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zu Kiel

**Recruitment processes in the larval phase:
the influence of varying transport on
cod and sprat larval survival**

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1 INTRODUCTION

Natural variations in the abundance of fish stocks can be the result of several factors acting on all life stages. In particular, factors acting on the early life-history stages have been identified to contribute to recruitment variability (e.g. Lasker, 1981; Cury and Roy, 1989). Among these, biotic factors such as starvation and predation have been considered to be of great importance. Investigations dealing with the impact of predation on recruitment success have been intensified only in more recent years (e.g. Sissenwine, 1984; Köster, 1994; Köster and Schnack, 1994). Food limitation during the phase of first feeding has already been discussed much earlier as important factor regulating recruitment success, e.g. by Hjort (1914). He formulated the 'critical period concept'. Cushing (1974) expanded the time period under investigation. In formulating his 'match-mismatch' hypothesis he argued the temporal coupling or decoupling of the production maxima of fish larvae and their prey organisms to be the mayor source of recruitment variability.

Iles and Sinclair (1982), however, propagated the outstanding importance of an abiotic factor, i.e. ocean circulation. According to the 'member-vagrant' hypothesis (Sinclair and Tremblay, 1984) recruitment success would be largely determined by the circulation system encountered by the larvae. Survival would be dependant on the retention of larvae in areas of characteristic environmental conditions. In the Baltic Sea there are generally high gradients in both abiotic and biotic variables, due to the strong vertical stratification and the limited exchange with the North Sea. Especially temperature, salinity, oxygen-content as well as prey and predator abundance vary in small horizontal and vertical scales, so that varying transport regimes might have a considerable influence on recruitment success.

In the Baltic Sea, two cod (*Gadus morhua* L.) stocks exist whose early life stages (eggs, larvae, juveniles) are subject to transport processes. These stocks are the western Baltic cod stock, considered to be located west of the island of Bornholm (Fig. 1.1), and the eastern stock, east of Bornholm (Bagge and Thurow, 1994).

The eastern Baltic cod stock is historically one of the largest in the North Atlantic region (Dickson and Brander, 1993) with a long-term mean abundance of 400 000 to 500 000 tons of spawning stock biomass. The stock is therefore of considerable commercial importance.

The western Baltic cod stock is historically of minor importance with a long-term mean of about 33 000 tons (ICES, 1994). As obtained from genotypic and phenotypic analysis (Sick, 1965; Jamieson and Otterlind, 1971; Schmidt, 2000), a distinction between both stocks occurs on either side of longitude 14°30' N with some area of overlap between both stocks. To the east, the eastern stock extends northwards to the Bothnian Sea area, whereas on the western side, the western stock can be traced back towards the southernmost part of the Kattegat (Bagge *et al.*, 1994).

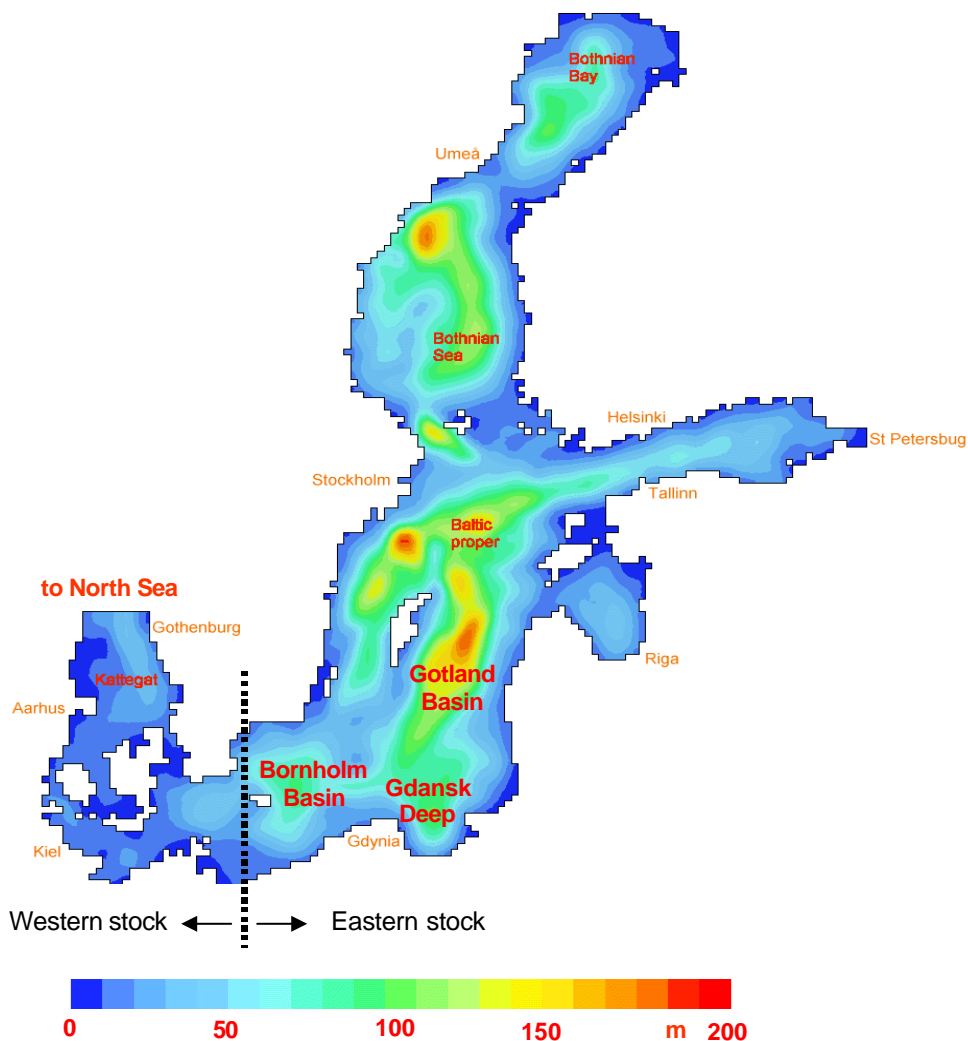


Figure 1.1: The Baltic Sea

Besides the differences in their genetic characteristics, the different cod stocks spawn at different times of the year within areas of different environmental conditions. The spawning grounds of the western stock cover the Danish Straits, Kiel Bay, Fehmarn Belt and Mecklenburg Bay. The spawning season in the western Baltic starts in February and by May spawning is completed (Kändler, 1949; Berner, 1960; Thurow, 1970; Bleil and Oeberst, 1997).

For the eastern Baltic cod stock there are three main spawning areas: the Bornholm and Gotland Basins as well as the Gdansk Deep (Fig. 1.1). During recent years, successful spawning of the stock has been limited to the Bornholm Basin due to anoxic conditions in the spawning layer at the other spawning sites (e.g. Bagge *et al.*, 1995; MacKenzie *et al.*, 2000). Consequently, reproductive success within the last 15 years was dependent mainly on the environmental conditions existing in the Bornholm Basin. The main spawning season (May to September) in the Bornholm Basin is characterized by a seasonal thermocline at approximately 20 to 30 m depth and a permanent halocline at between 50 to 75 m depth (Kullenberg and Jacobsen, 1981; Møller and Hansen, 1994). Oxygen content and salinity in the halocline and deeper layers have been shown to be the major environmental factors affecting the fertilization rate and survival of Baltic cod eggs (e.g. Westin and Niesling, 1991; Wieland *et al.*, 1994). Ephemeral inflows of well oxygenated saline water from the North Sea replenish oxygen in the deep layers which is lost due to the breakdown of organic material by bacteria.

Contrary to other cod stocks, where salinities are sufficient to keep eggs floating in the surface layer, in the central Baltic cod eggs occur exclusively in the intermediate and bottom water, concentrating in a narrow depth range within or below the halocline (Kändler, 1944; Wieland and Jarre-Teichmann, 1997). Thus, the Baltic cod stock, unlike others, is subjected to a clear environmental influence on reproductive success based on oxygen conditions in the spawning basins (e.g. MacKenzie *et al.*, 1996). Cod eggs are also subject to predation as high abundances of eggs are found in a relatively restricted area where they are heavily preyed upon by herring and sprat (Köster and Möllmann, 1997). The duration of the egg stage is temperature dependent with larvae typically hatching between 14 and 21 days (Wieland *et al.*, 1994). A few days after hatch, the larvae begin to migrate vertically through the halocline into less saline, shallower water layers to feed (Grønkjær and Wieland, 1997). First-feeding of cod larvae takes place around larval stages 5 to 6, at an age of 4 to 8 days after hatch (Fossum, 1986). Therefore, viable larvae of stages 6 and 7 should have just completed their vertical feeding migration and are mainly found above the halocline (Grønkjær and Wieland, 1997). Here, they concentrate in the depth range of approximately 25-40 m, while their abundance in the upper 20 m is generally low. The vertical migration of larvae has been shown to be a prerequisite

for survival with larvae in good feeding condition being found only in the upper 40 m (Grønkjær *et al.*, 1997).

Larvae of sprat co-occur with cod larvae in the area of the deep Baltic basins (Kändler, 1949). As for cod, the Bornholm Basin has been shown to be an important spawning ground for sprat (Köster *et al.*, 2001a). The spawning period extends from March to August, with peak spawning in May/June, depending to a certain extent on the temperature conditions (Elwertowski, 1960; Grimm and Herra, 1984). In contrast to cod, vertical distribution patterns of sprat larvae are not well investigated.

Biomass and recruitment levels of cod and sprat showed quite different time trends (Fig. 1.2). Due to a combination of reproduction failure and high fishing mortalities, the cod spawning stock biomass (SSB; Sub-division 25-32) decreased from ~700 000 to <100 000 tons from 1980 to 1992, reaching the lowest level on record in 1999 (75 000 tons). On the other hand recruitment of sprat generally increased since the mid 80s, with highly variable recruitment during the last years (ICES, 2001).

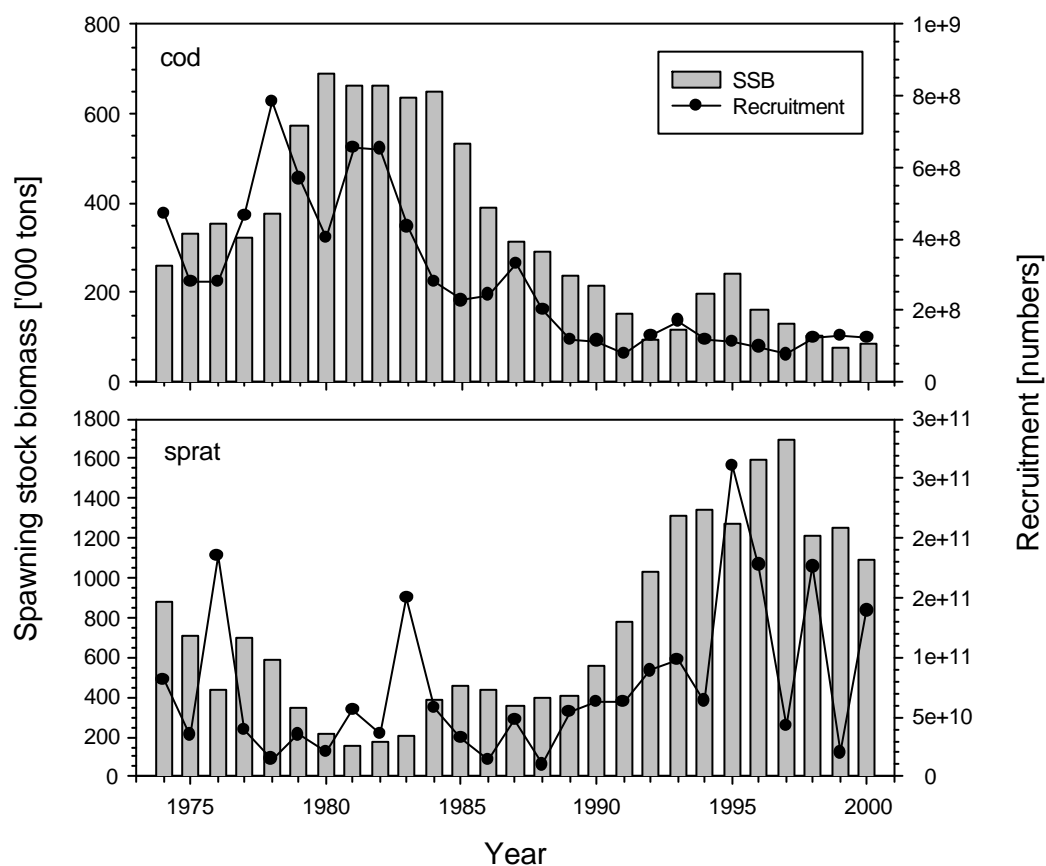


Figure 1.2: Stock development (Spawning stock biomass and recruitment) of cod (age 2) and sprat (age 1) in the central Baltic Sea; cod: ICES Sub-divisions 25-32; sprat Sub-division 22-32.

Accordingly, SSB values (Sub-division 22-32) showed a strong increase from ~350 000 tons in 1987 to ~1 700 000 tons in 1997. Afterwards the spawning stock biomass decreased slightly to approx. 1 000 000 tons in 2000.

Because of the prolonged spawning period in the Baltic (cod: Wieland and Horbowa, 1996; sprat: Grimm and Herra, 1984; Elwertowski, 1960), and age- and size-dependent timing of spawning (Tomkiewicz *et al.*, 1997; Tomkiewicz and Köster, 1999) the potential exists for eggs and larvae of differing quality (e.g. competitive ability; Buckley *et al.*, 1991) to be exposed to a temporally and spatially varying environment because of changes in food conditions (St. John *et al.*, 1995), oxygen conditions (MacKenzie *et al.*, 1996), predation (e.g. Köster and Schnack, 1994) and transport potential. The influence of varying transport potential on the survival of cod and sprat early life history stages in the Baltic is yet unclear.

A number of different models had already been used to investigate egg and larval transport when this study started. Bartsch *et al.* (1989) used a baroclinic numerical model to explain the drift of herring larvae in the North Sea towards their nursery areas. Investigations on larval transport of the Japanese sardine in the Kuroshio current were performed by Kasai *et al.* (1992) as well with simple one-dimensional as with two-dimensional numerical models. In the area of the Newfoundland shelf as well Helbig *et al.* (1992) as DeYoung and Davidson (1994) investigated the degree of retention of cod eggs and larvae on the shelf by means of current models. Campana *et al.* (1989) focused on the influence of varying transport for larval haddock spawned on Browns Bank (near Georges Bank). For the Baltic Sea Aro *et al.* (1991) formulated a two-dimensional two-layer model to estimate the drift of early life stages of cod. However, this model seemed not to be adequate for the planned investigations. Instead, a rather new 3-D eddy resolving baroclinic model of the Baltic Sea (Lehmann, 1995) should be used to model larval drift. First modelling attempts had already been undertaken for cod larvae by Hinrichsen *et al.* (1995) and Voss (1996), confirming the potential of larval drift to be modelled successively.

According to the original idea of Sinclair and Trembley (1984) 'retention' is thought to be beneficial for survival while 'dispersed' individuals have higher mortality rates. However, in the Baltic Sea this might be *vice versa*: retention of larvae on the spawning grounds in the central basin can be hypothesized as being detrimental for

recruitment success while a dispersal to shallow coastal areas could be beneficial: Production in the central basin appears to be nutrient limited with low prey availability potentially resulting in low growth and survival of cod (Kiørboe, 1991; St.John *et al.*, 1995; St.John and Lund, 1996). The shallow coastal regions of the Baltic Sea however have been identified as regions of high primary and secondary production due to the availability of nutrients caused by the interaction of the thermocline with bottom topography (e.g. St.John *et al.*, 1995; Josefson and Conley, 1997) and from terrestrial and benthic introduction. The significance of observed nutrient concentrations concerns nitrogen and phosphorus as limiting nutrients for the primary carbon flux in coastal water ecosystems (e.g. Sæderstrøm, 1996) and coastal upwelling (Haapala, 1994). Hence, the rapid transport of larvae to the shallow coastal regions may potentially result in increased feeding success, growth and survival relative to individuals retained in the central basins of the Baltic Sea. Additionally, it has to be taken into account, that recent investigations of the long-term dynamics of the main mesozooplankton species in the central Baltic revealed clear time-trends, with a decrease in biomass of *P. elongatus*, a species mainly distributed in the deep basins, since the 1980ies and an increase of the standing stock of the other abundant copepod species, especially *Acartia* spp. (Dippner *et al.*, 2000; Möllmann *et al.*, 2000).

In order to better understand the effects of physical forcing on the distribution and mortality of the early life stages of cod and sprat, physical modeling activities have been conducted. A three-dimensional eddy resolving baroclinic model of the Baltic Sea (Lehmann, 1995) in combination with a Lagrangian particle tracking technique (Hinrichsen *et al.*, 1997) has been used to investigate the temporal evolution of larval distributions in the Bornholm Basin.

2 OBJECTIVES OF THE STUDY

Field studies directed towards the larval stage of cod and sprat have been conducted since 1987 during several cruises in each year from the Institute of Marine Sciences in Kiel (Fig. 2.1). The results obtained in this work are structured into seven chapters, each of them dealing with different periods out of this time-series:

In the first chapter (4.1) the applicability of the Baltic Sea Model to simulate larval drift processes, the influence of small scale changes in the vertical distribution on the resulting modeled drift as well as possible influences of retention or dispersal on cod recruitment are investigated for May 1988 and August 1991. This part of the study has been published in Voss *et al.* (1999).

As the results suggested an influence of transport processes on Baltic cod recruitment, the larval drift hypothesis was tested for the period 1979-1994 in chapter 4.2. Special emphasis was laid on an inter-annual comparison of the years 1993 and 1994. This part of the study has been published in Hinrichsen *et al.*, (2001a).

The existence of two neighboring cod stocks in the Baltic lead to a further investigation (chapter 4.3), dealing with the potential for advective exchange of early life stages between these stocks. Due to a very different wind forcing situation, the years 1988 and 1993 were chosen for a corresponding modeling exercise. This part of the study has been published in Hinrichsen *et al.*, (2001b).

The Baltic Sea Model could also successfully be used to correct abundance estimates of larvae in the region of the Bornholm Basin for transport processes between two consecutive surveys. As a result, a model-supported estimation of mortality rates during different larval periods ('critical' periods) became possible (chapter 4.4; published in: Voss *et al.*, (2001).

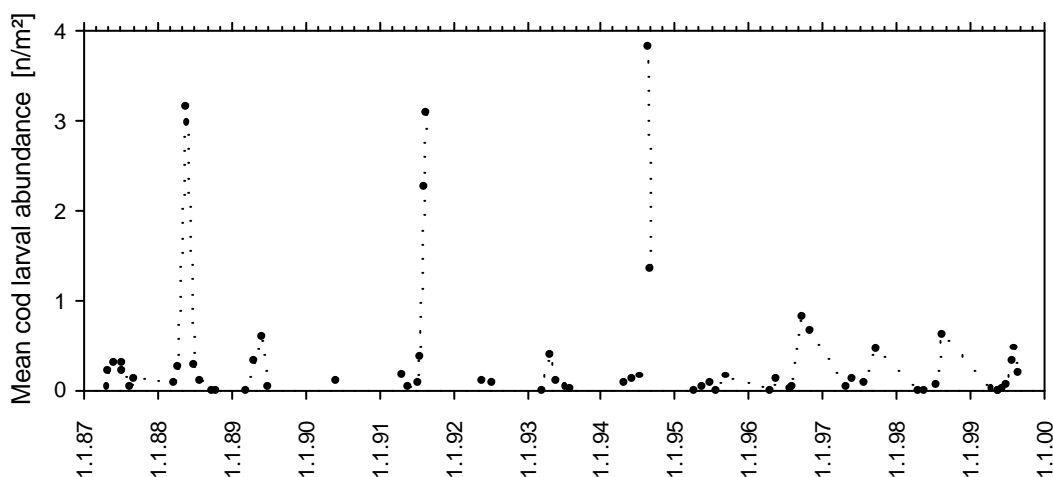


Figure 2.1: Time series of cod larval abundance in the Bornholm Basin 1987-2000.

As a next step it was planned to couple trophodynamic relationships to the hydrodynamic model, yielding an individual based model (IBM) of drift and feeding designed to examine growth and survival of Baltic fish larvae.

As a pre-requisite, in chapter 4.5 the feeding habits of cod and sprat larvae are investigated.

Information on the vertical distribution of sprat larvae, especially on potential diurnal migration patterns, is very scarce in the literature, but urgently needed for the implementation of an IBM, this topic is addressed in chapter 4.6.

The final results-chapter (4.7) describes the first set-up of an IBM constructed for Baltic cod, investigating the larval growth and survival in a changing environment.

This study was conducted within the frame of two EU-projects (AIR2-CT94-1226:CORE; FAIR-CT98-3959:STORE). The author was responsible for all project activities related to fish larval abundance, distribution, feeding, drift and mortality in relation to biotic and abiotic processes. However, much of this work was only possible to be carried out in close cooperation and with the help of many colleagues: Hans-Harald Hinrichsen (IfM, Kiel) carried out all hydrodynamic model runs, implemented model updates and run the IBM model for cod larvae.

The work presented in the chapters 4.1 and 4.2 benefited from valuable input to all tasks from Prof Dr. M. St. John (IHF, Hamburg). Chapter 4.2 comprises additionally work of Drs. E. Aro (FGFRI, Helsinki, Finland) and P. Grønkjær (IBS, Aarhus, Denmark) mainly related to the young fish distribution and larval behavior, respectively. Field work and otolith readings on 0-group cod as well as valuable discussions on the results in chapter 4.3 are due to U. Böttcher and R. Oeberst (BFA, Rostock). Mortality rates during hatch to first-feeding, as described in chapter 4.4, are partly based on egg stage IV abundance and distribution provided by Dr. K. Wieland (GINR, Nuuk, Greenland). Dr. F.W. Köster (IfM, Kiel) organized the field activities (especially with respect to chapters 4.5 and 4.7) prior to the start of the PhD project. Finally, Dr. C. Möllmann (IfM, Kiel) and G. Kornilovs (LATFRI, Riga, Latvia) helped in developing the IBM for cod larvae, especially by supplying zooplankton data.

3 MATERIAL AND METHODS

3.1 Basic biological data

3.1.1 Abundance and horizontal distribution of ichthyoplankton

Data were obtained from research programs carried out between March 1987 and August 1999. The horizontal distribution and abundance of cod and sprat eggs and larvae was obtained by double oblique Bongo sampling. The Bongo (60 cm diameter) was equipped with flowmeters in each of the nets. During the investigations used in this work the Bongo nets had mesh sizes of 0.3 and 0.5 mm. The samples were preserved on board in 4% formaldehyde/seawater solution and were later transferred to formaldehyde-free conservation fluid (Steedman, 1976). Fish eggs and larvae were sorted from the samples and staged and measured to the nearest 0.1 mm. At least a sub-sample of 100 specimen was processed for staging and measuring. The counts were finally standardized to 1m² by the volume of water filtered and the maximum depth of the tow (~2 m above the ground). Egg staging was performed according to a 5 stage system based on morphological criteria (Westernhagen, 1970; Thompson and Riley, 1981), which was adopted for the Baltic (Wieland, 1988; Wieland and Köster, 1996). Cod larvae were staged following a 10 stage system for Norwegian cod (Fossum, 1986). To check the applicability of this staging system, cod larvae from laboratory studies with known hatching date were sub-sampled daily for a period of two weeks to be able to compare the stage/age relationship. No significant deviations in development times were detected. The station grid in use comprised 30 stations in 1987-90, 36 stations in 1991-93 and finally 45 standard stations from 1994 on (Figure 3.1). The station grid was always sampled around the clock, i.e. catches were obtained both during day and night.

3.1.2 Vertical distribution

Cod and sprat early life history stages

Sampling was carried out on 35 surveys in the central part of the Bornholm Basin during the time span 1987-2001. The earliest samples used in this work were collected in 1989 with a MOCNESS (Wiebe *et al.*, 1976), while from 1990 on a BIOMOC was used instead. Both gears are multiple opening/closing nets operating with 9 nets and a mouth opening of 1 m². The BIOMOC is a MOCNESS system modified similarly to the BIONESS (Sameoto *et al.*, 1980). The nets had in both cases a mesh size of 335µm and were equipped with flowmeters (for a detailed

description see Wieland, 1995). The samplers were towed at a definite depth for ~3 minutes at a speed of 3 knots. Two combined hauls of the gear in use (up to 17 nets) allowed to investigate the vertical distribution in the water column with a resolution of 5 m depth intervals. As far as possible at least 3 parallels were performed. Fixation and further processing were done as described under section 3.1.1.

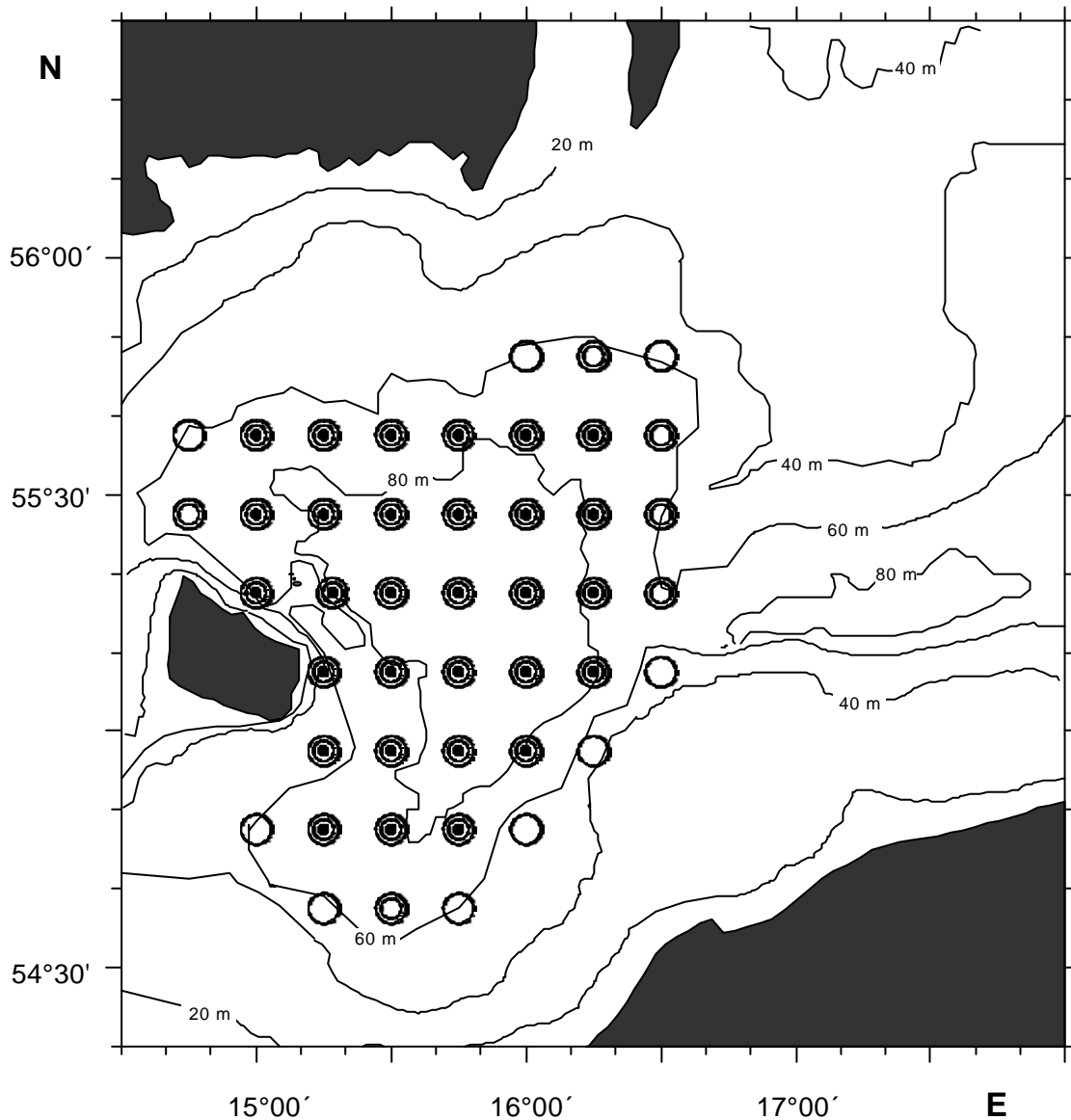


Figure 3.1: Bongo station grid in the Bornholm Basin. 1987-1990: 30 Stations (3 circles); 1991-1993: 36 stations (2 circles); 1994-2001: 45 stations (1 circle).

During 5 sampling occasions a 24-hours sampling was performed yielding sufficient numbers of sprat larvae to investigate potential diel vertical migration patterns. These were May 1989, June 1989, June 1990, May 1999 and April 2000. For different size groups (< 6mm; 6-10mm; >10mm), which were chosen according to morphological

criteria (Bartsch and Knust, 1994), weighted mean depth was calculated for each daytime and nighttime series of samples as:

$$WMD = (\sum n_{\Delta d} \Delta d d_i) / \sum n_{\Delta d} \Delta d \quad (1)$$

where n_d is abundance ($N \cdot m^{-3}$) in sampling depth interval d whose midpoint is d_i . To describe length-dependant vertical migration patterns, the vertical migration strength V (Bollens and Frost, 1989) was calculated for 1 mm larval length groups by calculating the difference between the fraction of the population above a given depth at night and the fraction of the population above that same depth during day. The reference depth was set for all sampling occasions to 17.5m, representing the lower part of the thermocline. Diel vertical migrations in the direction 'up at night' and 'down during the day' will result in positive values, while negative values indicate a vice versa migration pattern. Values of ± 100 indicate a diel vertical migration of the whole population, zero values show the complete absence of such migration patterns.

Zooplankton

To be able to describe the feeding environment for cod and sprat larvae, vertically resolving samples were analyzed for zooplankton during 2 sampling occasions: May 1989 and May 1999. Samples were obtained using 50 μ m liners, deployed in the middle of the 335 μ m MOCNESS (1989) and BIOMOC (1999) nets, respectively. For zooplankton a vertical resolution of 10m depth intervals was chosen. At least 1/100 of the total sample (~400 specimen) was counted and identified to species and stage of development, e.g. copepods were classified as:

- (a) nauplii, (b) copepodite stages I-III [C I-III], (c) copepodite stages IV-V [C IV-V],
- (d) adult males [C VI-m] or adult females [C VI-f]

The separation to copepod species was only done from the C I-III stage on.

3.1.3 Determination of the birthdates and the age/length characteristics from otolith analysis of 0-group cod

These investigations were carried out by Oeberst and Böttcher (Institute for Baltic Sea Research, Warnemünde; IOW), determining the birthdates of 0-group cod caught in the different nursery areas of the Baltic Sea from sagittal otolith microstructure analysis. This made it possible to assign the juveniles to their different spawning areas since timing of spawning, and hence the age of the 0-group cod, is different in the western and central Baltic stock.

The main aims of these investigations were to determine the origin of juvenile cod caught within the Arkona- and Bornholm Basin based on birthdate distributions and to carry out modeling exercises to examine the potential impact of different wind driven circulation patterns on the transport of cod early life stages between the western and eastern Baltic (see section 3.3).

The juveniles were sampled during 6 trawl surveys in the Arkona- and Bornholm Basin carried out in September and October 1993 to 1996 by the IOW, using pelagic, bottom or near bottom hauls. In the laboratory, the meristic parameters of the fish were determined and the otoliths were removed. Microstructure analyses were carried out on a sub-sample of sagittal otoliths from juveniles from 2 to 18 cm in total length. A total of 81 pelagic and 243 demersal individuals were analyzed.

The formation of the accessory growth center (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 reared cod with a well known age (48 days) showed that the development of the AGC started 41 to 43 days after hatch. Using these data, together with the results of the former analyses, gave an assumed mean value of 45 days from the hatchcheck to the beginning of the secondary increments.

A detailed description of the otolith microstructure analyses can be found in Oeberst and Böttcher (1998).

For estimation of the birthdates the following equation was used:

$$\text{Birthdate} = \text{Catchdate} - C1 - C2 - \text{NDI} \quad (2)$$

where

- C1 is the mean number of days for the development of the egg stages

- C2 is the mean number of days between the hatchcheck and the beginning of the secondary increments
- and NDI is the number of secondary increments.

For C1 a constant value of 20 days was taken. This value was derived from the observed temperature regime in the Baltic Sea applying egg-stage development/temperature relationships (Thompson and Riley, 1981) which agree well with results of Wieland *et al.* (1994).

3.1.4 Cod and sprat larval stomach content analysis

Sprat and cod larval stomach contents were analysed from 12 cruises in 1987 and 1988 covering the months March to October. Larvae were obtained from the regular Bongo station grid (see Fig. 3.1) and the gut content was analysed using a stereomicroscope. Copepod prey items were classified comparable to the vertically resolving zooplankton sampling. The separation to copepod species was only possible from the C I-III stage on for sprat larvae. Table 3.1 provides an overview about the cruises conducted, the numbers of larvae suitable for analysis as well as the numbers with empty stomachs. Not all larvae were included in the analysis, as some of them were destroyed during the sampling procedure.

The calculation of food selection indices is based on a vertically resolving sampling in May 1989. Sampling took place in the centre of the Bornholm Basin during daylight hours. The water column was sampled in 5m intervals down to 45m, covering the main vertical distribution range of feeding cod and sprat larvae (Wieland and Zuzarte, 1991; Groenkjaer and Wieland, 1997; Makarchouk and Hinrichsen, 1998). A total of 2 complete profiles was analysed. Vertical profiles of temperature, salinity and dissolved oxygen were recorded with a ME 1500 OTS probe concurrently to the net samplings.

According to the hydrography, the results were grouped in 10m depth-intervals (5-15m: warm surface layer, 20-30m: region of the thermocline; 35-45m: intermediate water with approx. constant temperature and density). The total of 564 sprat larvae with ingested food items were additionally grouped to 3 length classes (<8mm, 8-10mm, >10mm). Due to lower numbers caught (n=57 in analysis) and a restricted length distribution (4.5-8.4mm larval length), results for cod larvae were only splitted to depth strata.

Table 3.1: Overview about sampling times, numbers of sprat and cod larvae in stomach content analysis as well as numbers with empty stomachs

Date	sprat larvae in analysis (empty)	cod larvae in analysis (empty)
23-30 Apr 87	9 (9)	50 (37)
31 May - 1 Jun 87	13 (10)	33 (6)
3-9 Jul 87	513 (278)	78 (37)
17-18 Aug 87	457 (254)	5 (2)
8-9 Sep 87	243 (201)	20 (2)
6-7 Apr 88	39 (24)	45 (7)
18-19 May 88	1514 (1122)	1033 (228)
28-30 Jun 88	615 (463)	42 (4)
30 Jul -2 Aug 88	192 (120)	16 (1)
21-23 Sep 88	7 (5)	0
11-13 Oct 88	45 (29)	2 (0)

To describe the feeding selectivity (SEL) the logarithmic Shorigin index (Berg, 1979) was calculated:

$$SEL = \log_{10} (\%N_i \text{ in the ingested food} / \%N_i \text{ in the potentially available food}) \quad (3)$$

where $\%N_i$ is the numerical percentage of an item

In this index random feeding receives the value 0. Preference results in positive values calculated, while avoidance in analogy receives negative values (complete avoidance is assigned the value $-\infty$).

3.2 Baltic Sea Model

Numerical simulations of the Baltic Sea circulation were performed by application of a three-dimensional (3-D) eddy resolving baroclinic model of the Baltic Sea (Lehmann, 1995). The 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). The Baltic Sea model comprises the whole Baltic including the Gulf of Bothnia and Gulf of Riga as well as the Belt

Sea, Kattegat and Skagerrak. At the western boundary an idealized North Sea basin is attached to the model domain which is used to take up sea-surface elevations in the area of the Skagerrak and to provide the water masses necessary for the water mass exchange which have the typical characteristics of the North Sea. The model is driven by atmospheric data provided by the SMHI (Swedish Meteorological and Hydrological Institute) and river runoff taken from a monthly mean runoff database (Bergström and Carlsson, 1994). The meteorological database covers the entire Baltic Sea drainage basin with its parameters stored at a temporal increment of 6 hours. The horizontal resolution is 5 km. The experiments described under 3.3.1 and 3.3.2 were run with 28 vertical levels. Later on the model was enlarged to encompass 41 vertical levels. The thickness of the different levels was in each case chosen to best account for the different sill depths in the Baltic. For the region of the Bornholm Basin this results in a vertical resolution of 6 (3) m layers. A horizontal resolution in the order of the half Rossby Radius of deformation is required to resolve the whole spectrum of meso-scale motions. In the Baltic the internal Rossby Radius was determined to be in the range of 2 to 10 km (Fennel, 1991). Thus, the model is not fully eddy resolving for some regions of the Baltic, but in order to find a compromise between available computer capabilities and resolution of the model in space and time, a grid size of 5 km and a time-step of 5 minutes was chosen. Simulations were performed employing ground truth data of physical and biological parameters obtained on research cruises prior to the period of examination or utilizing the characteristic hydrography for the period of examination. For each depth level of the model, observational data were interpolated onto the model grid by objective analysis (Hiller and Kaese, 1983). Calculation of larval drift routes was performed by using a Lagrangian particle tracking technique (Hinrichsen *et al.*, 1997). Simulated three-dimensional velocity fields were extracted at 3-hourly intervals in order to develop a database for this Lagrangian particle tracking exercise on larval cod. The data set then offers the possibility to derive drift trajectories 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 initially released. 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, current velocity, etc.) along the trajectories. In order to

establish a Lagrangian view of the simulated circulation, drifters can be placed in the modeled 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.

3.3 Applications of the Baltic Sea Model

3.3.1 Variations in the drift of larval cod: Combining field observations and modeling exercises

Simulations were used to predict the potential transport of cod larvae observed on consecutive surveys carried out during the research programs in May 1988 and August 1991.

Comparison of model output with the ichthyoplankton surveys

The horizontal distribution of cod larvae from the first survey in each year was incorporated as an additional tracer in the model. Modeled distributions were then compared with observed distributions obtained during the second survey of each cruise program. Hence the transport of larvae for a period of 5 days was examined in May 1988 and for 6 days in August 1991. In order to account for the vertical migration behavior of first-feeding larvae, only the abundance of larval stages 6 and 7 (age 6-10 days) was used as input for the model run. These stages were chosen because viable larvae of these stages have been observed to occur above the halocline (Grønkjær *et al.*, 1997) with maximum abundance found at approximately 30 to 40 m depth (Grønkjær and Wieland, 1997). The initial vertical position of cod larvae in the water column can influence their horizontal distribution and advection, due to variations in current velocities at different depths. Therefore, the drift of cod larvae, which were initially inserted into the model fields at the 33 m level, was modeled using the mean current velocities for the depth range from 24 to 42 m, thereby making some allowance for their unknown 'real' vertical distribution patterns. This depth range represents the larval drift behavior within the upper part of the intermediate layer and the lower part of the surface mixed layer including the thermocline. The model output was then compared to the horizontal distribution of larvae observed during the second survey. As by the time of the second survey the larvae of stages 6 and 7 had now reached development-stage 8, only these older larvae were incorporated in the presentation of the survey results.

Influence of different vertical distributions on the drift

In order to determine the potential influence on transport of smaller scale variations in the vertical distribution of older larvae, i.e. variations in the depth of the maximum abundance of larvae (between 25 to 40 m depth), simulations were performed with particles released simultaneously at different vertical levels (27 m, 33 m, and 39 m) at the same locations. The simulations were run for a period of 21 days and the transport in each level was compared relative to the transport of larvae released at a depth of 33 m and experiencing the mean current velocities of the 24-42 m layer. The resulting drift trajectories were then analyzed in relation to the daily averaged wind stress data for May 1988 and August 1991.

Retention or dispersal of larvae

To check the development of the horizontal distribution patterns for the investigated time periods, other additional simulations were carried out: in regions of observed high abundance of the larval stages 6 to 7 during the first survey of each cruise program, simulated drifters were deployed on a regularly spaced grid and tracked for a period of 21 days (41 and 107 simulated drifters for May 1988 and August 1991, respectively). After 21 days these larvae would have reached the end of their larval phase and entered the young fish stage.

3.3.2 Testing the larval drift hypothesis: retention versus dispersion

The goal of this study has been to assess the potential for variable larval transport in the Bornholm Basin and to develop a technique for quantifying the inter- and intra-annual variation in larval transport and thereby identify the existence of particular transport regimes.

Two models of the age-dependent vertical distribution of Baltic cod larvae were developed on the basis of vertical profiles of larval abundance in 1993 and 1994 (Grønkvæ and Wieland, 1997). The distribution of newly hatched larvae is assumed to be identical to the distribution of the late stage eggs. In accordance with the egg distribution (Wieland, 1995; Włodarczyk and Horbowa, 1997) yolk-sac larvae (< 5 days) were restricted to depths exceeding 50 m. First-feeding (6 to 10 days) and older larvae (10 to 25 days) were most abundant at intermediate depths, but a

substantial fraction (ca. 30%) was caught above 30 m. During this phase there were indications of diurnal migration: larvae concentrated above 30 m at night but dispersed during daytime.

The vertical resolution of the circulation model was adapted to reflect these distributions (model 1): larvae remain within and below the halocline (48-84 m) for the first 5 days, below the surface wind-mixed layer (12-48 m) during the next 20 days, and between 12 and 30 m for the remaining 35 days.

To account for differences in the timing of upward migration seen for the oldest larvae a second model was investigated, in which the upward migration was delayed and the larger larvae allowed to migrate over a larger depth range (model 2): larvae remain within and below the halocline (48-84 m) for the first 10 days, within the halocline (48-66 m) for the next 5 days, then below the surface wind-mixed layer (12-48 m) for another 10 days, whereas larvae older than 25 days were assumed to be above the thermocline (12-30 m) for 12 hours per day and between 30 and 66 m for the other 12 hours.

To determine the wind energy required to transport cod larvae from the spawning site within the deepwater region of the Bornholm Basin to different potential nursery areas, idealized constant wind forcing (velocity 12 m/s) in space and time was applied.

Within- and between-year variation in the drift patterns of cod larvae were simulated for May-September 1993 and 1994. For both years, the initial conditions are realistic three-dimensional distributions of temperature and salinity, based on observations taken during quasi-synoptic hydrographic surveys in May at the beginning of the spawning season. The model was forced with realistic wind data based on observations obtained at the weather station at Christiansø. In the simulations, new batches of larvae were released into the modeled Eulerian flow fields at 5 days intervals and tracked for a period of 60 days. This time span approximately covers the entire duration of the larval phase of cod (Fossum, 1986). Release dates commenced on May 1 (Julian day 121) and ended July 30 (Julian day 211). A total of 1056 larval drifters were released at the appropriate depth on a regular spaced grid enclosed by the 80 m isobath encompassing the historical peak egg and larval abundance in the Bornholm Basin (Wieland, 1995).

The larvae were allowed to drift for a period of 60 days or until they reached the 30 m depth contour where their position remained fixed assuming settling. Each larval

drifter representing the four release centers was given an identifying code stipulating time of release, thereby allowing information on the source, time of hatch, and period of drift of each individual at each destination.

Because the same number of drifters was released at each five days interval, we compare simulated distributions between and within years and not the actual numbers of larvae.

Transport index

To identify historic variations of larval retention/dispersal owing to variations in wind forcing between and within years, a simple transport index was developed based on cumulative wind energy. Critical energetic levels were derived from the results of the numerical simulations with constant wind forcing in the model. The cumulative sum of the wind energy utilized is based on three hourly observations at the weather station at Christiansø. An earlier study (Hinrichsen *et al.*, 1995) suggests that larval drift towards the west and north is correlated to westerly and southerly winds, whereas easterly and northerly winds result in transport to the south and east. Thus, as a first step, the difference in cumulative wind energy between winds coming from southern to western (positive) and northern to eastern (negative) directions was calculated for each 60 days period (representing the period of larval drift) commencing at 5 days intervals during the main spawning season (May-September). For example, to get a total amount of wind energy of + 100000 Wm⁻², approximately 11 days with wind velocities of 12 ms⁻¹ from southerly and westerly directions are required. Periods of dispersal were considered to be those in which cumulative wind energy is sufficient to transport more than 50 % of initially spawned larvae to coastal areas, while periods with less wind energy are defined as periods of retention.

3.3.3 The potential for advective exchange of early life stages between the western and eastern Baltic basins

Under strong westerly wind conditions, the general stratification of the Baltic is broken down by mixing and a considerable amount of highly saline water can penetrate into the eastern Baltic. These mass transports can be accompanied by advective propagation of passively drifting particles such as eggs and larvae of different fish species and, thus, within the same area (central Baltic) possibly lead to mixing of the juvenile populations of both cod stocks. On the other hand, cod larvae

of the eastern stock, which are located in the central Baltic relatively close to surface waters (Grønkvæ and Wieland, 1997), might have the potential to drift to the west in the upper layers of the two-layer current system of the Baltic (Lehmann and Hinrichsen, 2000).

The main aims of this exercise were:

- to determine the origin of juvenile cod caught within the Arkona- and Bornholm Basin based on birthdate distributions derived from otolith microstructure analysis
- and to carry out modeling exercises to examine the potential impact of different wind driven circulation patterns on the transport of cod early life stages between the western and eastern Baltic.

The horizontal 0-group cod distribution within the potential nursery areas were not surveyed systematically on a standard station grid during the autumn cruises. Furthermore, the initial cod egg abundance data, as well their three-dimensional distribution patterns in the Danish Straits, in Kiel Bay and in Mecklenburg Bay are not available. Thus, it could not be the goal to simulate the drift patterns of the larvae for each of the years explicitly, but only to identify the principal factors influencing the transport of early life stages of cod between the western and eastern Baltic. Therefore, two scenarios with considerably different wind conditions (western Baltic cod spawning seasons of 1988 and 1993) were selected.

Because it has been assumed that eggs and young (non-feeding) larvae have no swimming behavior, their advection was simulated by incorporating a passive tracer into the model with the same diffusivities specified as for temperature and salinity. The particle drift was derived from the temporal evolution of the tracer field. With respect to the average duration of the egg and non-feeding larval stages, these simulations were performed for periods of 25 days. Within the spawning grounds of the western cod stock, eggs and young larvae are found below the pycnocline which, on average, is at 20 m depth (Bagge *et al.*, 1994). Thus, passive drifting tracers were incorporated at model grid points where this depth was exceeded. The initial abundance at every model grid point and within every depth cell of the model deeper than 20 m was set to a constant value (1 n/m^3). Generally, the major spawning ground of the western Baltic cod stock can be subdivided into four subareas (Fig. 3.2):

- Great Belt (I)
- Little Belt, Kiel Bay, Langeland Belt and Fehmarn Belt (II)
- Mecklenburg Bay (III)
- Øresund (IV)

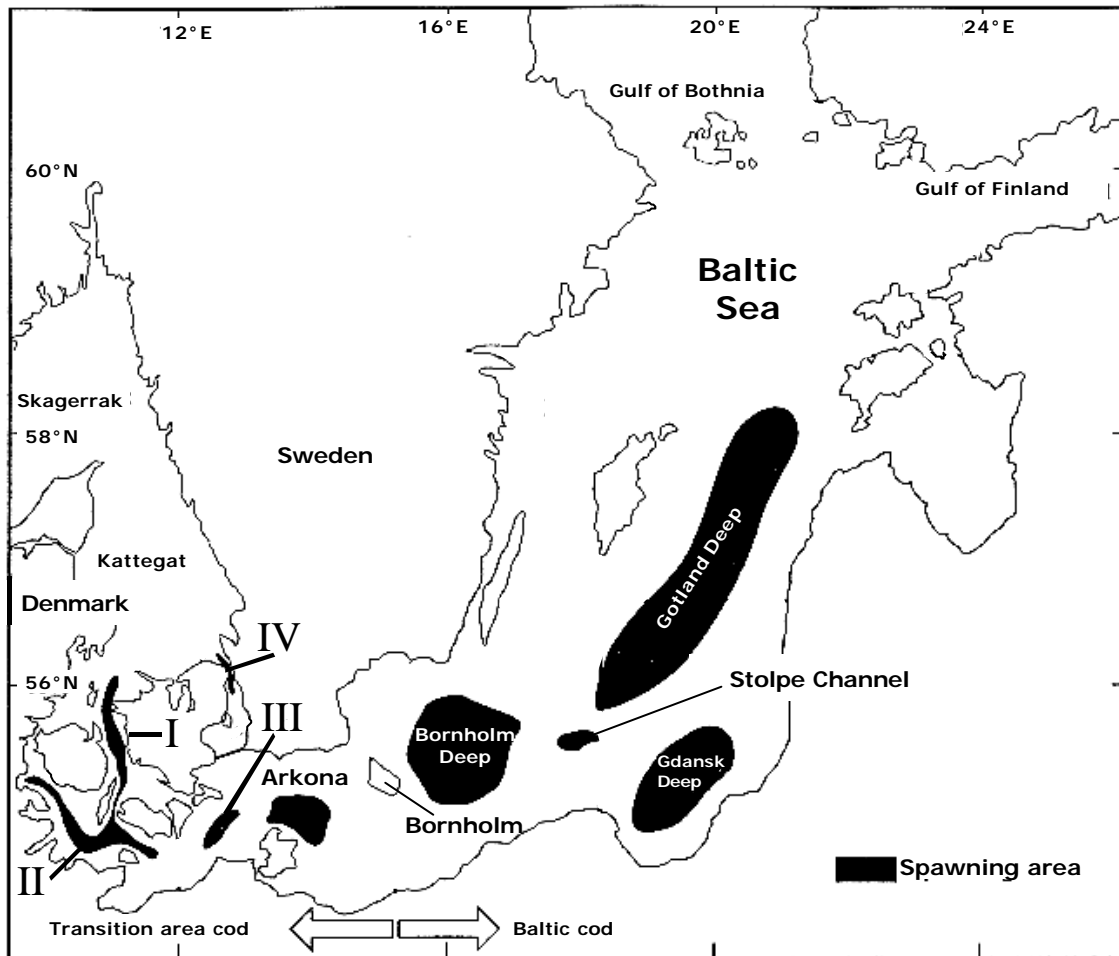


Figure 3.2: Spawning areas of Baltic cod (after Bagge and Thurow, 1994). Spawning areas of the western Baltic or transition area cod stock are marked by I (Great Belt), II (Little Belt, Kiel Bay, Langeland Belt and Fehmarn Belt), III (Mecklenburg Bay) and IV (Øresund).

Older cod larvae are usually found in the same geographical area as eggs and young larvae but mainly above the pycnocline (< 20 m).

In order to estimate the potentially different drift patterns of cod early life stages spawned in the western Baltic and in the Kattegat area, the circulation patterns were analyzed during the major spawning season (January to April) for two years with

considerably different wind forcing conditions (1988 and 1993). The spawning period of 1988 (Fig. 3.3) was regarded as a mild winter with relatively low and variable wind forcing during the winter as well as in early spring. In contrast, in January 1993 the recent major Baltic inflow to the Baltic Sea occurred (e.g. Matthäus and Lass, 1995). During this time there was a relatively long period of strong wind forcing, mainly from the west. The years 1988 and 1993 are specified as scenarios 1 and 2, respectively. During the simulations, older larvae and/or juveniles of cod were prescribed as Lagrangian drifters which were released into the modeled Eulerian flow fields within the spawning grounds of the western Baltic (Fig. 3.2) at depths above the pycnocline. Regardless their age, older larvae and juveniles are considered to be horizontally passive or to have only a random swimming behavior which is not taken into account utilizing our Lagrangian particle tracking technique. The release of drifters was repeated at 5 day intervals, i.e. every 5 days a new batch of drifters was inserted and tracked over a period of 45 days. The release dates commenced on Julian day 6 and ended on Julian day 80, whereas the analysis of the temporal evolution of the tracer fields (eggs and/or young larval abundance) also started on Julian day 6 but ended on Julian day 31 for both scenarios.

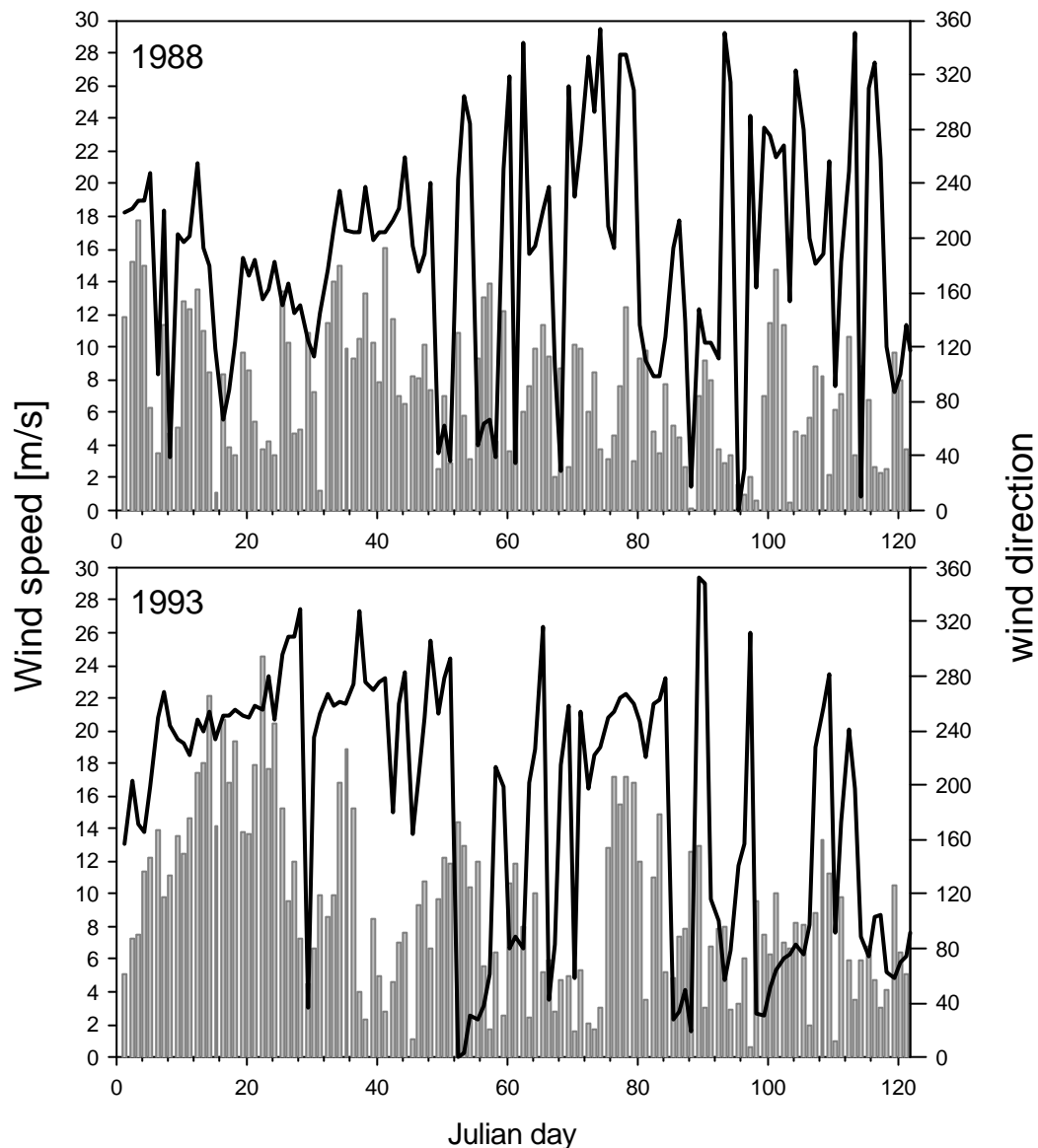


Figure 3.3: Daily mean wind direction and wind speed from January to April 1988 and 1993 taken from Christiansøweather station (line - wind direction; histogram bars – wind speed).

3.3.4 Model-supported estimation of mortality rates in cod larvae: the varying impact of ‘critical periods’

While stage specific mortality rates for cod eggs are available from both, laboratory and field studies (Wieland, 1995; Wieland *et al.*, 2000a), corresponding information for the larval stage is missing. Especially the estimation of field based mortality rates was hampered by generally too low numbers of larvae caught and advective losses from the survey area (Voss *et al.*, 1999). ‘Patch’ studies, i.e. to flag an aggregation of eggs or larvae with a free-drifting drogue and to monitor the developmental success of distinct cohorts (Fortier and Leggett, 1985; Heath and MacLachlan, 1987), are

additionally hampered by the fact that wind stress and current shear in the Baltic influence the trajectory of the drifter significantly (Wieland *et al.*, 2000a).

Due to the missing data on larval mortality in the field, it was not possible to investigate the influence of different processes on larval survival rates. In this approach we use basin-wide abundance estimates from two consecutive surveys to calculate mortality rates. Abundance estimates are corrected for transport processes using the initial horizontal distribution of larvae and applying the Baltic Sea Model. Mortality rates within two 'critical periods', from hatch (egg stage IV) to first feeding (larval stage 5-7) and from onset of feeding to the state of an established feeder (larval stage 8) were calculated.

Sampling related to the horizontal distribution and abundance of cod eggs and larvae was performed on 2 consecutive surveys, approximately 6 days apart, in May 1988 and August 1991. These programs constituted the only available surveys within the time series of ichthyoplankton surveys with sampling intervals and larval abundances having the potential for the determination of stage-specific larval mortality rates (MacKenzie *et al.*, 1996).

During cruises in May 1988 and August 1991 no vertical resolving sampling was performed. Therefore we used data from other cruises in the Bornholm Basin to determine the vertical distribution of the eggs and larvae to be incorporated as passive particles into the Baltic Sea Model, i.e. vertical resolving sampling was performed in July 1988 and 1991. In both cases cod eggs concentrated in a narrow depth layer below the halocline, with maximum abundance in 70 m depth (Wieland and Zuzarte, 1991; Wieland and Jarre-Teichmann, 1997). Feeding cod larvae (\geq stage 5) were generally found above the halocline with maximum abundance around 30 m depth (Grønkjær and Wieland, 1997; Grønkjær *et al.*, 1997). This was observed for July 1991 also, while for July 1988, due to very low numbers of larvae caught, no conclusive result could be obtained. Based on these observations the following relative vertical distribution was utilized to implement cod eggs and larvae as additional tracer into the flow fields:

- 25% in 27-30 m, 50% in 30-33 m and 25% in 33-36m for feeding cod larvae (stages \geq 5)
- 25% in 66-69 m, 50% in 69-72 m and 25% in 72-75 m for cod eggs and non-feeding larvae

Estimation of mortality rates

Mortality rates were estimated by comparing the daily production of a given developmental stage at the first sampling date with that of a corresponding stage at the second sampling date (cohort method). Temperature-dependent incubation time of eggs were calculated (Wieland *et al.*, 1994) with an estimated ambient mean temperature (Wieland and Jarre-Teichmann, 1997). As the consecutive surveys were approximately 6 days apart, the developmental stages had to be chosen accordingly. For the young (hatching) larvae mortality rates were calculated from egg stage IV (oldest egg stage) to larval stage L5-7 (first feeding). For the older larvae larval stages 5-7 were compared with larval stage 8 (established feeding; Table 3.2). As the time interval between the sampling dates did not match exactly the difference in age between developmental stages, the daily production observed at the second sampling date was adjusted according to Wieland *et al.* (2000a).

Table 3.2: Observed (n/m^2) and adjusted (n/m^2) abundance (n/m^2) and daily production ($n/m^2/d$) of different developmental stages inside the 80m depth contour line.

	May 1998 Time interval between surveys: 5.66 days;				August 1991 Time interval between surveys: 5.92 days;			
	1	2	1	2	1	2	1	2
survey								
stage	<i>Egg IV</i>	L 5	L 5-7	L 8	<i>Egg IV</i>	L 5	L 5-7	L 8
age [days] *	14.09	19.35	22.35	28.35	13.51	19.72	21.72	27.72
dt age	5.26		6.00		6.21		6.00	
n/m^2_{obs}	0.98	0.21	2.43	1.50	0.66	0.52	1.97	0.33
$n/m^2/d_{obs}$	0.39	0.10	0.41	0.25	0.27	0.26	0.33	0.06
$n/m^2/d_{adj}$		0.11		0.25		0.26		0.06

*: at mean ambient egg incubation temperatures of 5.75 °C in May 1998 and 5.87 °C in August 1991

While the station grids covered the area > 60 m depth, all calculations were based on the mean abundance (n/m^2) of the developmental stages inside the 80 m depth contour line. This was done, as abundance values outside the observation area were unknown and therefore no reliable exchange rates due to transport could be calculated. By restricting the calculations to the area > 80 m depth, reliable exchange rates between the areas 60-80 m depth and > 80 m depth could be derived from a hydrodynamic model.

While the initial stage specific abundance is known from the survey results for the areas >60m depth, the abundance for the area <60m depth was set to be 0. The initial horizontal distributions as obtained by the first surveys were entered into the model as a tracer and the exchange rates between the areas were calculated over time. By this, the abundance found during the second survey in the area > 80m depth could be corrected for transport gains or losses.

The two periods (19-28 May 1988 and 11-20 Aug 1991) exhibit contrasting wind forcing scenarios: In May 1988 wind forcing was relatively low in magnitude and variable in direction. In contrast, the simulation for August 1991 was affected by relatively strong wind forcing of mainly western directions.

To visualize the persistent circulation patterns averaged model results for different depth layers in the Bornholm Basin are presented. However, averaged currents give no information about their variability. Thus, the stability, defined as the ratio of the averaged vectorial velocity and the averaged arithmetic velocity, was calculated as:

$$B = \frac{(\bar{u}^2 + \bar{v}^2)^{\frac{1}{2}}}{\frac{1}{N} \sum_{i=1}^N (u_i^2 + v_i^2)^{\frac{1}{2}}} \quad (4)$$

with $\bar{u} = \frac{1}{N} \sum u$ and $\bar{v} = \frac{1}{N} \sum v$ as the averaged components of the flow, and N as the number of current observations at the location under consideration. The vectorial mean is obtained from individually observed current vectors, and the arithmetic mean velocity is calculated by averaging the speeds without regard to the current direction (Neumann and Pierson, 1967).

3.4 Bio-physical modeling of larval cod growth and survival

The coupling of a circulation model with trophodynamic relationships of larval fish can be utilized to examine starvation mortality and growth rates at the level of individual larvae (e.g. Werner *et al.*, 1993; Letcher *et al.*, 1996). A coupled hydrodynamic/trophodynamic individual based model (IBM) of drift and feeding designed to examine growth and survival of Baltic larval cod was constructed. This coupled model allows to examine feeding, growth and starvation mortality of larval cod in the Bornholm Basin in the context of their transports by utilizing trophodynamic relationships along their potential drift routes. Implementation of the coupled model required zooplankton abundance as well as turbulence and temperature fields as inputs to the larval

feeding, metabolic and growth components (Hinrichsen *et al.*, submitted). Utilization of this model allowed to examine how habitat and environment affect survival and growth variability.

The spatio-temporal variability of growth and survival is studied by modeling the fate of larvae for various scenarios in prey fields. The effect of a declining standing stock of *Pseudocalanus elongatus* (e.g. Möllmann *et al.*, 2000) was simulated by using prey fields with and without this copepod species.

The IBM tracks individuals through the larval stage thereby distinguishing four stages, i.e. yolk-sac larvae (< 4.5mm), first feeding larvae (4.5 to 6mm), larvae of 6 to 9mm and larvae > 9 mm. Within the model the encounter of food, foraging, growth and survival of individual cod larvae is simulated by specific submodels in 6 hour time steps. All larvae were initially defined to have equal length and weight at hatch. Along the drift trajectories within the coupled model the larvae's environment consists of the prey field and the ambient temperature determining both their growth and survival. Yolk-sac larvae before reaching their length at first-feeding (< 4.5 mm) were considered as passive drift particles, with growth exclusively determined by ambient temperature. In order to analyse the survival and growth of larval Baltic cod, the following simulation output parameters have been obtained by using the coupled model:

- survival dependent on minimum weight growth rates
- number of starvation periods
- condition of larvae in terms of weight at 6mm length
- growth in terms of mean length after 70 days of drift and feeding

3.4.1 Trophodynamic IBM

Encounter and turbulence submodels

Encounter rates of larval fish with their prey are functions of both larval fish size (l), prey size and density (Blaxter, 1986). An estimate of the number of the i th prey item $N(l,i)$ ($i=1,2,\dots,n$) encountered on a 24 hours basis depends on the search volume (SV) in which larvae perceive prey, and its concentration $p(i)$ (i th prey/liter). Baltic cod

larvae are visual predators (Last, 1978) and therefore the main daily feeding period can be expected only during the fraction of daylight hours H (Morse, 1989),

$$N(l, i) = SV(l, i) \times p(i) \times H \quad (5)$$

The search volume was defined as the product of the fish swimming speed $SS(l)$ and the area a fish of length l can scan for food (RA).

$$SV(l, i) = SS(l) \times RA(l, i) \quad (6)$$

For swimming speeds of larvae we used the summary relationship of Miller *et al.* (1988). This equation yields swimming speeds of approximately one body length per second. The reactive area (RA, mm^2) was assumed to be half a circle with a radius equal to the reactive distance (RD) and was defined for each prey type i as

$$RA(l, i) = 0.5 \times \mathbf{p} \times RD(l, j)^2 \quad (7)$$

The search volumes increase rapidly with increasing larval size and prey size. Prey sizes have been taken from Herrroth (1985). RD (mm) was defined as a function of both prey body length and larval length using the relationship of Breck and Gitter (1983).

Including turbulence in the calculation for prey encounter rates (Rothschild and Osborn 1988) results in the number of (i th) prey encountered estimated as

$$N(l, i) = H \times A(l, i) \times D(l, i) \quad (8)$$

instead of Eq. 5. The effect of turbulent velocities enters in the determination of $A(l, i)$, the velocity of larval fish relative to its prey and to turbulent motions. $D(l, i)$ is the product of the cross-sectional area of perception of the larvae RA and the prey concentration $p(i)$. Turbulent velocities required for the determination of $A(l, i)$ can be obtained by different methods. The simplified relationship utilized enables the calculation of turbulent velocities (MacKenzie *et al.*, 1994) directly dependent on the cube of wind speed and larval depth. Wind speed and direction were obtained from

the weather station Christiansø (up to 1994) as well as from atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden; from 1995 onwards).

Foraging submodel

Larval fish typically are not able to attack all prey encountered, thus time required for feeding reduces search time. In order to simulate this process, we utilized a submodel characterizing optimal foraging in dependency on the swallowing probability (SP) determined empirically for cod and haddock larvae by Laurence (1985). This rather simple approach is dependent on both the initial dry weight at hatch (w_{\min}) as well as on weight at age/length (w)

$$SP = 0.9 \times \left[1 - 0.667 \times e^{(-0.004 \times (w - w_{\min}))} \right] \quad (9)$$

Growth submodel

Temperature influences metabolic processes and is besides prey availability the most important factor that determines growth (Brett, 1979). As obtained from rearing experiments with Norwegian coastal cod (Otterlei *et al.*, 1999) somatic growth in length and weight increased with increasing temperature. Specific length growth rates as well as larval stage durations have been determined by these relationships adjusted to observed length growth rates of Baltic cod.

Larval growth is simulated by the standard bioenergetic supply-demand function, represented as the difference between the amount of food ingested by a larvae and the metabolic costs of its activities. The daily growth increment

$$G = AE \times g - m \quad (10)$$

is the difference between the weight gained through feeding (g) and the loss due to the weight dependent metabolic costs (m) (Werner *et al.*, 1996). The total food intake (g) of individual larvae is related to consumption from the foraging model times the assimilation efficiency

$$AE = 0.8 \times \left(1 - 0.25 \times e^{(-0.002 \times (w - 10))} \right) \quad (11)$$

which is the proportion of ingested food not egested by the larvae (Buckley and Dillmann, 1982). The assimilation efficiency strongly depends on the larval mass w ranging from 0.6 to 0.8 increasing rapidly with larval size. The ingested food provides energy exclusively used for growth after the energy for metabolic costs is totally covered.

Starvation submodel

A minimum weight (W_{\min}) at the end of the different larval stages is prescribed for each larvae. Maximum weight (W_{\max}) was taken from a length-weight relationship for Norwegian coastal cod (Otterlei *et al.*, 1999). Larvae were defined to die from starvation if the final weight in a specific stage was below a threshold value (a) times the maximum weight

$$W_{\min} = a \times W_{\max} \quad (12)$$

The threshold was set to 0.75 (Letcher *et al.*, 1996). Starvation obviously occurred if the metabolic costs are higher than the gained weight due to feeding. This submodel on starvation was able to firstly determine the mass of a larvae at death from starvation and secondly enables counting of the starvation periods.

Prey fields

Stomach content analyses (see 3.1.4) of larval cod from the Bornholm Basin revealed copepod nauplii and early copepodite stages to be the preferred prey organisms similar to what has been observed for other stocks (Goodchild, 1925; Wiborg, 1948; Last, 1978; van der Meeren and Naess, 1993; Fossum and Ellertsen, 1994). Additionally, cladoceran species, although playing a minor role, were identified as food for larval Baltic cod. The food composition of cod larvae is size-specific. Thus, for the present modelling approach we specified potential food organisms/stages for feeding larvae of a specific size:

- first feeding larvae (4.5 to 6 mm): nauplii of calanoid copepods
- larvae of 6 to 9 mm: nauplii and copepodite stages of calanoid copepods

- larvae > 9 mm: all life-stages of calanoid copepods as well as cladocerans.

Zooplankton abundance data were derived from an extensive database compiled by the Latvian Fisheries Research Institute in Riga within the EU-funded project "Baltic Sea System Study, BASYS" (<http://www.io-warnemuende.de/Projects/Basys.htm>). For detailed descriptions of the database as well as sampling and analysis procedures, see Dippner *et al.* (2000) and Möllmann *et al.* (2000). We included in the prey fields the dominant calanoid copepod (*P. elongatus*, *Acartia* spp., *T. longicornis*, *C. hamatus*) and cladoceran species (*B. longispina maritima*, *E. nordmanni*, *Podon* spp.). Densities of copepod nauplii, copepodites and adults as well as cladocerans were combined and assigned to water depth and seasonal occurrence.

In order to obtain a spatio-temporal resolution of prey, zooplankton abundances were fitted by a second order polynomial function:

$$F_{(d,t)} = \sum_{i=1}^N \sum_{j=1}^N A_{ij} * d^{(i-1)} * t^{(j-1)} \quad (13)$$

which is determined by a multiple regression analysis using the least square criteria. A_{ij} is the abundance of the above described size specific food organisms. d represents the bottom depth at any location whereas t is given in Julian days. Due to the variable vertical resolution in sampling the zooplankton data, average seasonal prey abundances have been determined for two depth layers: 0-25 and 25-50m.

3.4.2 Model simulations

First, coupled hydrodynamic/trophodynamic IBM runs were performed for the spawning periods of 1986 to 1999 in order to obtain the average intra-annual variability in survival and growth. Therefore, a total of 720 Lagrangian drifters were released at depth between 25 and 35m on a three-dimensional regular spaced grid enclosed by the 60 m isobath. The drifters were released into the modeled flow fields at 10 days intervals and were tracked for a period of 70 days, as this time period approximately covers the entire duration of the larval phase of cod (Fossum 1986). The first release date was April 1 and the last September 20, thereby encompassing the main spawning period of Central Baltic cod (MacKenzie *et al.*, 1996; Wieland *et al.*, 2000b). To investigate the effect of the strong decay in *P. elongatus* abundance,

simulations were performed with mean prey fields excluding and including this species. No effect of turbulence on the feeding of cod larvae was implemented in these simulations.

The inter-annual variability in survival and growth of larvae originating from peak spawning times was simulated for the years 1986-1999. Dates of peak spawning were estimated by Wieland *et al.* (2000b) using egg abundance data. Model simulations were initialized by ignoring turbulence and using prey fields without *P. elongatus*. In the following we successively modified the simulations by taking into account (i) the vertical distribution of the zooplankton prey, (ii) the effect of turbulence on contact rates between predator and prey, and (iii) the inter-annual trend in prey availability. As obtained from field investigations (Grønkjæ and Wieland, 1997), the vertical distribution of the small sized zooplankton particles has been given a marked peak (50% higher) in the upper part of the intermediate layer where Baltic cod larvae preferably dwell.

4 RESULTS

4.1 Variations in the drift of larval cod: Combining field observations and modeling exercises

4.1.1 Field results

Selected horizontal distributions of cod larvae obtained during the field campaign are shown in Fig. 4.1 (May 1988) and Fig. 4.2 (August 1991). For the first survey in each year the distribution of larval stages 1-5 (non-feeding) and 6-7 (first-feeding) are presented and during the second survey the distribution of stage 8 larvae (established feeders). The non-feeding larvae and can be expected to be distributed mainly below the halocline (Grønkjær and Wieland, 1997). Viable larvae of the stages 6 and 7 should have completed their vertical feeding migration and are mainly found above the halocline (Grønkjær and Wieland, 1997). These feeding larvae start to drift within the upper water masses and may be transported out of the deep basin. Larvae of stages 6-7 recorded during the first survey will have reached stage 8 by the second consecutive survey (5 and 6 day intervals between consecutive surveys for May 1988 and August 1991, respectively). The changes in horizontal distribution therefore give an indication of the drift of the larvae. Because older larval stages (9-10) would have been influenced by currents in the upper water layers for some time, their distributions are not presented.

The horizontal distribution of the stage 1-5 larvae sampled during the first survey in May 1988 (Fig. 4.1a) was restricted to the deeper part of the Bornholm basin with highest abundance in the southern central area. Stages 6 and 7 (Fig. 4.1b) were more abundant, but only a small proportion of the larvae were found outside the 80 m depth contour. Highest abundance of older larvae (stage 8) during the second survey (Fig. 4.1c) were also recorded in the central basin, indicating low transport during the 5 day interval. For May 1988, the low transport of larvae observed during the field experiment and the simulated transport are in good agreement (Fig. 4.1 cf. Fig. 4.4a). As a result, the modeled distribution (not shown) and the distribution found in the field (Fig. 4.1c) showed a high similarity, both indicating a concentration of larvae in the central basin.

In August 1991 the young larval stages were more abundant in the northern part of the sampled area (Fig. 4.2a). Stage 1-5 larvae were concentrated at two stations: one in the center of the deep basin, the other on the northern edge, slightly outside

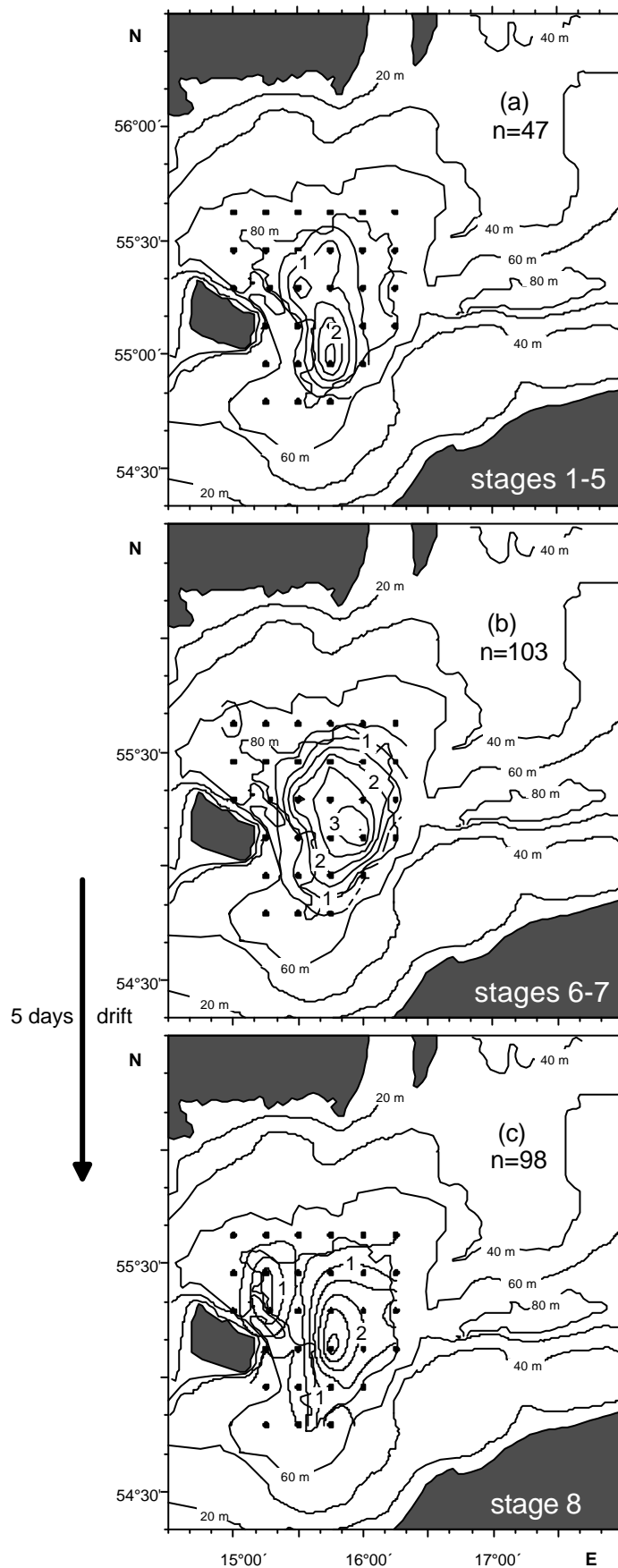


Figure 4.1: May 1988, horizontal distribution of cod larvae: a) first survey (19 May 1988), larval stages 1-5; b) first survey (19 May 1988), larval stages 6-7; c) second survey (24 May 1988) larval stage 8; contours of abundance are drawn as n/m² with the dots indicating sampling positions.

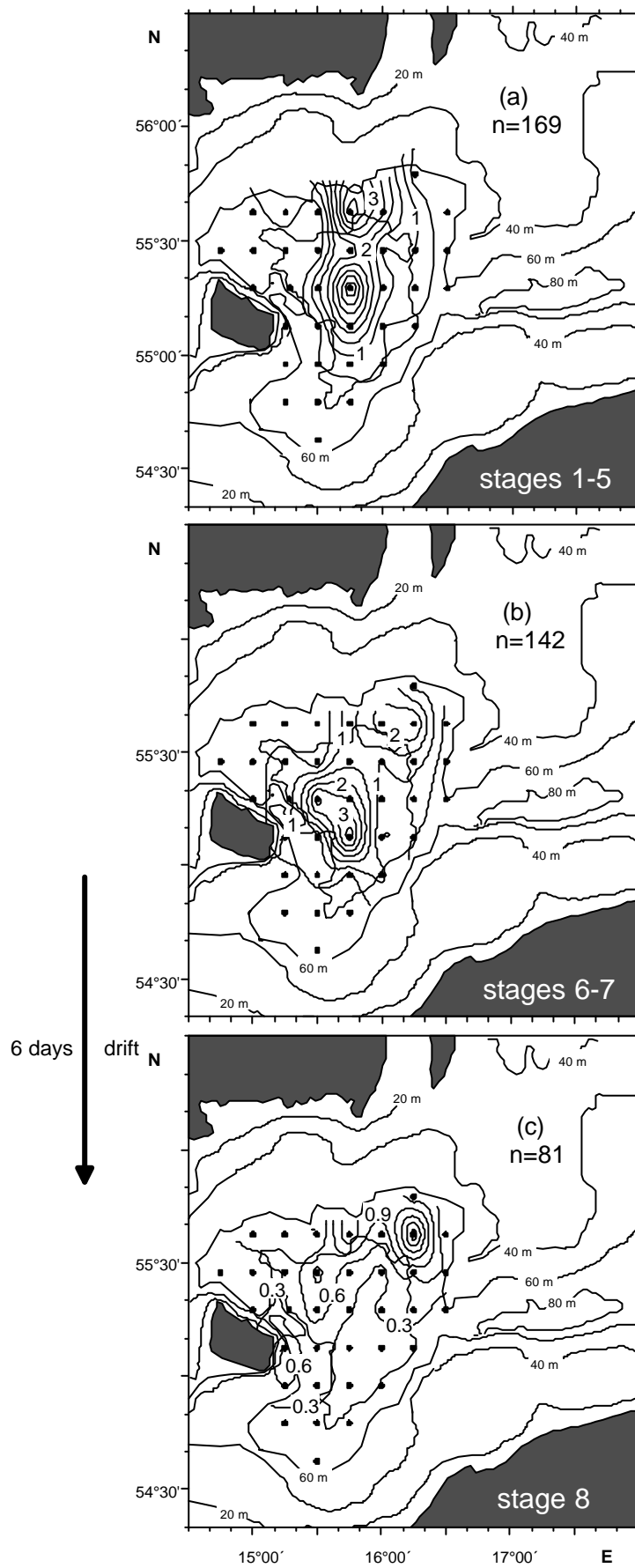


Figure 4.2: August 1991, horizontal distribution of cod larvae: a) first survey (11 August 1991), larval stages 1-5; b) first survey (11 August 1991), larval stages 6-7; c) second survey (17 August 1991), larval stage 8; contours of abundance are drawn as n/m^2 with the dots indicating sampling positions.

the 80 m depth contour. Figure 4.2b shows the horizontal distribution of cod larvae of stages 6-7, according to the first ichthyoplankton survey (11 August 1991). Two areas of high larval abundance were evident: one in the center of the Bornholm Basin, and the other in the north-eastern area. At stations in the southern and north-western parts of the basin no stage 6-7 larvae were sampled. For initialization purposes this larval distribution was introduced as an additional tracer in the simulation (see also Fig. 4.3a). The horizontal distribution of stage 8 cod larvae sampled during the second ichthyoplankton survey (17 August 1991) is shown in Fig. 4.2c. The distribution of these stages was used for comparison with the model output after 6 days of integration. A maximum of observed stage 8 larval abundance was situated in the north-eastern part of the basin with abundance declining towards the Stolpe Trench. In the south-eastern part of the sampled area only low numbers of larvae were caught, one exception being at a station located directly to the east of Bornholm ($> 0.6/m^2$). The maximum abundance in the central basin observed during the first survey was not detected on the second cruise.

4.1.2 Simulation results

Comparison of model output and ichthyoplankton survey results

Figure 4.3 summarizes the results of the comparison of model output and the results from the ichthyoplankton survey for August 1991. The horizontal distribution of stage 6-7 larvae observed during the first survey, as used for the model input is shown in Fig. 4.3a (see also Fig. 4.2b). The modeled drift trajectories for the time period between the first and second (6 days apart) ichthyoplankton surveys are presented in Fig. 4.3b. The simulated drifters launched into the model flow fields experienced the mean current velocities of the water body between depths of 24 and 42 m. Generally, the trajectories showed a northwards orientated component. In the north-eastern part of the basin this northerly drift component was rather weak, with simulated drifters heading mainly towards the east. In the region from the north-west to the south-east of the survey area, the drift trajectories showed an additional westerly component resulting in an area of divergence in the central basin. Figure 4.3c shows the horizontal distribution of cod larvae generated by the physical model after 6 days of integration. Abundance values for the positions of the stations sampled during the field campaign are shown in black, while additional positions used in the simulation, outside the survey grid, are marked in gray. According to the modeled drift

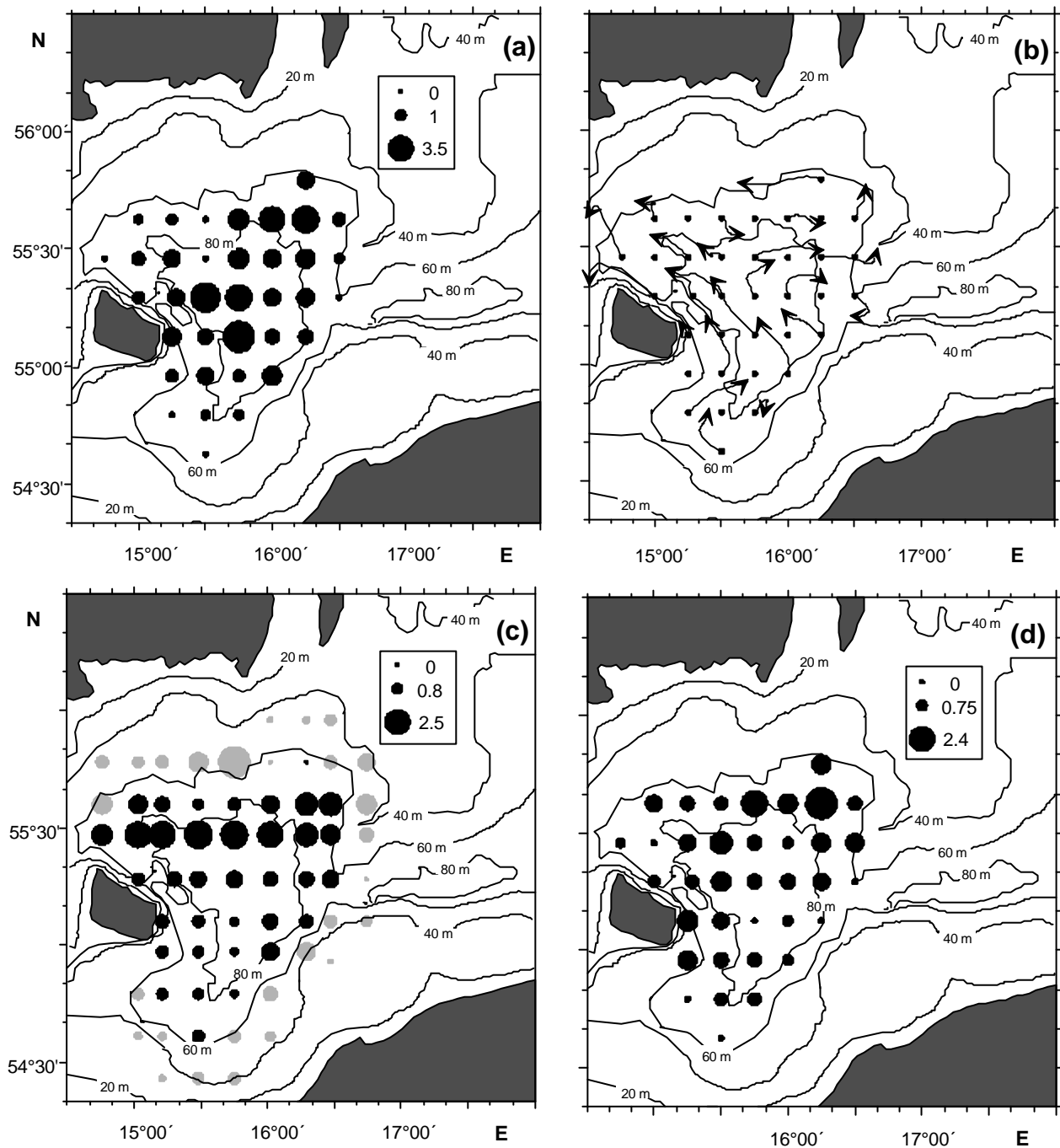


Figure 4.3: Comparison of model output and results from the ichthyoplankton surveys: a) observed horizontal distribution of larval stages 6-7 [n/m^2] for the first August 1991 survey (11 August 1991); b) modeled drift trajectories for the period between the first and second surveys (11 August – 17 August 1991), the drift relating to mean current velocities between depths of 24 and 42 m; c) modeled horizontal distribution of larval stage 8 [n/m^2] after 6 days of integration (17 August 1991), black dots indicate the actual station grid, shaded dots indicate additional positions used in the simulation; d) observed horizontal distribution of larval stage 8 [n/m^2] for the second August 1991 survey (17 August 1991).

trajectories the overall distribution has shifted northwards, high concentrations of cod larvae being found in the northern part of the basin. The maximum abundance found in the central part of the basin during the first survey may be the origin of the high abundance in the north-west in Fig 4.3c. The other maximum found initially in the north-east of the area (Fig. 4.3a) was displaced only slightly to the east, now being distributed over a broader area of four stations (Fig. 4.3c). In the southern part of the basin only low abundance values were generated by the model. The general features predicted by the model were confirmed by the second August 1991 ichthyoplankton survey (Fig. 4.3d). The overall shift in distribution towards the north, the low abundances in the southern areas and the high concentration in the north-eastern edge of the basin are in good agreement between the observations and the modeled results. However, the predicted increase in abundance in the north-west was not observed (Fig. 4.3c cf. Fig. 4.3d).

Influence of different vertical distributions on the drift

For the time periods examined, the particle trajectories generated by the Lagrangian drift model showed no significant differences related to the release of particles at different vertical levels. Deploying simulated larval drifters at different vertical levels generally gave a corresponding drift in the same direction, although the final destinations of the drifters varied. Table 4.1 shows the mean deviation of the drift end-positions after 21 days for the different levels compared with the transport based on mean current velocities for the 24-42 m depth layer.

Table 4.1: Mean deviation and standard deviation (s.d.) of the larval destinations for May 1988 and August 1991 after 21 days of drift for tracers released at different depths compared with transport for the mean current velocities of the 24-42m depth layer. Results are based on 45 start-positions.

Level	1988		1991	
	Mean deviation (km)	s.d.	Mean deviation (km)	s.d.
27m	9.338	7.834	12.772	9.601
33m	5.245	9.456	5.525	4.564
39m	13.233	14.902	15.423	11.857

For both time periods, the mean deviations at all depth levels were relatively small. The lowest deviations occurred at the 33m depth level (~5 km) while for the 39m depth level, mean deviations of approximately 15 km were calculated. The slightly higher values for August 1991 can be explained by stronger current transport during this time period. These results are in good agreement with the observations obtained from a drift modeling exercise performed for summer 1994 (Hinrichsen *et al.*, 1997). However, there were large differences between the different years in the actual drift routes. While in May 1988 the larval drifters tended to remain in the area of the deep basin during the 21 day simulation (Fig. 4.4a), in August 1991 a significant transport out of the basin occurred (Fig. 4.4b), mainly towards the east and north-west. The daily averaged wind data for May 1988 and August 1991 at the weather station at Christiansø (approximately 15 nautical miles north of Bornholm) are shown in Fig. 4.5. The lower drift velocities obtained from the simulation for May 1988 can be correlated with wind forcing which in magnitude was relatively low and strongly variable in direction. In contrast, for the 21 days simulation carried out for August 1991 the observed strong larval drift was affected by relatively strong wind forcing (10 m/s) in a mainly westerly direction.

Retention or dispersal of larvae

Figure 4.6 shows the final destinations of the simulated drifters deployed in regions of high larval abundance (shaded boxes, cf. Figs. 4.1b and 4.2b) after 21 days drift for larval stages 6-7. In accordance with the modeled drift trajectories, the resultant distributions varied considerably. In May 1988 the simulated drifters tended to remain in the deep part of the basin with a high proportion remaining within the 80 m depth contour. Higher concentrations were found in the northern part of the central deep basin with only some drifters being advected towards the south-west. In contrast, the final locations of the drifters in August 1991 were mostly outside the 80 m depth contour; generally, the final destinations of the larval drifters were widely dispersed within the northern half of the area, indicating a rapid transport out of the basin towards shallower regions. In August 1991, the area adjacent to the Swedish coast northwest of Bornholm might be considered an important nursery area for Baltic cod. A second important area is indicated to be the shallow water region to the north-east of the Bornholm Basin. Thus, for the two investigated time periods, two different drift

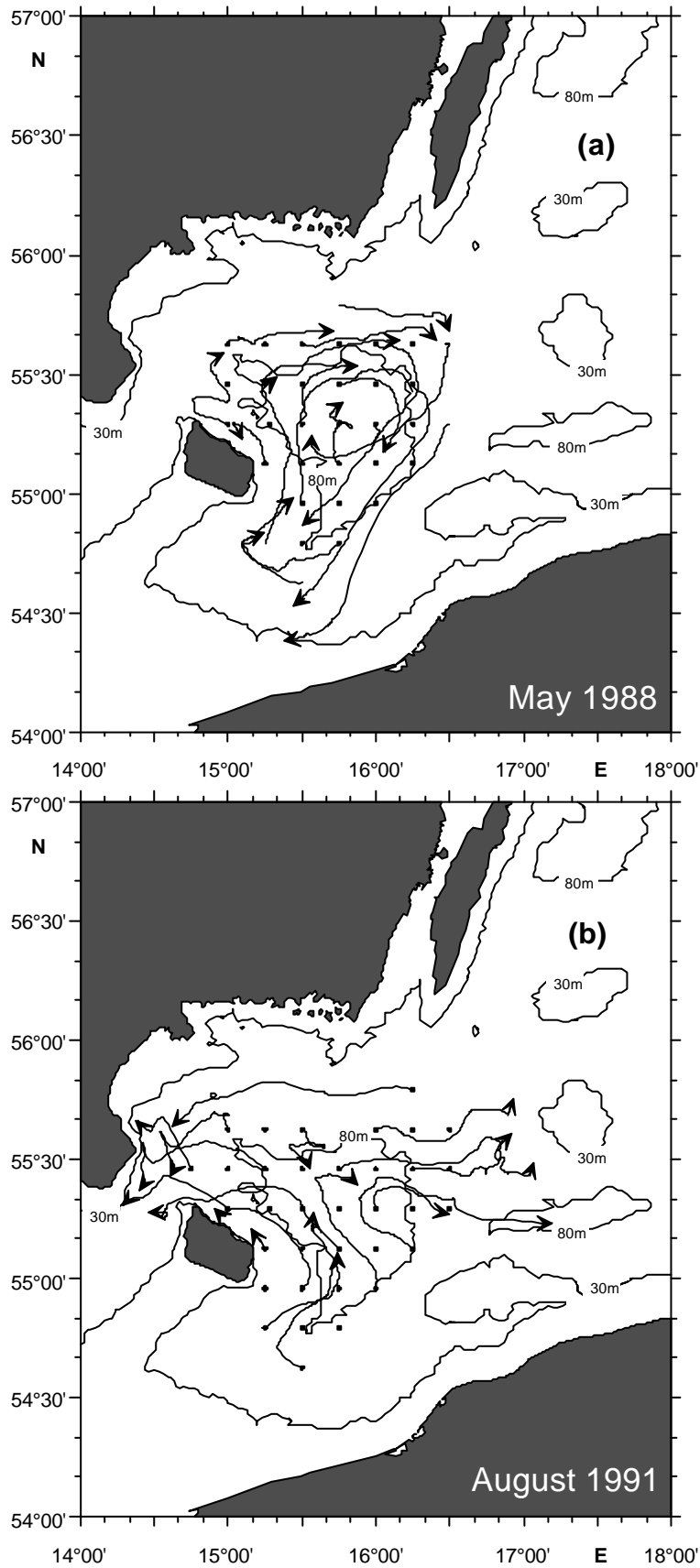


Figure 4.4: Modeled drift trajectories for a) May 1988 and b) August 1991 for a period of 21 days after the first survey based on mean current velocities in the 24 to 42 m depth layer.

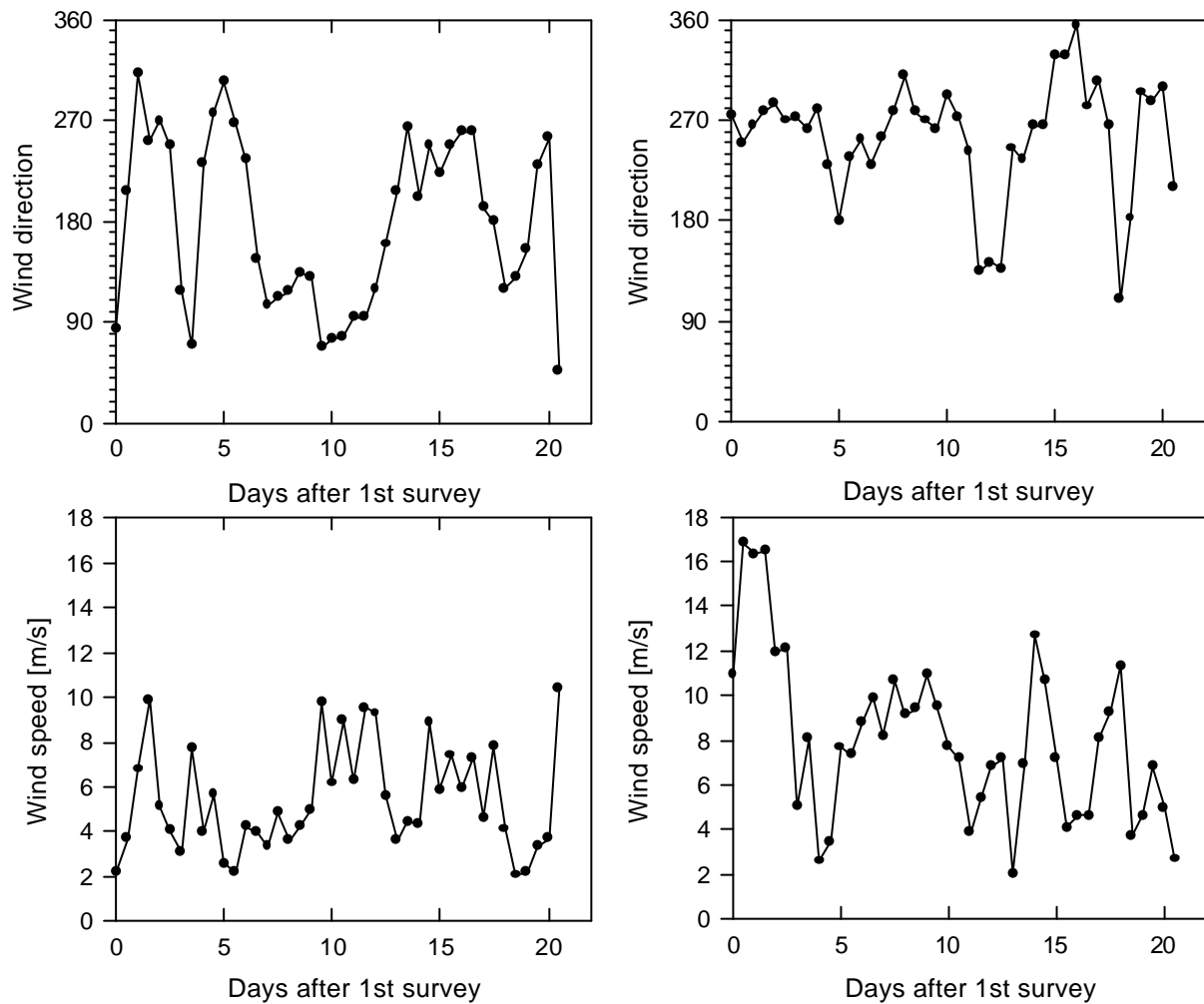


Figure 4.5: Time-series of averaged wind speed and direction (12 h means) at Christiansø weather station for May 1988 (left panels) and August 1991 (right panels).

scenarios were found: a situation of retention of larvae in the deep basin for May 1988 and a dispersal situation with larval transport towards shallow water regions for August 1991.

4.1.3 Distribution of juvenile cod and potential influence on recruitment

The spatial distribution patterns of 0- and 1-group cod based on the Baltic Young Fish Surveys (BYFS) has been investigated regularly in different areas of the central Baltic. Table 4.2 gives General Linear Model estimates (Sparholt, 1996) of age group 1 abundance for the central cod stock in the Bornholm Basin, divided into a northern and southern area and by depth strata for the years 1989 and 1992. As indicated by the physical circulation model for the 1991 year-class, relatively high abundance of 1-year-old cod was observed in 1992 in the northern shallow coastal area of the basin.

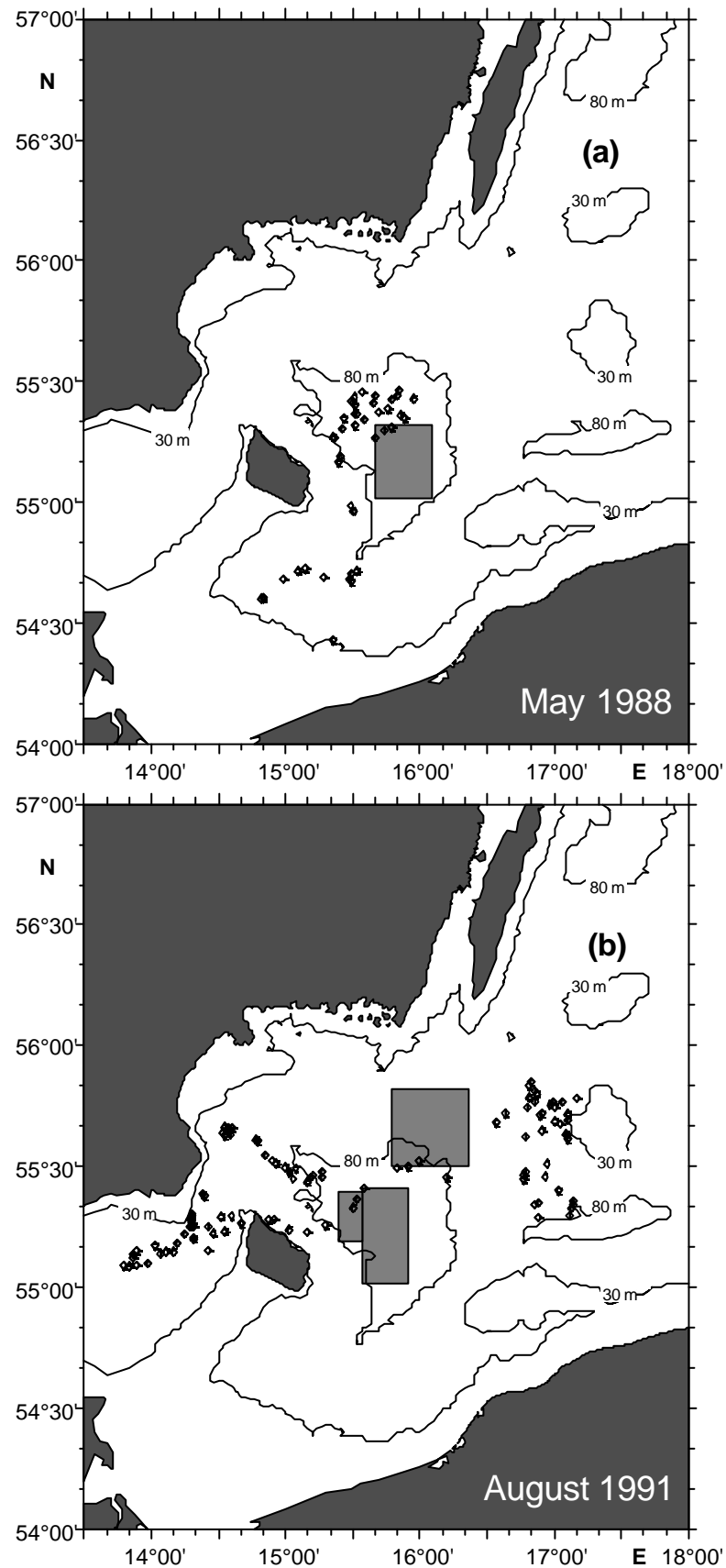


Figure 4.6: Larval drifter destinations for a) May 1988 and b) August 1991 after a 21 day drift simulation for stages 6-7. Drifters were released on a regular spaced grid in regions of high larval abundance (shaded boxes, cf. Figs. 4.1b and 4.2b).

In contrast, for the 1988 year-class, the observed distribution of age group 1 was more widely dispersed over the entire Bornholm basin.

Table 4.2: General Linear Model estimates of age group 1 abundance (numbers/hour trawling) for the central Baltic cod stock, divided into a northern and southern area and by depth strata for the years 1989 and 1992 (from Sparholt, 1996).

Year	Southern area				Northern area				
	10-40m	40-60m	60-80m	80-120m	10-40m	40-60m	60-80m	80-120m	
1989	0.0	3.7	7.0	3.4	-	3.5	0.2	0.0	Σ17.8
1992	-	43.1	7.5	22.4	-	205.5	29.9	9.8	Σ318.2

Table 4.3 shows the estimated cod egg production in the Bornholm Basin for the entire spawning seasons of 1988 and 1991 (Wieland, 1995) as well as the observed mean larval abundance for the two surveys and the resulting recruitment (age-groups 0, 1 and 2; total Baltic) according to MSVPA (ICES, 1997). The seasonal cod egg production in 1988 was estimated to be approximately the same as for 1991. For larval abundance no seasonal production values can be given. However, the sampled periods (May 1988 and August 1991) covered the peak larval abundance in each year (Grønkvæ *et al.*, 1995) and the larval abundance was of a comparable order of magnitude. The abundance of 0-group cod was calculated to be 1.22 times higher for the 1991 year-class, compared with 1988. A comparison of the abundance for the 1 and 2 year age-groups, however, shows a higher survival rate in 1991, resulting in a 1.68 and 1.78 times higher year-class strength for these age-groups, respectively. Such a comparison of cod recruitment data for the total Baltic with the conditions encountered in the Bornholm Basin might be appropriate, as the other spawning areas had only a minor impact on recruitment, due to anoxic conditions in the spawning layer (Bagge *et al.*, 1995).

Thus, recruitment success was higher in 1991, dominated by a dispersal situation in August, compared to 1988 when there was an observed retention situation in May.

Table 4.3: Estimated seasonal cod egg production for 1988 and 1991 (Wieland, 1995), observed mean larval abundance for May 1988 and August 1991 and resulting recruitment [age-groups 0 (3rd quarter), 1 (1st quarter) and 2 (1st quarter)] according to MSVPA (ICES, 1997).

	1988 year-class	1991 year-class
Egg production (numbers)	$3.65 \cdot 10^{12}$	$3.70 \cdot 10^{12}$
Larval abundance (n/m ²)	3.07 (May)	2.68 (August)
Age-group 0 (numbers)	$3.02 \cdot 10^8$	$3.67 \cdot 10^8$
Age-group 1 (numbers)	$1.58 \cdot 10^8$ (1989)	$2.65 \cdot 10^8$ (1992)
Age-group 2 (numbers)	$1.10 \cdot 10^8$ (1990)	$1.95 \cdot 10^8$ (1993)

4.2 Testing the larval drift hypothesis: retention versus dispersion

4.2.1 Within- and between-year variation

Comparisons of within- and between-year variability of larval drift and retention showed large differences between 1993 and 1994 caused primarily by variation in wind forcing. At the beginning of the spawning season (May), wind data time series (Fig. 4.7) showed low to moderate winds predominately from northern and eastern directions in both years. Larger differences occurred in the wind fields from June-August. In 1993, wind speeds varied but were mainly from the west. In contrast, 1994 showed a typical summer situation in July with, on average, low wind speeds (< 5 m/s) mainly from the east, while direction was highly variable during June and August/September, with wind speeds occasionally reaching 15 m/s.

To illustrate differences in the transport of larvae within and between years, destinations of the larval drifters are presented in Fig. 4.8 and 4.9.

Simulations for 1993 indicate larval transport to the Swedish coastal area from the central (Fig. 4.8a) and western spawning site (Fig. 4.8b) and less so from the southern spawning site (Fig. 4.8c), while drifters initially released in the northeastern spawning site ended up widely dispersed over deep water (Fig. 4.8d). In general, larval transport towards the northern coastal region is due to return flows in the interior of the basin, compensating for the circulation driven by wind forcing from the south and west (Krauss and Brüggel, 1991). Simulations for 1994 (Fig. 4.8a-d) indicate that much higher numbers were retained in deeper water and less

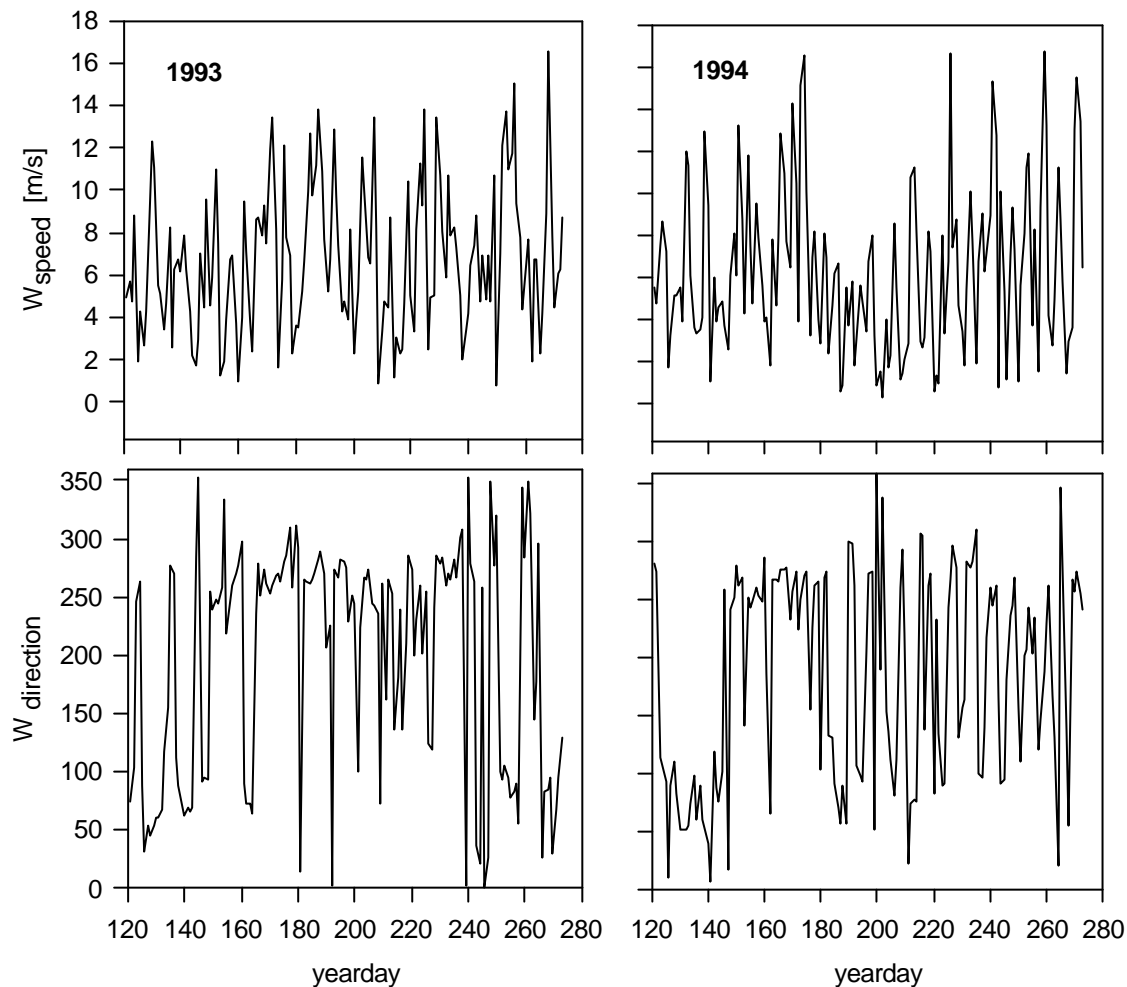


Figure 4.7: Time series of daily averaged wind speed and direction for the main spawning season of Baltic cod (May to September) in 1993 (left panels) and 1994 (right panels).

transport to shallow coastal regions because lower drift velocities predicted by the physical circulation model on the basis of the prevailing lower wind stress.

Table 4.4 summarizes the total number of drifters either remaining in the deep basins (retention) or being advected to shallow coastal waters (dispersal) based on the two vertical distribution models applied in each year. In general the annual variability in relation to wind forcing can be described as follows:

- high numbers of post-larvae end up in the Swedish coastal area during periods dominated by westerly winds (1993),
- a balance between retention and dispersal of larvae during periods with variable wind conditions (1994),
- low numbers of larvae are advected towards adjacent basins (Arkona, Gotland).

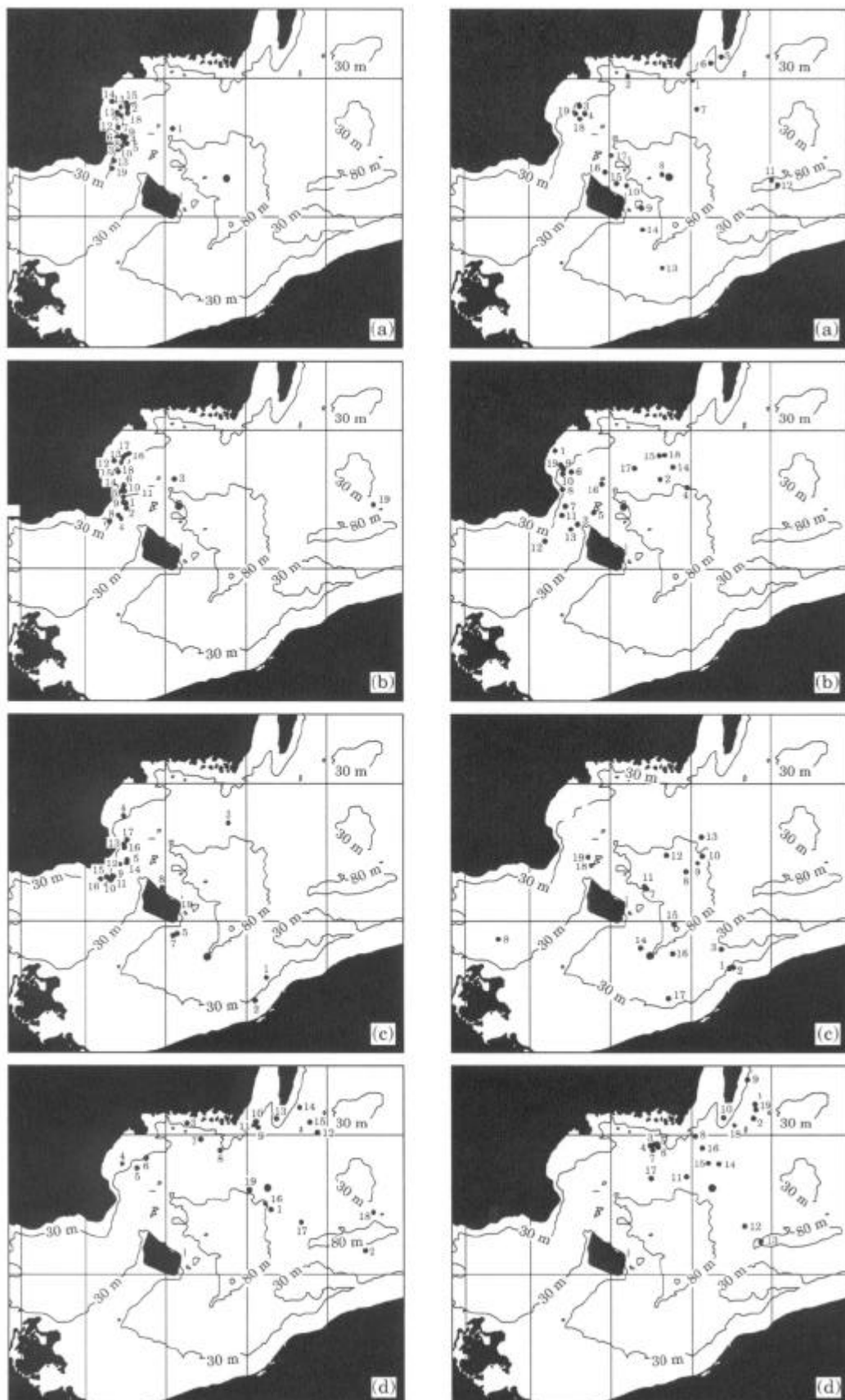


Figure 4.8: Larval drifter destinations after a 60 days drift simulation from subsequent release dates (1-19) onwards at 4 historical spawning centers (large dots; a-d in 1993 (left panels) and 1994 (right panels)).

Generally, the simulated distributions after 60 days by the two models differed only slightly (Table 4.4). However, model 2 (including vertical migration) resulted in higher retention, because mean current velocities in the intermediate layer, in which the larvae were assumed to descend during day-time, are lower than in the layer below the wind-induced mixed layer above the thermocline, where in model 1 all larvae were assumed to stay independent of the time of the day.

Table 4.4: Percentage of larvae observed (\pm s.d.) during the main spawning season in different regions after 60 days drift simulation according to two models applied to 1993 and 1994

Experiment	Bornholm basin	Gotland basin ^a	Arkona basin	Swedish coast	Polish coast ^b
1993 model 1	13.5 \pm 18.3	0.8 \pm 1.2	0.6 \pm 0.5	81.7 \pm 21.6	3.4 \pm 4.3
1993 model 2	21.5 \pm 23.9	0.9 \pm 1.8	1.6 \pm 1.1	72.2 \pm 26.9	3.9 \pm 3.8
1994 model 1	48.0 \pm 28.5	1.9 \pm 3.5	1.7 \pm 1.8	46.0 \pm 30.2	2.3 \pm 3.2
1994 model 2	60.9 \pm 27.3	2.0 \pm 2.3	2.0 \pm 2.3	31.3 \pm 27.7	1.9 \pm 3.5

^a incl. Stolpe Trench.

^b incl. Bornholm coastal area.

4.2.2 Temporal evolution of larval transport

Figure 4.9 shows the temporal evolution in the percentage of larval retention and dispersal to coastal areas over the duration of the main spawning season in relation to cumulative wind energy from different directions during the 60 days larval drift period in the two years. The x-axis indicates the date of larval batch release (hatch). Larvae hatching at the beginning and end of the spawning season in 1993 experienced a fair amount of low wind forcing from the eastern and northern direction. This resulted in a relatively low transport to northern coastal areas. Over most of the spawning season, the predominant wind forcing came from western and southern directions, causing the transport of most larvae to northern coastal areas. The influence of a period of low wind energy can be observed in the 1994 simulation. A period of quiet weather resulted in a strong decrease in the percentage of larvae transported to the northern coastal areas and retention of larvae over deep water.

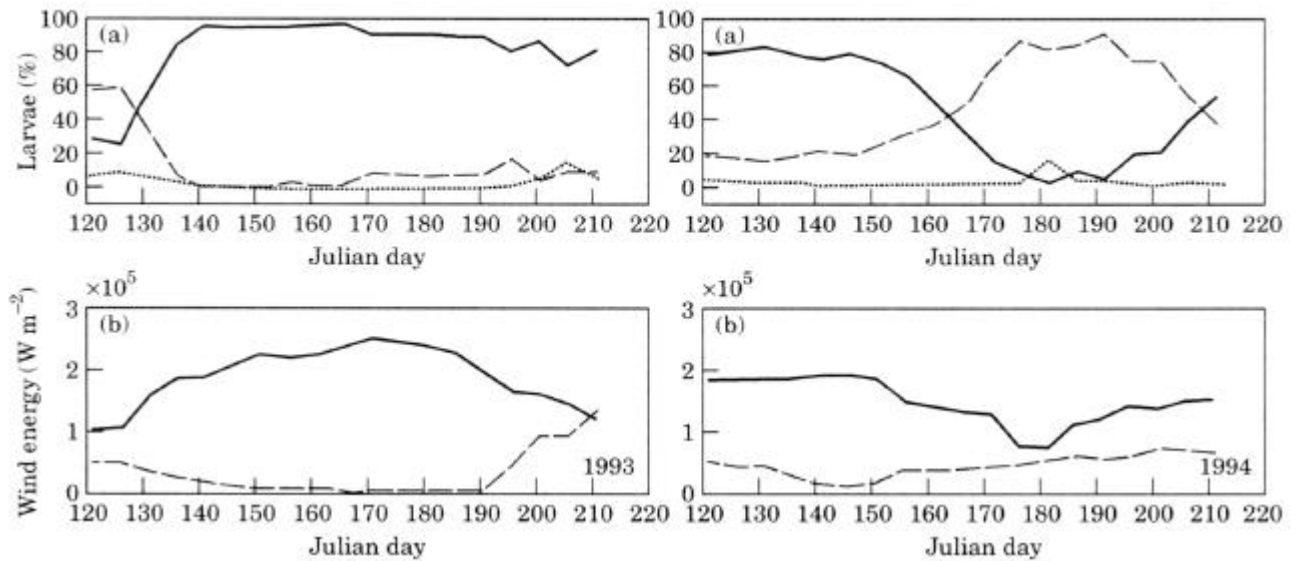


Figure 4.9: Relative frequency of simulated larval drifters (top panels) ending up in the deep basin (broken line), advected to northern coastal waters (full line), and advected to southern coastal waters (dotted line), and wind energy (bottom panels) from south to west (full line) and north to east (broken line) directions in relation to time of release during the spawning season, 1993 (left) and 1994 (right).

4.2.3 Developing a transport index

Figure 4.10 shows two examples of the fate of cod larvae under different constant windstress. For westerly winds, the percentage retained in deep water dropped rapidly when energy exceeded 100000 Wm^{-2} and a balance (50% retained and 50% advected) between transport of larvae to the northern coast and retention was reached at 140000 Wm^{-2} . For easterly winds, the percentage of larvae transported to the southern coast increased rapidly when energy exceeded 50000 Wm^{-2} and the balance was reached at 115000 Wm^{-2} . A similar simulation applying windstress from the north showed the potential for advection of larvae towards the eastern basins through the Stolpe Trench. Approximately 10% of the larvae ended up in this region when energy was 35000 Wm^{-2} .

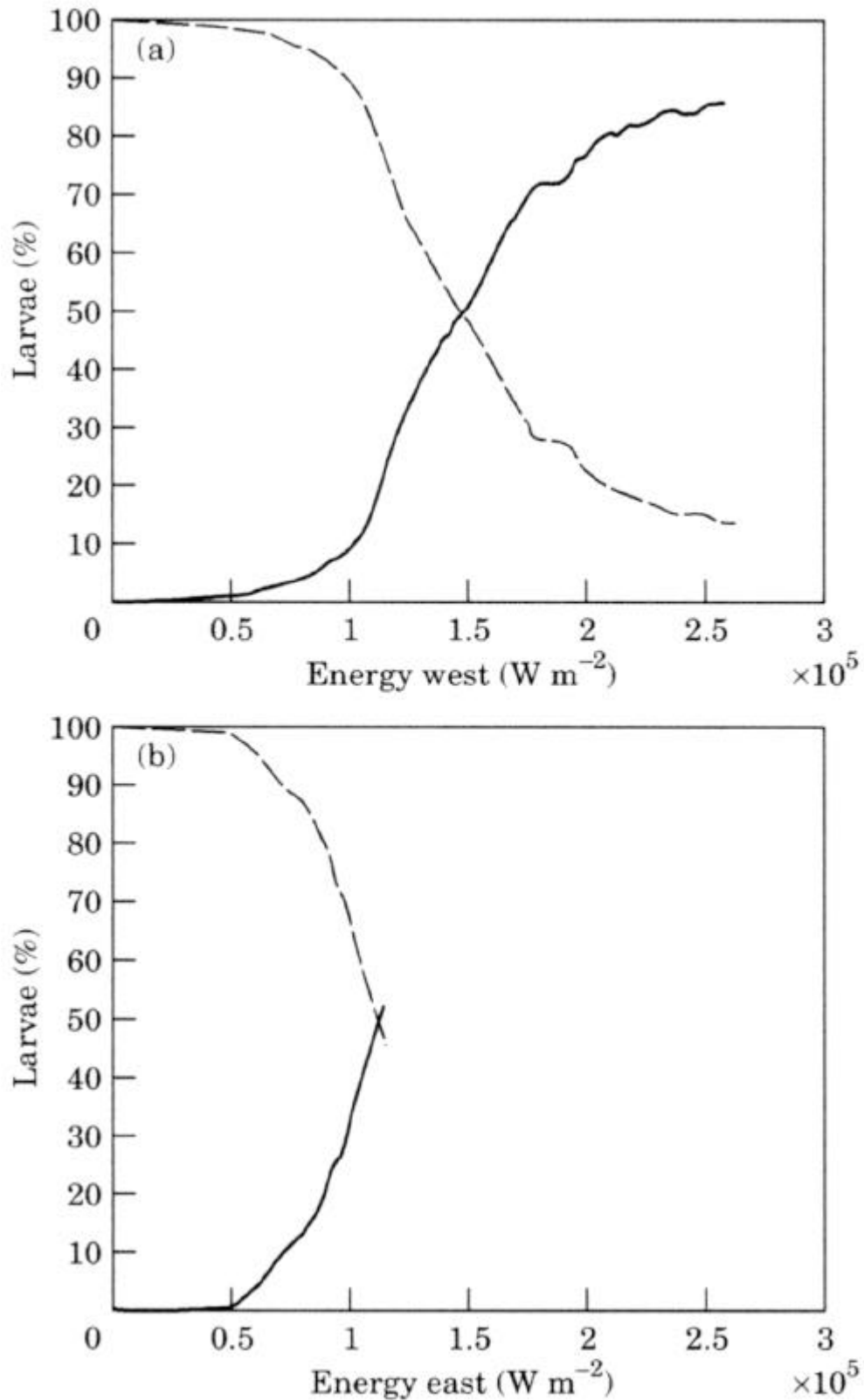


Figure 4.10: Percentage of larvae retained in the deep basin (broken line) and percentage advected to coastal area (solid line) in relation to wind energy derived from numerical simulations with constant wind forcing: (a) westerly winds and advection to northern coasts and (b) easterly winds and advection to southern coasts.

Based on the results obtained in the simulations under constant wind forcing, the transport index can be divided into three typical classes:

- Dn: transport to the northern coasts when wind energy $>140000 \text{ Wm}^{-2}$
- Ds: transport to the southern coasts when wind energy $<115000 \text{ W m}^{-2}$
- R: retention in the deepwater areas for intermediate values.

To illustrate differences between and within years, the calculated transport indices are presented in Fig. 4.11. Positive values, indicating westerly and southerly winds, predominate in all years, 1979-1994 with highest 60 days values observed in 1985 (283000 Wm^{-2}). Negative indices are absent in several years and exceeded the dispersal limit to southern coasts only in 1993 (133000 Wm^{-2}). Estimates of mean cod egg abundance at different times of the spawning season in the Bornholm Basin (Wieland *et al.*, 2000b) are also shown for 1985-1994 to allow an evaluation of the most critical period for larval transport. Unfortunately, no seasonal abundance data are available for the earlier years. However, historical data on gonadal maturation (Tomkiewicz and Köster, 1999) and egg abundance (Wieland *et al.*, 2000b) reveal a clear shift of spawning activity to later months within the last 10 years. This suggests that the spawning took place relatively early in 1979-1984, which would mark these years as typical retention years, with the possible exception of 1982. In 1985, there was a good chance for dispersal for larvae born after the spawning peak, but subsequently retention years continued until 1989. From 1990 onwards, a series of dispersal years occurred, during which larvae may have been rapidly transported to the northern coasts. High easterly wind energy observed during the late spawning season in 1993 might also have resulted in transport of a relatively large fraction of larvae to the southern coasts. In view of the extremely high egg abundance during a period of retention, 1994 must be considered as a retention year, although the number of eggs in August was still higher than in other years and these should have been advected towards the northern coastal area.

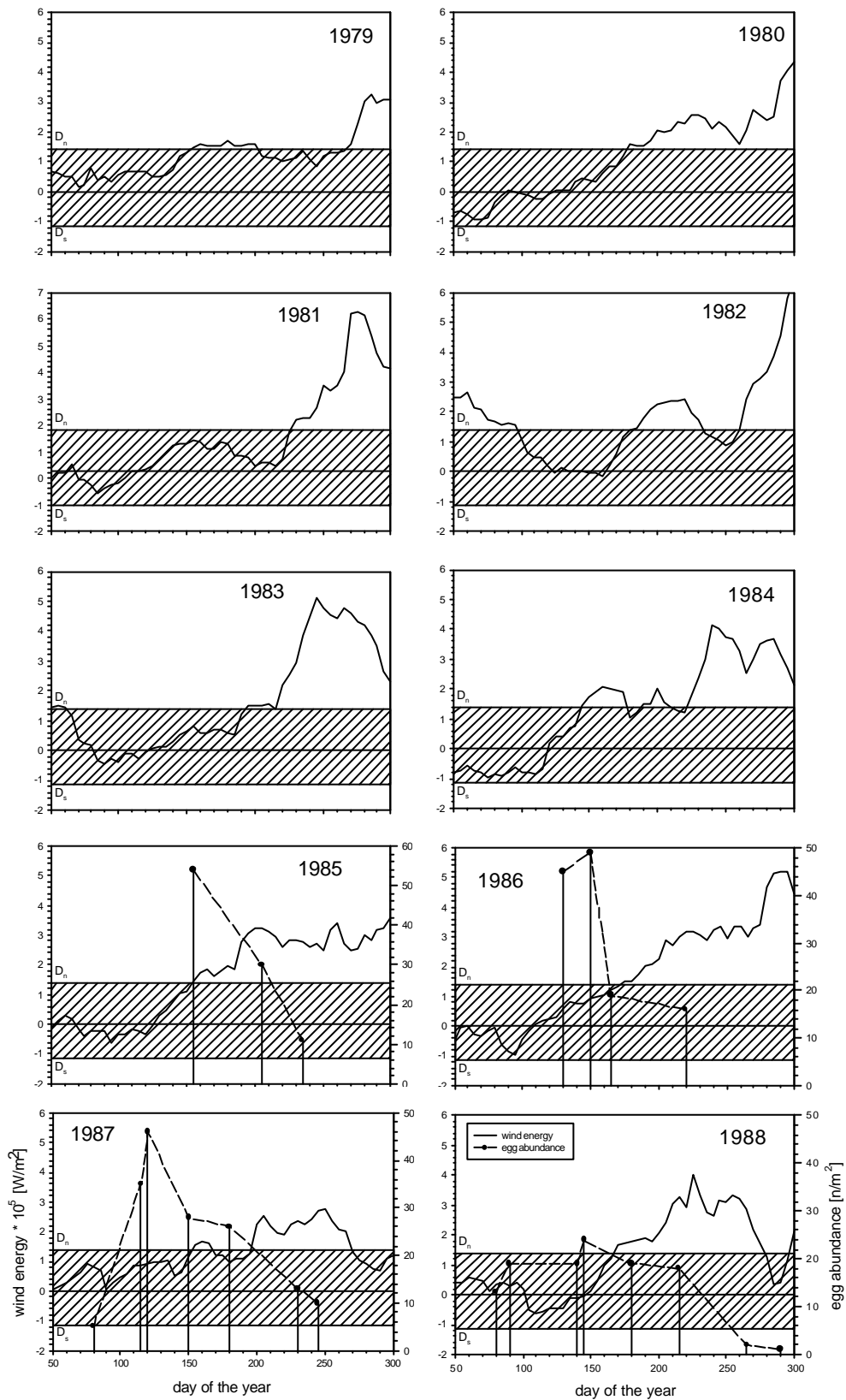


Figure 4.11: Variations in wind energy (solid line) (cumulative sums over 60 days at 5 days intervals; south to west: positive; north to east: negative), 1979-1994 (hatched interval indicates wind energy values that are expected not to result in advection to northern or southern coasts; see text). For 1985-1994, estimates of mean cod egg abundance (points) in the Bornholm Basin are also indicated.

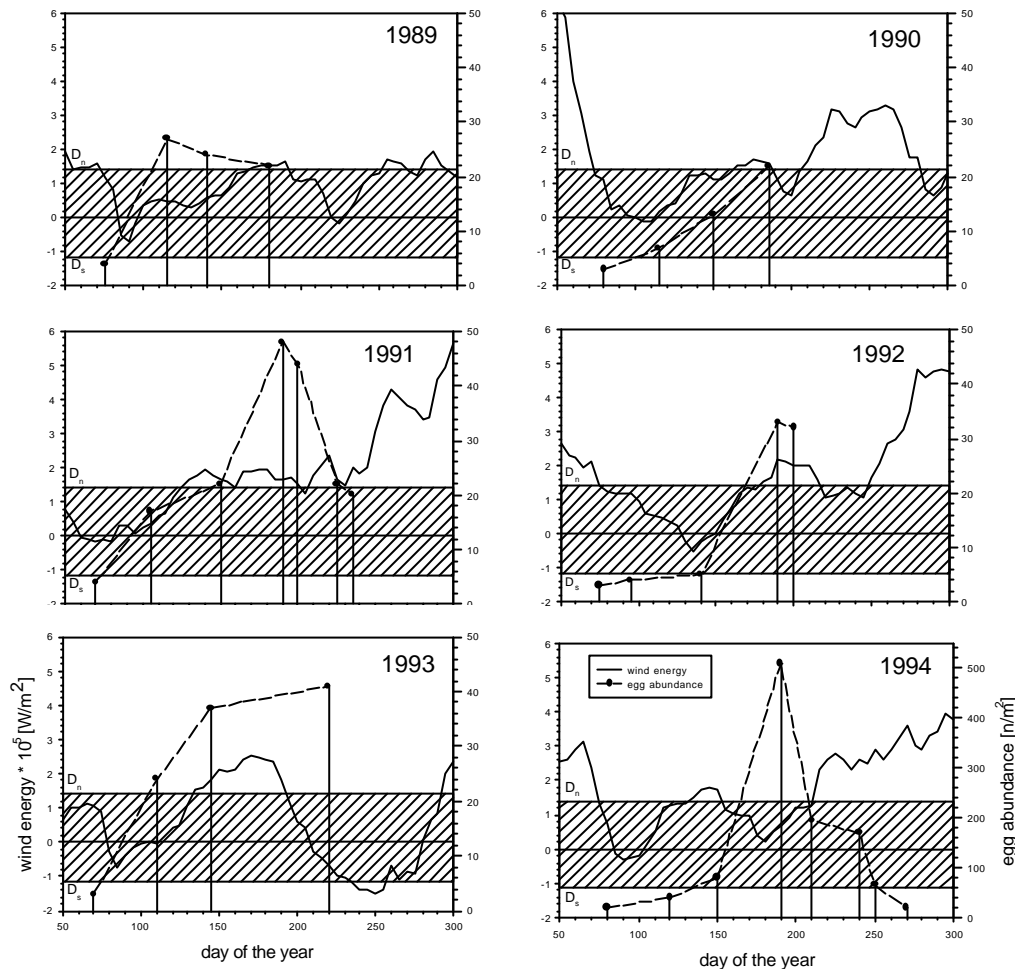


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4.2.4 Spatial distribution of juvenile cod

Information on spatial distribution patterns 1-group cod has been collected regularly in the Baltic Young Fish Surveys. Assuming that juvenile cod remain fairly stationary during winter, the estimates of abundance of 1-group by depth zone for the northern and southern compartments of the Bornholm Basin based on General Linear Modelling (Tab. 4.5; from Sparholt, 1996) have been qualitatively compared with the classification in retention and dispersal years. However, this comparison is restricted by the lack of samples from the shallow coastal zones in most years. Juvenile cod from the year classes 1991-1993 were most abundant in the northern part of the Bornholm Basin below 60m, which seems to correspond with dispersal to northern waters. However, this was also the case for the year classes 1987 and 1989, which were considered to be retention years. Year classes 1984 and 1994 were most abundant in the southern part <60m, which cannot be explained by the transport

indices in those years. All other year classes were more abundant in the southern part > 60m, which would correspond to retention in the deeper areas. The dispersal years 1985 and 1990 do not show corresponding shifts in juvenile cod abundance.

Table 4.5: Age 1-group cod estimates (number/hour) for different parts of Sub-division 25 (from Sparholt, 1996).

	South				North			
	10-40m	40-60m	60-80m	80-120m	10-40m	40-60m	60-80m	80-120m
1980	-	1.0	18.0	22.0	-	0.0	0.0	11.8
1981	-	-	887.4	-	-	-	174.9	-
1982	-	1.3	103.7	1.1	-	32.2	0.6	-
1983	-	23.1	79.6	29.0	-	13.7	38.2	39.2
1984	11.8	60.1	34.1	18.5	-	3.9	13.1	0.0
1985	-	4.9	40.6	18.3	-	2.0	8.4	0.0
1986	-	2.8	21.6	0.0	-	18.6	3.7	-
1987	-	0.0	91.3	0.0	-	-	1.4	0.0
1988	-	0.9	12.1	2.0	-	30.5	3.4	0.0
1989	0.0	3.7	7.0	3.4	-	3.5	0.2	0.0
1990	-	2.6	2.1	-	-	22.5	0.2	-
1991	-	23.4	11.5	2.0	-	3.0	0.2	-
1992	-	43.1	7.5	22.4	-	205.5	29.9	9.8
1993	2.9	13.1	11.8	1.9	-	196.2	37.3	-
1994	0.0	2.8	35.1	7.2	13.0	39.6	15.6	0.0
1995	1.7	120.2	76.2	3.6	23.0	72.1	2.4	-

4.3 The potential for advective exchange of the early life stages between the western and eastern Baltic basins

4.3.1 Length and age of juvenile cod in the Arkona Basin and Bornholm Basin

The 0-group cod caught in autumn in the Arkona Basin and the Bornholm Basin can be divided into two major size classes. The length groups of cod between 3 to 7 cm and 8 to 14 cm caught within the Arkona Basin during autumn were traced back to spawning activities in July to August and March to May (Fig. 4.12a). Figure 4.12b displays the distribution of birthdates of juveniles caught in the Bornholm Basin.

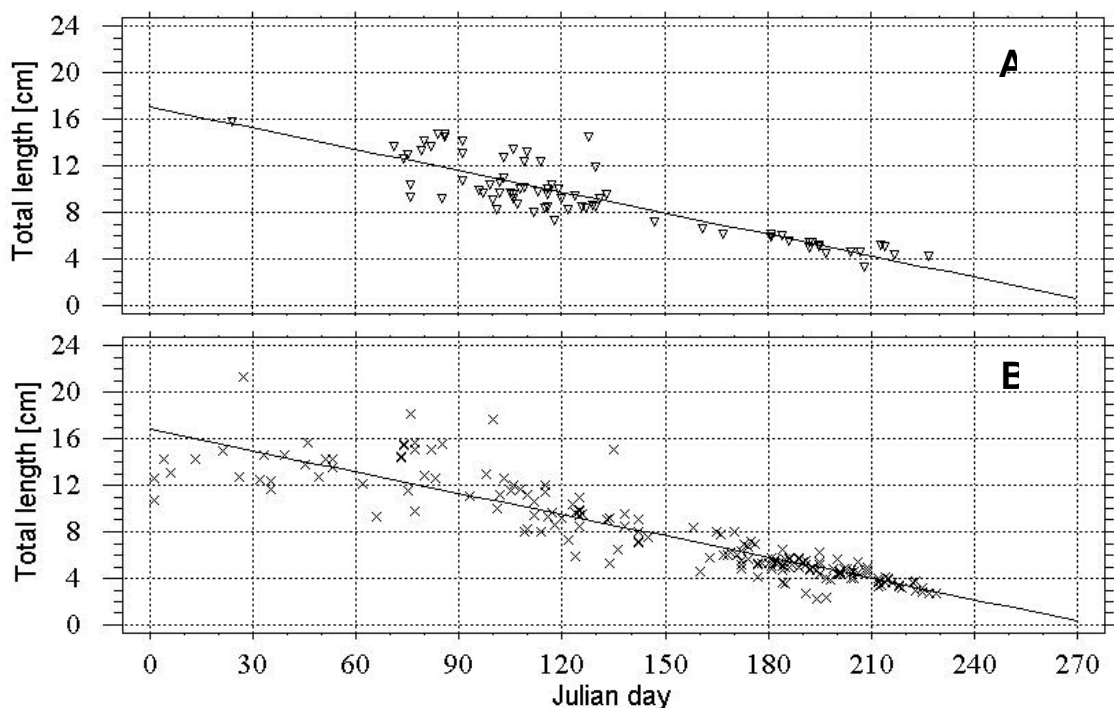


Figure 4.12: Distribution of total lengths and birthdates for juvenile cod caught from 1993 to 1996 in a) the Arkona Basin, and b) the Bornholm Basin with lines representing linear regressions.

According to data on the temporal gonad development of cod (Bleil and Oeberst, 1997), the distribution of the birthdate estimates agrees well with the observed peak spawning periods for different areas of the Baltic Sea. The spawning season in the Arkona Basin and the Bornholm Basin covers the same time range, from May to July/August, therefore individuals spawned in summer months (Julian day 150 - 250) can be assigned to these spawning regions. The spawning season in the western Baltic had starts already in February and ends in May. Within this region the development of the gonads started later from west to east. Individuals originating from this group made up the majority of 0-group cod caught in the Arkona Basin (Fig.

4.12a), but were also present in the Bornholm Basin (Fig. 4.12b). The additional fraction of juvenile cod found in the Bornholm Basin with back-calculated birthdates from January represents individuals spawned in the Kattegat region (Börje *et al.*, 1985).

4.3.2 Advection of early life stages from western to eastern basins

An overview of displacements of particles launched within the western Baltic can be obtained from Fig. 4.13, which shows the horizontally resolved but vertically integrated cod egg and/or young larvae concentrations generated by the circulation model. The figure shows the final locations of the arbitrarily chosen abundances after a 25-day integration period for scenarios 1 and 2 (Julian day 6 to 31; scenario 1: 1988 with low and variable wind forcing; scenario 2: 1993 with strong westerly wind forcing). By day 25, all particles, initially started as eggs, will have reached the stage of young larvae. In scenario 1 (1988), only low transport rates towards the Arkona- and Bornholm Basin were recognized (Fig. 4.13a). As a consequence, this resulted in a relatively high fraction of larvae remaining in the area where they were spawned. Individuals spawned in the Øresund, as well as in Kiel Bay and in Mecklenburg Bay, clustered as well near their spawning grounds. Individuals spawned in the area of the Little and Great Belt have completely disappeared from their area of origin and were transported mainly towards Kiel and Mecklenburg Bay. Conversely, in scenario 2, most of the individuals were advected towards the east (Fig. 4.13b). After 25 days of integration, the absolute maximum abundance of particles was found within the area of the Bornholm Deep (55°30' N, 15°30' E). Furthermore, from the numerical experiment, two intermediate maxima within the Arkona Basin were observed. The high particle transport in scenario 2 (1993) orientated from west to east was due to extremely high wind speeds from westerly directions (see Fig. 3.3). In contrast, wind forcing in scenario 1 was considerably lower and more variable in direction.

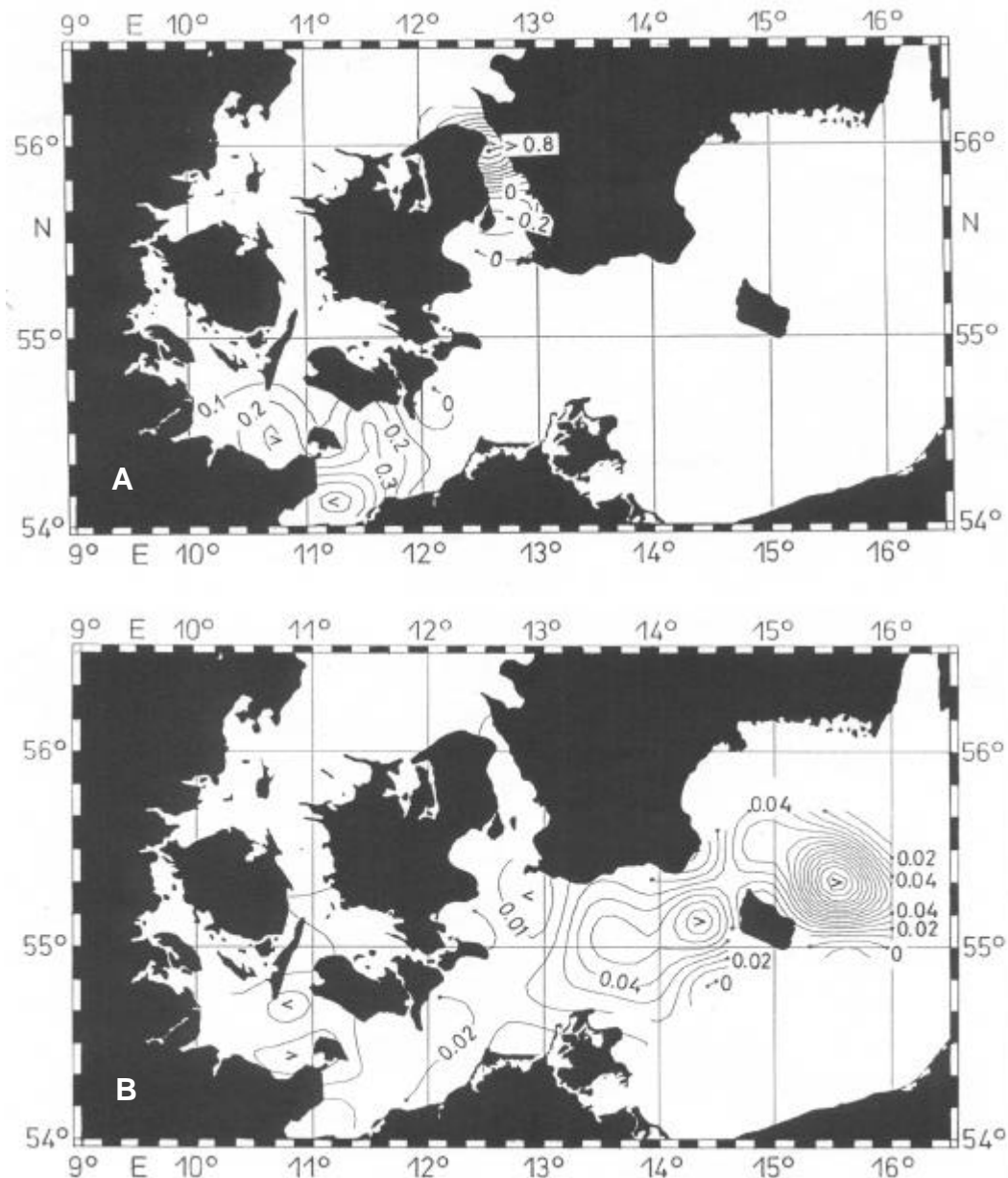


Figure 4.13: Horizontal distribution of tracers representing cod eggs and young larvae initially released within the spawning grounds of the western Baltic cod stock on 5 January of each year at a) the end of January 1988 (contour interval 0.1 n/m^3), and b) the end of January 1993 (contour interval 0.01 n/m^3).

A more detailed comparison of the particle transport for the two considered scenarios is given in Fig. 4.14. For scenario 1, at the beginning of the spawning period (Julian day 7), the flow fields showed only weak northward transport, whereas a stronger transport from Kiel Bay and Mecklenburg Bay towards the Øresund region occurred after the onset of a longer period of wind forcing from northeastern direction (Julian day 15). However, in general, particle transport towards the Arkona Basin was of minor importance only.

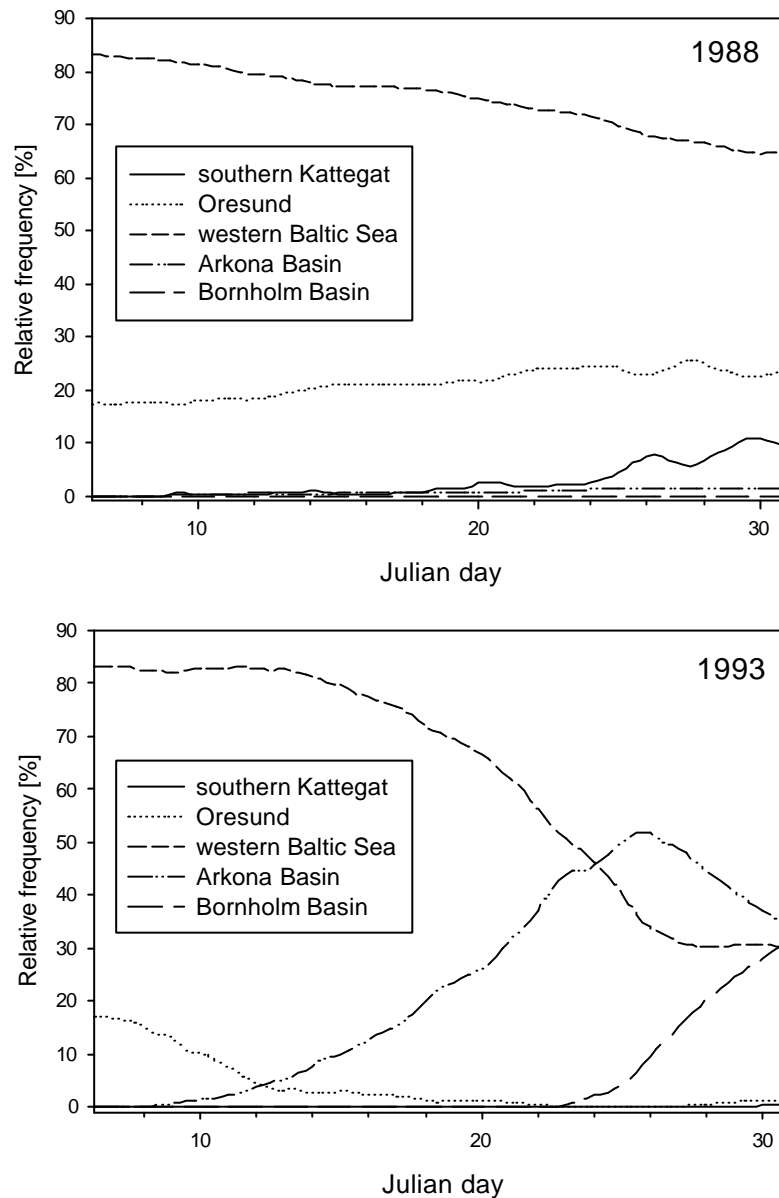


Figure 4.14: Time series (January 1988 and 1993) of relative frequency of cod eggs and young larvae initially released as tracers in the western Baltic ending their drift within different areas of the Baltic.

In contrast, scenario 2 depicted a typical inflow situation often accompanied by high wind speeds (>15 m/s) mainly from a westerly direction. The particle transport throughout the entire simulation period was dominated by advection of water masses from the Skagerrak/Kattegat region and the western Baltic towards the central Baltic. Correspondingly, after the 25 day simulation period, almost 70% of the particles representing eggs and/or young larvae left the spawning grounds of the western Baltic and were quickly advected into the Arkona Basin and, partly, further eastward into the Bornholm Basin. Compared to scenario 1, transport of particles from the

Danish Straits further northward towards the Skagerrak/Kattegat region was not detectable.

Further support for the results on annual variability of the circulation due to meteorological forcing, can be derived from the temporal development of the final destinations of Lagrangian drifters representing older (feeding) larvae as well as pelagic juveniles. Such investigations were performed for both scenarios over the entire duration of the major spawning period of the western Baltic as well as for the Kattegat cod stock (Fig. 4.15). The number of drifters advected into a specific region at a given time after release varies with wind forcing conditions, and thus can be used as a tool for understanding variability of particle drift induced by variability of the wind driven flow component. It should be noted that feeding larvae were initially inserted into the simulated flow fields higher (0 - 20 m) in the water column and thus, were more directly associated with the direct wind-driven component of the flow fields.

For scenario 1, Lagrangian drifters released either at the beginning of the spawning season or later than Julian day 40, primarily experienced moderate wind forcing from a southerly to an easterly direction during their 45 day drift periods. This resulted in a relatively high occurrence of particle transport towards the southern Kattegat. Drifters inserted between Julian day 20 and 40 were influenced mainly by winds of a westerly direction, thus, generally, particle transport towards the north decreased rapidly. Instead, an increase of particle drift towards the east (Arkona Basin) was observed. During the simulation period of scenario 1, no substantial transport towards the east of larvae originally spawned in the western Baltic or in the Kattegat can be derived from the model results. In contrast, during the major Baltic inflow (scenario 2), more than 30% of the larvae were advected through the Arkona Basin into the Bornholm Basin, caused by extremely high wind forcing from a westerly direction. As soon as the influence of these winds diminished, the number of particles showing transport towards the east decreased, whereas the number of larvae with final destinations in the Kattegat and the Danish Straits became more numerous. Drift towards the Bornholm Basin was not evident (Julian day 35) but occurred again afterwards, primarily due to the influence of single wind events mainly from a western direction at the end of March (Julian day 75 to 85).

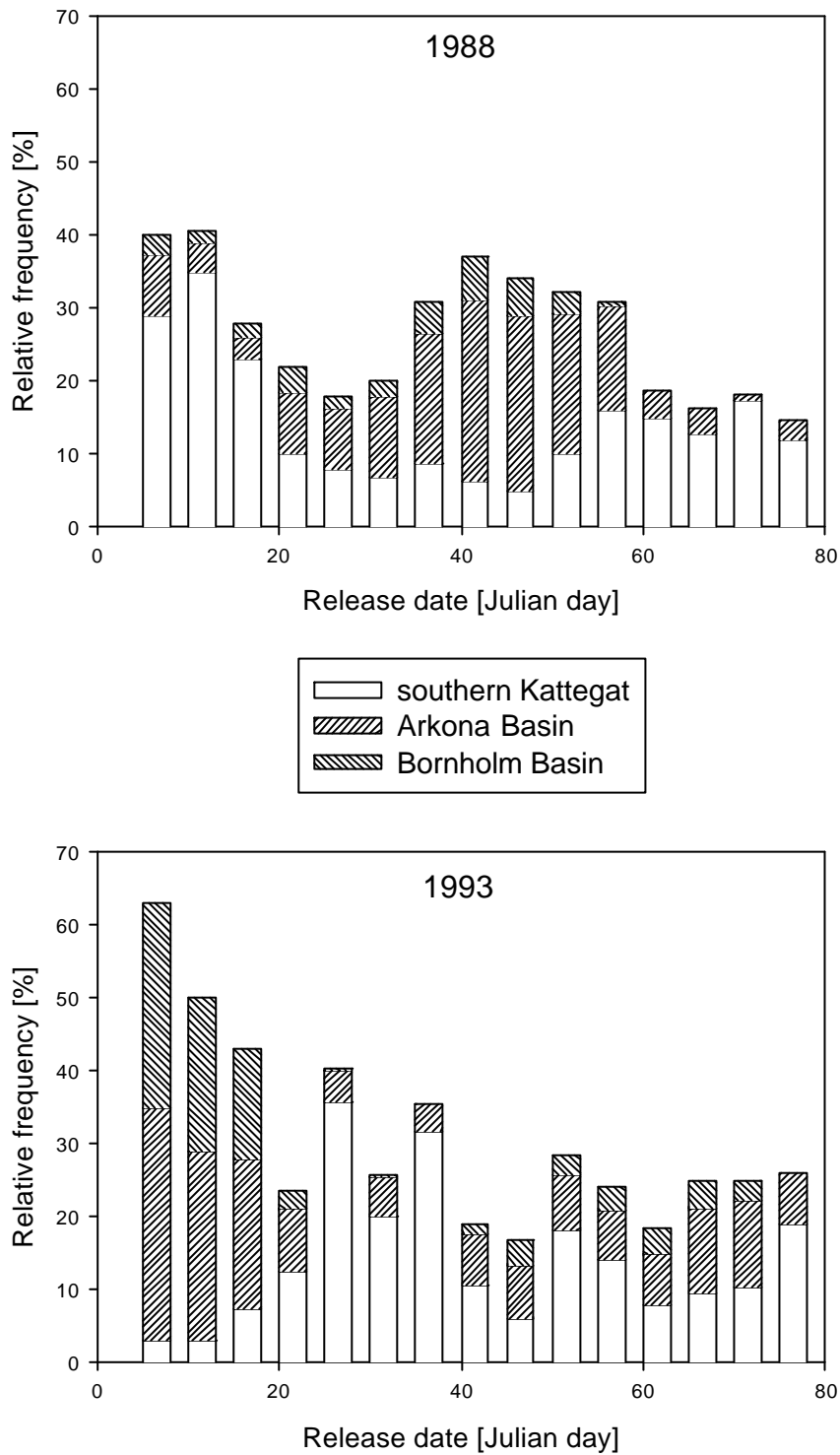


Figure 4.15: Time series (January to March 1988 and 1993) of relative frequency of Lagrangian drifters (drift duration 45 days) ending their drift within the southern Kattegat, the Arkona Basin, and the Bornholm Basin. The x-axis indicates the dates of release.

In order to identify differences in the eastwards transport of particles, the final destinations of drifters initially released in the western Baltic spawning grounds (area I-IV, see Fig. 3.2) are presented in Fig. 4.16. This analysis indicates that areas II and III can be identified as the main contributors of the western Baltic spawning stock to the juvenile population of the Arkona Basin and partly also of the Bornholm Basin. Enhanced transport from area I and IV towards the Arkona Basin was obtained only in cases of extremely strong wind forcing from a westerly direction.

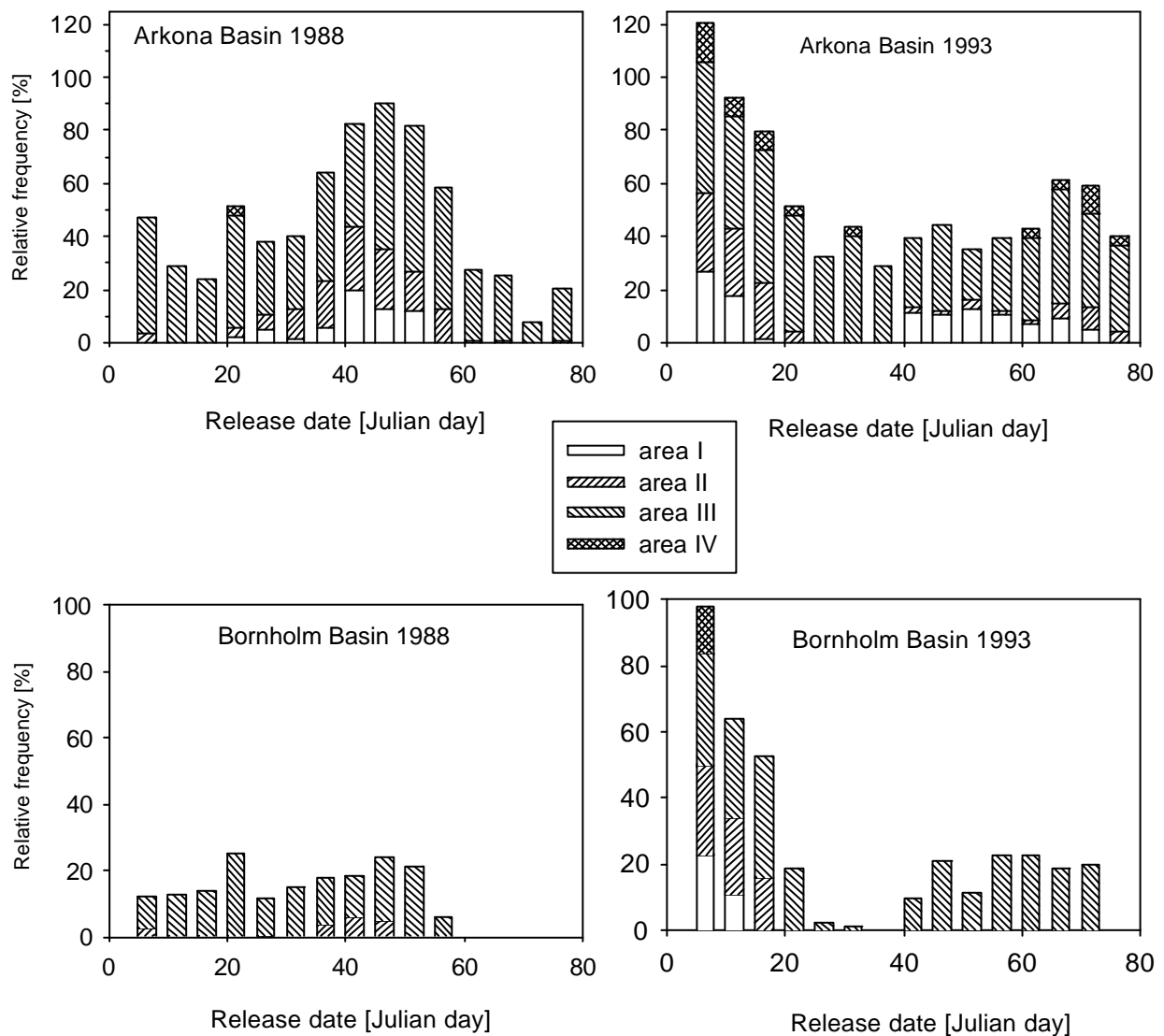


Figure 4.16: Time series (January to March 1988 and 1993) of relative frequency of Lagrangian drifters (drift duration 45 days) destined for the Arkona and the Bornholm Basin and initially released (see Fig. 3.2) in the Great Belt (I); the Little Belt, Kiel Bay, Langeland Belt and Fehmarn Belt (II); Mecklenburg Bay (III); and the Øresund (IV).

4.4 Model-supported estimation of mortality rates in cod larvae: the varying impact of 'critical periods'

4.4.1 Initial horizontal distributions

The horizontal distribution of cod egg stage IV and larval stage 5-7 as obtained from the first survey in each field campaign is shown in Figs. 4.17 and 4.18. In May 1988 the egg stage IV is concentrated in the area >80m water depth (Fig. 4.17a).

Especially 3 stations in the north, west and south of the Bornholm Basin showed higher concentrations. In the area outside the 80m depth contour only small numbers of cod egg stage IV were found. The distribution of larval stages 5-7 is somewhat wider (Fig. 4.17b), but the highest concentration are still found in the centre of the basin. Only to the east and south-east considerable numbers of larvae were recorded in the area < 80m depth. During the first survey in August 1991 the centre of the egg stage IV distribution was displaced to the north-western edge of the deep basin (Fig. 4.18a). The station with the maximum abundance was located just inside the 80m depth contour line, however, in this region eggs of developmental stage IV were also found shallower than 80m depth. Figure 4.18b displays the distribution of the larval stages 5-7. In contrast to egg stage IV, highest numbers were now obtained in the central part of the deep basin. However, considerable concentrations of larvae were also recorded in the area between 60-80m water depth, especially in the north-eastern part of the basin.

4.4.2 Hydrodynamic model runs

Figure 4.19 shows the mean circulation (speed, direction and stability) in the depth layer with maximum cod egg or larval abundance for May 1988. The circulation patterns were averaged over a 5 days period, beginning with the time point of the first survey. For the depth layer with the assumed maximum cod egg abundance (69-72 m) low transport speeds were found (Fig. 4.19a). Especially in the northern part of the basin and along the edges a high stability of the prevailing currents could be recognised. In the centre of the deep basin an almost circular transport regime was established. So, only limited transport rates across the 80 m depth contour line were to be expected. Figure 4.19b shows the mean circulation for the depth layer of maximum cod larval abundance (30-33 m). Also in this case a circular transport regime could be observed. However, the current speed is much higher and the southern edge of the circular transport extends towards shallower regions.

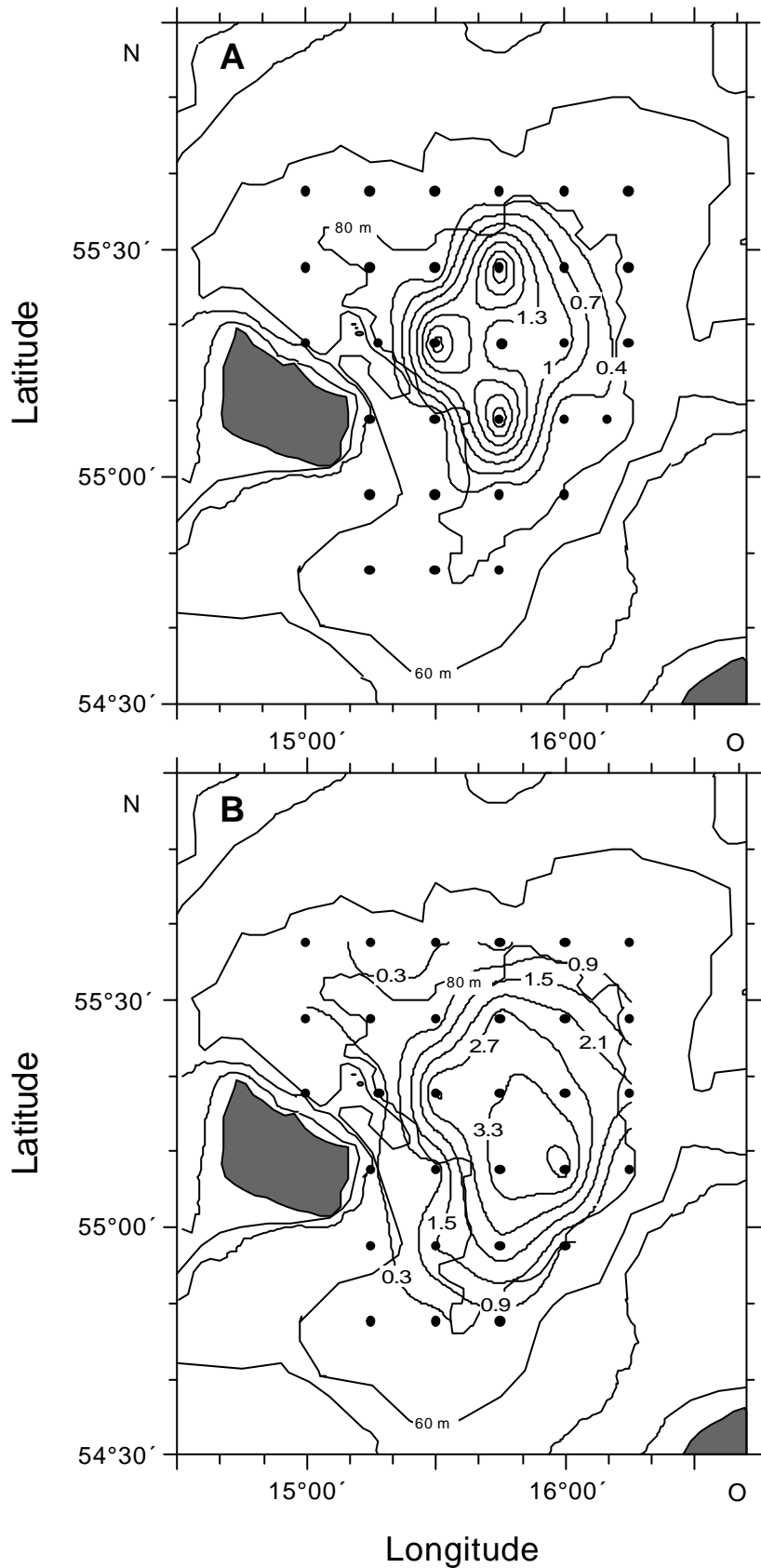


Figure 4.17: May 1988, first survey (19 May), horizontal distribution of cod early life stages: a) cod egg stage IV; b) cod larval stages 5-7; contours of abundance are drawn as n/m^2 with dots indicating sampling positions.

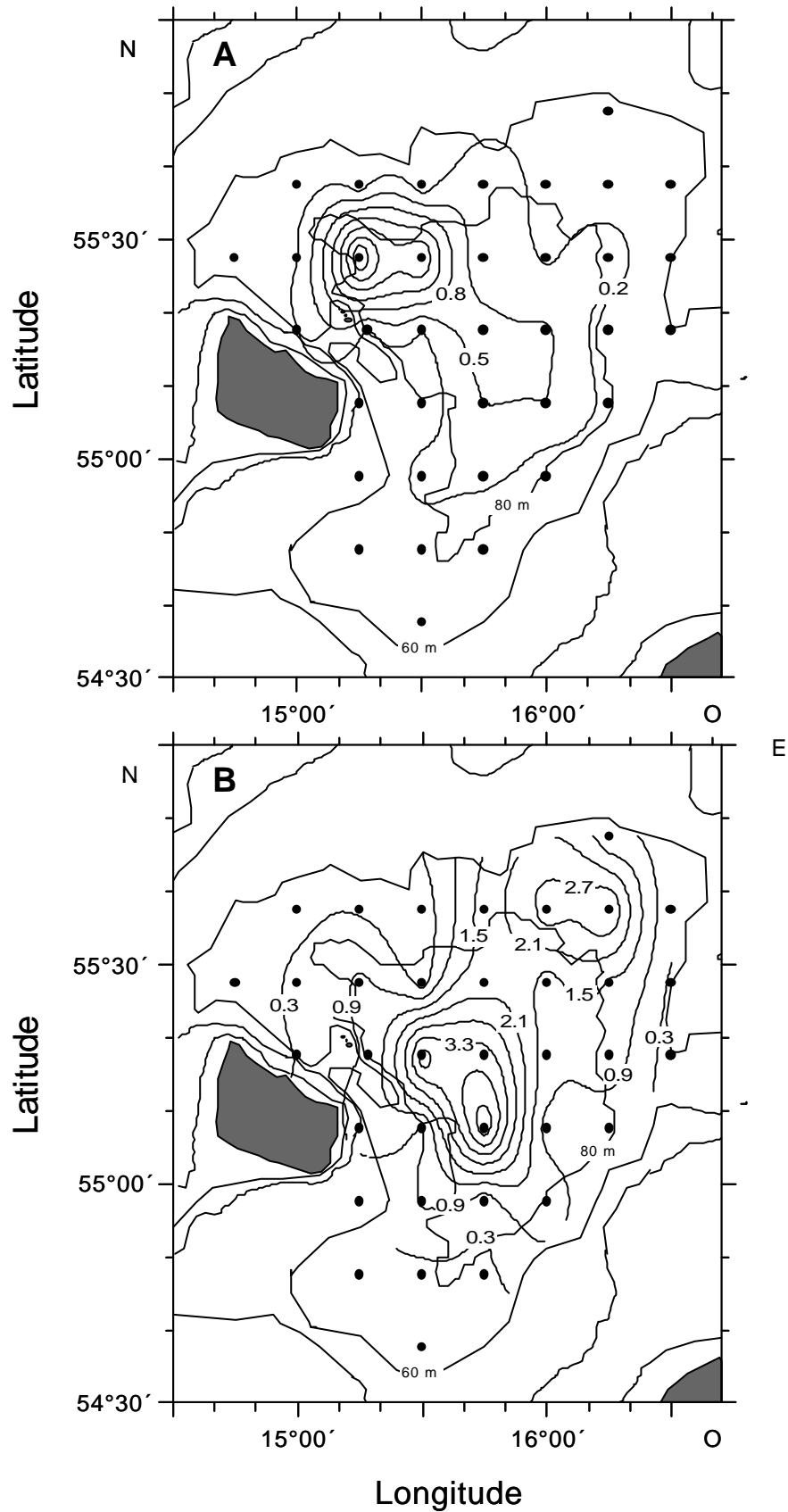


Figure 4.18: August 1991, first survey (11 August), horizontal distribution of cod early life stages: a) cod egg stage IV; b) cod larval stages 5-7; contours of abundance are drawn as n/m² with dots indicating sampling positions.

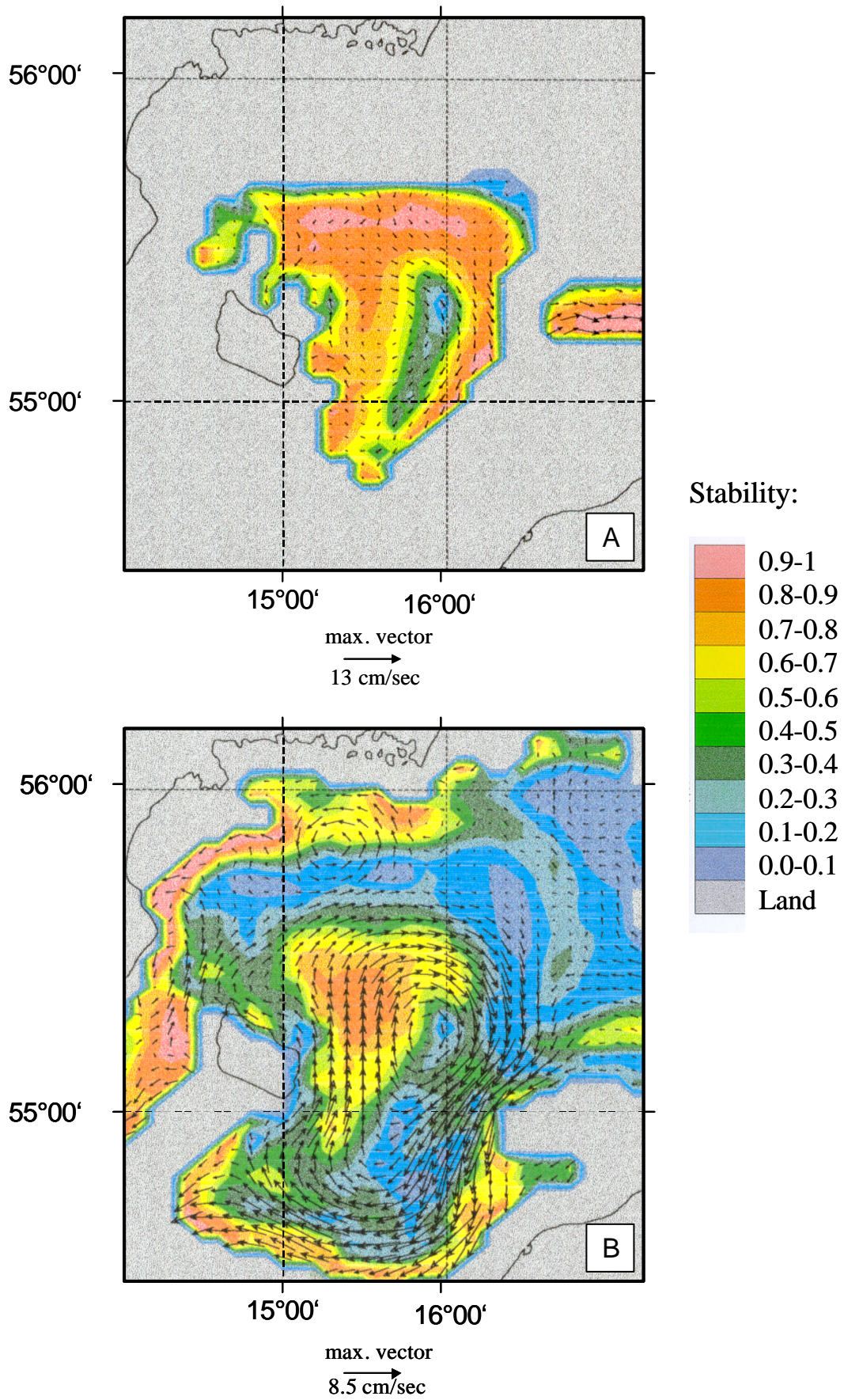


Figure 4.19: Mean current fields and stability averaged over 19-23 May 1988. a) depth layer 69-72m; b) depth layer 30-33m.

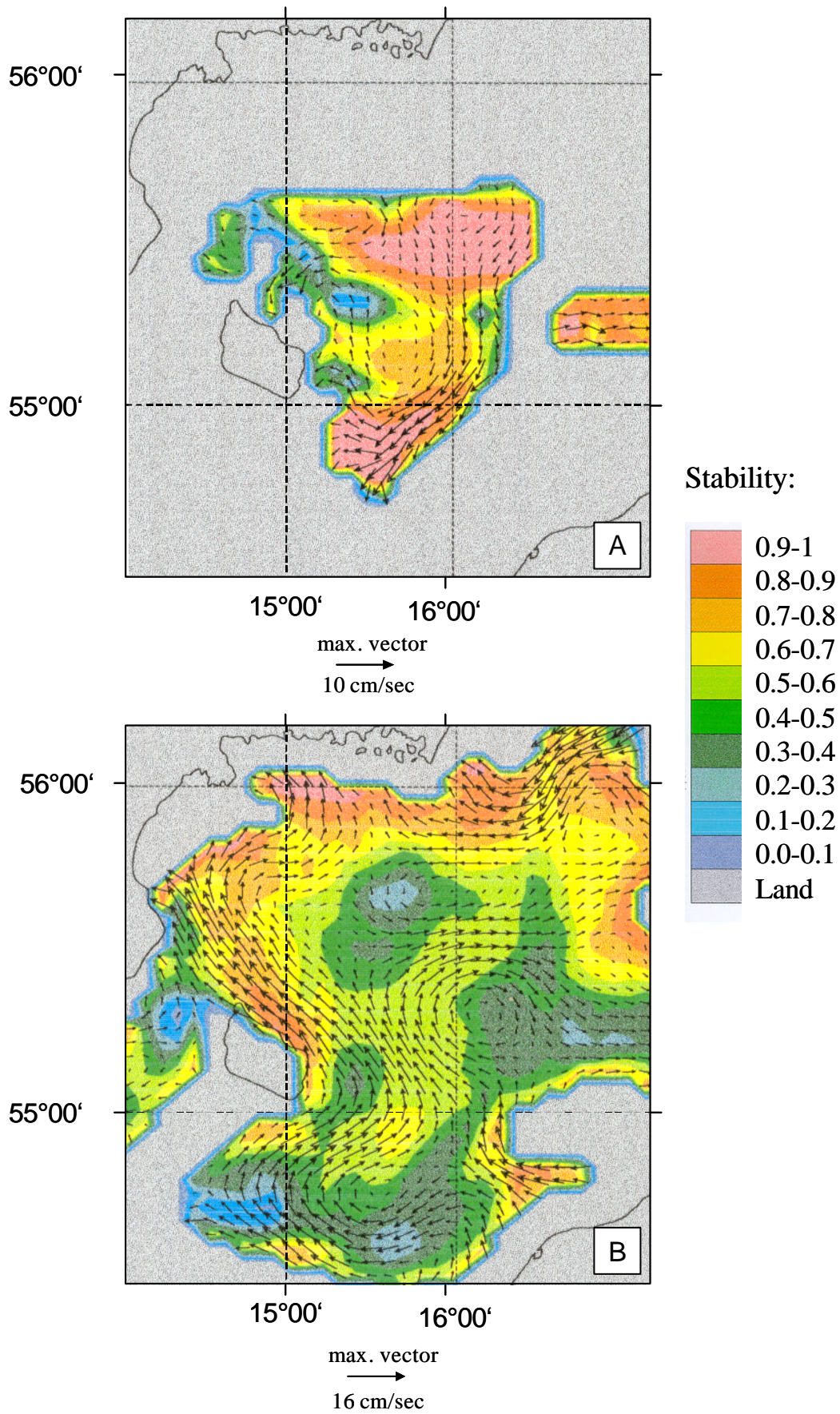


Figure 4.20: Mean current fields and stability averaged over 11-15 August 1991. a) depth layer 69-72m; b) depth layer 30-33m.

The corresponding results for August 1991 are given in Fig. 4.20. Compared to May 1988 the current speeds are generally higher. Beside these differences in transport speed, the mean circulation is quite similar for the depth layer of cod eggs (Fig. 4.20a). The mean circulation relevant for cod larvae (Fig. 4.20b) looks different: In the area of the deep basin an overall transport towards the north can be observed. Water masses are transported into the basin from the south, while they leave the deep basin in a strong and stable current directed to the north-west (western part of the basin) or towards the east, north-east (eastern part of the basin). In this case larvae found in the central basin during the first survey will have the tendency to be displaced towards shallower regions in the north.

Based on the model runs, the development of the relative distribution of cod eggs and larvae to different depth strata (> 80 m and <80 m) was calculated. These data were used to correct the abundance values found during the second survey in the area > 80 m depth for transport gains or losses. According to the circular transport regime and the rather low current speeds in May 1988 for both, eggs and larvae, only small changes in the relative distribution were found. After 5.66 days (the time interval between the surveys) the transport patterns resulted in net losses of only 6.7 and 3.4 % out of the area > 80 m depth for cod eggs and larvae, respectively. In August 1991 stronger changes in the relative distribution occurred (Fig. 4.21). Although the circulation patterns in the egg-relevant depth layer were quite similar to those observed in May 1988, the difference in the initial horizontal distribution led to a strong net transport out of the area > 80 m depth during the first 50 hours of the model run (Fig. 4.21). After that, a weaker net transport into the area > 80 m depth occurred. After 5.92 days (interval between surveys) the proportion of eggs distributed inside the area > 80 m depth had almost regained the starting value (61% vs. 58%). For cod larvae in August 1991 a steady transport out of the deep basin can be observed, as expected according to the flow fields. Initially 54% of the larvae were distributed in the deep part of the basin. At the time point of the second survey the proportion has declined to 42%, which means that the abundance found inside the 80 m depth contour line during the second survey will be underestimated by 12%.

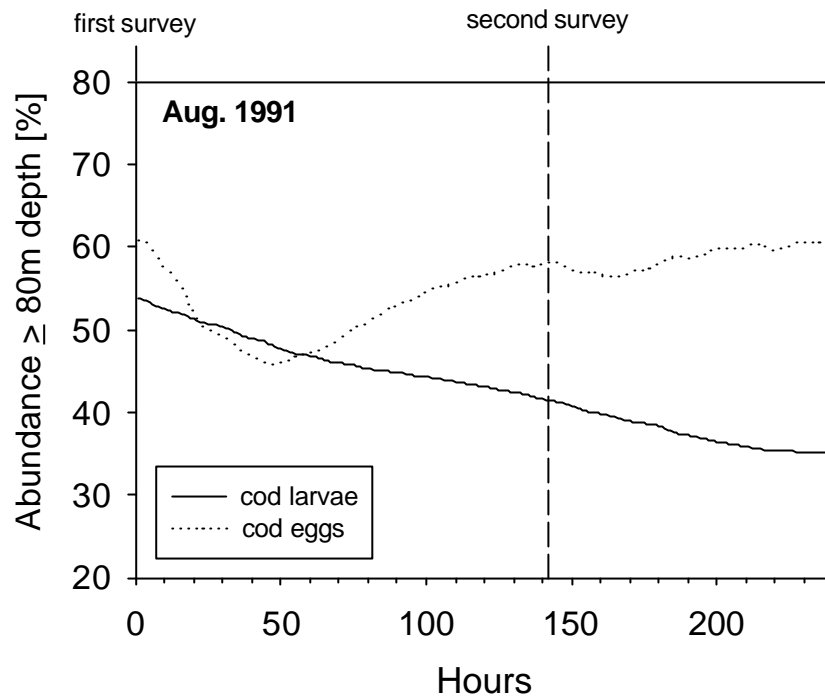


Figure 4.21: Proportion of cod eggs and larvae distributed inside the 80m depth contour line. Temporal evolution due to transport processes in August 1991 (11 – 20 Aug.). Vertical lines indicate the temporal midpoint of sampling.

4.4.3 Mortality rates

For both periods (May 1988 and August 1991) average mortality rates between the oldest egg stage (stage IV) and larval stage 5 (first feeding larvae) as well as between larval stage 5-7 and larval stage 8 (established feeders) were calculated. Table 4.6 shows the daily production values and the corresponding mortality rates with and without correction for transport. Especially for August 1991 the correction for transport had a considerable impact. In May 1988 the mortality between egg stage IV and larval stage 5 amounted to ~20% per day. Mortality rates during the onset of feeding (larval stage 5-7 to larval stage 8) were considerably lower with only 7% per day. In August 1991 the situation was vice versa. There was almost no mortality between hatch and the onset of feeding. Mortality rates of 0.08 % per day have to be regarded as extremely low for cod early life stages. The period to reach larval stage 8, i.e. to survive to the state of an established feeder, was more critical. Average mortality rates amounted to >22% per day. Obviously, during the two time periods investigated, different processes must have acted, limiting survival at different stages of development.

Table 4.6: Cod larval mortality rates: Observed (obs) and adjusted (adj) abundance (n/m^2) and daily production ($n/m^2/d$) of different developmental stages inside the 80m depth contour line, as well as resulting mortality rates (M) with and without correction for transport (corr) in May 1988 and August 1991.

	May 1988				August 1991			
	Time interval between surveys: 5.66 days;				Time interval between surveys: 5.92 days;			
survey	1	2	1	2	1	2	1	2
stage	Egg IV	L 5	L 5-7	L 8	Egg IV	L 5	L 5-7	L 8
age [days] *	14.09	19.35	22.35	28.35	13.51	19.72	21.72	27.72
dt age	5.26		6.00		6.21		6.00	
n/m^2_{obs}	0.98	0.21	2.43	1.50	0.66	0.52	1.97	0.33
$n/m^2/d_{obs}$	0.39	0.10	0.41	0.25	0.27	0.26	0.33	0.06
$n/m^2/d_{adj}$		0.11		0.25		0.26		0.06
M [1/d]	0.2359		0.0804		0.0078		0.2972	
M [%/d]	21.02		7.73		0.78		25.71	
$n/m^2/d_{corr}$	-	0.12	-	0.26	-	0.27	-	0.07
M [1/d] _{corr}	0.2226		0.0729		0.0008		0.2547	
M [%/d] _{corr}	19.95		7.03		0.08		22.49	

*: at mean ambient egg incubation temperatures of 5.75 °C in May 1998 and 5.87 °C in August 1991

4.5 Feeding ecology of sprat and cod larvae in the Bornholm Basin

4.5.1 Daily feeding cycle

In May 1988, at night time almost all sprat larval stomachs sampled were empty (Fig. 4.22a). At sunrise the percentage of empty stomachs decreased sharply, but stayed also during daylight hours at typical values of 20-40%. This clear dependence of feeding activity on daylight-hours was also obvious for all other analysed sampling occasions.

For cod larvae only during one survey sufficient numbers for such an analysis were caught (Fig. 4.22b). In this case there was no such obvious relationship between daytime and feeding activity. The proportion of empty stomachs tended to be higher

during the second part of the night, but the differences between day and night time were much less pronounced than for sprat larvae. In general the percentage of feeding cod larvae was higher, with values of >80% in most daylight samples.

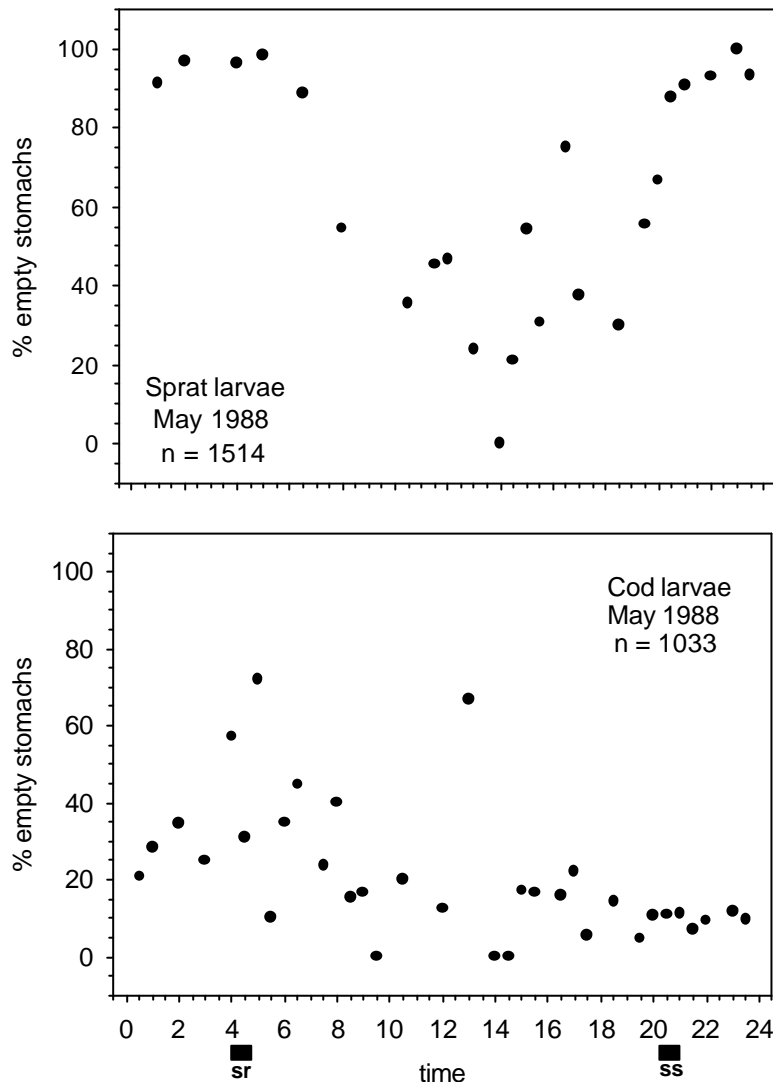


Figure 4.22: Percentage of empty larval stomachs for different times of the day in May 1988. Black bars indicate the time of sunrise (sr) and sunset (ss).

4.5.2 General diet composition

For sprat larvae a large range of prey types could be identified (Table 4.7). However, nauplii were the dominating prey items. Among the different copepods, the developmental stages of *Acartia* spp. (including *A. bifilosa*, *A. longiremis* and *A. tonsa*) were of major importance while other copepods were seldom found in the stomachs. Another important prey type was the cladoceran *Bosmina coregoni maritima*.

Table 4.7: Summary of prey items encountered in sprat larvae stomachs. Prey type, prey size, number of prey items found in the stomachs (n), number of larvae feeding on the prey type (N), percentage of the prey type on the total ingested prey items (D) and percentage of larvae feeding on the prey type (P).

Prey	Size (mm)	n	N	D(%)	P(%)
Nauplii	0.17-0.32	821	564	51.8	49.8
<i>Acartia spp.</i>					
C I-III	0.32-0.37	132	105	8.3	9.28
C IV-V	0.37-0.59	141	104	8.9	9.19
C VI - f	0.61-0.76	285	173	18.0	15.28
C VI - m	0.61-0.82	15	15	0.9	1.33
<i>Temora longicornis</i>					
C I-III	0.37	1	1	0.06	0.09
C IV-V	0.51-0.56	3	3	0.2	0.27
C VI - f	0.58-0.87	10	8	0.6	0.71
C VI - m	0.63-0.71	5	5	0.3	0.44
<i>Pseudocalanus elongatus minutus</i>					
C I-III	0.34-0.36	2	2	0.1	0.18
C IV-V	0.53-0.73	6	6	0.4	0.53
C VI - f	0.75	1	1	0.06	0.09
C VI - m	0.80	1	1	0.06	0.09
<i>Centropages hamatus</i>					
C VI - f	0.76-0.78	2	2	0.1	0.18
C VI - m	0.83	1	1	0.06	0.09
<i>Bosmina corigoni maritima</i>	0.21-0.56	126	42	7.9	3.71
<i>Evadne normannii</i>	0.36	1	1	0.06	0.09
<i>Podon spp.</i>	0.53-0.77	12	5	0.7	0.44
Polychaeta	0.81	1	1	0.06	0.09
Bivalvia	0.26-0.31	4	4	0.2	0.35
Gastropoda	0.09	1	1	0.06	0.09
Diatomacea	0.06-0.07	14	10	0.8	0.88

The analysis of the stomach content of cod larvae revealed an even higher importance of nauplii (Table 4.8). 2713 of 2972 prey items identified belonged to this group. While calanoid copepods were found relatively regularly in the diets,

cladocerans played only a minor role. For both species only low numbers of diatoms and dinoflagellates were found in the guts.

Table 4.8: Summary of prey items encountered in cod larvae stomachs. Prey type, prey size, number of prey items found in the stomachs (n), number of larvae feeding on the prey type (N), percentage of the prey type on the total ingested prey items (D) and percentage of larvae feeding on the prey type (P).

Prey	Size (mm)	n	N	D(%)	P(%)
Nauplii	0.17-0.34	2713	864	94.3	86.40
<i>calanoid copepods</i>					
C I-III	0.29-0.58	98	46	3.4	4.60
C IV-V	0.39-0.70	51	35	1.8	3.50
C VI	0.63-0.73	12	10	0.4	1.00
<i>Bosmina corigoni maritima</i>	0.41	2	1	0.1	0.10
<i>Evadne normannii</i>	0.37	1	1	0.03	0.10
<i>Podon spp.</i>	0	0	0	0.00	0.00
Polychaeta	0	0	0	0.00	0.00
Bivalvia	0	0	0	0.00	0.00
Gastropoda	0	0	0	0.00	0.00
Diatomacea	0.05	1	1	0.03	0.10

4.5.3 Seasonal changes in the diet composition

In sprat larvae on average 1.2 - 1.6 prey organisms per stomach were found, with no obvious seasonal trend in the total stomach content (Fig. 4.23a). Only in July 1988 an exceptional high value of ~4 prey organisms per stomach was observed. Throughout the spawning seasons of both years, the mean lengths increased while the importance of nauplii in the diet decreased. The outstanding value of July 1988 is mainly caused by high numbers of cladocerans found in sprat larval stomachs. For cod larvae nauplii and C I-III were the dominating food items throughout the year (Fig. 4.23b). Only in June and July 1988 adult calanoids contributed substantially to the diet of the larvae. The proportions of nauplii and C I-V stages exhibited a clear seasonal trend: In spring cod larvae fed mainly on nauplii, whereas later in the season C I-V stages increased in importance. In October 1988 nauplii were again the

dominating food item. Total stomach contents were on average higher (1.2 – 3.4 prey organisms / stomach) than for sprat larvae. Seasonal trends in the total stomach content differed between the years. While highest values were reached in 1987 in late summer, in 1988 maximum average stomach contents were recorded in spring.

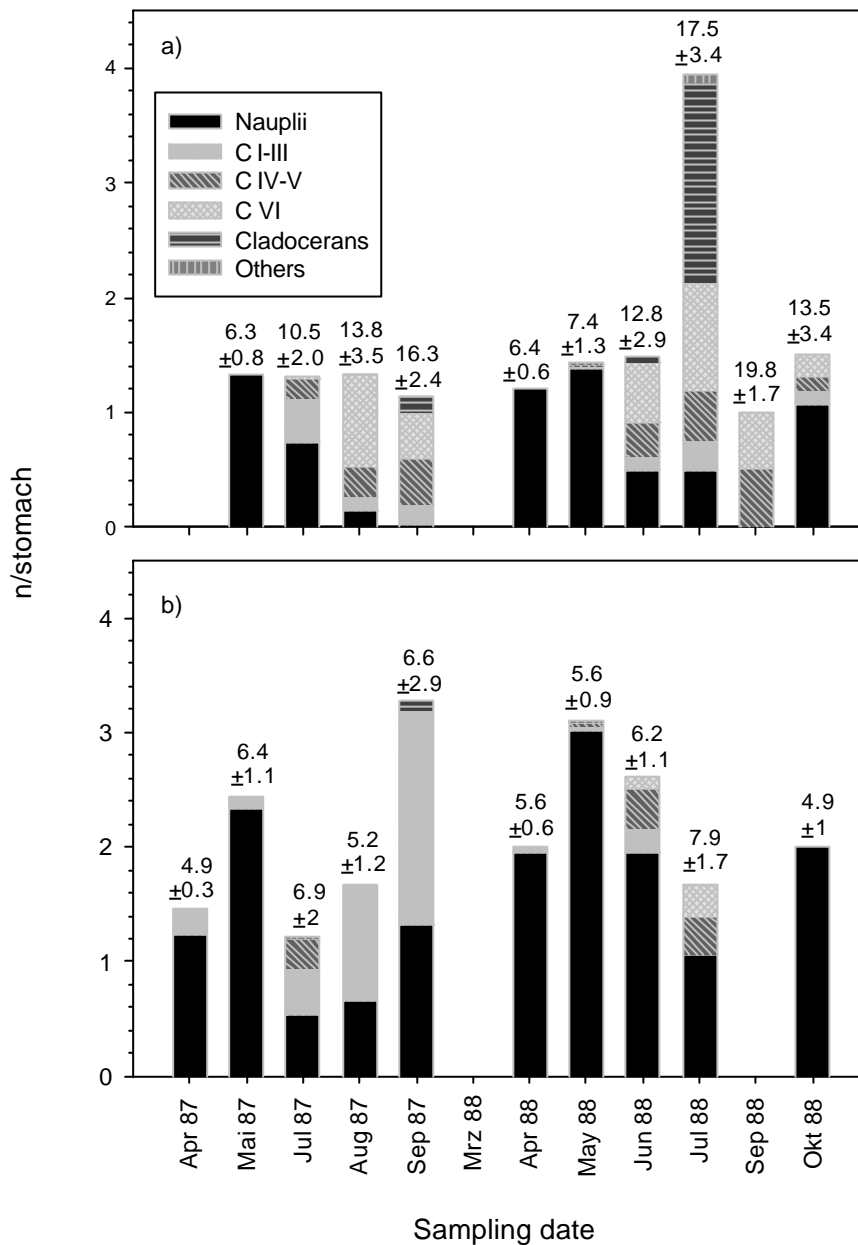


Figure 4.23: Average diet composition (n/stomach of feeding larvae) over the investigated time period for sprat larvae (upper panel) and cod larvae (lower panel).

4.5.4 Size-dependant diet composition

To investigate the dependence of larval length on the diet composition, the results were broken down to 2 mm (sprat) and 1 mm (cod) length classes. To obtain sufficient numbers per length group, some sampling dates were combined. Prey

numbers per stomach tended to be higher with increasing size of the larvae. However, this trend was not always obvious and the absolute changes were rather limited. Up to 20 mm length, the prey numbers per stomach stayed in the range of 0-3 items per stomach (Fig. 4.24). Only in the length group >20 mm in June/July 1988 (Fig. 4.24d) a maximum value of ~7 n/stomach was reached. For all observations a decline in the proportion of nauplii in the diets with increasing larval lengths was obvious. Anyhow, nauplii remained the dominating prey item (>50% in numbers) throughout the season for lengths up to at least 10 mm. Sprat larvae seemed to progressively include older copepod stages in their prey field. The length at which different stages were ingested changed between the surveys and seemed to be dependant on zooplankton abundance. Adult copepods were first found in considerable numbers in the length group of 10-12 mm (August and September 1987; Fig. 4.24b). Cladocerans were identified in small numbers starting at 8-10 mm larval length. However, cladoceran proportions of >10% in the diet were restricted to sprat larvae >16 mm.

The variations in the total stomach content between the sampling dates was higher for cod larvae (Fig. 4.25). The values ranged from 0-13 n/stomach, with highest stomach contents found in May 1988 (Fig. 4.25c). As for sprat larvae, nauplii were the dominating food items for small cod larvae. Substantial contributions of calanoid C I-V stages were first found in the length group 6-7 mm, C VI were included in higher numbers from 9 mm length on (Fig. 4.25b).

At the same total length cod larvae preyed on larger organisms compared to sprat larvae (Fig. 4.26). Minimum size of C I-III stages (see Tab. 4.7) falls within the standard deviation of the mean prey size for cod larvae of 6-7 mm length, and for sprat larvae at 9 mm length. Minimum size of C IV-V were included in the standard deviation of mean prey size of 7-8 mm cod and 11 mm sprat. Correspondingly, C VI sizes were suitable for 9-10 mm cod and 13 mm sprat larvae.

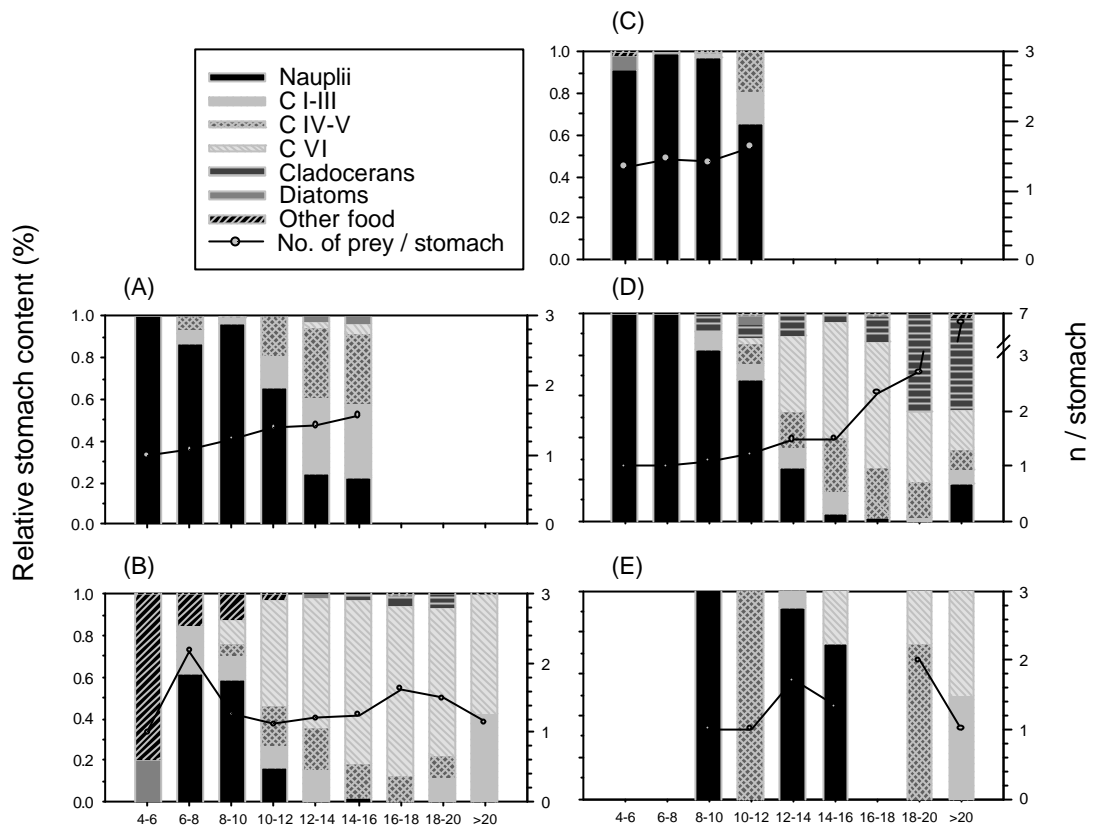


Figure 4.24: Relative stomach content [% of numbers] and average stomach content [numbers] for 2 mm length classes of sprat larvae (A: July 1987; B: August and September 1987; C: April and May 1988; D: June and July 1988; E: September and October 1988).

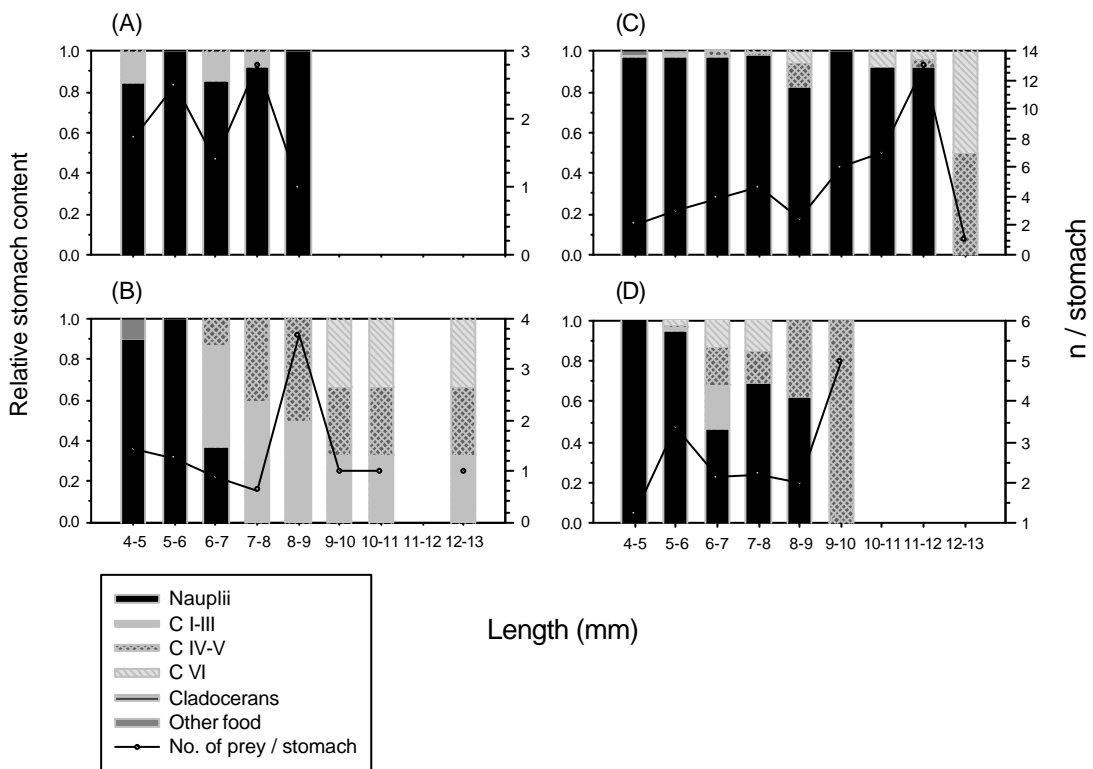


Figure 4.25: Relative stomach content [% of numbers] and average stomach content [numbers] for 1 mm length classes of cod larvae (A: April and May 1987; B: July 1987; C: April and May 1988; D: June and July 1988).

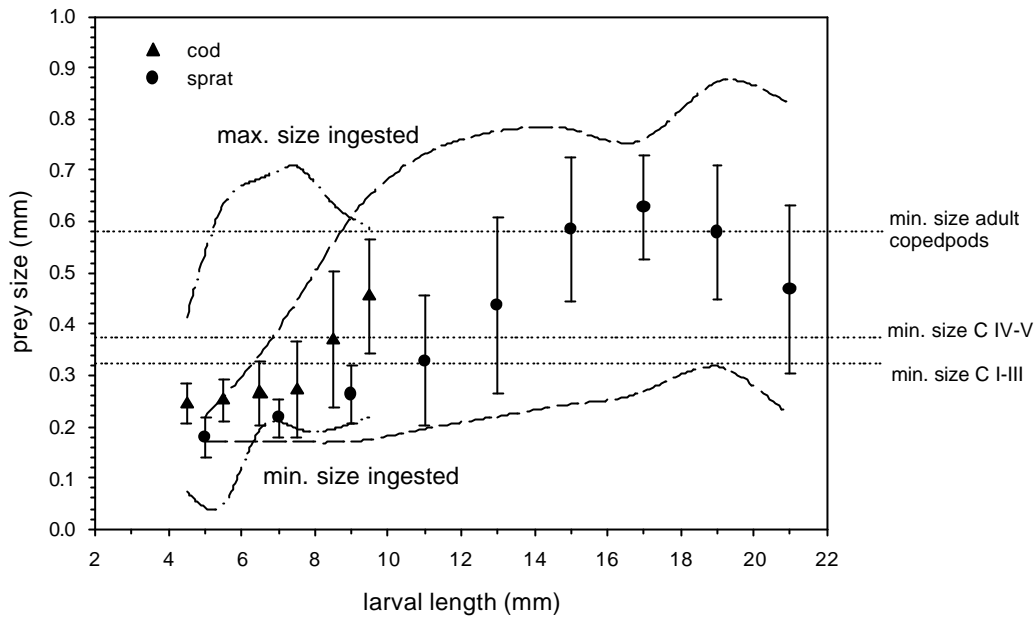


Figure 4.26: Mean, minimum and maximum ingested prey lengths for different sized sprat and cod larvae. Error bars indicate the standard deviation of the mean prey length, dotted lines indicate the minimum size of different prey organisms in the sea.

4.5.5 Prey selection

Sprat larvae positively selected nauplii, independently of larval length or depth stratum (Tab. 4.9). Although all main Baltic copepod species were available as potential prey in different developmental stages, sprat larvae of 8-10 mm generally selected *Acartia spp.* C I-III (with the exception of the 5-15 m depth stratum). C IV-V were actively selected from larvae >10 mm. Only two species of adult copepods were found in the stomachs, *Acartia spp.* and *Temora longicornes*, with lower prey avoidance values for *Acartia spp.* Further, C I-III of *T. longicornes* and individuals of the cladoceran *Evadne nordmanni* were identified in the larval stomachs, but they revealed as well rather negative selection indices.

Cod larvae also actively selected nauplii in all depths strata (Tab. 4.10). In contrast to sprat larvae, cod larvae showed a complete avoidance for all copepodite stages of *Acartia spp.* The only copepod species actively selected was *P. elongates*, revealing high selection indices for C IV-V and C VI-f. In the deepest investigated depth layer additionally the cladoceran *Podon spp.* showed a positive selection index (1.29).

Table 4.9: Food selection in different sized sprat larvae: Logarithmic Shorigin indices for different potential prey types in different depth layers (A. = *Acartia* spp.; T. = *Temora longicornes*; P. = *Pseudocalanus elongatus*; Evad. = *Evadne nordmannii*; Podon = *Podon* spp.)

Prey type	<8 mm			8-10mm			>10mm		
	5-15m	20-30m	35-45m	5-15m	20-30m	35-45m	5-15m	20-30m	35-45m
Nauplii	0.67	0.68	0.62	0.67	0.45	0.65	0.19	0.56	0.55
A. C I-III	-∞	-0.46	-0.27	-∞	0.38	0.36	0.64	0.57	0.67
A. C IV-V	-∞	-0.94	-∞	-∞	-0.46	-∞	0.58	-0.03	0.13
A. C VI-f	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-0.30	-0.51
T. C HIII	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-0.93	-1.35
T. C IV-V	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞
T. C VI-f	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-0.85
P. C I-III	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞
P. C IV-V	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞
P. C VI-f	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞
Evad.	-∞	-0.52	-∞	-∞	-∞	-∞	-∞	-∞	-∞
Podon	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞	-∞

Table 4.10: Food selection in cod larvae: Logarithmic Shorigin indices for different potential prey types in different depth layers (A. = *Acartia* spp.; T. = *Temora longicornes*; P. = *Pseudocalanus elongatus*; Evad. = *Evadne nordmannii*; Podon = *Podon* spp.)

Prey type	Depth		
	5-15m	20-30m	35-45m
Nauplii	0.51	0.80	0.49
A. C I-III	-∞	-∞	-∞
A. C IV-V	-∞	-∞	-∞
A. C VI-f	-∞	-∞	-∞
T. C HIII	-∞	-∞	-∞
T. C IV-V	-∞	-∞	-∞
T. C VI-f	-∞	-∞	-∞
P. C I-III	-∞	-∞	-∞
P. C IV-V	-∞	1.34	1.97
P. C VI-f	2.92	-∞	1.84
Evad.	-∞	-∞	-∞
Podon	-∞	-∞	1.29

4.6 Vertical migration pattern of sprat larvae

4.6.1 Diurnal migration pattern

The vertical distribution of sprat larvae in relation to day-time was studied during 5 cruises. 3 of these were performed more than 10 years ago (1989 and 1990), while the remaining took place in 1999 and 2000.

The abundance of larvae in the different depth layers usually varied over day-time. As an example, Fig. 4.27 illustrates the sprat larval distribution at 5 different sampling times in May 1989.

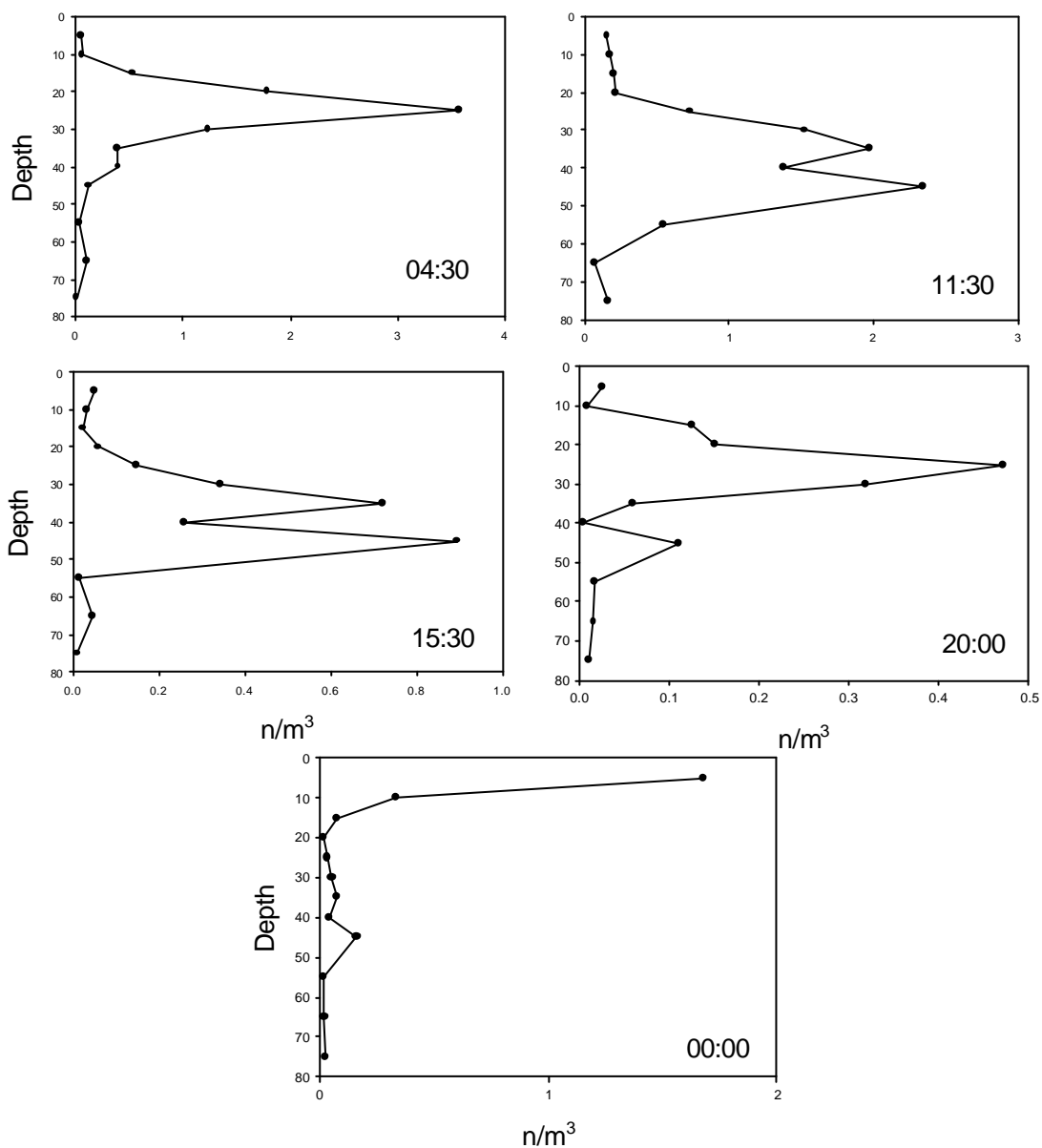


Figure 4.27: Vertical distribution of sprat larvae at 5 different times of the day in May 1989.

This result suggests the existence of a general migration pattern in the direction 'up g day' for May 1989. Anyhow, as sprat larvae do not hatch fully developed, the picture might be biased by the length distribution encountered in the samples. Therefore possible migration patterns were investigated for different size-groups of larvae for all sampling times. Two principle migration patterns could be differentiated (Fig. 4.28): Small (young) larvae (< 6mm length) showed only weak daily migration patterns for all sampling occasions. Larvae >6mm exhibited a clear

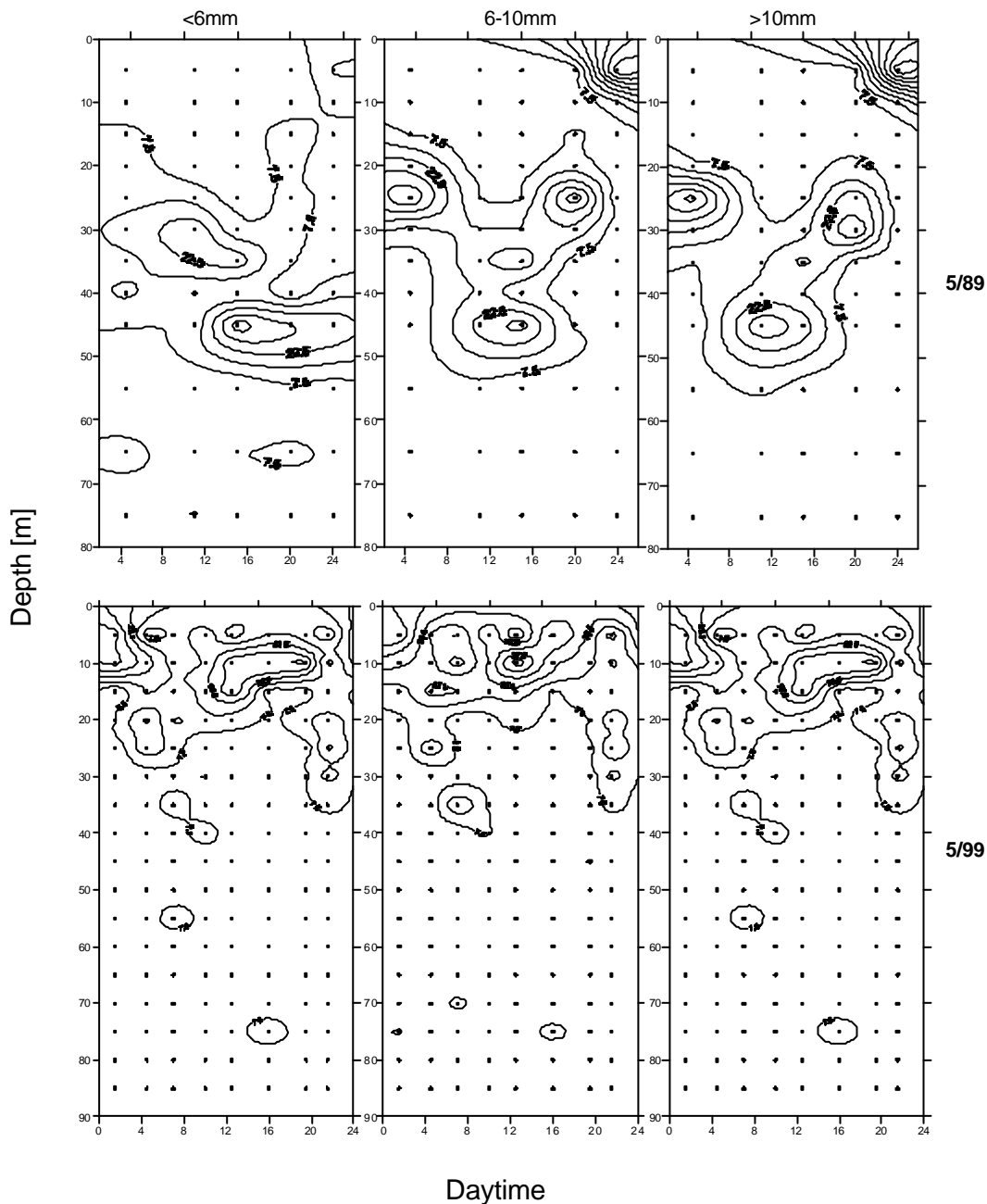


Figure 4.28: Time-dependant vertical distribution of 3 size-classes of sprat larvae in May 1989 (upper panel) and May 1999 (lower panel). Lines are contours of relative abundance (% per depth stratum); dots indicate sampled times/depths.

daily migration during 3 of the 5 investigations (May 1989, June 1989, June 1990). Larvae concentrated in shallow waters (<10m depth) at night, descended during dawn to depths of 30-50m where they stayed during day-light hours. At dusk the larvae ascended again to near-surface. As an example the situation encountered in May 1989 is shown in Fig. 4.28a. Contrary to this, in May 1999 and April 2000 also for larger larvae no signs of daily migration were identified (Fig. 4.28b). The larvae concentrated the whole day in upper water layers.

To further investigate at which length sprat larvae started to migrate, the vertical migration strength V (Bollens and Frost, 1989) was calculated for 1mm length groups (Fig. 4.29). Again, for May 1999 and April 2000 only very low values were obtained. For April 2000 the length groups of 8-10mm rather revealed negative migration strength values, indicating a weak 'anormal' migration in the direction 'down at night' and 'up at day'. During the investigations in 1989 and 1990, all size groups >10mm high positive migration strength values. The length at which the migration commenced was, however variable: While in June 1989 even the smallest larvae had high V -values, a strong increase in V could be found from 6mm and from 8 mm on in May 1989 and June 1990, respectively.

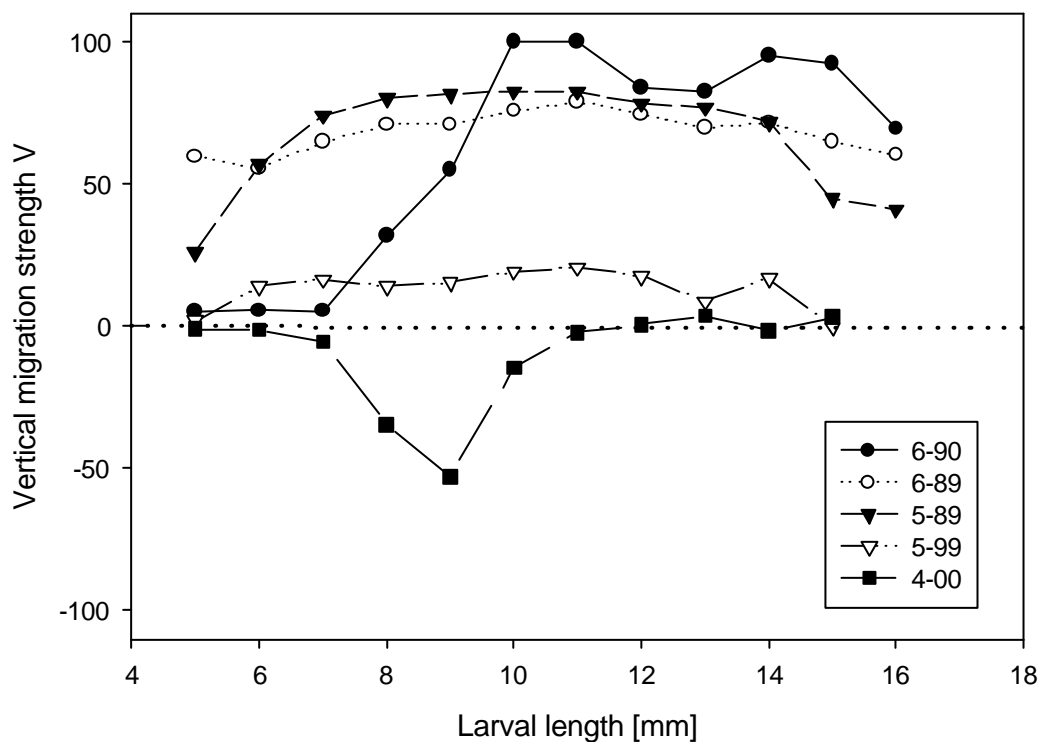


Figure 4.29: Vertical migration strength V (Bollens and Frost, 1989) for 1mm size classes of sprat larvae at different sampling dates.

The results from the different 24-hours samplings suggested a change in the migration patterns and thereby in the vertical day-time distribution of sprat larvae over the past 10-12 years. To further investigate this hypothesis, additional length-stratified data are only available for day-time distributions in May 1998 and June 1999. The calculations are based on larvae >10 mm, as for this group an absence of migration patterns can not be explained by larval size. Also in these investigations the mean weighted depth of larvae during day-time was found to be considerably shallower than in 1989 and 1990 (Fig. 4.30).

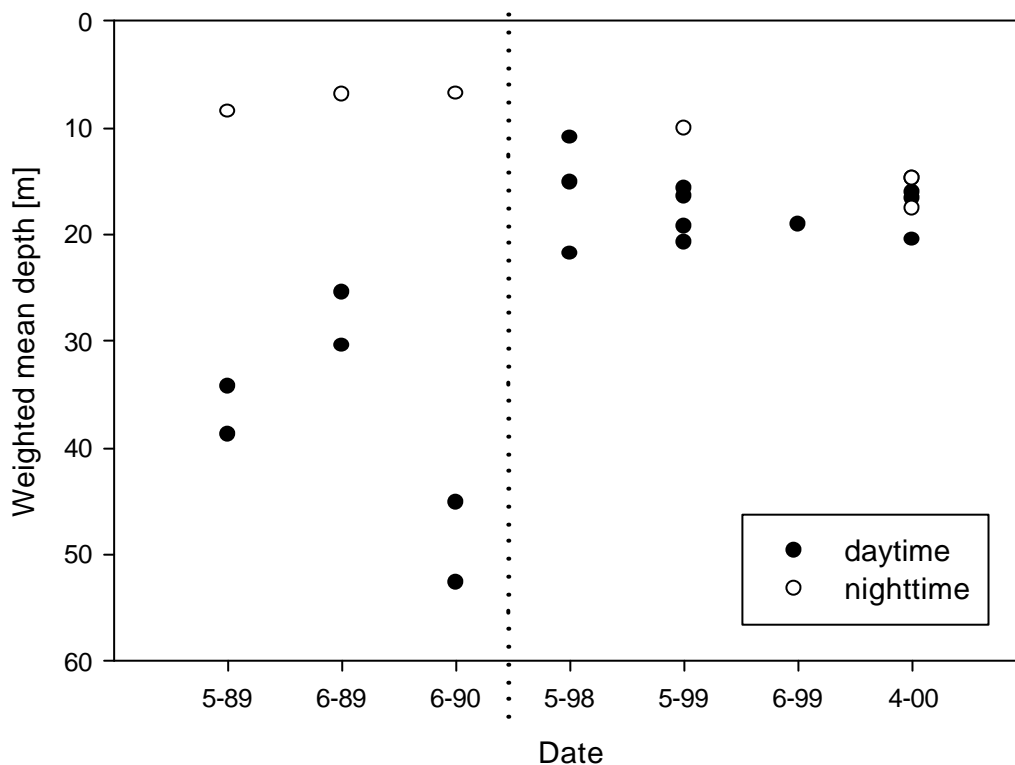


Figure 4.30: Weighted mean depths of sprat larvae >10mm from day-time samples (full circles; 1-4 replicates) and from night time samples (open circles; 1-2 replicates).

As the distribution over depth is asymmetric, the comparison of mean weighted depths might not be accurate. An alternative illustration, showing the depth of the highest abundance of larvae >10mm for each field campaign together with an indication of the depth layer containing ~75% of all larvae, is given in Fig. 4.31. For all 4 sampling occasions conducted in most recent years, the depth of highest abundance was found in 5 to 10m depth. The layers containing ~75% of larvae are as well clearly different from the layers calculated for the time period 1989-1990.

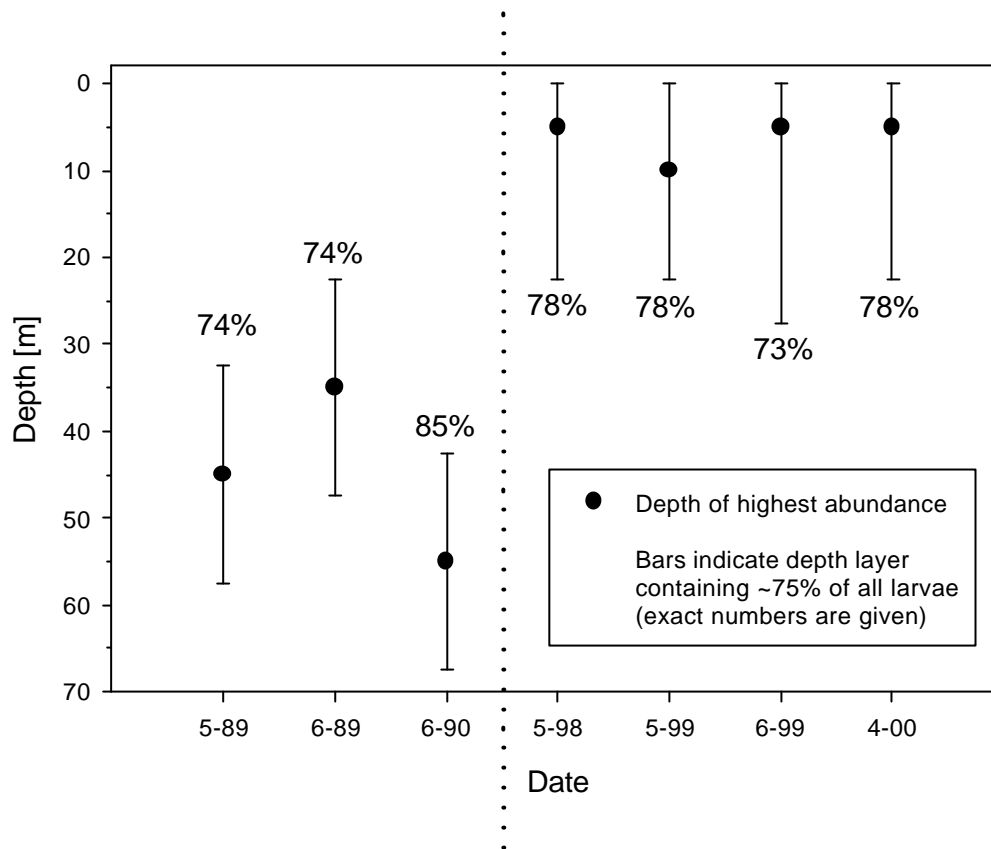


Figure 4.31: Depth of highest abundance of sprat larvae >10mm as well as depth layer containing the majority of larvae in this size class.

4.6.2 Potentially important environmental factors

The Baltic Sea is a highly stratified environment for fish larvae. Vertically especially salinity, temperature and oxygen content vary with depth. In spring surface warming leads to an increasing thermal stratification located above the permanent halocline. The beginning thermal stratification can be observed for the sampling dates in different intensities (Fig.4.32). Sub-surface temperature in May was generally about 8-10°C, being approximately 3-5°C higher than in the intermediate waters of 30-50m depth. In June sub-surface temperatures of up to 16°C were encountered (June 1999, June 1989), resulting in a temperature difference of >10°C to intermediate water layers (Fig.4.32). Salinity as well as the oxygen content varied only on small scales for upper water layers. Strong gradients below 50m should generally not affect the environment of larger sprat larvae, due to their vertical position in upper water layers.

The observed absence of a vertical migration to deeper water layers during day-time for the sampling dates 1998-2000, have therefore resulted in higher ambient water temperature for larger sprat larvae, compared to a situation in which a vertical

migration would have taken place. For May and June the respective increase in ambient water temperature is about 3-5°C and 6-10°C.

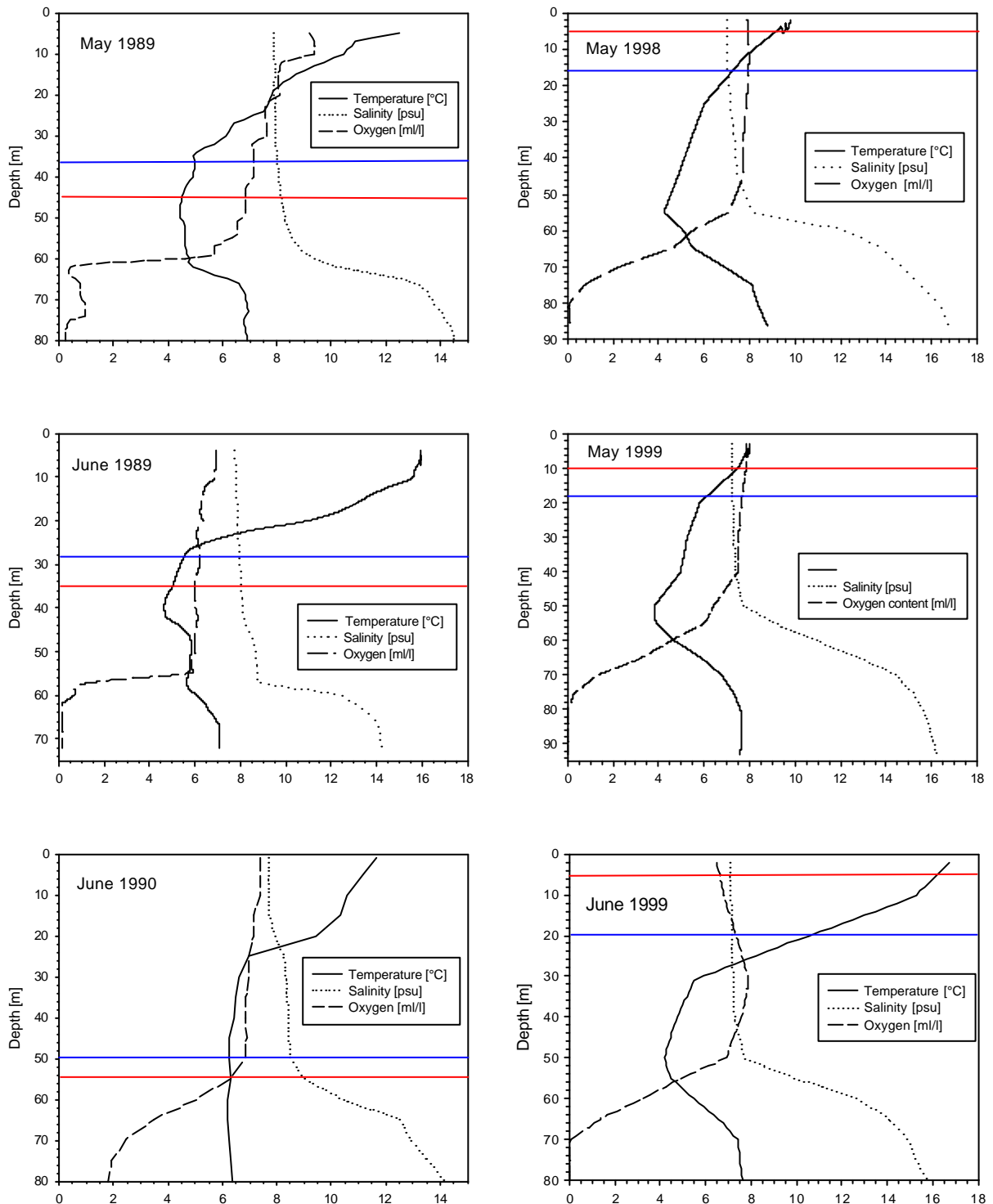


Figure 4.32: Hydrographic situations encountered at the position of vertically resolving sampling. Temperature (solid line), salinity (dotted line) and oxygen content (broken line) are shown. Horizontal red and blue lines indicate the depth of highest abundance and the mean weighted depth of sprat larvae >10mm, respectively.

Additionally to the changes in abiotic variables, depth of occurrence plays an important role for the biotic environment. For sprat larvae particularly the abundance of suitable food organisms has to be taken into account, as with higher ambient temperatures the metabolic and growth-related costs increase. Figure 4.33a shows the relative depth-distribution of all copepods encountered in May 1989.

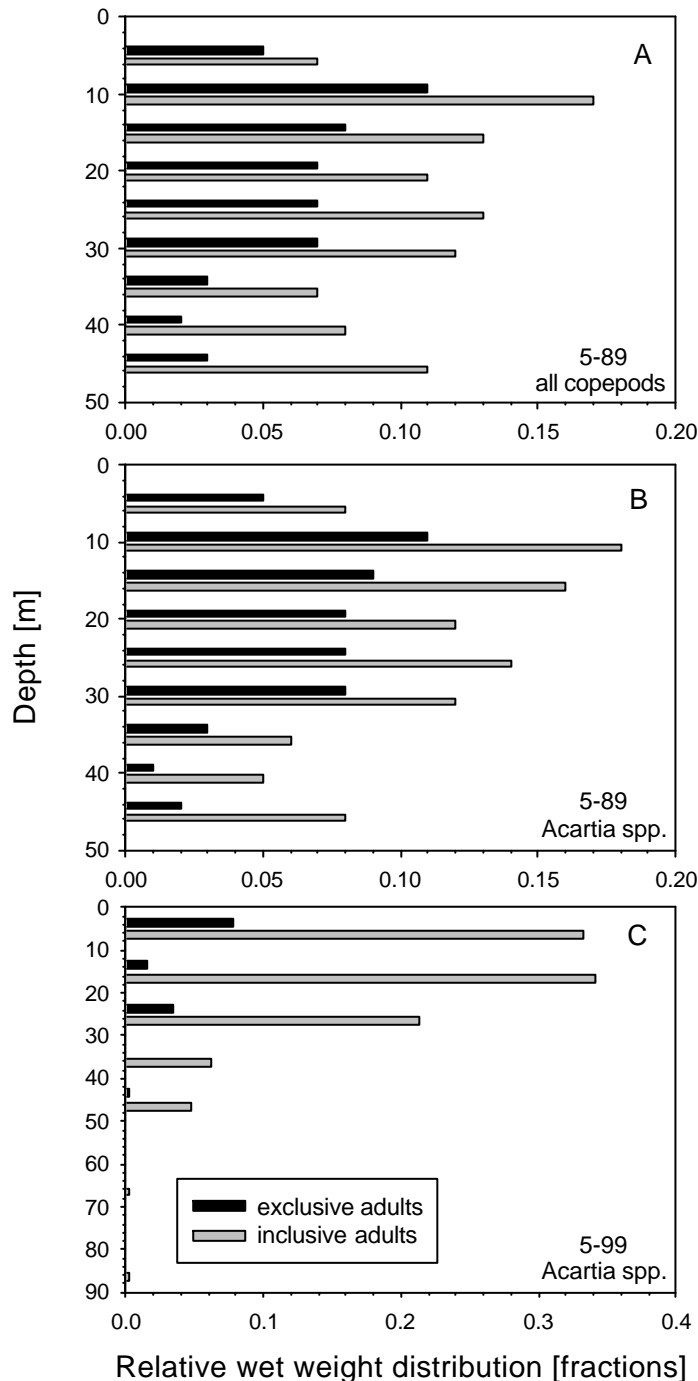


Figure 4.33: Vertical prey field distribution for sprat larvae; exclusive the adult copepod stages (grey bars) or inclusive the adult stages (black bars): (A) all copepod species in May 1989; (B) *Acartia* spp. in May 1989; (C) *Acartia* spp. in May 1999. Bars indicate the relative wet weight distribution over depth.

The values reflect the relative biomass distribution. Both scenarios, excluding and including the adult stages, are calculated relative to the total biomass including the adult stages. As sprat larvae almost exclusively feed on *Acartia spp* organisms (see 4.5), in Fig, 4.33b the results are restricted to this species. In both cases and both scenarios highest values were reached in 10m depth. Although there is a slight trend to decreasing biomass values deeper than 30m, there were still considerable proportions found down to 45m. The relative biomass distribution of *Acartia spp.* in May 1999 was quite different (Fig. 4.33c). The highest values were again recorded in the shallowest water layers, but the gradient towards greater depths was considerably more pronounced. It appears possible, that sprat larvae not performing a vertical migration in May 1999 benefited from higher suitable prey concentrations during day-time, ensuring prey concentration to be sufficient to counterbalance an increased energy demand due to increased ambient temperatures.

4.7 Bio-physical modeling of larval cod growth and survival

All simulations performed revealed optimal feeding conditions for cod larvae >6 mm. These larvae feed on copepod nauplii, copepodite stages, at larval length >9 mm also on adult copepods and cladocerans. The specified distribution and abundance of prey turned out to be sufficient for survival and optimal growth of these larvae. On the contrary, for larvae of length between 4.5 and 6 mm, exclusively feeding on copepod nauplii, pronounced differences in growth and survival were encountered and described in the following.

4.7.1 Idealized seasonal nauplii prey fields

The two-dimensional (depth and date dependent) distribution of copepod nauplii including *P. elongatus* showed a pronounced seasonal signature (Fig. 4.34). Peak nauplii abundance of about 3000 n*m⁻³ were observed in the upper layer (0-25m). Highest concentrations are found mainly in the deeper part of the basin with mean peak nauplii abundances between Julian day 100 and 150. In shallower coastal areas peak abundance lagged 50 days behind. The lower layer (25-50m) reflects similar conditions as for the near surface layer with the same time period of peak nauplii abundance but lower concentrations (~1100 n*m⁻³).

Mean prey fields including *Acartia* spp., *T. longicornis* and *C. hamatus* only, showed for both depth layers maximum abundance within coastal regions (Fig. 4.34).

Compared to prey fields including *P. elongatus*, the concentrations were approximately 2 times lower with maximum abundances occurring later in the year (around Julian day 300). During the period of peak abundance of nauplii coastal areas revealed twice the concentration as observed for the deep part of the basin.

4.7.2 Intra-annual variability in growth and survival of cod larvae

Firstly, we simulated the intra-annual variability in survival and growth of larvae between 4.5 and 6mm experiencing above described prey fields with and without *P. elongatus*. Model output parameters as well as ambient environmental variables of surviving larvae during the spawning period of Baltic cod were averaged over the whole observational period of years 1986-1999 (see Fig. 4.35a and b). Note, that the whole set of parameters exclusively describes the state of the surviving proportion of the initially simulated population.

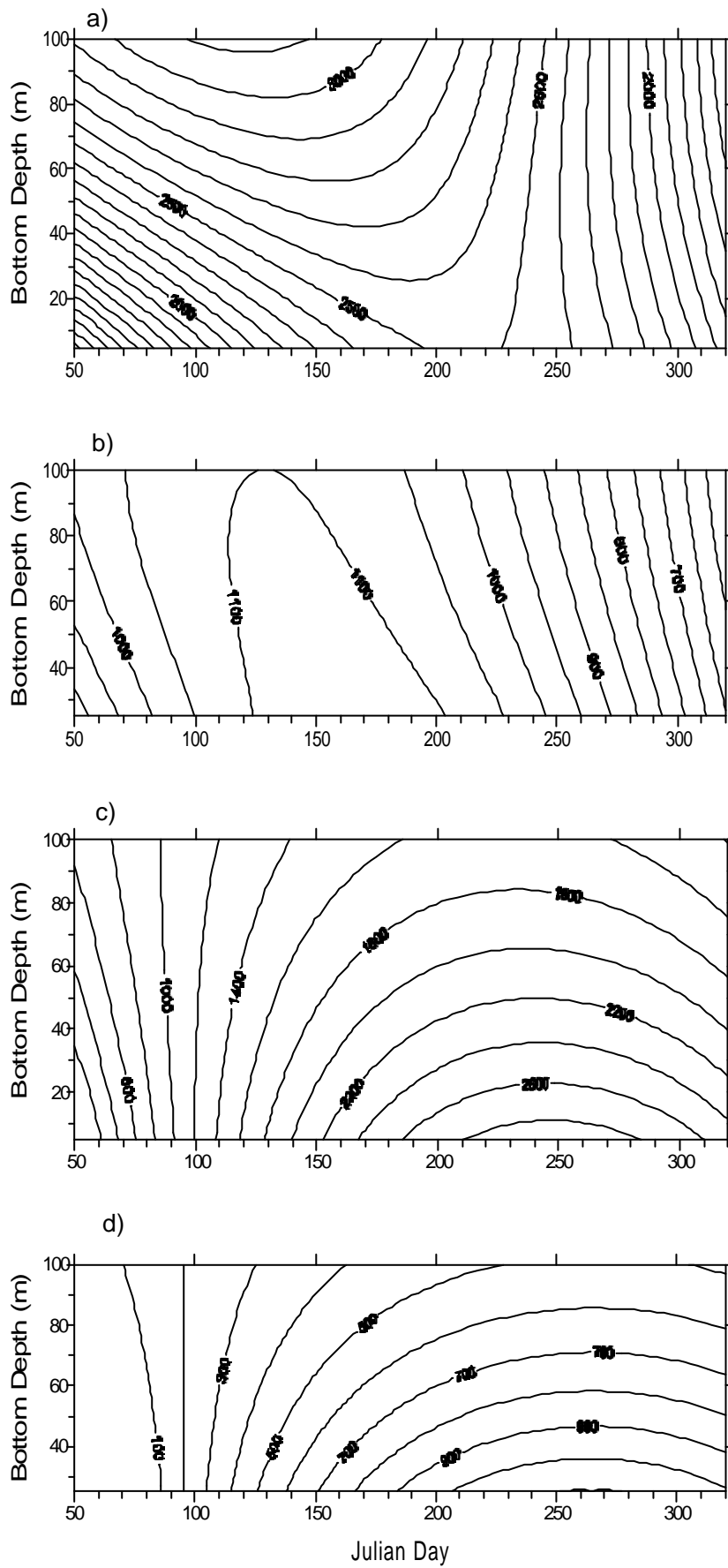


Figure 4.34: Idealized mean nauplii prey fields according to date and bottom depth, a) incl. *P. elongatus* (0-25m); b) incl. *P. elongatus* (25-50m); c) excl. *P. elongatus* (0-25m); and d) excl. *P. elongatus* (25-50m).

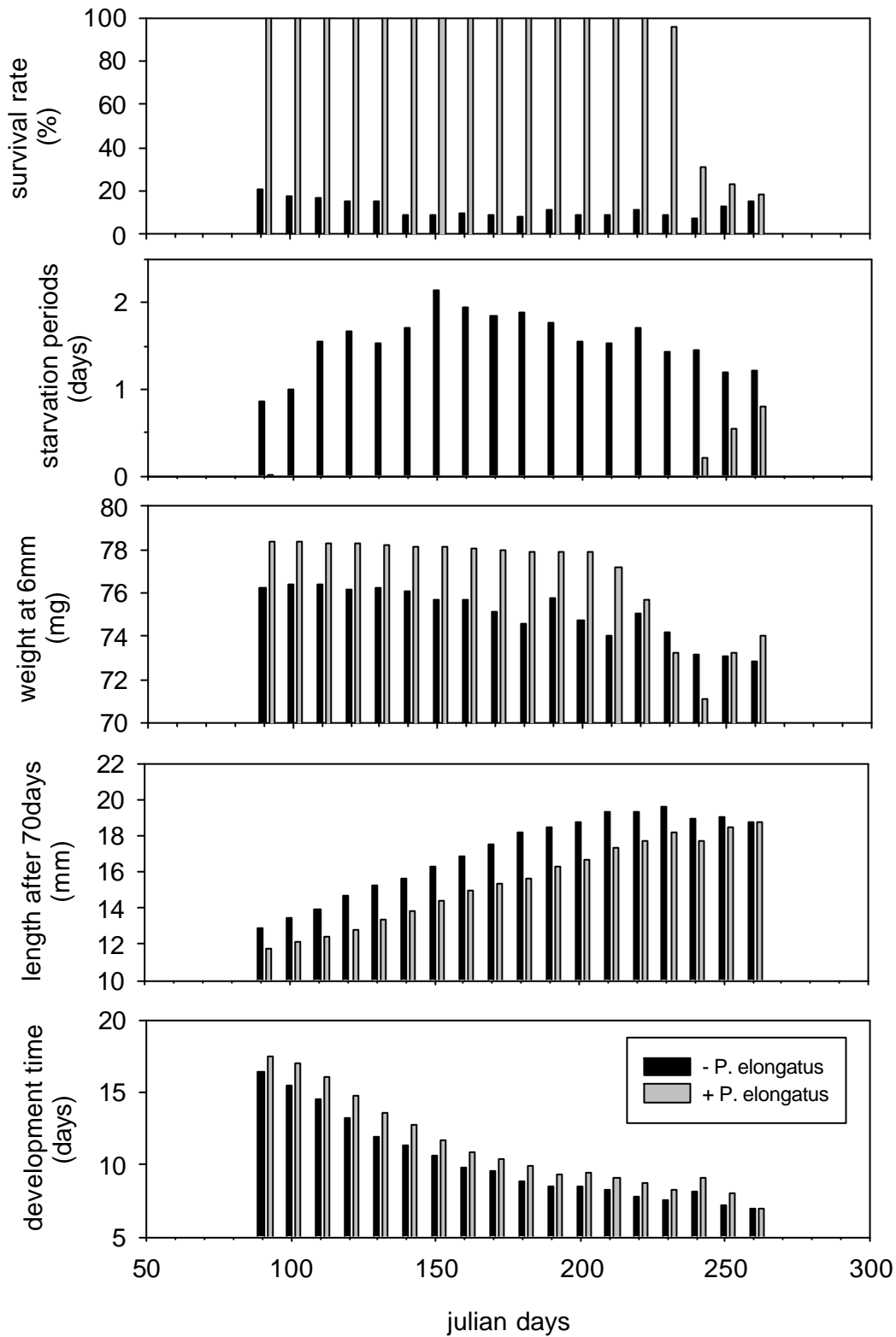


Figure 4.35a: Averaged (1986-1999) seasonal model output parameters of surviving larvae obtained from simulations with (+) and without (-) *P. elongatus*: survival rate, starvation periods, mean weight at 6 mm length, length after 70 days of drift and feeding as well as the development time until the end of the first-feeding stage.

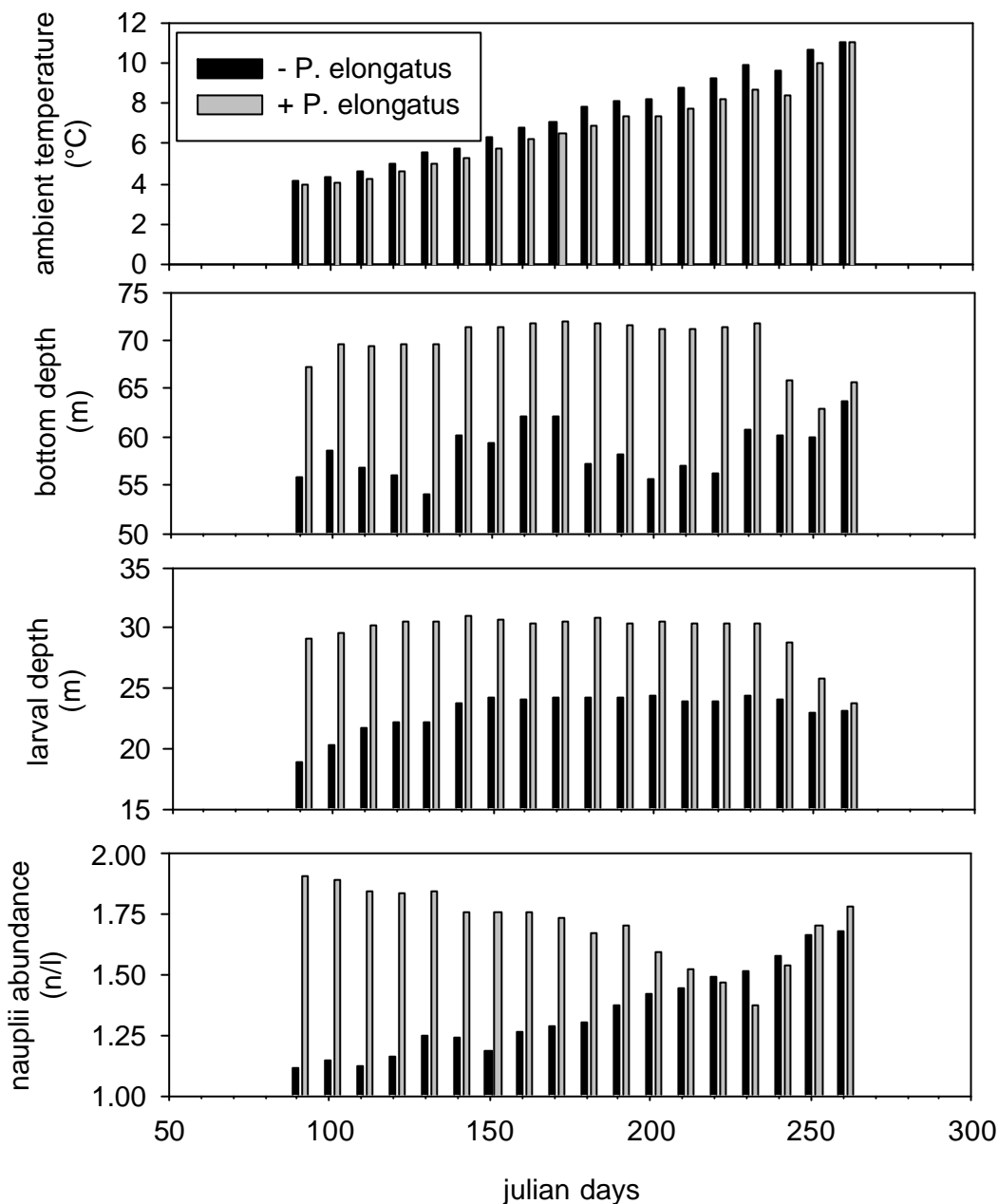


Figure 4.35b: Averaged (1986-1999) seasonal ambient environmental variables of surviving larvae obtained from simulations with (+) and without (-) *P. elongatus*: ambient temperature, bottom depth, larval depth and nauplii abundance.

The survival rate of larvae experiencing prey fields without *P. elongatus* seldomly exceeded 15% except during periods in early spring and at the end of the spawning season when environmental conditions enabled between 15 and 20% of the initially hatched larvae to survive. Consequently the same trend in starvation periods was observed within a range of 0.5 to 2 days. Higher survival in spring was a result of lower ambient temperatures yielding in lower specific larval growth rates. Thus a

lower amount of food is required to satisfy metabolic demands, allowing relatively high survival concurrent to low nauplii abundance. Contrary, in summer, although the available amount of food was higher, survival was lower. This was due to higher ambient temperatures encountered by the larvae resulting in shorter development times and high amounts of food needed daily for this rapid development.

Consequently, the number of starvation periods was high in early summer when drift into coastal areas with a high food abundance was also less frequent (not shown), compared to the beginning of the spawning period when temperature was lower. The mean larval condition expressed as the weight at 6mm length was also high in spring reflecting favourable environmental conditions. Finally, larval growth expressed as length-at-age at day 70 was found to be mainly driven by ambient temperatures. At the beginning of the spawning period, low growth rates resulted in smaller individuals at age, but nevertheless the larvae reached their length of metamorphosis (12 mm). Due to the seasonal warming growth accelerated towards summer months and early juvenile length after 70 days reached maximum values (18-20 mm) between Julian day 200 and 260. Consequently the average duration of the larval stage decreased throughout the season.

To evaluate the importance of *P. elongatus* for growth and survival of Baltic cod larvae, nauplii of this copepod species have been added to the mean prey fields. No starvation occurred in this scenario, with the exception of the final end of the main spawning time, i.e. releases at Julian days 231-261. This decrease in survival at the end of the season was accompanied by an increase in the number of starvation periods and resulted in worse larval conditions expressed by their low weights at 6mm. This bad condition was due to the high ambient temperature encountered by the larvae leading to a shortage in food supply although abundance of food at the end of the spawning season was relatively high. The simulations revealed, that maximum survival of first feeding cod larvae at high specific daily growth rates (due to high temperature) requires a food density of 1200-1500 nauplii* m⁻³. The encountered food resembles the spatial and horizontal distribution of the implemented input prey fields: at the beginning of the spawning period relatively high amount of food is available if *P. elongatus* is considered, whereas maximum nauplii abundance occurred during autumn without *P. elongatus*. The latter was due to potential drift routes within on average shallower water. The drift within deeper waters as well as

on average lower ambient temperature if *P. elongatus* was considered as prey is due to the higher number of surviving larvae dwelling in larger depth.

4.7.3 Inter-annual variability in growth and survival of cod larvae

We next simulated the inter-annual variability in survival and growth of larvae between 4.5 and 6mm originating from peak spawning times of years 1986-1999 (Wieland *et al.* 2000b). During the late 1980s, peak spawning took place between the beginning of May and mid-June. A remarkable shift in the timing of spawning to the end of July occurred in the 1990s. Model simulations were initialized by ignoring turbulence and using prey fields without *P. elongatus* (Fig. 4.36 a and b). The specified distribution and abundance of prey was mainly unfavorable for larval cod. This is reflected in low survival rates between 1 and 30% and a high number of starvation periods. Although the effect of the shift in spawning time is clearly visible in the ambient temperature, development time, nauplii abundance and an increasing length at age, survival and starvation as well as weight is highly variable. It becomes obvious that the strong year-to-year variations do not depend on a single process, but are influenced by a combination of different factors operating on different temporal and spatial scales (e.g. seasonality in temperature compared to transport into optimal feeding environment).

In the following we successively modified the simulations by taking into account

- (i) the vertical distribution of the zooplankton prey, and
- (ii) (ii) the effect of turbulence on contact rates between predator and prey.

Survival derived from the first analysis was generally higher and increased from on average 9% to 17%. In simulations with the two modifications larval survival increased further to approximately 20 % while the number of starvation periods decreased. The unusually strong increase in survival in 1999 can be explained by the fact that larvae dwelled in for this period of the spawning season unexpected low temperature. Thus, only low food supply was needed to enhance larval survival. In turn, larval weight at the end of the development was lower.

MacKenzie *et al.* (1994) demonstrated that encounter, expressed relative to the non-turbulent condition, linearly increases as the turbulent velocity or the windspeed increases. Assuming higher encounter rates to be related to higher survival success,

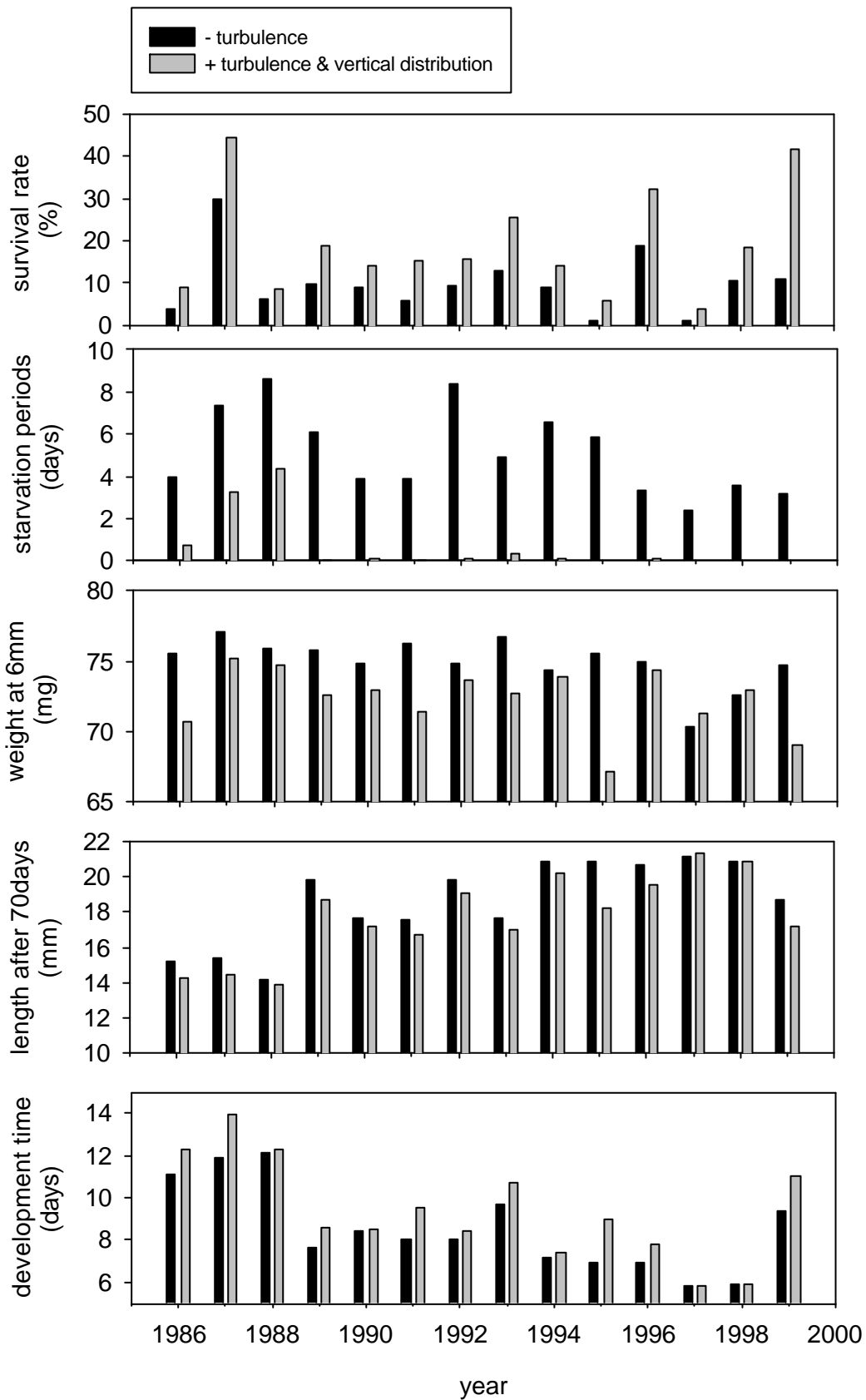


Figure 4.36a: Time-series (1986-1999) of model output parameters of surviving larvae originating from peak spawning obtained from simulations without *P. elongatus*, without (-) and with (+) turbulence and adjustment in zooplankton vertical distribution: survival rate, starvation periods, mean weight at 6 mm length, length after 70 days of drift and feeding as well as the development time.

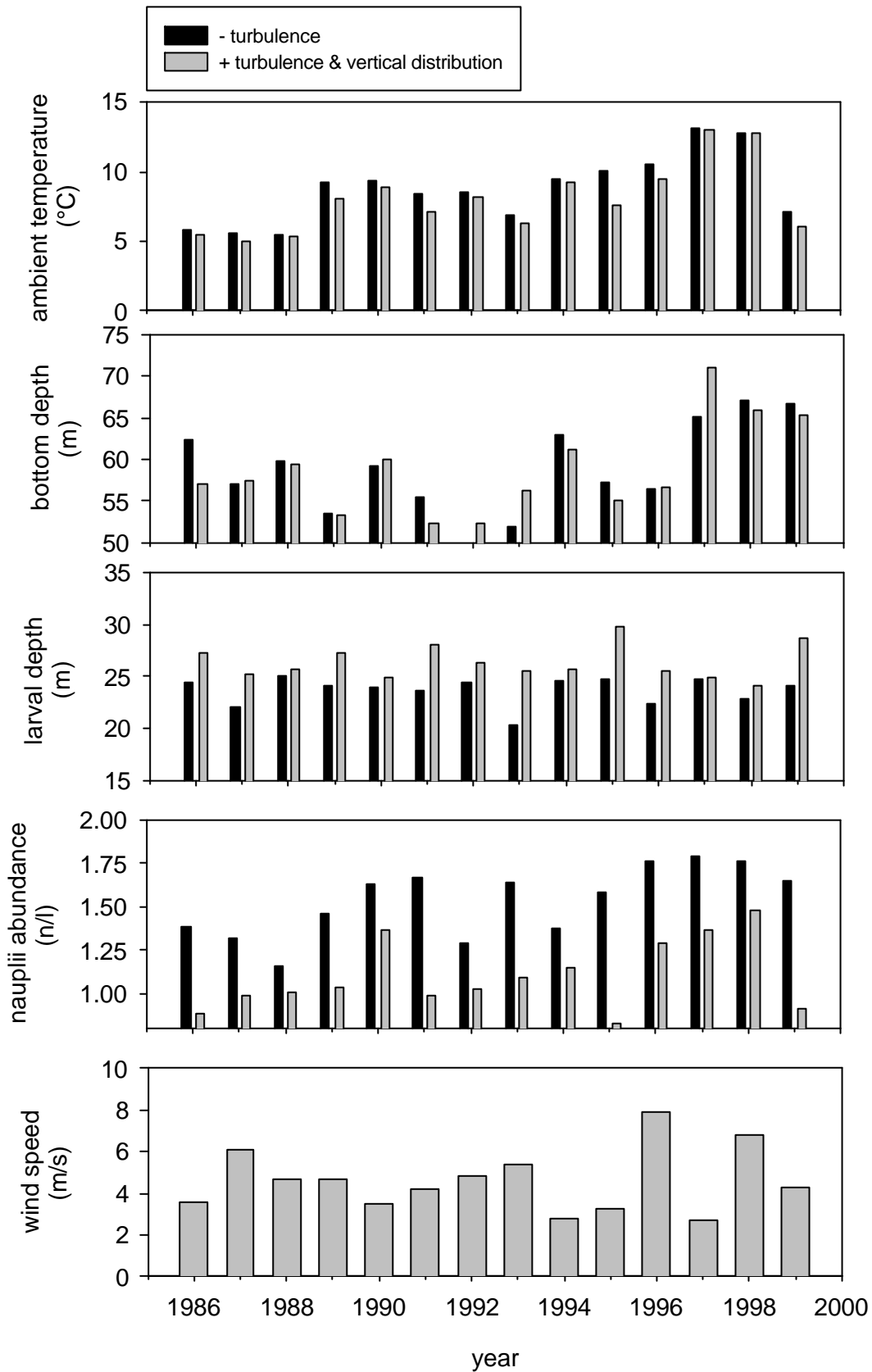


Figure 4.36b: Time-series (1986-1999) of ambient environmental variables of surviving larvae obtained from simulations without *P. elongatus*, without (-) and with (+) turbulence and adjustment in zooplankton vertical distribution: ambient temperature, bottom depth, larval depth and nauplii abundance; and additionally wind speed.

from our model results no such linear relationship between wind speed and survival success could be derived. Enhanced larval survival success may either occur during periods of peak prey abundance or is related to the occurrence of processes optimizing the physical environment (transport into optimal feeding environments, optimal turbulent conditions, low ambient temperatures).

Finally, we incorporated the inter-annual trend in prey availability in the simulations. As no highly temporally and spatially resolving zooplankton abundance data were available, a time series (1986-1997) of prey availability to larval cod was constructed by multiplying mean nauplii abundance by year specific weights (Table 4.11) derived from annual nauplii biomass estimates (Möllmann *et al.* 2000).

Table 4.11: Annual weighting factors for nauplii abundances derived from biomass estimates in the central Baltic Sea 1986-1997 (1992: no data).

Year	1986	1987	1988	1989	1990	1991	1993	1994	1995	1996	1997
weighting factor	0.95	1.03	0.55	0.70	0.87	1.33	0.23	0.29	0.24	0.45	0.36

These simulations, utilizing deviations from mean prey fields, have been performed for prey fields including *P. elongatus*. Additionally, the above mentioned simplified vertical distribution of nauplii as well as turbulence enhancing encounter rates between prey and predator have been included. These model runs illustrate optimal survival success until the beginning of the 1990s, while simulations for the most recent period resulted in relatively low survival rates (Fig. 4.37). The high survival success in the late 1980s/beginning of the 1990s was mainly due to low temperatures (low food requirement) and a high nauplii abundance at the beginning of the spawning season. These simulations show clearly the effect of the long-term as well as the seasonal dynamics of *P. elongatus* on larval cod survival and growth. The decreasing stock of this copepod since the late 1980s/beginning of the 1990s partly compensated by the delay in cod peak spawning resulted obviously in a restricted food availability for first-feeding larvae. Relatively high survival success in 1996 was caused by highest wind speeds (Fig. 4.36 b) registered during peak spawning periods from 1986 to 1999 as well as by low temperatures and relatively high food availability (Tab. 4.11).

Although the surviving larvae seldomly experienced starvation, their condition expressed by their weights at 6mm decreased. Obviously the minimum requirements

for preventing starvation was met, but resulting in bad condition. Again the increasing length after 70 days due to higher temperature reflects the shift in peak spawning.

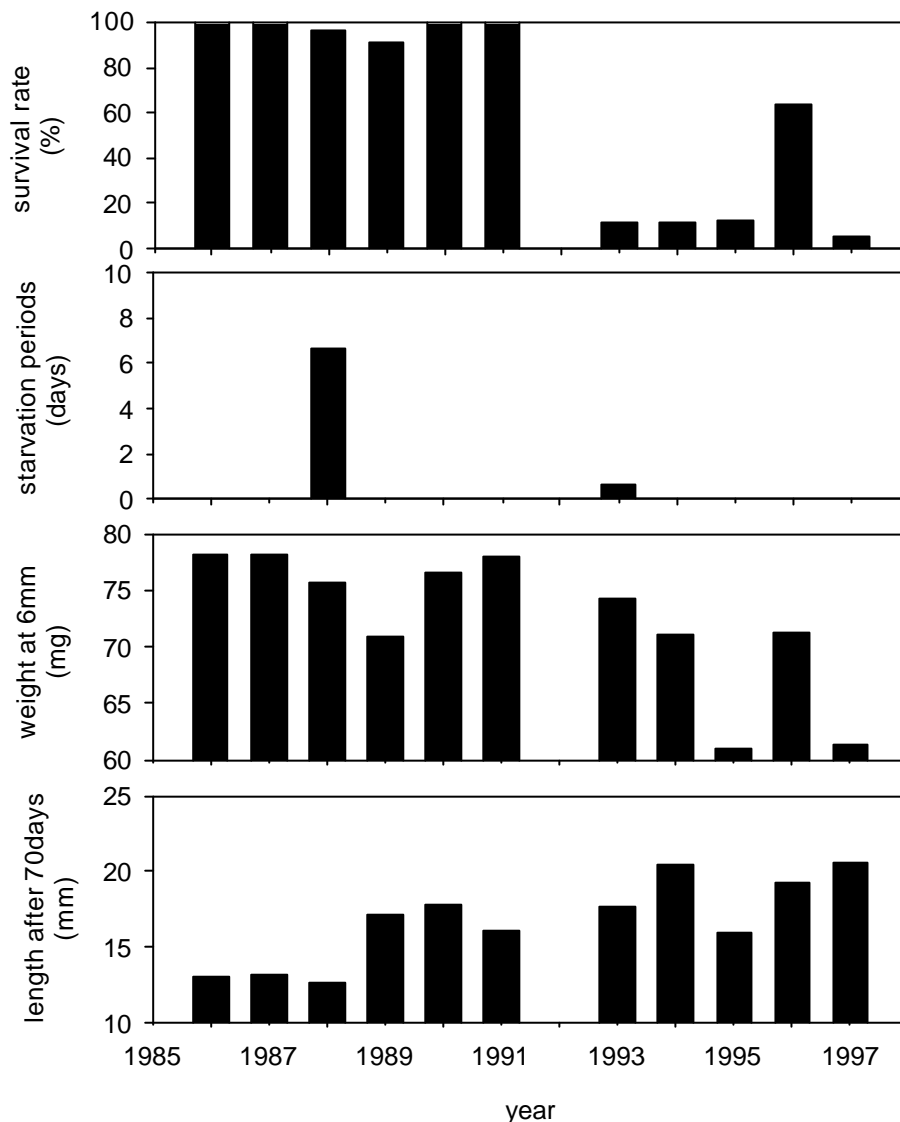


Figure 4.37: Time series (1986-1997; 1992-no data) of model output parameters of surviving larvae originating from peak spawning obtained from simulations with weighted nauplii abundance including *P. elongatus*, turbulence and adjustment in zooplankton vertical distribution: survival rates, starvation periods, mean weight at 6 mm length and length after 70 days of drift and feeding.

4.7.4 Spatial variability

The success of cod reproduction is dependent on certain minimum levels of salinity for egg fertilization (>11psu) and oxygen concentration for successful egg development (>2ml/l) (Nissling *et al.*, 1994; Wieland *et al.*, 1994). These conditions are normally met only within the area enclosed by the 60m isobath (MacKenzie *et al.*,

2000). Retention and dispersion from the main spawning ground (Bornholm Basin) has been identified to be one of the key processes influencing recruitment success of the eastern Baltic cod stock (Voss *et al.*, 1999; Hinrichsen *et al.*, 2001a). Thus, we analysed the average spatial distribution of survival of first-feeding larvae in years 1986-1999 (Fig. 4.38). If prey fields without the copepod *P. elongatus* were considered, larvae initially released as Lagrangian drifters at the outer edge of the deep Bornholm Basin area had considerably higher survival rates (20%), probably because of their lower drift distances towards the optimal feeding environments in more shallow coastal areas. In contrast, larvae hatching within the deep area of the Bornholm Basin during their first-feeding stage required too much prey for survival along their onshore oriented drift trajectories in less favourable feeding conditions. A similar analysis performed for prey fields including *P. elongatus* revealed no areas within the deeper part of the Bornholm Basin leading to significant starvation mortalities (not shown). Only a small area within the Bornholm Deep shows slightly less than 100% survival probability.

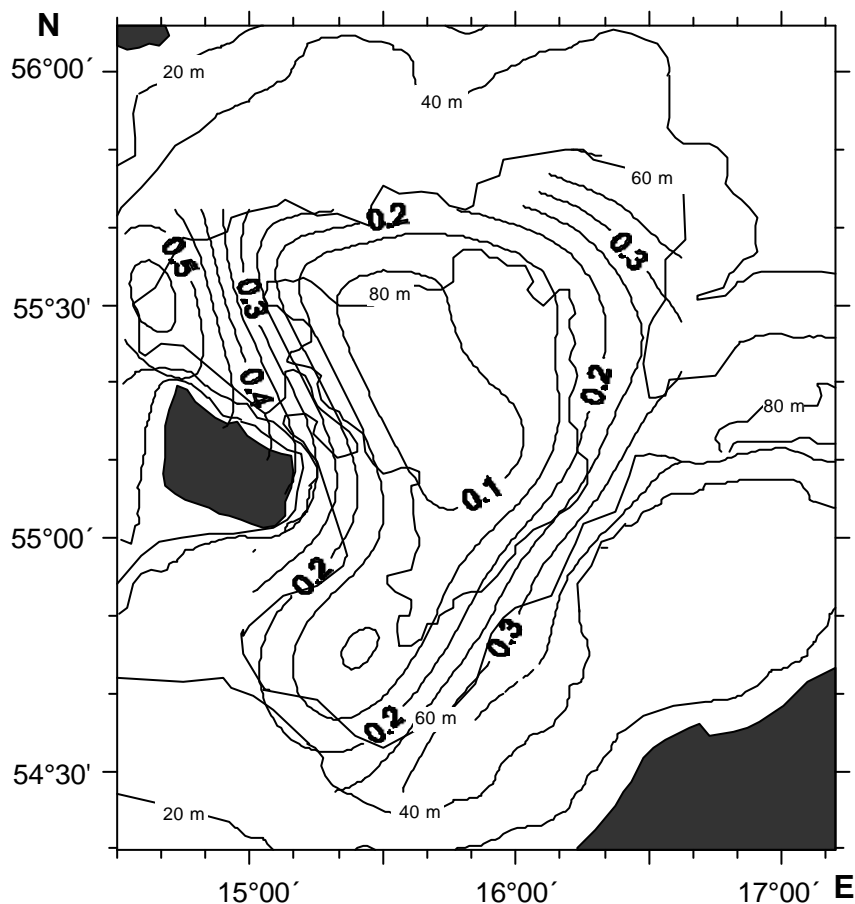


Figure 4.38: Average (1986-1999) horizontal distribution of mean larval survival probability in the Bornholm Basin obtained from simulations without *P. elongatus* and the impact of turbulence.

5 DISCUSSION

5.1 Larval transport

The complexity of the flow dynamics in the Baltic is well known and is mainly determined by the ephemeral character of wind stress, the baroclinic mass field and the complicated bottom topography (e.g. Lehmann, 1995). However, has the 3-D eddy resolving baroclinic model of the Baltic Sea successfully been utilized to simulate the drift of larval cod in the Bornholm Basin, a topographically complex area subject to seasonal variability of hydrographic and meteorological forcing.

In the first part of this study (chapter 4.1; Voss *et al.*, 1999), comparisons of the modeled output and the observed ichthyoplankton field data suggested that the larval distributions could be simulated with a considerable degree of confidence. When comparing modeled cod larval abundances and observations, one has to bear in mind that the model used known initial distributions of cod larvae in the Bornholm Basin only. Outside this area, the initial cod larvae abundance was set to zero, thus, uncertainties of the simulated distributions may be due to advection from neighbouring areas into the Bornholm Basin. Another limitation of the model is that it does not account for larval mortality, which might be different throughout the investigation area. A further source of error is the uncertainty in determining the horizontal distributions of cod larvae from the field samples. This might introduce errors both in setting the initial conditions for the simulation and in the reference distribution. Despite these problems, the modeling study was still able to identify regions where higher abundances of larvae were to be expected.

The simulated drift trajectories showed no significant differences related to differences in the depth of the considered flow field (27 m, 33 m, 39 m and mean of 24-42 m). Thus, at least within this depth range, a higher resolution of the vertical distribution appeared to be unnecessary for modeling purposes. For shallower as well as deeper depth layers (below the halocline), considerably different drift patterns can be expected (Voss, 1996). This is of importance if older larvae exhibit diurnal vertical migrations encompassing these regions, as observed for other cod stocks (e.g. Lough and Potter, 1993). For a reliable drift modelling of the complete early life stage such information would have to be incorporated.

A rapid transport of larvae from the spawning grounds towards the shallow coastal regions of the basin, as observed for August 1991, may be beneficial for larval growth and survival. Coastal areas exhibit a generally higher level of primary production, and hence food abundance, than more offshore regions (Cushing and Walsh, 1976). For the central Baltic, this is confirmed by many studies (e.g. HELCOM, 1993; Ochocki *et al.*, 1995) and in the Bornholm Basin, in particular, high production was found in shallow waters (< 30 m) where the thermocline and halocline reach the bottom (St. John *et al.*, 1995). In addition, larval transport to some coastal areas may offer higher survival probabilities for demersal 0-group cod due to the spatial differences in benthic habitat quality (e.g. substrate type, predator abundance).

From these results, it appeared that annual as well as inter-annual variations in larval drift, distribution of pelagic and demersal stages of juvenile cod and recruitment success have the potential to be examined with respect to variations in meteorological forcing.

Therefore, in the second part of the study (chapter 4.2; Hinrichsen *et al.*, 2001a), simulations were performed for the spawning seasons of 1993 and 1994, which clearly demonstrated the effect of atmospheric forcing on the destinations of larval drifters released at different locations in the Bornholm Basin. The results suggested that in years with a large number of low-pressure systems passing over the Baltic Sea characterized by strong westerly winds, 80-90% of larvae hatched in the centre of the Bornholm Basin may be transported to the northern coastal areas (extreme dispersal years). Conversely, high-pressure systems over Scandinavia and the eastern Baltic Sea during the spawning season result in weak easterly and/or northerly winds and the larvae might be largely retained within the deep-water region of the Bornholm Basin (retention years). Relatively long periods of easterly winds were identified as a prerequisite for enhanced larval transport to the south. Although such periods are rarely observed, the BITS (Baltic International Trawl Survey) data base shows for many year-classes high catch rates of juvenile cod in the southern part of sub-division 26, a fact not to be explained by this simple modelling approach. However, the development of a transport index based on the amount of wind energy required to transport larvae from the spawning site to the coastal regions allowed the identification of changes in transport regime within the spawning season and

between years. Examining the different transport regimes with respect to hatch date and growth rate of surviving 0-group individuals may help to identify the favourable conditions during temporal windows leading to enhanced survival. Such information might be combined temporally with an area- and age-specific egg production model to provide improved estimates of annual recruitment potential.

The analysis of the temporal gonad development of cod (Bleil and Oeberst, 1997) suggested that for juveniles caught during trawl surveys in the autumn in the Arkona as well as in the Bornholm Basin, a separation into origins from the western and eastern stock dependent on their different total length characteristics, was reasonable. However, several reasons existed why relatively high numbers of juveniles of the western as well as of the Kattegat stock could be observed within nursery areas of the eastern stock. The first, but non-verified alternative, was that for spawning purposes, cod of the western and the Kattegat stock migrate actively eastwards and afterwards remain in these nursery areas for longer. However, this seemed to be unlikely, as trawl surveys carried out during previous cruises from February to April have never revealed spawning cod in the eastern Baltic; spawning cod (maturity stage > 5) first occurred in this area in May.

In contrast, the third part of the study (chapter 4.3; Hinrichsen *et al.*, 2001b) suggested the probability of an advective exchange between the western and the eastern Baltic cod stocks during their early life stages. Depending on its strength and intensity, after an inflow of haline waters over the various sills (Drodgen and Darss), it can move as a dense bottom current through the Arkona Basin, the Bornholm Basin and through the Stolpe Channel into the eastern Gotland Basin (Matthäus and Franck, 1992). Following the phase of passive drift, associated with an eastward orientated water mass transport, it is also likely that early life stages of Baltic cod can be advected from the Kattegat and the western Baltic into the central Baltic. This was clearly demonstrated by the numerical experiments simulating the flow patterns in January 1993 by simply considering cod eggs and young larvae as passively drifting tracers. Field samplings from April 1993, yielding feeding cod larvae in the Bornholm Basin (Voss, unpublished), support these modelling results, as spawning had not yet started in this region. Moreover, the results of the drift studies on particles initially released within the spawning grounds of the western Baltic, yielded a clear tendency of direct wind-induced drift of cod early life stages towards the east. Although

transport from the Øresund as well as from the Great Belt can be assumed as being possible only during periods of strong westerly winds, significant eastwards orientated drift of eggs, larvae and pelagic juveniles from Kiel and Mecklenburg Bay was also evident during periods of minor westerly wind influence.

In summary, the potential of cod early life stages from the western Baltic cod stock to drift into the Arkona and the Bornholm Basin and to contribute there to the juvenile populations was shown to be affected mainly by strong westerly winds. Thus, during mild winters, when usually a high number of low air pressure systems with westerly winds pass across the Baltic, the contribution of the western to eastern cod stock may be at its highest level. In contrast, during cold winters with high air pressure over eastern Europe and mainly easterly winds, retention of eggs, larvae and juveniles within their original spawning grounds may predominate. Furthermore, the circulation of the Baltic Sea and water mass exchange with the Kattegat, and hence exchange of the eggs and larvae of cod, are influenced by ice coverage during the winter season, when wind-induced currents and associated sea level variations may decrease drastically.

Although, the interrelationships between both stocks are at present only poorly understood, the utilization of circulation models for elucidating transport of early life stages of fish together with extensive field programmes on the temporal and spatial distribution of 0-group cod may be helpful for quantifying the importance of eastwards orientated drift and the corresponding contribution of juveniles to the eastern Baltic cod stock. Oeberst (2000a,b) estimated that 20-50% of cod aged 2-3 caught in the Bornholm Basin were spawned in the Belt Sea. For 1 year-olds he calculated proportions of up to 90%. However, the importance of juveniles originating from the western spawning stock being caught in the Bornholm Basin might be overestimated, as a corresponding transport from juvenile stages originating from the Bornholm Basin to further eastern areas is not considered. Improved management advice for both stock components may be possible by additional incorporation of physical parameters (wind energy, inflow intensity etc.) in a modeling scheme, especially during periods for which the ratio between the spawning stock biomass of the western and the eastern stock is relatively high (as it is at present) compared to the long-term mean.

5.2 Mortality rates of cod larvae

Field-based mortality rates of Baltic cod larvae have so far only been calculated based on drift studies in the Bornholm Basin, relating the abundance of the oldest egg stage with different larval stages. Mortality rates varied between 1-42 % day⁻¹ (Wieland *et al.*, 2000a; Wieland and Voss, 1997), but all calculations were hampered by very low numbers of larvae caught and the problem of not quantifiable advective losses from the initially flagged aggregation (Wieland *et al.*, 2000a).

In this basin-wide study corrections for transport processes were applied and had a varying impact on the calculated mortality rates. Especially for high speed, non-circular transport regimes these advection processes had to be taken into account, although the principle differences in mortality rates could also be seen without a corresponding correction. The importance of such corrections will even increase for planned studies on sprat larval mortality, as these are distributed shallower in the water column (see section 4.6; Wieland and Zuzarte, 1991; Makarchouk and Hinrichsen, 1998) and therefore are subject to higher current speeds.

There is no indication for a strong small-scale patchiness of cod eggs or larvae, which would not be resolved by the applied meso-scale station grid and thereby considerably bias the abundance estimates, as results from high-resolution samplers like the Longhurst-Hardy Plankton Recorder (Raab, 1999) and the Ichthyoplankton Recorder (Mees, pers. comm., Inst. Marine Sciences, Kiel) demonstrated. The uncertainties in the abundance estimates arising from the non-synoptic sampling procedure as well as the spatial sampling resolution can so far not be quantified, but a theoretical study dealing with this problem has been conducted by Voss and Hinrichsen (subm.) showing mean errors in abundance estimates of 10-20%.

Even when accounting for these uncertainties, the results presented for cod larvae suggest a high variability in the importance of different 'critical periods' for recruitment. In May 1988 the period between hatch and the onset of feeding was characterised by high mortalities (~20 % day⁻¹), whereas during the same period in August 1991 very low mortality rates were observed. Different processes have been proposed to influence survival on this stage. Viable hatch requires a minimum oxygen level of 2 ml/l (Wieland *et al.*, 1994). To account for year to year variations in the hydrographic environment occupied by the eggs, the so called Reproductive Volume (RV) has been defined (Plikshs *et al.*, 1993; MacKenzie *et al.*, 1996). The RV defines the volume of water suitable of successful development of cod eggs by threshold

levels in temperature ($>1.5^{\circ}\text{C}$), salinity (>11 psu) and oxygen content (> 2 ml/l) as experimental studies have shown that below these limits development of cod eggs ceases before hatch (Thompson and Riley, 1981; Nissling and Westin, 1991; Wieland *et al.*, 1994). In 1991 the RV in the Bornholm Basin amounted to 184.7 km^3 , being substantially higher than in 1988 with 99.9 km^3 (Köster *et al.*, 2001b). Additionally taking into account the vertical distribution of the eggs, Köster *et al.* (2001b) calculated the oxygen related egg survival to be considerably higher in August 1991 (0.5) compared to May 1988 (0.08).

Even if hatching occurs, low oxygen concentrations negatively impact larval activity (Rohlf, 1999). Under such circumstances hatched cod larvae might sink to deeper, less oxygenated water layers, as specific gravity increases after hatch and the larvae are not able to counterbalance the sinking rate.

Another potentially important source of mortality during this stage is predation by the clupeids sprat and herring. Performed stomach content analysis of sprat and herring indicate considerable predation pressure on all egg stages in May 1988 (Köster *et al.*, 2001b), while for August 1991 the consumption of cod eggs by the clupeids was low (Köster and Möllmann, 2000). These processes might have the potential to explain the strong differences in mortality rates during the period from hatch to first feeding encountered in this study.

The second investigated 'critical period' ranges from the onset of feeding (larval stage 5) to the state of an established feeder (larval stage 8). During this phase the larvae have to migrate vertically into upper water layers with sufficient light conditions and higher prey concentrations for successful feeding (Grønkjær *et al.*, 1997).

Predation on these larvae is of less importance, as the vertical overlap between prey and predator is rather limited, with the clupeids feeding within and below the permanent halocline (Köster and Möllmann, 1997).

A possible source of variation in survival are differences in prey availability for the larvae. Unfortunately, there are no detailed data on abundance and distribution of suitable prey organisms, like copepod nauplii and small copepodite stages (Last, 1978; van der Meeren and Næs, 1993; Fossum and Ellertsen, 1994), available for these time periods. However, the total meso-zooplankton biomass in the Bornholm Basin was estimated to have been higher in July/August 1991 than in May 1988 (HELCOM, 1996; Schöler, 1995). Schöler (1995) calculated a ratio of 4807 mg/m^2 wet weight in July 1991 to 2818 mg/m^2 wet weight in May 1988, a fact which would *per se*

contradict higher mortality rates for first feeding cod larvae in summer 1991. On the other hand, Schöler (1995) estimated the share of *Pseudocalanus elongatus*, the preferred prey of cod larvae (see section 4.5), in the total meso-zooplankton to be much higher in May 1988 (48%) than in 1991 (May: 27%; with the composition of species being not different to July). Therefore, the impact of a higher total meso-zooplankton abundance is, at least partly, compensated by a different species composition.

Additionally; the ability of the larvae to migrate vertically and to establish as feeding larvae might be influenced by their energy reserves, i.e. the size and quality of their yolk sac. Egg size is a function of fish size and the batch number spawned (Vallin and Nissling, 2000). In the end of the spawning season the egg size is smallest. While it was main spawning time in May 1988, August 1991 corresponds to the late spawning season (Wieland *et al.*, 2000b). While there are no direct egg diameter measurements available for May 1988, investigations for August 1991 showed that egg diameter *in situ* were indeed small, compared to mean values (Wieland and Köster, 1996). Therefore yolk reserves should have been higher in May 1988, favouring survival of the larvae.

In conclusion, the different mortality rates found for the two investigated periods can not easily be attributed to inter-annual or seasonal differences in single processes. Due to the complex abiotic and biotic relationships in the Baltic Sea, it is likely that a combination of seasonal and yearly effects is responsible.

Analysis of long-term data series have shown, that there is a significant relationship between larval abundance and recruitment in Baltic cod (Köster *et al.*, 2001b). This study suggests that feeding-larval abundance is determined by variable mortality rates during the phase of hatching and during the onset of feeding.

Despite the relationship between larval abundance and recruitment, recruitment levels for the 1988 and 1991 year-classes were of a comparable order of magnitude (Köster *et al.*, 2001a, ICES 2001), while larval abundance was calculated to be much higher in 1988 (43.9 vs. 25.2 *10⁹ larvae in 1988 and 1991, respectively; Köster *et al.*, 2001b). From this example it becomes likely, that also after reaching the state of an established feeder processes can act as bottlenecks of survival, limiting year-class strength.

Anyhow, the larval abundance/ recruitment-relationship might be improved by incorporation of additional parameters, e.g. larval length distributions.

5.3 Stomach content analysis of cod and sprat larvae

Baltic sprat and cod larvae are visual predators and therefore the main daily feeding period can be expected during day-light hours. Similar results are presented by e.g. Last (1978) for North Sea cod larvae, with main feeding activity just before sunset. While the results for sprat larvae followed the expected daily feeding cycle very well, the findings for cod larvae revealed not such a clear picture. In May 1988 even in night-time a considerable percentage of the investigated cod larvae had some ingested food particles. The diet at night was dominated by nauplii independently of the length of the larvae. As feeding cod larvae usually stay around 30 m depth (Grønkjær and Wieland, 1997; Grønkjær *et al.*, 1997), where the abundance of nauplii is still high, an occasional feeding seems possible, especially as in laboratory experiments cod larvae were able to feed at very low illumination levels (0.1 to 0.4 lx; Huse, 1994). The sampling in May 1988 was not performed during full-moon, but there was only little cloud cover. So it remains unclear, whether feeding at night is caused by 'moonlight-feeding' as discussed by Last (1978), happens by incident or is a common phenomenon in the Baltic.

Nauplii and calanoid copepod stages I-V have been shown to be important prey organisms for both species. The importance of these items as food for cod larvae has also been described by several authors for different regions (Goodchild, 1925; Wiborg, 1948; Last, 1978; van der Meeren and Næss, 1993; Fossum and Ellertsen, 1994). Older sprat larvae (>16 mm) also included cladocerans (i.e. *Bosmina coregoni maritima*) in higher numbers in their diet, a fact not observed for cod larvae. This might be explained by slightly different vertical distribution patterns of the larvae, i.e. larger sprat larvae also occurring in surface layers (Wieland and Zuzarte, 1991; Makarchouk and Hinrichsen, 1998), the main distribution area of *B. coregoni maritima*.

Contrary to other investigations (Marak, 1960; van der Meeren and Næss, 1993; Fossum and Ellertsen, 1994), no relevant proportion of phytoplankton (diatoms or dinoflagellats) was found in the stomachs of the first-feeding larvae from the Bornholm Basin. This is confirmed by Russian results obtained from eastern Baltic spawning areas for cod larvae in 1978-1985 (Graumann *et al.*, 1989). This difference might be explained by the special environmental conditions in the Baltic, which lead to a temporal as well as spatial mismatch of larvae and high abundances of the above mentioned phytoplankton. In the central Baltic the bloom of diatoms can be

expected from the end of March to the beginning of May (Schulz *et al.*, 1992), i.e. before larvae occur in high numbers in the plankton. The abundance of dinoflagellats in spring, also suitable as food for larvae, has increased in recent years (HELCOM, 1996). However, abundance values were still rather low in 1987 and 1988 (HELCOM, 1996). The second bloom of diatoms occurs in general in October/November being too late to be used by larvae hatched in August/September as a food resource of considerable importance. Additionally to this temporal mismatch, the spatial overlap during spring is rather limited, i.e. highest concentrations of diatoms are encountered in 5-15 m depth (Dahmen, 1995), whereas first-feeding larvae show highest concentrations considerably lower in the water column (sprat: Makarchouk and Hinrichsen, 1998; cod: Grønkjæ and Wieland, 1997). In summer the thermocline increases in depth, thus phytoplankton occurs in relative high abundance also down to 30 m, but the absolute abundance values are considerably lower than in spring or autumn.

The dominating role of nauplii as food organisms in spring even in larger larval size classes, can be explained by the composition of the prey community: The abundance of C I-VI in this time of the year is rather low (Krajewska-Soltys and Linkowski, 1994; Dahmen, 1995). Instead, high numbers of nauplii can be found in the water column, especially *P. elongates* nauplii, as this species is having its reproduction peak at this time of the year. Highest copepod biomass values in the Bornholm Basin are usually reached in July (Möllmann *et al.*, 2000), a fact clearly mirrored in the diet composition of larger larvae. Anyhow, this change to enhanced availability of CHIII, CIV-V and CVI is not seen in enhanced total stomach contents. Extraordinary high abundance values of cladocerans recorded by the Baltic Monitoring Program (HELCOM, 1996) in late summer 1988 were used as prey source only by larger sprat larvae.

The observed shift from nauplii to copepodite/copepod feeding is related to different factors: with increasing length and age of the larvae the swimming ability as well as the mouth size increase. The larvae become able to cope with larger prey organisms. The increase in suitable prey size is more pronounced for cod larvae than for sprat larvae. Last (1978) found an increasing percentage of copepodites in the stomachs of North Sea cod larvae above 5 mm. The results for the Baltic suggest a significant incorporation of C I-III in the diets from 6-7 mm length (cod) and from 9 mm length (sprat).

The analysis of prey selection clearly indicated different 'key prey species' for sprat and cod larvae. In May 1989 sprat larvae strongly selected developmental stages of *Acartia* spp. This result is supported by the 1987 and 1988 Bongo sampling, as by far most identified copepods in sprat larval stomachs belonged to this species. So, a general preference of sprat larvae for *Acartia* spp. prey appears to be obvious. Cod larvae, on the other hand, strongly selected all developmental stages of *P. elongatus* in May 1989. The results from the Bongo sampling can not further support this finding, as the ingested C I-VI stages could not be identified to species. Additionally, the calculated selection indices might be influenced by sampling errors. Only two parallels have been investigated, these however showing the same results. Also in other areas, where the zooplankton composition resembles that of the Baltic, *Pseudocalanus* spp. has been shown to be important as larval food (Last, 1978; Kane, 1984; McLaren and Avendaño, 1995). In the Baltic Grønkjæ (pers. comm.) found that nauplii of *P. elongatus* was common prey in larval guts. Nauplii of *Acartia* spp. were on the other hand poorly represented in the gut contents. Taking into account these different sources of information also for cod larvae a general preference, in this case for *P. elongatus* prey, may be hypothesized. Thus, cod larvae might be affected by the recent decline in abundance of this copepod in the Baltic (e.g. Möllmann *et al.*, 2000). The decrease in biomass of *P. elongatus* since the early 1980ies coincided with a strong decrease in recruitment success of Baltic cod (ICES, 2001). However, both processes have also been shown to be linked to a decrease in ambient salinity (for *P. elongates*: e.g. Möllmann *et al.*, 2000; for cod via the RV: Jarre-Teichmann *et al.*, 2000; Köster *et al.*, 2001b). On the other hand the standing stock of *Acartia* spp., the prey most often consumed by sprat larvae, increased throughout the 1980's and 1990's, accompanied by a strong increase in reproductive success of sprat. But as sprat egg production and sprat egg survival (Köster *et al.*, 2001b) as well as *Acartia* spp. biomass (Möllmann *et al.*, 2000) increase with increasing temperature, also this correlation might be spurious. Therefore, the application of an individual based model for cod and sprat larvae including variable prey fields allows to further investigate the impact of these changing feeding scenarios on sprat and cod recruitment.

5.4 Vertical migration pattern of sprat larvae

In studies of vertical distribution visual avoidance of the sampling gear could be a major error source, as it would tend to skew the distribution to deeper layers where light is inadequate for visual detection of the nets. If this is true then visual avoidance should cause night/day catch ratios to be larger than 1. However, for both investigated time periods (1989-1990 and 1998-2000) we had ratios less than 1, suggesting that this is not a problem in this study.

The vertical distribution of newly hatched fish larvae is determined by the distribution of the late-stage eggs (Anderson and deYoung, 1995). In the Baltic Sea young stages of sprat eggs can be found in a wide range of depths, from sea surface to 140 m (in the periods with good saturation of deep water layers with oxygen). Recent investigations showed that the mean depth of sprat eggs was changing from year to year and during the spawning season (Wieland and Zuzarte, 1991; Makarchouk and Hinrichsen, 1998). Generally the mean depth of eggs decreased during the spawning season (Makarchouk and Hinrichsen, 1998), e.g. the depth layer containing 80% of eggs changed from 55-95 m in May (1996) to 43-65 m in July (1997) in the Gdansk Deep. Makarchouk (2001) developed a model to predict the vertical distribution of sprat eggs under changing hydrographic conditions.

In the Bornholm Basin the density of the sprat eggs and the hydrographic characteristics confined the late-stage and hatching eggs to the deeper water, where the youngest larvae are also found (Wieland and Zuzarte, 1991; Gonzalez-Balzar, 1994). The smallest size group of sprat larvae (<6mm) in this investigation showed almost no signs of diurnal vertical migrations. This is in accordance with results by Bartsch and Knust (1994) and Kloppmann (1991) from the German Bight, both showing only very limited or no diurnal vertical migration for newly hatched sprat larvae. In the size-class 6-10mm, larvae started diurnal vertical migrations in the sampling of 1989 and 1990, i.e. larvae ascended to the surface at night and descended to 30-50m at day-time. While Bartsch and Knust (1994) detected a similar behaviour of sprat larvae in the German Bight in June 1991, Kloppmann (1991) found contradicting results for an investigation around Helgoland: sprat larvae concentrated in the upper 10m at day-time while they dispersed at night.

Valenzuela *et al.* (1991) explained the vertical migrations they recorded in the German Bight by the attempt of sprat larvae to keep their position in a tidal system. Other authors hypothesized that larvae primarily seek depths according to optimal

feeding conditions, determined by a compromise between optimal light for feeding and optimal densities and sizes of prey (e.g. Munk *et al.*, 1989). For the Baltic Sea this is a more appealing theory due to the absence of tidal currents. Supporting results have been presented by Grønkjæ and Wieland (1997) for Baltic cod larvae. The effect of light on feeding of sprat larvae has so far not been investigated. However for herring larvae Blaxter (1968) found a feeding threshold of 0.1 lux (ca. $0.017\mu\text{E m}^{-2}\text{s}^{-1}$ at sunlight) and increasing feeding incidence of larvae up to 1000 lux (ca. $17\mu\text{E m}^{-2}\text{s}^{-1}$) where a level of 90-100% incidence was reached. Unlike for cod larvae no inhibition of feeding (above 12 lx; Huse, 1994) was found. Investigations from the North Sea in autumn (Munk *et al.*, 1989) indicated that lower feeding thresholds were reached at 45-60 m and 15-20 m depth, respectively (estimated from photon flux densities at noon and extinction coefficients). When prey distributions were not uniform, larvae migrated to depths with peak concentrations of suitable prey (ca. 40m) when light intensity increased above the threshold at this depth. With decreasing light intensity at dusk larvae ascended to the surface and continued feeding in the upper part of the water column (Munk *et al.*, 1989). A similar pattern of vertical migration of fish larvae linked to light and the distribution of prey has been found by many authors (e.g. Fortier and Leggett, 1983; Lough and Cohen, 1982; Bjørke *et al.*, 1986).

In this study, at day-time sprat larvae obviously choose the depth layers with maximum prey abundance and highest light intensities in the investigations from 1998-2000. However this did not result in a diurnal vertical migration pattern, as highest prey concentration were recorded in the upper water layers of 5-15m depth. Although in May 1989 suitable prey biomass and light levels were also highest in the surface layers (10-15m depth), larger sprat larvae concentrated in 35-40m depth. A fact also to be seen in the samplings from June 1989 and 1990. This might be explained by an additional environmental factor, i.e. temperature. Due to the thermal heating at the sea-surface a thermocline is developing in May, resulting in 3-5°C higher water temperatures in the surface layer (10-15m) compared to 35-40m depth. In June this difference is even more pronounced (6-10°C). The observed absence of a vertical migration to deeper water layers during day-time for the sampling dates 1998-2000 resulted in higher ambient water temperature, compared to a situation in which a vertical migration would have taken place. The existence of a vertical

migration pattern in May/June 1989 and 1990 has therefore, by reducing the ambient temperatures, also reduced the metabolic and growth-related costs.

The declining gradient in suitable food biomass towards greater depths was considerably more pronounced May 1999 than in May 1989. It appears possible, that sprat larvae not performing a vertical migration in May 1999 benefited from higher ambient temperature (i.e. higher growth rates), as prey concentrations might have been sufficient to counterbalance the increased energy demand due to increased ambient temperatures.

Due to the limited data on vertical zooplankton distribution, it remains unclear, if the observed steeper gradient in the *Acartia* spp. distribution in May 1999 has become a common feature in the Bornholm Basin and is therefore a possible explanation for all observation since 1998. However, positive changes in long-term abundance of *Acartia* spp. in the Baltic Sea have already been described (Möllmann *et al.*, 2000). In conclusion, from the present data it appears to be possible that sprat larvae changed their diurnal migration behaviour, due to the combined effect of temperature and light gradients as well as changes in vertical prey distribution. Additional analysis are ongoing, to further investigate this theory.

5.5 Bio-physical modelling of cod larval growth and survival

A spatially-explicit coupled biophysical model of larval survival and growth for Baltic cod was developed. The model allows to consider the relative effects of advective and trophodynamic processes on growth and survival. It combines a three-dimensional circulation model, and a bioenergetically-based individual model which tracks larval stages of Baltic cod, their growth and survival, through space and time. For the trophodynamics, with two exceptions (assimilation efficiency and starvation threshold taken from more generalized models; Letcher *et al.*, 1996), only submodels and parameters that have been developed or measured for cod larvae have been used, although mainly derived in other areas. The model is also able to assess the overall influence of small-scale turbulence on encounter rates, but does not consider that turbulence can have an overall detrimental effect on larval fish ingestion rate if exceeding a certain level depending also on larval behaviour (MacKenzie *et al.*, 1994).

The primary aim of the study was to examine the influence of abiotic and biotic environmental variability on the potential larval survival success of Baltic cod.

Although transport patterns of intermediate water layers, where post yolk-sac cod larvae mainly occur (Grønkjæ and Wieland, 1997), are relatively well known (Krauß *et al.*, 1999; Hinrichsen *et al.*, 2001a), validation of the results of our coupled physical/biological modelling approaches seems to be difficult. Several processes and factors are only partly resolved and thus parameterized in the model simulations. First, transport patterns of larvae are influenced by the initial spawning location assumed to be an even distribution, their initial vertical position in the water column and their behaviour, especially their diurnal vertical migration within the intermediate water layer, which may vary with stage and size (Grønkjæ and Wieland, 1997) not being incorporated here. Furthermore, transport rates of larvae are dependent on the timing of peak spawning. Secondly, trophodynamics are the most difficult processes to implement in models of larval growth, because of the difficulties in validating such models experimentally or by data obtained during field campaigns. Besides the strong non-linearity of trophodynamic relationships utilized, these relationships are often simplified to be computationally feasible. Finally, tests and validation of the IBM model results can only be performed for specific time periods and areas, for which sufficient information on spatially resolved egg and/or larval abundance, its prey and physical forcing data are available, an exercise presently conducted for 1999 (STORE, 2001).

A process not incorporated in the model is predation on larval Baltic cod. Results from extensive field investigations revealed only clupeid fish, i.e. herring and sprat, to be important predators of cod early life history stages (Köster and Schnack, 1994; Köster and Möllmann, 2000). In contrary to cod eggs, cod larvae are only marginally affected by clupeid predation due to a spatial mismatch between predator and prey (Köster and Möllmann, 1997).

We computed idealized prey fields by using a multiple regression technique on existing zooplankton abundance data. This procedure yielded seasonal trends in abundance of copepod nauplii which resemble the life-cycle patterns of the different species. The univoltine *P. elongatus* has an abundance maximum in April and May (Line, 1979 and 1984). Contrary *T. longicornis*, *Acartia* spp. and *C. hamatus* having multiple generations (Line, 1979 and 1984) accumulate in June to produce next summer generations. Also horizontal distribution patterns are found to be realistic. *P. elongatus* nauplii in the central Baltic are associated with the vertical distribution of adults, preferring higher salinities (Dippner *et al.*, 2000; Möllmann *et al.*, 2000)

encountered in deeper parts of the water column. This explains higher nauplii concentrations in the centre of the basin. *T. longicornis* and *Acartia* spp., not confined to high salinities but to warmer waters (Dippner *et al.*, 2000; Möllmann *et al.*, 2000), were generally found in the upper 50 m of the water column and are distributed in more shallower regions. Nauplii of *C. hamatus* were observed mainly in the centre of the basin which suggests a spawning in deeper layers similar to *P. elongatus*. However, the overall abundance of *C. hamatus* is low compared to other species. Although the constructed prey fields are considered to be realistic, simulating the decline in *P. elongatus* by excluding the abundance of this copepod in the low food environment scenario, underestimated the food abundance and thus probably also larval survival success.

The model results suggest the necessity of the co-occurrence of peak prey and larval abundances and favourable oceanographic conditions for high survival rates. Besides, inclusion of a more realistic description of the temporal and spatial distribution of the prey fields as well as prey aggregation influencing e.g. the vertical distribution of larval fish, future modelling activities have to consider larval survival success with respect to meso-scale horizontal patchiness of prey. Additionally, the intra-annual evolution of zooplankton prey fields has to be validated by data obtained from specifically designed field campaigns (STORE, 2001).

Our modeling results indicate central Baltic cod larvae > 6mm, feeding on all juvenile stages of copepods and later on adults and cladocerans (Zuzarte *et al.*, 1996) to be not food limited. Contrary, first feeding larvae (4.5 - 6 mm length), preying mainly on copepod nauplii are found to have changed from a non food-limited to a food limited state thus representing a critical early life history stage. This food limitation was caused by the decline in abundance of the copepod *P. elongatus* within the last two decades (Möllmann *et al.*, 2000). Zooplankton distributions suggest prey concentrations to strongly vary in time and space independent whether *P. elongatus* is considered or not. Including the abundance of this copepod, highest survival rates occurred during spring and early summer, whereas when neglecting *P. elongatus*, only late hatched larvae, although less in magnitude, had higher chances to survive due to increasing abundances of other copepod nauplii. The shift in peak spawning time of Baltic cod (Wieland *et al.*, 2000b) obviously accounts for the decline in *P. elongatus*. Larvae are now born later in the season, thus profiting from the increasing abundances of juvenile stages of the remaining copepod species *T. longicornis*,

Acartia spp. and *C. hamatus* accumulating at this time of the year. It is not clear yet, whether spawning in general is delayed or late spawners are the only surviving part of the eastern Baltic cod stock, caused by a combination of high fishing pressure on early spawning cohorts (ICES, 1999) or high mortalities of early life stages of early spawners. The spatial analysis of the model output, however, revealed that larvae in recent years had only a high survival probability when advected relatively fast to the margins of the Basin. This is due to the concentration of these copepods in more shallow areas.

In conclusion, our results show the dependence of Baltic cod larvae to climatic forcing conditions both directly in terms of transport and temperature and indirectly due to the impact on prey population development. In a recent study on the link between the North Atlantic Oscillation (NAO) and the Arctic sea ice export, Hilmer and Jung (2000) found that the NAO underwent a secular change in the longitudinal position of the two pressure centers during the last two decades. The eastward movement of the centers of inter-annual NAO variability resulted in an increasing influence of the NAO on the Baltic Sea area, which was accompanied by a reduced flux of saline water masses into the deep basins of the Baltic Sea and an increased river runoff. A result of the decreasing salinity is the decay of the calanoid copepod *P. elongatus* during the last two decades (Möllmann *et al.*, 2000). Our results showed that sufficient food to ensure high survival of Baltic cod larvae is strongly depended on the occurrence of *P. elongatus* in the prey field. Thus, from this study it can be concluded that variations of prey availability on a climatic time scale might be considered as input parameters for recruitment predictions of fish stocks.

5.6 Implementation of results in realized and future studies

Results presented in this work have been implemented in a number of other studies: After identifying variable transport and its coupling to the prevailing wind forcing as a potentially important factor in cod recruitment (e.g. Voss *et al.*, 1999; Hinrichsen *et al.*, 2001a; (chapters 4.1 and 4.2)), attempts have been made to include this factor in stock-recruitment relationships. Jarre-Teichmann *et al.* (2000) demonstrated that the cumulative wind energy at peak spawning time significantly affects cod recruitment, by incorporating a 'wind energy index' in the calculations. *et al.* (2001b) incorporated these transport processes in their exploratory analysis on cod recruitment processes by modifying the 'wind energy index' to consider explicitly the

direction of transport (larval transport index). Further, this 'larval transport index' was modified for sprat larvae (Köster *et al.*, 2002) by adjusting to the different vertical distributions (chapter 4.6) and main spawning season of the two species. In this work Köster *et al.* (2002) showed that wind stress as well as temperature might be critical for sprat recruitment by affecting survival in the period between the late larval and early juvenile stage.

Horizontal distributions from area-disaggregated multispecies virtual population analysis (MSVPA; Köster *et al.*, 2001a) and research surveys indicate that sprat and cod undergo migrations between the basins: e.g. cod recruits of age-group 1 concentrate in Sub-division 26 although main spawning takes place in Sub-division 25. A fact, which could be explained to a large degree by larval transport (Köster *et al.*, 2001a). However, the identified transport of cod early life stages from the western Baltic spawning sites to the eastern Baltic basins (Hinrichsen *et al.*, 2001b; (chapter 4.3)) and their potential impact on eastern Baltic cod recruitment is so far not accounted for in stock assessment.

The evaluation of cod and sprat larval abundance data, being a prerequisite for many tasks addressed in this work, has also contributed to the identification of 'critical life stages' of cod and sprat as performed by Köster *et al.* (2002) by relating observed abundance data between successive stages. For cod recruitment the phase between late egg and early larval stage was identified to be critical. The application of larval stomach content data (Voss and Köster, sub.; (chapter 4.5)) within an IBM for cod larvae (Hinrichsen *et al.*, sub.; (chapter 4.7)) revealed a possible biological explanation. Nevertheless, cod larval abundance was found to be significantly related to year-class strength while sprat recruitment was largely independent from larval abundance.

For cod it will be a future task to further elaborate, how accurate the larval abundance/ recruitment relationship is, to possibly enhance short-term predictions. A goal, which would be of considerable value for fisheries management. Especially the coupling of larval survival to zooplankton dynamics, transport in relation to horizontal hatching distribution and the influence of so far not sufficiently investigated patterns like plankton patchiness, up-welling and hydrographic fronts will have to be covered. Additionally, the impact of varying transport on the utilization of young fish nursery areas will have to be a focus of future work.

As cod and sprat are closely linked via trophodynamic relationships, it will be the overall goal for future work to better understand the implications of a varying and possibly changing environment on both species and their interactions, not at least concerning their reproductive success.

6 SUMMARY

The major aim of the present study was to investigate the influence of varying transport regimes on larval survival and subsequent recruitment of two major Baltic fish species, cod and sprat. A three-dimensional eddy resolving baroclinic model of the Baltic Sea in combination with a Lagrangian particle tracking technique has been used to model larval drift. The ability of the 'Baltic Sea Model' to simulate larval drift in the Bornholm Basin as well as different possible applications were tested for cod larvae:

Results of the Baltic Sea Model were evaluated for May 1988 and August 1991 by a comparison to field data, showing good agreement.

The strong dependence of larval transport (i.e. direction and speed) on the prevailing wind conditions could be shown from comparisons of periods exhibiting contrasting forcing scenarios (1988 vs. 1991; 1993 vs. 1994). The impact of varying transport regimes on horizontal young fish distribution and subsequent recruitment was shown by a comparison of modeled data and survey results for a time-series from 1979-1994. The suggested process influencing larval survival is transport of larvae and pelagic juveniles to coastal nursery habitats during periods of high wind stress and a retention in the less-suitable central basin during periods of low wind stress of variable wind direction.

Consequently, a transport index based on the amount of wind energy required to transport larvae from the spawning site to the coastal regions was developed, allowing the incorporation of this process into stock-recruitment models.

The existence of two cod stocks in the Baltic led to the question, to which extend their early life history stages might mix due to advection processes out of the spawning areas. Otolith investigations by colleagues within the STORE project revealed that a high percentage of juvenile cod caught in the Bornholm Basin originated from the western Baltic cod stock. Thus transport simulations were performed, confirming the potential of western Baltic cod early life history stages to be advected to the Bornholm Basin, especially under strong westerly wind forcing conditions.

For cod recruitment the period between the late egg and early larval stage is critical. This period encompasses as well hatching as the onset of feeding, both processes with potentially high mortality rates. A further application of the Baltic Sea Model was to simulate cod egg and larval drift and advection out of the surveyed

area, thereby enabling the calculation of production rates corrected for advection and subsequently mortality rates. A comparison of two periods revealed highly variable mortality rates, and hence a variable impact on recruitment during hatch and the onset of feeding, respectively.

To improve the understanding of key-processes affecting growth and survival of Baltic fish larvae in the context of their transports, the Baltic Sea Model was coupled to trophodynamic relationships, yielding an individual based model (IBM) of larval drift and feeding. As a pre-requisite the feeding habits of the target species cod and sprat were investigated. Both species showed a daily feeding cycle, with food intake being bound to sufficient light conditions. The dependence on day-light hours was more pronounced for sprat larvae than for cod. Both species fed mainly on developmental stages of copepods. Sprat larvae additionally included cladocerans in their diet, if these were abundant in the zooplankton community. Cod and sprat larval diet composition showed a clear dependence on the seasonal occurrence of different developmental stages of copepods as well as on larval length. With growing length, larvae included successively larger prey organisms in their diets. At a similar total length cod larvae ingested larger prey than sprat larvae. A study on prey selection revealed that cod larvae preferred all developmental stages of the copepod *Pseudocalanus elongatus*, while sprat larvae strongly selected *Acartia spp.*

To be able to adequately model larval transport, the vertical distribution and potential diurnal migration patterns have to be known. These question had already been investigated for cod larvae, but corresponding information for sprat larvae was not available. Thus the present work concentrated on sprat larval vertical distribution. During 3 sampling occasions in 1989 and 1990 sprat larvae performed vertical migrations in the direction 'up at night' (ca. 0-15m) and 'down at day' (ca. 30-55m). Larvae commenced the diurnal migration at length of 6-9mm. However, during the most recent samplings (1998 to 2000) no diurnal migration was detected. Larger larvae stayed also during day-time in the upper water layers (ca. 0-20m), thereby facing higher ambient temperatures. Changes in the composition and abundance of the zooplankton (i.e. increasing *Acartia spp.* biomass during the last years) might have the potential to explain these behavioral changes.

Finally, the first set-up and utilization of a hydrodynamic/ trophodynamic IBM for cod larvae resulted in new insights in the cod recruitment process:

Starvation mortality was found to be important, but exclusively for first feeding larvae, being restricted in their prey field to copepod nauplii.

Caused by the strong decay of *P. elongatus* during the last two decades, larval cod in the eastern Baltic Sea has changed from a non-limited to a food-limited stage.

The shift in peak spawning time of Baltic cod was found to account for the decline in standing stock of *P. elongatus*: Larvae had higher survival probabilities later in the year and if transported into shallower coastal regions, which depends on the prevailing forcing conditions and the horizontal distribution of the spawning effort (with hatching at the edges of the basin being obviously of advantage).

7 ZUSAMMENFASSUNG

Hauptziel der vorliegenden Arbeit war es, den Einfluss unterschiedlicher Transport-Regime auf das Überleben der Larvenstadien, sowie die spätere Rekrutierung zweier wichtiger Ostsee-Fischarten, Dorsch und Sprott, zu untersuchen. Ein dreidimensionales, wirbelauflösendes, baroklines Modell der Ostsee wurde in Kombination mit einer Lagrange'schen Partikelverfolgungs-Technik genutzt, um die Larven-Drift zu simulieren. Die Anwendbarkeit dieses ‚Ostseemodells‘, um die Drift von Fischlarven zu bestimmen, wurde zunächst exemplarisch für den Dorsch getestet:

Die Ergebnisse des Ostseemodells zur (Dorsch-) Larvendrift wurden an Hand zweier doppelter Aufnahmen, im Mai 1988 und August 1991, evaluiert. Der Vergleich von Modelldaten und Feldergebnissen zeigte dabei gute Übereinstimmungen.

Die starke Abhängigkeit des zu erwartenden Transportes (Richtung und Geschwindigkeit) von den Windbedingungen konnte durch den Vergleich meteorologisch unterschiedlicher Perioden (1988 und 1991; 1993 und 1994) deutlich gemacht werden. Auswirkungen unterschiedlicher Transport-Regime auf die Verteilung der Jungfische sowie den Rekrutierungserfolg konnten durch den Vergleich von Modelldaten und Felduntersuchungen für eine Zeitserie von 1979-1994 nachgewiesen werden. Die zugrunde liegende Theorie besagt, dass der Überlebenserfolg der Jugendstadien durch Änderungen im Windantrieb beeinflusst wird: während Phasen starken, gleichgerichteten Windantriebs erfolgt ein schneller Transport von Larven und pelagischen Juvenilen zu geeigneten Aufwuchsgebieten im Küstenbereich. Phasen mit geringem Windantrieb (bzw. aus wechselnden Richtungen) gehen dagegen mit einem Verbleib (Retention) dieser Stadien im weniger geeigneten tiefen Becken einher. Auf diese Ergebnisse aufbauend wurde ein Windenergie-basierter Transport-Index entwickelt. Dieser Index ermöglichte die Einbeziehung von Drift-Prozessen in Bestands/ Rekrutierungs- Modelle.

Die Existenz zweier getrennt gemanagter Dorschbestände in der Ostsee (westlicher und zentraler Ostseedorsch) führte zu der Frage, in wie weit sich deren Jugendstadien, durch Drift aus den Laichgebieten heraus, vermischen können. Untersuchungen an den Otolithen juveniler Dorsche aus dem Bornholm Becken (zentrale Ostsee), die von Kollegen aus dem STORE Projekt durchgeführt wurden, zeigten, dass diese zu einem hohen Prozentsatz in der westlichen Ostsee abgelaidet wurden. Daher wurden weitere Transport-Simulationen durchgeführt, welche die

Möglichkeit des Austausches von Jugendstadien zwischen den Beständen bestätigt. Besonders unter starken Westwind Bedingungen wurden hohe Transportraten aus der westlichen Ostsee ins Bornholm Becken beobachtet.

Die Phase zwischen dem späten Eistadium und dem frühen Larvenstadium ist bei der Dorschrekrutierung in der Ostsee besonders kritisch. In dieser Phase liegen sowohl der Schlupf, als auch der Beginn der exogenen Ernährung, beides Phasen in denen hohe Mortalitäten auftreten können. Der Einsatz des Ostseemodells ermöglichte erstmals die Berichtigung von Abundanzwerten aus aufeinander folgenden Felduntersuchungen, indem explizit die Transportprozesse berücksichtigt wurden. Dies machte die Bestimmung von korrigierten Sterblichkeitsraten möglich. Der Vergleich zweier Zeiträume (Mai 1988 und August 1991) zeigte, dass die Sterblichkeiten, die mit dem Schlupf bzw. dem Beginn der exogenen Ernährung verbunden sind, in hohem Maße variabel erscheinen.

Um die Schlüsselprozesse bestimmen und untersuchen zu können, die während des Transportes das Wachstum und die Sterblichkeiten von Fischlarven beeinflussen, wurde das Ostseemodell mit tropho-dynamischen Beziehungen von Fischlarven gekoppelt. Ziel war es, ein 'individual based model' (IBM) für Dorsch bzw. Sprottlarven zu erstellen. Als Voraussetzung wurde zunächst das Fressverhalten von Dorsch- und Sprottlarven untersucht. Die Nahrungsaufnahme beider Arten ist im wesentlichen auf die Tagesstunden beschränkt. Diese Beobachtung ist allerdings für Sprottlarven sehr viel ausgeprägter als für Dorschlarven. Beide Arten ernähren sich hauptsächlich von den verschiedenen Entwicklungsstadien von Copepoden. Sprottlarven fressen zusätzlich auch Cladoceren, sofern diese in hohen Abundanzen im Zooplankton auftreten. Der Mageninhalt beider Arten ist sowohl vom saisonalen Angebot der verschiedenen Entwicklungsstadien als auch von der Länge des Räubers stark abhängig. Mit steigender Länge beziehen die Larven zunehmend größere Beuteorganismen (Entwicklungsstadien) mit in ihr Nahrungsfeld ein. Bei gleicher Länge bewältigen Dorschlarven jedoch größere Nahrungsorganismen als Sprottlarven. Untersuchungen zur Nahrungsselektion zeigten, dass Dorschlarven alle Stadien des Copepoden *Pseudocalanus elongatus* bevorzugen, während Sprottlarven die Art *Acartia spp.* stark selektieren.

auftraten (ca. 30-55m). Die Sprottlarven begannen diese Wanderungen mit einer Länge von 6-9 mm. Untersuchungen aus den letzten Jahren (1998-2000) zeigten jedoch keine täglichen Vertikalwanderungen. Größere Larven blieben während des gesamten Tages nahe der Oberfläche (0-20m) und somit in wärmeren Wasserschichten. Diese beobachteten Änderungen im Verhalten der Sprottlarven können eventuell mit Änderungen in der Abundanz und der Zusammensetzung ihrer Nahrungsorganismen zusammenhängen.

Die Erstellung und der erste Einsatz des gekoppelten hydrodynamischen/ trophodynamischen IBMs für Dorschlarven resultierte in neuen Erkenntnissen zum Rekrutierungsprozess:

Der Prozess des Verhungerns spielt als Sterblichkeitsursache lediglich zum Beginn der Larvenphase eine Rolle, d.h. solange die Dorschlarven ausschließlich auf Nauplien als Nahrungsquelle angewiesen sind.

Ausgelöst durch den starken Rückgang der Biomasse von *P. elongatus*, hat sich der Ostseedorsch von einer nicht nahrungs-limitierten Art zu einer (im frühen Larvenstadium) nahrungs-limitierten Art entwickelt.

Die Verschiebung der Laichzeit des Dorsches zu späteren Monaten könnte mit der Abnahme von *P. elongatus* in Zusammenhang stehen: Ist diese Copepodenart nicht im Nahrungsangebot vorhanden, hatten Larven nur später im Jahr und bei zügigem Transport in Flachwassergebiete (abhängig von den Windbedingungen) höhere Überlebenschancen. Daher sind sowohl ein später Schlupfzeitpunkt als auch ein Schlupf am Rande des Beckens von Vorteil.

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