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Baltic cod recruitment – the impact of climate variability on key processes

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Large-scale climatic conditions prevailing over the central Baltic Sea resulted in declining salinity and oxygen concentrations in spawning areas of the eastern Baltic cod stock. These changes in hydrography reduced the reproductive success and, combined with high fishing pressure, caused a decline of the stock to the lowest level on record in the early 1990s. The present study aims at disentangling the interactions between reproductive effort and hydrographic forcing leading to variable recruitment. Based on identified key processes, stock dynamics is explained using updated environmental and life stage-specific abundance and production time-series. Declining salinities and oxygen concentrations caused high egg mortalities and indirectly increased egg predation by clupeid fish. Low recruitment, despite enhanced hydrographic conditions for egg survival in the mid-1990s, was due to food limitation for larvae, caused by the decline in the abundance of the copepod *Pseudocalanus* sp. The case of the eastern Baltic cod stock exemplifies the multitude effects climatic variability may have on a fish stock and underscores the importance of knowledge of these processes for understanding stock dynamics.

Keywords: eastern Baltic cod, egg survival, hydrography, larval prey availability, predation, recruitment.

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Introduction

The Baltic Sea is characterized by a series of deep basins separated by shallow sills. Besides the development of a thermocline in spring, the characteristic hydrographic feature in the deep central Baltic basins is a permanent halocline separating an intermediate cold water layer from a saline bottom water layer. Salinity and oxygen conditions in the bottom layer can only be enhanced by lateral intrusion of water originating from the Kattegat and the North Sea termed "Baltic inflows" (Matthäus and Franck, 1992). Usually, minor inflows will only enter the Bornholm Basin, with little or no eastern transport. Inflows reach the Gdańsk Deep and the Gotland Basin only if (i) the transported volume of water has a substantial magnitude, a "major inflow" (for definition see Matthäus and Nausch, 2003), (ii) the advected water is replaced by an even denser water mass in a subsequent inflow (ICES, 2004), or (iii) a subsequent inflow of less dense water glides over water from an earlier inflow (Matthäus and Nausch, 2003).

Hydrographic conditions in the central Baltic are affected by large-scale climatic conditions. Since the late-1980s, prevailing weather conditions with strong westerly winds resulted in mild winters, above normal rainfall, increased river run-off, and reduced frequency of major inflows (Matthäus and Schinke, 1994). Consequently, higher than normal temperatures in the intermediate and the bottom waters were recorded, while salinity and oxygen concentrations in the deep Baltic basins declined (Matthäus and Nausch, 2003).

Ambient salinity in the Baltic is insufficient to keep cod eggs floating in the surface layer, so they occur within and below the permanent halocline (Wieland and Jarre-Teichmann, 1997). Late yolk-sac larvae perform a vertical migration into the food-rich intermediate water, preferring depths below the thermocline (Grønkjær and Wieland, 1997). Cod eggs are often exposed to low oxygen concentrations, suggesting a negative impact of oxygen conditions on egg survival, and subsequent recruitment success during periods lacking inflows (e.g. Kosior and Netzel, 1989; Lablaika *et al.*, 1989).

The eastern Baltic cod stock declined to its lowest stock size on record in 1992 owing to a reduction in reproductive success in combination with increasing fishing pressure (Bagge *et al.*, 1994; Köster *et al.*, 2003b). The reproductive success of the stock is coupled to hydrographic conditions in spawning areas. Laboratory experiments confirmed that at least $2\ \mathrm{ml\,l^{-1}}$ oxygen is needed for successful egg development (Nissling, 1994; Wieland *et al.*, 1994). Further, low salinity affects the fertilization of marine fish species (Westin and Nissling, 1991). Experimental studies revealed a minimum salinity of 11 for activation of spermatozoa and thus successful fertilization in Baltic cod (Westin and Nissling, 1991). Combination of these two limiting factors, the oxygen and the salinity threshold, formed the basis for the definition of the so-called "reproductive volume" (RV), or the water volume allowing for successful cod egg development (Plikshs *et al.*, 1993; MacKenzie *et al.*, 2000). In addition to the frequency and the magnitude of inflows, the magnitude of the RV in the deep Baltic basins depends on the temperature of the inflowing water influencing oxygen solubility (Hinrichsen *et al.*, 2002b) and oxygen consumption rates by biological processes (MacKenzie *et al.*, 1996).

Despite being conceptually appealing, the RV explains only a limited amount of variance in cod recruitment (e.g. Sparholt, 1996). The reasons behind this may be (i) that the amount and quality of eggs produced by a unit of spawning-stock biomass vary significantly in relation to food availability (Kraus *et al.*, 2002) as well as stock structure (Vallin and Nissling, 2000), (ii) that the RV may not be the best proxy for egg survival, because egg mortality caused by low oxygen concentration above the threshold is not considered (Wieland *et al.*, 1994), and (iii) eggs may float outside the RV in water layers not sustaining their development (Köster *et al.*, 2001a). Finally, processes like food supply for larvae and early juveniles (Hinrichsen *et al.*, 2002a), predation on cod eggs by clupeids (Köster and Möllmann, 2000), and cannibalism on juveniles (Sparholt, 1994) affect early life stage survival.

The present contribution aims to disentangle interactions between reproductive effort of the eastern Baltic cod stock, climatic and hydrographic forcing conditions, and species interactions affecting early and juvenile life stage survival. Numerous biotic and abiotic factors influence cod recruitment. We attempt to summarize these influences in the following sections which are organized by cod life stage. Results describe *in situ* fieldwork, process studies, and modelling work, and condense an immense sampling effort executed over a long period by numerous investigators. Published, updated, and new time-series are presented. Based on identified important processes, an attempt is made to explain recent and historical stock dynamics.

Material and methods

Information on time-series used, sources, and applied methodology are summarized in Table 1.

Area disaggregated spawning stock

Spawning-stock biomass (SSB) of the eastern Baltic cod stock has been estimated annually by ICES (2003) since 1966. Estimates are now based on an XSA (Shepherd, 1999), tuned with catch rates from the first quarter international bottom trawl survey. Area disaggregated estimates for Subdivisions (SDs) 25, 26, and 28, assumed to represent the Bornholm Basin, the Gdańsk Deep, and the Gotland Basin, respectively (Figure 1), are available from area disaggregated Multispecies Virtual Population Analysis (MSVPA) runs for the period 1976—1996 (Köster *et al.*, 2001b), and have been updated to cover 1976—1999 (for technical set-up see ICES, 2001).

Potential egg production

Basin-specific seasonal potential egg production (PEP) by the spawning stock has been estimated by multiplying female SSB with relative individual fecundity values. Using relative instead of absolute age-specific fecundity is justified, because this measure is independent of body size in Baltic cod (Kraus *et al.*, 2000) and thus can be applied to the spawning stock without considering the size/age structure. Relative fecundity for each SD was predicted from prey availability (Kraus *et al.*, 2002) using MSVPA-derived area-specific herring and sprat abundances.

Abundance of eggs and larvae

Mean annual abundances of eggs and larvae were available for the different spawning areas from ichthyoplankton surveys during 1966—1999. Egg abundance estimates are averages of surveys conducted during 3-month periods encompassing the main spawning period, i.e. April—June up to 1989, then mid-April—July (1990), May—July

Table 1. Sources of information used and their temporal and spatial coverage as compiled from literature and after update (in bold), as well as applied methods.

	Available information			Present study		
Variable	Period	Subdivision	Reference	Period	Subdivision	Method (abbreviations, see text)
Spawning stock	1976–1996	25,26,28	Köster *et al.* (2001b)	1976–**1999**	25,26,28	MSVPA
Potential egg production	1976–1999	25	Kraus *et al.* (2002)	1976–1999	25,**26,28**	PEP
Egg abundance	1976–1996	25,26,28	Köster *et al.* (2001a)	**1966–1999**	25,26,28	Ichthyoplankton surveys
Realized egg production per egg stage	1976–1996*	25	Köster *et al.* (2003b)	1974–**1999***	25	Average daily egg production
	1987–1999*	25	Kraus *et al.* (2002)	1987–**1999***	25	Seasonal egg production
Reproductive volume	1966–1996	25,26,28	MacKenzie *et al.* (2000), Köster *et al.* (2001a)	1966–**1999**	25,26,28	RV
Egg mortality	1987–1993*	25	Wieland (1995)	1987–1993* & **1999**	25	Cohort development
	1987–1993*	25	Wieland (1995)	1974–**1999***	25,**26,28**	Daily/seasonal production
	1976–1996	25	Köster *et al.* (2001a)	**1966–1999**	25,**26,28**	OES
Egg predation	1976–1996	25	Köster *et al.* (2001a)	1976–**1999**	25	RPP
Larval abundance	1976–1996	25,26,28	Köster *et al.* (2001a)	**1966–1999***	25,26,28	Ichthyoplankton surveys
Larval food availability	1966–1997	25,26,28	Möllmann *et al.* (2000)	1966–**1999***	25,26,28	LatFRA plankton monitoring
	1991–1993	25,26	Krajewska-Soltys and Linkowski (1994)	1991–1993	25,26	Vertical sampling
				1999	**25**	Horizontal & seasonal sampling
				1987–1996	**25**	Displacement volumes
Larval growth and survival	1986–1997	25	Hinrichsen *et al.* (2002a)	1987–1997 & **1999**	25	Coupled bio/physical model
Recruitment and cannibalism	1976–1996	25,26,28	Köster *et al.* (2001b)	1976–**1999**	25,26,28	MSVPA

*Time-series incomplete.

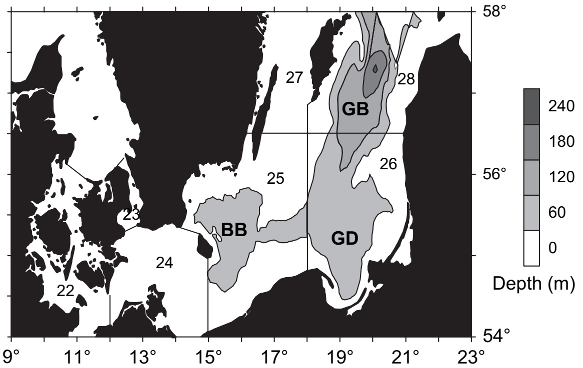

Figure 1. The southern and central Baltic with spawning areas of the eastern Baltic cod stock in ICES Subdivisions 25 (BB: Bornholm Basin), 26 (GD: Gdańsk Deep), and 28 (GB: Gotland Basin).

(1991—1992), mid-May—mid-August (1993—1995), and mid-June—mid-September (1996—1999), corresponding to the shift in spawning time (Wieland *et al.*, 2000a). Larval abundance data refer to a period similar to the 3-month period of egg abundance estimates, but delayed by 1 month to account for the period of egg development (Wieland *et al.*, 1994).

Realized egg production and observed egg survival

Daily production of egg stages I—IV (for definition see Thompson and Riley, 1981) were calculated by dividing stage-specific abundances by the development time of each egg stage. Stage-specific egg abundance data were computed for the Bornholm Basin from ichthyoplankton surveys in 1974—1978, 1983, 1985—1999 averaged over 2—4 surveys conducted during the main spawning period. The Gdańsk Deep and the Gotland Basin values were calculated from single surveys in hydrographically contrasting years with maximum spatial coverage of the spawning areas, i.e. 1974, 1976, 1989, and 1995—1996. Egg development times were calculated using temperature-dependent relationships developed by Wieland (1995), applied to the Bornholm Basin average ambient temperatures derived from the ICES hydrographic database for depths where eggs reside. The latter were predicted from vertical egg distribution models (see below). For the eastern spawning areas, temperatures at the depths of the highest cod egg concentration were used. Dead eggs were, in contrast to Köster *et al.* (2001b), distributed to the different egg stages according to the relative stage-specific distribution of live eggs. However, for estimation of mortality rates, dead eggs were excluded.

Seasonal egg production rates in the Bornholm Basin were estimated for years with the best survey coverage, as described by Kraus *et al.* (2002), applying daily production rates of egg stages IA, IB, II, and III (Thompson and Riley, 1981). Applying differences in age between stages, the seasonal production values were used to calculate stage-specific mortality rates per day and over the entire egg developmental period.

Repeated ichthyoplankton surveys during short time intervals (5—11 days) conducted in 1987—1993 and in 1999 allowed the estimation of mortality rates from egg stage IA or IB to III by following daily production rates of specific egg cohorts (Wieland, 1995; Wieland *et al.*, 2000b). If mortality rates could be determined only for shorter developmental periods, i.e. from stages IA to IB or II, and from II to III, an average daily mortality rate until egg stage III was calculated.

Oxygen-related egg survival

Incubation experiments were conducted under controlled oxygen and temperature conditions to estimate egg survival rates in relation to variable oxygen conditions (Wieland *et al.*, 1994; Rohlf, 1999). In all experiments, egg batches from single females caught by trawling in the Bornholm Basin were fertilized by sperm from several males. Subsets of these egg batches were incubated at different oxygen concentrations, and the viable hatch, i.e. larvae surviving through the yolk-sac stage, were expressed relative to the proportion surviving at normoxic conditions to separate the oxygen effect from other causes of mortality. A sigmoid survivorship function was fitted to the combined experimental data set.

Oxygen-related egg survival (OES) during the main spawning season was computed using predicted vertical distribution of cod eggs at 5-m depth intervals relative to water density and the oxygen concentration, as obtained from the ICES hydrographic database, and the relationship between oxygen concentration and cod egg survival derived from the incubation experiments. The vertical distribution of eggs was modelled according to Köster *et al.* (2001a) by fitting a parabolic function to the relationship among the log relative distribution of the youngest egg stage (IA), obtained from vertically resolving ichthyoplankton sampling in the Bornholm Basin in April—July 1986—1996 and measured water density profiles. Cod eggs are less buoyant after inflows, when salinity is highest in the bottom water (Wieland and Jarre-Teichmann, 1997). Furthermore, seasonal variation in the vertical distribution of cod eggs was detected (Köster *et al.*, 2001a), and consequently these hydrographic and seasonal situations were modelled separately, leading to the following combinations: (i) stagnation/early spawning, (ii) stagnation/late spawning, (iii) inflow/early spawning, and (iv) inflow/late spawning. For the Gdańsk Deep and the Gotland Basin, the stagnation scenario was applied throughout the time-series, because salinity values never exceeded the threshold set for the Bornholm Basin. However, a shift in spawning period was considered. Because the current models do not account for the effect of temperature on the vertical distribution (Wieland and Jarre-Teichmann, 1997), a correction was made for low temperatures (<1.7 °C) by transferring the predicted relative abundance of eggs to the next deeper water layer.

Reproductive volume and oxygen content

Estimates of the RV in different subareas were compiled as follows: (i) the period 1966−1973 (MacKenzie *et al.*, 2000) assumed peak spawning to be in May, with the data series labelled as "Kiel" applied for the Bornholm Basin and "LatFRA" for the Gdańsk Deep and the Gotland Basin, (ii) the period 1976−1996 as presented by Köster *et al.* (2001a), and (iii) the remaining years, i.e. 1974−1975 and since 1997, using updated "Kiel" estimates for the Bornholm Basin and updated "LatFRA" estimates for the eastern basins.

Cod egg predation by clupeids

Predation by herring and sprat has a significant impact on cod egg survival although remaining variable in time and space (Köster and Möllmann, 2000). In spring and early summer, sprat predation on cod is important due to the spatio-temporal overlap in sprat spawning time with cod. In summer, herring is the principal predator of cod after returning from their coastal spawning areas to their deep-water feeding grounds, while sprat have mainly left the area. Because the population of herring is currently substantially smaller than that of sprat, predation pressure is higher in spring than in summer (Köster and Möllmann, 2000). Egg predation was considerably lower in the Gdańsk Deep and Gotland than in the Bornholm Basin (CORE, 1998). Thus, only cod egg predation in the Bornholm Basin is considered in the present study.

Predation intensity in the Bornholm Basin depends on the vertical overlap between predator and prey. Köster *et al.* (2001a) modelled the daily consumption of cod eggs by individual clupeids in spring and early summer as linearly related to cod egg abundance, considering the vertical predator−prey overlap. The model is based on the observation that oxygen concentration in bottom water limits the clupeid vertical distribution during the daylight-feeding period, while the density regime determines the vertical distribution of cod eggs. This results in clupeids dwelling below cod eggs in inflow situations, whereas clupeids co-occur in high egg density water layers during stagnation years (Köster and Möllmann, 2000). Based on these observations, the average capture depth of clupeids and the average depth of highest cod egg concentration were combined into an index of vertical predator−prey overlap. Predation pressure by clupeids on cod eggs was determined over 1976−1992 using daily egg consumption rates by individual predators, predator population sizes from area-disaggregated MSVPA, and hydroacoustic survey results, as well as standing stocks of cod eggs (Köster *et al.*, 2001a). In the present analysis, these estimates are updated by revised predator population estimates from MSVPA runs, and the predation pressure is expressed relative to the maximum value determined (RPP). This approach is limited to spring and early summer situations only, as sprat tend to leave the Bornholm Basin in summer, and those remaining are distributed shallower during daytime while feeding on cladocerans (Köster and Möllmann, 2000). To accommodate the distributional shift, observed average daily egg consumption per abundance values calculated from summer survey results 1994−1997 were applied for 1993−1999.

Larval survival in relation to food availability

The major prey of first-feeding cod larvae in the Baltic are calanoid copepod nauplii (Voss *et al.*, 2003), especially nauplii of *Pseudocalanus* sp. (Hinrichsen *et al.*, 2002a). The importance of *Pseudocalanus* sp. (formerly named *P. elongatus*, see Möllmann *et al.*, 2005) nauplii for cod larval growth and survival was tested with a coupled hydro-/trophodynamic individual-based model. Simulated flow fields were used to investigate the potential drift of Baltic larval cod from the centre of spawning effort in the Bornholm Basin towards their different nursery areas, experiencing temporally and spatially resolved prey fields (Hinrichsen *et al.*, 2002a).

The prey fields represent the abundance of the dominant calanoid copepod (*Pseudocalanus* sp., *Acartia* spp., *Temora longicornis*, *Centropages hamatus*) and cladoceran species (*Bosmina longispina maritima*, *Evadne nordmanni*, *Podon* spp.) in the habitat of cod larvae (25−50 m). Zooplankton data compiled by LatFRA (Möllmann *et al.*, 2000) were used to determine seasonal and depth-dependent prey availability as averages over stations in all subareas. Interannual variability was added by applying a weighting factor derived from a time-series of average abundances (Hinrichsen *et al.*, 2002a). Model results are evaluated with respect to the validity of the applied prey field, using independent data on zooplankton availability in the Bornholm Basin from three sources: (i) Krajewska-Soltys and Linkowski (1994), covering three stations in the second and third quarters of 1991−1993, (ii) data from zooplankton sampling on a station grid in the Bornholm Basin in April, May, June, and August 1999, using a 150-μm mesh size Bongo net equipped with a 50-μm liner, and (iii) displacement volumes from 335-μm Bongo samples on 32−45 stations covering the second and third quarters of 1988−1997. Second, results of new coupled hydro-/trophodynamic model runs for 1999 (Hinrichsen, unpublished) are presented. These runs are based on directly measured prey fields in the Bornholm Basin.

Finally, simulated larval survival rates were compared with observations of independent mortality derived by relating age-0 recruitment to surviving egg production in the Bornholm Basin, either modelled as the product of PEP and OES or directly observed as average daily egg stage III production, age-2 recruitment in the entire central Baltic (shifted to the year of origin) to the sum of PEP and OES over all subareas.

Recruitment

Estimates of age-2 recruitment for the entire eastern Baltic stock are available since 1966 from ICES (2003). Age-0 recruitment values for the different SDs were derived by area-disaggregated MSVPA runs described above.

Results

Climate-induced hydrographic conditions

Bottom water salinity and oxygen in the Bornholm Basin during cod spawning were highly variable depending on the occurrence of inflows (Figure 2). Major inflows were frequent only in the first half of the time-series, and are characterized by low bottom water temperatures, as the inflowing water originates from near-surface layers in the western Baltic during winter. The increase in surface temperature during the 1990s (Figure 2) is primarily related to the shift of cod spawning to summer, but also to a general increase in water temperature. Major inflows resulted in a rise of the halocline, still visible in years following the inflow.

Bottom water oxygen concentrations of >3 ml l^{-1} were recorded in the Gdańsk Deep only in 1976, 1983, 1990, and 1991 (Figure 2). These situations are not characterized by high salinities, which occurred on other occasions, e.g. in 1970 and 1975, meaning that situations of enhanced oxygen conditions are not necessarily the same as when eggs float in the water column.

The Gotland Basin shows indications of a long-term freshening, with declining isohalines from the mid-1970s to 1994, e.g. a decline of the 11 psu isohaline from 100 to 200 m (Figure 2). Although this deepening of the halocline allows the vertical convection in winter to oxygenate lower water layers, oxygen concentrations below 100 m were in general <2 ml l^{-1}, with the exception of 1994, when an inflow introduced large quantities of water with oxygen concentrations >3 ml l^{-1}. Because of relatively high salinity, the inflowing water partly replaced the anoxic water, resulting in an intermediate oxygen-depleted water layer (Figure 2).

Potential egg production and reproductive volume

The PEP followed the general trend of SSB, with a maximum in the early 1980s, a sharp decline during the late 1980s, and a minor peak in the 1990s (Figure 3a). Changes in PEP are, however, more pronounced than in SSB. High PEPs in the early 1980s resulted from high egg production in all three spawning areas, while a second peak in the 1990s was due only to spawning in the Bornholm Basin. PEP in SD 28 has been extremely low since the late 1980s.

Comparing PEP with RV at spawning indicates that a large portion of the egg production in the Gotland Basin spawned during the late 1970s and early 1980s in unsuitable environments (Figure 3a, b). Since the early 1980s hydrographic conditions have also been adverse in the Gdańsk Deep when, especially from 1986 to 1992, virtually no RV was present. The only spawning site regularly sustaining successful egg development was the Bornholm Basin. After the major inflow in 1993, oxygen concentrations allowed successful egg development in the Gdańsk Deep in 1993 and 1994, and resulted in one of the highest RV on record in the Gotland Basin in 1994. While a substantial PEP was estimated in the Gdańsk Deep, the corresponding production in the Gotland Basin was very low.

Oxygen-related egg survival

The oxygen–egg survival relationship ($r^2 = 0.94$) showed that oxygen concentrations above the threshold level of 2 ml l^{-1}, used in the definition of the RV, have a pronounced impact on egg survival (Figure 4). Using this function to estimate the fraction of the egg production surviving in each spawning season requires use of modelled egg stage IA vertical distribution in relation to the ambient density. Explained variances in these models ranged between 72% and 82% for the four environmental scenarios. Coupling predicted vertical distributions, measured oxygen concentrations, and the oxygen–survival relationship allowed the construction of a time-series of oxygen-related egg survival (OES) (Figure 3c). OES values indicate that egg survival was always highest in the Bornholm Basin, while egg survival especially in the Gotland Basin has always been low. Observations on RV (Figure 3b) are contradictory to the relatively high egg and larval abundance observed by ichthyoplankton surveys during the 1970s and 1980s (Figure 3d, e).

To validate the OES and the RV as measures of egg survival, the realized egg production at stage III derived from ichthyoplankton surveys in the Bornholm Basin was regressed on the PEP, with and without multiplying PEP by OES, and adding RV as an additional variable. While the latter decreased the explained variance ($r^2 = 0.58$) compared to the simple model utilizing only PEP ($r^2 = 0.61$), multiplying the PEP with the OES increased the r^2 to 0.73 (Figure 5).

The OES correlated to the egg survival from ichthyoplankton surveys in corresponding years (Figure 6a, $r^2 = 0.64$). A linear regression of observed and predicted survival until egg stage III indicates a slope of 0.41 ($p < 0.01$) (intercept insignificant), indicating that mortality causes other than oxygen depletion affect egg development success. Although egg survival derived from seasonal egg production curves and cohort development are closely related ($r^2 = 0.82$, $n = 8$), the relationship between OES and egg survival from seasonal production curves is less satisfactory ($r^2 = 0.36$, $p = 0.153$, $n = 7$). This can be explained by large residuals in 1991 and especially 1996 (Figure 6b). The latter deviation, however, did not enter the comparison to the survival from cohort development (Figure

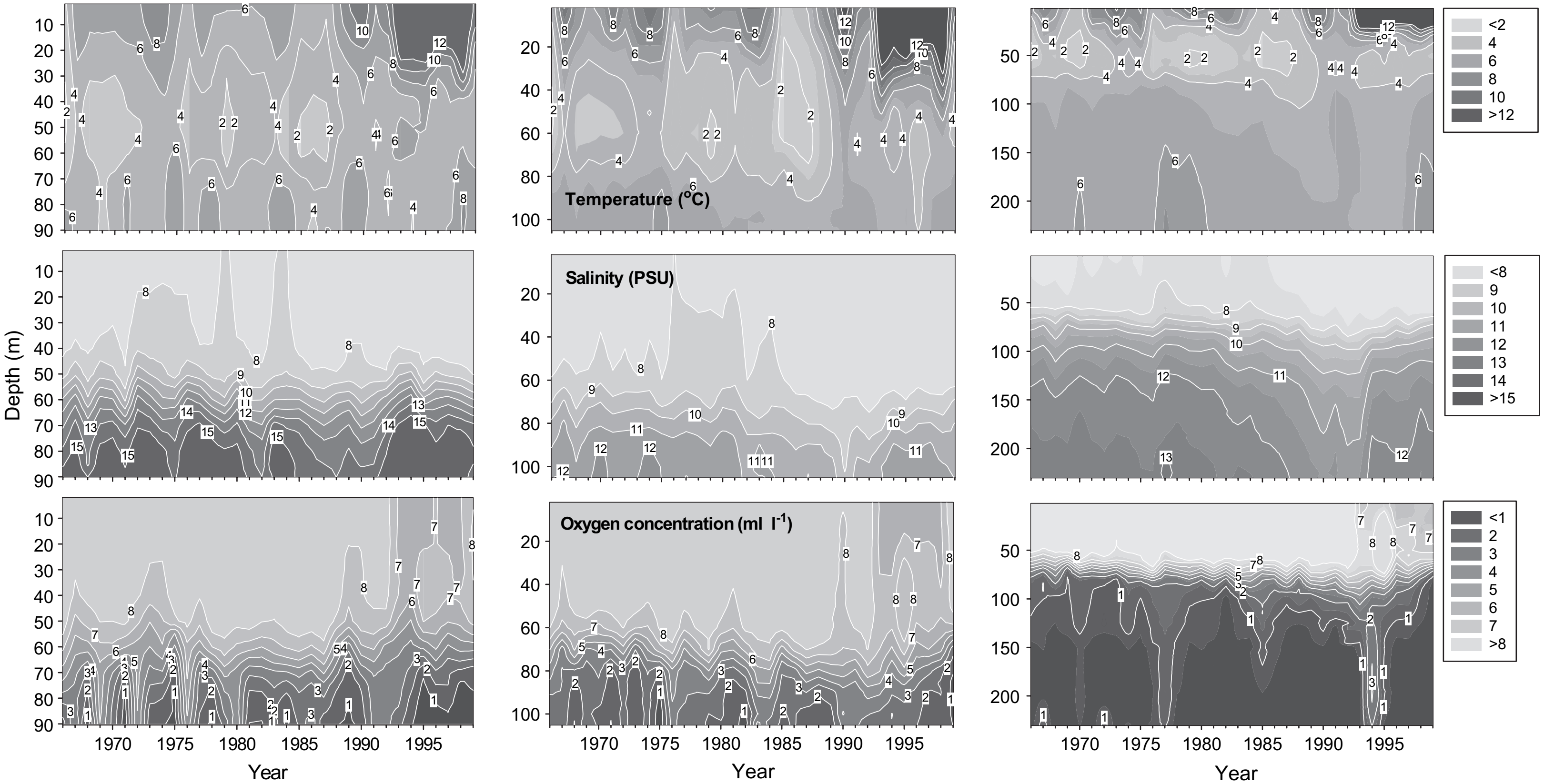

Figure 2. Temperature, salinity, and oxygen concentrations during the main spawning season (second quarter 1966−1989, third quarter 1990−1999) in the Bornholm Basin (left), the Gdańsk Deep (middle), and the Gotland Basin (right).

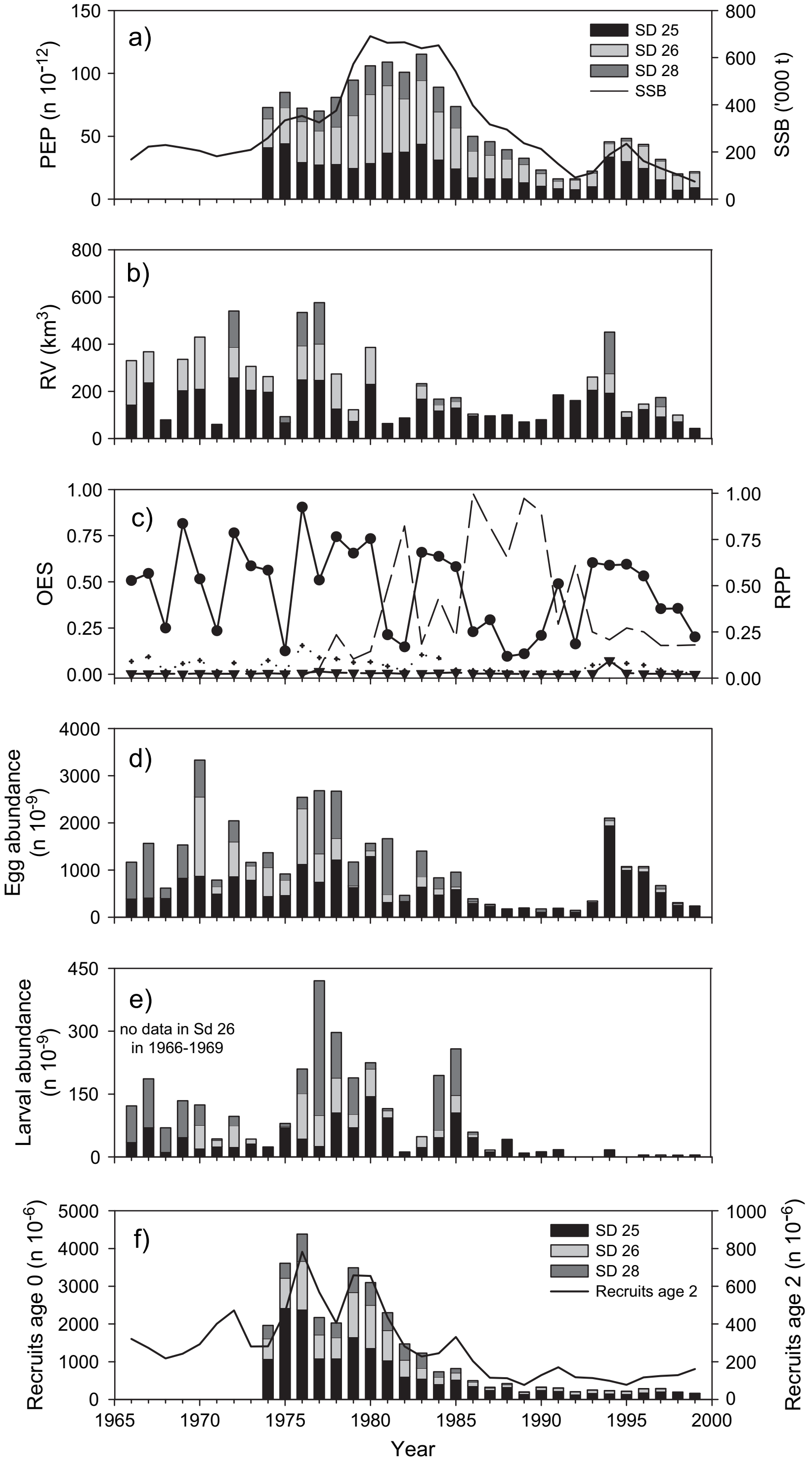

Figure 3. Time-series of (a) spawning-stock biomass (SSB) in Subdivisions 25, 26, and 28 and the entire central Baltic (SSB) and potential egg production (PEP), (b) reproductive volume (RV), (c) oxygen-related egg survival (OES) and relative egg predation pressure in SD 25 (RPP – thin dashed line), (d) egg abundance, (e) larval abundance, and (f) recruitment at age-0 in Subdivisions 25, 26, and 28 and recruits at age-2 in the entire central Baltic.

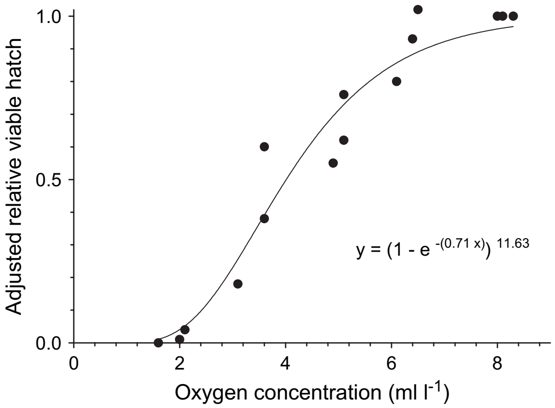

Figure 4. Relative viable hatch of cod eggs at different levels of oxygen concentration during egg incubation, adjusted to survival at normoxic conditions.

6a) and, as in 1996, no repeated ichthyoplankton surveys were performed. Interestingly, the highest predicted and observed egg survival was encountered in 1993 and 1994, despite low observed larval abundance (Figure 3e).

Average daily egg mortality rates in different spawning areas are compared in Table 2 for contrasting environmental conditions within areas. Egg mortality rates were mainly low in 1974 and 1976. These years were typical inflow years with in general high RVs and OES (Figure 3b, c). Differences in mortality rates between the different areas, however, are not consistent with the OES, suggesting that egg mortality should have been lowest in the Bornholm Basin. While this is the case in 1976, mortality was lowest in 1974 in the Gdańsk Deep (Table 2). In a typical stagnation year like 1989, egg mortalities were relatively low in the Bornholm Basin only, but extremely high in the eastern spawning areas, consistent with theory. In 1995 and 1996, years characterized by favourable conditions in the Bornholm Basin, egg mortality rates were again low in this area, while they were very high in the Gotland Basin. Thus, flushing of the Baltic from the west determines conditions for cod egg development in the three deep Baltic basins, and egg survival depends on the strength of the inflow.

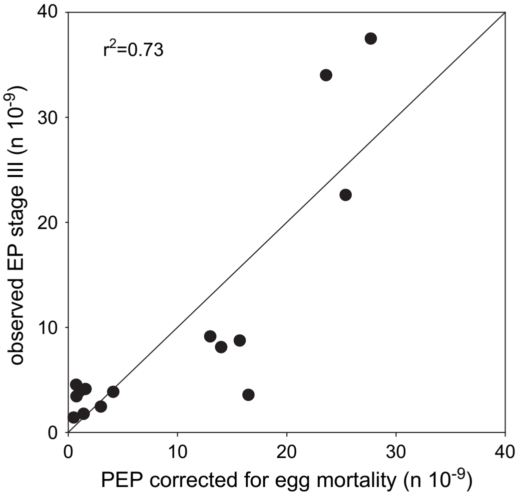

Figure 5. Linear regression of daily production of cod egg stage III (EP) in the Bornholm Basin on potential egg production (PEP) corrected for oxygen-related egg survival.

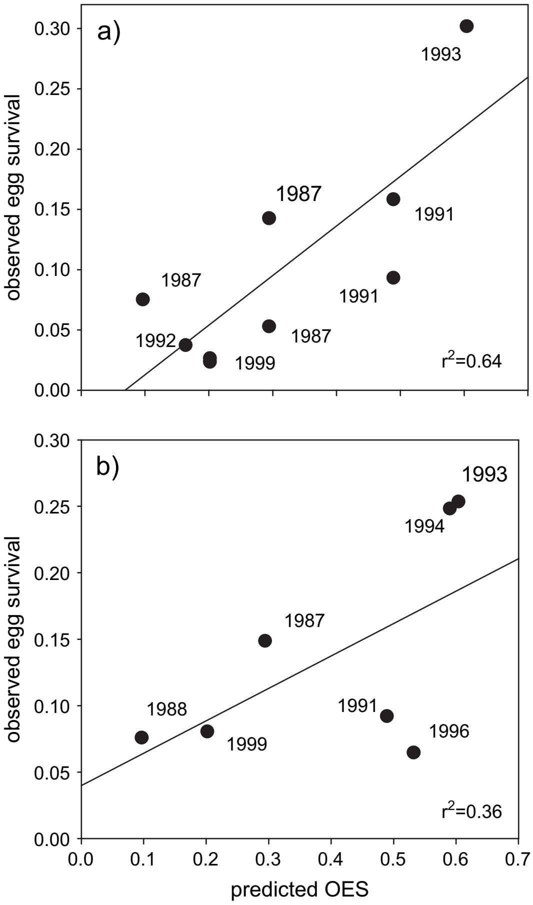

Figure 6. Observed egg survival from ichthyoplankton surveys (proportion surviving to stage III) from following cohort development (a) and from seasonal stage-specific egg production curves (b) vs. predicted oxygen-related egg survival (OES).

Table 2. Average daily mortality rates from egg stage I to III in different spawning areas in years with contrasting environmental conditions, i.e. 1974, 1976, and 1989 (April—June) and 1995 and 1996 (July/August).

Year	Bornholm Basin	Gdańsk Deep	Gotland Basin
1974	0.272	0.122	0.164
1976	0.051	0.247	0.524
1989	0.191	1.247	1.217
1995	0.268	—	1.041
1996	0.199	—	1.322

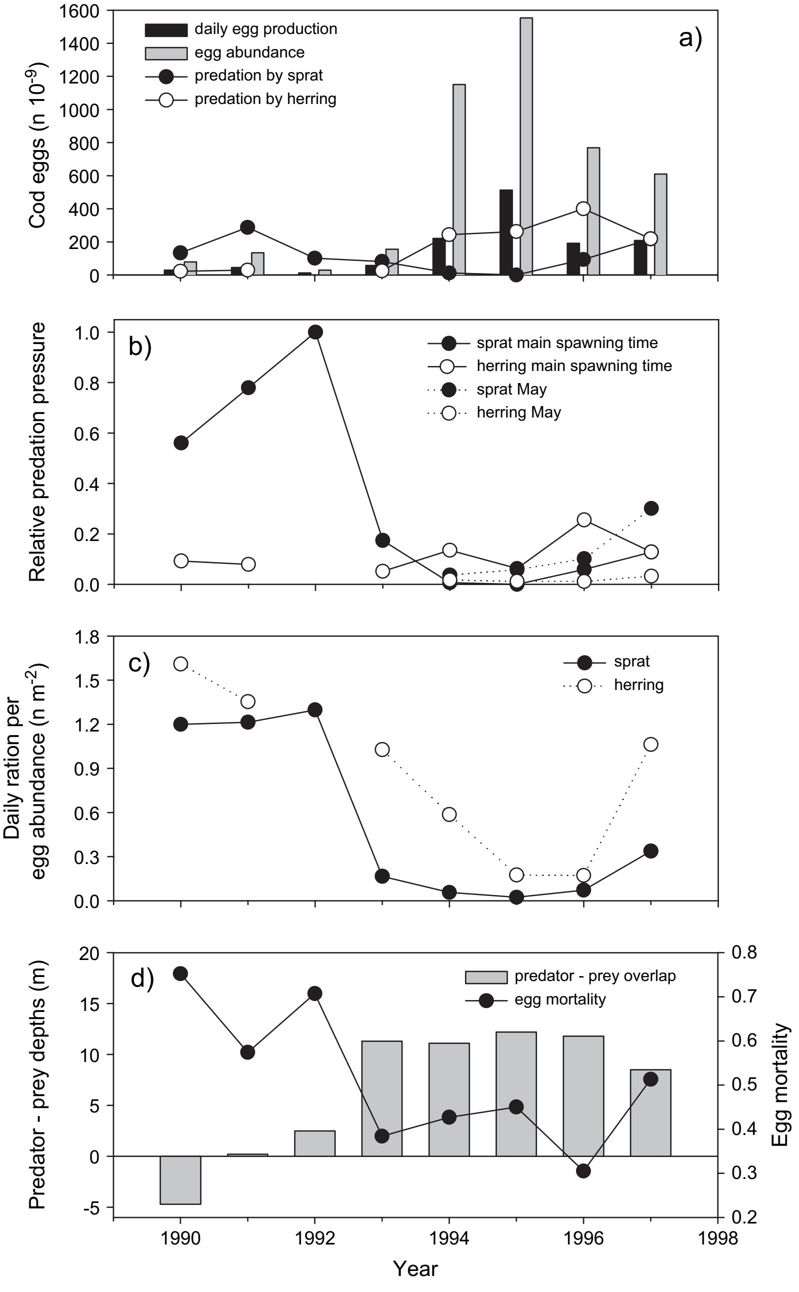

Figure 7. Daily cod egg consumption by clupeids in the Bornholm Basin during main spawning periods in comparison with daily production rates and standing stocks of eggs (a); corresponding relative predation pressure (b); daily ration by individual sprat and herring per egg abundance (c); spatial overlap between predator and prey and daily cod egg mortality based on vertical resolved ichthyoplankton and hydrography sampling during stomach sampling cruises (d).

Egg predation by clupeids

Comparing daily cod egg consumption rates by sprat and herring populations in the Bornholm Basin during cod spawning periods with daily production rates and standing stocks of cod eggs confirmed high predation by sprat during the early 1990s, when the cod spawning season was still in spring and early summer (Figure 7a). Predation was estimated to be above daily production and standing stocks in 1990–1992 and above production in 1993. After the shift of cod spawning to summer, the importance of predation by herring increased, consuming 50 to >100% of the daily production and up to 50% of the standing stock. Assuming that these consumption estimates were unrealistically high, and expressing the predation pressure in relative terms, i.e. as the ratio of daily consumption to production scaled to the maximum determined for sprat in spring 1992 (Figure 7b), revealed a minimum of egg predation in 1993—1995. This can be explained by a combination of limited vertical overlap between predator and prey after the 1993 major inflow, and the shift of cod spawning to summer.

The effect of the shift in spawning season can be inferred from a seasonal comparison of the relative predation pressure during May/June and July/August 1994—1997. The predation pressure by sprat was approximately 2.5 times higher in spring/early summer than in summer, while the predation pressure by herring was approximately 8 times higher in summer than in spring (Figure 7b). The effect of the vertical predator—prey overlap can be deduced from a comparison between May/June 1990—1992 and 1993—1996. Sprat and herring predation decreased by a factor of 6.0 and 3.5, respectively (Figure 7b).

Comparing average daily rations of cod eggs by individual sprat and herring with egg abundance (Figure 7c) confirms that the individual egg predation by sprat follows closely the predator—prey overlap (Figure 7d), though the relationship is less obvious for herring. Comparing the oxygen-related egg mortality during stomach sampling cruises (determined similar to the OES) revealed a similar trend in hydrography-induced egg mortality and predator—prey overlap and hence predation pressure (Figure 7d). This can be explained by the same hydrographic parameters affecting the vertical predator—prey overlap and oxygen-related egg mortality, i.e. salinity and oxygen. This is also obvious from a comparison of modelled relative predation pressure (RPP) and OES for the period 1966 until the mid-1990s (Figure 3c). Deviations in most recent years are caused by the shift of cod spawning from spring to summer.

Model simulations of larval survival in relation to food availability

Model simulations revealed food limitation for first-feeding cod larvae during the 1990s, caused by a decline in the abundance of the calanoid copepod *Pseudocalanus* sp. Model output suggests further retention and dispersal from the main spawning ground to be a key process influencing larval survival (Hinrichsen *et al.*, 2002a). If *Pseudocalanus* sp. was available in the modelled prey fields, food limitation occurred only late in the spawning season (Figure 8a). Prey fields without *Pseudocalanus* sp. resulted in higher survival at the beginning and the end of the spawning season (Figure 8a). Higher survival early in the spawning season is caused

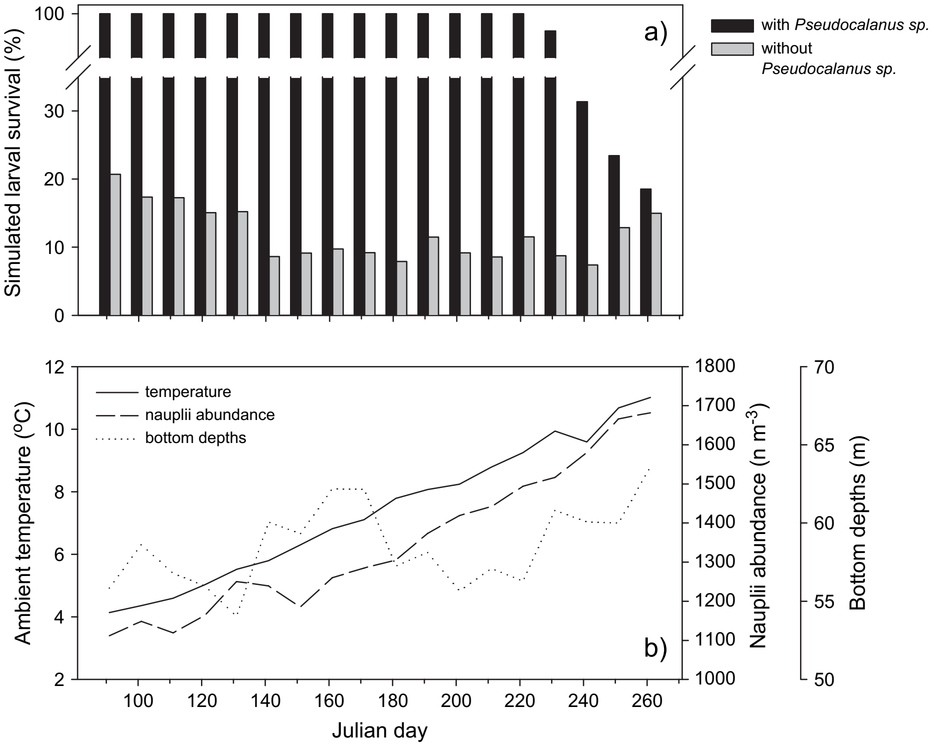

Figure 8. Seasonal variability in simulated larval survival (averaged 1986—1999) in SD 25 from a2 coupled hydro-/trophodynamic model based on an idealized prey field, with and without *Pseudocalanus* sp. (a), and average ambient environmental variables encountered by surviving larvae (runs without *Pseudocalanus* sp.), i.e. nauplii abundance, temperature, and bottom depth after drift period as a measure of transport (b), modified after Hinrichsen *et al.* (2002b).

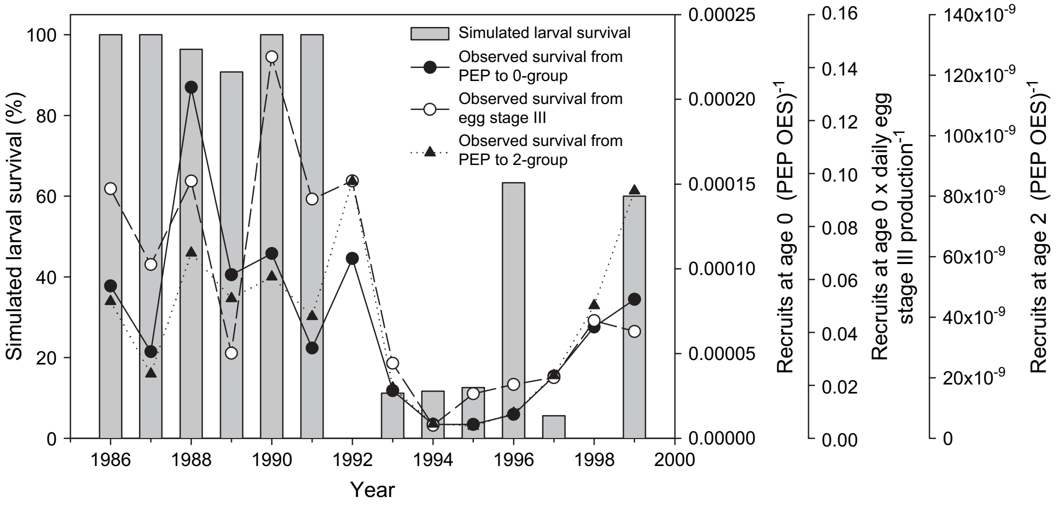

Figure 9. Interannual variability in simulated larval survival in SD 25 from a coupled hydro-/trophodynamic model based on idealized prey field, with the exception of 1999, based on observed zooplankton abundance; measures of larval survival as recruits at age-0 per surviving egg production (PEP times OES) and per observed average daily egg stage III production as well as recruits at age-2 in the entire eastern Baltic per sum of surviving egg production in each SD (PEP times OES).

in the model by lower temperatures on average (Figure 8b) and related lower food requirements for sustaining standard metabolism. Higher survival later in the spawning season is due to an increased abundance of nauplii other than *Pseudocalanus* sp., and enhanced transport into productive shallow-water areas.

Interannual variability in larval survival from peak spawning activity as derived by coupled model runs (Hinrichsen *et al.*, 2002a) suggested low survival from 1993 to 1997, with the exception of 1996 (Figure 9). The latter can be explained by relatively high wind speeds (affecting transport and prey encounter via turbulence), below average temperatures (Figure 2), and relatively high *Pseudocalanus* sp. availability (Figure 10b). Low survival through the larval stage during the 1990s is also evident in the ratio of egg to larval abundance for the Bornholm Basin (Figure 3d, e), and confirmed by relating 0-group recruitment to different measures of surviving egg production (Figure 9). Simulated and observed larval survival rates were lowest during 1993—1995, a period of favourable oxygen conditions for egg survival. Before 1992, observed survival rates were lower in general and more variable than the coupled model output, pointing to other larval or early juvenile mortality. Despite the general agreement of simulated and observed low larval survival during the 1990s, the relatively high larval survival suggested by the model for 1996 is not confirmed by observations.

New model simulations with directly observed prey fields for 1999 demonstrated that early-hatched cod larvae were not food limited, whereas late hatched survivors were transported to coastal areas because of insufficient food supply in the centre of the basin (Hinrichsen *et al.*, unpublished). In general, there was no starvation mortality of individuals spawned in April and May 1999, whereas survival of larvae hatched in June—August decreased to about 60%. The high survival of early-hatched larvae contradicts earlier model results for the 1990s (Hinrichsen *et al.*, 2002a). This may indicate either an improvement of food availability from the mid- to the late-1990s, or that prey fields used in the earlier coupled model runs were underestimated.

Pseudocalanus sp. abundance measured in the Bornholm Basin in 1999, the basis for 1999 model runs, was similar to values determined for the eastern basins by LatFRA in spring and summer 1999 (Figure 10a). This indicates that establishing average zooplankton abundances for the entire central Baltic did not bias the food availability used in earlier model runs. Polish investigations determined that abundances of *Pseudocalanus* sp. nauplii in the Bornholm Basin in spring 1992 and 1993 (Krajewska-Soltys and Linkowski, 1994) were well below the average *Pseudocalanus* sp. abundance from the LatFRA time-series (Figure 10a). This confirms lower than normal food supply for early cod larvae in those years. In contrast, Polish *Pseudocalanus* sp. nauplii abundances in summer were above the long-term average of the LatFRA series (Figure 10b), indicating better than normal food supply for late-hatching larvae.

All zooplankton data sets show a decline in prey availability from the early- to the mid-1990s. This includes displacement volumes, measured on many stations from 1988 to 1997, showing a significant reduction in mesozooplankton biomass from 1992 to 1995 (Figure 10a). A high survival from main spawning activity in 1999, indicated by the coupled model simulations for 1999, is

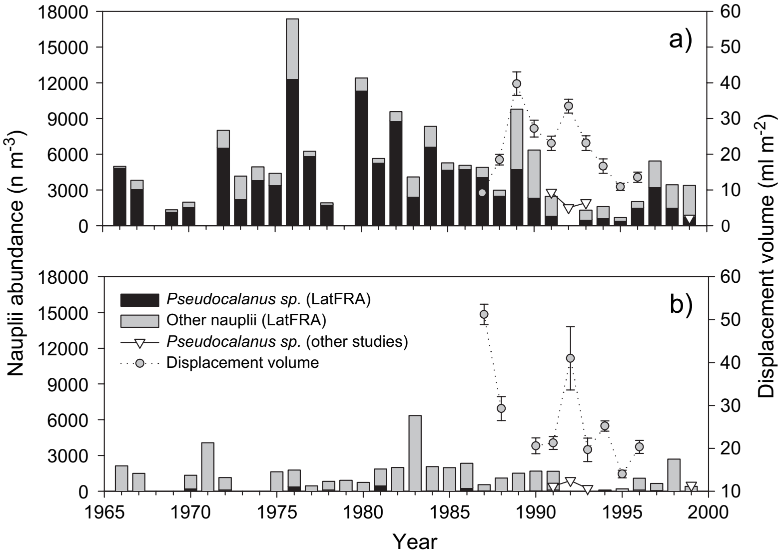

Figure 10. *Pseudocalanus* sp. and other nauplii abundance (whole water column) in SDs 26 and 28 in the second (a) and third quarters (b) from LatFRA monitoring (no data available in the second quarter in 1968, 1971, 1979, and 1992 and in the third quarter in 1968−1969, 1972−1973, and 1992−1993), in SD 25 from Polish studies in 1991−1993 (water samples), in 1999 (50 μm net), and zooplankton displacement volume ± s.e. (335 μm Bongo samples).

confirmed by available observations of survival from egg production to recruitment (Figure 9).

Survival in the juvenile stage

Larval abundance and recruitment at age-0 were significantly related in SDs 25 and 26 ($r^2 = 0.33$ and $r^2 = 0.49$, respectively; $p < 0.01$). However, recruitment in SD 28 was regularly observed despite the absence of larvae in the ichthyoplankton surveys, a fact which is true also for SD 26 (Figure 3e, f). Comparing the time-series of cod larval abundance in the central Baltic, i.e. the integrated abundance of all spawning areas, which should be unaffected by transport between spawning areas, with recruitment from the standard assessment revealed a highly significant relationship ($r^2 = 0.53$, $p < 0.01$). This, however, does not imply that mortality from the larval to the early juvenile stage is constant. On the contrary, high larval abundance observed in all spawning areas in 1984 and 1985 did not result in massive recruitment, indicating situations with higher than normal mortalities at the early juvenile stage.

Cannibalism is a significant source of mortality in juvenile cod (Sparholt, 1994), which, however, is accounted for in the present analysis, as 0-group abundance from

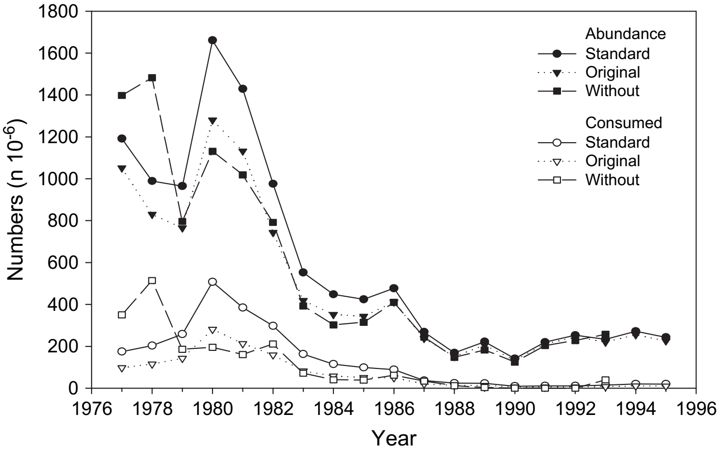

Figure 11. Juvenile cod (age group 1) abundance and consumption (cannibalism) estimated by MSVPA runs with the standard suitability model implemented in the Baltic, the original model suggested by Gislason and Sparre (1987) and without suitability model, modified after Neuenfeldt and Köster (2000).

MSVPA runs are used. According to Neuenfeldt and Köster (2000), recruitment estimates from MSVPA runs are substantially affected by the choice of the suitability submodel and whether a suitability model is used at all. Deviations in recruitment estimates from MSVPA runs using different suitability models are obvious for the beginning of the time-series (Figure 11). An MSVPA run without a suitability model (i.e. based on observed stomach content only) suggested highest recruitment for year classes 1976 and 1977, while next highest year classes were determined for 1979 and 1980. The former result fits better the larval abundance (Figure 3e), indicating that the 1977 year class may be underestimated and the 1980 year class overestimated by the present MSVPA runs (Figure 3f). Independent of how prey selection is modelled in the MSVPA, cannibalism is confirmed to be a significant source of juvenile mortality at high cod stock size.

Discussion

The decline of the eastern Baltic cod stock was caused by reduced reproductive success in combination with increasing fishing pressure (Bagge *et al.*, 1994; Köster *et al.*, 2003b). The reproductive success of the stock is closely coupled with hydrographic conditions in spawning areas. The importance of interacting climatic and hydrographic forcing, reproductive effort by the stock, and species interactions are discussed below.

Potential egg production and reproductive volume

A comparison of the PEP in the three spawning grounds with the RV at spawning time indicated that, during the late-1970s and early 1980s, a large portion of the PEP was spawned in unsuitable environments in the Gdańsk Deep and the Gotland Basin. The estimate of the PEP depends on the distribution of the adult stock derived from area-disaggregated MSVPA runs, and thus on the distribution of commercial catches in the different SDs (Köster *et al.*, 2001b). MSVPA results may be sensitive to spawning migrations from eastern areas into the Bornholm Basin, which regularly has the best reproductive conditions. Analyses of results from bentho-pelagic trawl surveys (Tomkiewicz and Köster, 1999) and commercial cpue data (Lablaika and Lishev, 1961) confirmed this spawning migration. However, egg abundance data presented here indicate large-scale spawning in the eastern spawning areas even in unfavourable oceanographic conditions. This confirms observations on pelagic prespawning and spawning concentrations from trawl surveys in the Gotland Basin also in years with unfavourable oxygen conditions (Uzars *et al.*, 1991). Consequently, a mismatch of reproductive effort and spawning habitat quality was one of the main causes of the declining reproductive success and recruitment failure of the stock during the 1980s.

Oxygen-related egg survival

The relationship established between oxygen concentration and egg survival confirmed that, below 2 $\mathrm{ml\,l^{-1}}$ oxygen concentration, no successful egg development occurs. However, it clearly indicates that survival success is also negatively affected above this threshold, as earlier reported by Wieland *et al.* (1994).

Egg survival rates determined from ichthyoplankton surveys for favourable hydrographic conditions in the Gdańsk Deep and the Gotland Basin, i.e. in 1974 and 1976, are substantially higher than suggested by the OES. One reason for the discrepancy may be the rapid loss of newly spawned eggs with insufficient buoyancy from the system, resulting in mortality rates being underestimated on ichthyoplankton surveys. According to the applied vertical distribution model, only 6−37% of the eggs produced were able to obtain neutral buoyancy in the Gdańsk Deep, while the percentage in the Gotland Basin was higher, i.e. 22−52%, due to the greater depths of the basin. Because the hydrographic conditions in the bottom water of the Gotland Basin are less favourable than in the Gdańsk Deep this does not, however, translate into a higher estimated egg survival.

High abundances of larvae in eastern spawning areas during the 1970s and mid-1980s clearly indicated substantial egg survival. An extensive drift of larvae from the Bornholm Basin into eastern spawning areas, which may explain high larval abundance despite low egg survival, could not be confirmed by drift modelling studies (Hinrichsen *et al.*, 2003). More likely, the applied vertical distribution model, based on data from vertical resolving net sampling in the Bornholm Basin, underestimates the buoyancy of cod eggs produced in eastern spawning areas. A possible explanation may be that lower salinities at gonad maturation and during the fertilization process positively affect egg buoyancy . Larger females produce on average more buoyant eggs (Nissling and Vallin, 1996), so a substantial spatial difference or change in spawning stock structure in terms of size or age may additionally affect the vertical distribution of cod eggs. In addition, a potential dependence of egg size and buoyancy on female condition, described for various cod stocks (e.g. Trippel, 1998), is not considered in the model.

Comparing the OES and field-based egg survival rates from the Bornholm Basin revealed highly significant relationships, but also indicated other sources of egg mortality. Other processes potentially affecting egg developmental success are: (i) salinity-dependent fertilization rate (Westin and Nissling, 1991), (ii) predation (see below), and (iii) endogenous processes such as chromosome aberrations during embryonic development (Kjørsvik, 1994), contamination by toxicants (e.g. Schneider *et al.*, 2000), and endogene parasites (e.g. Pedersen and Køie, 1994).

Egg predation by clupeids

Estimated cod egg consumption by herring and sprat populations in the Bornholm Basin exceeded corresponding egg production rates in spring and early summer dates of 1990−1992, demonstrating either an overestimation of the consumption or an underestimation of egg production. Currently, there is no indication that the applied sampling scheme is unable to resolve intra- and interannual variability in the diet of clupeids, or that the applied procedure to estimate daily egg consumption rates by individual predators is biased (Köster and Möllmann, 2000). However, a hydroacoustic survey conducted in May/June 1999 revealed a possible overestimation of the predator population. The applied sprat distribution pattern within SD 25 from historical hydroacoustic surveys, used to downscale area-disaggregated MSVPA results (Köster and Möllmann, 2000), was found to be invalid at the large population sizes of the 1990s. Assuming the 1999 hydroacoustic survey distribution to be representative of the entire time-series would result in approximately 50% lower population consumption rates. Estimates of the sprat population size in the Bornholm Basin in 1999 using the daily egg production method (Kraus and Köster, 2004), confirmed the hydroacoustic survey results. No bias could be detected for herring. Expressing predation pressure in relative terms, as in the present study, does not account for an overestimation of sprat predation relative to herring. This implies that the relative predation pressure modelled for early spawning times may hold, though still being sensitive to shifts in distribution of the predator over time, but that the predation pressure after the shift of cod spawning to summer may not be directly comparable.

With respect to a potential underestimation of the daily cod egg production, it should be noted that, although the PEP is significantly related to the realized egg production, the former is about twice as high as seasonal production values from ichthyoplankton surveys (Kraus *et al.*, 2002). This indicates an underestimation of the egg production derived by ichthyoplankton surveys or an overestimation by the PEP, e.g. due to atresia. Another factor explaining the discrepancy between both production estimates may be limited fertilization success. Even if not fertilized, eggs are preyed upon.

Despite uncertainties in the estimates, it is evident that egg predation intensity by clupeids depends on ambient hydrographic conditions. In stagnation periods, when oxygen and salinity are low, the vertical overlap between predator and prey is high, while opposite conditions release cod eggs from clupeid predation. Furthermore, egg predation pressure depends on predator abundance. Herring stock sizes declined throughout the 1980s and 1990s (Köster *et al.*, 2003b), while sprat stock size increased to the highest levels on record in the mid-1990s, mainly because of favourable thermal conditions for reproduction (MacKenzie and Köster, 2004). Timing of spawning defines the major predator species, late spawning enhancing the horizontal overlap with herring, but releasing predation pressure by sprat. The shift of the cod spawning season to summer during the first half of the 1990s has thus been an advantage for cod reproductive success.

Larval survival

Comparing the abundances of eggs and larvae as well as observed and modelled egg survival with larval abundances indicated high mortality rates during hatching or in the early larval stage during the mid-1990s. While information on endogenous factors impacting hatching success is limited, there are at least three different processes that can explain high mortality in the early larval stage: (i) sub-lethal effects of egg incubation at low oxygen concentrations and/or direct effects of low oxygen concentrations on larval survival (Nissling, 1994), (ii) predation by clupeids (Köster and Möllmann, 2000), and (iii) food limitation and starvation (MacKenzie *et al.*, 1996).

Experimental studies demonstrated that low oxygen concentration at egg incubation impacts larval activity and the start of the vertical migration into upper water layers (Rohlf, 1999). Further Nissling (1994) demonstrated that low oxygen concentration negatively affected larval survival. However, given the favourable hydrographic conditions within and below the halocline after the 1993 major inflow, it appears unlikely that sub-lethal oxygen effects during egg incubation or low oxygen concentrations at the depths larvae live were responsible for the low larval survival in the mid-1990s.

There is little evidence of substantial predation on cod larvae by clupeids (Köster and Möllmann, 1997). This can be explained partly by limited vertical overlap of larvae dwelling in upper water layers and clupeids feeding in bottom water layers. Only newly hatched larvae concentrate in relatively high quantities within or below the halocline, where they are available as prey to herring and sprat. However, herring, the dominant predator in summer, the main spawning time of herring in the mid-1990s, seldom fed on these small larvae, possibly owing to a mismatch in size preference (Köster and Möllmann, 1997).

The impact of food availability on larval growth and survival has been tested by Hinrichsen *et al.* (2002a) with a coupled hydro-/trophodynamic model. Model results indicated the importance of a match in calanoid nauplii and cod larval abundance in space and time for good survival of early larvae. High nauplii abundance of *Pseudocalanus* sp. in spring or cod spawning in summer and a rapid transport into shallower areas with higher production of other calanoid copepod species assure high survival (Hinrichsen *et al.*, 2002a). The strong decline of

Pseudocalanus sp. since the end of the 1980s, associated with a decrease in salinity (Möllmann *et al.*, 2000, 2003), resulted in low simulated larval survival in 1993–1995 and 1997.

Apart from various potential improvements in the trophodynamic IBM formulation and model parameterization (Hinrichsen *et al.*, 2002a), the modelling approach had to cope with a relatively sparse temporal and spatial resolution of zooplankton data from the entire central Baltic derived by LatFRA. However, newly available zooplankton data from 1999 in the Bornholm Basin as well as Polish abundance data (Krajewska-Soltys and Linkowski, 1994) indicated that the prey fields used in Hinrichsen *et al.* (2002a) appeared to be a valid representation of the food availability for cod larvae.

A further test of the coupled hydro-/trophodynamic model output is possible by inspecting instantaneous protein growth rates of cod larvae (older than 6 days) sampled in the Bornholm Basin in May–July 1994 and May 1995 (Grønkjær *et al.*, 1997). Compared with protein growth rates from cod larvae reared experimentally poor, intermediate, and good nutritional conditions, 85% and 62% of the larvae caught in May 1994 and 1995, respectively, were classified in poor condition, likely beyond the point of no return, while 0% and 15% were in good condition. In June and July 1994, more than half the larvae were in poor condition, but an increased fractions of 20% and 37% were in good condition. Overall, these data suggest substantial larval cod mortality in 1994 and 1995 and confirm an enhanced nutritional status of larvae spawned later in the season, as suggested by the coupled model output.

Poor larval survival during the mid-1990s was also suggested by the ratio of egg to larval abundance. However, the shift in cod spawning time to summer may have resulted in a mismatch of high larval production and ichthyoplankton survey timing in 1993 and 1994. Furthermore, no larval size or age data are available to compute larval mortalities directly. Therefore a validation of the simulated larval mortalities was only possible by relating 0-group recruitment to different measures of surviving egg production. These measures of larval survival confirmed the simulated larval mortalities, with the exception of the relatively good larval survival suggested by the model for 1996.

Survival at the juvenile stage

Significant relationships between larval abundance and 0-group recruitment in SDs 25 and 26 confirmed that the later larval and early juvenile stages are less critical for cod recruitment than the egg and the early larval stages (Köster *et al.*, 2003a). An insignificant relationship in SD 28, where recruitment is regularly observed despite the absence of larvae in the ichthyoplankton surveys, can be explained by (i) drift of larvae from the Gdańsk Deep into the Gotland Basin, and (ii) an immigration of juvenile cod from the coastal nursery areas in SD 26, indicated by bottom trawl surveys in the Gotland Basin (Plikshs, 1996).

MSVPA-derived recruitment at ages 1 and 2 match trawl survey results, especially in SDs 26 and 28 (Köster *et al.*, 2003a). However, the outstanding 1979 year class was not confirmed by survey results. According to simulations by Neuenfeldt and Köster (2000), the application of constant suitability coefficients artificially inflated the strength of the 1979 and 1980 cohorts, while it underestimated year classes 1976 and 1977. In contrast, a significant impact of the suitability submodel on the recruitment estimates in 1984 and 1985 could not be detected. Therefore, the mismatch between good larval abundance and declining recruitment success in those years cannot be explained by methodological problems in estimating recruitment.

During the juvenile stage of demersal fish stocks, year-class strength is thought to be regulated primarily by density-dependent processes mediated through competition for a limiting food resource and predation (Myers and Cadigan, 1993). Evidence exists that growth of juvenile Baltic cod in shallow water may be affected by density-dependent competition for food (Hüssy *et al.*, 2003) and density-dependent cannibalism (Uzars and Plikshs, 2000). Therefore, transport to suitable nursery areas and away from adult cod concentrations may be an important process governing juvenile growth and survival.

Hinrichsen *et al.* (2003) investigated the drift of larvae and pelagic juveniles from the spawning area of the Bornholm Basin to nursery areas from 1986 to 1999 by combining 3-D hydrodynamic model simulations and spatial distributions of juvenile cod from 0-group surveys. The results suggest that juveniles caught in different areas of SD 25 hatched at different times. Because of seasonal differences in circulation pattern, on average, southern coastal nursery areas are most important for early and late spawned individuals, whereas larvae hatching in June–mid-July were transported towards the north or, to a greater extent, retained in the Bornholm Basin (Hinrichsen *et al.*, 2003). This implies that the transport pattern and the importance of nursery areas change with shifts in spawning time. While in the 1980s and early 1990s northern nursery areas were of greater importance, transport to southern areas dominated in the remaining period. Whether this general change in the transport regime has affected juvenile growth and survival is unclear at present.

Summary

Hydrographic conditions in the central Baltic are affected by large-scale climatic conditions during the last two decades, resulting in higher than normal temperatures in the intermediate and bottom water, and declining salinity and oxygen concentrations in the deep Baltic basins.

The decline in recruitment during the 1980s was related to these climate-induced changes in the physical environment. Anoxic conditions in deep layers at important spawning sites caused severe egg mortalities. Declining salinities and oxygen concentrations enhanced the vertical overlap between eggs and clupeid predators in the remaining productive spawning area of the Bornholm Basin. A temperature-related increase in the sprat stock intensified egg predation further.

The lack of recovery in recruitment in the mid-1990s, despite improved hydrographic conditions for egg development, is related to poor larval survival. A decline in the abundance of the copepod *Pseudocalanus* sp., related to lower salinity, caused food limitation for first-feeding cod larvae.

The case of the eastern Baltic cod stock exemplifies the multitude of effects climate variability may have on a fish stock, and it underscores the importance of knowledge of these processes for understanding the dynamics of such a fish stock. It is further evident that adequate long-term fisheries management has to consider climate forcing on recruitment and species interactions in order to achieve optimal resource utilization and conservation.

Acknowledgement

The present study evaluates the state-of-the-art in Baltic cod recruitment research based on results from the Commission of the European Communities, Agriculture and Fisheries (AIR and FAIR), specific RTD-programmes CT94-1226 (CORE) and CT98-3959 (STORE), as well as the German Federal Ministry of Education and Research funded project GLOBEC Germany, as a contribution to EU FP6, TP 8.8 Specific Targeted Research Projects 502482 (BECAUSE) and 513670 (PROTECT). Contributions from participants of these projects are acknowledged.

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