Vertical distribution of Baltic sprat larvae: changes in patterns of diel migration?

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Ontogenetic and diurnal vertical migration patterns of Baltic sprat larvae were investigated for the periods 1989–1990 and 1998–2002. Comparison of the results led to the hypothesis that the diel vertical migration behaviour of sprat larvae >10 mm has changed. In 1989 and 1990, sprat larvae migrated to the surface at night, whereas they stayed 30–50 m deep by day. From 1998 to 2002, sprat larvae showed no signs of diel vertical migration, remaining in warmer, near-surface water by day and night. This behavioural change coincided with a more general change in the Baltic ecosystem, i.e. an increase in near-surface temperature and a general increase in abundance of the major prey organism (*Acartia* spp.) of Baltic sprat larvae, with more pronounced aggregation in surface waters.

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Introduction

Variation in the vertical distribution of planktonic organisms has long been recognized as an important factor controlling the structure and dynamics of marine foodwebs (Russell, 1927; Cushing, 1951; Banse, 1964; Longhurst, 1976; Lampert, 1989). The impact of such variation is amplified when there are strong vertical gradients, such as in the Baltic Sea. There, vertical distributions of different developmental stages and species are strongly affected by fluctuating hydrographic conditions (Grønkjaer and Wieland, 1997; Hansen *et al.*, 2006; Schmidt, 2006), and predator–prey interactions are influenced by variable vertical overlap (Neuenfeldt, 2002; Köster *et al.*, 2003; Neuenfeldt and Beyer, 2003; Möllmann *et al.*, 2004).

In the Baltic Sea, sprat (*Sprattus sprattus*) are an ecologically important pelagic fish species (Rudstam *et al.*, 1994; Kornilovs *et al.*, 2001), being prey for top predators (e.g. cod, harbour porpoise) and predator on zooplankton and fish eggs (Arrhenius and Hansson, 1993; Bagge *et al.*, 1994; Köster and Schnack, 1994; Möllmann and Köster, 1999; Köster and Möllmann, 2000a, b). Currently too, sprat represent the most abundant, commercially exploited species in the Baltic (ICES, 2006), and optimal management is challenged by large fluctuations in stock size.

The spawning of sprat and the distribution of its planktonic eggs is restricted to the central part of the deep basins in the Baltic, with vertical concentration in the upper part of the halocline, typically between 45 and 70 m. The Bornholm Basin in the central Baltic Sea is an especially important spawning ground for sprat (Köster *et al.*, 2001). During the main spawning season in spring, the Bornholm Basin is characterized by a seasonal thermocline at ∼20–30 m deep and a permanent halocline at 50–75 m, which separates less-saline surface waters (salinity 7–8) from more-saline bottom waters (salinity 10–18) (Kullenberg and Jacobsen, 1981; Møller and Hansen, 1994). Renewal of the bottom waters follows irregular saline water inflows into the Baltic Sea (Matthäus and Lass, 1995).

From the early 1980s to the late 1990s, there was a regime shift in the Baltic Sea, as shown by a profound change in fish and zooplankton abundance and species composition (Alheit *et al.*, 2005). The copepod *Pseudocalanus acuspes*, major prey for cod larvae (Voss *et al.*, 2003), generally decreased in abundance (Möllmann *et al.*, 2000). The copepod *Acartia* spp., major prey of sprat larvae (Voss *et al.*, 2003), increased in abundance likely because of an increase in water temperature (Möllmann *et al.*, 2000). The sprat stock gained substantially from decreased predation pressure by the declining cod stock (Köster and Möllmann, 2000b), and from improved recruitment success, though there was increased variability too.

Sound scientific explanation for the increased variability is missing. Spawning-stock biomass is a poor predictor of recruitment success of sprat (Köster *et al.*, 2003; MacKenzie and Köster, 2004). Recent research has shown that recruitment depends to some degree on temperature conditions influencing gonad development and egg survival (MacKenzie and Köster, 2004). The critical periods in the sprat life cycle are, however, the larva and the early juvenile stage (Köster *et al.*, 2003; Voss *et al.*, 2006). Mechanisms influencing survival of sprat larvae are only poorly understood, at least partly because of missing knowledge of vertical distribution patterns of larvae, so hampering process-orientated research.

Here, we investigated the vertical distribution and migration of sprat larvae and zooplankton in the Bornholm Basin, based on samples obtained from 1998 to 2002 and a decade earlier, in

Table 1. Sampling for sprat larvae and zooplankton in terms of number of profiles investigated and larvae analysed, type of sampling device, and vertical resolution.

Sampling month	Number of profiles by day	Number of profiles by night	Number of larvae	Number of profiles of zooplankton	Ontogenetic sampling	Sampling device
May 1989	2	2	6471	5[a,d]	No	MOCNESS, 50 μm liners[d]
June 1989	2	2	2225	–	No	MOCNESS[d]
June 1990	2	2	5278	–	No	BIOMOC[d]
May 1998	3	–	3096	–	Yes	BIOMOC[d]
May 1999	4	2	12 837	3[a,c]	Yes	BIOMOC, 50 μm liners[d]
April 2000	4	2	15 678	–	Yes	BIOMOC[d]
June 2002	2	2	236	9[b,c]	Yes	BIOMOC, 50 μm multinet[d]

[a]Sampling at one station, MOCNESS or BIOMOC 335 μm and 50 μm liners; [b]Sampling on one date but at six different stations, Multinet 50 μm; [c]Vertical resolution 10 m; [d]Vertical resolution 5 m.

1989 and 1990. The purpose of the studies was to document the vertical distribution of sprat larvae and their potential prey. Differences in results between the two periods led to a hypothesis that there have been gradual changes in the diel vertical migration behaviour of sprat larvae >10 mm, perhaps linked to changes in the Baltic Sea ecosystem.

Material and methods
Sampling and laboratory analysis

Vertically resolved sampling was conducted during seven spring cruises between May 1989 and June 2002 (Table 1) in the central part of the Bornholm Basin, central Baltic Sea (Figure 1). The earliest samples used were collected in 1989 with a MOCNESS (Wiebe *et al.*, 1976); from 1990, a BIOMOC was used instead. Both gears are multiple opening/closing nets operating with nine nets and a mouth opening of 1 m^2. The BIOMOC is a MOCNESS system modified similarly to the BIONESS (Sameoto *et al.*, 1980), but still using vertically operated opening/closing bars. In both cases, the nets had a mesh size of 335 μm and were equipped with calibrated flowmeters (for a detailed description, see Wieland, 1995). The samplers were towed at a fixed depth for ~3 min at a speed of 3 knots. Two combined hauls of the gear in use (up to 17 nets) allowed investigation of vertical distribution in the water column with a resolution of 5 (10) m depth intervals, resolving the water column down to a maximum of 5 m above the sea floor.

For sampling of small zooplankton (e.g. nauplii, N), 50-μm liners mounted inside the multiple opening/closing nets were used, a technique already successfully applied to analyse vertical distribution patterns of zooplankton (Hansen *et al.*, 2004, 2006). Alternatively (in June 2002), a vertically towed 0.25 m^2 multinet was used. Samples were immediately fixed in borax-buffered formaldehyde–seawater solution (4% final concentration) for later analysis in the laboratory.

Sprat larvae were sorted from the samples and measured to the nearest 0.1 mm, applying no correction for shrinkage. Several zooplankton subsamples were taken for subsequent microscope identification (magnification 50×) until at least 500 individuals in total were counted. All individuals were identified to developmental stage [grouped in nauplii, copepodites (C1–C3), copepodites (C4 and C5), adult males (C6–m) and females

(C6–f), and species]. Abundances of sprat larvae and copepods per m^3 were calculated based on counts and filtered volumes.

In parallel with plankton sampling, vertical profiles of temperature, salinity, and oxygen were taken, using a conductivity, temperature, depth (CTD) probe with calibrated oxygen sensor mounted on a water-rosette sampler [Meerestechnik Elektronik (ME), Kiel, Germany].

Data analysis

As an index of vertical location of larvae, weighted mean depths (WMD) (Bollens and Frost, 1989) were computed as WMD $=(\sum n_i\,d_i)/\sum n_i$, where n_i is the abundance of individuals in depth stratum i with midpoint depth d_i.

Additionally, relative abundances per 5 m depth were calculated based on daylight sampling averaged over sampling dates. Sprat larvae were classified into three length groups (2 to <5; 5 to <10; ≥10 mm) according to morphological criteria, relevant to their swimming ability (Bartsch and Knust, 1994). Vertical distribution profiles are presented for copepods and size groups of
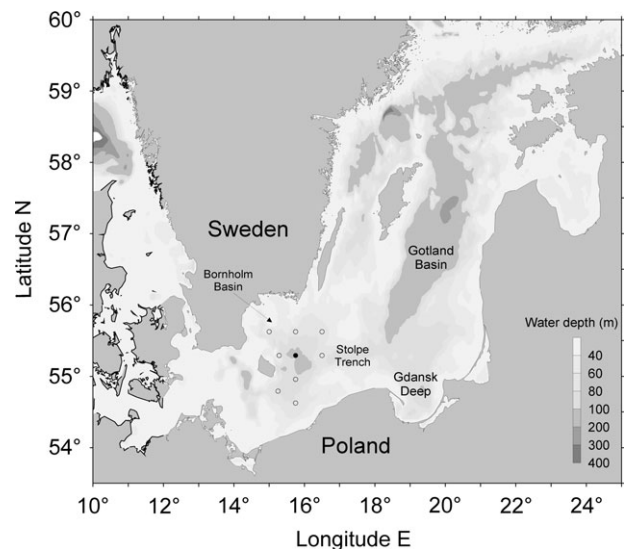

Figure 1. Map of the central Baltic Sea. Open circles indicate the positions of vertically resolved zooplankton sampling in June 2002, and the black dot the position of sampling on all other dates.

sprat larvae for the daylight period 08:00–18:00 (local time) and for the period of darkness 23:30–04:00, i.e. for the sampling times with potentially most pronounced day–night differences.

We applied the Paul–Banerjee statistic (Paul and Banerjee, 1998) to test for significance of differences in vertical distribution. The method considers patchiness and requires replicate samples. It is a complement to the test of Solow et al. (2000), which is used in cases when replicate samples are not available. The null hypothesis tested states that the shapes of the depth profiles of mean abundance are the same under all different conditions (Beet et al., 2003). Test statistic B has an approximate χ^2 distribution with $(T - 1) \times (D - 1)$ degrees of freedom at T different conditions and D depths.

As sprat larvae feed almost exclusively on Acartia spp. (Voss et al., 2003), the vertical distribution of that taxon is presented (g wet weight per m^3). Biomass values for the different developmental stages were taken from Hernroth (1985). For a simple illustration of change in the vertical distribution of Acartia spp., the surface fraction (SF) was calculated by dividing Acartia spp. biomass in the 0–20 m stratum by total Acartia spp. biomass in the 0–50 m stratum. The vertical axis was restricted to 50 m in all cases to preclude influence from differences in vertical extension of the zooplankton sampling.

Results
Ontogenetic migration
Ontogenetic changes in vertical distribution of sprat larvae were studied on the basis of daylight sampling between May 1998 and June 2002. Yolk-sac larvae, which mainly depend on endogenous energy reserves (size class 2 to <5 mm), had WMDs between 43 and 70 m (Figure 2). Mean relative abundance per 5-m depth layer was greatest at around 70 m. An ontogenetic migration to upper water layers was found for larger size classes: larvae of 5 to <10 mm length were more widely spread through the water column; mean relative abundance peaked in two different layers, deep in the water column, at around 70 m, and near the surface, at around 10 m. Large larvae (≥10 mm) were concentrated exclusively near the surface (WMD 10–18 m); mean larval length per
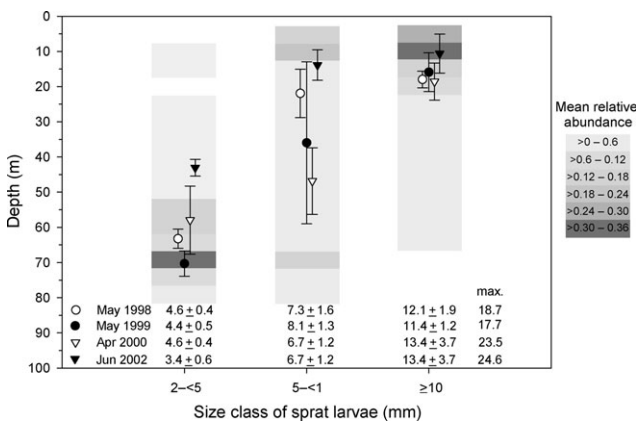

Figure 2. Ontogenetic changes in vertical distribution of sprat larvae represented by three size classes. WMD (symbols, mean ± s.d.) for individual surveys is given as well as mean relative abundance per 5 m depth layer (shading), averaged over sampling dates and daylight periods. Additionally, length of larvae per size group (mean ± s.d.) is provided along with maximum size caught.

size class varied between samplings, but with only small absolute differences (Figure 2).

Diurnal vertical migration
Diurnal vertical migration was investigated for the largest size class of sprat larvae (≥10 mm), because this group is least restricted by limited swimming ability (Figures 3 and 4). In the period 1999–2002, these larvae stayed mainly in less-saline surface waters (7–8), in the depth range where the seasonal thermocline develops. Using Paul–Banerjee statistics, we found no significant day–night differences in vertical distribution in the period 1999–2002 ($p > 0.05$ for all cases; Figure 3), indicating the absence of any substantial diurnal migration. Hydrographic conditions showed the typical vertical structure of the deep, central Baltic basins in spring: a developing warm, low salinity surface layer, cooler intermediate waters below the seasonal thermocline, and higher salinity, sometimes oxygen-depleted water below the permanent halocline.

During the earlier sampling period of 1989 and 1990, larvae ≥10 mm were mainly near the surface at night (Figure 4), as in the more recent period. Daylight profiles, however, were significantly different between the two periods (Paul–Banerjee statistics, $B = 39.32$; $p < 0.001$), showing deeper distribution in 1989 and 1990, with abundance maxima in the 35–55 m depth range (Figure 4). Testing daylight against night-time distribution for the earlier period revealed statistically significant differences (Paul–Banerjee statistics, $B = 67.77$; $p < 0.001$) and therefore the existence of diurnal vertical migration by larvae ≥10 mm. Larvae experienced lower ambient temperature by day as well as slightly increased salinity. Day–night differences in the ambient temperature amounted to 3–5°C in May and 6–10°C in June. Mean size of larvae was always slightly bigger by night than by day, but the differences were small and the size ranges sampled did not indicate any change in the sampled cohort of larvae between day and night.

Prey distribution
The SF of Acartia spp. biomass, the preferred prey for sprat larvae, ranged from 0.46 to 0.78 depending on sampling dates and stages included (Figure 5). In 1989, the SF of Acartia spp. was significantly lower in the water column than in 1999 or 2002 (Student's t-test, $t = 4.15$, $p < 0.01$ excluding adults; $t = 3.26$, $p < 0.01$ including adults).

Discussion
Ontogenetic migration
In the Bornholm Basin, the gravity of sprat eggs and the hydrographic characteristics confine late-stage eggs to deeper water (Wieland and Zuzarte, 1991; Nissling et al., 2003), where younger larvae were also found. The gravity of the eggs and their vertical distribution shows seasonal and annual variation (Nissling et al., 2003), along with corresponding fluctuations in the WMD of newly hatched larvae. The results presented here show that yolk-sac and feeding larvae are spread throughout the water column in a non-uniform manner. The bimodal distribution might be the result of either or both of the late-stage egg distribution and the necessity to migrate to the surface for optimal feeding.

Ontogenetic vertical migration of sprat larvae is expected to be coupled to feeding, as already shown for Baltic cod larvae (Grønkjær and Wieland, 1997). Alternatively, an upward
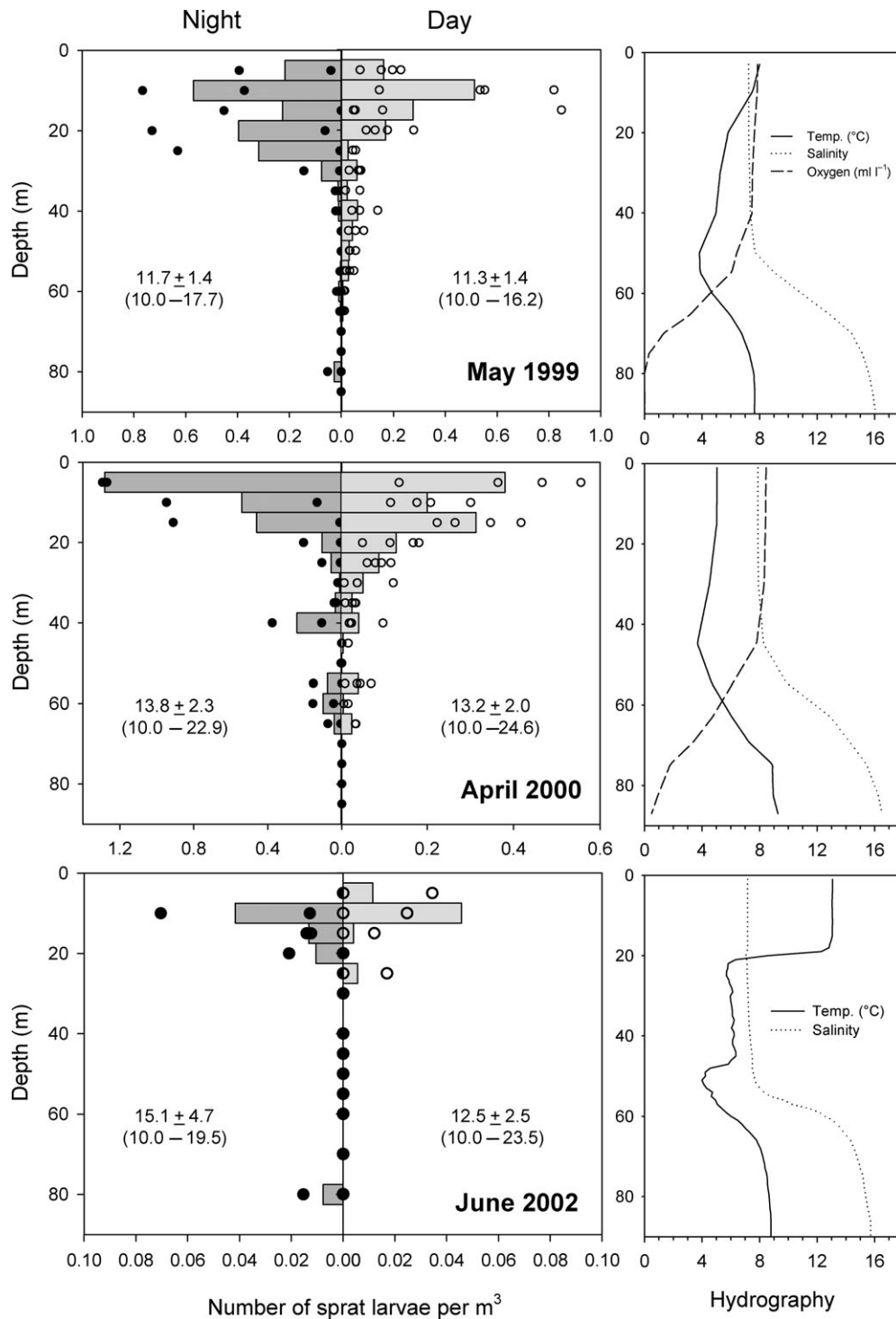
Figure 3. Vertical distribution of sprat larvae compared with hydrographical profiles in spring of 1999–2002. By night (left) and day (right), the distribution of larvae ≥10 mm is shown, circles representing single measurements, and bars mean values. Larva length is given as mean ± s.d. and size range.

ontogenetic vertical migration might reduce predation risk, because adult sprat and herring concentrate to feed in depths >50 m (Köster and Schnack, 1994; Köster and Möllmann, 2000b).

The fraction of larger larvae found below the halocline probably consisted to a great extent of starving larvae with reduced condition and swimming ability, which were not able to perform a first-feeding migration or to maintain their vertical position in optimal feeding conditions. These assumptions are supported by short-latency proxies of larval condition, showing depth dependence (A. Dänhardt, pers. comm.).
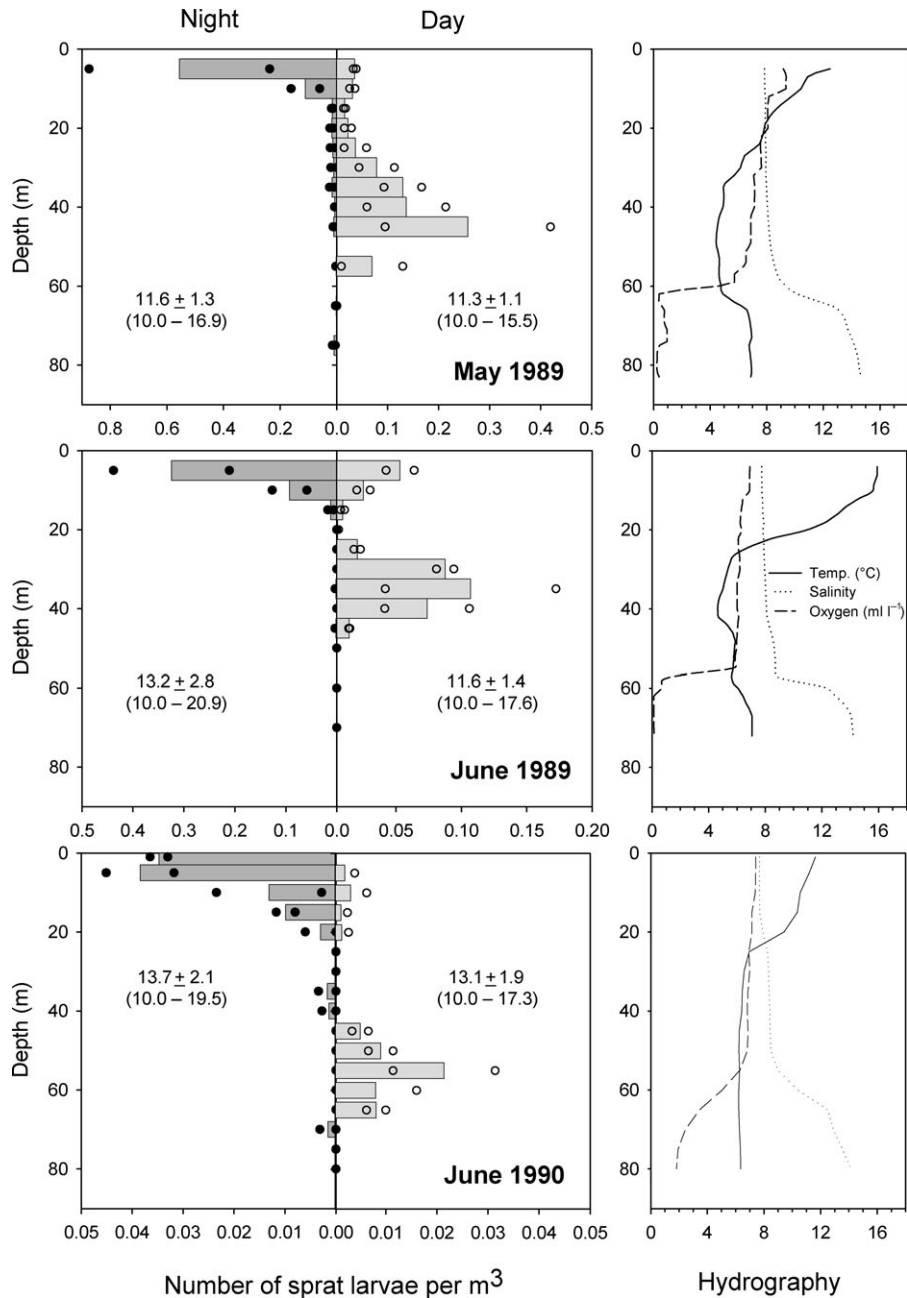
Figure 4. Vertical distribution of sprat larvae in comparison to hydrographical profiles in spring of 1989–1990. By night (left) and day (right), the distribution of larvae ≥10 mm is shown, circles representing single measurements, and bars mean values. Larva length is given as mean ± s.d. and size range.

Vertical migration patterns

Larger larvae showed clear vertical aggregation patterns in all profiles sampled. Vertical aggregation of feeding larvae is often determined by a combined effect of food abundance and suitable light level (Munk *et al.*, 1989; Gilbert *et al.*, 1992; Ponton and Fortier, 1992; Grønkjær and Wieland, 1997). Light level is important because sprat larvae are visual predators. Unlike the more dusk and/or dawn feeding behaviour of cod larvae (Last, 1978; Kane, 1984), the main daily feeding period of sprat larvae is around midday, i.e. when light levels are greatest (Voss *et al.*, 2003). The effect of light intensity on feeding of sprat larvae has not,

however, been investigated to date. The biomass of *Acartia* spp. was always greatest at depths of 5–15 m, and because they do not perform diurnal vertical migrations in the Baltic Sea (Schmidt, 2006), the combined effect of light level and prey abundance should favour sprat larval growth and survival near the surface. However, the hypothesis of larvae primarily seeking depths according to optimal feeding conditions, as determined by an optimal light for feeding and optimal densities and sizes of prey (Fortier and Leggett, 1983; Lough and Potter, 1993), does not explain the downward migration by day in 1989 and 1990. We therefore suggest a combined effect of a changed vertical
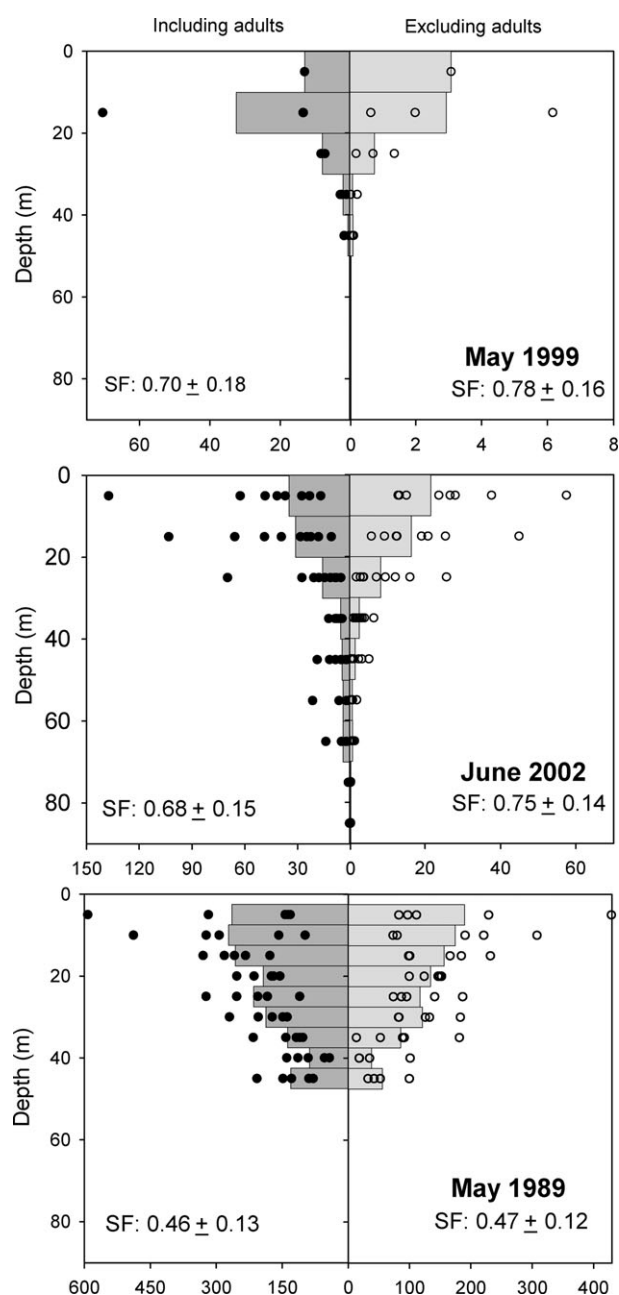
Figure 5. Vertical distribution of *Acartia* spp. in May 1999, June 2002, and May 1989. Results are given for all stages inclusive (left) and for adult stages excluded (right). Dots indicate single measurements, bars indicate mean values. SF of zooplankton (mean ± s.d.). The number of profiles is given in Table 1.

distribution pattern of *Acartia* spp. and temperature on larval migration. Since the beginning of the 1990s, the abundance of *Acartia* spp. has generally increased in the eastern Baltic. Greater abundance has been related to an overall increase in water temperature (Möllmann *et al.*, 2000). Our data demonstrate a significantly greater SF of *Acartia* spp. in 1999 and 2002 than in 1989, which might be linked to an increase in the temperature of surface waters in the Bornholm Basin. However, the data do not confirm an increase in total *Acartia* spp. biomass, so we propose further research into temperature and prey as potential drivers

of behavioural change in larval Baltic sprat, because this might considerably impact larval survival probability and therefore recruitment.

Acknowledgements

References

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., and Wasmund, N. 2005. Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES Journal of Marine Science, 62: 1205–1215.

Arrhenius, F., and Hansson, S. 1993. Food consumption of larval, young and adult herring and sprat in the Baltic Sea. Marine Ecology Progress Series, 96: 125–137.

Bagge, O., Thurow, F., Steffensen, E., and Bray, J. 1994. The Baltic cod. Dana, 10: 1–28.

Banse, K. 1964. On the vertical distribution of zooplankton in the sea. Progress in Oceanography, 2: 53–125.

Bartsch, J., and Knust, R. 1994. Simulating the dispersion of vertically migrating sprat larvae [*Sprattus sprattus* (L.)] in the German Bight with a circulation and transport model system. Fisheries Oceanography, 3: 92–105.

Beet, A., Solow, A. R., and Bollens, S. M. 2003. Comparing vertical plankton profiles with replication. Marine Ecology Progress Series, 262: 285–287.

Bollens, S. M., and Frost, B. W. 1989. Predator-induced diel vertical migration in a planktonic copepod. Journal of Plankton Research, 11: 1047–1065.

Cushing, D. H. 1951. The vertical migration of planktonic Crustacea. Biological Reviews, 26: 158–192.

Fortier, L. C., and Leggett, W. C. 1983. Vertical migrations and transport of larval fish in a partially mixed estuary. Canadian Journal of Fisheries and Aquatic Sciences, 40: 1543–1555.

Gilbert, M., Fortier, L., Ponton, D., and Drolet, R. 1992. Feeding ecology of marine fish larvae across the Great Whale River plume in the seasonally ice-covered southeastern Hudson Bay. Marine Ecology Progress Series, 84: 19–30.

Grønkjaer, P., and Wieland, K. 1997. Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Marine Ecology Progress Series, 154: 91–105.

Hansen, F. C., Möllmann, C., Schütz, U., and Hinrichsen, H-H. 2004. Spatio-temporal distribution of *Oithona similis* in the Bornholm Basin (central Baltic Sea). Journal of Plankton Research, 26: 659–668.

Hansen, F. C., Möllmann, C., Schütz, U., and Neumann, T. 2006. Spatio-temporal distribution and production of calanoid copepods in the central Baltic Sea. Journal of Plankton Research, 28: 39–54.

Hernroth, L. 1985. Recommendation on methods for marine biological studies in the Baltic Sea. Mesozooplankton biomass assessment. The Baltic Marine Biologist, 10. 45 pp.

ICES. 2006. Report of the Baltic Fisheries Assessment Working Group. ICES Document CM 2006/ACFM: 24. 622 pp.

Kane, J. 1984. The feeding habits of co-occurring cod and haddock larvae from Georges Bank. Marine Ecology Progress Series, 16: 9–20.

Kornilovs, G., Sidrevics, L., and Dippner, J. W. 2001. Fish and zooplankton interaction in the central Baltic Sea. ICES Journal of Marine Science, 58: 579–588.

Köster, F. W., Hinrichsen, H-H., Schnack, D., St John, M. A., MacKenzie, B. R., Tomkiewicz, J., Möllmann, C. *et al.* 2003. Recruitment of Baltic cod and sprat stocks: identification of critical life stages and incorporation of environmental variability into stock–recruitment relationships. Scientia Marina, 67: 129–154.

Köster, F. W., and Möllmann, C. 2000a. Egg cannibalism in Baltic sprat *Sprattus sprattus*. Marine Ecology Progress Series, 196: 269–277.

Köster, F. W., and Möllmann, C. 2000b. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science, 57: 310–323.

Köster, F. W., Möllmann, C., Neuenfeldt, S., St John, M. A., Plikshs, M., and Voss, R. 2001. Developing Baltic cod recruitment models. 1. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat. Canadian Journal of Fisheries and Aquatic Sciences, 58: 1516–1533.

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

Kullenberg, G., and Jacobsen, T. S. 1981. The Baltic Sea: an outline of its physical oceanography. Marine Pollution Bulletin, 12: 183–186.

Lampert, W. H. 1989. The adaptive significance of diel vertical migration of zooplankton. Functional Ecology, 3: 21–27.

Last, J. M. 1978. The food of three species of gadoid larvae in the eastern English Channel and the southern North Sea. Marine Biology, 48: 377–386.

Longhurst, A. L. 1976. Vertical migration. *In* The Ecology of the Seas, pp. 116–137. Ed. by D. H. Cushing and J. J. Walsh. Blackwell, Oxford. 331 pp.

Lough, R. G., and Potter, D. C. 1993. Vertical distribution patterns and diel migrations of larval and juvenile haddock *Melanogrammus aeglefinus* and Atlantic cod *Gadus morhua* on Georges Bank. Fishery Bulletin US, 91: 281–303.

MacKenzie, B. R., and Köster, F. W. 2004. Fish production and climate: sprat in the Baltic Sea. Ecology, 85: 784–794.

Matthäus, W., and Lass, H. U. 1995. The recent salt inflow into the Baltic Sea. Journal of Physical Oceanography, 25: 280–286.

Møller, J. S., and Hansen, I. S. 1994. Hydrographic processes and changes in the Baltic Sea. Dana, 10: 87–104.

Möllmann, C., Kornilovs, G., and Sidrevics, L. 2000. Long-term dynamics of main mesozooplankton species in the central Baltic Sea. Journal of Plankton Research, 22: 2015–2038.

Möllmann, C., and Köster, F. W. 1999. Food consumption by clupeids in the central Baltic: evidence for top-down control? ICES Journal of Marine Science, 56: 100–113.

Möllmann, C., Temming, A., Stepputtis, D., Bernreuther, M., Köster, F. W., and Hirche, H-J. 2004. Fish predation control of key copepod species in the Bornholm Basin. ICES Document CM 2004/L: 28. 28 pp.

Munk, P., Kiørboe, T., and Christensen, V. 1989. Vertical migrations of herring, *Clupea harengus*, larvae in relation to light and prey distribution. Environmental Biology of Fishes, 26: 87–96.

Neuenfeldt, S. 2002. The influence of oxygen saturation on the distributional overlap of predator (cod, *Gadus morhua*) and prey (herring, *Clupea harengus*) in the Bornholm Basin of the Baltic Sea. Fisheries Oceanography, 11: 11–17.

Neuenfeldt, S., and Beyer, J. E. 2003. Oxygen and salinity characteristics of predator–prey distributional overlaps shown by predatory Baltic cod during spawning. Journal of Fish Biology, 62: 168–183.

Nissling, A., Müller, A., and Hinrichsen, H-H. 2003. Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. Journal of Fish Biology, 63: 280–299.

Paul, S. R., and Banerjee, T. 1998. Analysis of two-way layout of count data involving multiple counts in each cell. Journal of the American Statistical Association, 93: 1419–1429.

Ponton, D., and Fortier, L. 1992. Vertical distribution and foraging of marine fish larvae under the ice cover of south-eastern Hudson Bay. Marine Ecology Progress Series, 81: 215–227.

Rudstam, L. G., Aneer, G., and Hildén, M. 1994. Top-down control in the pelagic Baltic ecosystem. Dana, 10: 105–129.

Russell, F. S. 1927. The vertical distribution of plankton in the sea. Biological Reviews, 2: 213–262.

Sameoto, D. D., Jaroszynski, L. O., and Fraser, W. B. 1980. BIONESS, a new design in multiple net zooplankton samplers. Canadian Journal of Fisheries and Aquatic Sciences, 37: 722–724.

Schmidt, J. O. 2006. Small and meso-scale distribution patterns of key copepod species in the central Baltic Sea and their relevance for larval fish survival. PhD thesis, University of Kiel, Germany. 99 pp.

Solow, A. R., Bollens, S. M., and Beet, A. 2000. Comparing two vertical plankton distributions. Limnology and Oceanography, 45: 506–509.

Voss, R., Clemmesen-Bockelmann, C., Baumann, H., and Hinrichsen, H-H. 2006. Baltic sprat larvae: coupling food availability, larval condition and survival. Marine Ecology Progress Series, 308: 243–254.

Voss, R., Köster, F. W., and Dickmann, M. 2003. Comparing the feeding habits of co-occuring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fisheries Research, 63: 97–111.

Wiebe, P., Burt, K. H., Boyd, S. H., and Morton, A. W. 1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. Journal of Marine Research, 34: 313–326.

Wieland, K. 1995. Einfluß der Hydrographie auf die Vertikalverteilung und Sterblichkeit der Eier des Ostseedorsches (*Gadus morhua callarias*) im Bornholm Becken, südliche zentrale Ostsee. Berichte aus dem Institut für Meereskunde Kiel, 266. 114 pp.

Wieland, K., and Zuzarte, F. 1991. Vertical distribution of cod and sprat eggs and larvae in the Bornholm Basin (Baltic Sea) 1987–1990. ICES Document CM 1991/J: 37. 12 pp.