

Testing the larval drift hypothesis in the Baltic Sea: retention versus dispersion caused by wind-driven circulation

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Retention or dispersion of larvae from the spawning grounds has been identified as one of the key processes influencing recruitment success in fish stocks. To examine the potential effects of transport on recruitment, numerical simulations were performed utilizing a three-dimensional physical oceanographic model of the Baltic Sea. Cod larvae were represented as Lagrangian drifters released in the deepwater region of the Bornholm Basin, the main spawning ground for Baltic cod. Simulations were performed for the major spawning seasons of 1993 and 1994, when annual and interannual variability of meteorological forcing was large. The principal goals of the modelling exercise were first to identify the physical processes influencing the demersal distribution of the early life stages and second to describe the transport of the pelagic stages in response to variations in windstress, thereby identifying the meteorological and hydrodynamic mechanisms influencing retention and/or dispersal. The results suggest that periods of low wind, especially from northern and eastern directions, retain early life stages of cod within the deepwater region of the Bornholm Basin. Periods of higher windstress and duration from the west and south resulted in a rapid transport of larvae into shallow coastal regions. Based on the results obtained from these drift experiments and a wind data time series from the meteorological station Christiansø, a transport index has been developed, variations in annual retention/dispersal have been identified, and comparisons with variations in recruitment success are presented.

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Keywords: Baltic cod, larval drift, recruitment success, retention and dispersal, wind-driven circulation.

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Introduction

In recent years increased attention has been given to the influence of ocean circulation on the transport of early life stages of fish. Justification for this approach is based on the observation that in some cases larval fish are dependent on circulation patterns for transport from the spawning grounds to the nursery areas. Variations in transport have subsequently been suggested to be an important parameter influencing recruitment variability in fish stocks (Iles and Sinclair, 1982; Fortier and Leggett, 1985; Smith and Stoner, 1993; Lough *et al.*, 1994). Although conceptually appealing, verification of

the effect of transport on recruitment success is difficult for various reasons, such as a lack of a suitable recruitment time-series, problems in identifying spawning and nursery areas, or accurate quantification of the reproductive effort.

There are two separate cod stocks in the Baltic: a western stock inhabiting areas west of Bornholm and an eastern stock inhabiting areas east and north of Bornholm. Historically, there have been three main spawning areas for the eastern Baltic cod stock: the Bornholm Basin, the Gotland Basin, and the Gdansk Deep (Figure 1). However, during recent years successful spawning has been limited to the Bornholm Basin

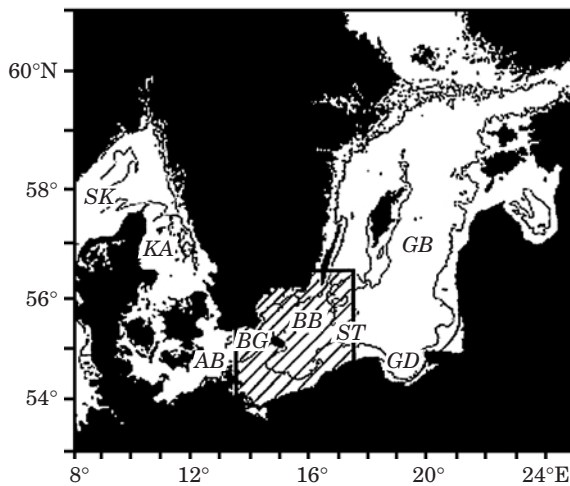


Figure 1. Map of the Southern Baltic with the study area (hatched; SK: Skagerrak; KA: Kattegat; AB: Arkona Basin; BG: Bornholm Gat; BB: Bornholm Basin; ST: Stolpe Trench; GD: Gdansk Deep; GB: Gotland Basin).

owing to anoxic conditions in the spawning layers at the other primary spawning sites (Bagge *et al.*, 1994). Neutral buoyancy and peak abundance of cod eggs in the Bornholm Basin occurs in the region of the halocline, with small quantities occurring in the more saline deep layer (Kändler, 1944; Müller and Pommeranz, 1984; Wieland, 1995). Duration of the egg stage is temperature-dependent, with larvae typically hatching within 15 days (Wieland, 1995). After a few days, the larvae start to migrate vertically through the halocline (Grønkjær and Wieland, 1997) into the low saline surface layers for feeding. The peak abundance of feeding larvae is found between 30 and 40 m. The vertical migration has been identified as a prerequisite for larval survival (Grønkjær *et al.*, 1997).

The transport of larvae is primarily determined by the wind-driven circulation of the Baltic Sea (Voss *et al.*, 1999). Windstress acting at the sea surface results in Ekman transport in cross direction to the wind in the near surface layers, with coastal jets produced in the direction of the wind along both coasts of the basin. The Ekman flow is compensated by a mainly topographically steered return flow in the central interior of the basin (Krauss and Brüggge, 1991), which is generally in a direction opposite to the prevailing winds.

The analysis of the vertical distribution suggests that larval drift in the Bornholm Basin mainly occurs in the depth range of the compensating return flow below the Ekman layer (Hinrichsen *et al.*, 1995; Grønkjær *et al.*, 1997). Hinrichsen *et al.* (1995) observed that westerly and southerly winds cause larval drift towards the west and north, while easterly and northerly winds result in transport to the south and east. Besides the in- and outflow through the entrance area, precipitation

and evaporation rates through river run-off might interact with the wind-induced structures to affect the thermohaline circulation (Lehmann and Hinrichsen, 2000).

The importance of larval transport from the spawning grounds in the centre of the basin to shallow coastal areas for recruitment success is as yet unclear. Production in the central basin appears to be nutrient limited, with low prey availability potentially resulting in low growth and survival of cod (Kirøboe, 1991; St. John *et al.*, 1995; St. John and Lund, 1996). In contrast, the shallow coastal regions have been identified as having high primary and secondary production, owing to input of nutrients through interaction of the thermocline with bottom topography (St. John *et al.*, 1995; Josefson and Conley, 1997), from terrestrial sources and benthic releases. The significance of limiting nutrient concentrations for the primary carbon flux in coastal water ecosystems (Søderstrøm, 1996) and coastal upwelling (Haapala, 1994) concerns nitrogen and phosphorus. Hence, 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.

Our goal is to assess the potential for variable larval transport in the Bornholm Basin by developing a technique for quantifying inter- and intra-annual variation and thereby to identify the existence of particular transport regimes. The primary aim of the study was to examine the influence of physical factors on the horizontal distribution of the early life stages. Transport of cod larvae is influenced by hydrographic and meteorological forcing, the initial spawning location and timing, the vertical position in the water column and larval behaviour, especially the diurnal vertical migration that varies with stage and size (Grønkjær and Wieland, 1997). To better understand the effects of physical forcing on the distribution of the early life stages of cod, physical modelling activities have focused on the description of the circulation of the Baltic.

Materials and methods

Baltic Sea model

A three-dimensional eddy resolving baroclinic model of the Baltic Sea was applied for numerical simulations of the circulation. 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). A detailed description of the equations and modifications necessary to make the model suitable for the Baltic Sea can be found in Lehmann (1995). The model comprises the entire Baltic, including the Gulf of Bothnia, Gulf of Riga as well as the Belt Sea, Kattegat,

and Skagerrak. The horizontal resolution is 5 km, with 28 vertical levels specified. The simulations incorporated physical and biological parameters obtained during research cruises prior to the period of examination, thus utilizing the characteristic hydrographical situation.

The model was forced with actual wind data registered at the Christians weather station, which is located approximately 15 nautical miles northeast of Bornholm (ca. 55°10'N 15°10'E). Routes of larval drift were calculated by utilizing a Lagrangian particle tracking technique (Hinrichsen *et al.*, 1997) based on a 4th-order Runge-Kutta scheme. Simulated three-dimensional velocity fields were extracted to develop a database for the Lagrangian particle tracking exercise. The data set offers the possibility to derive drift trajectories by calculating the advection of "marked" water particles.

Vertical distribution of cod larvae

Two models of the age-dependent vertical distribution of cod larvae were developed on the basis of vertical profiles of larval abundance in 1993 and 1994 (Grønkjær and Wieland, 1997). First, age was determined from otolith increment counts according to methods described by Stevenson and Campana (1992). Second, a length-stage key was made allowing an approximate ageing of all larvae measured (Grønkjær 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 d) were restricted to depths exceeding 50 m. First-feeding (6–10 d) and older (10–25 d) larvae 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 d, below the surface wind-mixed layer (12–48 m) during the next 20 d, and between 12 and 30 m for the remaining 35 d.

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

To determine the wind energy required to transport larvae from the spawning site within the deepwater region of the Bornholm Basin to different potential 0-group nursery areas, idealized constant wind forcing (velocity 12 m/s) in space and time was applied.

Initialization, forcing, and experimental design

Within- and between-year variation in drift patterns of larvae was 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 (Figure 2).

In the simulations, new batches of larvae were released into the modelled Eulerian flow fields at 5-d intervals and tracked for a period of 60 d. This time span approximately covers the entire duration of the larval phase of cod (Fossum, 1986). Release dates commenced on May 1 (yearday 121) and ended July 30 (yearday 211), thereby encompassing the peak spawning period of eastern Baltic cod (MacKenzie *et al.*, 1996). 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 d or until they reached the 30-m depth contour where their position remained fixed. Each larval drifter representing the four release centres 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 5-d interval, we compare simulated distributions between and within years and not the actual numbers of larvae.

Simulations were also carried out under constant wind conditions from different directions and of different strength.

Transport index

To identify historic variations of larval retention/dispersal owing to variations in wind forcing between and within years, a simple wind 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 3-h 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

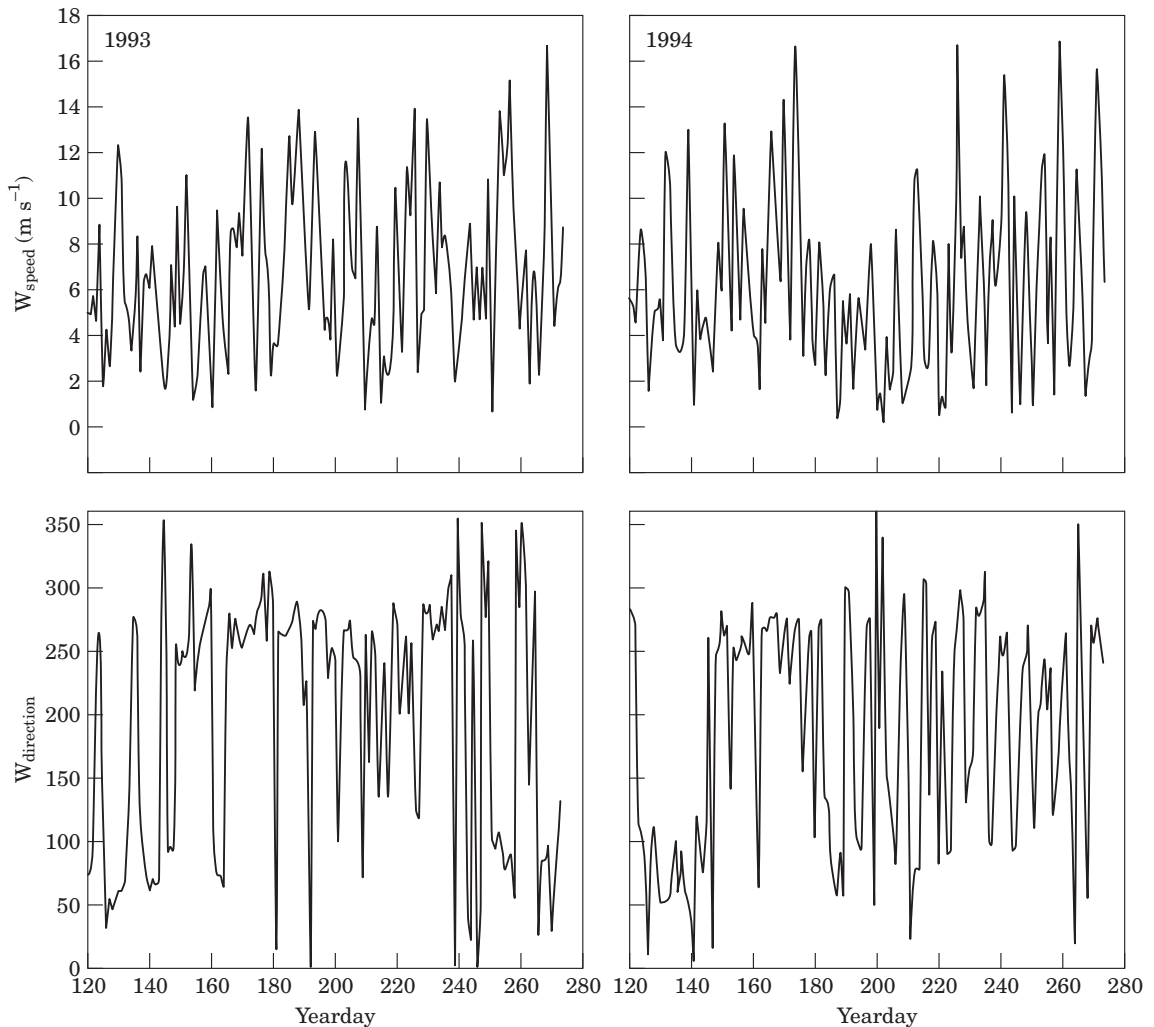


Figure 2. Time-series of daily averaged windspeed (top panels) and direction (bottom panels) during the main spawning season of Baltic cod (May–September) in 1993 and 1994.

westerly and southerly winds, whereas easterly and northerly winds result in transport to the south and east. 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-d period (representing the period of larval drift) commencing at 5-d intervals during the main spawning season (May–September). For example, to get a total amount of wind energy of $+100\,000\text{ W m}^{-2}$, approximately 11 d with wind velocities of 12 m s^{-1} from southerly and westerly directions are required. Furthermore, we consider that periods of dispersal are 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.

Results

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 main spawning season (May), wind data time-series (Figure 2) showed low to moderate winds predominantly 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 windspeeds ($<5\text{ m/s}$) mainly from the east, while direction was highly variable during

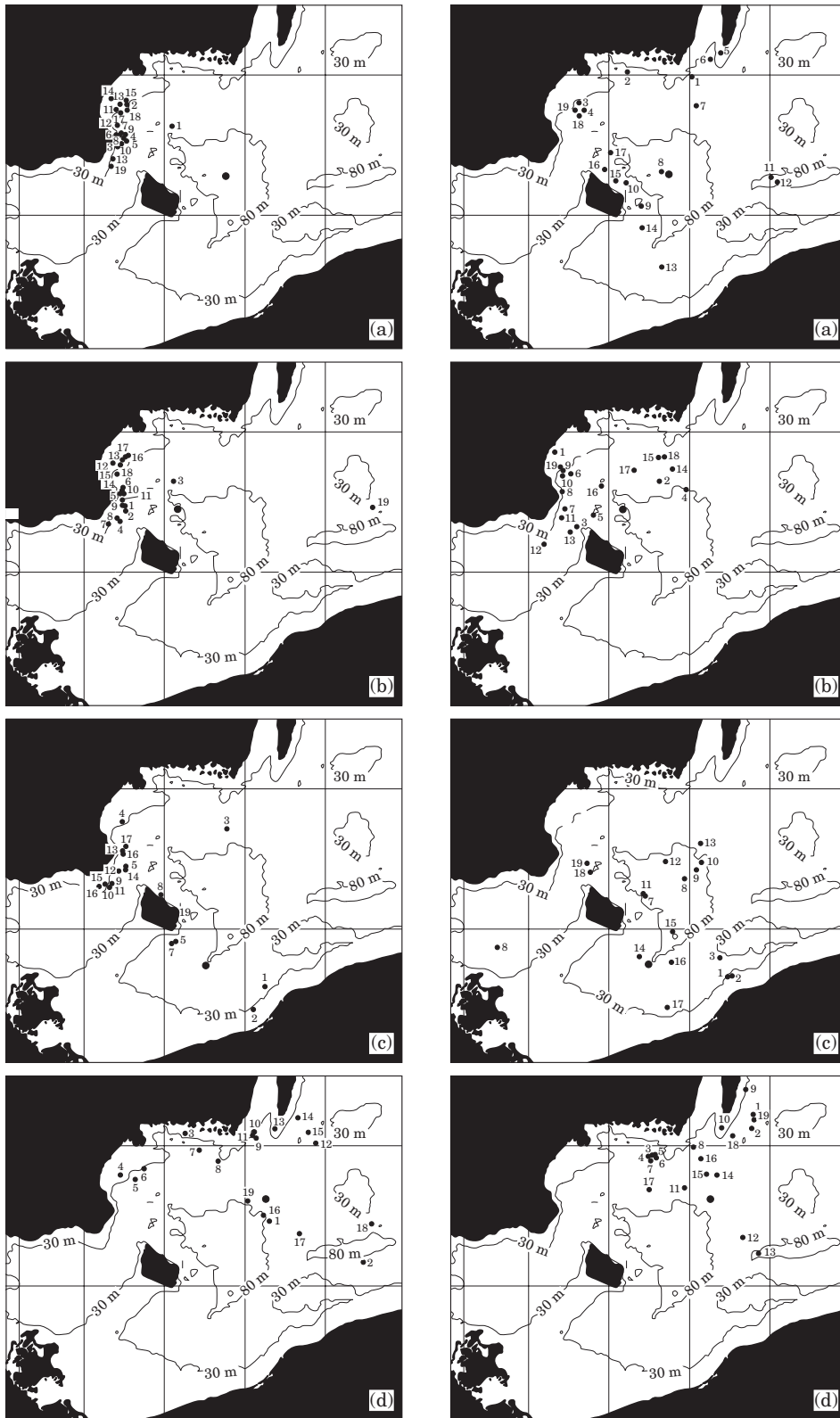


Figure 3. Larval drifter destinations after a 60-d drift simulation from subsequent release dates (1–19) onwards at four historical spawning centres (large dots; a–d) in 1993 (left panels) and 1994 (right panels).

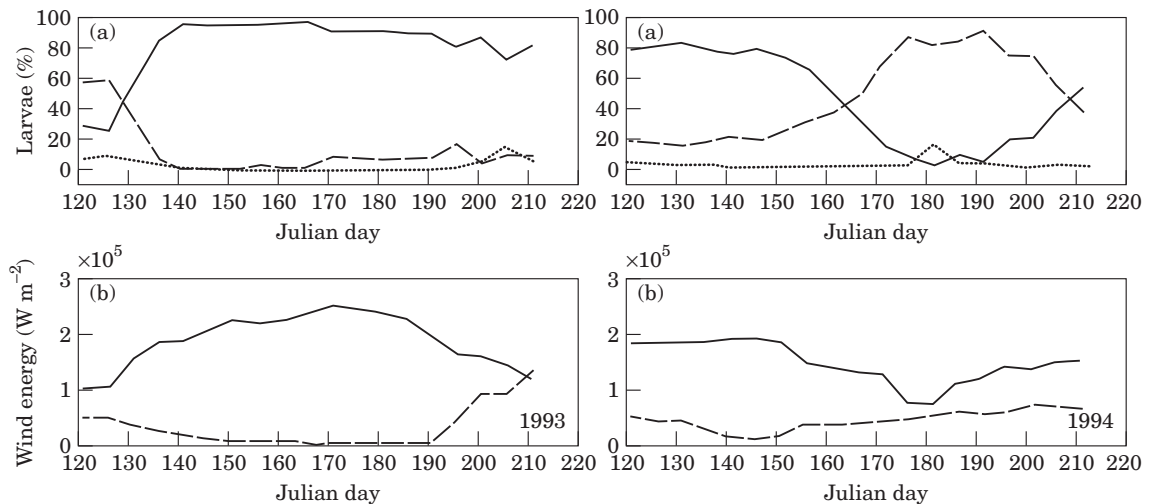


Figure 4. Relative frequency of simulated larval drifters (top panels) ending up in the deep basin (broken line), advected to northern coastal waters (full line), and advected to southern coastal waters (dotted line), and wind energy (bottom panels) from south to west (full line) and north to east (broken line) directions in relation to time of release during the spawning season, 1993 (left) and 1994 (right).

Table 1. Percentage of larvae observed (\pm s.d.) during the main spawning season in different regions after 60-d drift simulation according to two models (see methods) 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	3.9 \pm 5.8	2.0 \pm 2.3	31.3 \pm 27.7	1.9 \pm 3.5

^aIncluding Stolpe Trench.

^bIncluding Bornholm coastal area.

June and August/September, with speeds occasionally reaching 15 m/s. Wind events (as estimated by mean daily windspeed and direction) were generally westerly in 1994 and their frequency was lower than in 1993, when wind events came predominantly from the south and west.

To illustrate differences in the transport of larvae within and between years, destinations of the larval drifters are presented in Figures 3 and 4. Simulations for 1993 indicate larval transport to the Swedish coastal area from the central [Figure 3(a)] and westerly spawning site [Figure 3(b)] and less so from the southerly spawning site [Figure 3(c)], while drifters initially released in the north-eastern spawning site ended up widely dispersed over deep water [Figure 3(d)]. 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 Brügge, 1991). Simulations for 1994 [Figure 3(a)–(d)] indicate that much higher numbers

were retained in deeper water and less transport to shallow coastal regions because of the lower drift velocities predicted by the physical circulation model on the basis of the lower windstress in this year.

Table 1 summarizes the total numbers of drifters either remaining in the deep basins (retention) or being advected to shallow coastal waters (dispersal) based on the two models applied in each year. In general, the annual variability in relation to wind forcing can be described as follows:

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

Generally, the simulated distributions after 60 d by the two models differed only slightly (Table 1).

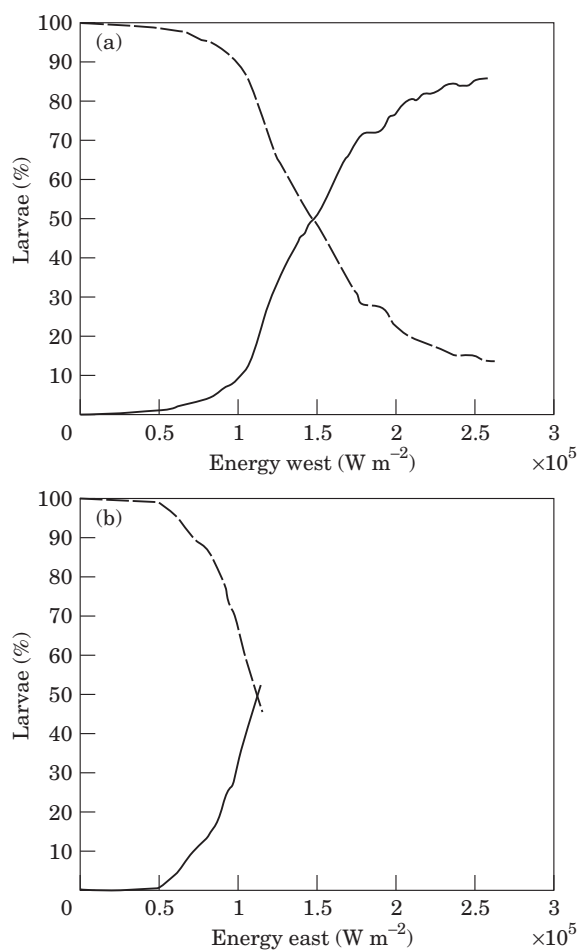


Figure 5. Percentage of larvae ending up in the deep basin (broken line) and percentage advected to coastal area in relation to wind energy derived from numerical simulations with constant wind forcing: (a) westerly winds and advection to northern coasts and (b) easterly winds and advection to southern coasts.

However, model 2 (including vertical migration) resulted in higher retention, because mean current velocities in the intermediate layer are lower than in the layer below the wind-induced mixed layer and above the thermocline.

Temporal evolution of larval transport

Figure 4 shows 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-d 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. The 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.

Simulations with constant wind forcing

Figure 5 shows two examples of the fate of cod larvae under constant windstress. For westerly winds, the percentage retained in deep water dropped rapidly when energy exceeded $100\,000\text{ W m}^{-2}$ and a balance between transport of larvae to the northern coast and retention was reached at $140\,000\text{ W m}^{-2}$. For easterly winds, the percentage of larvae transported to the southern coast increased rapidly when energy exceeded $50\,000\text{ W m}^{-2}$ and the balance was reached at $115\,000\text{ W m}^{-2}$. 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 the energy was $35\,000\text{ W m}^{-2}$.

Transport index

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

- (i) Dn: transport to the northern coasts when wind energy $> +140\,000\text{ W m}^{-2}$
- (ii) Ds: transport to the southern coasts when wind energy $< -115\,000\text{ W m}^{-2}$
- (iii) R: retention in the deepwater areas for intermediate values.

To illustrate differences between and within years, the calculated transport indices are presented in Figure 6. Positive values, indicating westerly and southerly winds, predominate in all years, 1979–1994, with highest 60-d values observed in 1985 ($283\,000\text{ W m}^{-2}$). Negative indices are absent in several years and exceeded the dispersal limit to southern coasts only in 1993 ($133\,000\text{ W m}^{-2}$). Estimates of mean cod egg abundance in the Bornholm Basin (Wieland *et al.*, 2000) are also shown for 1985–1994 to allow an evaluation of the most critical period for larval transport. Unfortunately, no data are available for the earlier years. However, historical data on gonadal maturation and egg abundance reveal a clear shift of spawning activity to later months within the last ten years (Wieland *et al.*, 2000). This suggests that spawning took place relatively early in 1979–1984, which would mark these years as typical

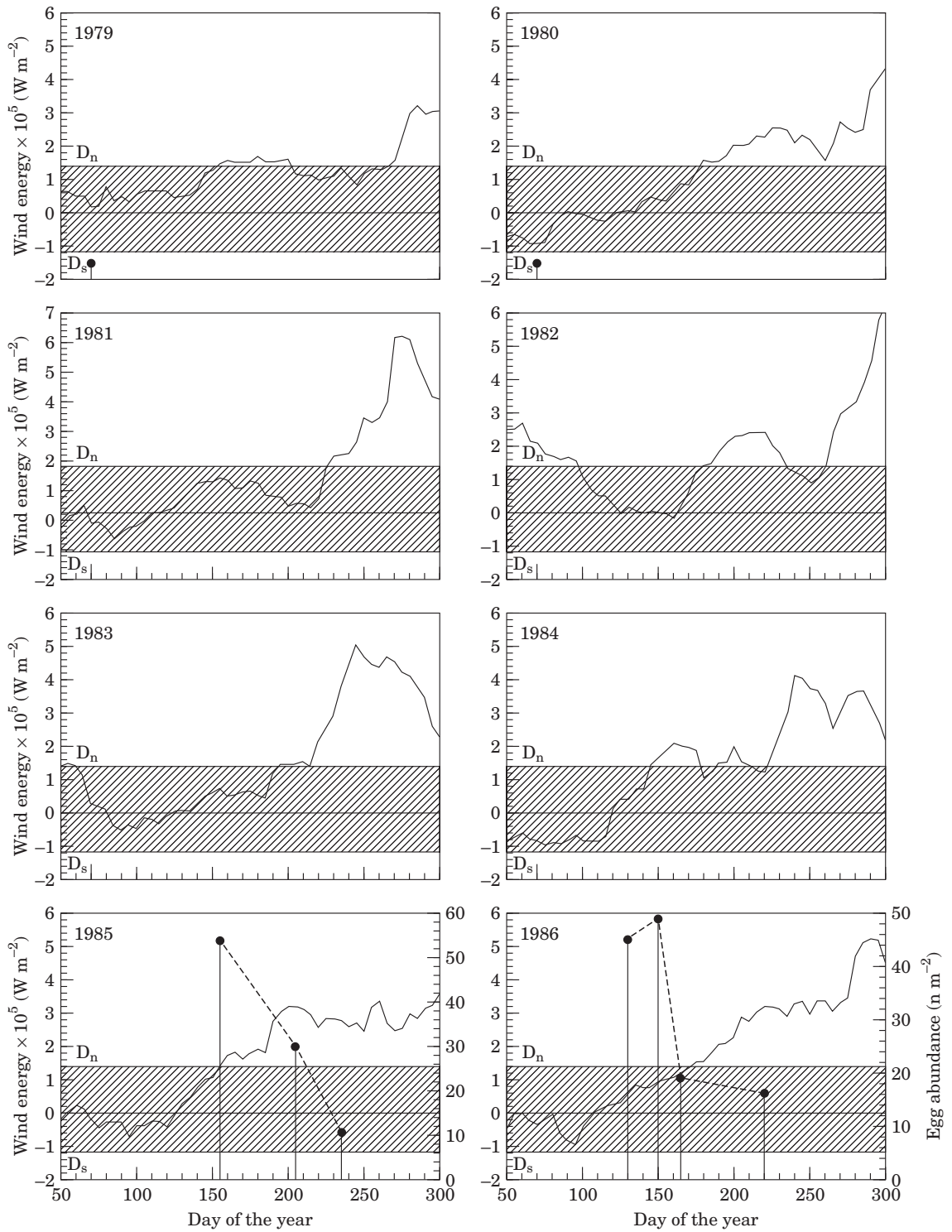


Figure 6.

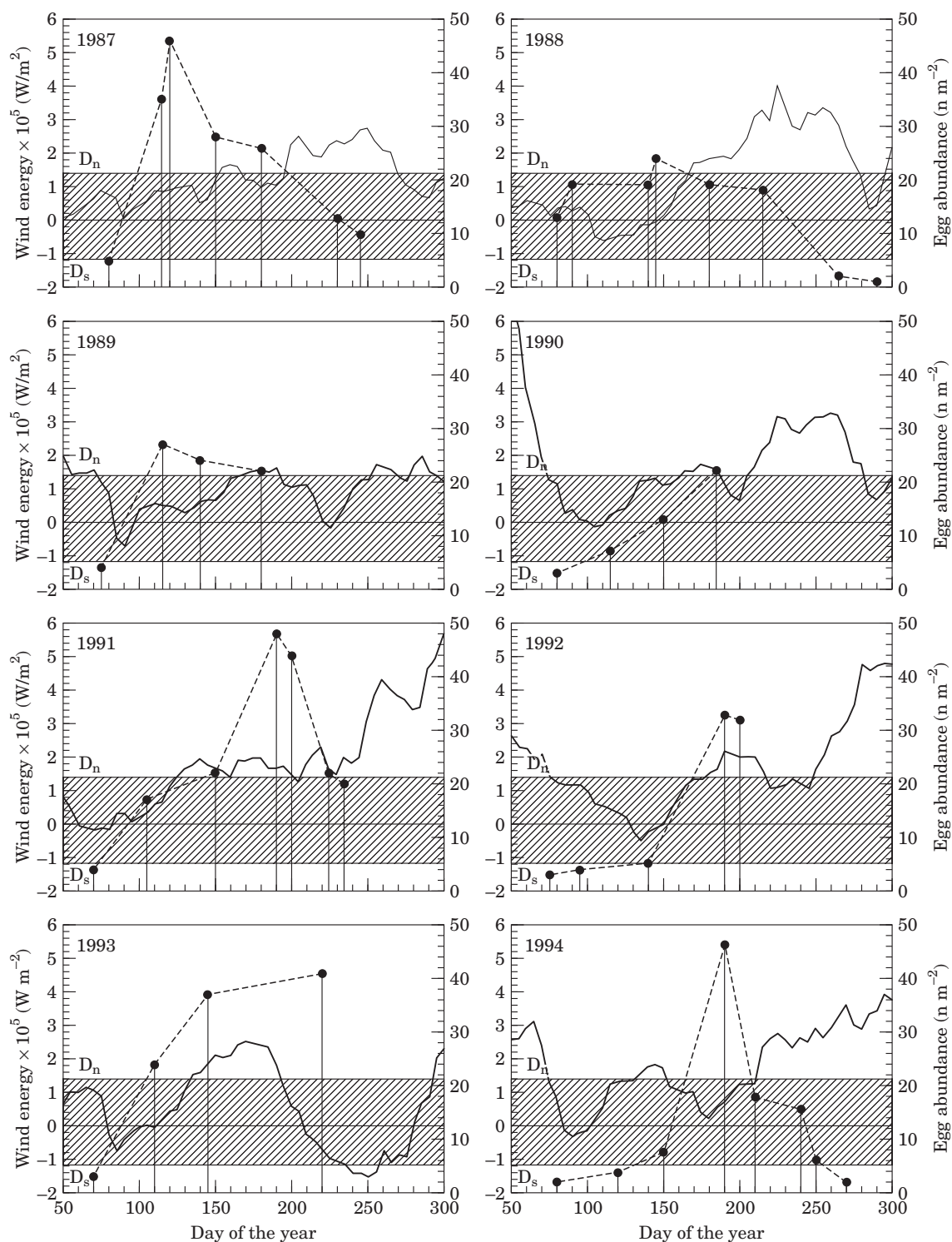


Figure 6. Variations in wind energy (—) (cumulative sums over 60 d at 5-d intervals; south to west: positive; north to east: negative), 1979–1994 (hatched interval indicates wind energy values that are expected not to result in advection to northern or southern coasts; see text). For 1985–1994, estimates of mean cod egg abundance (—●—) in the Bornholm Basin are also indicated.

Table 2. Age 1-group cod estimates (number/h) for different parts of the Bornholm Basin (from Sparholt, 1996).

	South				North			
	10–40 m	40–60 m	60–80 m	80–120 m	10–40 m	40–60 m	60–80 m	80–120 m
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	—

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 clearly should have been advected towards the northern coastal area.

Spatial distribution of juvenile cod

Information on spatial distribution patterns of 0- and 1-group cod has been collected regularly in the Baltic Young Fish Surveys. The amount of data referring to 0-group cod in the Western and Central Baltic is limited and not particularly useful because the surveys are carried out early in the year. 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 (Table 2; 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 60 m, which would seem to correspond with

dispersal to northern waters. However, this was also the case for year classes 1987 and 1989, which were considered retention years. Year classes 1984 and 1994 were most abundant in the southern part <60 m, which cannot be explained by the transport indices in those years. All other year classes were more abundant in the southern part >60 m, which would correspond to retention in the deeper areas. The dispersal years 1985 and 1990 do not show corresponding shifts in juvenile cod abundance.

Discussion

Recruitment is determined by a series of stochastic processes affecting survival during early life. These biological and physical processes act to create windows of episodic survival (Houde, 1989), which may be determined by better growth (Campana, 1996; Meehan and Fortier, 1996), reduced predation (Houde, 1989; Paradis *et al.*, 1996), and enhanced transport (Campana *et al.*, 1989). These external conditions are superimposed on the susceptibility of an individual to mortality via the energetic reserves contained in the egg and the genetic attributes of the larvae. These attributes endowed by the adults influence hatching success (Nissling and Westin, 1997), larval size, and competitive ability (Buckley *et al.*, 1991). Thus, larvae of varying viability and with a varying growth potential are injected into an environment where stochastic processes act to determine their survival.

Because of the prolonged spawning period of Baltic cod (Wieland and Horbowa, 1996), and age- and size-dependent timing of spawning (Tomkiewicz *et al.*, 1997), the potential exists for eggs and larvae of differing

quality 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 (Köster and Schnack, 1994) and transport potential.

The temporal and spatial co-occurrence of larvae and favourable conditions will strongly influence the probability of larval survival. In addition to effects on transport, winds could have effects on production and survival in the system, for instance through mixing and turbulence (Kirøboe and MacKenzie, 1995) on nutrient distribution (Rothschild *et al.*, 1999), and predator-prey encounter rates (Kirøboe and MacKenzie, 1995; MacKenzie *et al.*, 1994).

From the numerical simulations it appears that variations in larval transport and hence horizontal distribution of pelagic and demersal stages of juvenile cod is caused by intra-annual as well as interannual variations in meteorological forcing. The simulations for 1993 and 1994 clearly show the effect of atmospheric forcing on the destination of larval drifters released at different locations in the Bornholm Basin. The results suggest 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 deepwater region of the Bornholm Basin (retention years). Although rarely observed, relatively long periods of easterly winds can be identified as a prerequisite for enhanced larval transport to the south.

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 allows the identification of changes in transport regime within the spawning season. Examining the different transport regimes with respect to hatch date and growth rate of surviving 0-group cod may help to identify the favourable conditions during temporal windows leading to enhanced survival. Such information might be combined temporally with an age-specific egg production model to provide improved estimates of annual recruitment potential.

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