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Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea

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ABSTRACT: Cod eggs in the Baltic Sea are neutrally buoyant at depths exceeding 55 m. When these eggs hatch the larvae must enter the upper photic portion of the water column to locate and capture sufficient prey to feed and grow. In this study we investigated the time during ontogenetic development at which this vertical migration occurs. The vertical distribution of cod larvae, microzooplankton, light intensity and the physical characteristics of the water column in the Bornholm Basin were investigated during 3 cruises in May, June and July 1994. Larvae designated as pre-feeding were usually located at the depths where they had hatched. After larvae had begun to feed, their distributions moved closer to the water's surface. Since larvae are negatively buoyant relative to the density of water in the upper layers of the Baltic, this migration requires active swimming. Hence the hydrographic structure of the water column in the Baltic likely imposes a modest metabolic cost on larvae. We also investigated factors determining the vertical distribution of feeding larvae. The distribution of these larvae was poorly correlated with prey abundance (i.e. concentration of copepod stages). However, distributions were correlated with prey availability as estimated by combining measures of light-dependent larval feeding incidence with the measured prey concentrations. Our observations suggest that a vertical migration among Baltic cod larvae is necessary for 2 reasons. This migration enables larvae to obtain suitable feeding conditions, and to avoid mortality that could be induced by exposure to the low oxygen conditions typical for the sub-halocline layer.

KEY WORDS: Larval cod · Estuarine · Vertical distribution · Migration · Developmental stage · Aggregation · Prey availability

INTRODUCTION

The distribution of fish larvae in relation to hydrographic and biotic factors (Ellertsen et al. 1981, Heath et al. 1988, Stephenson & Power 1988, Munk et al. 1989, Lough & Potter 1993) is considered to strongly influence recruitment processes (e.g. Sinclair & Iles 1985), and attention has been paid in particular to tidal, estuarine or otherwise stratified areas (e.g. Boehlert & Mundy 1988).

The vertical structure of the Baltic Sea deep basins is defined by strong variations in salinity, temperature and oxygen. A permanent halocline at 50 to 75 m separates low saline (<8 psu) surface water from the more saline deep water originating from episodic inflows of North Sea water. In periods without salt water inflow the oxygen conditions below the halocline deteriorate (Matthäus & Franck 1992). A 3-layer structure is formed in spring, when a thermocline at approximately 20 to 30 m depth develops, dividing the water column into the upper mixed layer, the intermediate layer and the deep water layer. These 3 layers persist until late autumn when the thermocline breaks down.

This vertical structure has been examined in relation to the spawning success of Baltic cod (Grauman 1973, Kosior & Netzel 1989), in particular the distribution, hatching and survival of eggs (Wieland 1988, Nissling

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& Westin 1991), whereas the larval distribution and survival in relation to hydrography have only recently been addressed (Nissling et al. 1994a).

In the Bornholm Basin, cod spawning starts in March, peaks in May/June and finishes in September (Bagge & Thurow 1993). Eggs are spawned below the halocline and are neutrally buoyant at a salinity of approximately 14.5 psu (Nissling et al. 1994b). Due to the low saline surface water, hatching eggs are confined to depths exceeding 55 m (Wieland 1995). This is in contrast to most other cod stocks, in which buoyancy of the eggs ensures that they hatch near the surface (e.g. Anderson & deYoung 1995). However, this deep distribution of cod eggs characteristic of the Baltic Sea may also be found in other stocks due to variability in egg buoyancy and hydrographic regime (Kjesbu et al. 1992, Oullet 1997) and, hence, situate newly hatched larvae below the upper mixed layer where feeding conditions are suggested to be optimal (Ellertsen et al. 1981, 1984, Munk et al. 1989, MacKenzie & Kiørboe 1995).

Sub-optimal feeding conditions in the deep water may be caused by reduced light intensities. Ponton & Fortier (1992) showed that Arctic cod *Boreogadus saida* and sand lance *Ammodytes* sp. larvae accumulated at the depth where food availability (light × prey density) was maximum, and that the larvae's feeding incidence (% of larvae with prey in gut) decreased with depth below the pycnocline. In laboratory experiments cod larvae are able to feed at very low illumination levels (0.1 to 0.4 lx), but the feeding incidence (percentage of larvae feeding) and feeding rate (numbers of food items in the gut) have been shown to increase at 1 to 12 lx (Ellertsen et al. 1980, Huse 1994), after which it again decreases. Cod larvae residing at hatching depth in the deep water may therefore experience sub-optimal feeding success.

Consequently, a migration towards optimal feeding conditions should take place prior to first feeding, i.e. Days 5 to 6 (Ellertsen et al. 1980, Fossum 1986), or at least before the point of no return around Days 9 to 11 (Ellertsen et al. 1980, Kjørsvik et al. 1991). This energetic limitation implies that the vertical migration must take place at a developmental stage without a functioning swimbladder to aid in the ascent (Ellertsen et al. 1980). In the Baltic Sea, the low density of the water constitutes a buoyancy problem. The early upwardly migrating larvae will experience a high sinking rate upon reaching the pycnocline, necessitating a high swimming frequency in order to complete the migration and maintain themselves in the surface layer. Some of the larvae may not be able to maintain this high frequency, due to the effect of low oxygen concentrations below the pycnocline, as proposed by Wieland et al. (1994), or as a consequence of the poor nutritional condition of post yolk-sac larvae in the deep water. Hence we expect these larvae to constitute a group of moribund, deeply distributed larvae.

In the present study we investigated how the vertical distribution of cod larvae during their early development varies with respect to the physical discontinuities and food abundance within the water column of the Bornholm Basin, Baltic Sea.

Our first hypothesis is that the larvae migrate towards the upper mixed layer during early development. This 'first-feeding migration' is necessitated by the low illumination levels at hatching depth, as well as the hypoxic conditions below the halocline in the Baltic deep water basins.

Secondly we put forward the hypothesis that the more advanced larvae should aggregate in relation to food availability as defined by the combined effect of food abundance and illumination levels.

This paper presents the results of 3 cruises examining the vertical distribution of cod larvae during spring and summer 1994 in the Bornholm Basin and considers the consequences of the estuarine conditions on vertical distribution of cod larvae and the possible implications for larval survival.

MATERIALS AND METHODS

Sampling procedure. Field studies were carried out in the Bornholm Basin from the FS 'Alkor' on 2 to 3 May, 1 to 3 June and 12 to 13 July 1994 (Fig. 1) during the Baltic cod spawning season. Sampling positions were located at the site of highest cod larvae abundance as determined on the basis of a bongo (500 µm mesh) grid inside the 60 m isoline. This grid was sampled 1 to 2 d in advance. The May (55° 22.5' N, 15° 52.5' E) and June (55° 17.5' N, 15° 45.0' E) stations were fixed, while that for July (start: 55° 13.43' N, 15° 55.55' E) was a drift station tracking an Argos buoy. The drogue was located at 55 m depth. Each of the 3 stations were sampled for approximately 24 h.

Physical variables (conductivity, temperature, density and oxygen) of the water column were measured with a ME OTS 1500 CTD/O^2 at the beginning and end of each sampling period (i.e. ~24 h apart). In order to ensure that oxygen measurements were reliable, the CTD was halted every 5 m below 40 m and every 10 m above 40 m until readings were stable.

Light profiles measuring total downwelling quanta (µE m^{-2} s^{-1}) were made with a quantum irradiance meter (Li Cor LI-192SA). Irradiance was measured in 2 m intervals and recorded on a data logger as 10 s averages in the upper 31 m and in 10 m intervals as 25 s averages below 31 m. The light profiles were performed from dawn to dusk between 2 combined

BIOMOC hauls. Wind speed and direction was obtained from the nearby Christiansø meteorological station, as well as from an anemometer on the vessel's mast.

Sampling of cod larvae in discrete depths was conducted with a 1 m^2 BIOMOC multiple opening/closing net (modified MOCNESS system; Wiebe et al. 1976) equipped with nine 335 µm nets. Prey organisms (microzooplankton) were sampled with 50 µm liners (diameter of opening 4 cm) inserted in the BIOMOC at selected depths.

Two combined BIOMOC hauls, 17 nets in 5 m intervals, constituted a depth profile from 5 to 85 m. Towing time in a specific depth was 3 min, after which the BIOMOC was lowered 2 m. Here a new net was opened and the BIOMOC was lowered 3 m to the correct sampling depth. When possible this profile was sampled every 4 h, otherwise every 6 h. Towing speed was 3 knots, and a mechanical flowmeter recorded volume filtered for each net (approximately 400 m^3).

The liners were inserted at selected depths, normally 10 m intervals, to determine the vertical distribution of microzooplankton. Microzooplankton samples were fixed in 1% buffered formaldehyde-seawater. In the laboratory subsamples were identified as nauplii and copepodite Stages I–III and IV–V. They were then counted under a dissecting microscope (25×). From the May samples both copepodite groups were identified to species or genus before being counted.

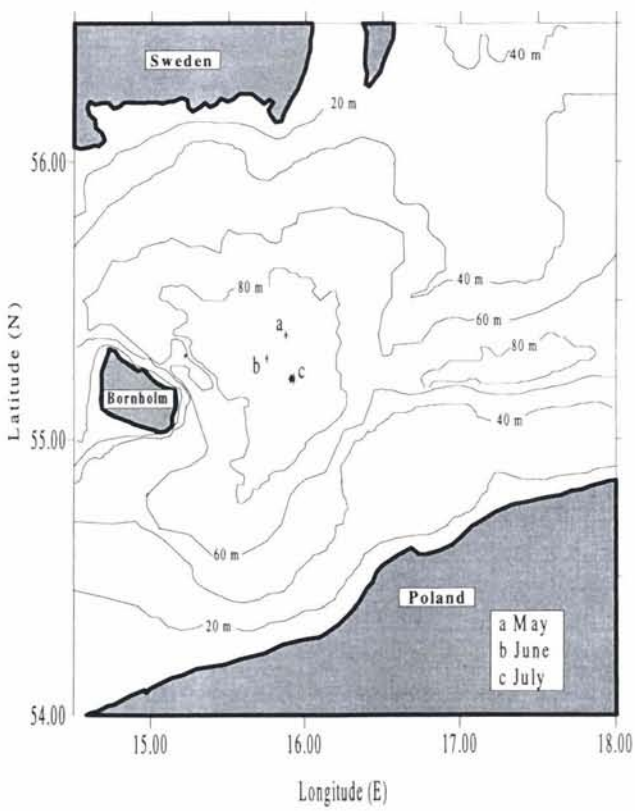

Fig. 1. Sampling stations in the Bornholm Basin, Baltic Sea 1994. The May (a) and June (b) stations were fixed, whereas the July (c) station tracked a drift buoy

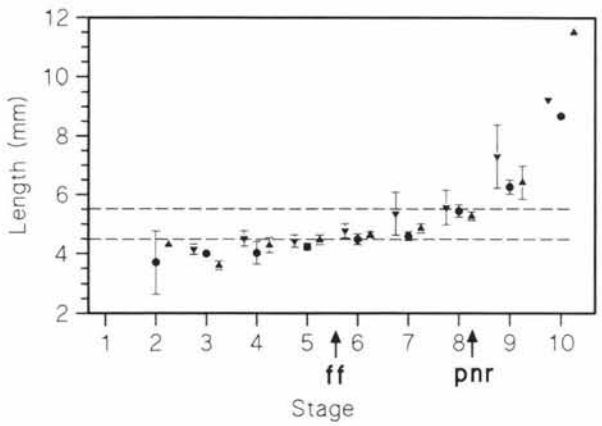

Fig. 2. Baltic cod larvae length/stage key based on Fossum's (1986) stages. Mean length ± 1 SD at stage is shown for the May (▼), June (●) and July (▲) crusies. SD for Stage 10 is not shown (Stage 10 May SD = 1.1 mm, Stage 10 June SD = 4.6 mm). Dashed lines indicate the distinction between size groups. Larvae <4.5 mm correspond roughly to larvae before first-feeding (ff), larvae from 4.5 to 5.5 mm to first-feeding larvae before point of no return (pnr), and larvae >5.5 mm to established feeders

The 335 µm samples containing the cod larvae were immediately fixed in 4% buffered formaldehyde-seawater. After minimum 3 wk fixation the cod larvae were sorted out and preserved in 70% ethanol. Standard lengths of the cod larvae were measured using a dissecting microscope (6×) fitted with a video camera. Images of the larvae were digitised (Pippin Image Analysis version 1.92) to enable measurements of the often wrinkled larvae. No correction for shrinkage was performed. In order to examine the vertical distribution of the larvae in relation to developmental stage, non-damaged larvae were staged according to Fossum (1986). Furthermore a length/stage key allowing an approximate staging of all the length-measured larvae was made (Fig. 2). Fossum's (1986) staging is based on yolk absorption in Arcto-Norwegian cod, but the stage/age relationship has been verified for laboratory-reared Baltic cod (R. Voss pers. comm.).

Data analysis. To test the 2 null hypotheses that larvae were uniformly distributed with depth and that no differences in vertical distribution existed between day and night we used ANOVA on $\ln(x + 1)$-transformed data. Samples of larval cod were classified as night catches if the hauls were commenced after sunset and before sunrise (Lough & Potter 1993). Vertical distribution of cod larvae was calculated on the basis of total number of larvae m^{-2} in each depth strata.

We then compared larval vertical distribution with environmental variables. Since our hypotheses related to the association of feeding larvae with their potential prey, we restricted our comparisons to larvae which had a high probability of having initiated feeding on copepod prey. According to Fossum (1986) first feeding takes place between Stages 5 and 6, but only a few larvae in these stages are found with gut content in the field (Ellertsen et al. 1984). Based on our length/stage key we therefore excluded larvae <4.5 mm (~ < Stage 6) from our comparisons because these larvae are unlikely to have been feeding on copepods (Last 1978, Ellertsen et al. 1980, Fossum & Ellertsen 1994, Zuzarte 1996), which were the main prey item retained by our sampling gear.

The mean depth of larvae >4.5 mm was then calculated using the formula for centre of mass:

$$Z_{cm} = \sum_{i=1}^{n} P_i Z_i$$

where Z_i is the depth of the ith sample and P_i the proportion of larvae at depth Z_i (Fortier & Leggett 1983). Furthermore, in order to determine the degree of aggregation of these feeding larvae, the aggregation of cod larvae >4.5 mm during the investigations was described utilising Lloyd's index of patchiness (Lloyd 1967):

$$LI = 1 + (s^2/D - 1)/D$$

D and s^2 being the mean and the variance of the abundance (no. m^{-2}) estimates, respectively.

Correlation between cod larvae bigger than 4.5 mm and prey distribution was performed utilising the Spearman Rank Correlation Coefficient (Sokal & Rohlf 1981). Here, we assumed that food availability was the combined effect of prey density and light intensity, reflecting the fact that most visual feeders have an optimum illumination level for foraging as well as a threshold below which feeding does not take place (Batty 1987, Huse 1994).

We therefore developed a theoretical index of prey availability based on laboratory studies (Huse 1994) of the effect of illumination on larval feeding activity. These studies showed that both feeding incidence (% of larvae with food in gut) and intensity (no. of prey per larvae) in cod larvae are optimal at an illumination of 1 to 12 lx. Estimates of food availability were then derived by calculating the percentage of food particles (D) found in a depth stratum times the laboratory estimate of feeding incidence for the illumination level [f(L)] found in that depth stratum:

$$\text{Food availability at depth } i = f(L_i) \times D_i$$

Before calculating the food availability we first converted the light levels from quanta (µE m^{-2} s^{-1}) to lux. For green coastal waters such as the Baltic (optical classification 3, Jerlov 1976) a very precise conversion covering all depths can be made. N. K. Højerslev (pers. comm.) has calculated the conversion factor and found 1 klx to equal 6.8 µE m^{-2} s^{-1}.

RESULTS

Physical characteristics

The sampling period from May to late July was characterised by calm weather conditions (Fig. 3). During the actual sampling days winds never exceeded 10 m s^{-1}, but in May and June short episodes (6 to 9 h) of 15 to 18 m s^{-1} were recorded the day before sampling.

Water depths at the May and June stations were 95 and 98 m. The July drift station varied between 90 and 98 m. CTD profiles were typical of the estuarine conditions in the Baltic (Fig. 4). A halocline was located at approximately 45 m depth, varying from 42 to 52 m during the sampling period. Salinity in the upper 45 m was stable at ~7.2 psu, while the salinity below 45 m increased to a maximum of 18.0 psu. Density (sigma-t) of the water in May and June varied along with the salinity from 5.5 to 14.5. Water temperature in May was 6°C down to a thermocline at 22 m, after which the temperature fell to 3°C. In June surface warming had increased the stratification intensity and deepened the thermocline to 33 m, with surface temperatures of 8 to 9°C decreasing to 3°C in the deep water. On both occasions there were indications of a slightly warmer bottom water layer. In May and June, 50% oxygen saturation was found at 77 m, dropping below 30% near the bottom. Large saturation differences were found between the 2 CTD casts made at the same station.

In July, density ranged from 4 to 14.5, reflecting the increased surface temperatures. A second thermocline was present in July, stretching from 8 to 20 m with temperatures from 19 to 12°C. The 50% oxygen saturation depth was at 60 m in July, with 20 to 25% saturation near bottom.

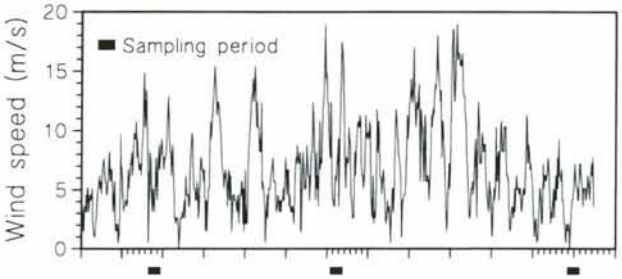

Fig. 3. Wind speed (m s^{-1}) in the study area from 20 April to 19 July recorded from nearby Christiansø

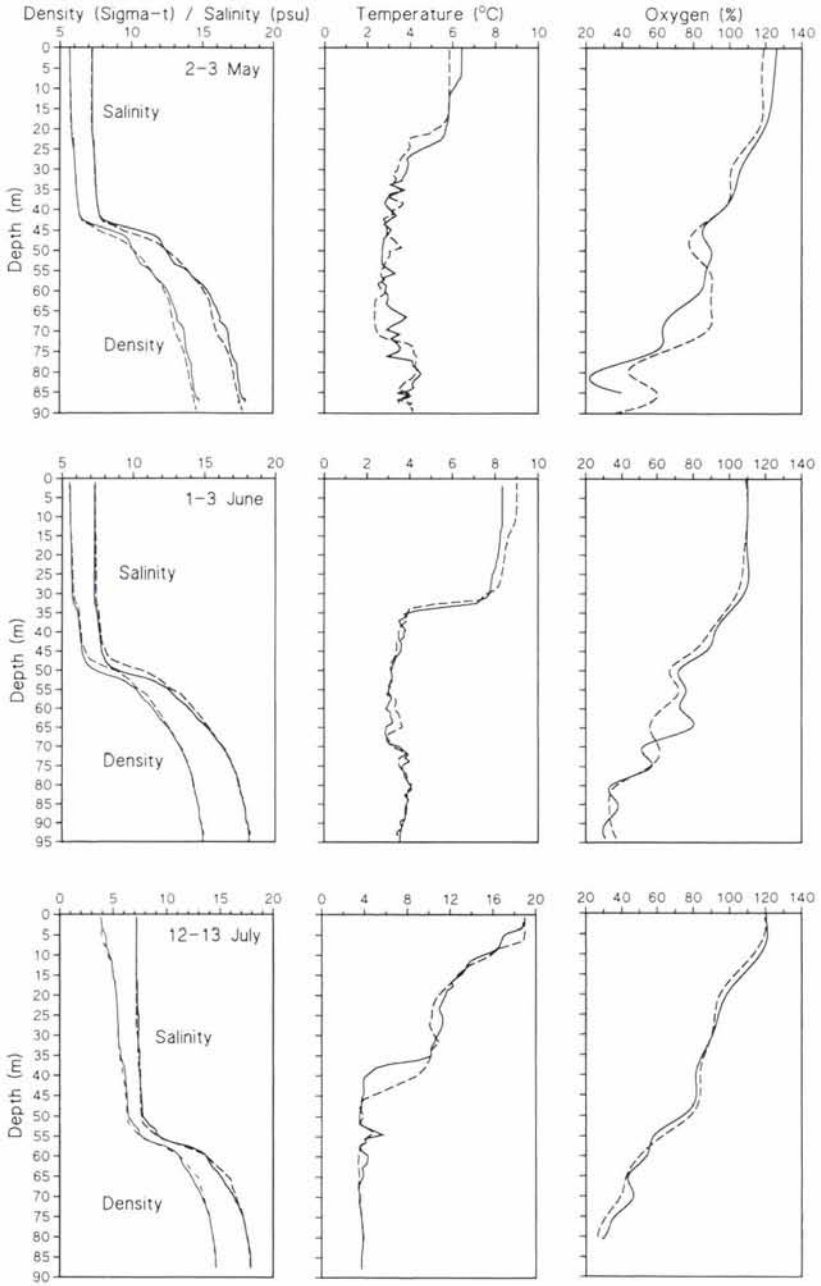

Fig. 4. Hydrographic conditions at the start (solid line) and at the end (dashed line) of each investigation

Microzooplankton

The abundance of nauplii, and the 2 groups of copepodites was determined at 9 depths with the mean (±SE) of 3 profiles (morning, afternoon and midnight) shown in Fig. 5. No indication of vertical migrations between the 3 profiles was evident for any of the zooplankton groups examined, hence the data were pooled. The vertical distribution of the microzooplankton changed between cruises. No distinct peak of nauplii was found in May, although the abundance on average was higher above the halocline than below. In June the highest mean abundance of nauplii was found in the deep water at 65 to 75 m, whereas in July it peaked at 15 m. The abundance of copepodite Stages I–III and IV–V revealed no consistent pattern, except low abundance in the lower halocline region (55 m) and in the deepest samples (75 to 85 m).

Based on the May samples, 3 species of copepods were common in the study area. *Pseudocalanus minutus* was spread throughout the water column, making up for the deep water peaks of copepodites, while *Acartia* spp. and *Temora longicornis* were found mainly above the halocline. Furthermore, *Centrophagus hamatus* was found in low numbers in surface waters, and *Oithona similis*, also in low numbers, was found in deep waters.

Cod larvae

A total of 607 cod larvae were caught during the 3 investigations (Table 1). The frequencies of the different length groups are shown in Fig. 6. Most (54 to 59%) larvae were 4.25 to 5.00 mm standard length (SL). No significant ($F_{2,586} = 2.31$, $p = 0.10$) difference in mean length was found between cruises for larvae <7.5 mm. The percentage of larvae larger than 7.5 mm decreased from May to July. The night:day catch ratio varied between 0.7 and 0.4, yielding no indication of visual gear avoidance with all larval sizes combined. Ten out of 12 larvae larger than 7.5 mm were caught during daylight.

Vertical distribution

Cod larvae were found in all 17 depth intervals (Fig. 7). The depth intervals with the highest mean abundances during the day were from 30 to 40 and 60 to 75 m, while during the night peaks were observed from 25 to 30 and 70 to 75 m. Below 75 m the low oxygen content (<2.8 mg O_2 l^{-1}) probably made the condi-

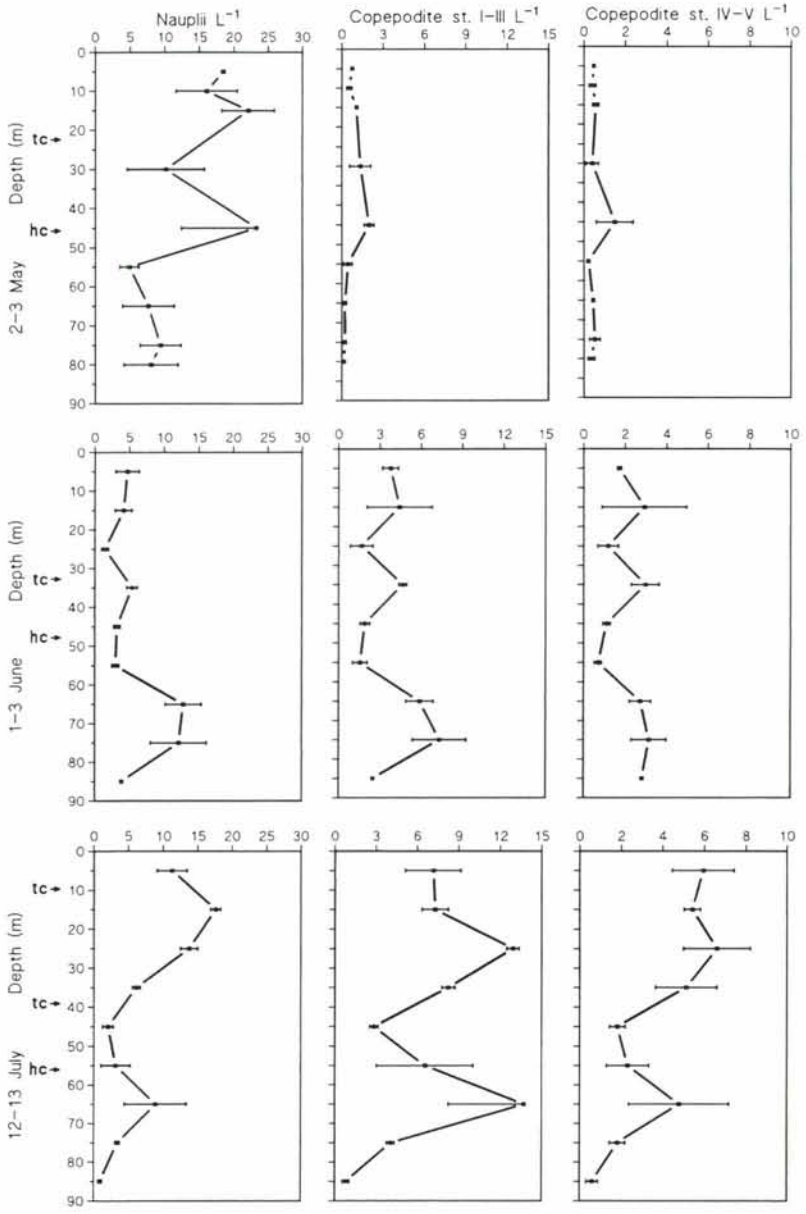

Fig. 5. Vertical distribution (mean ± SE) of prey items (no. l^{-1} nauplii and copepodite Stages I–III and IV–V) of larval cod. tc: thermocline; hc: halocline. n = 3

tions unfavourable, as yolk-sac cod larvae experience high mortality below 3.0 mg O_2 l^{-1} (Nissling 1994). Only during the investigations in July did we find a significant effect of depth on the abundance of larvae ($F_{16,85}$ = 6.74, $p < 0.01$). During May, June and July, 46.2 ± 18.1, 38.8 ± 15.7 and 64.6 ± 13.2% (mean ± SD) of the larvae were caught in the interval from 5 to 45 m.

On all 3 stations the mean length of larvae above the halocline was significantly larger than it was below (May, T_{137} = 4.81, $p < 0.001$; June, T_{158} = 7.82, $p < 0.001$; July, T_{288} = 6.28, $p < 0.001$), and based on the July samples there was no significant effect of sampling time (day/night) on the mean length of larvae above (T_{174} = 1.74, p = 0.08) and below the halocline (T_{110} = −0.34, p = 0.74), suggesting that larger individuals concentrated in the upper 45 m both day and night.

A total of 64, 81, and 119 larvae were staged from the May, June and July samples respectively (Table 2). The null hypothesis that there was random distribution of Stages 3 to 10 above and below 45 m was rejected on the basis of pooled data from the 3 mo (chi-squared = 35.2, df = 7, $p < 0.01$). Larvae in Stages 3 and 4 were abundant below, whereas larvae in Stage 8 were found almost exclusively above the halocline.

The vertical distribution of larvae in relation to developmental stages illustrates that larvae start migrating through the halocline at about Stage 4 to 5 (approximately 4 to 8 d post hatch) which coincides with first-feeding (Fig. 8). The largest relative amount of cod larvae above the halocline was found to be in Stage 8 (approximately 10 to 16 d post hatch). Stages 9 and 10 (approximately Day 17 post hatch to metamorphosis) were spread throughout the water column, but with more than 50% above 45 m.

On the basis of the length/developmental-stage key, we partitioned all length-measured larvae into 3 size groups, roughly corresponding to developmental Stages 1 to 5, 6 to 8 and 9 to 10, which confirmed the ontoge-

Table 1. Total number, abundance and mean length (± SE for all values) of cod larvae caught during the cruises in May, June and July 1994. Number of vertical profiles sampled (5 to 85 m in 5 m intervals) shown in parentheses

Larvae	May	June	July
Total no.	145	160	302
No. 1000 m^{-3}	4.14 ± 1.19 (5)	4.67 ± 1.12 (6)	7.89 ± 0.89 (6)
No. m^{-2}	0.34 ± 0.11 (5)	0.36 ± 0.09 (6)	0.66 ± 0.07 (6)
No. m^{-2} day	0.44 ± 0.14 (3)	0.42 ± 0.12 (3)	0.73 ± 0.12 (4)
No. m^{-2} night	0.19 ± 0.15 (2)	0.29 ± 0.14 (3)	0.53 ± 0.09 (2)
Mean length (mm)	4.90 ± 0.1	4.74 ± 0.08	4.57 ± 0.04

netic differences in vertical distribution of the larvae (Fig. 9).

The larvae <4.5 mm were mainly yolk-sac larvae before first feeding. It was apparent that these larvae were concentrated below the halocline, although the July data showed a more uniform distribution than did May and June. Larvae larger than 4.5 mm and smaller than 5.5 mm (first-feeding larvae) showed clear peaks in abundance above and below the halocline in May and June, while in July these larvae were concentrated in the upper 45 m. The 5.5 to 7.5 mm group (feeding larvae) aggregated in the upper 45 m during the night and spread throughout the water column during day (day/night data not shown). Few larvae larger than 7.5 mm were obtained (n = 12) and these were almost

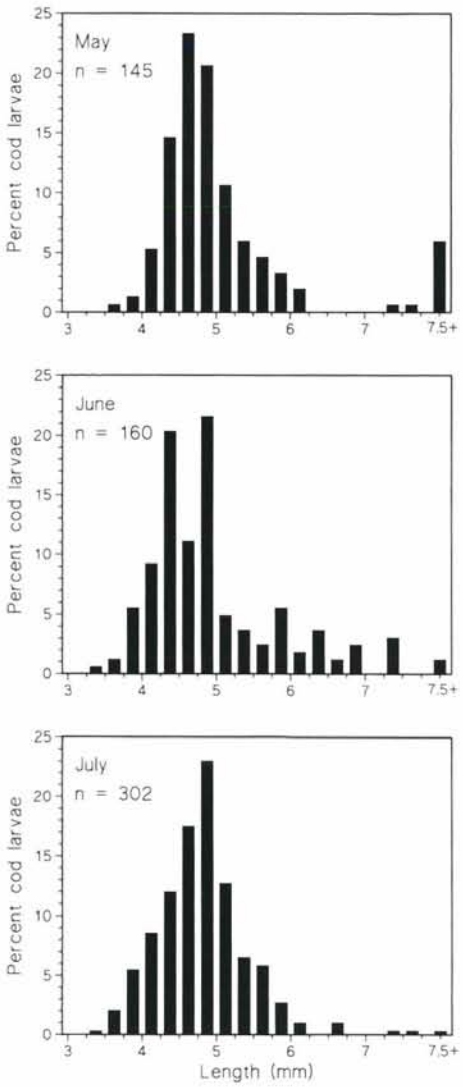

Fig. 6. Length frequencies of cod larvae caught in May, June and July

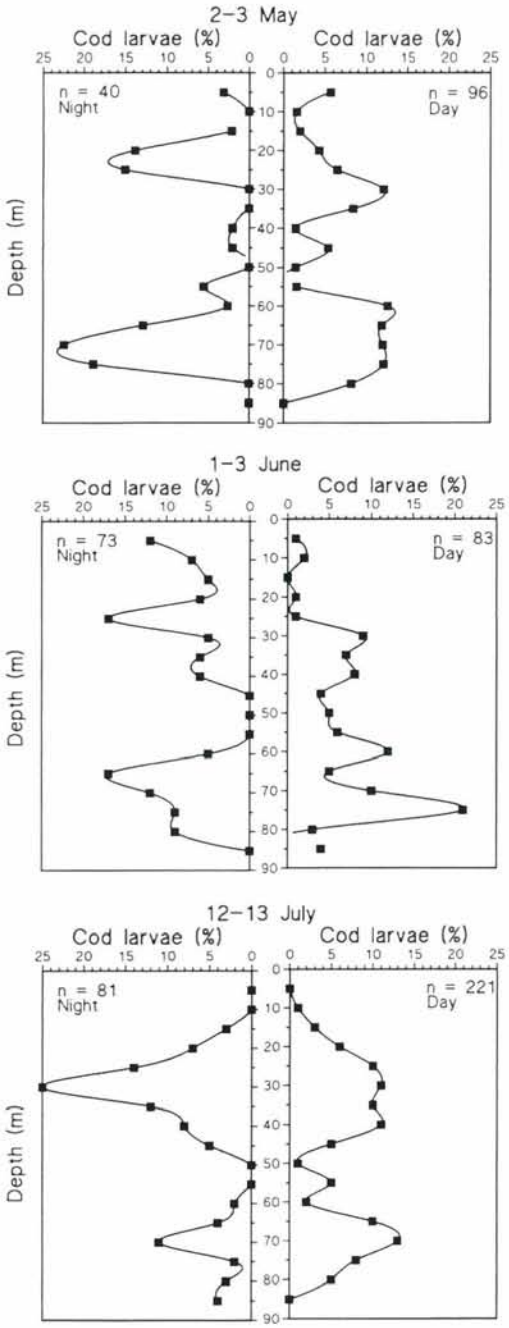

Fig. 7. Day and night vertical distribution of cod larvae in May, June and July. Percentages calculated based on no. m^{-2} in each 5 m depth interval (5 to 85 m). Gaps in the smoothed line are due to excessive curvature

exclusively caught during the day, when they were found scattered over the water column.

The distribution pattern for the 2 smallest larval groups in July differed somewhat from the pattern found in May and June. This difference suggests that the larvae migrating to the upper 45 m were smaller in July than in May and June, a finding further supported

Table 2. Number and stage of non-damaged cod larvae staged from each cruise. Larvae were developmentally staged according to Fossum (1986)

Stage	May	June	July
1	1	0	0
2	0	2	1
3	8	1	7
4	7	6	7
5	14	7	17
6	15	14	33
7	4	14	22
8	4	12	24
9	2	22	7
10	9	3	1
Total	64	81	119

by the occurrence of Stage 4 larvae above the halocline in July.

Based on all larval sizes, no vertical migration could be detected between day and night samples in June ($F_{16,68} = 1.02$, $p > 0.05$). In May and July the day/night data sets were unbalanced, but supported the results from June.

Larval aggregation

The highest degree of patchiness, as measured by Lloyd's index, was found from sunset to midnight on all 3 occasions, while the largest scatter was found at midday (Fig. 10).

Calculation of the larval centre of mass (Z_{cm}) is often used to detect changes in vertical position. Applied to each profile, the centre of mass of larvae larger than 4.5 mm showed large fluctuations during 24 h (Fig. 11). Two patterns of movement seemed evident: the centre of mass rose to shallower layers during the dawn to late morning period and descended to deeper layers during mid-day (e.g. between 10:00 and 16:00 h). However, the exact timing and magnitude of ascents and descents varied between dates.

The centre of mass of larvae larger than 4.5 mm is plotted with the 0.0068 µE m^{-2} s^{-1} (~1 lx) and 0.068 µE m^{-2} s^{-1} (~10 lx) isolumes in Fig. 11. Within these 2 isolumes, cod larvae in the laboratory are found to have their highest feeding incidence (Ellertsen et al. 1980, Huse 1994). This graph yields no indication of aggregation with respect to a specific isolumen, but shows some association between interval of optimum feeding isolumes and centre of mass from sunrise to sunset. Around midday the larvae tend to be above optimum light levels.

A Spearman Rank Correlation test showed no significant association during the day between the average density of cod larvae (mean of 3 profiles) and any of the 3 prey groups (Table 3). Replacing the food density with food availability significantly improved the correlation coefficients. Strong correlation was then found between cod larvae and copepodite Stages I–III in June and July. The correlation between copepodite Stages IV–V and cod larvae was only marginally insignificant in June. In May correlation between prey and cod larvae distribution was weak. Fig. 12 shows the vertical distribution of cod larvae and the availability of the food items. It is obvious that the poor correlation in May is related to the high density of larvae in the deep water. This peak was not prominent in June and July, where correlations were better.

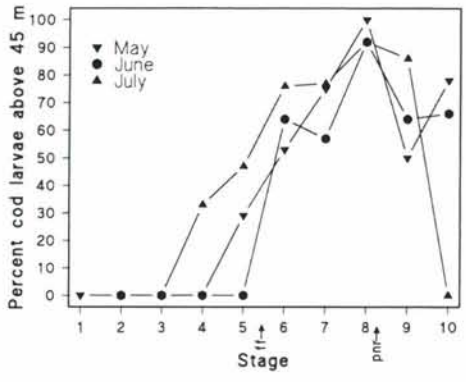

Fig. 8. Percentage of larvae in each stage above the halocline (5 to 45 m). See Table 2 for no. of larvae staged

DISCUSSION

Cod larvae

During May, June and July 1994 abundances of cod larvae were 0.34 to 0.66 m^{-2}, which is consistent with results from cruises conducted in the years 1987 to 1993 (Grønkjær et al. 1995a, Wieland 1995). However, these abundances are much lower than those observed historically in the same area (MacKenzie et al. 1996). For example, Müller (1988) found 100 times more larvae in June 1973, and Krenkel (1981) found 10 to 20 times more larvae during 1977 to 1980. This difference might be due to the large reduction in spawning biomass of Baltic cod from 700000 t in 1980 to approximately 70000 t in 1994 (ICES 1994), as well as to processes affecting growth and survival of eggs and larvae (review by MacKenzie et al. 1996).

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

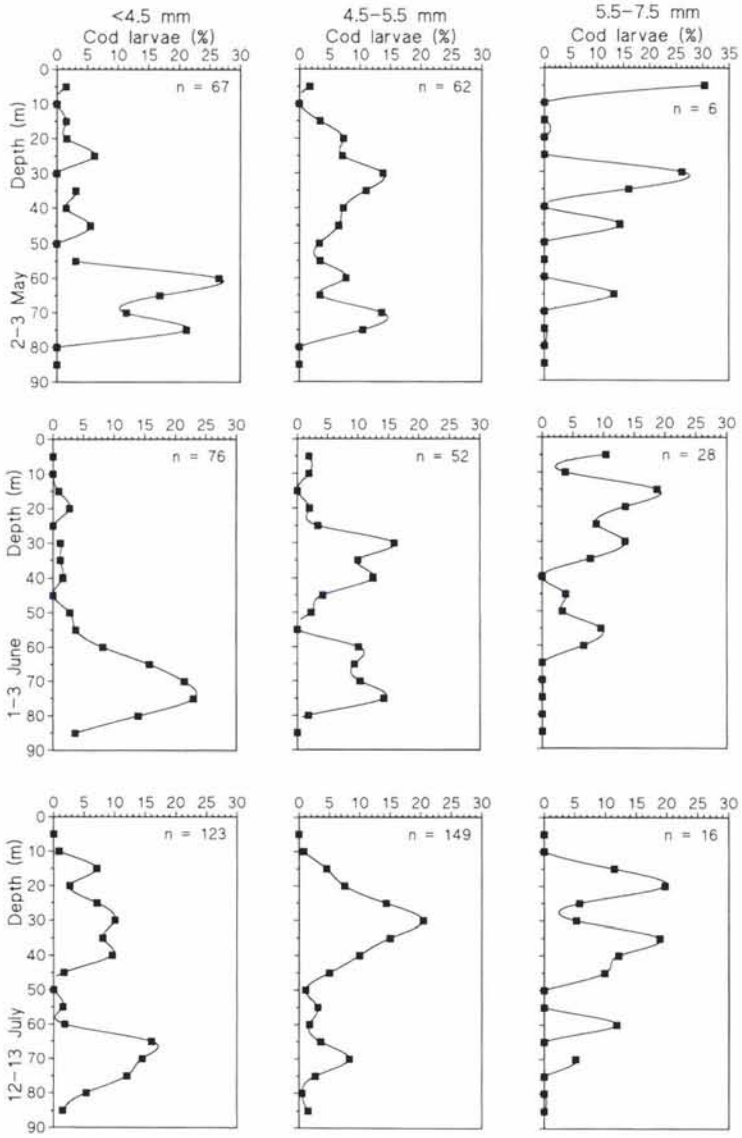

Fig. 9. Vertical distribution of 3 size groups of larvae. The 3 size groups correspond approximately to developmental Stages 1 to 5, 6 to 8 and 9 to 10. Percentages are calculated on the basis of no. m^{-2} in each 5 m depth interval (5 to 85 m). Gaps in the smoothed line are due to excessive curvature

nets. If this is true then visual avoidance should cause night:day catch ratios to be larger than 1. However we had ratios less than 1, suggesting that this was not a problem in our study. We note that Lough & Potter (1993) consider visual avoidance of a 1 m^2 MOCNESS to be relatively small in cod larvae <13 mm (live length).

The mean length of the larvae was similar during the 3 cruises, possibly indicating a steady-state process in which larger larvae above the halocline are advected from the main spawning area and new smaller larvae are being added due to local spawning or advective input from other areas. In support of this possibility, Kändler (1944) found that larvae and 0-group cod drifted to shallow-water feeding grounds, and Hinrichsen et al. (in press) have used 3-D circulation models to demonstrate that larvae exit the Bornholm Basin.

Alternatively, a constant size distribution could be maintained by higher mortality of the larger larvae. Herring in particular primarily prey on larger larvae (Köster & Schnack 1994), which could cause the absence of these size classes in our catches. The relative importance of these 2 factors are difficult to assess, but it is likely that in combination they determine the size pattern of cod larvae in the Bornholm Basin.

Vertical distribution

The vertical distribution of newly hatched fish larvae is determined by the distribution of the late-stage eggs (Anderson & deYoung 1995).

In the Bornholm Basin the density of the cod eggs and the hydrographic characteristics confines these late-stage and hatching eggs to the deep water, where the youngest larvae are also found (Nissling et al. 1994b, Wieland 1995). In other cod stocks, this deep distribution of hatching eggs may be found when high-density eggs are spawned (Oullet 1997). Density of eggs has been observed to correlate with quality, poorer eggs being denser than high-quality eggs (Kjesbu et al. 1992, Anderson & deYoung 1994). Consequently, in other stocks a variable fraction of the larvae may hatch at depths assumed to be sub-optimal for feeding and survival.

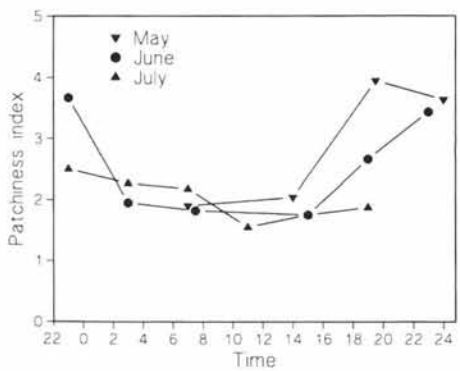

Fig. 10. Changes in Lloyd's patchiness index (Lloyd 1967) for larvae >4.5 mm (feeding larvae) during the 24 h studies

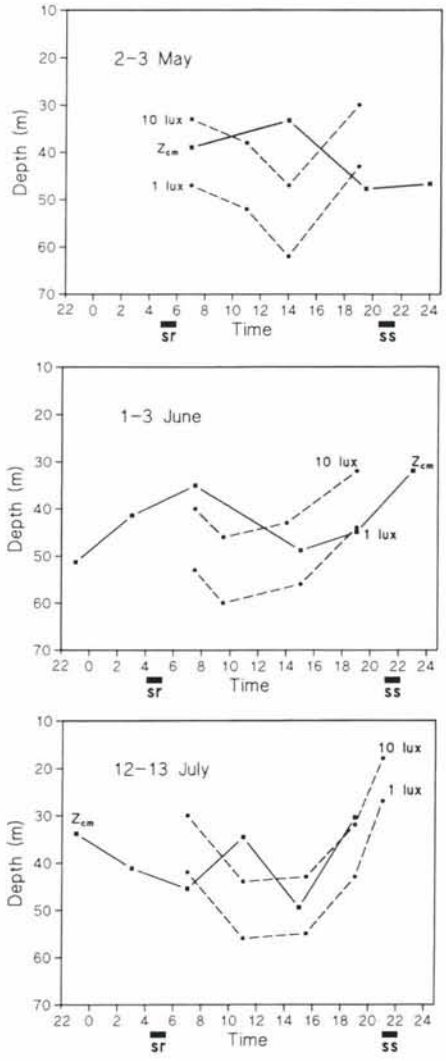

Fig. 11. Depth of the optimal light levels for cod larval feeding (1 to 10 lx), as determined by Huse (1994), and larval centre of mass (Z_{cm}) for larvae assumed to have initiated feeding (larvae >4.5 mm) during the 24 h studies. sr: sunrise; ss: sunset

The results presented here show that yolk-sac and feeding Baltic cod larvae are spread throughout the water column in a non-uniform manner. The bimodal distribution observed is expected to be the result of (1) the egg distribution and (2) the necessity of migrating to the surface for optimum feeding conditions.

First-feeding migration

We suggested that larvae originating from deeply distributed eggs should migrate towards the upper mixed layer in order to optimise foraging. The existence of a this first-feeding migration becomes evident when the cod larvae are split into size groups and

Table 3. Spearman Rank Correlation coefficients between vertical distribution of food items (nauplii and copepodite Stages I–III and IV–V) and cod larvae at 9 depths (n = 9). Correlations are restricted to cod larvae >4.5 mm as only these larvae are assumed to primarily feed on copepod prey. Food availability represents the combined effects of light and food abundance. Significance levels are based on sequential Bonferroni correction for number of simultaneous correlations within months ($^{*}p < 0.05$)

	Nauplii	CI–CIII	CIV–CV
Food density			
May	0.27	0.33	0.53
June	0.75	0.42	0.42
July	0.27	0.43	0.25
Food availability			
May	0.20	0.28	0.26
June	0.66	0.75*	0.75
July	0.63	0.83*	0.67

staged. Our hypothesis that the upper layer group consists of older and probably feeding individuals was confirmed by a chi-squared test with pooled data from the 3 months.

Looking into details of the distribution we found almost no larvae <4.5 mm, or younger than Stage 5, above the halocline in May and June. As first feeding is found to take place around Stages 5 to 6 (Fossum 1986), when the larvae are approximately 4.5 mm, as estimated from the length stage key made for each of the 3 months, we believe this migration is coupled to feeding. In July 40% of the larvae <4.5 mm were in the upper 45 m. That this is not due to reduced length at age in July, but due to an earlier start of the upward migration, is evident from the vertical distribution of the different stages, showing a large fraction of Stages 4 and 5 larvae above the halocline during the July survey.

The timing of migration in all 3 months (Stages 4 to 7) coincides with the time of highest swimming activity (Days 5 to 7 post hatch) (Solberg & Tilseth 1984). Hence the one-way first-feeding migration of Baltic cod larvae is undertaken long before the onset of diel migration of cod larvae, as reported by Ellertsen et al. (1981) and Lough & Potter (1993).

The proportion of larvae above the halocline reached its maximum after Stage 8, ~14 d post hatch. This is very late, considering that the point of no return is estimated to be on Day 11 at 5°C (Ellertsen et al. 1981). Starved cod larvae are found to die around Day 11 at 8°C. (Grønkjær et al. 1995b). Raae et al. (1988) found 80% of starved cod larvae to survive until Day 12, after which mortality increased and all larvae were dead at Day 17. The high proportion of Stage 8 larvae in the upper water masses could therefore, besides the upward migration of earlier

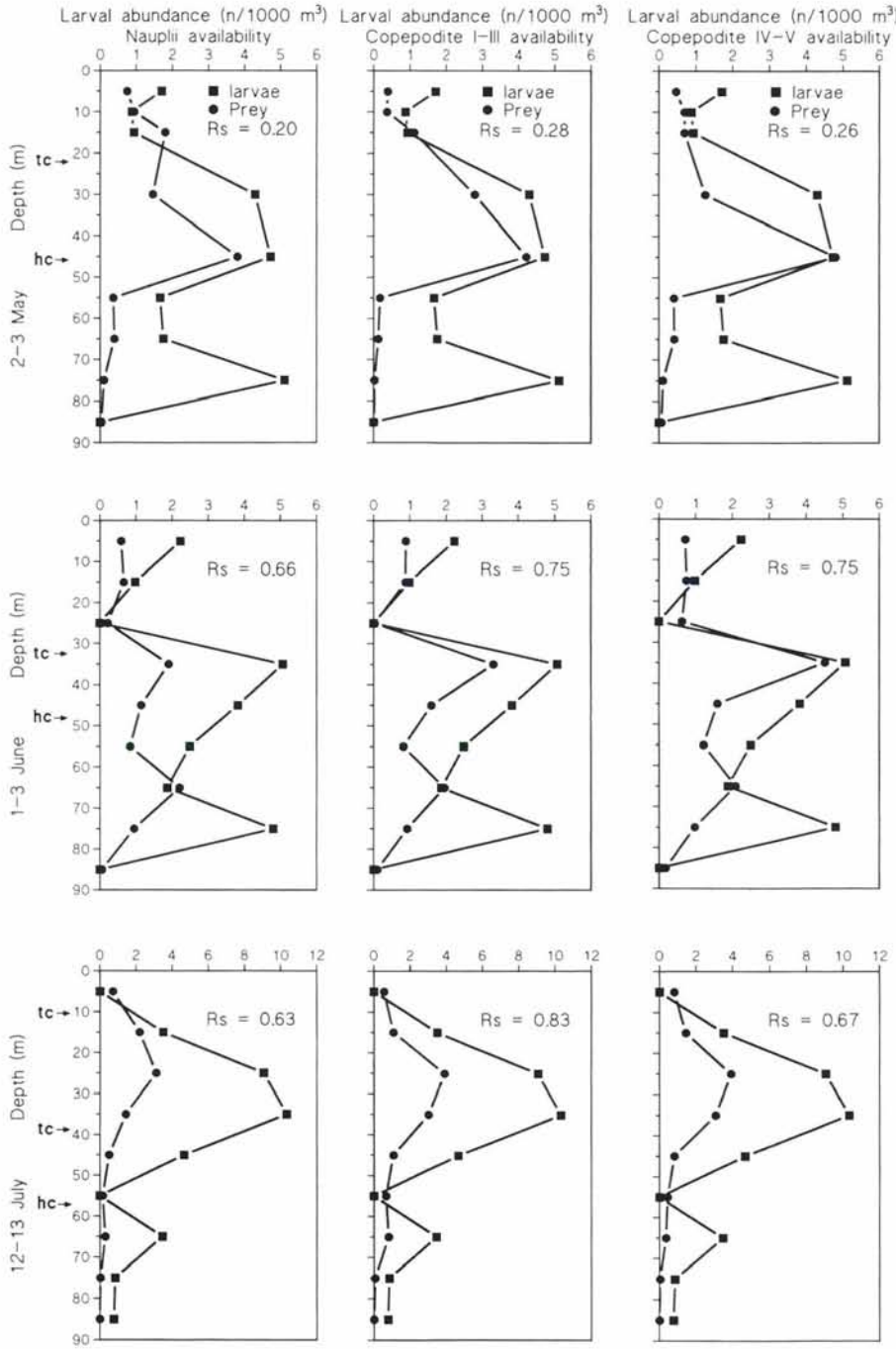

Fig. 12. Mean abundance of larvae >4.5 mm (no. 1000 m^{-3}) and availability of nauplii and copepodite Stages I–III and IV–V (relative scale). Spearman Rank Correlation coefficients (Rs) between larval abundance (mean of 3 d samples) and prey availability (mean of 2 d samples) at 9 depths are shown. Correlations are restricted to cod larvae >4.5 mm as only these larvae are assumed to primarily feed on copepod prey

stages, be attributed to increased mortality of deeply distributed larvae in Stage 8 due to starvation.

Late-migrating larvae may also experience reduced survival, as they show delayed development of swimbladder and alimentary tract, and subsequently reduced growth, when compared to early feeding larvae (feeding before yolk-sac exhaustion) (Ellertsen et al. 1981). These differences may persist into the juvenile stage (Rosenberg & Haugen 1982) and contribute to a large variability in survival potential of Baltic cod larvae. Prolonged stay in the deep water may also increase the predation-induced mortality, as sprat and

herring concentrate feeding below 50 m (Köster & Schnack 1994), and chaetognaths, which have been identified as fish larvae predators (Brewer et al. 1984), are concentrated here (Arndt & Stein 1973).

Finally the low oxygen levels found in the deep water layer may reduce the survival chances of the deeply distributed larvae. Nissling (1994) found increased mortality in Baltic cod larvae at oxygen levels below 3.0 mg O_2 l^{-1}. These oxygen levels were recorded at 65 to 75 m depth during our studies.

The migration can probably only be performed by larvae in good condition, in particular those having strong swimming abilities. Specific gravity of cod larvae hatched from eggs incubated at 10 and 30 psu salinity was at Day 4 approximately 1.012 and 1.018 g cm^{-3} (Nissling & Vallin 1996). Since the density of water in the surface layer and halocline is less than 1.006 g cm^{-3}, any larvae located in this layer will quickly sink to denser water, unless they actively swim to counteract the high sinking rate (Waller & Rosenthal 1995). Consequently larvae must maintain a high level of swimming activity if they are to avoid sinking below the halocline again. Good nutritional condition, i.e. large yolk sac, and large size at hatch might be critical parameters determining which larvae are able to migrate to the surface. Furthermore, if the ability to migrate and avoid sinking is dependent upon larval buoyancy large differences in migration and vertical distribution could be due to maternal effects on the egg and larval characteristics (e.g. yolk-sac size, length at hatch) and the salinity in which the eggs develop (Nissling & Vallin 1996).

Larval aggregation

Upon reaching low-salinity surface water, the larvae showed clear vertical aggregation patterns. These patterns were consistent across cruises in spite of large differences in the physical and biotic environment.

The distribution of nauplii, the principal prey of the smaller cod larvae (Last 1978), was very different between cruises. The abundance of the copepodites did not show large differences through the water column, but increased significantly over the 3 mo period. This increase in copepodite abundance through spring and summer has been shown to be reflected in the diet composition of Baltic cod larvae. Zuzarte et al. (1996) showed a shift from nauplii to copepodite dominated diet from April/May to July/August in 1987 and 1988 among larvae larger than 6 mm.

However, the vertical distribution of the larval food items per se did not explain the distribution of the larvae. Very poor correlations were found between larval and prey abundances over the 9 depths sampled.

Ponton & Fortier (1992) also found poor correlation between vertical distribution of Arctic cod and sand lance larvae and their prey items, but by scaling the food abundance with available light they obtained significant correlation, especially between larger larvae and their prey. The effect of a combination of light and food abundance on vertical distribution and feeding of fish larvae has also been suggested by, e.g., Munk et al. (1989) and Gilbert et al. (1992).

Hence, we compared larval abundance with food availability, which was the combined effect of illumination and food abundance. To calculate this we assumed that the feeding of Baltic cod larvae was dependent on light in the same manner as for the Atlantic cod used by Huse (1994). Huse (1994) found a dome-shaped relation between feeding incidence and intensity and illumination. Feeding was low below 0.1 lx, peaked at 1 to 12 lx and was inhibited by light levels above 12 lx.

This yielded strong correlations in June and July, but the correlations in May remained poor. The poor correlations in May were caused by a high abundance of larvae >4.5 mm in the 75 m stratum. This peak, although not as pronounced, was also evident in June and July. A closer examination of these larvae showed that 22 out of 26 staged larvae in this depth were younger than Stage 7 and longer than 4.5 mm. This is also evident from the length/stage key (Fig. 2). Based on Fossum's cod development stages, these larvae probably had not yet commenced feeding, and therefore functionally should belong to the group <4.5 mm (larvae before first-feeding), which were not included in the correlation. Substituting the abundance in the 75 m interval with the mean of the abundance in the interval above and below further improved most correlation coefficients (range 0.55 to 0.80, n = 9). As expected improvement was largest in May.

The highest correlations were found with the copepodite stages as food items. This can be explained by the observed preference of these stages in the diets of the larger larvae in the Baltic Sea (Zuzarte et al. 1996). Moreover, Last (1978) found that cod larvae from the North Sea were able to feed on *Pseudocalanus minutus* copepodites from 4 mm; and, from 6 mm, these copepodites made up 60% of the stomach content biomass.

Last (1978) found that cod larvae in the North Sea were dusk and dawn feeders, and Kane (1984) found that cod larvae on Georges Bank were primarily dusk feeders. If cod larvae in the Baltic Sea exhibit the same general feeding periodicity as larvae in these other areas, then we would anticipate that vertical distributions of larvae in the Baltic might coincide with the depth range where light intensities were optimal for feeding, especially at the time of day when feeding activity is expected to be most intense. Our results sup-

port this possibility, because larvae at dawn and dusk were either located within, or close to, the depth range encompassed by the 1 and 10 lx isolumes. During the day the larvae were on average found at a higher than optimum light level, although never far from the 10 lx isolume.

These results are therefore consistent with several studies which suggest that food concentration alone is an incomplete description of the availability of food for larval fishes (Munk et al. 1989, MacKenzie & Leggett 1991). In our case, associations between larval abundance and food availability increased when light conditions were considered. Hence these 2 factors together explained much of the vertical variation in larval distributions, although other factors (e.g. turbulence, predators) can also affect larval vertical distributions.

Diel vertical migrations

Based on all larval sizes from the June data set, it was not possible to demonstrate any significant vertical migration between day and night using an ANOVA. Although the larvae had completed the first-feeding migration, only small variations in depth distribution between day and night were seen in the 4.5 to 5.5 mm larvae (data not shown). The data on larvae from 4.5 to 5.5 mm indicated a shift towards greater depth during the day in May and to a lesser extent in June, but interpretation of this as vertical migration is difficult due to the inconsistency of the data, the short sampling period and the low numbers of larvae caught. When the larvae reach the size group 5.5 to 7.5 mm, indications of vertical migration are seen in the scattering of the larvae during day.

The centre of mass of larvae >4.5 mm varied with a periodicity less than 24 h in June and July, which would render pooling in day and night unsuitable to detect vertical migrations. Furthermore, the occurrence of larvae >4.5 mm in the deep water is a problem in the calculation of centre of mass. These larvae can skew the centre of mass downward if they are caught in larger number. Caught in variable numbers they might introduce fluctuations in centre of mass not discernible from migrations. Hence strong conclusions regarding diel vertical migrations cannot be made from the present study.

The above results are similar to findings of Ellertsen et al. (1981) on Arcto-Norwegian cod indicating that no diel migration exists around first feeding, and those of Lough & Potter (1993) on Georges Bank stating that diel migrations of cod larvae may be initiated when the larvae are 6 to 8 mm (live length), depending on the physical structure of the water column, but not until they are >9 mm are clear patterns seen.

Contrary to studies on, e.g., herring larvae (Heath et al. 1998, Munk et al. 1989), it was found that the Baltic cod larvae aggregated during the night and that these patches dispersed during the day. The aggregational patterns seen are, however, in agreement with the observations that cod larval feeding incidence and intensity is maximum at dusk (Last 1978, Kane 1984). The vertical distribution and aggregational patterns seen indicate that feeding Baltic cod larvae aggregate in relation to the combined effects of food abundance and light regime during this period.

In conclusion, our studies of the vertical distribution of cod larvae in the Bornholm Basin have shown that the large-scale (above/below halocline) distribution in the water column is determined by the larval age, as reflected in the distribution of larval sizes and stages. The upward migration of first-feeding larvae suggests that the distribution in the deep water is sub-optimal with regard to feeding.

Small-scale (~5 m) distribution of the larger feeding larvae seems to be governed by food abundance and light regime through their combined effects on food availability. The larvae on all cruises aggregated in the depth of optimum light conditions during the 2 periods considered to be the principal feeding times, namely at sunrise and sunset. Furthermore, this aggregation was consistent in spite of large differences in temperature, thermocline depth and subsequent water density between cruises.

This leads us to believe that the fraction of the larger larvae found below the halocline to a large extent are larvae in which condition and swimming ability have deteriorated so that they are unable to migrate to, and remain within, optimum feeding depths. If this is true we hypothesise that large larvae located in deep water will have low growth rates and survival probability. These ideas are presently being investigated.

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LITERATURE CITED

Anderson JT, deYoung B (1994) Stage dependent density of cod eggs and larvae (*Gadus morhua*) in New Foundland waters. ICES Mar Sci Symp 198:654–665

Anderson JT, deYoung B (1995) Application of a one-dimensional model to vertical distribution of cod eggs on the

northeastern Newfoundland Shelf. Can J Fish Aquat Sci 52:1978–1989

Arndt EA, Stein H (1973) Das Zooplankton von vier Terminfahrten des Internationalen Ostseejahres 1969, 1970. Beitr Meereskd 32:33–35

Bagge O, Thurow F (1993) The Baltic cod stock, fluctuations and the possible causes. ICES Mar Sci Symp 198:254–268

Batty RS (1987) Effect of light intensity on activity and food-searching of larval herring *Clupea harengus*: a laboratory study. Mar Biol 94:323–327

Boehlert GW, Mundy BC (1988) Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas. Am Fish Symp 3:51–67

Brewer GD, Kleppel GS, Dempsey M (1984) Apparent predation on ichthyoplankton by zooplankton and fishes in nearshore waters of southern California. Mar Biol 80: 17–29

Ellertsen B, Fossum P, Solemdal P, Sundby S, Tilseth S (1984) A case study on the distribution and availability of prey organisms in relation to physical processes in Lofoten. Flødevigen Rapportser 1984(1):453–477

Ellertsen B, Solemdal P, Strømme T, Tilseth S, Westgård T, Moksness E, Øiestad V (1980) Some biological aspects of cod larvae (*Gadus morhua* L.). Fiskerdir Skr Ser Havunders 17:29–47

Ellertsen B, Solemdal P, Sundby S, Tilseth S, Westgård T, Øiestad V (1981) Feeding and vertical distribution of cod larvae in relation to availability of prey organisms. Rapp PV Réun Cons Int Explor Mer 178:317–319

Fortier L, Leggett WC (1983) Vertical migrations and transport of larval fish in a partially mixed estuary. Can J Fish Aquat Sci 40:1543–1555

Fossum P (1986) A staging system for larval cod (*Gadus morhua* L.). Fiskerdir Skr Ser Havunders 18:69–76

Fossum P, Ellsertsen B (1994) Gut content analysis of first-feeding cod larvae (*Gadus morhua* L.) sampled at Lofoten, Norway 1979–1986. ICES Mar Sci Symp 198:430–437

Gilbert M, Fortier L, Ponton D, Drolet R (1992) Feeding ecology of marine fish larvae across the Great Whale River plume in the seasonally ice-covered southeastern Hudson Bay. Mar Ecol Prog Ser 84:19–30

Grauman GB (1973) Investigation of factors influencing fluctuations in abundance of Baltic cod. Rapp PV Réun Cons Int Explor Mer 164:73–76

Grønkjær P, Jørgensen SB, Frederiksen M, St. John M, Clemmesen C, Støttrup JG (1995b) The influence of essential fatty acids composition on growth of larval cod (*Gadus morhua*) larvae. Preliminary observations. ICES Comm Meet 1995/J:19

Grønkjær P, Möllmann C, Voss R (1995a) Abundance and distribution of larval cod (*Gadus morhua*) in the Bornholm Basin. ICES Comm Meet 1995/J:24

Heath MR, Henderson EW, Baird DL (1988) Vertical distribution of herring larvae in relation to physical mixing and illumination. Mar Ecol Prog Ser 47:221–228

Hinrichsen HH, Lehmann A, St John M, Brügge B (in press) Modelling of the cod larvae drift in the Bornholm Basin in the summer 1994. Cont Shelf Res

Huse I (1994) Feeding at different illumination levels in larvae of three marine teleost species: cod, *Gadus morhua* L., plaice, *Pleuronectes platessa* L., and turbot, *Scophthalmus maximus* (L.). Aquacult Fish Manage 25:687–695

ICES (1994) Report of the working group on the assessment of demersal stocks in the Baltic. ICES Comm Meet 1994/ Assess:17

Jerlov NG (1976) Marine optics. Elsevier Oceanography Series no. 14. Elsevier Scientific Publishing Company, Amsterdam

Kändler R (1944) Untersuchungen über den Ostseedorsch während der Forschungsfahrten mit dem RFD 'Poseidon' in den Jahren 1925–1938. Ber Dtsch Wiss Kommn Meeresforsch 11:137–245

Kane J (1984) The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Mar Ecol Prog Ser 16: 9–20

Kjesbu OS, Kryvi H, Sundby S, Solemdal P (1992) Buoyancy variations in eggs of Atlantic cod (*Gadus morhua* L.) in relation to chorion thickness and egg size: theory and observations. J Fish Biol 41:581–599

Kjørsvik E, van der Meeren T, Kryvi H, Arnafinnson J, Kvenseth PG (1991) Early development of the digestive tract of cod larvae, *Gadus morhua* L., during start-feeding and starvation. J Fish Biol 38:1–15

Korsior M, Netzel J (1989) Eastern Baltic cod stocks and environmental conditions. Rapp PV Réun Cons Int Explor Mer 190:159–162

Köster FW, Schnack D (1994) The role of predation on early life stages of cod in the Baltic. Dana 10:179–201

Krenkel K (1981) Über das Vorkommen der Eier und Larven von Sprott (*Sprattus sprattus*) und Dorsch (*Gadus morhua*) in der Ostsee in den Jahren 1977–1980. Fisch-Forsch 19(2):31–36

Last JM (1978) The food of three species of gadoid larvae in the eastern English Channel and southern North Sea. Mar Biol 48:377–386

Lloyd M (1967) Mean crowding. J Anim Ecol 36:1–30

Lough RG, Potter DC (1993) Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fish Bull US 91:281–303

MacKenzie BR, Kiørboe T (1995) Encounter rates and swimming behavior of pause-travel and cruise larval fish predators in calm and turbulent laboratory environments. Limnol Oceanogr 40:1278–1289

MacKenzie BR, Leggett WC (1991) Quantifying the contribution of small scale turbulence to the encounter rates between larval fish and their zooplankton prey: effects of wind and tide. Mar Ecol Prog Ser 73:149–160

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

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

Müller A (1988) Vertical distribution of ichthyoplankton in the Bornholm Basin. Kiel Meeresforsch Sonderh 6:341–347

Munk P, Kiørboe T, Christensen V (1989) Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environ Biol Fish 26:87–96

Nissling A (1994) Survival of eggs and yolk-sac larvae of Baltic cod (*Gadus morhua* L.) at low oxygen levels in different salinites. ICES Mar Sci Symp 198:626–631

Nissling A, Kryvi H, Vallin L (1994b) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. Mar Ecol Prog Ser 110:67–74

Nissling A, Solemdal P, Svensson M, Westin L (1994a) Survival, activity and feeding ability of Baltic cod (*Gadus morhua*) yolk-sac larvae at different salinities. J Fish Biol 45:435–445

Nissling A, Vallin L (1996) The ability of Baltic cod eggs to maintain neutral buoyancy and the opportunity for survival in fluctuating conditions in the Baltic Sea. J Fish Biol 48:217–227

Nissling A, Westin L (1991) Egg mortality and hatching rate of Baltic cod (*Gadus morhua*) in different salinities. Mar Biol 111:29–32

Oullet P (1997) Characteristics and vertical distribution of Atlantic cod (*Gadus morhua*) eggs in the northern Gulf of St. Lawrence, and the possible effect of cold water temperature on recruitment. Can J Fish Aquat Sci 54:211–223

Ponton D, Fortier L (1992) Vertical distribution and foraging of marine fish larvae under the ice cover of southeastern Hudson Bay. Mar Ecol Prog Ser 81:215–227

Raae AJ, Opstad I, Kvenseth P, Walther BT (1988) RNA, DNA and protein during early development in feeding and starved cod (*Gadus morhua* L.) larvae. Aquaculture 73: 247–259

Rosenberg AA, Haugen AS (1982) Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. Mar Biol 72:73–77

Sinclair M, Iles TD (1985) Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian shelf area in relation to oceanographic features. Can J Fish Aquat Sci 42:880–887

Sokal RR, Rohlf FJ (1981) Biometry. WH Freeman and Co, New York

Solberg T, Tilseth S (1984) Growth, energy consumption and prey density requirements in first feeding larvae of cod (*Gadus morhua* L.) Flødevigen rapportser 1984(1):145–167

Stephenson RL, Power MJ (1988) Semidiel vertical movements in Atlantic herring *Clupea harengus* larvae: a mechanism for larval retention? Mar Ecol Prog Ser 50:3–11

Waller U, Rosenthal H (1995) The migratory behaviour of yolk-sack larvae of cod, *Gadus morhua*. ICES Comm Meet 1995/L:14

Wiebe P, Burt KH, Boyd SH, Morton AW (1976) A multiple opening/closing net and environmental sensing system for sampling zooplankton. J Mar Res 34:313–326

Wieland K (1988) Distribution and mortality of cod eggs in the Bornholm Basin (Baltic Sea) during two patch studies in 1986. Kiel Meeresforsch Sonderh 6:331–340

Wieland K (1995) Einfluß der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (*Gadus morhua callarias*) im Bornholmbecken, südliche zentrale Ostsee. Berichte aus dem Institut für Meereskunde an der Christian-Albrechts-Universität zu Kiel, no. 266

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

Zuzarte F, Köster FW, Möllman C, Voss R, Grønkjær P (1996) Diet composition of cod larvae in the Bornholm Basin. ICES Comm Meet 1996/J:19

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