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Drift patterns of cod early life stages in the Baltic: exchange between the western and eastern stock, a physical modelling approach

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Abstract

In order to clarify mechanisms influencing reproductive success of Baltic cod a modelling exercise was performed to examine the effect of the wind driven circulation on the transport of early life stages between the western and eastern Baltic. Because the different stocks spawn within different environments at different times of the year, the occurrence of variable age/length distributions of juveniles within the different potential nursery areas can be explained by the difference of circulation patterns. A three-dimensional circulation model of the Baltic Sea was utilized to investigate the temporal evolution of egg and larval fields of the western Baltic stock which preferably spawns in the Kattegat and the Belt Sea. Comparison of within and between year variability of egg and larval transport showed large differences between 1988 and 1993 primarily due to variations in wind forcing. The wind conditions during the main spawning periods of western Baltic cod differed significantly. In 1988 relatively low and variable wind forcing prevailed, whereas due to a relatively long period of strong wind mainly from western directions, in January 1993 the recent major Baltic inflow to the Baltic Sea occurred. Estimates of egg and larval drift as well as the identification of spawning areas of the western Baltic stock which potentially can contribute to the juvenile population within the eastern Baltic will be presented and discussed.

1 Introduction

In the Baltic Sea, two cod stocks exist whose early life stages (eggs, larvae, juveniles) are subject to advection by non-stationary three-dimensional current fields. These stocks are the western Baltic cod stock, considered to be located west of the island Bornholm (Fig. 1), and the eastern stock, east of Bornholm (Bagge and Thurow, 1993). As obtained from genotypic and phenotypic analysis (Sick, 1965; Jamieson and Otterlind, 1971) a distinction between both stocks occurs on either side of longitude $14^0 30' N$ with a rather narrow area of overlap between both stocks.

Historically, for the eastern Baltic cod stock three main spawning areas have been identified (the Bornholm Basin, the Gdansk Deep and the Gotland Basin). In the western Baltic, cod begin to spawn in different areas (Danish Straits, Kiel Bay, Fehmarn Belt and Mecklenburg Bay) early in the year with peak spawning in March. In May the spawning is completed (Kändler, 1949; Berner, 1960; Thurow, 1970; Bleil and Oeberst, 1997). Spawning of cod in the eastern Baltic (May to July) is delayed compared to the western Baltic (Wieland et al., 1999). Thus, within the different nursery areas of the Baltic juveniles with different age and length characteristics can be expected.

The Baltic Sea can be described as a large estuary with an upper layer of brackish water and a lower layer of saline water. The Danish Straits connect the Baltic Sea and the Kattegat. The outflow of brackish water masses in near surface waters and a compensating inflow of haline water near the bottom establish a haline stratification in the Danish Straits most time of the year (Wyrtki, 1953). Generally, during periods of weak and moderate winds, this stratified two-layer system prevails. Under strong west wind conditions, the stratification is broken up by mixing and a huge amount of highly saline water can penetrate into the Baltic Sea. After passing the major sills (Drodgen and Darss Sill) the highly saline water sinks down to the bottom. Due to river runoff (Bergström and Carlsson, 1994) and more or less continuous inflows of haline water originating in the Skagerrak/Kattegat area, a permanent halocline in the central Baltic is maintained.

The main aims of this study were:

- to determine the birth-dates of juvenile cod caught within different potential nursery areas of the Baltic Sea (Arkona- and Bornholm Basin) in order to obtain informations about their origin, and
- to perform modeling exercises, to examine the effect of and the sensivity to different wind driven circulation patterns on the transport of cod early life stages between the western and eastern Baltic

Due to the lack of time, during the autumn cruises from 1993 to 1996 the horizontal 0-group cod distribution within the potential nursery areas were not surveyed systematically and with only less spatial resolution. Thus, it could not be the goal to simulate the circulation patterns for each of the years explicitely, but to identify the principal factors influencing the transport of early life stages of cod between the western and eastern Baltic. Therefore, two years with considerably different wind conditions (1988 and 1993) were chosen.

2 Material and methods

2.1 Determination of the birth-dates and the age/length characteristic from otolith structure analysis of 0-group cod

Spawning of cod in the eastern Baltic Sea is delayed compared to the western Baltic, the Kattegat and the Skagerrak areas (Bleil and Oeberst, 1997), and if mixing of early life stages between different stocks can be assumed, populations of juvenile cod originating from different spawning areas will probably show varying age and size distributions. Thus, the investigations were focused on determining birth-dates of the 0-group cod caught in the different nursery areas from sagitta otolith microstructure analysis in order to assign the juveniles to their different spawning areas.

The juveniles were sampled during 6 surveys in the Arkona- and Bornholm Basin performed by R/V "Solea" in September and October of the years 1993 to 1996. The individuals were caught in pelagic hauls ($>$ 15 to 20 m above the bottom) and in bottom or near bottom hauls. The microstructure analyses were carried out at a subsample of sagitta otoliths from juveniles with a total length from 2 to 18 cm. A total of 81 pelagic and 243 demersal individuals were analysed.

Because of damages or overgrinding 20% of the otoliths were not suitable for the microstructure analysis. The first 10 to 20 increments following the hatchcheck were very thin and with low contrast and could often not be clearly determined. Furthermore, counting of the 5 to 15 increments closest to the accessory growth center (AGC) was difficult due to substructures, whereas the numbering of the secondary increments, which started after the AGC was possible without any problems. The formation of the AGC was found from 42 to 56 increments (mean=49.3) after the hatchcheck taken from a subsample of well prepared otoliths (n=18). Similar investigations from 18 juvenile cod with a well known age (48 days) yielded that the development of the AGC started 41 to 43 days after hatching. Using these data together with the results of the former analyses a mean value of 45 days from the hatching check to the beginning of the secondary increments can be assumed. A more detailed description about microstructure analysis of otoliths can be found in Oeberst and Böttcher (1998).

The spawning periods of the western Baltic, the Arkona-, and the Bornholm Basin are very different, thus the estimation of the juveniles birth-dates will not lead to substantial errors for the assignment back to their different spawning areas. From these investigations follow that the different pelagic stages of cod (eggs, larvae and juveniles) stay about 105 days in pelagic waters and thus are susceptible for drift processes.

2.2 Baltic Sea Model

In order to calculate the advection of eggs and larvae of Baltic cod, numerical simulations of the circulation of the Baltic Sea were performed by application of the three-dimensional eddy-resolving baroclinic model of the Baltic Sea (Lehmann, 1995). The horizontal resolution is 5 km with a discretisation of 28 levels in the vertical. The model comprises the whole Baltic Sea, including Bothnian Sea, Gulf of Finland as well as Belt Sea, Kattegat and Skagerrak. At the western boundary an idealised 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 Norrköping, Sweden) and river runoff taken from a monthly mean runoff data base (Bergström and Carlsson, 1994).

Because eggs and young (non-feeding) larvae have only minor swimming behaviour their advection was simulated by the incorporation of 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. Within the spawning grounds of the western Baltic cod stock eggs and young larvae are found at depth below 20 m (Bagge et al., 1994), thus, passive drifting tracers were incorporated here at every model grid point where depths of 20 m were exceeded (Fig. 2). Generally, the major spawning ground of the western Baltic cod stock can be subdivided into four typical subareas:

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

The concentrations representing cod eggs and/or larvae were totally arbitrary because the 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).

Older (feeding) cod larvae usually are found in the same area as eggs and young larvae but mainly above the pycnocline ($<$ 20 m). In order to develop a data base for a Lagrangian particle tracking exercise on feeding larvae and pelagic juvenile cod simulated three-dimensional velocity fields were extracted. This data base offers the possibility to derive routes of simulated Lagrangian drifters by calculating the advection of "marked" water particles (Hinrichsen et al., 1997). The drifters were allowed to leave the layers where they were launched, thus, the geographic positions of the drifters varied over time as the result of the three-dimensional velocities that they experienced.

In order to estimate the potential advection of cod early life stages spawned in the western Baltic and in the Kattegat area, the circulation patterns during the major spawning season (January to April) for two years with considerably different wind forcing conditions (1988 and 1993) were analysed. The two selected years differ significantly from their overall wind conditions. The spawning period of the year 1988 (Fig. 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 (Fig. 4) the recent major Baltic inflow to the Baltic Sea occurred (e.g. Matthäus and Lass, 1995). This time period can be identified by a relatively long period of strong wind forcing of mainly western direction.

During the simulations older larvae and/or juveniles of cod were prescribed as Lagrangian drifters which were released into the modelled Eulerian flow fields within the spawning grounds of the western Baltic (Fig. 2) at depths above the pycnocline (3, 8, 13 and 18 m). The release of drifters was repeated at 5 days 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 January 6 and ended March 21, whereas the analysis of the temporal evolution of the tracer fields (eggs and/or young larval abundance) also started January 6 but ended January 31 for both considered years.

3 Results

3.1 Length and age of juvenile cod in the Arkona- and Bornholm Basin

The 0-group cod caught in autumn in the Arkona- and the Bornholm Basin (total length 2 - 17 cm) can be divided into two size classes with regionally different frequencies. The Bornholm Basin was dominated by pelagically sampled individuals of size classes 2 - 7 cm, whereas within the Arkona Basin predominately the size classes 8 - 14 cm have been observed, with the latter exclusively caught by bottom trawls.

The length groups between 3 to 7 cm and 8 to 14 cm of cod caught within the Arkona Basin during the autumn cruises were traced back to spawning activities in July to August and April to May (Fig. 5a). Fig. 5b displays the distribution of birth-dates of juveniles caught in the Bornholm Basin.

According to data sampled from 1992 to 1996 on the temporal gonadal development of cod (Bleil and Oeberst, 1997), the distribution of the birth-dates estimates agrees well with the observed peak spawning periods for different areas of the Baltic Sea. The spawning season in the Arkona- and the Bornholm Basin covers the same time range, from June to August. Individuals spawned in the summer months (Julian day 180 - 250) can therefore be assigned to these spawning regions. The spawning season in the western Baltic started already in February, ending in May. Within this region the development of the gonads started succesfully later from west to east. Individuals originating from this spawning group made up the majority of 0-group cod caught in the Arkona Basin (Fig. 5a), but were also present in the Bornholm Basin (Fig. 5b). Investigation on the timing of spawning in the Kattegat area led to the assumption that the spawning process started here even earlier than in the western Baltic (Börje et al., 1985). The additional fraction of juvenile cod found in the Bornholm Basin with back calculated birth-dates from January to the middle of march could therefore represent individuals spawned in the southern Kattegat or in the Øresund.

3.2 Advection of eggs, larvae and juveniles of Baltic cod

An overview of displacements of particles launched within the western Baltic can be obtained from Fig. 6, which shows the horizontal vertically integrated cod egg and/or young (non-feeding) larvae concentrations generated by the physical circulation model. The diagramm represents the final locations of the arbitrarily chosen abundances after a 25 days integration period for January 1988 and 1993 (January 6 to 31). By day 25 of the year 1988 when all initially as cod egg started particles must have reached the stage of young larvae only low transport rates towards the deep basins of the central Baltic (Arkona- and Bornholm Basin) were recognised (Fig. 6a). As a consequence, this resulted in a relatively high fraction of larvae remaining in the area where they were spawned. For the 1988 model run, individuals spawned in the Øresund as well as in the Kiel Bay and in the Mecklenburg Bay clustered near their spawning grounds. Individuals originally representing eggs and/or larvae spawned in the area of the Little- and Great Belt have been completely disappeared from this area and were mainly transported towards the Kiel Bay as well as to the Mecklenburg Bay. Conversely, in January 1993, most of the individuals were advected towards the east by crossing the Darss Sill (Fig. 6b). After 25 days of integration, the absolute maximum abundance of particles was found within the area of the Bornholm Deep ($55^0 30'$N, $15^0 30'$ E). The high particle transport in January 1993 orientated from west to east was due to extremely high wind speeds from westerly directions (Fig. 4). In contrast, wind forcing in January 1988 was considerably lower in wind speed and more variable in direction (Fig. 3).

A more detailed comparison of the particle transport for the two considered years is given in Fig. 7. As a result of interannual variability in wind conditions, the two considered years exhibit significantly different circulation patterns. In January 1988, at the beginning of the spawning period (Julian day 7) the flow fields moved particles further northward only weakly, whereas a stronger transport from the Kiel and Mecklenburg Bay towards the Øresund region occurred after the onset of a longer period of wind forcing from northeasterly direction (Julian day 15). However, during January 1988, particle transports across the Darss Sill towards the Arkona Basin were only of minor importance.

In contrast, January 1993 depicted a typical inflow situation with, on average, high wind speeds ($>$ 15 m/s) of mainly western direction. As a consequence, the particle transport throughout the entire simulation period was predominated by advection of well oxygenated highly saline water masses from the Skagerrak/Kattegat region and the western Baltic towards the central Baltic. Correspondingly, after the 25 days simulation period almost 70% of the particles representing eggs and/or young larvae left the spawning grounds of the western Baltic and were advected into the Arkona Basin and partly farther eastward into the Bornholm Basin. Furthermore, from this analysis, durations of about 15 to 25 days for particle transports over such long distances were estimated. Compared to 1988, a similar transport of particles from the Danish Straits further northward towards the Skagerrak/Kattegat region was not detectable in the model results.

Further support for the results on annual variability of circulation patterns due to variations of meteorological forcing conditions can be derived from a detailed examination of the temporal development of the final destinations of Lagrangian drifters representing older (feeding) larvae as well as juvenile cod of pelagic habitat. Fig. 8 displays the trajectories of a selection of drifters initially released in the spawning grounds of the western Baltic in January 1993. Due to strong westerly winds the particles preferably drifted into the Bornholm Basin across the shallow Rønne Bank southwest of Bornholm, while a second route through the Bornholm

Gat area (between Bornholm and the southern coast of Sweden) seems to be of only minor importance.

The investigations were performed over the whole duration of the major spawning period of the western Baltic as well as of the Kattegat cod stock for the years 1988 and 1993 (Fig. 9). 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 in the wind-induced flow component. The x-axis of the figure indicates the dates of drifter release (at 5 days intervals). Note, compared to particles such as cod eggs and young larvae incorporated into the model as a specific tracer field, these drifters were initially inserted into the simulated flow fields higher in the water column and thus, were more directly associated with the direct wind-driven component of the flow fields.

In 1988, Lagrangian drifters either released at the beginning of the spawning season or later than Julian day 40, primarily experienced moderate wind forcing from southern to eastern direction during their 45 days drift periods. This resulted in a relatively high occurrence of particle transport rates towards the southern Kattegat area. Drifters inserted between Julian day 20 and 40 were mainly influenced by winds of westerly directions, thus, generally the particle transport towards the north rapidly decreased. Consequently, due to the change in atmospheric conditions an increase of particle drift towards the east (Arkona Basin) was observed. During the simulation period of 1988 no substantial transports towards east of larvae originally spawned in the western Baltic or in the Kattegat can be derived from the model experiment. Controversy, during the major Baltic inflow in January 1993 about 30% of the cod larvae were advected across the Darss Sill through the Arkona Basin into the Bornholm Basin. 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 region and within the Danish Straits became more numerous. Drift towards the Bornholm Basin completely vanished (Julian day 35) but slightly recovered afterwards primarily due to the influence of single wind events of mainly western direction at the end of March (Julian day 50 and 75 to 85).

In order to identify differences in the eastward transport of particles, the final destinations of drifters which were initially released within the different spawning grounds of the western Baltic cod stock are presented in Fig. 10. This analysis indicates that the subareas II and III (see chapter 2.2) can be identified as the main contributors of the western Baltic spawning stock biomass to the juvenile population of the Arkona Basin and partly also of the Bornholm Basin. Enhanced transport from subarea I and IV across the Darss Sill was only obtained in cases of extremely strong wind forcing conditions of westerly direction. As a consequence, the mean drift durations towards the east were considerably shorter in 1993 compared to 1988 (not shown).

4 Discussion

The analysis of the temporal gonadal development of cod (Bleil and Oeberst, 1997) suggests that for juveniles caught during trawl surveys in autumn in the Arkona- as well as in the Bornholm Basin a separation into origins from the western and eastern stock in dependency on their different total length characteristics seems to be reasonable. However, it remains an open question to debate, why relatively high numbers of juveniles of the western as well as of the Kattegat stock can be observed within nursery areas of the eastern stock. The first but presently non-verified alternative is, that for spawning purposes cod of the western and the Kattegat stock migrates actively eastward and that afterwards the juveniles remain in these nursery areas for longer time periods. However, this seems to be very unlikely, because as obtained from trawl surveys carried out during previous cruises from February to April spawning cod never was detected in the eastern Baltic. For the first time spawning cod (maturity stage > 6) occurs in May.

In contrast, the present study suggests the probability of an advective exchange between the western and the eastern Baltic cod stocks' early life stages. Following the phase of passive drift, associated with an eastward orientated water mass transport it is 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 our numerical experiments simulating the flow patterns in January 1993 by simply considering cod eggs and young larvae as passively drifting tracers. Moreover, the results of the more extended temporally highly resolved drift study 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 of being possible only during periods of strong westerly wind events, significant eastward orientated drift of eggs, larvae and pelagic juveniles of cod from the Kiel and Mecklenburg Bay also was evident during periods of minor westerly wind influence.

In summary, the potential for transport 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 population was tested and has been recognized as being mainly affected by strong westerly winds. Thus, during mild winters, when usually a high number of low air pressure systems with winds of western direction passing the Baltic, contribution of the western to eastern cod stock may be on its highest level. In contrast, during strong winters high air pressure over eastern Europe associated with mainly easterly winds, retention of eggs, larvae and juveniles within their original spawning grounds may be predominated. Furthermore, the circulation of the Baltic Sea and the water mass exchange with the Kattegat are influenced by ice coverage during the winter season. Due to a reduced momentum transfer at the air-sea surface interface, wind-induced currents and associated sea level variations may drastically decrease. Under maximum ice extent the sea level difference between Kattegat and Baltic which is mainly controlling the inflow of haline water into the Baltic, will be different from those of mild winters. Differences in contributions of the western to the eastern stock in dependency of physical forcing conditions may hint that this mechanism is controlled by the North Atlantic Oscillation (NAO) index.

Baltic cod is managed as one unit covering the whole Baltic Sea. However, ICES considers the stock in two units (western and eastern) and advice is provided separately on them. Changes in atmospheric conditions as well as in the physical environment afftecting the variability in reproductive success of cod are very hard to predict and presently beyond of fisheries management control. 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 programs on the temporal and spatial distribution on 0-group cod may be helpful to quantitatively estimate the importance of an eastward orientated drift and a corresponding contribution of juveniles to the eastern Baltic cod stock. This indicates, that improved management advices for both stock components may be possible by additional incorporation of physical parameters (wind energy, inflow intensity etc.), especially during periods for which the ratio between the spawning stock biomasses of the western and the eastern stock is relatively high (as it is at present) compared to the long-term mean.

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Figure captions

Fig. 1: Western and central Baltic Sea. Ø:Øresund, GB(west):Great Belt, LB:Little Belt, KB:Kiel Bay, FB:Fehmarn Belt, MB:Mecklenburg Bay, AB:Arkona Basin, BB:Bornholm Basin, GD:Gdansk Deep, GB(east):Gotland Basin

Fig. 2: Spawning grounds of the western Baltic cod stock. I:Great Belt; II:Little Belt, Kiel Bay, Langeland Belt and Fehmarn Belt; III:Mecklenburg Bay; and IV:Øresund

Fig. 3: Wind direction (lower panel) and wind speed from January to April 1988 taken from Christiansø weather station

Fig. 4: Wind direction (lower panel) and wind speed from January to April 1993 taken from Christiansø weather station

Fig. 5: Distribution of total lenghts and birthdays for juvenile cod caught from 1993 to 1996 in a) Arkona Basin, and b) Bornholm Basin

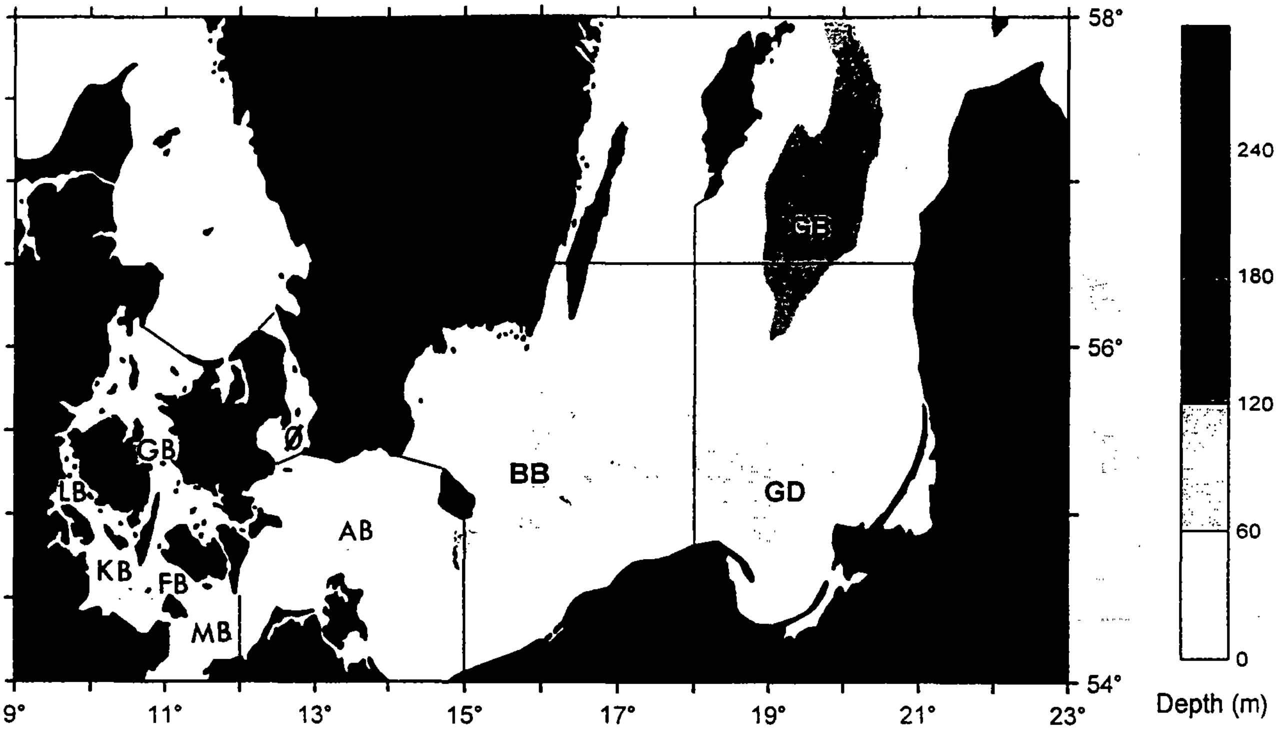
Fig. 6: Horizontal distribution of tracers representing cod eggs and young larvae (initially released within the spawning grounds of the western Baltic cod stock at the 5th of January of each year at a) end of January 1988, and b) end of January 1993

Fig. 7: Relative frequency of cod eggs and young larvae initially released as tracers within the western Baltic a) southern Kattegat 1988 b) southern Kattegat 1993 c) Øresund 1988 d) Øresund 1993 e) western Baltic Sea (except Øresund 1988) f) western Baltic Sea (except Øresund 1993) g) Arkona Basin 1988 h) Arkona Basin 1993 i) Bornholm Basin 1988 and j) Bornholm Basin 1993

Fig. 8: Lagrangian drifter (drift duration 45 days) representing older (feeding) larvae and pelagic juvenile cod initially released within the western Baltic at the 5th of January, 1993

Fig. 9: Relative frequency of Lagrangian drifter (drift duration 45 days) within a) southern Kattegat 1988 b) southern Kattegat 1993 c) Arkona Basin 1988 d) Arkona Basin 1993 e) Bornholm Basin 1988 f) Bornholm Basin 1993. x-axis indicates the dates of release

Fig.10: Relative frequency of Lagrangian drifter (drift duration 45 days) observed within the Arkona Basin initially released in (see Fig. 2) a) area I 1988 b) area I 1993 c) area II 1988 d) area II 1993 e) area III 1988 f) area III 1993 g) area IV 1988 h) area IV 1993, and observed within the Bornholm Basin initially released in i) area I 1988 j) area I 1993 k) area II 1988 l) area II 1993 m) area III 1988 n) area III 1993 o) area IV 1988 p) area IV 1993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Depth (m)

Fig. 1

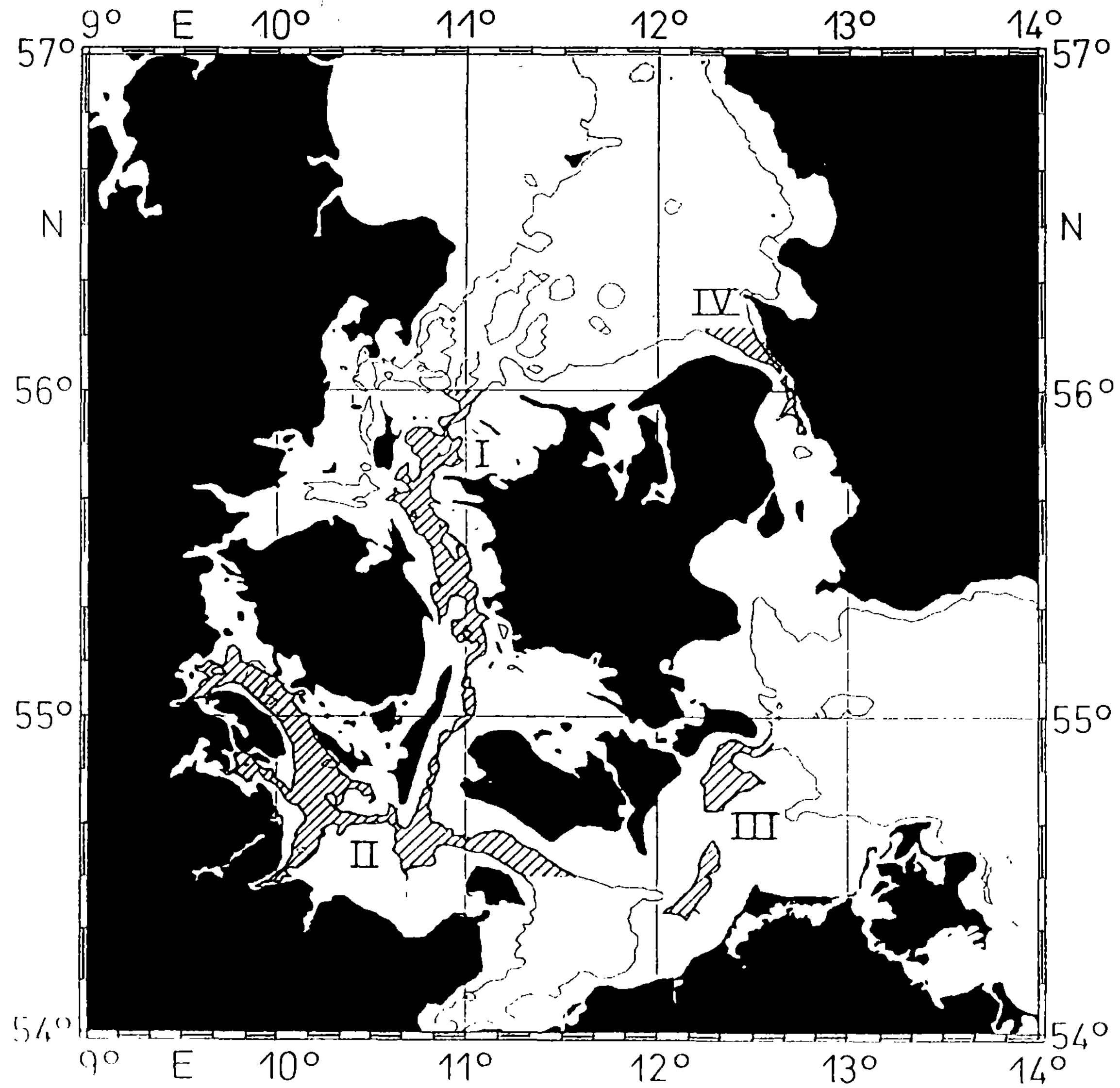
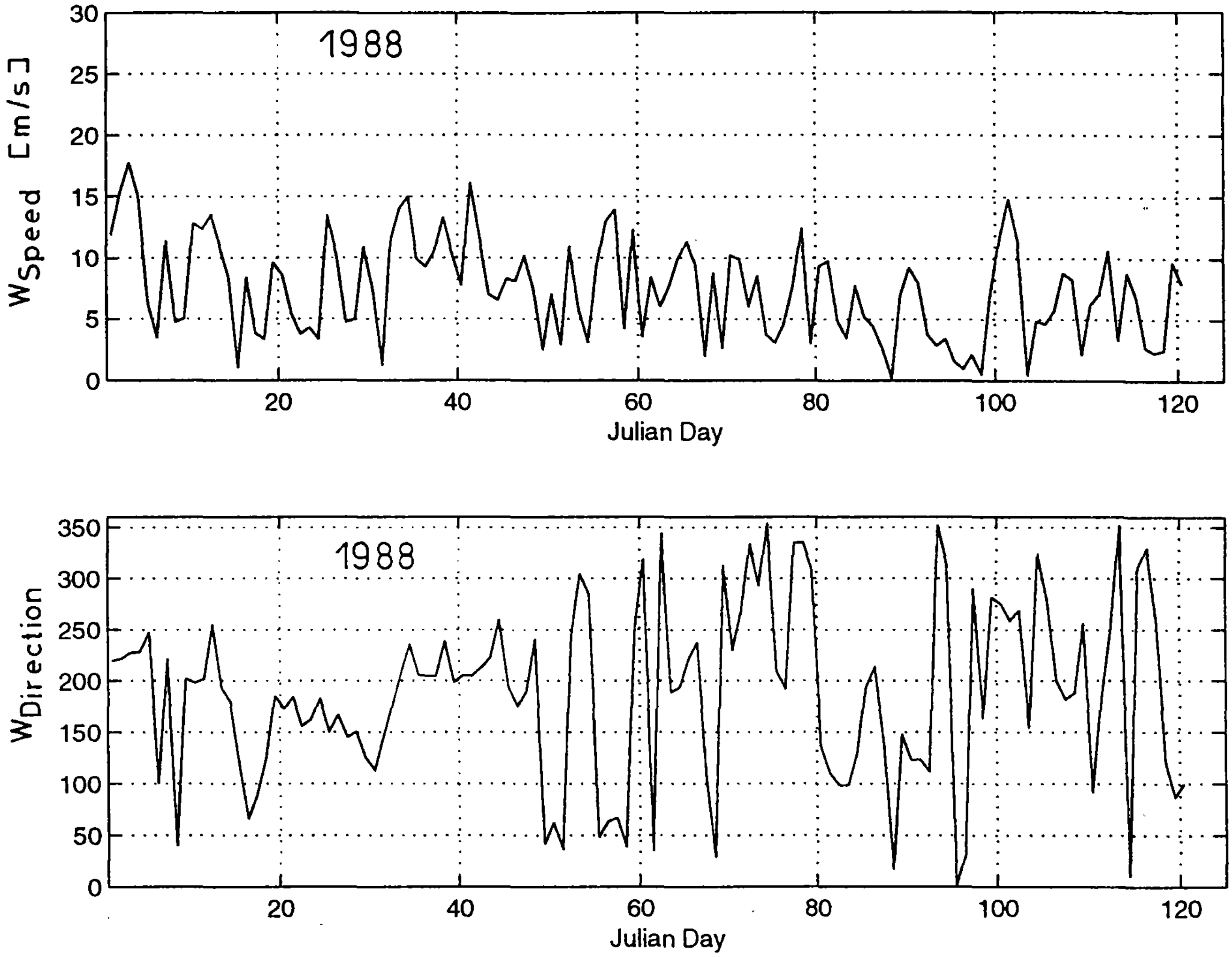


Fig. 2

1988
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5
10
15
20
25
30
20
40
60
80
100
120
Julian Day
1988
W_Direction
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Julian Day

Fig. 3

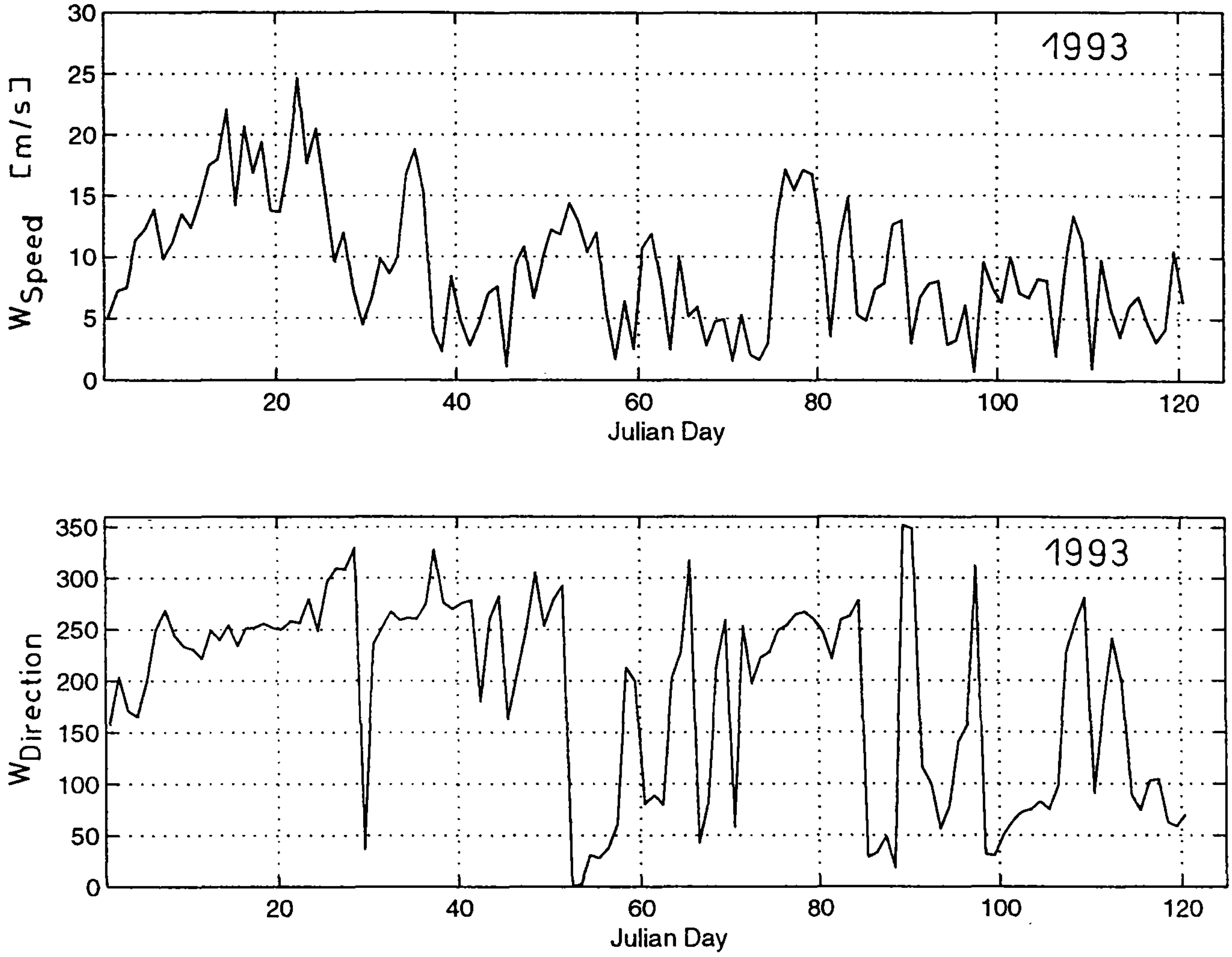
1993
W_Speed [m/s]
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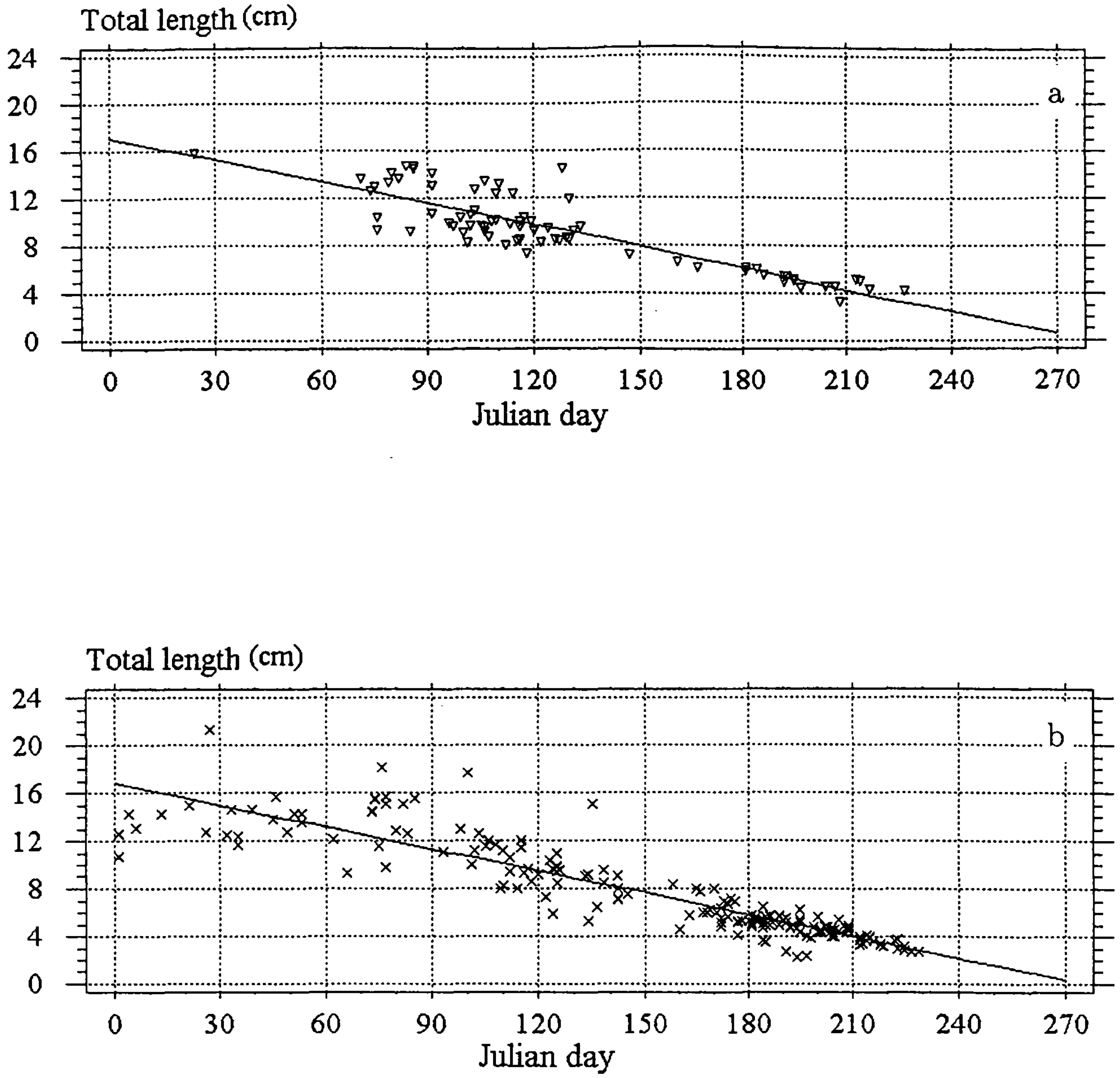
Fig. 4


Total length (cm)
24
20
16
12
8
4
0
a
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30
60
90
120
150
180
210
240
270
Julian day
Total length (cm)
24
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Julian day

Fig. 5

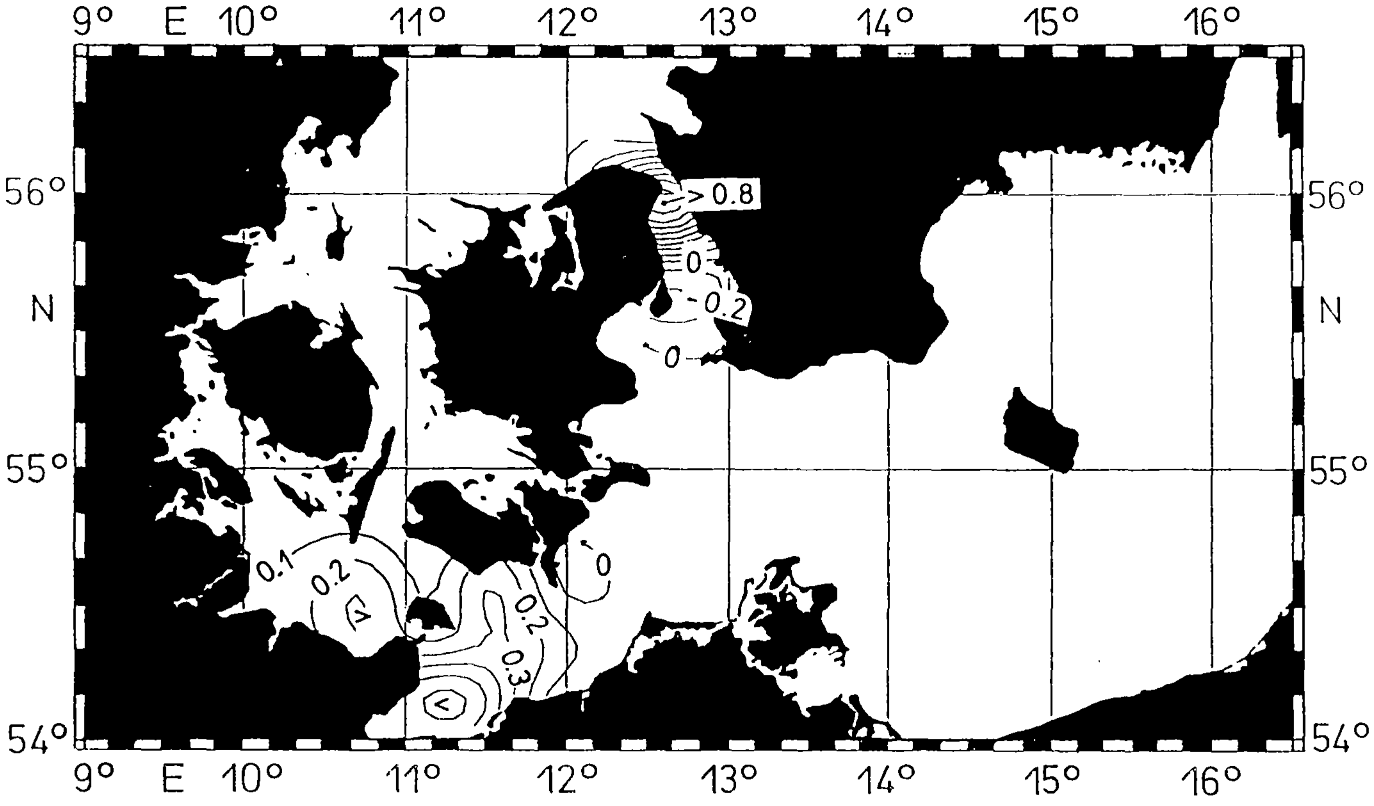
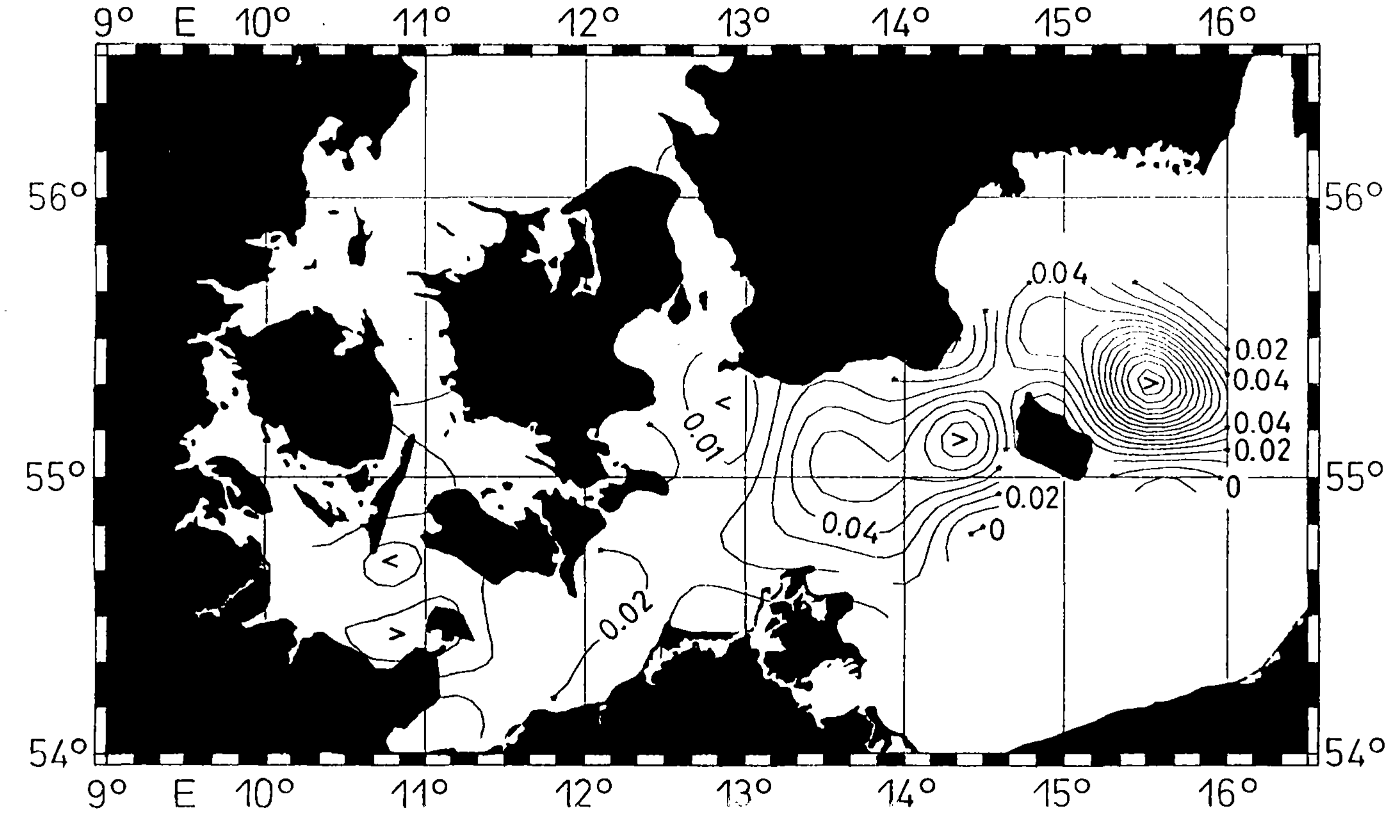


Fig. 6a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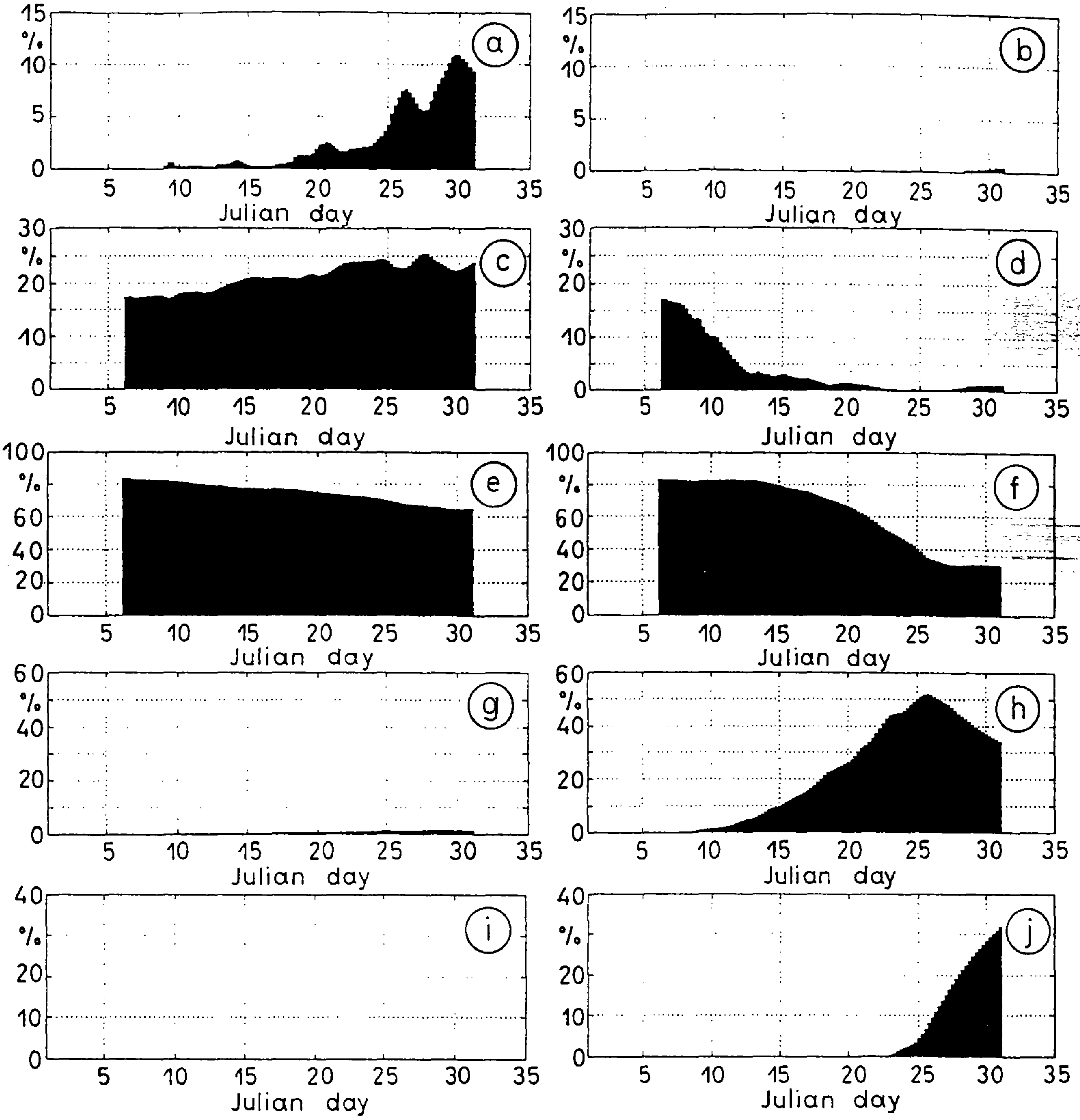
9° E 10° 11° 12° 13° 14° 15° 16°

Fig. 6b


a
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40

Fig. 7

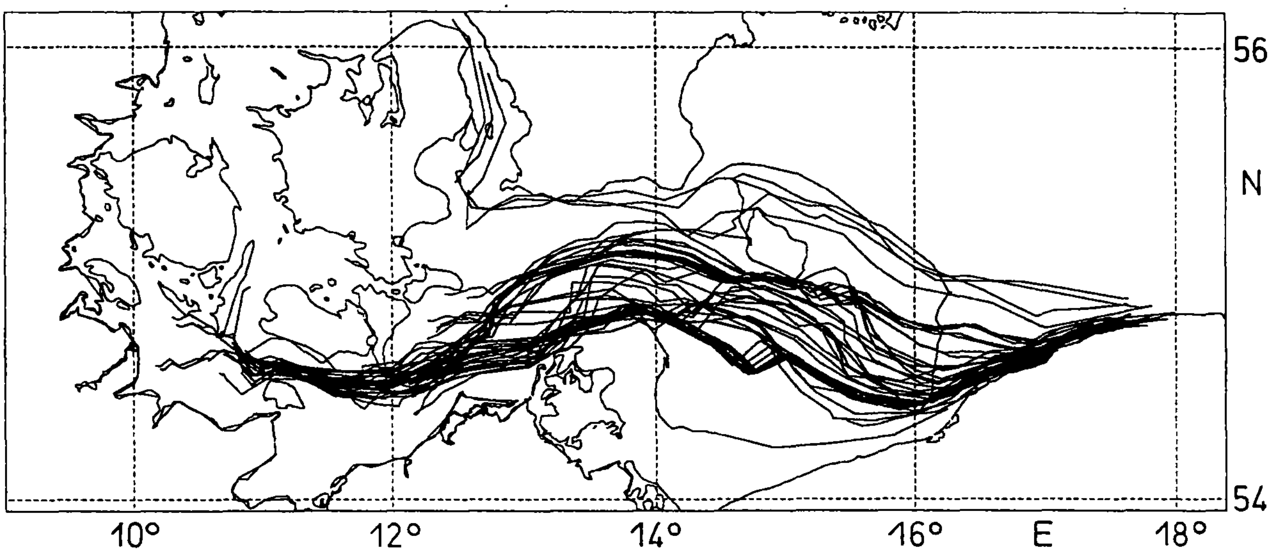

Fig. 8

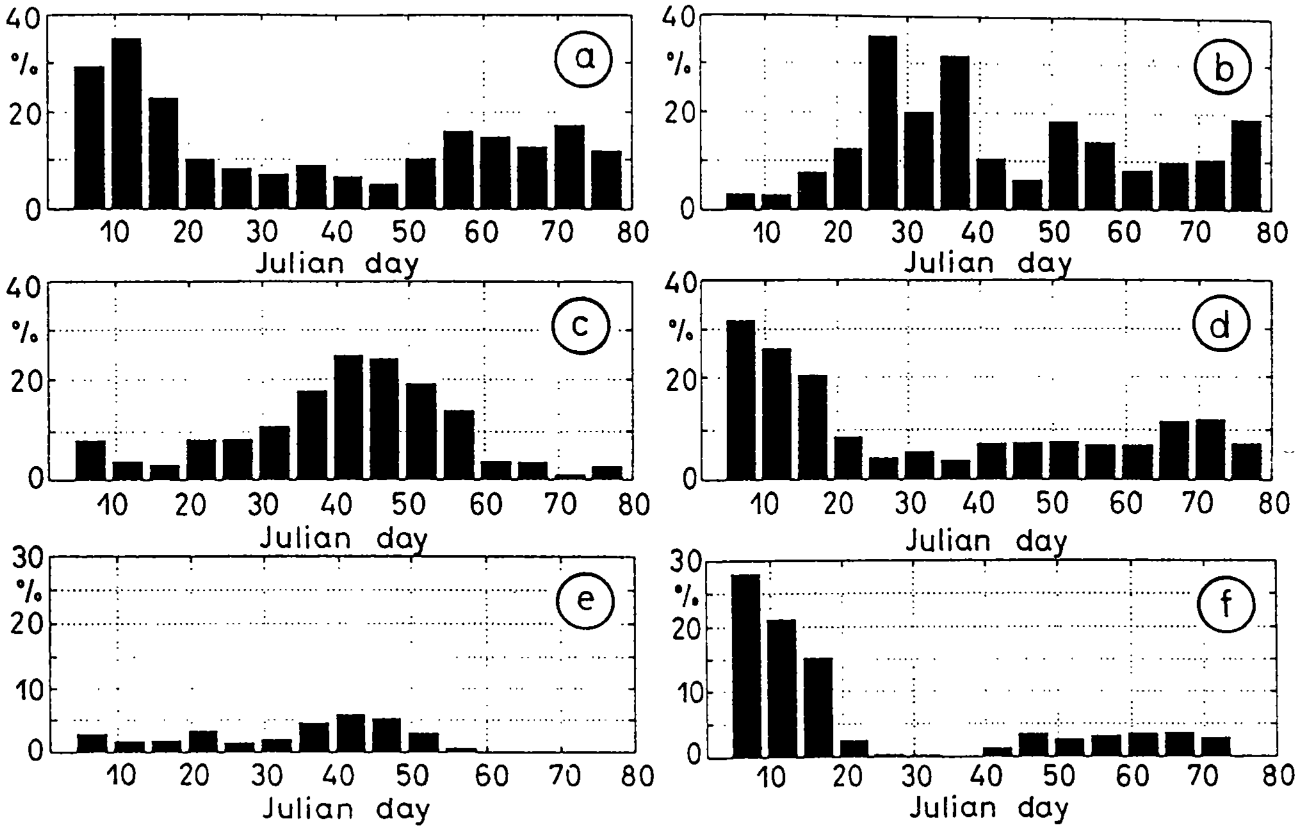

Fig. 9

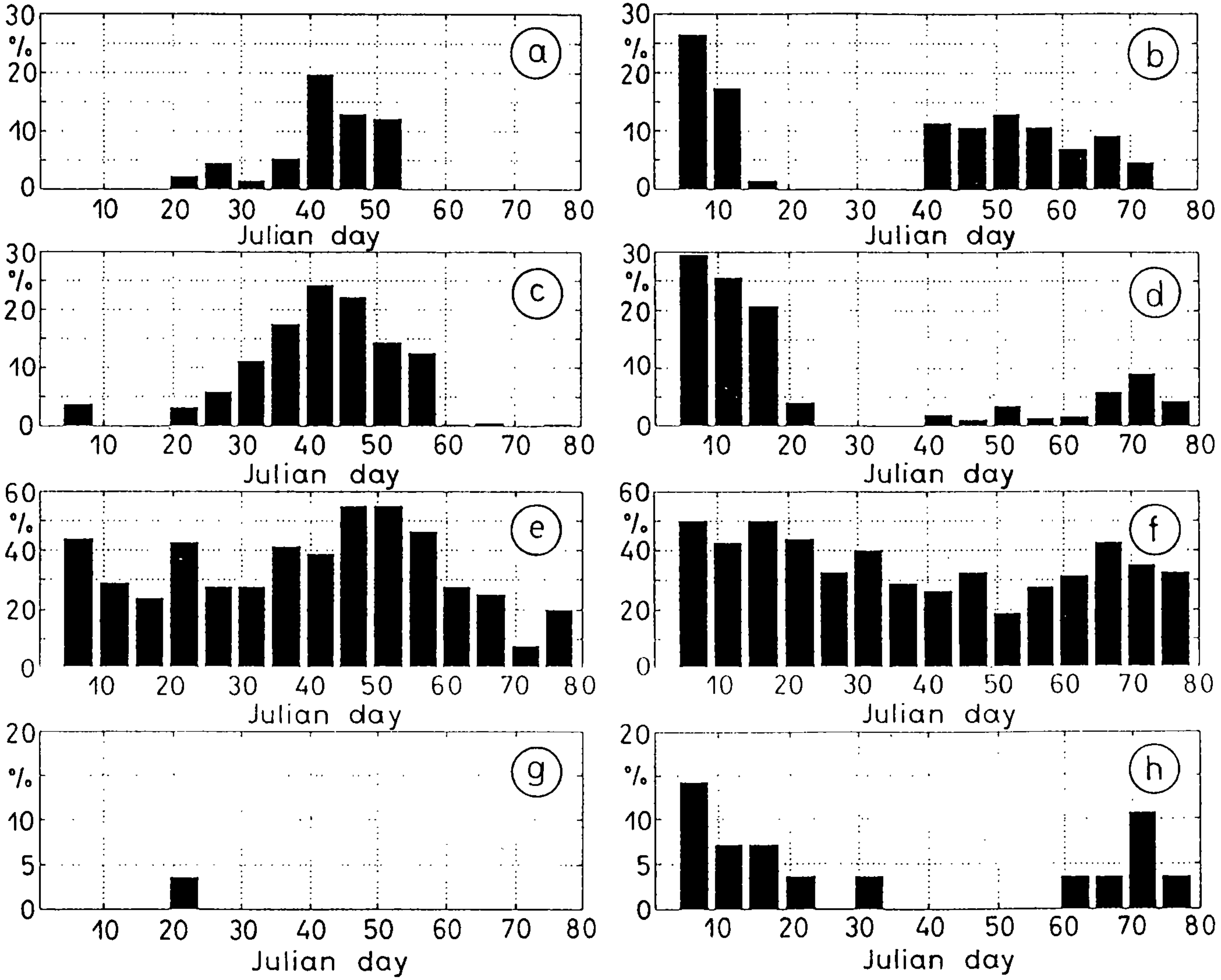

Fig. 10

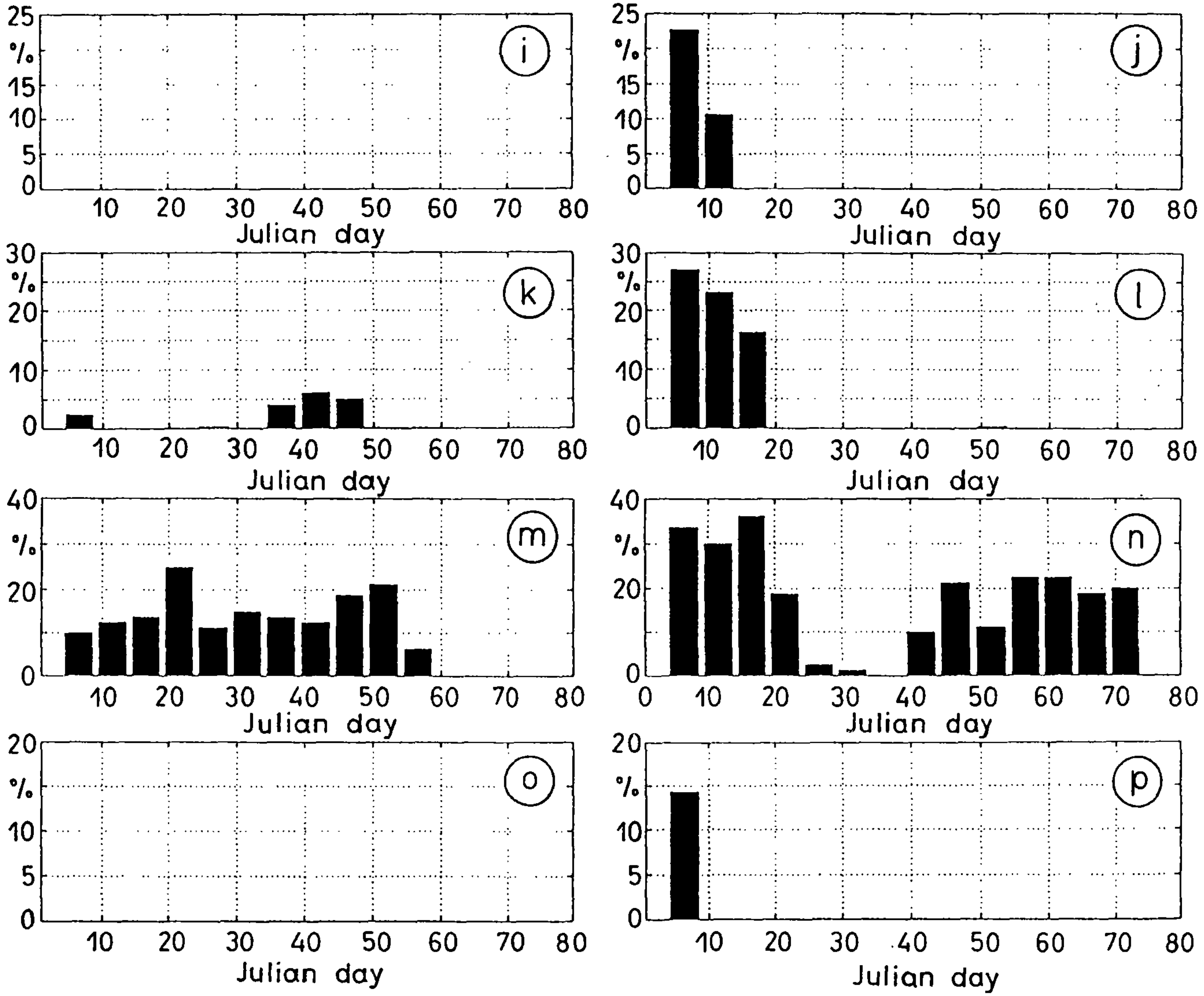

Fig. 10 (cont.)