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Survival probability of Baltic larval cod in relation to spatial overlap patterns with their prey obtained from drift model studies

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Temporal mismatch between the occurrence of larvae and their prey potentially affects the spatial overlap and thus the contact rates between predator and prey. This might have important consequences for growth and survival. We performed a case study investigating the influence of circulation patterns on the overlap of Baltic cod larvae with their prey. A three-dimensional hydrodynamic model was used to analyse spatio-temporally resolved drift patterns of larval Baltic cod. A coefficient of overlap between modelled larval and idealized prey distributions indicated the probability of predator–prey overlap, dependent on the hatching time of cod larvae. By performing model runs for the years 1979–1998 investigated the intra- and interannual variability of potential spatial overlap between predator and prey. Assuming uniform prey distributions, we generally found the overlap to have decreased since the mid-1980s, but with the highest variability during the 1990s. Seasonally, predator–prey overlap on the Baltic cod spawning grounds was highest in summer and lowest at the end of the cod spawning season. Horizontally variable prey distributions generally resulted in decreased overlap coefficients. Finally, we related variations in overlap patterns to the variability of Baltic cod recruitment success.

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Introduction

Recruitment success of marine fish stocks can to a large degree be related to the feeding success of their early life stages, i.e. larvae and juveniles (Mullin, 1993). The survival of fish larvae and juveniles depends on their ability to encounter, capture, and ingest a sufficient quantity of appropriate prey in order to avoid starvation and assure growth. According to the "match–mismatch" hypothesis, variability in recruitment depends on the temporal match/mismatch of the annual reproductive cycle of fish and the prey of their larvae (Cushing, 1973). Differences in the match between larvae and their prey may thus generate variability in larval feeding success, including both interannual (Cushing, 1996) and spatial variability. Thus, the

transport of eggs and larvae into sub-optimal feeding environments may influence recruitment success (e.g. Sinclair, 1988; Heath and Gallego, 1998; Hinrichsen et al., 2002).

The deepwater area off the island of Bornholm (Baltic Sea) is the major spawning ground of Baltic cod (Figure 1). Larval cod prey mainly on nauplii of the dominant calanoid copepods in the area, i.e. *Pseudocalanus elongatus*, *Temora longicornis*, *Acartia* spp., and *Centropages hamatus* (Voss et al., 2003). Based on long-term data sets (Möllmann et al., 2000), idealized spatio-temporal distributions of the seasonal abundance of nauplii of the main copepod species have been constructed (Figure 2). In deepwater areas, where *P. elongatus* is most abundant owing to its deeper vertical distribution compared with the other calanoid species
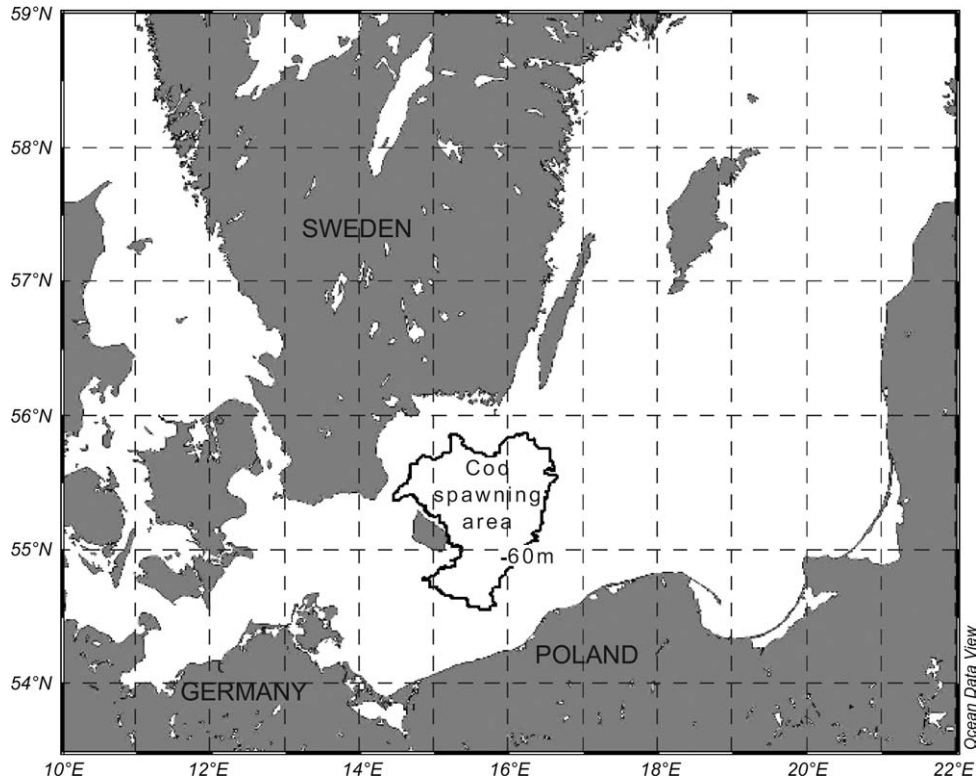
Figure 1. Map of the Bornholm Basin (Baltic Sea) and statistical rectangles. Thick line represents the spawning area of Baltic cod (60-m isobath).

(Möllmann and Köster, 2002), mean nauplii abundance strongly increases during late winter, with peak abundance between April and May (Figure 2a). In late summer and autumn, *P. elongatus* abundance decreases whereas the abundance of all other species peaks later in the year. Shallow areas at the margins of the deep basin show a similar temporal trend to the deepwater areas, with the maximum of the "other" copepods in late summer being significantly higher than the *P. elongatus* maximum (Figure 2b).

The described spatio-temporal variability in occurrence of food for larval cod indicates the possibility of a spatial mismatch between the appearance of larval predators and their planktonic prey, depending on the hatching time of larvae. It can be assumed that the degree of this spatial mismatch strongly depends on the intra- and interannual variability in circulation patterns. In the present study we use data on the location and timing of spawning of Baltic cod as input into a particle-tracking model (Hinrichsen *et al.*, 1997). Utilizing currents from a three-dimensional circulation model of the Baltic Sea (Lehmann, 1995), cod larvae were tracked through space and time. Modelled distributions of larvae were then compared with assumed distributions of prey, reflecting the spatio-temporal variability in occurrence of copepod species. The utilization of an overlap coefficient (Horn, 1966) provided an integrative

view, indicating the probability of the simultaneous spatial occurrence of cod larvae and their prey.

Material and methods
Hydrodynamic model and particle tracking

The hydrodynamic model is based on the free surface Bryan–Cox–Semtner model (Killworth *et al.*, 1991), which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and the modifications made to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann *et al.* (2002). Physical properties simulated by the hydrodynamic model agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann, 1995; Hinrichsen *et al.*, 1997; Lehmann and Hinrichsen, 2000a).

The model domain comprises the entire Baltic Sea including the gulfs of Bothnia, Finland and Riga, as well as the Belt Sea, Kattegat, and Skagerrak. The horizontal
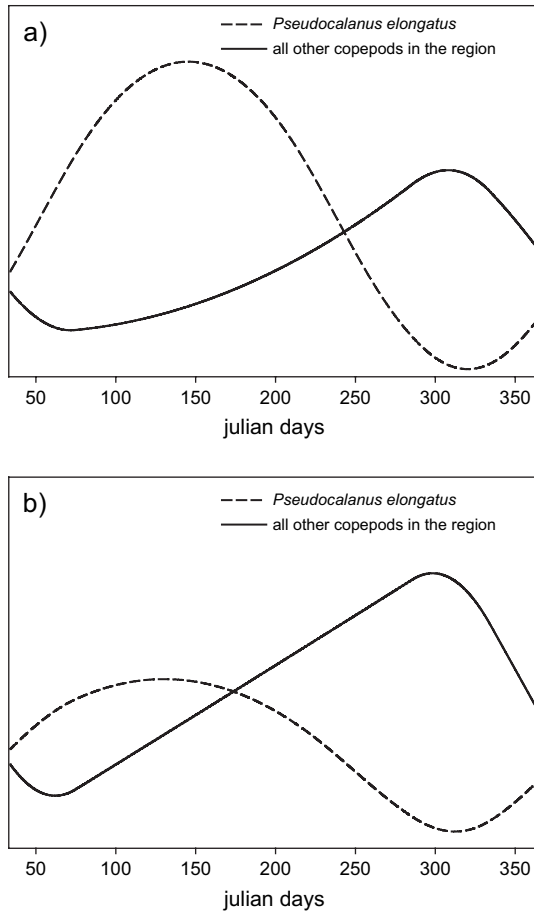
Figure 2. Schematic of seasonal copepod abundances in the Central Baltic (a) deepwater areas, and (b) shallow-water areas. n − number of replicates.

resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norr-köping, Sweden) and river run-off taken from a mean run-off database (Bergstrøm and Carlsson, 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of $1° \times 1°$ squares. Meteorological parameters such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness, and precipitation are stored with a temporal increment of 3 h.

Simulated three-dimensional velocity fields were extracted (at a 6-h interval) in order to develop a database for a Lagrangian particle-tracking exercise for larval cod. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of "marked" water particles. Vertical velocities were calculated from the divergence of the horizontal velocity fields. The drifters

were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced.

In order to establish a Lagrangian view of the simulated circulation, drifters can be placed in the modelled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independently from the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a fourth order Runge−Kutta scheme (Hinrichsen *et al.*, 1997).

First, the hydrodynamic model on Baltic cod larval drift was utilized for the time period 1979−1998 in order to obtain means of intra-annual variability in distribution and transport patterns. In order to consider seasonal variability in relation to spatial and temporal variations in larval transports, 720 Lagrangian drifters were released at depths between 25 and 35 m (depths at which feeding larvae occur after vertical feeding migration) on a regularly spaced grid enclosed by the 60-m isobath, representing the main spawning area of the Bornholm Basin (Figure 1). The main spawning area of Baltic cod is also known as one of the main reproductive areas of the calanoid copepod *P. elongatus* (Möllmann *et al.*, 2000). Drifters, at their release representing first-feeding larvae, were inserted into the modelled flow fields at 10-day intervals, and were tracked for certain time periods. The release dates commenced on 1 April and ended on 20 September, thereby encompassing the historic as well as the present peak spawning period of eastern Baltic cod (Wieland *et al.*, 2000).

Overlap calculation

Our main goal was to estimate the overlap between successively released batches of larval cod and their prey (Figure 2). To determine how many larvae and prey were simultaneously present in the specified subareas of the central Baltic Sea (Figure 1), a coefficient of overlap (C) was calculated (Horn, 1966), which is 0 when there is no overlap, and 1 when two distributions are identical:

$$C = 2 \sum_{i=1}^{n} (A_i \times B_i) / \left(\sum_{i=1}^{n} A_i^2 + \sum_{i=1}^{n} B_i^2 \right)$$

where n is the number of statistical rectangles (Figure 1) covering the main spawning area as well as the whole Bornholm Basin. The latter is the area of most likely larval and juvenile appearance (Hinrichsen *et al.*, 2003). The statistical rectangles have an approximate size of 15 nautical miles in both latitudinal and longitudinal direction. For our analysis, A and B are the proportions of larvae found in each rectangle at hatch (A) and after a given time period of larval drift (B), respectively.

High values of this coefficient indicate retention of larvae in the region of initial larval release (water depth > 60 m). Low values indicate dispersal and hence transport of larvae out of the area where they originally hatched. In order to generate temporal mismatches between larval predators and prey, the delayed time periods for which final larval drift locations were calculated have also been assumed to be the dates of peak prey occurrence. Hence, owing to the intra- and interannual variability of drift patterns, considerable spatial mismatches between larvae and their potential prey might have occurred. According to the mean seasonal evolution of prey fields (Figure 2), during spring and early summer retention in the deep area can be related to optimum encounter rates between predator and its pre-dominant prey (*P. elongatus*), whereas low values might indicate low survival success and growth of larvae. On the other hand, a low spatial overlap coefficient obtained for the late spawning period (late summer and autumn) might lead to higher prey encounter only in shallower coastal regions outside the main spawning area. There, at the same time of year, the abundances of "other" copepods are significantly higher than those of *P. elongatus* (Figure 2b).

In order to obtain measures for maximum accepted temporal mismatches between larval fish and zooplankton species/stages as their potential prey, we performed laboratory rearing experiments on starvation mortality of Baltic cod first-feeding larvae (Petereit, 2004). Parts of these experiments were conducted to determine the time until death of starved cod larvae. The results revealed a significantly high dependence of the maximum duration of survival on temperature. At a temperature of about 2°C larvae survived for about 39 days (Figure 3), while larvae under warmer temperature conditions survived for a shorter time (e.g. 13 days at 10°C). The experiments showed a significant impact of temperature on the maximum survival duration of non-fed larvae; however, larval fish usually die before reaching this age at the so-called "point
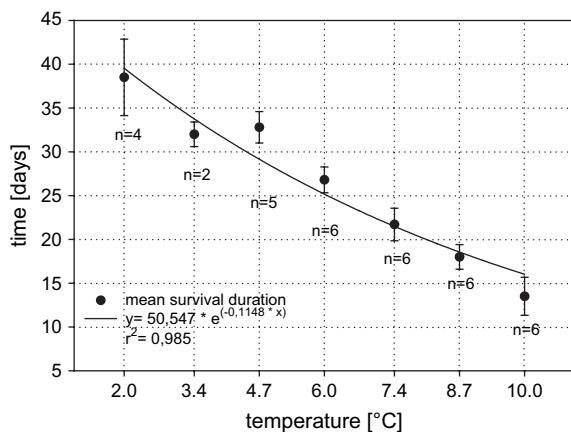
of no return". This "point of no return" is defined as the larval age after which a restart of feeding and subsequent recovery is impossible. For North Sea cod, the "point of no return" has been identified to be 11 days at 7°C and 10 days at 9°C (Yin and Blaxter, 1987). Ellertsen *et al.* (1980) found in their experiments a "point of no return" of 11 days at 5°C. In order to account for the average prevailing temperature conditions within the larval Baltic cod habitat, for our numerical model simulations we decided to chose temporal mismatches between the occurrence of larvae and their prey not to exceed 15 days, which is in good accord with the observed "points of no return" of non-fed or less optimal fed larvae.

In order to analyse how geographically variable larval cod distributions impact the spatial overlap between larvae and their prey, we performed three case studies with different horizontal distributions of larvae; i.e. (i) basin-wide (water depth > 60 m) mean abundance, as well as peak abundance (ii) within the basin centre area, and (iii) at the margins (approximately in the area of 60−80-m water depth) of the spawning area of cod (Figure 4).

Results

Generally, results of the overlap probability between larval cod predators and their prey focused on the analysis of the within- and between-year variations of larval drift. To obtain a general impression of the magnitude of the coefficient of overlap, examples of two contrasting years are displayed in Figure 5. The temporal evolution of the spatial overlap patterns between prey and predator caused by a temporal delay in peak prey abundance is considered here. At the beginning of the spawning period in 1981, the probability of a high overlap between a predator cohort released as larval drifters at Julian day 111 and its larval drift endpoints obtained for specific drift periods remained high for a time period of about 15 days. This indicates good retention of larvae in the spawning ground area (water depth > 60 m). During the spawning season of Baltic cod, retention leads to a high overlap between predator and prey, which at this time of the year is most likely concentrated in the deep basin area (Figure 2a). The opposite was observed for the early spawning period in 1995, when the spatial overlap was significantly lower than in 1981. The co-efficient rapidly decreased to values below 0.4 within less than one week, which can be related to strong dispersal and high transport of larvae out of the spawning ground caused by strong windforcing.

Analyses of the intra- and interannual variability of the spatial overlap coefficient between initial larval release locations and the final larval drift endpoints, showed large differences if a drift period of 10 days was considered (Figure 6). The coefficient of overlap ranged from 0.29 to 0.87 with the highest variability observed during the

Figure 3. Temperature-dependent average maximum survival duration of non-fed Baltic cod larval.
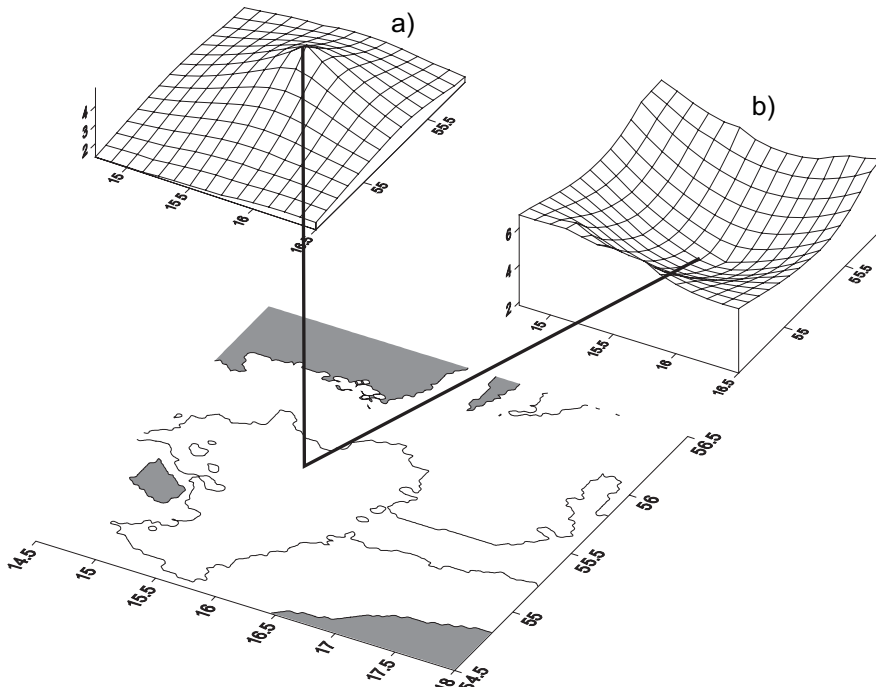
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Figure 4. Horizontal distribution patterns used for the calculation of the coefficients of overlap of (a) maximum abundance in the centre area, and (b) at the margins of the main spawning ground of Baltic cod.

1990s. The lowest value was obtained for autumn 1993, whereas the highest spatial overlap was in late spring 1995. Compared with the early 1980s, spatial overlap was lower from the mid-1980s, especially early and late in the spawning season. Only for the late 1980s and early 1990s, throughout the seasons, anomalously high coefficients of overlap were found. Generally, the overlap coefficient remained at a relatively high level during summer months. The latter is confirmed by seasonally averaged overlap coefficients obtained for the 20-year simulation period, (Figure 7). If a delay of peak prey abundance of 10 days compared with the occurrence of larval cod has been considered, an uniform horizontal distribution of larvae resulted in higher spatial overlap in summer than in spring and autumn. However, on average the overlap during the late spawning period was lowest. Assuming horizontal variability in prey abundance with maximum occurrence either in the centre or at the margins of the basin yielded generally a strong decrease in spatial overlap. However, during the early spawning period, larval growth, survival, and subsequent recruitment benefits from retention. Hence, the best survival rates of larvae could be expected where a uniform horizontal larval distribution dominates. Because high larval prey concentrations usually occur in shallow-water areas only late in the spawning season (third quarter), optimal late spawner survivorship might result during periods of dispersal if larvae originally hatched at the margins of the spawning area.

Recruitment as obtained from MultiSpecies Virtual Population Analyses (MSVPA) runs and the overlap coefficients calculated for the early and late spawning period showed generally declining trends towards the end of the 1990s (r = 0.55, p < 0.015), with extraordinarily high values from 1979 to 1983 (Figure 8). An overestimation of recruitment at age 0 was potentially encountered for 1979 (Köster *et al.*, 2001). Although the potential egg production was lower than in preceding years and the reproductive volume (habitat of successful egg development) of Baltic cod was well below average conditions (MacKenzie *et al.*, 2000),
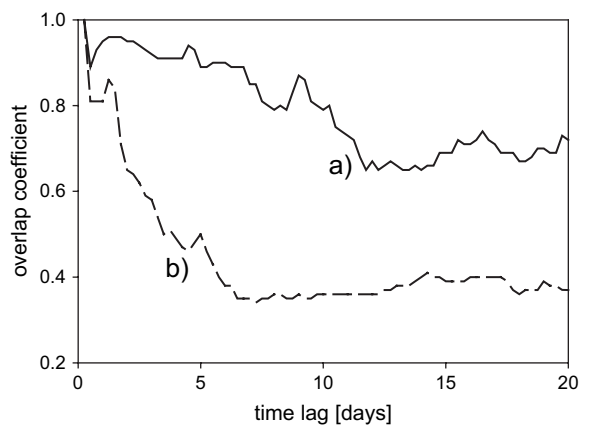

Figure 5. Temporal evolution of the coefficients of spatial overlap (a) May 1981, and (b) May 1995.
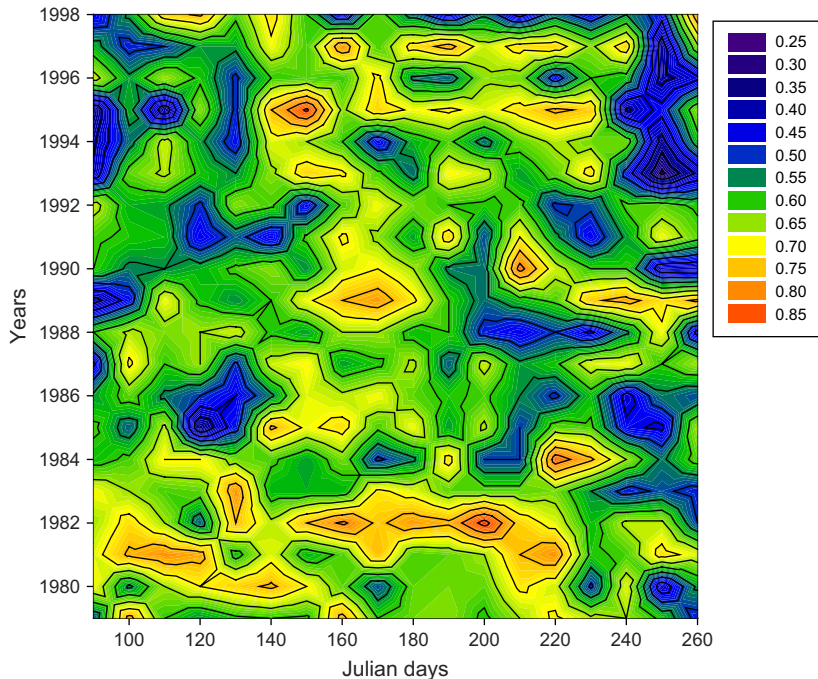
Figure 6. Coefficients of overlap between larval cod and their potential prey (time-lag 10 days).

recruitment at age 0 as determined by MSVPA was highest. 0-group abundance indices from trawl surveys in 1980 were above average but not extraordinarily high (ICES Baltic trawl survey database). Excluding the 1979 data from the model fitting increased the explained variance to 52% (p < 0.001). Accompanied by changes in the timing of spawning of Baltic cod (Wieland *et al.*, 2000), the slight recovery of recruitment at the end of the 1990s might be due to a high spatial overlap between peak abundance of larvae and prey late in the spawning season in shallower and coastal areas of the basin.

Discussion

Hinrichsen *et al.* (2002) utilized a spatially explicit coupled biophysical model to analyse the influence of abiotic and biotic environmental variability on the larval and juvenile survival success of Baltic cod. It turned out that variations of the feeding conditions (temporal and spatial variations of suitable prey availability) had a strong impact on survival of first-feeding larval stages. Their study suggests that food limitation for first-feeding larvae during the last two decades was caused by a pronounced decline of the copepod *P. elongatus*, the main food of larval cod. In the absence of this copepod, larvae hatched only at the outer edges of the Bornholm Basin at the end of the spawning period had good survival probability, because of their short drift distances towards the optimal

feeding environments in more shallow coastal areas. In contrast, larvae hatched within the deep part of the Bornholm Basin required more prey to survive along their drift routes than was available.

In this study, information on temporally and spatially resolved larval drift patterns can be applied in determining larval prey encounter, by coupling transport regimes to temporal and spatial differences of the feeding environment. The model results suggest, for Baltic cod spawning
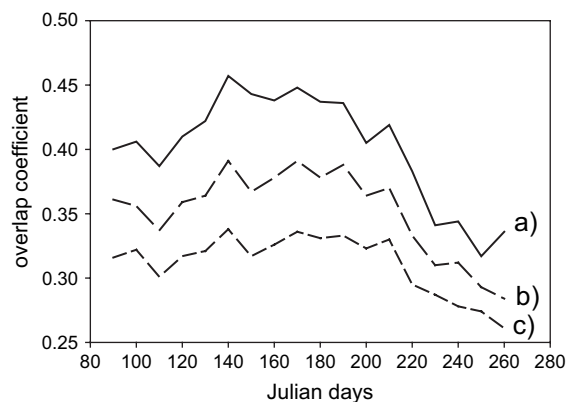

Figure 7. Seasonally averaged coefficients of overlap between larval cod and their prey (time-lag 10 days) (a) uniform even distribution, (b) maximum distribution in the centre, and (c) at the margins of the cod spawning area.
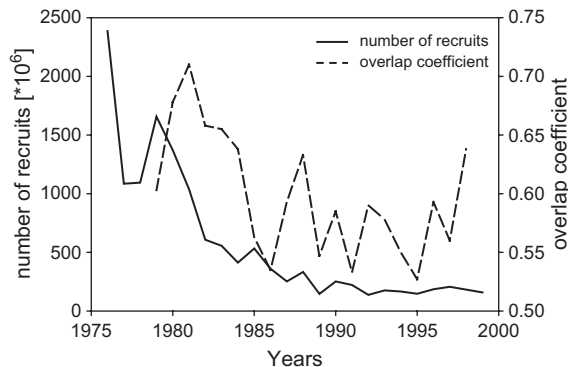
Figure 8. Baltic cod recruitment obtained from MultiSpecies Virtual Population Analysis (solid line) and averaged overlap coefficients after 10 days of larval drift during the early spawning season (dashed line).

seasons during the last 20 years, strong variability in the potential co-occurrence of peak prey and larval abundance, which allowed us to re-address the question of food limitation in larval Baltic cod. Thus, this spatial predator—prey overlap might be considered to be a key process and a candidate parameter for reducing uncertainty in the prediction of recruitment. From numerical simulations it appeared that variation in larval transport and hence in horizontal distribution are mainly controlled by the local atmospheric conditions over the Baltic Sea (Hinrichsen *et al.*, 2001, 2003). We investigated the influence of retention/dispersal of Baltic larval cod in the Bornholm Basin on overlap with their prey, dependent on the time of hatching. High overlap values could be related to periods in which larvae are retained on the spawning ground, so suggesting beneficial feeding conditions with a positive effect on growth, survival, and subsequent recruitment for spring and early summer spawners. Those time periods are characterized by weak windforcing conditions and occur mainly in summer. On the other hand, relatively strong windforcing results in limited spatial overlap and was highest late in the cod spawning season. Thus, larvae hatched within the spawning area are transported to shallower coastal areas and potentially could only contribute to recruitment if they are in contact with good food abundance late in the spawning season.

The coefficients of overlap have been calculated with respect to some simplifications. Detailed information on spatial and temporal variability in availability of larval cod and prey in combination with variation in ambient physical conditions was lacking. Although transport patterns of water layers where post-yolk-sac larvae mainly occur (Grønkjær and Wieland, 1997) are relatively well known (Krauss and Brügge, 1991; Voss *et al.*, 1999; Hinrichsen *et al.*, 2003), validation of the modelling results is difficult. Transport patterns of larvae are influenced by the initial spawning location, assumed here to be an even horizontal

distribution, their initial vertical position in the water column, and their behaviour. These processes and factors were not incorporated in our study. Furthermore, resolving the importance of co-occurrence of larvae and the peak abundance of their prey requires the analysis of growth characteristics of larvae and juveniles over the range of potential prey abundance available to them during the season. Grønkjær *et al.* (1997) clearly identified the importance of prey abundance for the successful growth of larval cod. As obtained from a comparative analysis of simulated coefficients of spatial overlap and observed recruitment, temporal and the corresponding spatial mismatches between predator and prey potentially have an impact on the reproductive success of Baltic cod.

Acknowledgements

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