Modelling the influences of atmospheric forcing conditions on Baltic cod early life stages: distribution and drift

H.-H. Hinrichsen[a,*], U. Böttcher[b], F.W. Köster[a], A. Lehmann[a], M.A. St.John[c]

[a] *Department of Fishery Biology, Institut für Meereskunde an der Universität, Düsternbrooker Weg 20, D-24105 Kiel, Germany*
[b] *Bundesforschungsanstalt für Fischerei, An der Jägerbek 2, D-18069 Rostock, Germany*
[c] *Institut für Hydrobiologie und Fischerei, Olbersweg 24, D-22767 Hamburg, Germany*

Abstract

Retention or dispersion of larvae from the spawning ground has been identified as one of the key processes influencing recruitment success in fish stocks. An exercise combining 3-D hydrodynamic model simulations and field data on spatial distributions of juvenile Baltic cod was utilised to investigate the potential drift of larvae from the centre of main spawning effort in the Bornholm Basin, Baltic Sea. In the simulations cod larvae were represented as Lagrangian drifters. Habitats in which larvae and juvenile cod potentially dwell and where juveniles settle were identified to ascertain the importance of predicting transport. The transport of Baltic cod larvae was investigated by detailed drift model simulations for the years 1986 to 1999. The results yielded a clear dependency on wind-induced drift of larval cod, which is mainly controlled by the local atmospheric conditions over the Baltic Sea. Seasonally averaged distributions of drifters were compared with actual distributions of 0-group cod, as determined from bottom and pelagic trawl surveys conducted in autumn of the years 1993 to 2000 in and around the Bornholm Basin. The results suggest that juveniles caught in different areas can be assigned to different times of the spawning season. Because of seasonal differences in the circulation patterns, the southern coastal environment is on average most important for early and late spawners, whereas larvae hatching in mid-summer were on average transported towards the north or to a higher degree remained in the spawning ground.
© 2003 Elsevier Science B.V. All rights reserved.

Keywords: Baltic Sea index; Hydrodynamic modelling; Juvenile cod; Otolith microstructure analysis; Overlap coefficient

1. Introduction

The Baltic Sea is characterised by specific patterns of horizontal and vertical hydrographic and biological variability which have significant influence on the spatial distribution of species and regional community structure (Arndt, 1989; Remane, 1940). As typical for estuaries, also in the Baltic Sea marine and freshwater organisms are found in a regional succession with different species-specific ranges of distribution. Depending on their specific adaptation and tolerance for hydrographic property levels (e.g. temperature, salinity and oxygen), many species approach the border of their general area of distribution in the Baltic Sea and may thus also show an increased vulnerability and stock size variability related to changes in the environmental conditions.

* Corresponding author.
E-mail address: hhinrichsen@ifm.uni-kiel.de
(H.-H. Hinrichsen).

It is evident that variations in fish stock structure and condition of the adults can affect the level of egg production (Marshall et al., 1998; Marshall and Frank, 1999; Marteinsdottir and Thorarinsson, 1998) and impact egg viability and buoyancy, with the latter influencing the survival probability of eggs and larvae (e.g. Kjesbu et al., 1996; Trippel, 1998; Nissling et al., 1998). Furthermore, the effects of predation on fish eggs and larvae (e.g. Bailey and Houde, 1989; Köster and Schnack, 1994) have the potential to reduce reproduction of a stock. Besides shifts in upper trophic levels of the central Baltic Sea from a cod to a clupeid dominated system, substantial changes in the mesozooplankton community have been described as well (e.g. Vuorinen et al., 1998; Möllmann et al., 2000). Spatial and temporal variability in abundance and species composition of zooplankton affects the food supply for cod larvae and pelagic juveniles (MacKenzie et al., 1996; Hinrichsen et al., 2002). Thus, the loss of eggs and larvae due to transport to sub-optimal feeding environments (e.g. Sinclair, 1988; Heath and Gallego, 1998) can influence recruitment success.

The Baltic Sea physical environment shows substantial seasonal and short-term fluctuations as well as pronounced long-term trends, depending on changes in the pattern of inflow conditions of highly saline and oxygenated water from the North Sea with only so-called major inflows penetrating far enough into the central Baltic to improve the oxygen conditions in the deep basins (Matthäus and Franck, 1992). As apparent from the 1980s, exceptionally long periods of stagnation are possible.

Within the deep water and bottom layers (>60 m) oxygen depletion has often been observed. Within the halocline (depths between 40 and 60 m) well-oxygenated water is normally found, resulting in good environmental conditions. In shallower depths, upwelling influences the nutrient distribution and may lead to enhanced primary and secondary production.

Cod in the eastern Baltic is genetically and morphometrically well separated from the cod stock in the western Baltic (Bagge et al., 1995) and has even been considered a subspecies (*Gadus morhua*). The success of cod reproduction in the eastern Baltic is restricted to the deep basins (Gotland Basin, Gdansk Deep, and Bornholm Basin), as a minimum salinity of 11 psu is

required for fertilisation of eggs and attaining neutral buoyancy (Westin and Nissling, 1991). The vertical distribution of cod eggs is thus confined to depths within and below the halocline (Wieland and Jarre-Teichmann, 1997). Since the mid-1980s successful spawning has been possible only in the Bornholm Basin, and the depth range with at least minimum conditions for egg development (salinity >11 psu, oxygen content >2 ml/l) showed a generally declining trend down to a minimum in 1989 (MacKenzie et al., 2000). Hatching occurs 17-22 days after spawning, depending on water temperature (Thompson and Riley, 1981; Wieland et al., 1994). Ten days after hatching, larvae start to undertake dial vertical migrations. After five days, first feeding larvae perform an active feeding migration through the halocline (Grønkjær and Wieland, 1997) into the low-saline surface layers, with peak abundance below the thermocline between 20 and 40 m depth. This initial vertical migration is a prerequisite for larval survival (Grønkjær et al., 1997), because only upper water layers have enough suitable prey and light conditions to allow successful foraging. Metamorphosis occurs at 12 mm length after about 25–50 days depending on the larval growth rate (Grønkjær et al., 1997). The transition from pelagic to demersal life stages usually occurs around a length of 4-6 cm (Hüssy et al., 1997; Oeberst and Böttcher, 1998). Until reaching the demersal life stage, the different pelagic early life stages (eggs, larvae and juveniles) are susceptible to drift within different depths for approximately 3 to 4 months.

The retention in or dispersion from the main spawning ground (Bornholm Basin) may be one of the key processes influencing recruitment success of the eastern Baltic cod stock (Hinrichsen et al., 1997, 2001a). Production in the central basin appears to be nutrient limited with relatively low prey availability resulting in low growth and potentially limited survival of cod (Kiørboe, 1991; St.John and Lund, 1996). In contrast, the shallow coastal regions of the Baltic Sea have been identified as regions of high primary and secondary production due to the introduction of nutrients by upwelling in combination with terrestrial (e.g. river runoff) and benthic input (Haapala, 1994). Hence, the rapid transport of cod larvae to the shallow coastal regions potentially results in increased feeding success, growth and survival relative to individuals

retained in the central basins of the Baltic Sea. The transport of Baltic cod larvae is primarily determined by wind stress (Voss et al., 1999). Wind stress acting at the sea surface results in Ekman transport to the right of the wind in surface layers, with coastal jets produced in the direction of the wind along both coasts of the basin. The Ekman dynamics and flow are compensated by a mainly topographically steered return flow in the central interior of the basin (Krauß and Brügge, 1991; Lehmann et al., 2002), which is generally opposite in direction to the prevailing winds.

The primary aim of this study is to examine the influence of physical factors on the spatial distribution of early life stages of Baltic cod. In order to better understand the effects of physical forcing on the distribution of early life stages of cod, physical modelling activities have been focussed on the description of the circulation of the Baltic Sea and its influence on the seasonal and the inter-annual distribution and transport of larvae originating in the Bornholm Basin (the centre of the stock's spawning activity). Three-dimensional models have reached a sufficient state of accuracy that a coherent picture of the circulation of the entire Baltic Sea and its varia-bilities can be presented (Lehmann et al., 2002). Two-layer hydrodynamic diagnostic models (box models) and prognostic models (two-dimensional hydrody-namic-ecosystem models) were used and tested for cod eggs and larval drift simulation studies in the 1980s and early 1990s with varying degrees of success (e.g. Aro et al., 1992). Utilising the present 3-D hydrodynamic model (Lehmann, 1995), simu-lated meso-scale distribution patterns of larval cod for two specific years were validated by field-based data (Voss et al., 1999). In order to investigate the drift of fish eggs and larvae in the Baltic Sea with respect to variable atmospheric forcing conditions, Hinrichsen et al. (2001a) developed a transport index which allows the identification of changes in transport regime within and between spawning seasons. This index was based on drift scenarios calculated with the same hydrodynamic model of the Baltic Sea as has also been utilised to clarify the potential mixing of early life stages between the western and eastern Baltic cod stocks (Hinrichsen et al., 2001b). In order to consider the relative effects of advective and trophodynamic processes on growth and survival of larval cod,

Hinrichsen et al. (2002) developed a spatially-explicit coupled biophysical model on drift and feeding of larval Baltic cod. It combines a three-dimensional circulation model, and a bioenergetically-based indi-vidual model which tracks larval stages through space and time.

The present study uses a coefficient of overlap (Horn, 1966) to obtain information on the probability of occurrence of larval cod within specified subareas of the Central Baltic Sea, thus indicating under what feeding conditions larvae and juvenile cod potentially dwell. This overlap coefficient has been utilised ear-lier to compare final distributions of simulated particle drifts with observed distributions of juvenile sandeels in the North Sea (Proctor et al., 1998). Moreover, usage of this coefficient allows identification of the environment in which larvae and juveniles change from pelagic to demersal habitat. Results of these investigations have been compared with age-depend-ent horizontal 0-group cod distributions within their potential nursery areas obtained from pelagic and demersal trawl surveys.

2. Material and methods

2.1. Baltic Sea model and Baltic Sea index

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; Semt-ner, 1974; Cox, 1984). A detailed description of the equations and modifications required 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 simu-lated 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 Gulf of Bothnia, Gulf of Finland, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km, with 41 vertical

levels specified. The thickness of the different levels was chosen to best account for the different sill depths in the Baltic. Several observations of eddy-like structures in the Baltic revealed a typical length scale of mesoscale features of about 25–60 km (Aitsam and Elken, 1982; Cooperative Research Report, 1989). The internal Rossby radius in the Baltic, which was determined to be 2–10 km (Fennel, 1991), showed a strong seasonal and regional dependence. For model purposes, a high horizontal resolution in the order of half the internal Rossby Radius (at least in the order of the Rossby Radius) is required to resolve the whole spectrum of mesoscale motions. To find a compromise between available computer resources and the resolution in space and time, a grid size of 5 km was chosen. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergström and Carlsson, 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of $1° × 1°$ 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 6-h intervals) to develop a data base for a Lagrangian particle tracking exercise on 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. Furthermore, the data contain information on the temporal evolution of the hydrographic property fields (temperature, salinity, oxygen, etc.) along the trajectories.

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 independent of the vertical resolution of the model's grid. Simulated drift routes were obtained from Eulerian flow fields by utilisation of a Lagrangian particle-tracking technique. The three-dimensional trajectories

of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen et al., 1997).

First, the hydrodynamic model on Baltic cod larval drift was utilised for the time period 1986 to 1999 to obtain means of inter-annual variability in distribution and transport patterns. In order to consider its seasonal variability in relation to spatial and temporal variations in larval transports, a total of 720 Lagrangian drifters were released at depth between 25 and 35 m (depths at which feeding larvae occur after vertical feeding migration) on a regular spaced grid enclosed by the 60 m isobath encompassing the main spawning area of the Bornholm Basin (Fig. 1—release areas: I, II, III and IV with depths between 60 and 80 m and release area V deeper than 80 m). Drifters, at their release representing first feeding larvae, were inserted into the modelled flow fields at 10-d intervals and tracked for 45 d. No correlation for a seasonal increase in water temperature resulting in shorter developmental times was introduced, because feeding larvae experience a rather stable temperature below the developing thermocline and above the halocline. The release dates ranged from 1 April to 20 September, thereby encompassing the historical as well as the present main spawning period of eastern Baltic cod (Wieland et al., 2000).
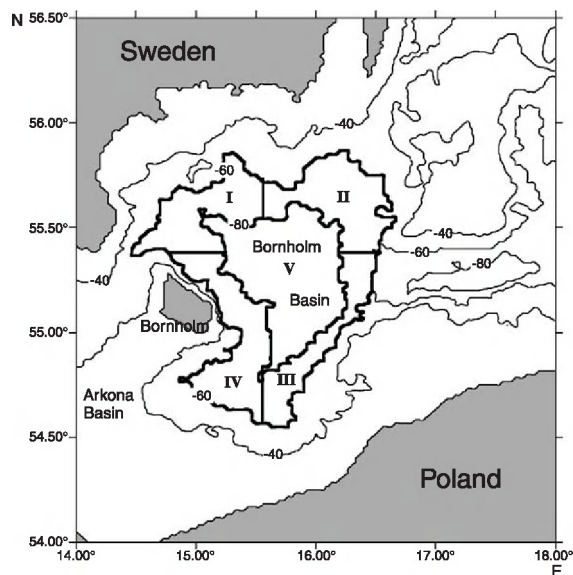

Fig. 1. Map of the Bornholm Basin. Thick lines represent subareas of Baltic cod spawning ground (see Table 1).

To determine how many larvae were present in which subarea of the central Baltic Sea during their 45-d drift and where pelagic life stages potentially settle, a normalised time-integrated version of the coefficient of overlap C (Horn, 1966) was applied, which is 0 when there is no overlap and 1 when the two distributions are identical. This was calculated from:

$$C(t) = (1/t) \sum_{t=0}^{t=45} 2*A*B/(A^2 + B^2)$$

where A at any time t gives the number of larvae initially released at depths >60 m, and B gives the actual number of larvae in any of the subareas into which larvae could be transported. Time-integrated values at any given time are a measure of residence probability of the number of larvae within specified subareas (see Table 1).

To obtain a general impression of meteorological impacts on larval transport, we related the relative residence probabilities within the above-mentioned specific environmental subareas of the Baltic to atmospheric conditions. Relevant to the atmospheric forcing are the local conditions over the Baltic Sea embedded in the large-scale atmospheric patterns. With respect to local forces, Lehmann et al. (2002) defined a Baltic Sea index, which is the difference of normalised sea level pressure anomalies between Oslo (Norway) and Szczecin (Poland). To account for the local atmospheric conditions in the area under consideration (Bornholm Basin) we calculated the normalised sea level pressure difference along a line at 15°E from 57° 30′ N to 52° 30′ N representing the u-component of the wind (hereafter BSI_u), whereas the sea level pressure

gradient at 55°N between 12° 30′ E and 17° 30′ E is a measure of the v-component (hereafter BSI_v). Daily mean sea level pressures at each position obtained from NCEP/NCAR re-analysis data (Kalnay et al., 1996) are normalised by dividing them by the long-term mean (1948–1999) standard deviation. For example, a positive BSI_u corresponds to an anomalous sea level pressure difference associated with westerly winds over the Bornholm Basin, in near-surface layers leading to transport towards the east. In contrast, a negative BSI_u corresponds to easterly winds, favouring currents towards the west near the sea surface. BSI_u values have been calculated and subsequently averaged for each of the 45-d drift simulations.

2.2. Age determination of 0-group

2.2.1. Otolith analysis

During this study, the birth dates of the 0-group cod caught in the different nursery areas were determined by microstructure analysis of sagittal otoliths. The juveniles were sampled during 6 trawl surveys in the Bornholm Basin carried out in September and October 1993 to 1996, using pelagic or demersal trawls. Unfortunately, the horizontal 0-group distributions within the potential nursery areas were not surveyed systematically on a standard station grid during the autumn cruises. Thus, the goal to simulate the drift patterns of larvae and juveniles for each of the years explicitly was not attained. Instead, to identify the principal factors influencing the transport of early life stages of cod spawned in the Bornholm Basin, we have utilised pooled data (1993–1996) for comparison with the seasonal averaged drift patterns.

Table 1
Correlation coefficients between BSI_u and overlap coefficient (45 days) derived for different areas; larvae released in different subareas (see Fig. 1) of the Bornholm Basin

Release area		Potential settling areas after 45 days drift						
Code	Depth	>60 m	40–60 m S	40–60 m N	<40 m S	<40 m N	<14E	>18E
I–V	>60 m	− 0.48*	− 0.59*	0.65*	− 0.54*	0.68*	0.77*	− 0.25
V	>80 m	0.04	− 0.62*	0.83*	− 0.48*	0.85*	0.00	− 0.06
I–IV	<80 m	− 0.53*	− 0.43	0.60*	− 0.50*	0.73*	0.05	− 0.15
IV	<80 m SW	− 0.56*	− 0.06	0.58*	0.13	0.69*	0.54*	0.05
III	<80 m SE	0.63*	− 0.77*	0.77*	− 0.69*	0.75*	− 0.64*	− 0.07
II	<80 m NE	− 0.08	− 0.81*	0.72*	− 0.79*	0.62*	0.10	− 0.25
I	<80 m NW	− 0.74*	0.27	0.23	0.28	0.53*	0.24	− 0.02

* Statistically significant at 95% level.

In the laboratory, the meristic parameters of the fish were determined and the otoliths removed. Microstructure analyses were carried out on a subsample of sagittal otoliths from juveniles from 2 to 18 cm in total length. Readings of the daily increments were performed on transverse sections of the otoliths at a video monitor, where the structure was clear, and directly at a microscope if the structure was unclear.

The first 10 to 20 increments following the hatch check were very thin and, for lack of contrast, could often not be determined clearly. Furthermore, counting of the 5 to 15 increments closest to the accessory growth centre (AGC) was difficult due to substructures, whereas the numbering of the secondary increments, which started after the AGC, presented no problems. The formation of the AGC was found from 42 to 56 increments (mean = 49.3) after the hatchcheck

taken from a subsample of well-prepared otoliths (n = 18). Similar investigations from 18 juvenile cod with known age (48 d) showed that the development of the AGC started 41 to 43 d after hatch. Using these data, together with the results of the former analyses, gave an assumed mean value of 45 d from the hatch check to the beginning of the secondary increments. A detailed description of otolith microstructure analyses can be found in Oeberst and Böttcher (1998).

For estimation of the birth dates the following equation was used:

$$\text{Birth date} = \text{Catch date} - C1 - C2 - NDI$$

where C1 is the mean number of days for the development of the egg stages, C2 is the mean number of days between the hatch check and the beginning of the
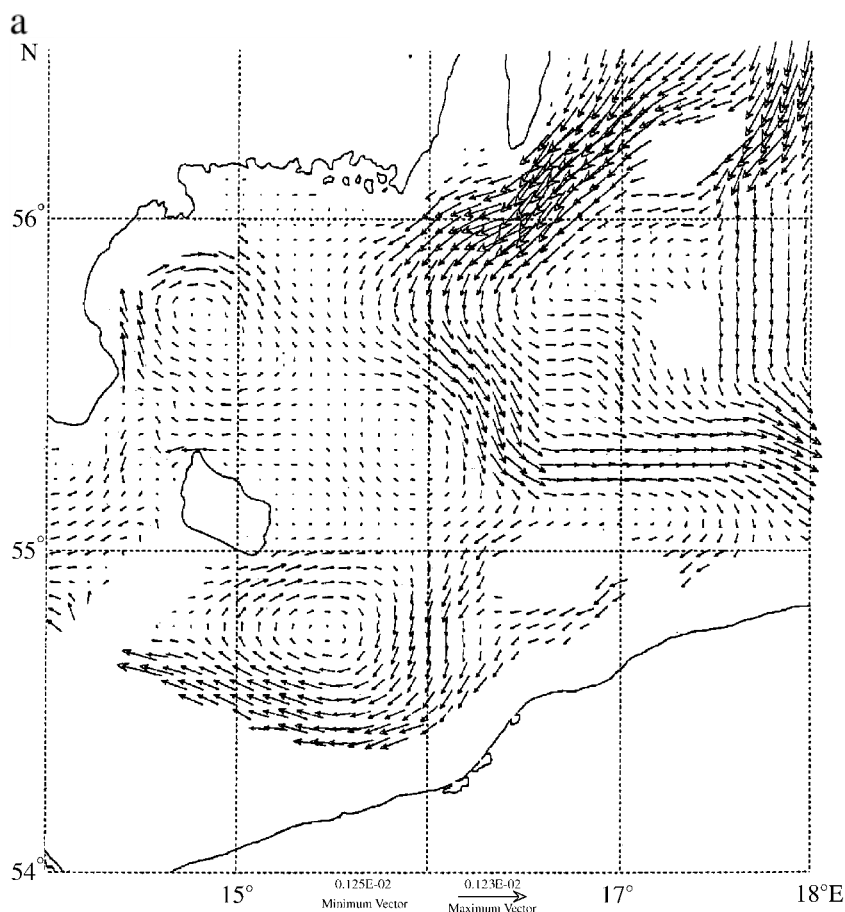

Fig. 2. Monthly means of the vertically averaged flow between 30 and 40 m a) July 1991 and b) September 1995.
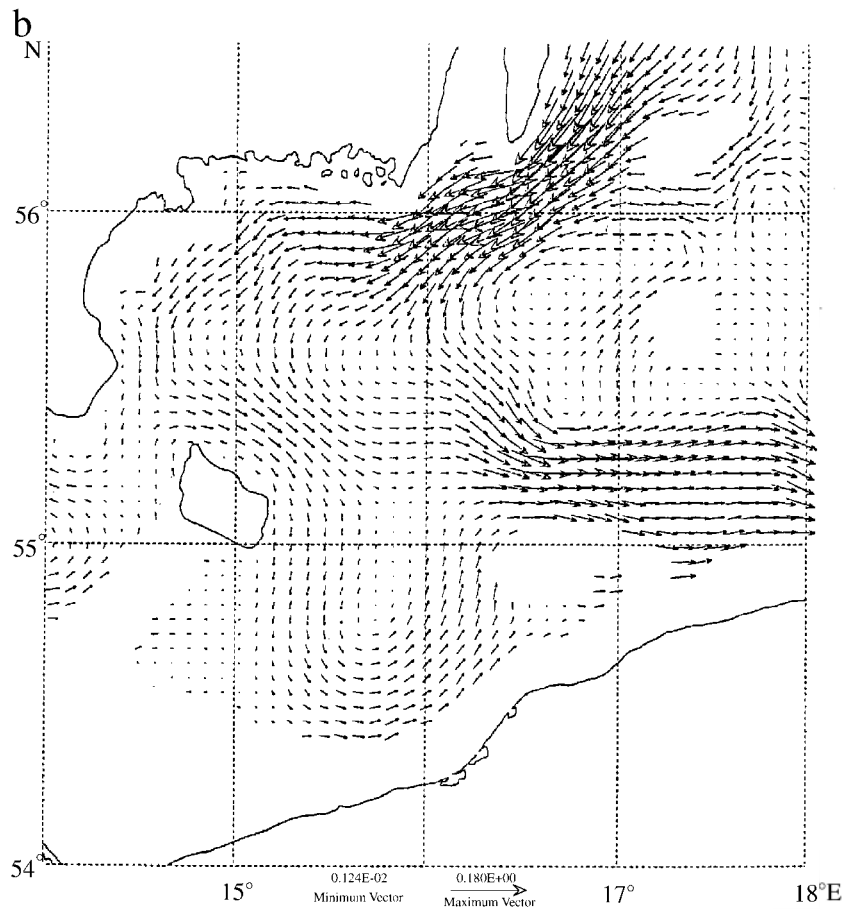
Fig. 2 (*continued*).

secondary increments and NDI is the number of secondary increments.

As described, a mean value of 45 d was used for C2, whereas for C1 a constant value of 20 d was taken. This value was derived from the observed temperature regime in the Baltic Sea and from the analysis by Thompson and Riley (1981). Their results agree with the investigations of Wieland et al. (1994) and with observations of naturally spawned eggs from Baltic cod held in a marine hatchery (Bleil, Bundesforschungsanstalt für Fischerei, Rostock, Germany, pers. comm., 2001).

The 0-group cod caught in autumn in the Bornholm Basin can be divided into two major size classes (Hinrichsen et al., 2001b). The length groups of cod between 3–7 cm and 8–14 cm caught within the Bornholm Basin during the autumn were traced back to spawning activities in July to August and April to May, respectively.

2.2.2. Use of published age/length keys

The birth dates of pelagic 0-group cod caught in the different nursery areas were obtained from an age/length relationship (Oeberst and Böttcher, 1998) with a high coefficient of determination ($r^2 = 0.61$):

$$Age = 52.48 + 9.18*TL$$

with TL the total length.

The juveniles were sampled during 4 trawl surveys in the Bornholm Basin carried out in October/November 1996, 1997, 1998 and 2000 using an Isaacs-Kidd-Midwater-Trawl (IKMT).

3. Results

Before describing individual or mean larval drift, it is useful to describe the general transport patterns of larval cod in the Bornholm Basin chosen to illustrate the typical behaviour of the drifter trajectories.

Monthly means of the vertically averaged flow between 30–40 m obtained from simulations performed for July 1991 (Fig. 2a) indicate a transport of larvae from the northern part of the main spawning area to the north-west Swedish coastal area, whereas larvae located in the southern part remained within an anticyclonic eddy-like feature. In general, transport of larvae towards the northern coastal region is due to return flows in the interior of the basin, compensating for the direct wind-driven circulation caused by wind from the south and west (Krauß and Brügge, 1991). In contrast, intense easterly winds observed during the late spawning season in 1995 resulted in a transport of a relatively large fraction of larvae towards the southern coastal environment (Fig. 2b).

3.1. Seasonal variability in transport

First results of the residence probability of larvae focussed on the analysis of the general seasonal variability of larval drift. In the model runs, we addressed the question to which area larvae were most likely to be transported. Fig. 3 displays averaged seasonal overlap coefficients within the different specific subareas of the Baltic covering the spawning period of Baltic cod for the whole observational period (1986–1999). The highest coefficients after 45 d of simulation resulted for the initial spawning ground (>60 m; Fig. 3a). This pattern appears to be relatively stable and constant in time; only at the end of the spawning period was a slightly higher transport rate out of the spawning ground indicated. By the beginning of the spawning season, considerable amounts of larvae were evident within the southern environment (<60 m; Fig. 3b). Occurrence in this area decreased with time showing a potential minimum level of overlap during mid summer. At the end of the spawning season larval transport towards the south was again more likely. Conditions in the northern part of the Bornholm Basin were quite the opposite (Fig. 3c). Small fractions of larvae found at the beginning of the spawning period were followed
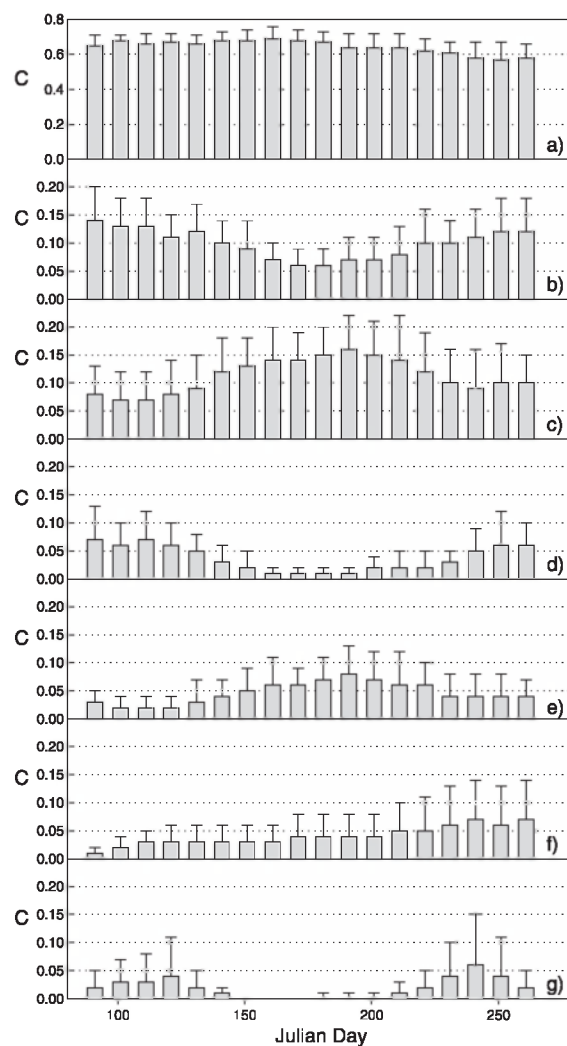

Fig. 3. Averaged seasonal residence probability of larval cod in different subareas of the Central Baltic expressed by overlap coefficients (1986–1999); a) depths >60 m, b) depths 40–60 m south, c) depths 40–60 m north, d) <40 m depths south, e) depths <40 m north, f) west of 14°E, and g) east of 18°E; bars showing mean values and solid lines its standard deviations.

by a strong increase during mid-summer. Late-season larvae were less likely to be transported towards the northern shallow areas. In contrast, larval transport from the spawning ground in the Bornholm Basin to adjacent basins (the Arkona Basin to the west; Fig. 3f, the Gdansk Deep and the Gotland Basin to the east; Fig. 3g) was generally low. Drift towards the east shows a clear time-dependent pattern, with most

larvae being transported away from the initial spawning ground at the beginning and at the end of the spawning activity. Generally, transport patterns into the areas between 40 and 60 m are fairly stable. Transport towards the coastal environments (<40 m) follows a pattern similar to that of the intermediate depth range, but is less probable and stable.

3.2. Coupling of transport to atmospheric conditions

The overall changes in residence probability of larval cod within the different subareas of the central Baltic (Fig. 3) are connected with local atmospheric forcing conditions for larval drift. To demonstrate this, linear regression analysis between the time-integrated overlap coefficients for these different subareas and the averaged BSI_u values was performed. Table 1 summarises the results of this analysis (see also Fig. 1—release areas I to V). Below the wind-induced Ekman layer, highest transport rates towards the southern shallower water regimes are related to low BSI_u values (easterly winds), whereby destinations of larvae initially released within the more eastern part of the deep Bornholm Basin show strongest correlations. In contrast, transport towards the north is mainly caused by westerly wind (high BSI_u). For these nursery areas the analysis revealed strong linear regressions which are statistically significant at the 95% confidence level, except for larvae initially inserted in the northwest of the Bornholm Basin. Correlations of larval transport towards the adjacent basins vary strongly. Similarly, the fraction of larvae which finally remained in the spawning ground (>60 m) after 45 d of drift was not related to changes of the local atmospheric forcing conditions over the Baltic.

A corresponding analysis utilising the v-component (BSI_v) of sea level pressure anomalies yielded no statistically significant correlations. Nor did multi-linear regression analyses considering both components (BSI_u and BSI_v) improve the explained variance of overlap coefficients.

3.3. Inter-annual variability of distribution and drift

We next simulated the inter-annual variability of cod larvae drift originating from peak spawning times of years 1986–1999 (Wieland et al., 2000). During the late 1980s, peak spawning, defined as dates of

maximum egg abundance obtained by successive ichthyoplankton surveys, took place between early May and mid-June. A remarkable shift in the timing of peak spawning to July/August occurred in the early 1990s (Wieland et al., 2000).

Because the mean pressure gradient between Oslo and Szeczin, controlling wind speed and direction over the Central Baltic, shows a strong seasonal variability (Lehmann and Hinrichsen, 2001), local atmospheric conditions might have an impact on larval drift. From 1986 to the early 1990s the averaged BSI_u values right after peak spawning time remained on an almost constant level (Fig. 4). Since peak spawning shifted towards later periods in summer, the anomaly of the sea level pressure gradient has varied strongly, with extremely low values observed in 1995 and in 1996. Higher than average values were recorded in 1997 and 1999, implying influence of stronger westerly wind forcing. Fig. 5 displays the overlap coefficients for the different subareas of the Bornholm Basin for larval transport originating from peak spawning times. Drift towards the northern coastal environment was evident for the first half of the time series. Later spawning in 1995 and 1996 (July) resulted in higher transport to the south. The potential for the existence of larval cod within the most shallow area (<40 m) was relatively low. Southward-oriented transport of larvae is a more pronounced pattern since the mid-1990s, caused by wind events of easterly directions. Transport towards the Arkona Basin was extremely high at the end of the time series, whereas drift in eastern directions was generally negligible. Only for 1995 and 1996, did a significant number of larvae have the potential for transport towards the east. Generally, the potential for cod larval transport out of the spawning area is relatively low. The cumulative overlap coefficient between the number of initially released simulated larval drifters and the number of larvae retained within
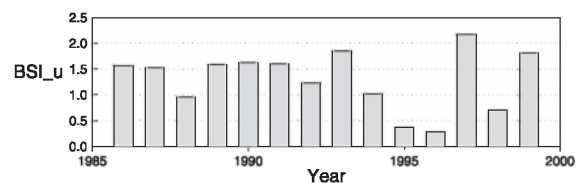

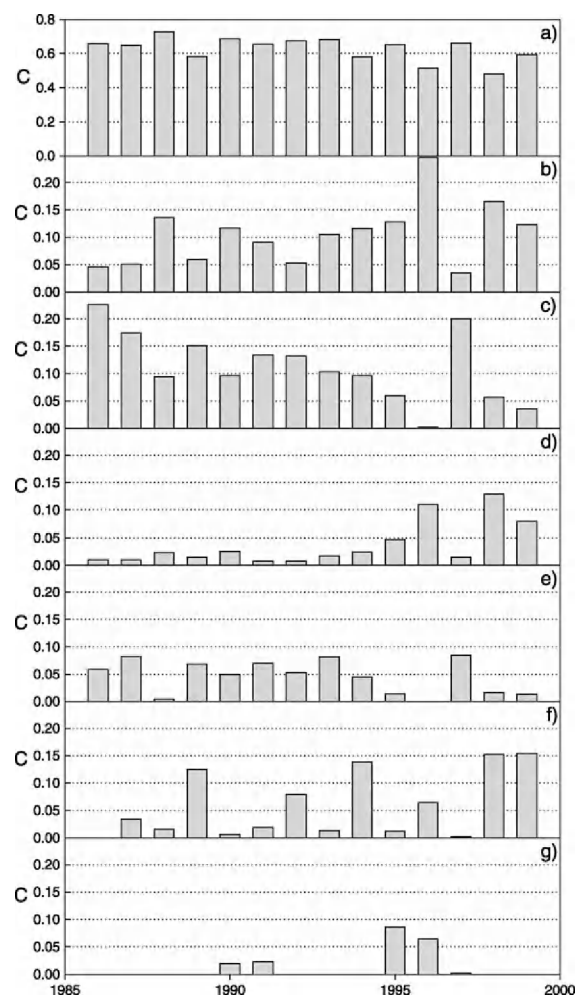Fig. 4. BSI_u values averaged over 45 days after peak spawning (1986–1999).

Fig. 5. Occurrence of larval cod in different subareas of the Bornholm Basin after peak spawning expressed by overlap coefficients (1986–1999) a) depths >60 m, b) depths 40–60 m south, c) depths 40–60 m north, d) <40 m depths south, e) depths <40 m north, f) west of 14°E, and g) east of 18°E.

the deep part of the Bornholm Basin is on average higher than 0.6.

3.4. Comparison between simulated residence probability of larval cod and observed distribution of 0-group cod

In the present analysis, the distribution of simulated larval or 0-group cod locations is partly consistent with the observed distribution of 0-group cod. Only low numbers of 0-group cod were caught by

bottom trawls within the northern coastal environment and in the deep Bornholm Basin (Fig. 6a, c). For these patterns no specific time trend could be identified. Peaks in abundance of 0-group cod encountered in this southern region from the beginning and the end of the spawning actually confirmed the pattern obtained by our numerical simulations. Highest concentrations of juveniles were mainly found in the southern coastal area (Fig. 6b). This temporally resolved pattern is in good agreement with the simulated distributions (Fig. 3), predicting that by the beginning and end of the spawning season, relatively high numbers of simulated larval drifters were transported to the southern coastal environment (Fig. 3b, d). On the other hand, the potential appearance at the northern coast of larvae hatched in summer (Fig. 3c, e) was predicted, but could not be validated by the field data.

Pelagic 0-group cod caught by IKMT hauls partly confirmed the pattern as obtained for demersal juveniles. Juveniles spawned in August were mainly caught south to the island of Bornholm (Fig. 7), whereas juveniles spawned in July were only found in low numbers in the trawls independent of the location. This is because at the date of catch (October/November) early spawned cod had already changed from pelagic to demersal habitat. The observed distribution pattern corresponds only to juvenile cod caught within the

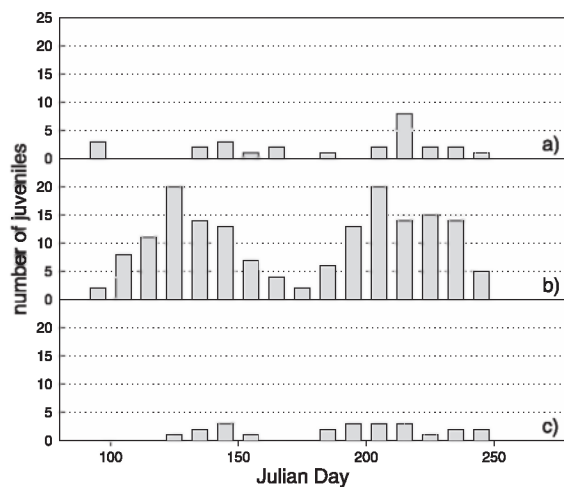

Fig. 6. Demersal 0-group cod caught in different areas of the Bornholm Basin according to birthdates (1993–1996), a) depths <40 m north, b) depths <40 m south, and c) depths >40 m deep basin.
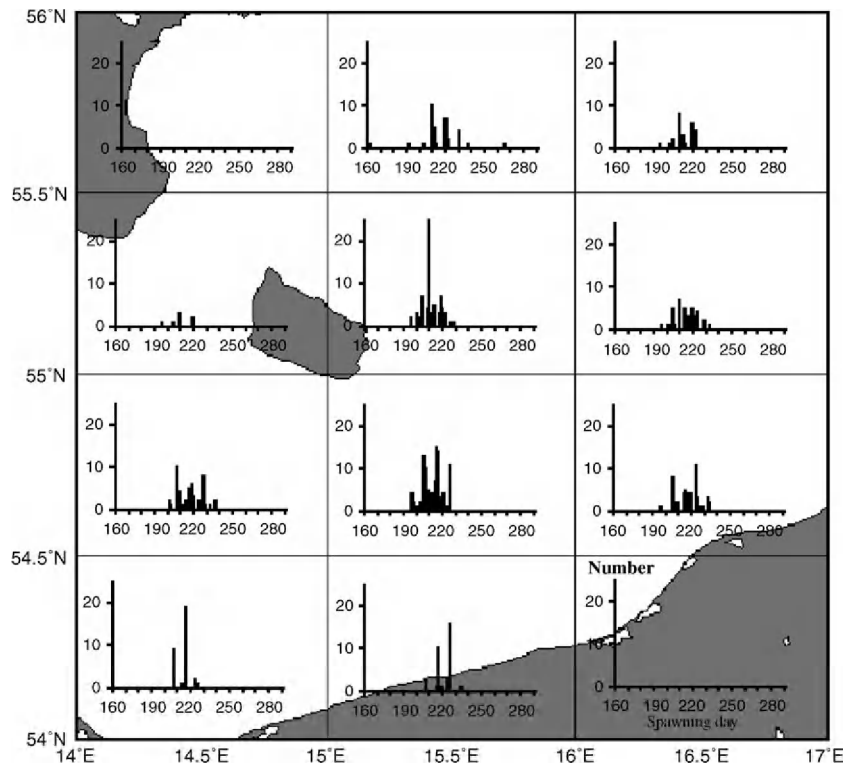
Fig. 7. Age distribution of pelagic 0-group cod per rectangle.

time period of the second peak in abundance (late spawning) of demersal cod (Fig. 6).

4. Discussion

Recruitment of Baltic cod critically depends on egg survival (Köster et al., 2001). Oxygen concentration at dwelling depths and to a lesser extent predation by clupeids are important factors affecting egg mortality rates. Egg survival and larval abundance are hardly correlated in cod, but larval abundance is significantly related to year-class strength (Köster et al., 2001). This indicates that either hatching or the early larval stage, or both, are critical periods for cod recruitment.

In the present study, the transport of eastern Baltic cod larvae spawned within the only presently important spawning ground, the Bornholm Basin, was investigated by detailed drift model simulations for the years 1986 to 1999. In order to investigate in which habitats larvae and juvenile cod potentially dwell and

where larvae and juvenile might change from pelagic to demersal habitat, a coefficient of overlap (Horn, 1966) was utilised instead of simply counting the number of larval destinations within the different subareas of the Bornholm Basin. The relative spatial distributions of larval cod drift endpoints only provide snapshots for single days. In contrast, the utilisation of an overlap coefficient revealed an integrative view indicating the probability of occurrence within the different subareas. The results of these exercises on particles initially released within this spawning ground yielded a clear dependency on wind-induced drift of larval cod, which is mainly controlled by the local atmospheric conditions over the Baltic Sea.

Averaged seasonally simulated distributions were compared with field observations. The results suggest that juveniles caught during autumn trawl surveys in different areas of the Bornholm Basin can be assigned to different times of the spawning season. The observed patterns are very similar to our simulations, suggesting that numerical experiments on cod larval

drift can explain broad trends in 0-group distributions of cod in and around the Bornholm Basin. Because of seasonal differences in the circulation patterns, the southern coastal environment is on average the most important for early and late spawners, whereas larvae hatched in mid-summer were on average transported towards the north or to a higher degree remained in the spawning area. Observed lower abundance of settled juveniles within the deep basin area might be explained by non-optimal feeding conditions.

The suitability of our hydrodynamic model of the Baltic Sea for predicting the circulation and consequently the transport of larval cod in the Bornholm Basin is clearly demonstrated in this coupled field and modelling exercise. Occurrence of larvae within the different subareas of the central Baltic can be explained by strong coupling with local atmospheric forcing conditions. When subdivided into more specific regions, these relationships partly became relatively weak, especially in the more western subareas of the Bornholm Basin. Here, larval transport might be influenced significantly by other processes (e.g. inflows from the west, complex bottom topography). However, the predictive power of larval drift patterns can be regarded as relatively high, because areas of the Bornholm Basin for which intense spawning activity has been observed (see Table 1; area II, III and V) are highly correlated with atmospheric forcing (BSI$_u$).

Cod reproduction is dependent on certain minimum levels of salinity and oxygen concentration for egg fertilisation and survival (Nissling and Westin, 1991). These conditions are met exclusively within the 60 m isobath (Wieland et al., 1994). Retention and dispersion from the main spawning area have been identified as key processes influencing recruitment success of the eastern Baltic cod stock (Voss et al., 1999; Hinrichsen et al., 2001a). Hinrichsen et al. (2002) utilised 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 feeding component of larval cod. By the absence of this copepod, only

larvae hatched on the outer edges of the Bornholm Basin at the end of the spawning period had higher 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 too much prey for survival along their drift routes in less favourable feeding conditions. Thus, enhanced larval survival success may either occur during periods of peak prey abundance or must be related to the occurrence of favourable environmental processes such as transport into optimal feeding environments (Hinrichsen et al., 2002), optimal turbulent conditions (MacKenzie et al., 1994), or low ambient temperatures (Otterlei et al., 1999) reducing the daily rations of food necessary for covering the standard metabolism.

Larval transport is dependent on the temporal and spatial distributions of late egg or early larval stages in conjunction with the timing of spawning activity. At present, although dependent on actual food availability, only larvae survive if hatched in areas from where rapid drift into optimal feeding environments is possible (Hinrichsen et al., 2002). The mean distribution of youngest egg stage IA (Wieland et al., 1994) during mean spawning periods 1994 to 1996 is presented in
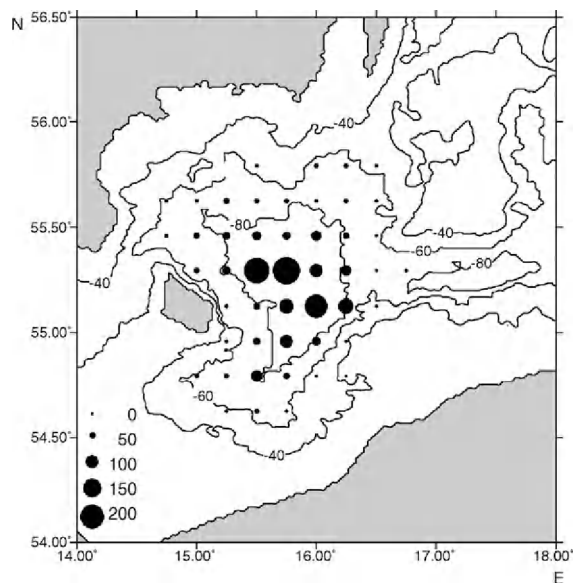

Fig. 8. Mean spatial egg distribution (number of eggs stage Ia) in the Bornholm Basin during main spawning time 1994–1996.

Fig. 8. Sampling of cod eggs was carried during ichthyoplankton surveys by utilisation of a Bongo net (60 cm diameter) with mesh sizes of 0.3 and 0.5 mm. Main spawning effort has been observed within the centre of the Bornholm Basin suggesting a subsequent mismatch between larval appearance and food availability for first-feeding larvae.

The present study suggests the applicability of hydrodynamic models to assess temporal and spatial egg and larvae distributions in the Bornholm Basin. The modelling approach showed that the influence of different wind conditions on the larval distribution patterns was high. For larvae, found mainly in the upper layers, significant advective losses from the spawning ground may occur depending on the wind forcing (Voss et al., 2001; Voss and Hinrichsen, 2002). Thus, the results suggest that in particular historical fish larval abundance estimates have to be assessed with caution.

In general, the information on temporally and spatially resolved larval drift patterns obtained here can be employed in short and medium stock projections by coupling transport regimes to feeding environments and habitat quality of nursery areas. The modelling exercise has clearly demonstrated that traditional sampling methodology is unable to identify potential habitats of cod early life stages without considering flow dynamics and the impact of physical forcing conditions. Thus, besides the incorporation of stock structure data (e.g. maturity ogives, age and sex diversity) as well as information on environmental variability (e.g. reproduction volume) into stock-recruitment models, it is of interest whether the predictive power of a process-oriented recruitment model for Baltic cod may benefit from simplified but 'online' accessible physical forcing parameters (e.g. Baltic Sea index).

Acknowledgements

References

Aitsam, A., Elken, J., 1982. Synoptic scale variability of hydrophysical fields in the Baltic proper on the basis of CTD measurements. In: Nihoul, J.C.C. (Ed.), Hydrodynamics of Semi-enclosed Seas. Elsevier, Amsterdam, pp. 433–468.

Arndt, E.A., 1989. Ecological, physiological, and historical aspects of brackish water fauna distribution. In: Ryland, S., Tyler, A. (Eds.), Reproduction, Genetics and Distribution of Marine Organisms. Olsen & Olsen, Fredensborg, pp. 327–338.

Aro, E., Myrberg, K., Bagge, O., Bay, J., 1992. Estimation of Baltic cod eggs and larvae drift in the Southern Baltic in July–August 1991 by a two-layer, two-dimensional linear flow model: sensitivity tests and verification of the model. ICES C.M. 1992/J, 5.

Bagge, O., Thurow, F., Steffensen, E., Bray, J., 1995. The Baltic cod. Dana 10, 1–28.

Bailey, K.M., Houde, E.D., 1989. Predation on early developmental stages of marine fishes and the recruitment problem. Adv. Mar. Biol. 25, 1–83.

Bergström, S., Carlsson, B., 1994. River runoff to the Baltic Sea: 1950–1990. Ambio 23, 280–287.

Bryan, K., 1969. A numerical method for the study of the circulation of the world ocean. J. Phys. Oceanogr. 15, 1312–1324.

Cooperative Research Report, 1989. Baltic Sea Patchiness Experiment PEX-86. ICES, Copenhagen.

Cox, M.D., 1984. A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Tech. Rep. No. 1, GFDL/Princeton University.

Fennel, W., 1991. Rossby radii and phase speeds in the Baltic Sea. Cont. Shelf Res. 11, 23–36.

Grønkjær, P., Wieland, K., 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Mar. Ecol. Prog. Ser. 154, 91–105.

Grønkjær, P., Clemmesen, C., St.John, M.A., 1997. Nutritional condition and vertical distribution of Baltic cod larvae — migrate or die. J. Fish Biol. 51 (Suppl. A), 352–369.

Haapala, J., 1994. Upwelling and its influence on nutrient concentration in the coastal area of the Hanko Peninsula, entrance of the Gulf of Finland. Est. Coast. Shelf Sci. 38, 507–521.

Heath, M.R., Gallego, A., 1998. Bio-physical modelling of the early life stages of haddock, *Melanogrammus aeglefinus*, in the North Sea. Fish. Oceanogr. 7, 110–125.

Hinrichsen, H.-H., Lehmann, A., St.John, M.A., Brügge, B., 1997. Modelling the cod larvae drift in the Bornholm Basin in summer 1994. Cont. Shelf Res. 17, 1765–1784.

Hinrichsen, H.-H., St.John, M., Aro, E., Grønkjær, P., Voss, R., 2001a. Testing the larval drift hypothesis in the Baltic Sea: retention vs. dispersion due to influence of wind driven circulation. ICES J. Mar. Sci. 58, 973–984.

Hinrichsen, H.-H., Böttcher, U., Oeberst, R., Voss, R., Lehmann, A., 2001b. The potential for advective exchange of the early life stages between the western and eastern Baltic cod (*Gadus morhua* L.) stocks. Fish. Oceanogr. 10, 249–258.

Hinrichsen, H.-H., Möllmann, C., Voss, R., Köster, F.W., Kornilovs, G., 2002. Bio-physical modelling of larval Baltic cod

(*Gadus morhua* L.) growth and survival. Can. J. Fish. Aquat. Sci. 59, 1858–1873.

Horn, H.S., 1966. Measurement of 'overlap' in comparative ecological studies. Am. Nat. 100, 419–424.

Hüssy, K., St.John, M.A., Böttcher, U., 1997. Food resource utilization by juvenile Baltic cod *Gadus morhua*: a mechanism potentially influencing recruitment success at the demersal juvenile stage? Mar. Ecol. Prog. Ser. 108, 21–31.

Kalnay, E., Kanamitsu, M., Kistler, R., Collins, W., Deaven, D., Gandin, L., Iredell, M., Saha, S., White, G., Woollen, J., Zhu, Y., Chelliah, M., Ebisuzaki, W., Higgins, W., Janowiak, J., Mo, K.C., Ropelewski, C., Wang, J., Leetmaa, A., Reynolds, R., Jenne, R., Joseph, D., 1996. The NCEP/NCAR 40-year reanalysis project. Bull. Amer. Meteorol. Soc. 77, 437–470.

Killworth, P.D., Stainforth, D., Webbs, D.J., Paterson, S.M., 1991. The development of a free-surface Bryan-Cox-Semtner ocean model. J. Phys. Oceanogr. 21, 1333–1348.

Kiørboe, T., 1991. Pelagic fisheries and spatio-temporal variability in zooplankton productivity. Proceedings of the Fourth International Conference on Copepoda. Bull. Plank. Soc. Japan, Spec. Vol., pp. 229–249.

Köster, F.W., Schnack, D., 1994. The role of predation on early life stages of cod in the Baltic. Dana 10, 179–201.

Köster, F.W., Hinrichsen, H.-H., St.John, M.A., Schnack, D., MacKenzie, B.R., Tomkiewicz, J., Plikshs, M., 2001. Developing Baltic cod recruitment models II: Incorporation of environmental variability and species interaction. Can. J. Fish. Aquat. Sci. 58, 1534–1556.

Kjesbu, O.S., Solemdal, P., Bratland, P., Fonn, M., 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. 53, 610–620.

Krauß, W., Brügge, B., 1991. Wind-produced water exchange between the deep basins of the Baltic Sea. J. Phys. Oceanogr. 11, 415–433.

Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus 47A, 1013–1031.

Lehmann, A., Hinrichsen, H.-H., 2000a. On the thermohaline variability of the Baltic Sea. J. Mar. Syst. 25, 333–357.

Lehmann, A., Hinrichsen, H.-H., 2000b. On the wind driven and thermohaline circulation of the Baltic Sea. Phys. Chem. Earth (B) 25, 183–189.

Lehmann, A., Hinrichsen, H.-H., 2001. The importance of water storage variations for water balance studies of the Baltic Sea. Phys. Chem. Earth (B) 26, 383–389.

Lehmann, A., Krauß, W., Hinrichsen, H.-H., 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus 54A, 299–316.

MacKenzie, B.R., Miller, T.J., Cyr, S., Legett, W.C., 1994. Evidence for a dome-shaped relationship between turbulence and larval fish ingestion rates. Limnol. Oceanogr. 39, 1790–1799.

MacKenzie, B.R., St.John, M.A., Wieland, K., 1996. Eastern Baltic cod: perspectives from existing data on processes affecting growth and survival of eggs and larvae. Mar. Ecol. Prog. Ser. 134, 265–281.

MacKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., Wieland, K., Zezera, A.S., 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Ga-*

dus morhua eggs in the Baltic Sea. Mar. Ecol. Prog. Ser. 143, 143–156.

Marshall, C.T., Frank, K.T., 1999. The effect of interannual variation in growth and condition on haddock recruitment. Can. J. Fish. Aquat. Sci. 55, 347–355.

Marshall, C.T., Kjesbu, O.S., Yaraginaga, N.A., Solemdal, P., Ultang, Ø., 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? Can. J. Fish. Aquat. Sci. 55, 1766–1783.

Marteinsdottir, G., Thorarinsson, K., 1998. Improving the stock-recruitment relationship in Icelandic cod (*Gadus morhua* L.) by including age diversity of spawners. Can. J. Fish. Aquat. Sci. 55, 1372–1377.

Matthäus, W., Franck, H., 1992. Characteristics of major Baltic inflows -a statistical analysis. Cont. Shelf Res. 12, 1375–1400.

Möllmann, C., Kornilovs, G., Sidrevics, L., 2000. Long-term dynamics of main zooplankton species in the Central Baltic Sea. J. Plankt. Res. 22, 2015–2038.

Nissling, A., Westin, L., 1991. Egg buoyancy of Baltic cod (*Gadus morhua*) and its implications for cod stock fluctuations in the Baltic. Mar. Biol. 111, 33–35.

Nissling, A., Larsson, R., Vallin, L., Frohlund, K., 1998. Assessment of egg and larval viability in cod, *Gadus morhua* - methods and results from an experimental study. Fish. Res. 38, 169–186.

Oeberst, R., Böttcher, U., 1998. Development of juvenile Baltic cod described with meristic, morphometric and sagitta otolith parameter. ICES C.M. 1998/CC, 15.

Otterlei, E., Nyhammer, G., Folkvord, A., Stefansson, S.O., 1999. Temperature-and size-dependent growth of larval and early juvenile Atlantic cod (*Gadus morhua*): a comparative study on Norwegian coastal cod and northeast Arctic cod. Can. J. Fish. Aquat. Sci. 56, 2099–2111.

Proctor, R., Wright, P.J., Everitt, A., 1998. Modelling the transport of larval sandeels on the north-west European shelf. Fish. Oceanogr. 7, 347–354.

Remane, A., 1940. Einführung in die zoologische Ökologie der Nord- und Ostsee. In: Grimpe, G., Wagler, E. (Eds.), Die Biologie des Brackwassers. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart. 216 pp.

Semtner, A.J., 1974. A general circulation model for the World Ocean. UCLA Dept. Meteorology Tech. Rep. No. 8. 99 pp.

Sinclair, M., 1988. Marine Populations: an Essay on Population Regulation and Specification. University of Washington Press, Seattle, USA.

St.John, M., Lund, T., 1996. Lipid Biomarkers: Linking the utilization of frontal plankton biomass to enhanced condition of juvenile North Sea cod. Mar. Ecol. Prog. Ser. 131, 75–85.

Thompson, A.B., Riley, J.D., 1981. Egg and larval developmental studies in the North Sea cod (morhua L.). Rapp. P. Réun. Cons. Int. Explor. Mer 178, 553–559.

Trippel, E.A., 1998. Egg size and viability and seasonal offspring production of young Atlantic cod. Am. Fish. Soc. 127, 339–359.

Voss, R., Hinrichsen, H.-H., 2002. Sources of uncertainty in ichthyoplankton surveys: Influence of wind forcing and survey strategy on abundance estimates. J. Mar. Syst. (in press).

Voss, R., Hinrichsen, H.-H., St.John, M., 1999. Variations in the drift of larval cod (*Gadus morhua* L.) in the Baltic Sea: combining field observations and modelling. Fish. Oceanogr. 8, 199–211.

Voss, R., Hinrichsen, H.-H., Wieland, K., 2001. Model-supported estimation of mortality rates in Baltic cod (*Gadus morhua callarias* L.) larvae: the varying impact of 'critical periods'. BioMed Central. BMC Ecology 1, 4.

Vuorinen, I., Hänninen, J., Vitasalo, M., Helminen, U., Kuosa, H., 1998. Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. ICES J. Mar. Sci. 55, 767–774.

Westin, L., Nissling, A., 1991. Effects of salinity on spermatozoa motility, percentage of fertilized eggs and egg development of Baltic cod *Gadus morhua*, and implications for cod stock fluctuations in the Baltic. Mar. Biol. 108, 5–9.

Wieland, K., Jarre-Teichmann, A., 1997. Prediction of vertical distribution and ambient development temperature of Baltic cod, *Gadus morhua* L., eggs. Fish. Oceanogr. 6, 172–187.

Wieland, K., Waller, U., Schnack, D., 1994. Development of Baltic cod eggs at different levels of temperature and oxygen content. Dana 10, 163–177.

Wieland, K., Jarre-Teichmann, A., Horbowa, K., 2000. Changes in the timing of spawning of Baltic cod: possible causes and implications for recruitment. J. Mar. Sci. 57, 452–464.