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Egg mortality: predation and hydrography in the central Baltic

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Cod and sprat are the dominant fish species in the Baltic pelagic ecosystem, both of great economic importance and ecologically strongly interlinked. Management of both species is challenged by highly variable recruitment success. Recent studies have identified predation and hydrographic conditions during the egg phase to be of critical importance. Two years of extensive field investigations in the Bornholm Basin, central Baltic Sea, were undertaken. In 2002, a typical stagnation situation characterized by low salinity and poor oxygen conditions was investigated, and in early 2003, a major inflow of North Sea water completely changed the hydrographic conditions by increasing salinity and oxygen content, thereby altering ecological conditions. The goal was to quantify egg mortality caused by predation and hydrography, and to compare these estimates with independent estimates based on cohort analysis. Results indicated high intra-annual variability in egg mortality. Cod and sprat egg mortality responded differently to the major Baltic inflow: mortality related to hydrographic conditions increased for sprat and decreased for cod. On the other hand, predation mortality during peak spawning decreased for sprat and increased for cod.

Keywords: Baltic inflow, Bornholm Basin hydrographic processes, cod, recruitment, sprat.

Introduction

Year-class strength of marine fish can generally be determined by several processes operating to affect the mortality rates experienced by all life stages. In particular, processes acting during early life history have been identified as contributing most to recruitment variability and hence stock abundance (Cury and Roy, 1989). Mortality can be attributed to abiotic factors that limit vital rates, e.g. unsuitably low or high temperature, light, turbulence, or low oxygen concentrations. Those abiotic factors interact with key biotic factors, such as prey availability and encounter with predators, to influence mortality (Bailey and Houde, 1989).

Nearly a century ago, Hjort (1914) first formulated his recruitment hypothesis, and since then, a number of additional recruitment hypotheses have evolved, many linked to the ideas of Hjort and most focusing on the exogenously feeding stages (reviewed by Houde, 2008). Today, however, it is generally accepted that a combination of processes acts to determine recruitment success, leading to the formulation of the "integrated process" hypotheses (Houde, 2008).

Predation was not among the processes initially suggested by Hjort (1914) when formulating his groundbreaking recruitment hypothesis. In various marine systems, from coral reefs (Connell, 1997) and large estuaries (Cowan and Houde, 1993) to temperate shelf seas such as Georges Bank (Overholtz *et al.*, 1991) and the North Sea (Pope, 1991), predation is thought to structure the fish community and its impact on prerecruits is thought to be the key factor influencing year-class strength. However, explicit hypotheses are seldom tested (Houde, 2008). This is because direct measurement of rates of predation is challenging in the wild, with most estimates being generated from studies conducted in large mesocosms (e.g. Cowan and Houde, 1993).

Variations in mortality resulting from physical oceanographic conditions have been studied in many areas. Here, we focus on processes affecting survival during the egg stage of Baltic cod (*Gadus morhua*) and sprat (*Sprattus sprattus*). Cod and sprat are the dominant fish species in the central Baltic. Both spawn pelagic eggs, are strongly interlinked ecologically, and are of great economic and ecological importance (Kornilovs *et al.*, 2001).

The Bornholm Basin ecosystem

The Bornholm Basin (Figure 1) is an important spawning ground for cod and sprat. For cod, it is frequently the only successful spawning ground in the central Baltic Sea because of unfavourable oxygen levels on the other potential spawning grounds (Gdańsk

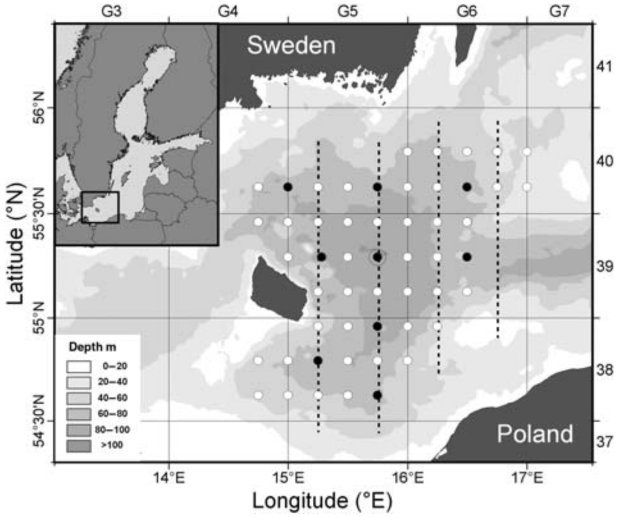

Figure 1. Map of the Bornholm Basin, Baltic Sea. Dots indicate the sampling positions. White dots, hydrography and ichthyoplankton abundance; black dots, hydrography, ichthyoplankton abundance, and vertical distribution; encircled black dot: central basin sampling position using towed multinet; dotted lines indicate the locations of hydroacoustic transects, fine lines the borders of ICES statistical rectangles.

Deep and Gotland Basin). Generally, the Bornholm Basin is characterized by a permanent halocline 50–75 m deep that separates the less-saline surface waters (salinity 7–8 psu) from more-saline bottom water (salinity 10–18 psu; Møller and Hansen, 1994). In winter, a cold mixed water mass is generated above the halocline by convective processes and vertical mixing caused by strong winds. The abiotic environmental conditions (temperature, oxygen, salinity) below and within the halocline are influenced mainly by the renewal of dense waters resulting from lateral inflows of saline water from the North Sea into the Baltic Sea (Matthäus and Lass, 1995). Major inflows usually take place during winter; in spring, a seasonal thermocline starts to form ~20–30 m deep and is coupled with the onset of the spring phytoplankton bloom. Historically, the sprat peak spawning in the Baltic has been in May (Elwertowski, 1960), though there has been some interannual variability related to temperature. Because of their specific gravity, sprat eggs tend to accumulate at and below the halocline in spring, but higher in the water column later in the season (Nissling *et al.*, 2003). Cod also begin their seasonal spawning in spring, but peak spawning is in early to midsummer. Cod eggs are usually found deeper in the water column than sprat eggs. The region below the halocline also represents the main feeding area of adult sprat, which feed on zooplankton as well as the cod and sprat eggs. The importance of cod egg predation and/or cannibalism, however, is temporally variable, and it seems to depend on predator abundance and the extent of vertical overlap between adults and eggs, which in turn is influenced by hydrographic conditions (Köster and Möllmann, 2000a, b). After hatching, sprat and cod larvae actively migrate to the upper water layers to feed (Voss *et al.*, 2007), greatly decreasing the vertical overlap with feeding adult sprat and hence minimizing that potential source of predation mortality. During summer, the intensity of spawning by sprat decreases, and portions of the sprat population begin to migrate out of the deep basin towards coastal feeding grounds, with the remaining sprat feeding mainly on cladocerans in or above the upper halocline. Cod spawning peaks in summer (July/August), with some spawning still ongoing until autumn. By autumn, large parts of the cod and sprat populations have left the deep basin and migrated towards their feeding grounds.

Mortality during the egg stage is usually high for cod as well as sprat (Wieland *et al.*, 2000a; Voss *et al.*, 2006), varying between years and over the course of the spawning season. In addition to predation, cod eggs are affected by oxygen deficiency (Wieland *et al.*, 1994) as a result of their greater abundance deep in the water column, whereas sprat eggs are strongly influenced by temperature (Baumann *et al.*, 2006). For both processes, functional relationships have been determined from laboratory experiments (cod, Köster *et al.*, 2005; sprat, Petereit *et al.*, 2008). For predation, the impact of adult sprat is probably most important, especially when the sprat stock is abundant, as it is currently (ICES, 2010). For this reason, we focus on quantifying predation mortality caused by sprat, but neglecting that which may be caused by other potential predators, such as herring (Köster and Möllmann, 2000b) or jellyfish (Barz and Hirche, 2005).

Extensive field investigations were carried out over a 2-year period in the Bornholm Basin, central Baltic Sea, encompassing prolonged spawning season of both species (February–October). Hydrographic conditions varied considerably between the 2 years. During 2002, the hydrography was characterized as a typical stagnation year, with generally lower salinity, a deep halocline, and hypoxia in the bottom waters of all deep basins. The situation resembled earlier years as a consequence of minor or no renewal of bottom water by inflow of North Sea water. In early 2003, there was a major inflow of North Sea water (according to the definition given by Matthäus and Lass, 1995) into the Baltic, before the spawning seasons of both cod and sprat, which completely changed the hydrographic conditions within the deep basin. Inflowing water masses reached the Bornholm Basin and started to spread into the Gotland Basin, accompanied by lower temperatures (ca. 5°C difference in the deep Bornholm Basin), a rise in salinity, a shallowing of the halocline, and much enhanced oxygen levels in deep water (up to >5 ml l^{-1} at the bottom).

The aim of this study is to quantify and partition egg mortality into two causative factors: hydrographic conditions (temperature and oxygen concentration) and sprat predation. Quantification of the importance of each factor under contrasting hydrographic conditions would aid understanding of the recruitment processes. The goal is to enhance the precision of recruitment predictions considering species-specific impacts of anticipated climate change.

Material and methods

Egg abundance

Sprat and cod eggs were collected during 14 cruises in 2002 and 8 cruises in 2003 to the Bornholm Basin (Table 1). During each cruise, a standard station grid of 52 stations was occupied (Figure 1). At each station, one double-oblique bongo-net haul was performed at a speed of 3 knots. The bongo (60 cm diameter per net) was equipped with 335 and 500 μm meshed nets and a flowmeter at the mouth of each net. Samples from the 335 μm net were preserved in 4% buffered formaldehyde/seawater solution immediately after collection, and fish eggs were subsequently sorted and at least 100 per sample staged. Egg-staging was performed according to the four-stage system of Thompson *et al.* (1981) for sprat eggs and Thompson and Riley (1981) for cod eggs, with stages Ia and Ib combined. The stage-specific counts were standardized to spatial densities (m^{-2}) based on the volume of water filtered and the maximum depth of the tow (down to ~2 m above bottom).

Given the typical problems associated with the inherent variability in distributional data for fish eggs, we calculated basin-wide abundances for each survey using objective analysis (Bretherton *et al.*, 1976), a standard interpolation algorithm in oceanography. This approach is based on the Gauss–Markov theorem, which provides an expression for the linear least-square error estimate of abundance. The analysis uses a spatial covariance function based on observations and assumptions concerning sampling variability, and small-scale errors inferred from the egg-abundance data at each station. The stage-specific, basin-wide abundance estimates were divided by the species- and stage-specific egg development times to produce an average daily net production estimate for each stage during each sampling period. As stage duration is temperature-dependent, ambient temperatures for the egg stages had to be calculated. We used vertical egg distribution data collected during the same research cruises (see below) and monthly temperature profiles from the ICES hydrographic database to calculate mean ambient temperatures per month. Mean ambient temperatures for cod and sprat eggs as well as the resulting stage duration from mid-stage I to mid-stage IV are listed in Table 2. For sprat eggs, the temperature/stage duration relationships from Petereit *et al.* (2008) were applied; for cod eggs, data from Wieland *et al.* (1994) were used. To obtain daily production estimates for all days between the first and the last sampling period, a linear interpolation was performed between successive survey estimates.

Table 1. Overview of the cruises, temporal midpoint of sampling, and mortality estimates.

Year	Cruise	Midpoint	Mortality caused by hydrography	Mortality caused by predation
2002	1	18 March	+	–
	2	5 April	+	+
	3	17 April	+	+
	4	7 May	+	+
	5	14 May	+	+
	6	22 May	+	+
	7	18 June	+	+
	8	3 July	+	–
	9	25 July	+	+
	10	16 August	+	+
	11	24 August	+	–
	12	5 September	+	+
	13	5 October	+	–
	14	14 November	+	+
2003	15	18 January	+	+
	16	12 February	+	–
	17	12 March	+	+
	18	21 April	+	+
	19	23 May	+	+
	20	7 July	+	–
	21	13 August	+	+
	22	29 November	+	+

Vertical distribution of eggs

The vertical distribution of eggs was investigated during all surveys using two different approaches. In June 2002, a towed multinet (9 nets, 0.5 m^2 opening, 335 μm mesh) equipped with a flowmeter was used on a single station in the central part of the basin (water depth >80 m). The nets were towed at a known depth for 3 min at a speed of 3 knots. Three daylight hauls were combined to determine the vertical distribution in the water column in 5-m depth intervals. For all other cruises, a vertical resolution of 10 m was obtained, using a vertically operated small multinet (5 nets, 0.25 m^2 opening, 335 μm mesh) at nine stations spread over the survey area. Results from all hauls were pooled for subsequent analysis. Sample fixation and analysis in the laboratory were the same as described above for sampling egg abundance. For the months where no sampling took place (Table 1), the results were interpolated from adjacent surveys.

Table 2. Weighted mean ambient temperature for cod and sprat eggs, and the corresponding stage duration from mid-stage I to mid-stage IV.

		Cod eggs		Sprat eggs	
Year	Month	Temperature (°C)	Stage duration I–IV (d)	Temperature (°C)	Stage duration I–IV (d)
2002	March	7.90	8.2	7.04	5.0
	April	7.12	9.3	6.34	5.8
	May	6.94	9.6	5.62	6.7
	June	6.47	10.3	6.11	6.0
	July	7.68	8.5	5.49	6.9
	August	8.83	7.1	7.27	4.8
	September	12.03	4.3	10.03	3.2
	October	9.69	6.2	12.98	2.3
	November	9.46	6.4	9.46	3.5
2003	January	9.16	6.8	5.60	6.7
	February	4.59	13.8	4.06	10.1
	March	3.66	15.9	3.53	12.01
	April	3.26	17.0	3.27	13.2
	May	3.09	17.4	3.26	13.3
	June	3.50	16.3	4.34	9.3
	July	4.22	14.6	4.83	8.1
	August	5.12	12.7	7.44	4.7
	September	7.51	8.7	10.65	3.0
	October	7.90	8.2	9.13	3.6
	November	8.31	7.7	9.88	3.3

Experimental studies showed that specific gravity (and therefore the buoyancy) of eggs might change during development owing to changes in osmolarity of water in the perivitelline space and the embryonic tissue (Craig and Harvey, 1987). Female Baltic cod show considerable individual variation in egg buoyancy (Nissling *et al.*, 1994); egg buoyancy is also significantly correlated with chorion thickness and batch number. Field observations from the Bornholm Basin, on the other hand, have only confirmed a slightly deeper distribution of egg stage IV so far; changes for egg stages I–III could not be detected. As a result, the calculations were not adjusted to stage-specific differences in vertical distribution, because the absolute changes were expected to be within the vertical resolution used in the analysis (i.e. <5 m).

Total egg mortality in the field

To calculate field-based rates of total egg mortality, a cohort analysis based on the following equation was used:

$$Z_{\mathrm{FIELD}} = \frac{-\ln(\mathrm{EPI}_{t1}/\mathrm{EPIV}_{t2})}{\mathrm{Age}_{\mathrm{IV}} - \mathrm{Age}_{\mathrm{I}}}, \qquad (1)$$

where Z_{FIELD} is the instantaneous daily mortality coefficient in the field from mid-egg stage I to mid-egg stage IV, EPI_{t1} the daily production estimate of stage I at time t1, EPIV_{t2} the daily production of stage IV at time t2, $\mathrm{Age}_{\mathrm{I}}$ the age at mid-stage I, and $\mathrm{Age}_{\mathrm{IV}}$ the average age at mid-stage IV. The value of t2 was calculated as t1 plus temperature-dependent development time from mid-stage I to mid-stage IV. This calculation was performed from the first sampling period to the latest possible one.

This approach explicitly focuses on mortality during the pelagic development of eggs observed in the field, and excludes mortality during the very early and very late egg phases, that could be caused by lack of fertilization or losses at hatch.

Mortality caused by hydrographic factors

For cod eggs, potential oxygen-dependent mortality was calculated for each month in 5-m depth strata. We used potential mortality, because the results are based on a modelled egg survival function, not on direct field observations. Ambient oxygen contents were derived from the ICES hydrographic database and were inserted into an egg-survival function (Köster *et al.*, 2005) based on experimental data:

$$y_{\mathrm{o}} = 100(1 - ((1 - \mathrm{e}^{-0.71x})^{11.63})), \qquad (2)$$

where y_{o} is the oxygen-dependent mortality before hatch (%) and x the oxygen content in ml l^{-1}. The function ($r^2 = 0.94$) describes a sigmoid curve with almost total mortality at 2 ml l^{-1} oxygen content, ~50% mortality at 4 ml l^{-1}, and <10% mortality at 7 ml l^{-1}. Mortality at <2 ml l^{-1} was set to 100%, and to 0% at >7.8 ml l^{-1}.

For sprat eggs, temperature-dependent egg mortality until hatch could be parametrized following the approach of Hinrichsen *et al.* (2007a):

$$y_t = 100 - \left(\frac{99.07}{1 + (T/3.361)^{-5.178}}\right), \qquad (3)$$

where y_t is the temperature-dependent mortality (%) and T the temperature in °C. The function results in >95% mortality at 1.9°C, ~50% mortality at 3.4°C, and almost total survival (2% mortality) at 8°C.

For each month, mean daily egg mortality caused by hydrographic conditions was calculated. We used mortality estimates per depth stratum, and applied the vertical distribution of eggs as a weighting factor. Applying the ambient temperature estimates to calculate overall egg development time facilitated the calculation of daily rates of mortality resulting from temperature and oxygen conditions, respectively.

Predator consumption

We used systematic hydroacoustic investigations in combination with pelagic trawling on four transects in the Bornholm Basin to estimate the spatio-temporal distribution of adult sprat (Figure 1). Acoustic measurements were conducted during the daylight feeding period (Cardinale *et al.*, 2003). Simrad scientific echosounders were used (EK 60 and EK 500). Calibration of the gear was performed using the standard copper-sphere method. The procedure and the settings of the acoustic measurements, as well as the data processing, were conducted according to the "Manual for the Baltic International Acoustic Survey" (ICES, 2001). Digitized echograms were corrected for bottom topography and non-fish echo-scattering layers and other unwanted echoes, such as air bubbles below the ship. Echo data were integrated as nautical area backscattering coefficient [NASC (m^2 nautical mile^{-2})] from 10 m below the surface to 0.5 m above bottom. Pelagic trawling was carried out with a Kombitrawl (formerly Engel trawl) along hydroacoustic transects, targeting observed schools of pelagic fish. After each haul, the total catch composition and its length distribution were recorded. Stock sizes were computed per ICES statistical rectangle according to ICES (2001; Figure 1). Adult sprat were collected for dietary analysis according to a length-stratified sampling scheme using 1-cm length classes. If available, three fish per length class were analysed per trawl station, resulting in total numbers per cruise ranging from 86 (August 2002) to 416 (May 2003; Supplementary Table S1).

Individual daily food ration dependence on temperature (F_T) was estimated using a general model of gastric evacuation, which incorporates predator weight as variable:

$$F_T = R'' \mathrm{e}^{AT} W^C (1 - (1(1 + \mathrm{e}^{-\mathrm{a2}(T - T_{50})})^{-1})) S^B 24, \qquad (4)$$

with R'' a food type constant, A the temperature coefficient, T the average ambient temperature, W the sprat weight (g dry), C the weight coefficient, a2 and T_{50} additional parameters, and S the mean of the individual field stomach content (g dry) raised to the power of $B = 0.668$ (Bernreuther *et al.*, 2009). The daily ration of fish eggs was derived following the approach of Köster and Möllmann (2000a). The observed average number of eggs per stomach was multiplied by the ratio between modelled total daily food intake and observed average stomach content.

To evaluate the effect of temporal and spatial variability on individual daily ration, i.e. in the stomach contents, stomach content data were averaged over successively increasing scales. Results were compared using mean individual ratios based on (i) cruise-specific stomach and predator abundance data, spatially resolved per ICES statistical rectangles, (ii) cruise-specific data averaged over the whole basin, and (iii) seasonally averaged whole-basin estimates. Further, we varied the number of eggs eaten per predator size class by ±20% to account for identification errors.

For all three approaches, total population consumption was computed by multiplying mean individual daily ration by the scaled population estimate, and summing up over all investigated rectangles, if needed. We used ICES rectangles 38G5, 39G5, 39G6, 40G5, and 40G6 to best represent the spawning area of cod and sprat, always (Figure 1).

Mortality caused by sprat predation

For all cruises where consumption estimates were available, daily mortality estimates attributable to sprat predation were calculated. Calculations were made for cod eggs and sprat eggs separately, using the three alternative calculations of total daily population consumption. We compared the number of eggs eaten per day (daily population consumption) with the total number of eggs dying per day, using an adaptation of the catch equation in the Beverton and Holt model of population dynamics (Beverton and Holt, 1957):

$$Z_{\mathrm{PRED}} = \frac{Z_{\mathrm{FIELD}} \times N_{\mathrm{EC}}}{\mathrm{SS}_{\mathrm{EGGS}} \times (1 - \mathrm{e}^{-Z_{\mathrm{FIELD}}})}, \tag{5}$$

where Z_{PRED} is the instantaneous daily mortality coefficient attributable to sprat predation, Z_{FIELD} the total instantaneous daily mortality coefficient derived from field sampling [Equation (1)], N_{EC} the population daily egg consumption, and $\mathrm{SS}_{\mathrm{EGGS}}$ the standing stock of eggs. Whereas N_{EC} and $\mathrm{SS}_{\mathrm{EGGS}}$ are estimated directly from survey results and can be applied to the temporal midpoint of sampling, estimated Z_{FIELD} values refer to periods between surveys and had to be interpolated to best match the consumption and standing stock estimates. Monthly mean values of total egg mortality were used as calculated above, so encompassing the sampling periods.

Results

Total egg mortality in the field

There were considerable numbers of eggs in the water column from February to August (sprat) and May to October (cod), in both years. Basin-wide egg abundance indicated peak spawning of sprat in spring (Figure 2); peak spawning in 2003 was, however, ~1 month earlier than in 2002, and eggs were more abundant. The abundance of cod eggs was also greater in 2003, and peak spawning was observed in summer of both years, though in 2003 started later and lasted longer.

Other than these differences in seasonal occurrence, the depth distribution of eggs of each species differs. Eggs of both species show overlapping depth ranges, but sprat eggs are generally closer to the surface (Figure 3). At the start of the 2002 spawning season (March), sprat eggs were mostly at depths of 60–70 m, but they had moved progressively shallower, up to 30–40 m, by July (Figure 3a). Cod eggs were mainly between 60 and 80 m deep throughout the 2002 spawning season (Figure 3c). After the inflow of North Sea water in early 2003, eggs of both species generally were more widespread in terms of depth. Over the course of the season, sprat eggs tended to be found shallower (Figure 3b), but cod eggs were mainly between 40 and 70 m deep, without a clear seasonal trend (Figure 3d).

Monthly means of daily mortality of sprat eggs in the field ranged between 14 and 73% in 2002 (Figure 4), but lower in 2003 when the seasonal differences were also less pronounced. Although egg mortality showed a steady increase over time in 2002, the situation in 2003 was characterized by a decline in mortality rates between May and July. As observed for sprat, mortality of cod eggs was lower after the inflow in 2003. In both years, mortality rates were higher during summer than during early spawning.

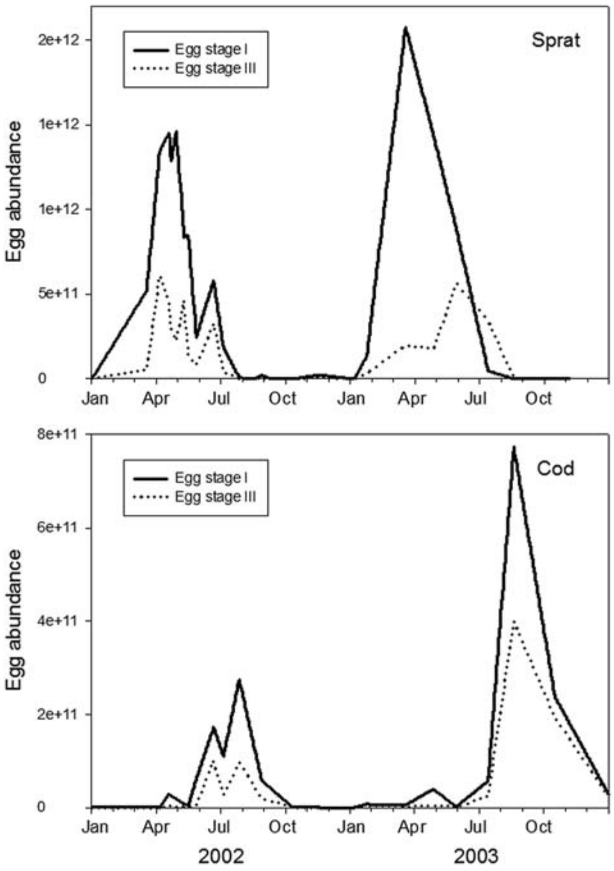

Figure 2. Seasonal, basin-wide egg abundance of sprat (upper panel) and cod (lower panel) in 2002 and 2003. The youngest egg-stage I and egg-stage III are shown.

Mortality caused by hydrographic factors

Depth-resolved potential mortality of sprat eggs resulting from temperature conditions showed great variability (Figure 5a). Mortality rates were high (>50% until hatch) above the halocline during winter and early spring. The effect of winter cooling was more pronounced in 2003, after the severe winter of 2002/03. Additionally, the major Baltic inflow in January 2003 transported highly saline, oxygenated, cold water into the deep layers of the Bornholm Basin, and potential egg mortality was then higher, including in the water layer below the halocline from March to June.

Potential cod egg mortality was high below the halocline throughout 2002 (depth >60 m; Figure 5b), and mortality estimates increased from spring to summer. After the inflow in early 2003, egg mortality resulting from low-oxygen conditions was almost negligible, but steadily increasing egg mortality resulting from deterioration in the oxygen conditions became obvious after June 2003. Mean daily rates of sprat egg mortality, taking the observed vertical egg distribution into account, were <4% throughout 2002 (Figure 5c), but in 2003, they were higher, >6% per day in April. In contrast to sprat, cod egg mortality

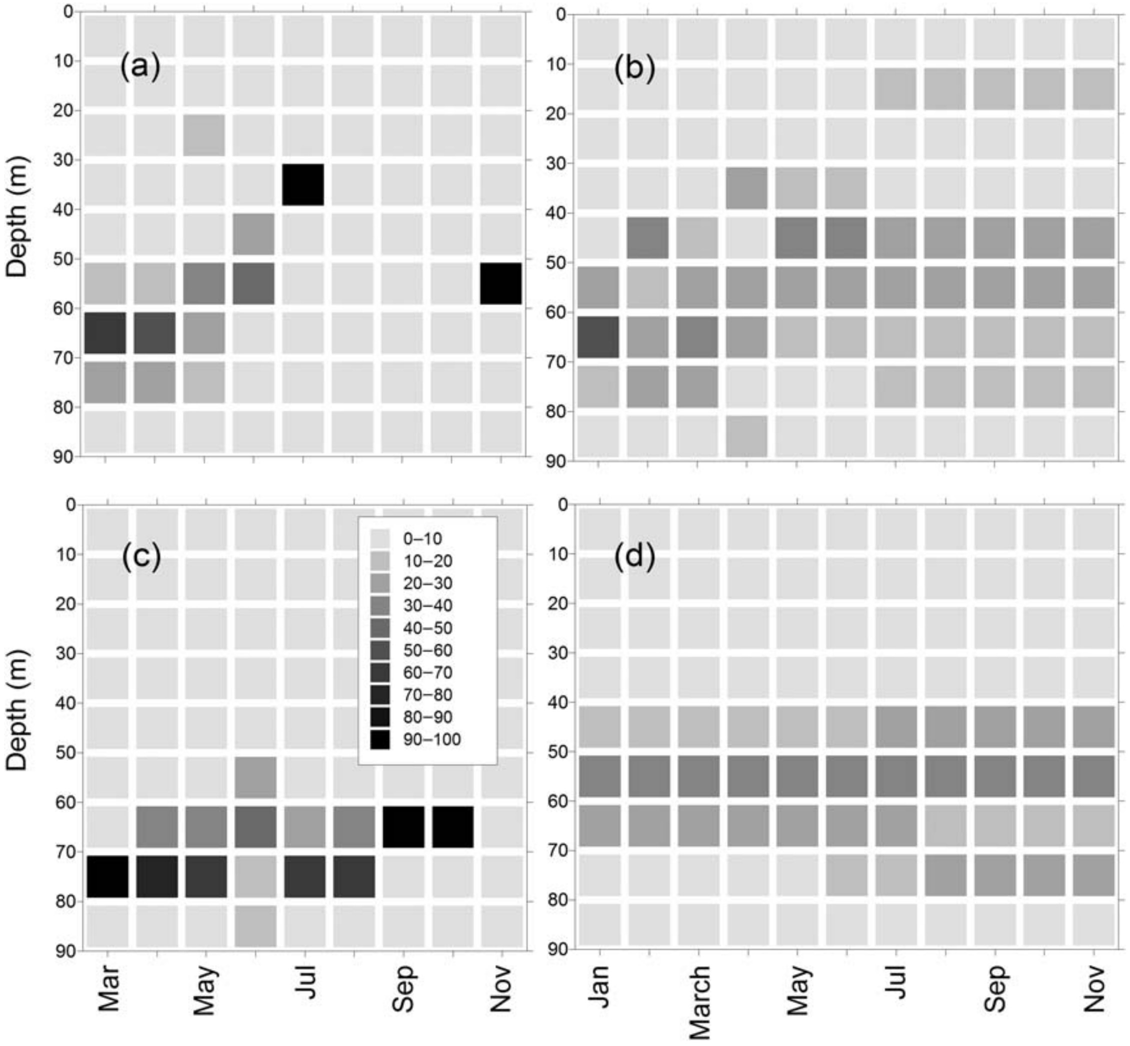

Figure 3. Relative vertical egg distribution (%). Sprat eggs in (a) 2002 and (b) 2003 compared with cod eggs in (c) 2002 and (d) 2003.

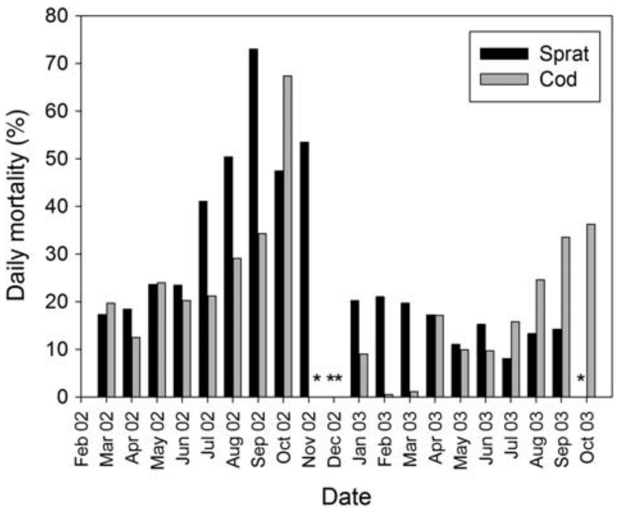

Figure 4. Field-based total mortality estimates (% daily mortality) for cod and sprat eggs in 2002 and 2003. Missing values are marked by asterisks.

from hydrographic conditions was higher in 2002 than in 2003 (Figure 5c). Daily mortality of almost 30% caused by oxygen deficiency was found in summer 2002, but in spring and early summer 2003, cod egg mortality was <5%, then increasing from August 2003 on, to 17% daily mortality in September.

Mortality caused by predation

Abundance and vertical distribution of adult sprat varied throughout the seasons (Figure 6). A decrease in abundance from April to September was accompanied by a decreasing depth of occurrence in 2002. Greatest densities were at 70 m in April, rising to 50 m in August/September. In January 2003, prespawning aggregations were found 55 m deep. Following the major Baltic inflow, the depth of greatest sprat abundance deepened to 75 m in April, and abundance was much lower than in 2002. As in 2002, however, abundance declined from April to August, and sprat were found shallower. A new annual cycle of reproduction started in October, with pre-spawning adults concentrating again at greater depth.

Predation mortality estimates are only available for selected months (Figure 7). Always, calculations using spatially resolved predator and prey data resulted in lower mortality estimates than for basin-wide and seasonal means. Variations in stomach

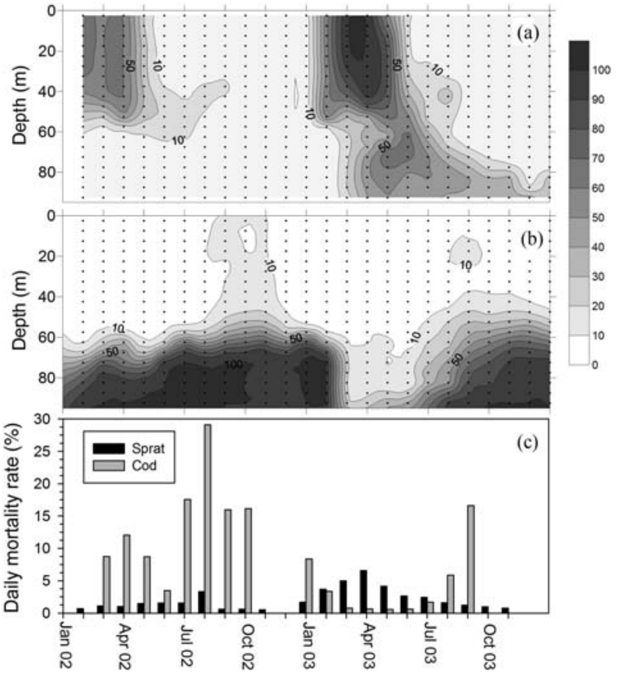

Figure 5. Mortality caused by hydrographic conditions: (a) vertically resolved sprat egg mortality attributable to critical temperature levels (% mortality until hatch), (b) vertically resolved cod egg mortality attributable to poor oxygen conditions (% mortality until hatch), and (c) monthly mean cod and sprat egg mortality, taking the observed egg distribution into account (% daily mortality).

content data by 20% translate into variations in daily mortality rates of <1–14%. Irrespective of the calculation method and the assumed error, general trends were seen: for sprat, predation mortality was higher during spring than in summer in both years. However, daily mortality rates were much higher in 2002 (stagnation) than in 2003 (post-inflow).

Cod egg mortality resulting from predation showed seasonal differences between the two years. Predation mortality rates were higher in spring than in summer 2002, but the situation was reversed in 2003. Mean seasonal mortality estimates were of comparable order of magnitude in spring 2002 and summer 2003, but in summer 2002 and spring 2003, predation was almost negligible.

Discussion

An *in situ* process study on the respective role and quantitative impact of predation and hydrographic conditions on sprat and cod egg mortality in the Bornholm Basin, Baltic Sea, revealed that the intra- and interannual importance of both mortality factors changed after the large-scale environmental variation caused by the inflow of North Sea waters in early 2003.

Despite large changes in hydrographic conditions, total egg mortality during peak spawning (cod, summer; sprat, spring) did not change much between the two years (Figure 8). Daily mortality of cod eggs during peak spawning is high (∼30%) compared with similar estimates on Georges Bank (12–14%; Mountain *et al.*, 2003), but within the range of earlier estimates in the Baltic (Wieland *et al.*, 2000a). In 2003, just after the major inflow event, survival of early-spawning cod eggs and late-spawning sprat eggs was higher than at other spawning times during that year, as well as relative to 2002. This is in line with the recruitment success of both stocks being higher by a factor of 1.9 (sprat) and 1.6 (cod) in 2003 compared with 2002. Correlation of better recruitment success with inflow situations, as observed for cod (Köster *et al.*, 2003), might therefore be related to greater egg survival of early-spawning adults. As older fish tend to spawn earlier in the season (Wieland *et al.*, 2000b), a healthy age distribution of the cod stock would amplify the positive effect of North Sea water inflow on cod recruitment success. For Atlantic cod (Buckley *et al.*, 2010) and Baltic sprat, the importance of such windows of survival outside peak spawning for recruitment success is clear (Baumann *et al.*, 2006). Increased total mortality of sprat eggs after oxygen-rich, cold Baltic inflow, leading to lowered recruitment success (MacKenzie *et al.*, 2008), was not observed in the Bornholm Basin in 2003.

For both species, the relative stability in total egg mortality during peak spawning, as well as the differences during early or late spawning, can be explained by changes in the relative importance of predation mortality and mortality associated with hydrographic conditions. We have attempted to disentangle total egg mortality into that caused by (i) hydrography and (ii) predation (Figure 8). Variability in physical factors are key elements of several recruitment hypotheses (Lasker, 1981; Cury and Roy, 1989). These hypotheses have been tested in many field studies (e.g. Gallego *et al.*, 1996). In this study, we concentrated on the basic physical parameters: temperature influencing mainly sprat egg survival, and oxygen conditions influencing cod egg survival. As expected (Wieland *et al.*, 1994), cod egg mortality resulting from low oxygen conditions was lower in 2003 than in 2002, in both spring and summer (Figure 8). In 2002, the share of total mortality resulting from low oxygen rose from 40% in spring to 71% in summer. In 2003, there was an increase from 5 to 30%. Major Baltic inflows are irregular (Matthäus and Lass, 1995), so are unpredictable and beyond the scope of any management options. In contrast, the speed of oxygen degradation is fast (Hinrichsen *et al.*, 2007b), and related to eutrophication levels, which are still regarded to be too high in the Baltic (HELCOM, 2007), and can be predicted and managed.

For sprat egg mortality, the situation is reversed. The inflow of oxygen-rich cold water in early 2003 resulted in increased egg mortality caused by the hydrographic conditions. The hydrographic share of total egg mortality was ca. 5% in 2002 but 25% in 2003, irrespective of season. This increase in egg mortality caused by lower temperature did not translate into an increase in total egg mortality, because predation mortality changed concomitantly.

Predation is known to have the potential to control or regulate recruitment levels (Bailey and Houde, 1989), but explicit hypotheses are rarely tested (Houde, 2008). Bradbury *et al.* (2001) postulated the effects of predation on cod egg survival to be relatively small, compared with coupled advective/temperature effects in Placentia Bay, Newfoundland. On the other hand, a study on larval inland silverside (*Menidia beryllina*) by Gleason and Bengtson (1996) showed a stronger relative importance of predation to larval rates of mortality when compared with food availability. Krautz *et al.* (2007) studied euphausiid predation on anchoveta (*Engraulis ringens*) eggs in the Humboldt Current, and quantified mortality rates attributable to predation, which accounted for 24–27% of total mortality. In our investigation, predation mortality accounted for a broad range (0–98%) of total mortality (Figure 8). Predation rates would be expected to be high in cases of predator abundance and strong spatial overlap of predator and prey (Neuenfeldt and Beyer, 2006). For the Bornholm Basin, it is an obvious issue for predation rates on sprat

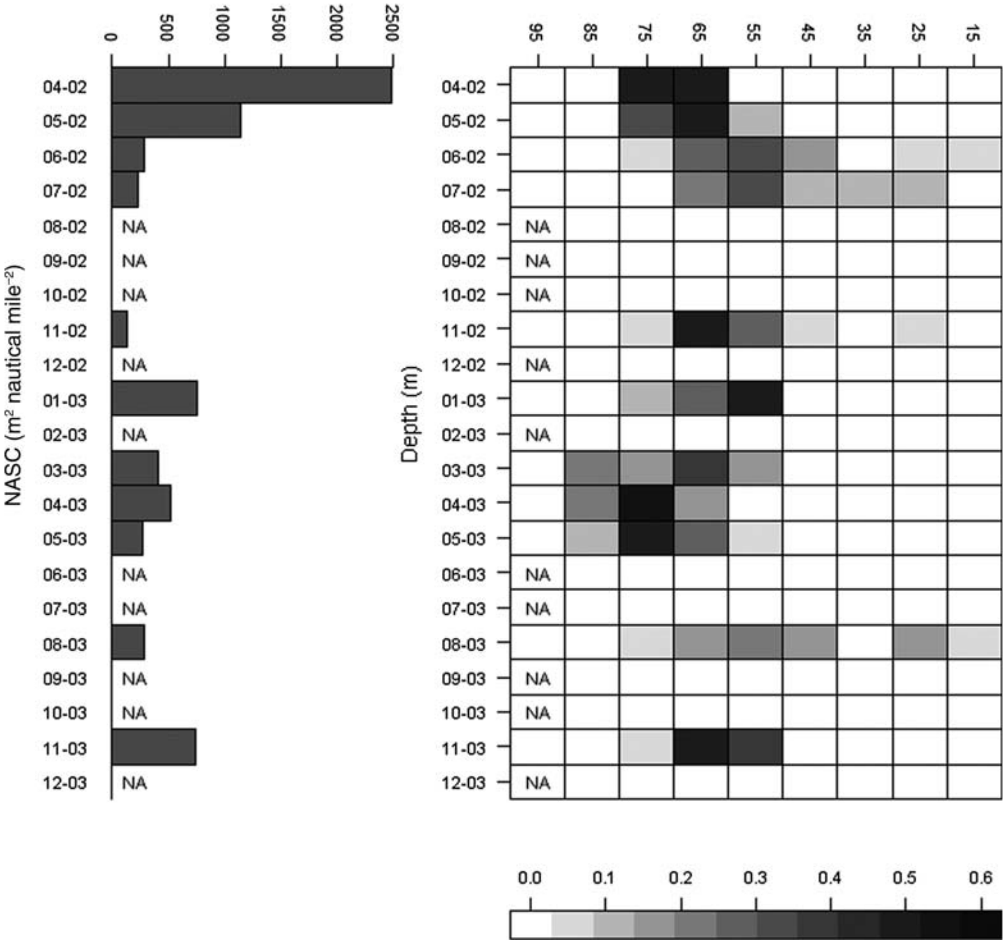

Figure 6. Vertical distribution and abundance of adult clupeids: NASC (m^2 nautical mile^{-2}) as a measure of abundance (left panel), and relative vertical distribution by month (right panel).

eggs. Predation is high in spring, at high predator abundance (adult sprat) and high vertical overlap of adults and eggs. In summer, predation on sprat eggs is minimal, however, because predator abundance decreases and vertical overlap diminishes as a result of changes in both adult sprat distribution and egg buoyancy. Adult sprat distribution seems to be related to hydrography (Stepputtis *et al.*, 2007), but the seasonal change in vertical distribution of sprat eggs is less well understood. It seems, however, to be related to the mean weight-at-age of spawners (Makarchouk, 2001). In 2002, spring predation was stronger than in spring 2003, when predator–prey overlap and adult sprat abundance were both higher.

The dynamics of cod egg predation mortality are more complicated. Comparing 2002 and 2003, egg predation mortality decreased in spring 2003 and increased in summer 2003. In spring, predation on eggs is less evident for cod than for sprat. However, in summer 2003, predation mortality accounted for ca. 40% of the total egg mortality. Above-average year classes of Baltic cod recorded in several recent years (ICES, 2010) might be linked to (i) a smaller sprat stock than in the early 2000s, (ii) a change in the horizontal distribution of the sprat stock, with them being more concentrated in eastern areas (leading to better survival during peak spawning in summer), and (iii) a rebuilding of cod stock age structure, resulting in increased spring spawning of that species (Wieland *et al.*, 2000b).

Estimates of total egg mortality exceed the combined effect of sprat predation mortality and mortality induced by critical levels of oxygen (cod) or temperature (sprat). This unaccounted for mortality (Figure 8) can be explained by several potential candidates. Spring-spawning herring feed on cod and sprat eggs in summer (Köster and Möllmann, 2000b) after returning from their coastal spawning grounds. Invertebrate predators (jellyfish, crustaceans) exist, but their predation potential is low (Barz and Hirche, 2005). Mortality associated with drift away from the spawning ground (Bradbury *et al.*, 2001) and mortality caused by solar radiation (Beland *et al.*, 1999) are regarded to be of little importance for fish eggs, especially given the deep distribution and associated low transport rates of the species and areas researched here (Voss and Hinrichsen, 2003). Egg mortality attributable to viruses, bacteria (Sandlund *et al.*, 2010), or fungal decay has been recorded in the laboratory (C. Petereit, pers. comm.), but its effect in the field is unknown.

There are several sources of error in our work, potentially influencing the results. Temporally insufficient coverage of the survey area, not resolving the principle dynamics, would influence the findings. We have, however, no indication from earlier investigations (covering the years 1986–present) of abrupt changes in spawning intensity, which would result in a bias in the calculations. A comparable approach was performed by Rijnsdorp

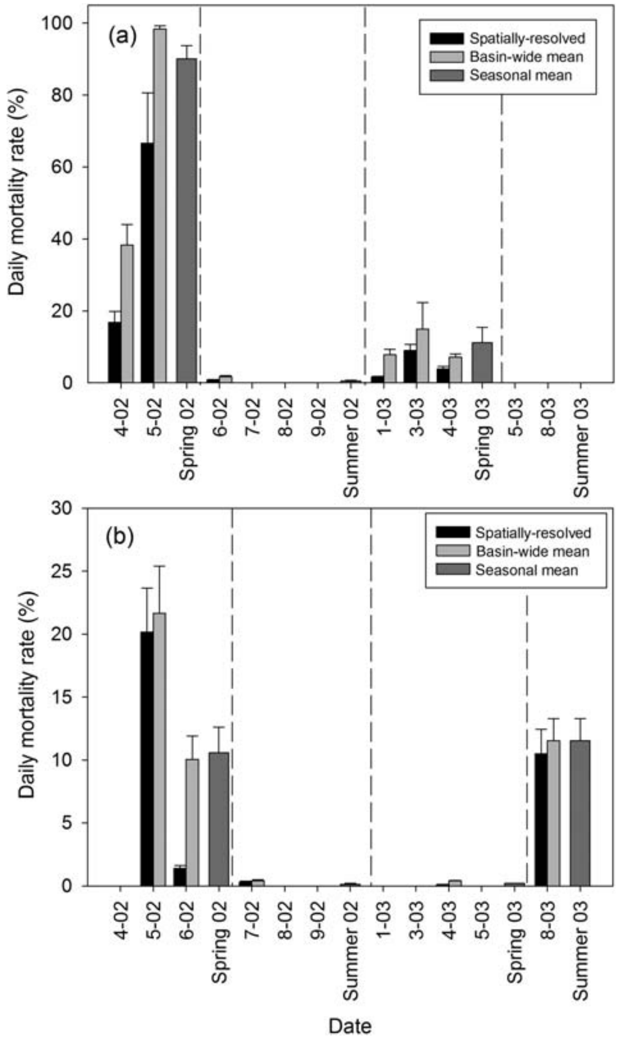

Figure 7. Predation mortality estimates (% daily mortality) for three different scales of data aggregation: (i) spatially resolved (ICES statistical rectangle) predator abundance and stomach data, black bars, (ii) basin-wide means, light grey bars, (iii) seasonal means of basin-wide estimates (dark grey bars) for (a) sprat eggs and (b) cod eggs. Error bars show the results of sensitivity analysis varying daily predator egg ratios by +20%, and dashed vertical lines separate early from late spawning time (species-specific).

and Jaworski (1990) in determining mortality in plaice and cod eggs in the North Sea. In their analysis, surveys were 27–28 d apart, similar to our temporal resolution in 2003; in 2002, coverage was better.

Our estimates of field-based total mortality rates rely on daily production values of different egg stages. Spawning activity is mainly restricted to the area where water depth exceeds 60 m (Hinrichsen *et al*., 2007b), but eggs could be transported out of the survey area during their development. Because of their slow rates of transport, potential bias caused by underestimating the abundance of older eggs would, though, seem to be negligible.

The magnitude of egg mortality caused by hydrographic conditions depends largely on vertical structure of the water column, because the Bornholm Basin is characterized by strong vertical gradients. In the region of hydrographical discontinuities, a vertical resolution of 10 m depth layers, as applied in this analysis, may result in bias. Additionally, horizontal mesoscale variability in hydrographic conditions (Hinrichsen *et al*., 2007b), contributing to variation in mortality rates (Hinrichsen *et al*., 2002), is ignored.

To calculate the daily food intake by individual sprat, we used a gastric evacuation model approach, which has been shown to yield low estimates compared with alternative bioenergetic models (Hansson *et al*., 1996). Consequently, we consider our estimates to be rather conservative and potentially an underestimate of true consumption. Nevertheless, predation mortality on sprat eggs in May 2002 might have been overestimated for two reasons. First, large numbers of egg integuments were recorded and assigned to sprat. Instead, these could have been egg integuments from flounder, which produce pelagic eggs in spring in the Bornholm Basin and whose range in egg diameter is similar to that of sprat. Unfortunately, we do not have flounder egg-abundance values to test this hypothesis. Second, egg integuments might have longer digestion times. However, no experiments on digestion times of egg integuments have been performed, as far as we could ascertain. Finally, positive selection of older egg stages as a result of their better visibility (Wieland and Köster, 1996), as well as stage-specific mortality rates (Wieland *et al*., 2000a), means that estimating daily consumption rates for individual egg stages in future would be beneficial.

Hypoxia, as frequently found in the Baltic, might influence foodweb structure, system productivity, and processes in pelagic communities, as observed in the Benguela Current (Ekau *et al*., 2010). In the Baltic Sea, the cod stock declined as a result of overfishing and climate-induced low oxygen levels diminishing recruitment success in the late 1980s (Köster *et al*., 2005). This led to a trophic cascade, involving cod, sprat, and the copepod *Pseudocalanus acuspes* (Möllmann *et al*., 2009). Climate-induced changes in inflow intensity influence the recruitment of both species through changes in abundance of larval prey (Voss *et al*., 2006), overall temperature regime (Baumann *et al*., 2006), or larval transport scenarios (Hinrichsen *et al*., 2002). Changes in the spatial distribution of adults in response to climate forcing have been recorded in the North Sea (Rindorf and Lewy, 2006) and elsewhere. In the Baltic, changes in the spatial distribution of adults do occur, probably linked to variability in hydrographic conditions (Stepputtis *et al*., 2007). The need to spawn in the deep basins of the Baltic Sea (owing to the specific gravity of eggs aligned with the Baltic's particular hydrography) prevents reallocation of spawning effort towards shallower areas. Therefore, Baltic cod and sprat might be especially vulnerable to climate change. The present state of a sprat-dominated system will not necessarily revert to a cod-dominated one (Köster *et al*., 2003), even under increased inflow intensity. However, rebuilding of the age structure of Baltic cod might be of considerable importance, because increased egg survival can only be expected during spring, when the older fish start to spawn.

Quantification of the rates of egg mortality under different environmental scenarios, as done here, is clearly only a first step towards integrating biological information in stock–recruitment functions, stock forecast models, and eventually bioeconomic models under environmental uncertainty.

Supplementary material

Supplementary material is available at the *ICESJMS* online version of this manuscript in the form of a table of the numbers of sprat stomachs analysed per length class.

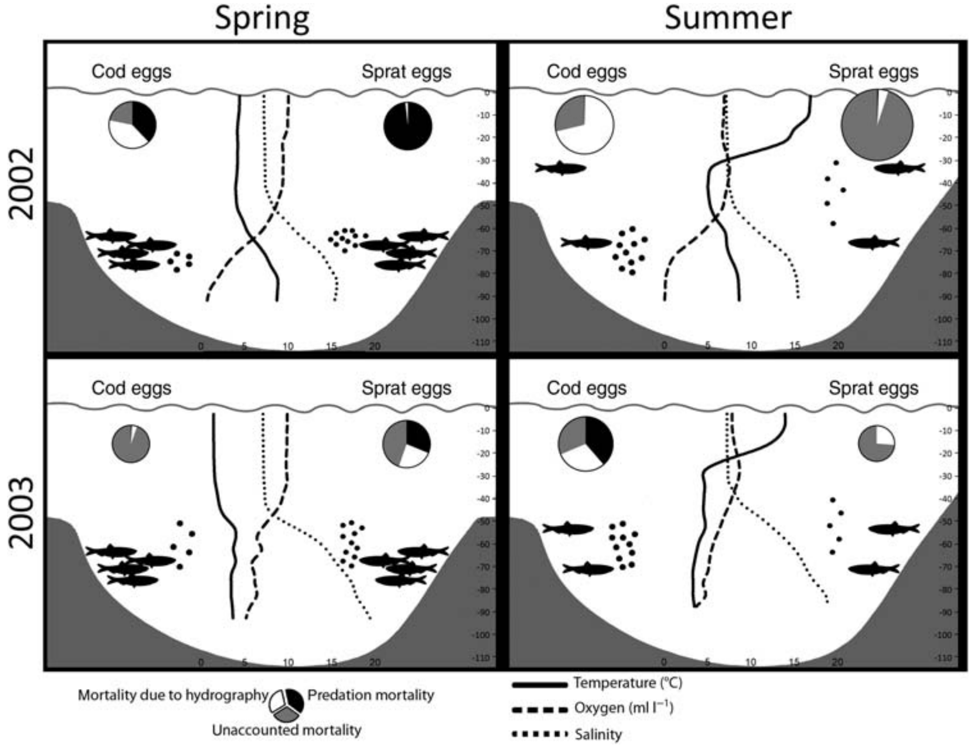

Figure 8. Conceptual diagram of cod and sprat egg mortality in the Bornholm Basin in spring and summer of 2002 and 2003: hydrography (lines), predator distribution and abundance (black fish silhouettes), egg distribution and abundance (small black dots), and total mortality (diameter of the pie chart), and the relative importance of mortality sources (pie chart).

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