e. food, predators). The objective of this study is to assess the importance of variability in environmental conditions within different western Baltic cod spawning grounds for egg survival. Habitat identification was based on environmental threshold levels for egg survival and development and ambient hydrographical conditions at different times during the spawning season. The long-term resolution of environmental conditions allowing survival of western Baltic cod eggs indicates that favourable conditions predominantly occurred during the late spawning season in April/May, while minimum survival rates could be expected from January to March. Unsuitable time periods and habitats exhibiting the highest mortality rates are exclusively characterized by ambient water temperatures below the critical survival threshold. Despite the strong influence of water temperature on habitat suitability, the impact of habitat suitability on recruitment was not clearly defined, suggesting that other mechanisms regulate year class strength.

**Keywords:** egg survival, environmental thresholds, hydrography, recruitment, spawning habitat suitability, western Baltic cod.

## Introduction

The western Baltic is the transition area connecting the Kattegat with the central Baltic through the channel-like inlets of the Sound, the Great Belt, and the Little Belt (Figure 1). The Kattegat is a shallow area with a mean depth of only 23 m. The Belt Sea is on average 13 m deep, with deep and narrow channels, i.e. the Great and Little Belt, the Fehmarn Belt, and the Sound, through which most of the water mass exchange between the Kattegat and the central Baltic occurs. With its two sills of < 8 m depth, water mass exchange through the Sound is limited. For management purposes, the Baltic Sea has been partitioned into Subdivisions (SD) by the ICES, where SD 21 encompasses the Kattegat and SDs 22–24 the western Baltic Sea, from the Belt Sea to the Arkona Sea.

The hydrographic conditions of the western Baltic Sea are controlled by inflows of high saline Atlantic water and outflows of surface water from the Baltic, which is brackish due to river run-off and precipitation (Lehmann *et al.*, 2002). Baltic inflows are mainly caused by persistent, strong westerly winds over the eastern North Atlantic and northern Europe (Schinke and Matthäus, 1998). The highly fluctuating in- and outflow, which is forced by the sea level inclination between the Kattegat and the western Baltic Sea, is the cause for the highly dynamic hydrographic environment in this area (Lehmann *et al.*, 2002).

One of the fish species that is faced with reproductive challenges resulting from this variable hydrography is cod (*Gadus morhua*), one of the most important commercial species in the Baltic Sea. Cod are generally distributed throughout the western Baltic Sea (Thurow, 1970; Oeberst, 2008). Adult cod undertake distinct seasonal migrations from their feeding grounds in near-shore and shallow waters to their spawning grounds (Aro, 1989). Major cod spawning grounds are located in the deeper, saline water of the Kattegat, the Sound, the Little and Great Belt (Thurow, 1970), Kiel Bay, the Fehmarn Belt, and to a limited degree in Mecklenburg Bay (Thurow, 1970; Bleil and Oeberst, 2000, 2002) and in the Arkona Basin (Bleil and Oeberst, 2004; Bleil *et al*., 2009). The spatial distribution of the spawning grounds seems to be rather stable over the years (Hüssy, 2011, and references therein). The timing of spawning is subject to a pronounced spatial gradient, with progressively later spawning from north to south (Bleil and Oeberst, 1997; Bleil *et al*., 2009). In the Kattegat and Sound, peak spawning occurs in January/February (Vitale *et al*., 2005), whereas in the Great Belt, Kiel Bay, and Mecklenburg Bay it occurs in March/April (Bleil and Oeberst, 2004; Bleil *et al*., 2009). The entire spawning season may last up to 7 months, while peak spawning is usually restricted to 1–2 months (Thurow, 1970; Bleil and Oeberst, 1997, 2004; Vitale *et al*., 2008; Bleil *et al*., 2009). It is thus evident that the spatio-temporal variability in environmental conditions over the spawning season is considerable. Environmental factors such as salinity, temperature, and oxygen concentration affect an area's suitability as a spawning ground through their power to limit survival of early life stages (Hinrichsen *et al*., 2007). Eggs drift passively with the currents and are thus particularly vulnerable to adverse conditions. Salinity levels below 20–22 psu, for example, cause the eggs to sink to the bottom where they fail to develop and eventually die (von Westernhagen, 1970; von Westernhagen *et al*., 1988, C. Petereit, pers. comm.). Another factor of considerable importance is temperature. Egg development time is strongly temperature dependent, where successful development is possible at temperatures >2°C, but best in the range of 5–8°C (von Westernhagen, 1970; Bleil, 1995). Under suboptimal conditions, egg mortality increases because of an increase in development time (von Westernhagen, 1970). Survival of cod eggs, and hence potentially recruitment success, is thus highly dependent on the geographical location of the spawning ground as well as on the timing of spawning.

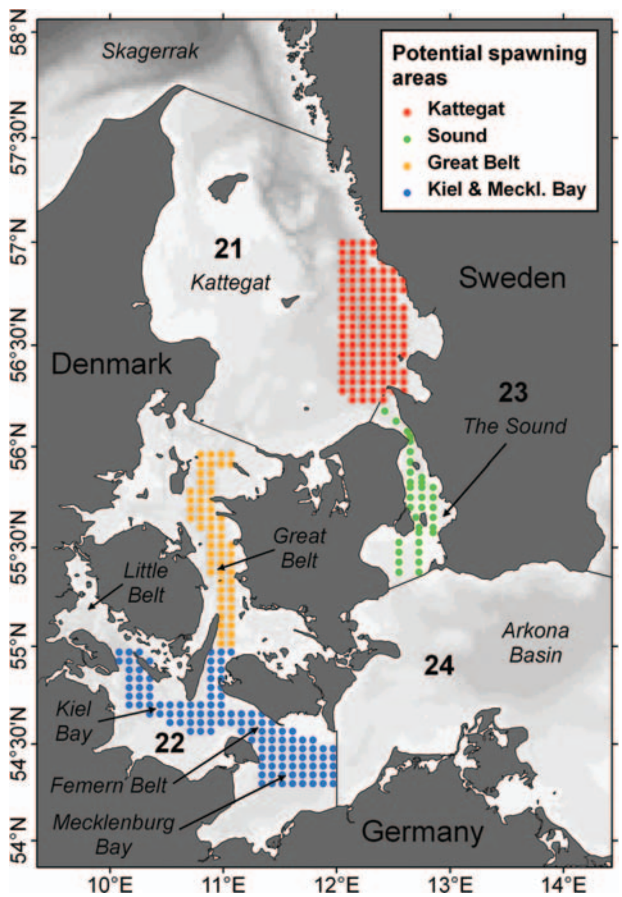


**Figure 1.** Map of the western Baltic Sea with the sampling locations for the estimation of spawning habitat suitability shown in different colours (red = Kattegat, green = Sound, yellow = Great Belt, blue = Kiel/Mecklenburg Bays).

The present study aims to examine how the spatio-temporal variability of the ambient hydrography in the main spawning areas affects the suitability of these areas for successful egg survival of western Baltic cod. The objectives of this study are to (i) perform long-term assessments of the impact of temperature and salinity on the suitability of spawning habitat for western Baltic cod spawning grounds; (ii) assess the impact of the timing of western Baltic cod spawning on spawning habitat suitability; and (iii) identify the relationship between spawning grounds and spawning times and stock recruitment.

## Material and methods

### Spawning areas and environmental threshold levels for egg survival

#### *Spawning areas*

The spawning grounds examined in this study were selected based on the review of all existing information on western Baltic cod's spawning activities by Hüssy (2011).

#### *Spawning time*

The period selected for this study covered the entire spawning season of cod in the different areas. Due to the considerable inter-annual variability, the period examined was chosen to encompass the entire period from the earliest to the latest reported spawning activities (Table 1).

#### *Environmental threshold levels for egg survival*

For successful egg development and survival, environmental conditions must fulfil a range of criteria. The critical threshold levels used in this study are summarized in Table 2, where salinity and oxygen values are required to be above the indicated threshold values. The salinity range from 18 to 33 psu (von Westernhagen, 1970) represents the levels at which eggs are neutrally buoyant

**Table 1.** Duration of the spawning season of cod in different areas of the western Baltic Sea.

| Area | Spawning season | Peak spawning | References |
|---|---|---|---|
| Kattegat | September–May | January/February | Vitale *et al.* (2005) |
| Sound | November–May | January/February | Vitale *et al.* (2005) |
| Kiel Bay | December–June | March/April | Thurow (1970), Müller (1988), Bleil *et al.* (2009) |
| Mecklenburg Bay | February–June | March/April | Kändler (1949), Bleil *et al.* (2009) |
| Arkona | March–September | June/July | Bleil *et al.* (2009) |

**Table 2.** Environmental threshold values for egg development and survival in the different spawning areas of the Baltic Sea.

| Parameter | Stock | Optimal value | Threshold value | Reference |
|---|---|---|---|---|
| Salinity | Kattegat | >21.2 ± 1.2 psu | 18 psu | Nissling and Westin (1997) |
| | Western Baltic | >20–22 psu | 18–33 psu | von Westernhagen (1970), Westerberg (1994), Nissling and Westin (1997) |
| Temperature | Western Baltic | 4–8.5°C | 2°C | von Westernhagen (1970), Bleil (1995) |
| Oxygen | Eastern Baltic | >2 ml $O_2$ $l^{-1}$ | 2 ml $O_2$ $l^{-1}$ | Wieland *et al.* (1994), Rohlf (1999) |

(float in the water). At salinities below this range, they sink and presumably die on contact with the bottom. Oxygen levels below a threshold level of 2 ml $l^{-1}$ result in development failure and death. Egg development is possible within a range of temperatures, while both higher and lower temperatures become increasingly lethal. In the present study, only the lowest possible threshold for egg development of 2°C is relevant, as temperatures during the spawning season do not exceed the upper limit of 10°C (Petereit, 2004). The duration of the egg stage is temperature dependent, and lasts between 7 and 18 d depending on the prevailing temperature conditions in the spawning period (Petereit, 2004). Retention within the spawning grounds is highly dependent on the prevailing drift patterns (Hinrichsen *et al.*, this issue).

## Hydrographic data

Temperature, salinity, and oxygen distributions provided as prognostic variables by the hydrodynamic Bryan–Cox–Semtner model (Bryan, 1969; Semtner, 1974; Cox, 1984; Killworth *et al.*, 1991) were selected and form the database for the subsequent long-term analysis on the habitat suitability in the different spawning areas of western Baltic cod for the entire spawning period.

## Spawning habitat suitability

Physical habitat suitability for western Baltic cod eggs was defined based on the threshold values for their survival in Table 2. As oxygen conditions in the investigated areas were generally above the threshold level of 2 ml $l^{-1}$ and temperatures at levels where cod eggs float never exceeded 10°C, the suitable habitat was defined as the water body exhibiting salinities between 18 and 33 psu and temperatures >2°C.

In order to resolve the spatial and temporal variability of the spawning habitat in relation to ambient hydrography, time-series of hydrography data covering the years 1979–2005 were used. Within each of the four investigated spawning areas (Figure 1), positions on the regularly spaced, 5 × 5 km hydrodynamic model grid were selected. At these grid points, the model provided hydrographic data profiles at a vertical resolution of 3 m intervals. For further calculations (see below), the vertical profiles were interpolated to obtain 1 psu salinity intervals. Based on the duration of the cod spawning season from December to May, 19 spawning dates at 10 d intervals from 1 December to 30 May were defined. This formed the basis for the calculation of the maximal possible suitable spawning habitat size for each of the four spawning areas ($HS_{\max,\,A}$), defined as:

$$HS_{\max,\,A} = \mathrm{n}_{\mathrm{ht},\,A} \times \mathrm{n}_{\mathrm{vt},\,A}$$

where $A$ refers to the four spawning grounds, $\mathrm{n}_{\mathrm{ht},\,A}$ is the total number of horizontal locations in each of the four spawning grounds, and $\mathrm{n}_{\mathrm{vt},\,A}$ is the total number of vertical egg buoyancy levels at 1 psu steps between 18 and 33 psu (a total of 16 levels) at these horizontal locations.

For each of the 19 individual dates during each spawning season from 1979/1980 to 2004/2005, the number of locations (in the horizontal and vertical dimension) which fulfilled the requirements for egg survival were determined, and the corresponding spawning habitat suitability ($HS_A$) in relation to the maximal possible suitable spawning habitat size ($HS_{\max,\,A}$) was calculated for each of the four spawning areas:

$$HS_A = \mathrm{n}_{\mathrm{h},\,A} \times \mathrm{n}_{\mathrm{v},\,A} \times HS_{\max,\,A^{-1}}$$

where (for each individual date) $\mathrm{n_h}$ is the number of horizontal locations at which a number ($\mathrm{n_v}$) of required egg buoyancy levels between 18 and 33 psu (at 1 psu steps) were available. Values were not taken into account as a suitable spawning habitat, if for a given buoyancy level the corresponding oxygen and temperature values were below their thresholds.

## Impact on year class strength

Data on recruitment and spawning stock biomass (SSB) of cod in the Kattegat (SD 21) and the western Baltic Sea ( SDs 22, 23, and 24) for each year were obtained from ICES (2011). The underlying data used to estimate these indices were obtained from DATRAS (2011). The available indices of SSB and $R$ cover the entire western Baltic, consisting of SDs 22, 23, and 24. In order to evaluate the influence of habitat suitability on relative year class strength, the indices of $R$ and SSB were estimated for each of these areas separately, excluding SD 24 which is outside the area of investigation. $R$ in SD 22 and 23 ($R_{22}$ and $R_{23}$) were estimated based on the proportions of age 1 cod in SD 22 and SD 23 ($\mathrm{p}_{\mathrm{age}\ 1,\ 22}$ and $\mathrm{p}_{\mathrm{age}\ 1,\ 23}$) caught during the Baltic International Trawl (BITS) surveys in the first quarter of each year (data from DATRAS, 2011) and $R$ in the western Baltic ($R_{22/23/24}$) as:

$$R_{22} = \mathrm{p}_{\mathrm{age}\ 1,\ 22} \times \mathrm{R}_{22/23/24}$$

$R_{23}$ was calculated accordingly. Based on the proportional contribution of mature cod ($\mathrm{p}_{\mathrm{mature},\ 22}$ and $\mathrm{p}_{\mathrm{mature},\ 23}$), $SSB_{22}$ and $SSB_{23}$ were estimated in the same way as:

$$SSB_{22} = \mathrm{p}_{\mathrm{mature},\ 22} \times SSB_{22/23/24}$$

$SSB_{23}$ was calculated accordingly.

Western Baltic cod are considered as recruits at age 1. Year class strength (YC) was therefore approximated by back-shifting the number of recruits $R$ by 1 year. In order to remove the effect of SSB size, relative year class strength was calculated as YC × $\mathrm{SSB}^{-1}$ rather than using total abundance.

To analyse the impact of spawning habitat suitability on recruitment, average monthly habitat suitability was calculated for each area. Each of the 19 spawning dates was assigned to the month in which they occurred, and the habitat suitability estimates for these dates were averaged by month. The impact of the spawning habitat suitability on relative year class strength was analysed in a multiple regression analysis with months nested within areas, with stepwise backward elimination of parameters for each SD separately.

### Baltic Sea Index (BSI)

To analyse the effect of atmospheric forcing conditions over the Baltic Sea on the spawning habitat suitability of western Baltic cod, the Baltic Sea Index (BSI) (Hinrichsen *et al.*, 2001; Lehmann *et al.*, 2002), which represents the 3 hourly resolved normalized sea level pressure differences between Oslo (Norway) and Szczecin (Poland) as a proxy for the general wind forcing conditions, was used. In this study, the BSI was averaged over a 5 d period prior to the 19 spawning dates. The main purpose was to provide estimates of spawning habitat suitability in terms of the vertical salinity distribution generated by wind-induced currents over the investigation area up to 5 d before the spawning dates. Positive indices correspond to anomalous sea level pressures associated with westerly winds, whereas negative values indicate predominantly easterly winds over the Baltic Sea. As the BSI has to be considered as a more large-scale measure of the atmospheric conditions over the Baltic, determination of the relationship between averaged BSIs and the spawning habitat suitability of the whole region was performed by simple correlation analysis. Habitat suitability representing the entire region was calculated following the procedure above, by combining the respective horizontal and vertical levels of all areas.

## Results

### Geographic patterns

Spatial patterns showed a pronounced decreasing gradient in average levels of spawning habitat suitability from north to south (Figure 2). The highest overall levels occurred in the Kattegat, with average values between mid-60% and 90% throughout the years and seasons. The average levels of suitable habitat gradually decreased from the Kattegat over the Sound ( ~ 45%) to the Kiel/Mecklenburg Bays (30–40%), while the variability increased considerably. In the Great Belt, the habitat suitability was similar to Sound levels for the first half of the spawning season (40–60%), increasing to Kattegat levels (90%) towards the end of the season.

The 5 d backward-averaged BSI was found to be significantly and negatively correlated to the corresponding spawning habitat suitability representing all four spawning grounds. Generally, the relationship indicated that differences in sea level pressure associated with westerly winds led to relatively low habitat suitability, while negative BSIs, representing easterly winds, provided higher values. For all spawning grounds (except the Sound), the highest habitat suitability occurred at the end of the spawning period



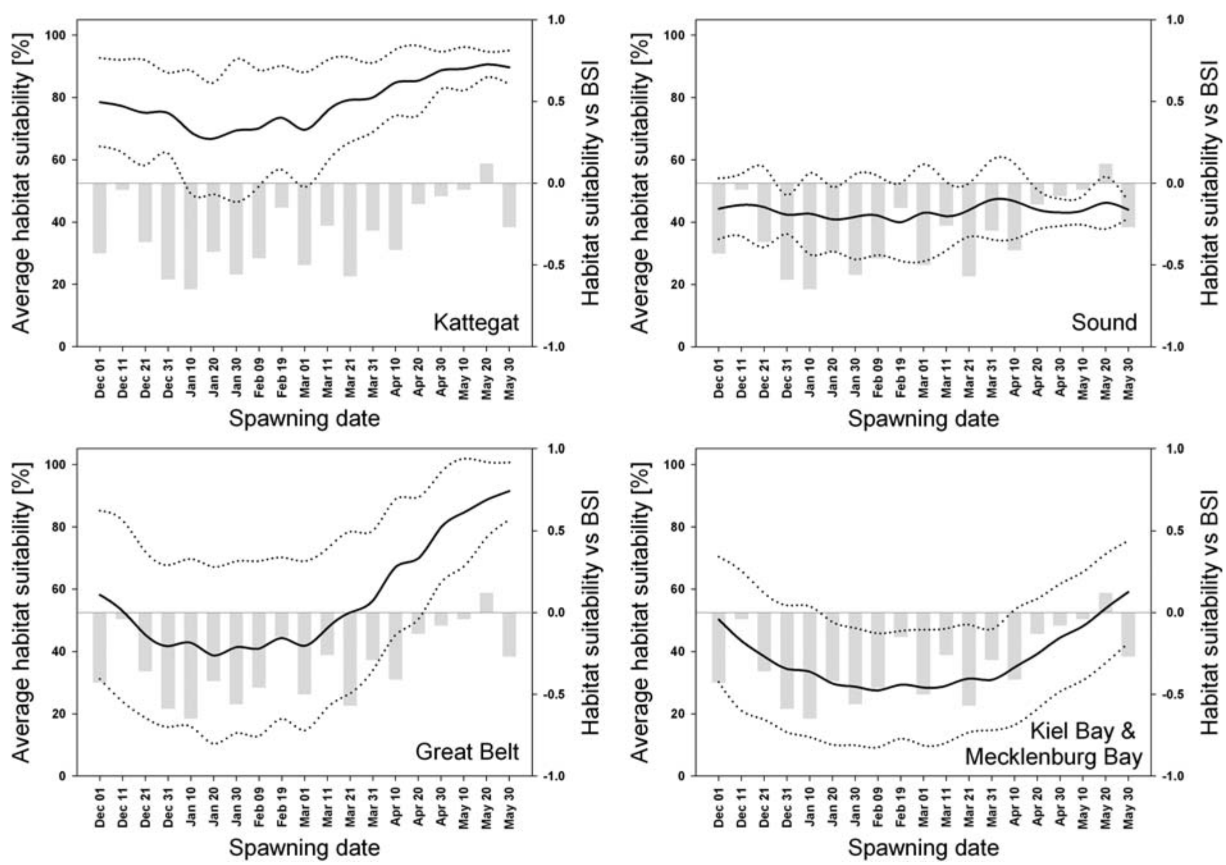


**Figure 2.** The spawning habitat suitability of cod over the spawning season for each of the four different spawning areas within the western Baltic Sea (solid lines, average; broken lines, ± SD). Also shown is the correlation between the BSI and total survival potential in the western Baltic Sea (columns), where negative values indicate correlation with easterly winds and positive values correlation with westerly winds.

(Figure 2); a period which is mainly characterized by outflow situations with high pressure over the Baltic and, accordingly, low wind forcing conditions. However, the predictability of the habitat suitability was only low during this period, while the highest negative correlations between the habitat suitability and the BSI were found between the end of December and the beginning of April.

## Temporal patterns

In all areas, the environmental conditions for successful reproduction were relatively high for early spawners (December), decreasing to the lowest levels during the main spawning season in January–March, and were most favourable during the late spawning season in April/May. These patterns were particularly pronounced during a period from the mid 1980s to the early 1990s, in the late 1990s, in 2001, and in 2004. In contrast to this, during the period 1979–1983, relatively low spawning habitat suitability was found in the early and middle part of the spawning season. This seasonal pattern in habitat suitability was almost exclusively caused by the prevailing salinity conditions. In all areas, the spawning seasons 1999/2000 and 2002/2003–2003/2004 were characterized by very good conditions throughout the season.

The Kattegat revealed an almost constant and high habitat suitability (Figure 3). The lowest values were observed in the spawning seasons 1982/1983, 1989/1990, and in 1999/2000, which was predominantly caused by low salinity levels.

Although much smaller in magnitude, the same seasonal variations were evident in the Great Belt (Figure 3). In the years 1988–

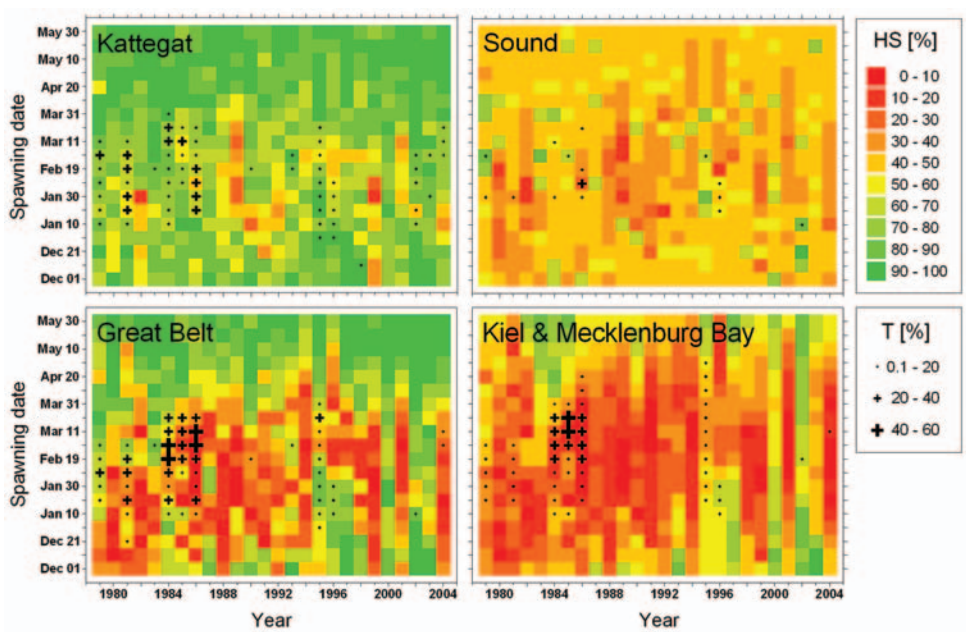


**Figure 3.** The spawning habitat suitability (HS, coloured squares) of western Baltic cod based on salinity and temperature conditions in relation to year and date within each spawning season for the Kattegat, the Sound, the Great Belt, and the Kiel/Mecklenburg Bays. In squares without crosses the spawning habitat suitability depends exclusively on salinity. The crosses indicate what percentage of the potential spawning locations are unsuitable for egg survival due to low temperatures.

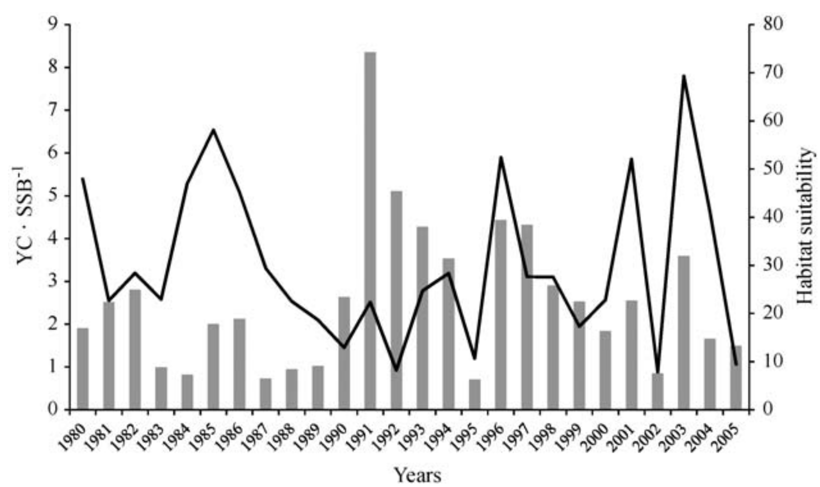


**Figure 4.** Relative year class strength of western Baltic cod in SD 22 (bars) and spawning habitat suitability (line) during March in the Kiel/Mecklenburg Bays (the only month and area with a significant correlation).

1992, 1999, 2001, and 2004, spawning habitat suitability during the main spawning season was low, as well as during the early spawning season in 1980 and 1982, with low temperatures as the main limiting factor.

In the Kiel/Mecklenburg Bays (Figure 3), conditions during the main spawning time in March–April were below average in the years 1980–1982, 1986–1994, 1996–1999, 2001, and 2004. The years 1995, 2000, and 2002 showed very high habitat suitability in this area also.

In the Sound (Figure 3), the spawning habitat suitability appears to be more constant but lower throughout the spawning season than in the other areas, exclusively due to lower salinity conditions.

### Impact on year class strength

In the Kattegat, relative year class strength ($YC_{21}$) was not related to the spawning habitat suitability within any month (d.f. = 20, all $p > 0.05$). Relative year class strength in the Great Belt and Kiel/Mecklenburg Bays ($YC_{22}$) depended particularly on the hydrographical conditions in the Kiel/Mecklenburg Bays in March only (d.f. = 13, $r^2 = 0.20$, $p = 0.05$). Relative year class strength in SD 22 and habitat suitability in the Kiel/Mecklenburg area during March (the only significant area–month combination) are shown in Figure 4. Also in the Sound relative year class strength ($YC_{23}$) was not correlated with spawning habitat suitability (d.f. = 13, all $p > 0.05$). These results indicate that spawning habitat suitability during the main spawning period does seem to have a certain influence on relative year class strength in the main spawning area of the Kiel/Mecklenburg Bays, but that this influence is neither strong nor consistent over the years and areas.

## Discussion

The habitat suitability of different spawning areas was evaluated by contrasting environmental conditions throughout the spawning season and over a range of years with known threshold levels for cod egg survival. However, the results on spawning habitat suitability alone are not sufficient to explain the variability of western Baltic cod stock size and recruitment. It was not in the aim of this study to explain early life stage survival, but it was intended as a baseline, providing the necessary information for subsequent studies of survival mechanisms of specific life stages throughout ontogenetic development (e.g. Hinrichsen *et al.*, this issue).

Spatial differences in habitat suitability were detected, with decreasing levels along a gradient from north to south. Lower values were generally associated with an increase in variability within and between years. In all areas except the Sound, spawning habitat suitability was predicted to be moderately high in the beginning of the spawning season, lowest during mid-season, and increasing steadily thereafter. However, the predictability of the spawning habitat suitability using regional atmospheric conditions (BSI) over the Baltic area was high during periods of low spawning suitability, while the lowest predictability was found to be during periods of relatively high spawning suitability. This seasonal pattern was exclusively associated with the prevailing seasonal salinity regimes and their impact on the eggs‘ ability to float in the water column. Since the mid 1990s, spawning habitat suitability has predominantly been determined by prevailing salinity conditions, while temperature-dependent mortality of eggs has been limited. In contrast to this, the habitat suitability was reduced over a prolonged period of cold years during the early to mid 1980s.

The estimation of habitat suitability relies on the threshold values selected for egg survival at the spawning location. These values were derived from published studies of both laboratory experiments and field observations. When discrepancies in reported values occurred, the most extreme values were selected in order to obtain as precautionary a measure of spawning habitat suitability as possible.

For salinity, the experimentally determined minimum level necessary to prevent Belt Sea cod eggs from sinking was 19–22 psu in the Kattegat, Sound, and Belt Sea (Nissling and Westin, 1997). In the field, cod eggs were found floating at salinities of 18–20 psu in the Kattegat and Sound (Westerberg, 1994) and in Kiel Bay (von Westernhagen *et al.*, 1988). The laboratory-derived values were based on relatively few individuals, which may have restricted the range of salinities for neutral buoyancy. The field observations on the other hand are based on a large number of eggs presumably spawned by a large number of females. A cross-effect with temperature has been observed, in that eggs survive lower salinities at low temperatures (von Westernhagen, 1970). Based on field measurements, von Westernhagen (1970) observed a relatively broad range of neutral egg buoyancy levels (18–33 psu). In order to obtain a conservative measure of spawning habitat suitability, this salinity range was therefore used for all areas.

Cod eggs are known to develop at a wide range of temperatures (Thompson and Riley, 1981; Page and Frank, 1989), but specific stocks have an optimal range within which egg survival and development are highest. For the western Baltic cod stock, this range has been reported as 5.5–8.5°C (Bleil, 1995) and 4–8°C (von Westernhagen, 1970), both based on laboratory studies. Outside this range, egg mortality increases abruptly, even though egg development is possible at temperatures down to 2°C. No field observations are available due to the difficulty in separating temperature from sampling effects. Due to the good overlap in optimal temperature range, despite a lag of 25 years between the two studies, a conservative approach was chosen by selecting the lowest threshold level for egg development (>2°C).

For western Baltic cod, no information on oxygen requirement for successful egg development and survival exists. This threshold level was thus inferred from other cod stocks, where oxygen levels below 5 ml $l^{-1}$ affect egg survival and levels below 2 ml $l^{-1}$ are lethal to Pacific cod (Alderdice and Forrester, 1971) as well as to Eastern Baltic cod (Wieland *et al.*, 1994). A precautionary threshold level of 2 ml $l^{-1}$ was therefore selected.

The peculiar hydrographic environment in the main spawning grounds of the eastern Baltic cod stock is known to result in high egg mortalities (Hinrichsen *et al.*, 2007), which, amongst other factors, such as, for example, egg predation by clupeids (Köster and Möllmann, 2000) and food limitation for larvae (Huwer *et al.*, 2011), is affecting recruitment success (Köster *et al.*, 2005). In the western Baltic Sea, the highly dynamic hydrographical conditions result in a complex environmental scenario which may likewise limit the survival success of cod early life stages. However, while the main hydrographic impact on egg survival of the eastern Baltic cod stock is mainly caused by the combined effects of salinity and oxygen conditions, the present study has shown that spawning habitat suitability of the western stock is mostly affected by salinity and in cold years by temperature, but not by adverse oxygen conditions. Furthermore, the resulting impact on recruitment seems to be limited. Albeit that recruitment was significantly correlated with habitat suitability during March, i.e. the main spawning season, in the Kiel/Mecklenburg Bays, the signal was not strong and was not consistent across areas, thus indicating that environmental conditions during spawning alone do not determine relative year class strength.

This study suggests that even though recruitment of western Baltic cod may be limited by environmental conditions during spawning, other factors have a much stronger influence on year class strength. Not only interannual changes in habitat suitability and timing of spawning determine the survival of eggs, but also subsequent drift, destination, and survival of eggs, yolk-sac, and feeding larvae. Generally, the analysis of the importance of habitat suitability in relation to relative year class strength suffers from the determination of the origin of juvenile fish and the SSB that produced these recruits. Extensive advective transport of the cod early life stages documented by Hinrichsen *et al.* (this issue) as well as active migration of juveniles towards their nursery grounds could have a large impact on recruitment and corresponding SSB estimates. Besides detailed spatially and temporally resolved information on the physical environment, stock structure data and egg production estimates are required to better understand the recruitment processes in the highly dynamic spawning areas of the western Baltic cod stock. However, this approach provides a guideline for the spatial distribution and temporal windows of high survival for the egg stage, which may serve as baseline for subsequent biophysical modelling of cod early life stage drift and survival success (Hinrichsen *et al.*, this issue).

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