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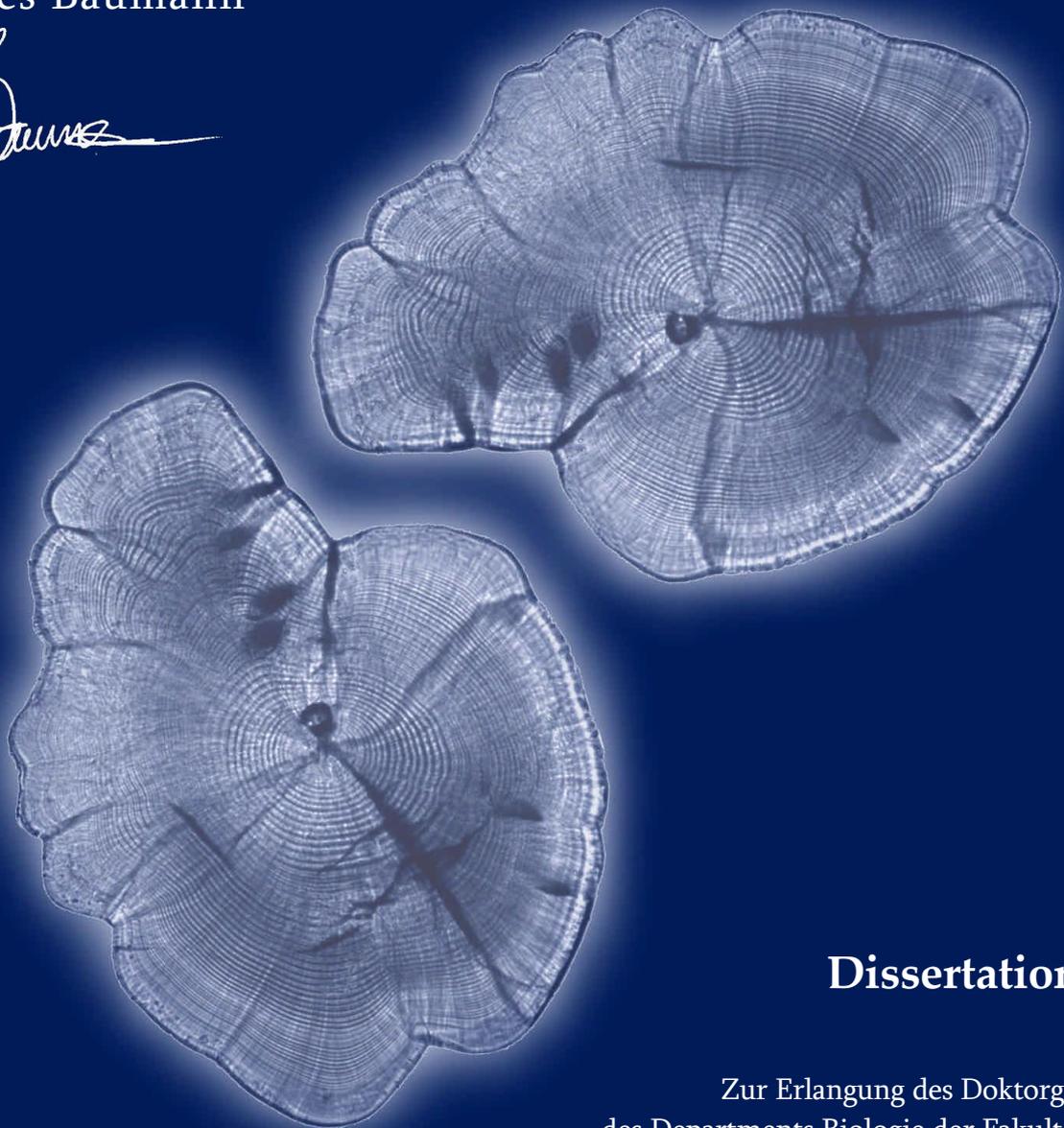
**Young-of-the-Year Baltic Sprat, *Sprattus sprattus* L:  
Growth Characteristics, Transport Patterns &  
Implications for Recruitment Variability**

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**Suhl**



**Dissertation**

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## CONTENTS

<b>Summary</b>	<b>5</b>
<b>General introduction</b>	<b>9</b>
<b>Paper 1: “Linking growth- to environmental histories in central Baltic young-of-the-year sprat, <i>Sprattus sprattus</i>: an approach based on otolith microstructure analysis and hydrodynamic modelling”</b>	<b>27</b>
Baumann, H., Hinrichsen, H.-H., Voss, R., Stepputtis, D., Grygiel, W., Clausen, L.W. & Temming, A. <i>Fisheries Oceanography</i> (in press).	
<b>Paper 2: “Temperature-induced regional and temporal growth differences in Baltic young-of-the-year sprat, <i>Sprattus sprattus</i>”</b>	<b>49</b>
Baumann, H., Gröhler, T., Kornilovs, G., Makarchouk, A., Feldman, V. & Temming, A. <i>Marine Ecology Progress Series</i> (in press).	
<b>Paper 3: “Sprat recruitment in the Baltic Sea: the importance of temperature and transport variability during the late larval and early juvenile stages”</b>	<b>71</b>
Baumann, H., Hinrichsen, H.-H., Malzahn, A.M., Möllmann, C., Köster, F.W. & Temming, A. <i>Canadian Journal of Fisheries and Aquatic Sciences</i> (under review).	
<b>Paper 4: “Starving early juvenile sprat, <i>Sprattus sprattus</i> L., in Baltic coastal waters: evidence from combined field and laboratory observations in August/September 2003”</b>	<b>91</b>
Baumann, H., Götze, E., Peck, M.A. & Temming, A. <i>Journal of Fish Biology</i> (submitted).	
<b>Paper 5: “Short-term decoupling of otolith and somatic growth induced by food level changes in post-larval Baltic sprat, <i>Sprattus sprattus</i>”</b>	<b>109</b>
Baumann, H., Peck, M.A. & Herrmann, J.-P. 2005. <i>Marine and Freshwater Research</i> <b>56</b> , 539-547.	
<b>Paper 6: “Baltic sprat larvae: coupling food availability, larval condition and survival”</b>	<b>125</b>
Voss, R., Clemmesen, C., Baumann, H. & Hinrichsen, H.-H. <i>Marine Ecology Progress Series</i> (in press).	
<b>Paper 7: “The general distribution pattern and mixing probability of Baltic sprat juvenile populations”</b>	<b>147</b>
Hinrichsen, H.-H., Kraus, G., Voss, R., Stepputtis, D. & Baumann, H. (2005). <i>Journal of Marine Systems</i> <b>58</b> , 52-66.	
<b>Conclusions, contributions &amp; acknowledgements</b>	<b>167</b>





# YOUNG-OF-THE-YEAR BALTIC SPRAT, *SPRATTUS SPRATTUS* L: GROWTH CHARACTERISTICS, TRANSPORT PATTERNS & IMPLICATIONS FOR RECRUITMENT VARIABILITY

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## SUMMARY

The present thesis has investigated patterns of growth, feeding and transport variability in Baltic sprat in order to better understand how these processes act during the pre-recruit life stages and determine sprat year-class strength.

In **paper 1**, otolith microstructure analysis and hydrodynamic modelling were combined to study growth patterns in young-of-the-year (YoY) sprat, which were sampled in October 2002 in the central Baltic Sea. The observed “window of survival”, approximated by the distribution of back-calculated days-of-first-feeding (*DFE*), was narrow compared to the extended spawning season of sprat in the Baltic Sea (mean $\pm$ SD = 22 June $\pm$ 14.1d) and indicated that only individuals born in summer survived until October 2002. Within the group of survivors, individuals born later in the season exhibited faster larval, but more rapidly decreasing juvenile growth rates than earlier born conspecifics. Back-calculated *larval* growth rates of survivors (0.48 – 0.69 mm day<sup>-1</sup>) were notably higher than those previously reported for average larval sprat populations, suggesting that the YoY-population was predominantly comprised of individuals which grew fast during the larval stage. Daily mean temperatures, experienced across the entire YoY-population, were derived from Lagrangian particle simulations and correlated to (1) detrended otolith growth and (2) back-calculated, daily somatic growth rates of survivors. The results showed that abrupt changes in ambient temperature can be detected in the seasonal pattern of otolith growth, and that higher temperatures led to significantly faster growth throughout the entire age-range of YoY-sprat.

In the **second paper**, we report on spatial and temporal differences in growth patterns of young-of-the-year sprat (YoY), that were again sampled in October 2002, but synchronously in 4 different regions of the Baltic Sea (i.e. western, central, eastern, north-eastern Baltic). Sagittal otoliths of 427 individuals from 64 sampling sites were

analysed for their microstructure to infer the day of first feeding (*DFE*) and the growth history of YoY-survivors. *DFE*-distributions were markedly different between Baltic areas, showing a shift to later mean *DFE*'s and narrower distributions from west to north-east. This was consistent with the shift in mean seasonal spawning effort of Baltic sprat, derived from long-term observations (1973-2002) of sprat egg abundance in these areas. Otolith growth trajectories (i.e. increment widths-at-age) showed a characteristic shape depending on the sampling area, but more importantly on the time of the year the individual started feeding (*DFE*). During the larval stage, individuals from the north-eastern area and those born later in the year had higher growth rates than their earlier born conspecifics, while the pattern was reversed during the juvenile stage. Weekly means of satellite-based sea surface temperature were used to approximate the potential temperature history of YoY-survivors, which significantly influenced the shape of the otolith growth trajectory. We conclude that different *DFE*'s and therefore different temperature histories were primarily responsible for the large-scale spatial growth variability between newly recruited Baltic YoY-sprat in 2002.

In **paper 3**, we tested the hypothesis that variable temperature conditions and larval drift patterns significantly influence inter-annual recruitment strength of age 0 sprat, *Sprattus sprattus*, in the Baltic Sea. Temperatures were compiled from the ICES Oceanographic database and analysed per month and depth-stratum, while drift patterns were studied by means of a hydrodynamic circulation model coupled to Lagrangian particle simulations. From the latter, we derived the annual ‘bottom-depth anomaly’ (*BDA*), an index that likely reflected the variable degree of annual larval transport from the central, deep spawning basins to the shallow coastal areas of the Baltic. *BDA*'s based on drifter cohorts released late in the season (July) were highly significantly correlated to sprat recruitment success and explained 80% and 75% of the overall variability during the periods 1979-1990 and 1991-2003, respectively. The drift index suggested that years of strong larval displacement towards southern and eastern Baltic coasts corresponded to relative recruitment failure, while retention within the deep basins was linked to relative recruitment success. The strongest correlation between temperature and recruitment occurred during August in surface waters, explaining 73% of the overall variability. The two synergistic approaches allowed to conclude that new year classes of Baltic sprat are predominantly comprised by individuals born late in the season and are determined in strength mainly by processes acting during the late-larval and early juvenile stages. The two proxies could prove valuable for recruitment predictions, although the mechanisms underlying the strong coupling between temperature, drift, and recruitment are not yet fully understood, mainly because of unresolved spatial zooplankton and predation dynamics in the Baltic Sea.

Paper 3 and other recent studies have suggested that the post-larval and early juvenile stages of Baltic sprat play an important role in regulating the strength of new year classes. In **paper 4**, we thus compared growth histories, inferred from otolith

microstructure analysis, between Baltic sprat early juveniles (26-42 mm total length, *TL*) and age 0 recruits (60-95 mm *TL*), sampled in August in shallow coastal waters and October 2003 in the entire western Baltic Sea (Sub-division 22), respectively. Recent growth rates of sprat juveniles, but not those of similarly old, prospective recruits, had declined very rapidly at the end of August. We suggest that this decline most likely resulted from a severe food deprivation of early juveniles in nearshore waters, given that (1) juveniles and recruits likely experienced similar temperature conditions, (2) that almost all juvenile sprat had empty stomachs on the sampling day, and because (3) field-collected early juveniles responded immediately with increasing growth rates when provided *ad libitum* food rations in the laboratory, while fish kept under zero food conditions showed a similarly rapid growth decline as observed prior to sampling. Starvation of early juvenile fish in the field has not been documented before, but may – at least in the case of Baltic sprat – comprise a density-dependent mechanism operating in coastal nursery areas. The unusually high abundance of age 0 sprat in the western Baltic in 2003 (hydroacoustic estimates) appears to support this concept.

In **paper 5**, the effects of food level changes on otolith and somatic growth were studied in post-larval Baltic sprat reared initially for a period of 11 days under zero, low, and *ad libitum* feeding conditions. During a subsequent 11d period, feeding regimes were reversed in half of the low and *ad libitum* feeding treatments, and starved fish were re-fed *ad libitum* rations. Somatic growth rates under low and *ad libitum* food rations ranged between 0.15-0.22 mm d<sup>-1</sup> and 0.48-0.63 mm d<sup>-1</sup>, respectively, and led to significant differences in length and weight between feeding regimes. Previously starved fish, however, grew only 0.25-0.28 mm d<sup>-1</sup> under *ad libitum* conditions. During the first period, significant linear relationships were found for otolith vs. length and vs. weight growth across all treatments. After changing feeding regimes, increment widths failed to significantly predict somatic growth for 9 days, after which a significant relationship between otolith and somatic growth became re-established. Recent otolith growth was a good predictor of fish condition after the first, but not after the second period. The results suggest that perturbations in environmental conditions can temporarily decouple otolith from somatic growth in post-larval sprat, which needs to be considered in field studies.

The **sixth paper** reports on the seasonal abundance of Baltic sprat eggs and larvae, which were collected during 14 cruises covering the spawning season in 2002 in the Bornholm Basin. Main egg and larval production was recorded in April, with a second small peak in June 2002. The *in situ* larval abundance was corrected for transport processes by using hydrodynamic model runs. Corrected larval abundance estimates were related to initial larval production to derive an index of larval mortality. This index suggested a much higher survival of summer over spring born sprat larvae, with pronounced differences in survival for larvae > 11 mm. Independent evidence for this survival pattern was gained by measured RNA:DNA ratios in sprat larvae hatched

from April-July 2002 and was linked to temporal variability in potential prey abundance. We found higher mean but less variable RNA:DNA ratios in spring- than in summer-born larvae, indicating a strong selection for fast growth in April/May but a less selective environment in June/July. Zooplankton data revealed high nauplii concentrations of *Acartia* spp., a key diet component of sprat, in April/May but very low concentrations of larger prey items like copepodites or adults. In contrast, abundance of larger prey increased considerably in June/July. The results suggest that larger sprat (>11 mm) in April/May 2002 may have been food limited and, therefore, had lower rates of survival, thereby supporting the underlying hypothesis of size-specific, temporally limited 'windows of survival' which are linked to the availability of suitable prey.

In **paper 7**, the average transport patterns of Baltic sprat larvae from different spawning grounds were investigated by detailed drift model simulations for the years 1979-2002. Modelling approaches with and without diurnal vertical migration were applied. We used recently collected data on spawning location, vertical distribution and the timing of spawning as input to a particle tracking model. Results of this modelling study enabled the identification of potential nursery grounds for sprat originating from different spawning grounds. On average, westerly winds are prevailing over the Baltic Sea. This leads to on average higher abundance of juvenile sprat along the southern and the eastern coast lines of the Baltic. The horizontal distribution of simulated larval or 0-group sprat is consistent with the observed distribution of 0-group sprat obtained from the hydroacoustic field surveys. In addition, this analysis identifies the potential for advective mixing between juveniles originating from different spawning sites or from the same spawning site throughout the spawning season. High spatial overlap was found between Arkona- and Bornholm Basin larvae hatched at the beginning of the spawning season. Mixing probability of sprat juveniles between Arkona- and Gotland Basin as well as between Bornholm- and Gotland Basin were on relatively low levels.

# **YOUNG-OF-THE-YEAR BALTIC SPRAT, *SPRATTUS SPRATTUS* L: GROWTH CHARACTERISTICS, TRANSPORT PATTERNS & IMPLICATIONS FOR RECRUITMENT VARIABILITY**

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## **GENERAL INTRODUCTION**

### *The ecological & economical importance of Baltic sprat*

The sprat, *Sprattus sprattus*, is a small, pelagic and zooplanktivorous clupeid that occurs over a broad geographical range from the Black and Mediterranean Seas in the south to the European Atlantic shelf, including the North and Baltic Seas in the north (Muus & Nielsen, 1999). Together with herring, *Clupea harengus*, sprat is an important element of the Baltic ecosystem because of its dual role, first as a significant predator on the zooplankton community (Kornilovs *et al.*, 2001) and second as a major prey species for Baltic cod, *Gadus morhua*, marine birds, and mammals (Bagge *et al.*, 1994). Over the recent two decades, the population dynamics of Baltic sprat have increasingly received scientific attention, as it was recognized that the large decadal trend in sprat stock abundance was part of a profound regime-shift that occurred in the Baltic ecosystem. Due to a combination of high fishing pressure and unfavourable hydrographical conditions, Baltic cod stocks declined dramatically at the end of the 1980s (Bagge & Thurow, 1993). The concurrent increase in sprat stock abundance to its highest levels on record in 1997 (> 2 Mio tons, ICES, 2005a) is thought to be a result of a release from predation pressure by cod, high reproductive success, and a relatively low fishing mortality (Parmanne *et al.*, 1994). It was postulated that the formerly cod-dominated Baltic ecosystem, where cod exert a top-down control on clupeid fish stocks, has shifted to a clupeid-dominated regime (Rudstam *et al.*, 1994), where clupeid predation on cod eggs and early life stages now predominantly controls Baltic cod recruitment (Köster & Schnack, 1994; Köster & Möllmann, 2000). Other researchers have pointed out that a regime shift in the Baltic Sea was not only apparent in the fish community, but affected almost all trophic levels (Wasmund *et al.*, 1998; Möllmann *et al.*, 2000) and was paralleled by a similar, climate-related shift in the North Sea ecosystem (Alheit *et al.*, 2005). Therefore, the future state of the Baltic ecosystem likely depends not only the levels of fishing pressure on Baltic cod or sprat, but on climate-

related changes in biotic and abiotic conditions, which determine recruitment strengths and therefore overall stock abundance of both Baltic fish species.

Along with its ecological importance, sprat now also comprises the most abundant, commercially exploited fish species in the Baltic Sea where reported landings exceeded 370,000 tons in 2004 (ICES, 2005b). However, after a period of relatively low and constant recruitment levels during most of the 1980-ies, sustainable management of Baltic sprat stocks has been challenged by unprecedented high and highly variable recruitment levels during the 1990s (ICES 2005a). Despite the wealth of studies on Baltic sprat biology, the mechanisms responsible for this recruitment variability are not yet sufficiently understood. As pointed out by Köster *et al.* (2003) and MacKenzie & Köster (2004), the size of the sprat spawning stock is only a poor predictor of the strength of new year classes, which entails that variable, environmentally influenced survival patterns during the pre-recruit stages are critical for recruitment determination.

*Baltic sprat year classes: Are they determined during the egg and early larval stage?*

Given that initial abundance and mortality rates are generally highest during the egg and early life stages of fish (Bailey & Houde, 1989; Houde, 1997a), small changes in relative survival have the highest potential to precipitate substantial fluctuations in the number of successful recruits (Houde, 1997b). This may be particularly true for marine fish species, which have generally a 45 times lower survival rate until metamorphosis than freshwater fish, leading Houde (1992) to conclude that processes acting during the early ontogenetic stages of marine fish may be most relevant for recruitment determination. Not surprisingly, thus, Baltic sprat recruitment research has focused to a large extent on processes acting during the egg and early larval stages.

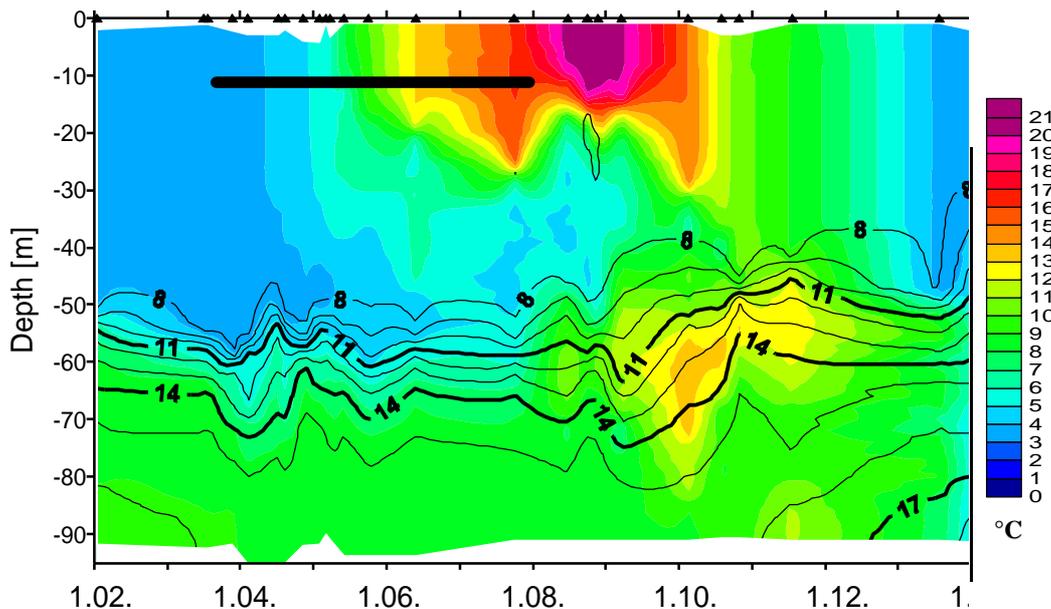


Fig.1: Seasonal development of water stratification patterns in 2002 in the Bornholm Basin. Colours and isolines refer to water temperature (°C) and salinity (psu), respectively (Graph produced by V. Mohrholz, IOW). The black line shows the extent of the average spawning season of Baltic sprat.

Baltic sprat is known to spawn over an extended period from March/April to July/August (Grimm & Herra 1984; Karasiova, 2002). Spawning takes place from the Kiel and Mecklenburg Bays in the west to the major basins in the central and eastern Baltic, the Arkona, Bornholm, and Gotland Basin and the Gdansk Deep (Grauman, 1975; Elwertowski, 1976; Sjöblom & Parmanne, 1976; Grauman & Krenkel, 1986). Because hydrographical conditions vary between Baltic regions as well as during the spawning season (Winsor *et al.*, 2001; MacKenzie *et al.*, 2002), sprat offspring are bound to experience a wide range of different environmental conditions due to differences in both the timing and the location of their production. Furthermore, the Baltic Sea is a highly stratified water body, with a permanent halocline at 50-75 m (Bornholm Basin, Fig. 1) separating a low salinity upper water layer from more saline waters at the bottom, the latter being renewed only by irregular inflow events of North Sea water into the Baltic proper (Wojewódzki, 1991). In spring and summer, i.e. during the spawning season of sprat, a thermocline develops at depths of about 20-30 m (Fig. 1), separating the cold, intermediate waters (also referred to as 'winter water') from the warmer surface layer. Sprat eggs are spawned in this surface layer but, due to their specific gravity, sink down to intermediate water depths (Wieland & Zuzarte, 1991) where they develop under substantially colder temperature conditions (Fig. 1). The potential importance of these vertical gradients in hydrographical conditions for sprat egg viability was emphasised by Nissling *et al.* (2003), who found that sprat eggs spawned in April had a higher specific gravity and would therefore develop in greater depths than later spawned eggs. In laboratory experiments, sprat eggs incubated at temperatures below 5°C were significantly less viable (Nissling, 2004), which led to the hypothesis that early spawning after cold winters could induce substantial egg and early larval mortality and therefore result in relatively weak year classes (Paramanne *et al.*, 1994). Other studies have corroborated the strong temperature influence by extending it to the spawning and even pre-spawning stock (Karasiova & Zezera, 2000; MacKenzie & Köster, 2004). Köster *et al.* (2003) noted that 63% of the variability in sprat egg production could be explained by 3 variables: spawning stock biomass (SSB), winter water temperature, and weight-at-age anomaly. In addition, the significant egg cannibalism by sprat, reported by Köster & Möllmann (2000) and increased egg mortalities due to high wind stress in summer (Grauman, 1965) have also been put forward as potential recruitment-relevant processes during the egg stage.

The problem, however, with all of these 'important' recruitment-determining processes affecting the spawning stock and the egg and early larval stages of Baltic sprat is that they have so very little to do with sprat recruitment variability. In other words, they may have a statistically significant influence but generally explain only small proportions of the overall variability (e.g. 27-30%, MacKenzie & Köster, 2004). Following Paulik's (1973) approach to examine the entire life history process for critical periods and relationships between successive life stages (Rothschild, 1986),

Köster *et al.* (2003) found that (1) SSB was closely related to egg abundance, that (2) egg abundance predicted larval abundance generally well, but that (3) larval abundance was unrelated to the number of age 0 recruits (Fig. 2). Given that sprat age 0 abundance was again a good predictor of age 1 recruitment (when fish become targeted by the commercial fishery), the authors concluded that the ‘critical’ recruitment-determining processes are likely to act during the larval and possibly even during the early juvenile

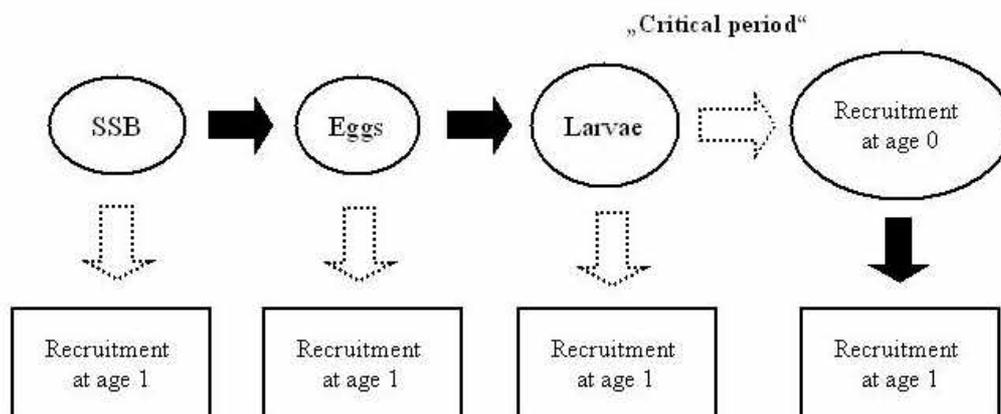


Fig.2: Schematic representation of Köster *et al.*'s (2003) correlation analyses between successive live stages of Baltic sprat. Black/empty arrows indicate that a strong/poor correlation, respectively, was found between the abundance of the different developmental stages.

stages of Baltic sprat.

Similar conclusions previously emerged out of analyses by Bradford (1992) and Leggett & Deblois (1994) who evaluated evidence for the hypothesis that recruitment levels in marine fish are established during the egg and early larval stages (a paradigm dating back to Johan Hjort's (1914) ‘critical period’ concept). Bradford (1992) summarized: “Recruitment is a complex process in which variation in all life stages contributes substantially to the variability in final abundance; therefore, researchers should recognize the importance of the later pre-recruit stages and the interactions among all stages.” Leggett & Deblois (1994) later remarked that a better “understanding of recruitment processes in fishes will clearly require a broader exploration of regulatory processes than has been common to date” and concluded further: “The link between recruitment and abundance/survival during pre-juvenile life stages of marine fishes is sufficiently well documented to justify a continued interest in factors regulating survival and abundance in the egg and larval stages. It should be noted, however, that processes operating during the post-larval stages can significantly moderate, and *may regulate recruitment* in some fishes”.

*Concepts of recruitment-regulation during the larval stage*

What are the processes that influence survival during the larval and post-larval stages of fish? The most general answer, i.e. that predation and starvation are the two major sources of larval fish mortality (Bailey & Houde, 1989; Heath, 1992), is also the least helpful one, given that both starvation and predation are often not directly observable in the field (Houde, 1978; Paradis & Pepin, 2001). “Thus, it may be difficult to establish which factors are influencing larval fish survival unless predation and starvation affect *measurable* characteristics of the survivors” (Pepin, 1989). Larval growth rates have always been regarded as one the most important of these characteristics, because they are thought to reflect an individual's survival probability (i.e. its susceptibility to predation/starvation, Houde, 1997b; Rilling & Houde, 1999) as well as the influence of the environment. The key role of growth as a potential survival criterion is emphasised by the number of growth-related, conceptual frameworks that have emerged over the last decades. The “bigger-is-better” hypothesis has focused on the fact that growth variability leads to size-at-age differences within a larval cohort, where larger individuals would be vulnerable to fewer predators and less susceptible to starvation. The “stage duration” hypothesis emphasised that faster growth of a larval cohort would result in lower cumulative mortalities, because the “high mortality period” would effectively be shorter (Houde, 1987; Sogard, 1997). As just another variation of these “growth-mortality” concepts, the “growth-selective predation” hypothesis pointed out that faster growing larvae may be able to escape predators better than slower growing conspecifics (Takasuka *et al.*, 2004). All three concepts have been used to explain the positive correlation between population growth rate and recruitment potential found, for example, in Atlantic cod (Meekan & Fortier, 1996), plaice *Pleuronectes platessa* (Hovenkamp, 1992), and some coral reef fish species (Bergenius *et al.*, 2002). However, it is noteworthy that field evidence is in some cases equivocal (Leggett & Deblois, 1994) and laboratory studies have even produced contrary results (e.g. Litvak & Leggett, 1992; Pepin *et al.*, 1992). For the juvenile stage, Sogard (1997) concluded that the available evidence generally supported the bigger-is-better hypothesis (e.g. Campana, 1996), with major size-selective processes encompassing overwinter mortality and predation. In addition, density-dependent processes may be more important during the juvenile than during the larval stage.

Growth rates of fish larvae are known to vary widely within any set of individuals sampled at the sea. There is a general consensus that this variability is a consequence of intrinsic factors, determining the growth potential of an individual larva, and environmental effects determining the actual outcome of this potential (Parma & Deriso, 1990). Ambient temperature comprises the most important abiotic growth determinant (Heath, 1992), and its significance for cohort survival and subsequent recruitment has been widely demonstrated (Limburg, 1996; Fowler & Jennings, 2003). Food availability

has been recognized as the most important biological agent governing growth in larval fish (Heath, 1992). Therefore, both abiotic and biotic factors are potentially relevant for recruitment variability, although fisheries ecologists have engaged in controversial debates regarding the relative importance of one over the other. The major concept linking food production in the sea to growth and thus recruitment variability has become known as the “match/mismatch hypothesis” (Cushing, 1974; Cushing, 1990), which states that the seasonal timing of fish offspring production has evolved to match the *average* seasonal phyto- and zooplankton peaks, whereby any environmentally induced shift in either fish or food production would lead to a mismatch situation and thus relative recruitment failure. Other feeding related theories, like Hjorts (1914) “critical period” and the “stable ocean hypothesis” (Lasker, 1981; Bakun & Parrish, 1982) can be regarded as special scenarios most relevant for first feeding larvae. The superior role of abiotic processes for recruitment determination was advocated by Iles & Sinclair’s (1982) “member/vagrant” and Cury & Roy’s (1989) “optimal environmental window” hypotheses, which proposed that ocean circulation/upwelling patterns need to retain larvae within areas of favourable conditions (or advect them into such areas) *and* have to guarantee cohort integrity in order to enable successful recruitment. However, both biological and physical processes are inextricably intertwined, and a better understanding of growth- and recruitment-relevant mechanisms likely requires a separate assessment of these factors for each species, developmental stage, and marine system (Sogard, 1997). In today’s fisheries science, there is an unmitigated interest in further exploring the specific sources of larval/juvenile fish growth variability.

#### *Otolith microstructure analysis*

Referring to somatic growth rates as a ‘measurable characteristic’ in larval and juvenile fish is – strictly speaking – wrong. To directly calculate growth, at least two subsequent size (or weight) measurements and knowledge of the time that has passed between these two measurements would be necessary. Larval fish in field samples, however, can usually be measured only once. To overcome this predicament, researchers have tried to estimate individual ages in a given sample in order to establish size-at-age relationships and then calculate mean population growth rates. Alternatively, they have identified a number of suitable growth *proxies*, such as condition factors (Ferron & Leggett, 1994), histological indices (Suthers, 1998), or RNA/DNA ratios (e.g. Buckley, 1984; Clemmesen & Doan, 1996). The most valuable growth proxies, however, have arguably been discovered in larval fish otoliths (Stevenson & Campana, 1992).

Otoliths are acellular, mineralised structures in a fish’s inner ear (vestibular system) and consist of calcium carbonate crystals (aragonite) embedded in a proteinaceous matrix (Carlstrom, 1963). Otoliths could be envisioned as ‘highly sensible measurement systems’ which aid a fish’s balance and hearing senses (Popper *et*

*al.*, 2005) and therefore need to grow continuously as a fish grows. The deposition of aragonite crystals, however, is discontinuous, resulting in translucent (calcium + protein) and opaque bands (protein only), together known as otolith increments. The daily nature of this increment formation has first been suggested by Panella (1971) and is now recognized as a widespread phenomenon in most marine and freshwater fishes (Campana & Neilson, 1985). The total count of all daily increments in an otolith yields a size-independent estimate of larval fish age and has been used extensively to infer larval/juvenile fish population growth rates from size-at-age relationships (e.g. Bolz & Lough, 1983; May & Jenkins, 1992). However, the true potential of otolith increments as a tool in larval/juvenile growth studies lays in the fact that otolith growth is strongly correlated to somatic growth (Stevenson & Campana, 1992). Therefore, and unlike all other available proxies, otolith microstructure analysis cannot only be used to infer

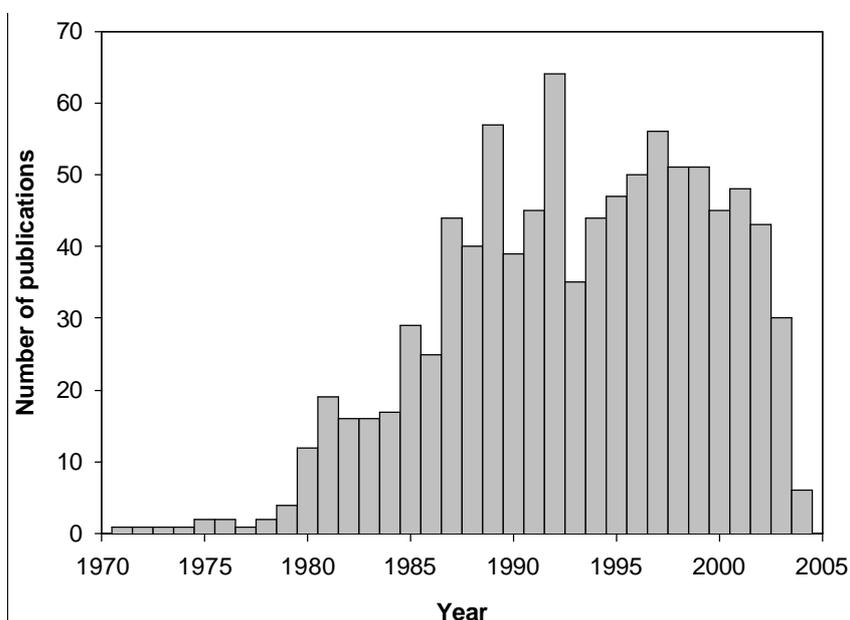


Fig.3: Number of published studies since 1971 using microstructure analysis in fish otoliths (Source: Aquatic Sciences & Fisheries Abstracts 2004)

recent growth rates, but also the entire growth *history* of an individual. Consequently, otolith microstructure analysis is now considered as one of the most powerful research tools in larval fish ecology and recruitment studies (Fig. 3). Not surprisingly, it has also played an important role in studies on larval sprat from the North and the Baltic Sea.

#### *Previous studies on larval sprat growth and feeding*

After the onset of exogenous feeding, the daily periodicity of otolith increment formation has been verified for sprat by Alshut (1988). In the North Sea, studies on otolith-derived growth patterns of larval sprat have often been conducted to test the hypothesis that growth (and thus survival probability) is promoted in the vicinity of frontal zones due to enhanced food availability. Munk (1993), for example, found that larval sprat growth increased from the stratified to the mixed side of a tidal front in the German Bight, with values ranging between  $0.28 - 0.49 \text{ mm}\cdot\text{d}^{-1}$  for 12 mm larvae and between  $0.12 - 0.45 \text{ mm}\cdot\text{d}^{-1}$  in the 16 mm length class. Similar values were reported by Shields ( $0.28 - 0.49 \text{ mm}\cdot\text{d}^{-1}$ , 1989), Ré & Gonçalves ( $0.41 \text{ mm}\cdot\text{d}^{-1}$ , 1993), and

Valenzuela & Vargas (0.36 – 0.40 mm·d<sup>-1</sup>, 2002), although the latter two were unable to detect significant growth differences across fronts. Laboratory calibration at 15°C on first-feeding North Sea sprat larvae resulted in daily growth rates of 0.31 – 0.37 mm·d<sup>-1</sup> (Alshut, 1988). In the Baltic Sea, larval sprat growth rates have been studied in the field by Dänhardt *et al.* (submitted), Reglero (2004), and Kamal (2004), resulting in a similar range in growth rates (0.2 – 0.46 mm mm·d<sup>-1</sup>). Feeding patterns of larval Baltic sprat were investigated by Voss *et al.* (2003) and Dickmann *et al.* (submitted), who found that larvae fed primarily on different developmental stages of *Acartia* spp. and *Temora longicornis* copepods and also appear to rely on cladocerans as an important additional food source. Voss *et al.* (2003) suggested that the pronounced increase in *Acartia* and *Temora* standing stocks in the Baltic since the 1980s could have contributed to the observed increase in sprat stock abundance.

#### *Why study recruits?*

Given that the vast majority of fish die before reaching the juvenile stage (>95%, Fuiman, 2002) and assuming non-random early life mortality, an inherent constraint of all larval studies is that *average* characteristics (e.g. growth rate, hatch-date, etc.) are highly unlikely to reflect the small group of survivors that eventually manage to recruit into the adult population (Miller *et al.*, 1988). Thus, in order to recognize traits that characterise predominantly those individuals with a higher survival probability, it may be necessary to describe such traits first in samples of successful survivors. In the case of Baltic sprat and for the purpose of the present thesis, survivors are considered those individuals that have joined the adult stock at the end of their initial year, which coincides with the time when the ‘Baltic International Acoustic Survey’ first estimates sprat recruitment strength in the Baltic Sea (ICES 2005c). Throughout this work, survivors are also referred to as recruits, young-of-the-year (YoY), 0-group, or age 0 sprat. Otolith microstructure analysis comprised an appropriate tool to estimate the temporal origin and describe growth patterns of Baltic YoY-sprat, thereby providing information that has not been available so far but may aid in better understanding Baltic sprat recruitment variability.

#### *Specific goals of the thesis*

1. The temporal origin of sprat recruits

Given the extended spawning season of Baltic sprat and the temporal variability in environmental conditions, one fundamental question is whether survival probabilities are seasonally invariant or whether recruits may predominantly be produced during specific ‘survival windows’. To resolve this, the temporal origin of newly recruited sprat has to be determined. An indirect approach to this question was used by Reglero *et al.* (in press) who first established a relationship between otolith increment widths and temperature for sprat larvae during the season 1999. This relationship was then applied

to predict the temperature experienced during the larval stage in age 1 individuals of 3 year classes (1997-1999) and to infer the ‘date of first increment formation’ by finding the time where predicted and observed temperatures were most similar. However, a direct back-calculation of recruit hatch-date distributions from otolith microstructure may yield more precise estimates, but has not been conducted before. Thus, in **paper 1**, **paper 2**, and **paper 4** the “day of first feeding” (DFF, the best available proxy for hatch day) was estimated based on the number of daily increments in sagittal otoliths of YoY-sprat. **Paper 1** focuses on individuals caught in October 2002 in the central Baltic Sea (ICES sub-division 25, Bornholm Basin), because this area was covered extensively in 2002 by the German-GLOBEC survey programme, monitoring the seasonal abundance of sprat eggs and larvae and their prey (**paper 6**). In the **conclusions** of this thesis, the findings of **paper 1** and **paper 6** are compared to infer the “window of survival” for YoY-sprat in 2002 and to identify potential processes responsible for this outcome.

In **paper 2**, the ‘otolith approach’ has been broadened to encompass YoY-recruits from the entire Baltic Sea. Previous studies have shown that large-scale spatial differences in spawning patterns and sprat morphology exist in the Baltic Sea, possibly induced by spatially different environmental conditions (Aps *et al.*, 1988; Shvetsov *et al.*, 1992; Grygiel, 1999). In order to better understand the sources of this spatial variability, the DFF-distributions of YoY-survivors in 2002 were described for 4 broadly defined Baltic regions (i.e. western, central, eastern, north-eastern Baltic).

## 2. Linking growth to temperature histories

Because the width of an otolith increment closely reflects the somatic growth rate on a given day, otolith growth trajectories (i.e. the series of increment widths-at-age) allow to infer the somatic growth history of an individual. However, in order to understand how growth histories are influenced by environmental variability, it is necessary to approximate the *environmental histories* of the individuals, too, and link them to the observed growth patterns. Given that temperature comprises the most important, abiotic growth factor, temperature-dependent growth patterns of YoY-recruits were investigated in this thesis by three different approaches. In **paper 1**, the temperature experience of YoY-sprat was estimated by means of a hydrodynamic circulation model of the Baltic Sea (see below), which provided a high temporal resolution of experienced temperature (day) and accounted for average transport patterns of sprat larvae. In **paper 2**, a larger spatial but temporally coarser approach was tested, by estimating the temperature histories of YoY-survivors from weekly means of satellite-based sea surface temperatures in the different Baltic areas. This facilitated conclusions on the general form of the temperature-dependence of somatic growth patterns over the entire pre-recruit age range. Finally, in **paper 3**, an extensive data set was obtained from the ICES Oceanographic database to derive month- and depth-specific temperature means for a time-series of 30 years (1974-2003). In combination

with the time-series of sprat age 0 abundance (ICES, 2005a), this approach produced new insights when and where (vertically) during the season temperature has the strongest impact on recruitment variability.

### 3. Feeding

Food availability is undoubtedly the most important biological factor controlling growth rates in fish (Heath, 1992). However, unlike temperature, prey availability is likely to act on much smaller temporal and spatial scales (patchiness), which have yet to be adequately sampled or appropriately modelled (Pepin et al. 2003). Ongoing research activities within the GLOBEC-Germany project currently attempt to construct modelled prey fields for Baltic sprat larvae in 2002, which may then be used to infer the feeding history of larvae or possibly even YoY-recruits. However, these data are not available yet and could therefore not be used in the present thesis. In addition, feeding-related growth variability is usually tightly coupled to temperature-related processes, which makes it difficult to disentangle both effects in the growth trajectories of field sampled individuals. It may therefore be necessary to study the effect of different feeding regimes first under laboratory conditions, where temperature can be controlled. In **paper 4** and **paper 5**, this approach was adopted to investigate the influence of different food levels on the growth of sprat post-larvae and early juveniles. As pointed out before, processes acting during the late pre-recruit stages may be of particular importance for sprat recruitment determination, yet these late stages have not been studied before in Baltic sprat. In **paper 5**, two main questions were addressed. First, how do somatic growth rates of post-larval sprat react to different and abruptly changing feeding conditions? As a second objective, experimental data were used to investigate the general correlation of otolith and somatic growth in post-larval sprat and to test potential scenarios that could lead to a disruption of this relationship. In **paper 4**, the field growth rates of post-larval sprat, sampled at the end of August 2003, were combined with those from the laboratory and compared to growth trajectories of similarly old, prospective YoY-recruits that were sampled later in October 2003. This produced new insights, how density-dependent food limitation during the post-larval and early juvenile stage of Baltic sprat may influence recruitment variability. In **paper 6**, the importance of food abundance and prey composition for early and late larval sprat survival was addressed. For sprat larvae that were sampled between April and July 2002 in the Bornholm Basin, an estimated survival index was related to the seasonal variability in stage-resolved *Acartia* and *Temora* copepod abundance (**paper 6**), while larval condition was assessed by means of RNA:DNA ratios.

### 4. Transport

The initially poor swimming abilities of pelagic fish larvae entail that they are susceptible to variable ocean circulation patterns, which do not only determine the spatial distribution of a larval cohort but also potentially influence the environmental conditions the larvae experience. Researchers have therefore emphasised that larval/juvenile growth histories may only be appropriately linked to environmental histories, if the *advective* history of the studied individuals is considered, too. Due to the considerable advances made in predicting ocean circulation patterns, reliable hydrodynamic models have been developed for many marine systems and now comprise an invaluable tool in fisheries research. For example, hydrodynamic modelling has been used successfully to identify spawning and nursery grounds (e.g. Allain *et al.*, 2003, Hinrichsen *et al.*, 2003), to develop coupled bio-physical individual based models (IBM's, e.g. Werner *et al.*, 1996; Hinrichsen *et al.*, 2002), or to reconstruct daily environmental histories at the level of individual fish (e.g. Baumann *et al.*, 2003).

The Baltic circulation model by Lehmann (1995) and Lehmann & Hinrichsen (2000) has played a key role in the present thesis, and was applied in various ways in 4 out of 7 papers. In **paper 1**, the average advective history of YoY-recruits was modelled by means of Lagrangian particle simulations, thereby enabling daily temperature estimates to be linked with the growth histories of YoY-recruits from the central Baltic Sea. In **paper 3**, the transport patterns of larval/juvenile sprat from the entire Baltic were modelled for an extensive time series of 25 years to determine their potential importance for sprat recruitment variability. In **paper 6**, hydrodynamic modelling was applied to correct larval mortality estimates by accounting for potential advective losses out of the study area (Bornholm Basin). Finally, in **paper 7**, the long-term Lagrangian simulations were used to address the question, to what degree sprat larvae produced in different areas of the Baltic Sea are likely to mix, which has important implications for the current understanding of Baltic sprat stock separation. Furthermore, by demonstrating the utility and the limitations of transport modelling, the results in **paper 7** also comprise a necessary pre-requisite for appropriately inferring the advective history of YoY-recruits.

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## General introduction

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

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**- PAPER 1 -**

**LINKING GROWTH- TO ENVIRONMENTAL HISTORIES IN CENTRAL BALTIC  
YOUNG-OF-THE-YEAR SPRAT, *SPRATTUS SPRATTUS*: AN APPROACH BASED  
ON OTOLITH MICROSTRUCTURE ANALYSIS AND HYDRODYNAMIC  
MODELLING**

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**ABSTRACT**

Otolith microstructure analysis and hydrodynamic modelling were combined to study growth patterns in young-of-the-year (YoY) sprat, *Sprattus sprattus*, which were sampled in October 2002 in the central Baltic Sea. The observed “window of survival”, approximated by the distribution of back-calculated days-of-first-feeding (DFF), was narrow compared to the extended spawning season of sprat in the Baltic Sea (mean±SD = 22 June±14.1d) and indicated that only individuals born in summer survived until October 2002. Within the group of survivors, individuals born later in the season exhibited faster larval, but more rapidly decreasing juvenile growth rates than earlier born conspecifics. Back-calculated *larval* growth rates of survivors (0.48 – 0.69 mm day<sup>-1</sup>) were notably higher than those previously reported for average larval sprat populations, suggesting that the YoY-population was predominantly comprised of individuals which grew fast during the larval stage. Daily mean temperatures, experienced across the entire YoY-population, were derived from Lagrangian particle simulations and correlated to (1) detrended otolith growth and (2) back-calculated, daily somatic growth rates of survivors. The results showed that abrupt changes in ambient temperature can be detected in the seasonal pattern of otolith growth, and that higher temperatures led to significantly faster growth throughout the entire age-range of YoY-sprat.

**Key words: Baltic sprat, otolith microstructure analysis, young-of-the-year, hydrodynamic modelling, temperature-dependent growth**

## INTRODUCTION

The Baltic sprat, *Sprattus sprattus*, has become the most abundant, commercially exploited fish species in the Baltic Sea (ICES, 2004). Over the past decade, not only absolute recruitment strengths but also inter-annual recruitment variability have reached historically high levels (ICES, 2004). While the positive trend in sprat stock abundance is generally explained by a regime shift from a cod-dominated to a clupeid-dominated system (Köster *et al.*, 2003), the recent, strong fluctuations in recruitment success remain insufficiently understood.

Previous field studies in the Baltic Sea have investigated the sprat egg and larval stages (e.g. Voss, 2002; Nissling *et al.*, 2003), because they are considered critical for recruitment variability (Köster *et al.*, 2003; MacKenzie and Köster, 2004). However, an inherent limitation of larval studies is that average characteristics (e.g. growth rate, hatch date) are unlikely to reflect the small fraction of individuals that will eventually survive until recruitment (Sharp, 1987). Therefore, a better understanding of processes influential to sprat recruitment may require complementary studies that describe characteristic traits in successful sprat recruits.

Otolith microstructure analysis is a promising tool to accomplish this, as it provides a wealth of information about present and past characteristics in larval and juvenile fish (Stevenson and Campana, 1992). Its two pre-requisite assumptions, daily periodicity of increment deposition and coupled otolith and somatic growth, have been confirmed for sprat, at least after the onset of exogenous feeding (Alshut, 1988; Shields, 1989). Yolk-sac sprat larvae, on the other hand, appear not to deposit regular micro-increments. Thus, for sprat survivors, otolith microstructure analysis can be used to back-calculate the day of first feeding as a proxy for hatch-day (Valenzuela and Vargas, 2002) and to reconstruct age- and day-specific histories of otolith growth as a proxy for somatic growth. These data may later serve as a basis for comparing characteristics of survivors with those of non-survivors sampled earlier in the season (e.g. Allain *et al.*, 2003).

The present paper focuses on sprat survivors that were caught in October 2002 as young-of-the-year (YoY) or 0-group individuals in the Bornholm Basin and adjacent coastal areas (Fig. 1). The Bornholm Basin has been shown to be an important spawning ground for sprat in the central Baltic (Köster *et al.*, 2001), where the spawning season usually extends from March to August (Elwertowski, 1960). Sprat eggs and newly hatched larvae develop in intermediate water depths of 45-65 m (Wieland and Zuzarte, 1991), whereas feeding sprat larvae typically occur in surface waters (Voss, 2002). Depending on the circulation pattern, larvae and juveniles may either be retained in the basin or advected into shallower nursery grounds, where they likely stay until the end of the growing season. Later, YoY-sprat are thought to join adult schools during their overwintering migration into the deep basins (ICES, 2004).

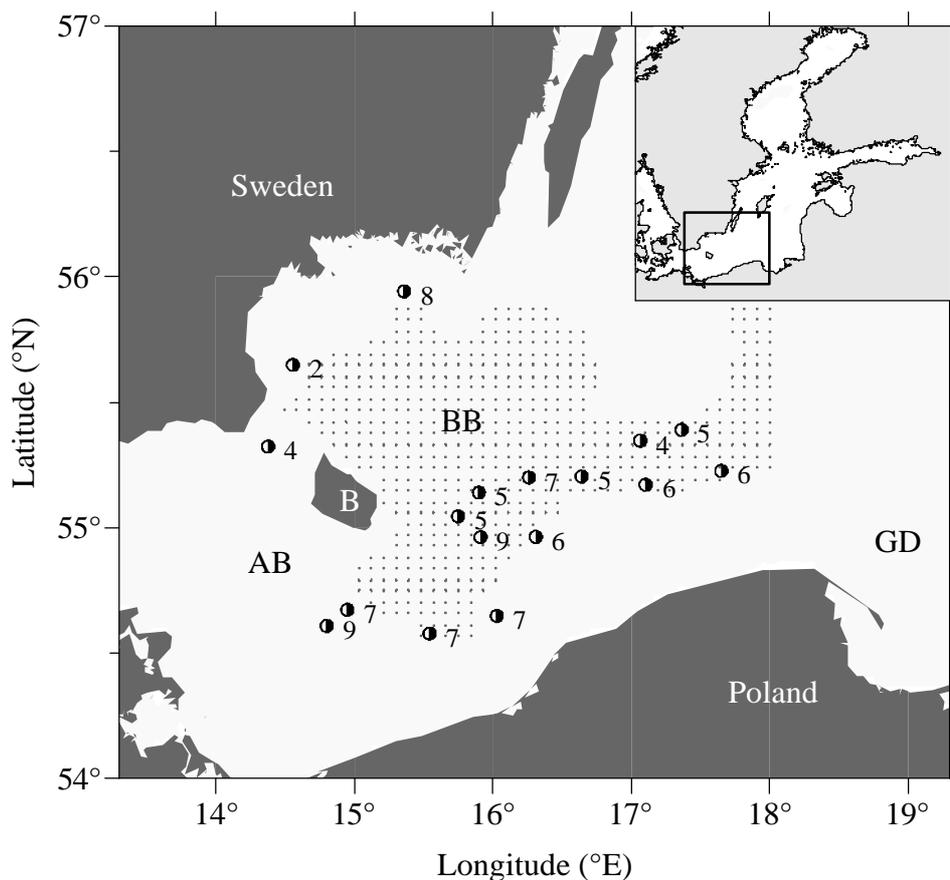


Fig. 1: Study area with bathymetry shading (inlay Baltic Sea) and positions of YoY-sampling sites between 7.-23.10.2002. Numbers refer to otoliths randomly selected for analysis. Grey dots show seeding positions of 618 Lagrangian drifters used in the hydrodynamic circulation model. AB = Arkona Basin, B = Bornholm Island, BB = Bornholm Basin, GD = Gdansk Deep

One of the main factors influencing growth and survival of larval and juvenile fish is ambient temperature (Heath, 1992). Given the extended spawning season of sprat, it is likely that fish hatching at different times of the year will experience considerably different temperature conditions. To understand how temperature affected the past growth of survivors, it is necessary to reconstruct their temperature histories and link them to growth patterns inferred from otolith microstructure analysis. The most obvious approach, i.e. taking direct temperature measurements from field surveys, is typically hampered by the relatively low temporal resolution of survey data and the uncertainty about the spatial distribution of individuals at a given time.

An alternative approach is to use a realistic hydrodynamic circulation model, where the average drift of larval and juvenile cohorts is simulated by means of passive Lagrangian particles seeded into the model domain. Apart from the spatial distribution, such models are also able to provide temperature data associated to particles on a daily (or even hourly) basis. Lagrangian studies have been used successfully to identify spawning and nursery grounds (e.g. Allain *et al.*, 2003, Hinrichsen *et al.*, 2003), to develop coupled bio-physical IBM's (e.g. Werner *et al.*, 1996), or to reconstruct daily environmental histories at the level of individual fish (e.g. Baumann *et al.*, 2003). In the

present approach, however, Lagrangian particles are not used to investigate individual drift patterns but to derive a spatially integrated, average index of daily temperature conditions, which the majority of survivors potentially experienced throughout their first months of life.

By applying these approaches, the main goals of this study were first to determine the potential “window of survival” for YoY-sprat in 2002 based on the back-calculated dates of first feeding, and secondly, to combine otolith analysis with hydrodynamic modelling in order to describe environmentally influenced changes in the growth of survivors.

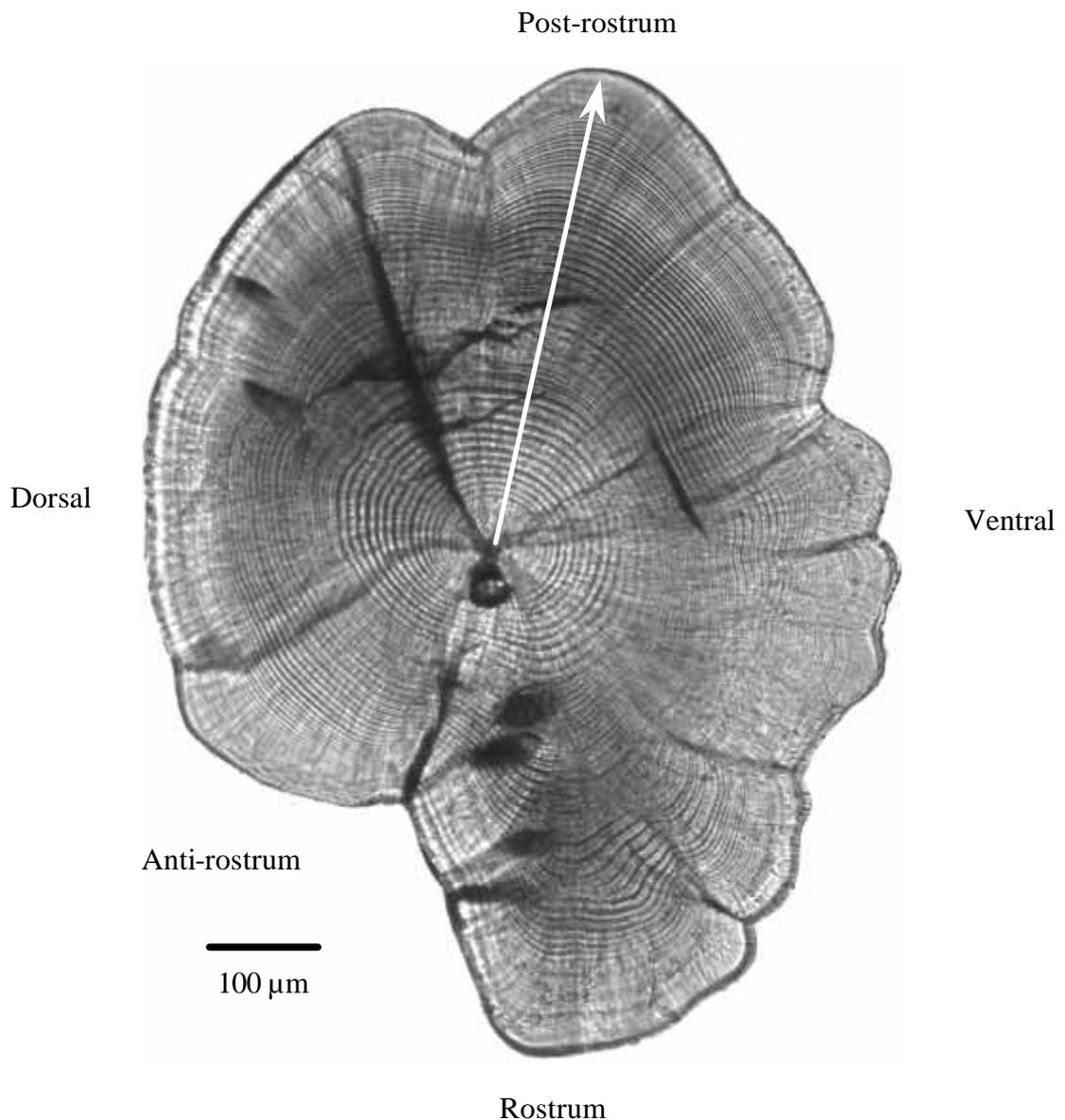


Fig.2: Polished sagittal otolith of a juvenile sprat aged 84 days after first feeding (DFF). All increments were counted and measured along the same axis from core to post-rostrum (arrow).

## MATERIAL AND METHODS

### *Field sampling and otolith analysis*

Young-of-the-year sprat were sampled in October 2002 from two research vessels participating in the annual Baltic International Acoustic Surveys (BIAS). From 18 - 23 October 2002, 15 hauls were conducted by the RV “Baltica” (Poland) in central and southern parts of the Bornholm Basin (Fig. 1) using a standard pelagic trawl net with a 22 mm mesh opening in the cod end. On 7 and 8 October 2002, three hauls with catches of YoY-sprat were conducted by the RV “Argos” (Sweden) in northern areas of the Bornholm Basin (Fig. 1) using a similar trawl type. From each haul, up to 20 YoY-sprat were randomly selected and immediately preserved in 95% ethanol. The preservative was replaced approximately three weeks after sampling.

Prior to otolith extraction, sprat were individually measured (nearest mm) for total (*TL*) and standard length (*SL*) and assigned a unique identification number. From each specimen, both sagittal otoliths were removed and mounted individually on microscopic slides with a drop of Crystal Bond® thermoplastic glue. All otoliths were subsequently ground from one side and, after re-heating and repositioning, from the other side with a 3 µm lapping film (266x Imperial PSA 3M®) until all increments were sufficiently visible. Irrespective of left or right, the otolith with the most distinct increments was chosen for analysis. Measurements took place under 400x magnification with a digital camera (Leica®DC300, 3132 x 2328 pixels) connected to an image analysis system (ImagePro Plus 4.5.1) allowing for a theoretical resolution of 0.078 µm pixel<sup>-1</sup>. All increments were measured along the same axis from core to postrostrum of the otolith (Fig. 2). Depending on the size of the otolith, this axis was covered by up to four consecutive and overlapping image sections. Each section was photographed 4-7 times in different focal planes that were later merged into a single multi-frame image. Multi-frame images (.tiffs by default) are simple but effective means to digitally “focus” through an otolith’s microstructure during measurements, which generally improved the confidence of interpretation. During measurements, the reader also judged the quality of each interpreted otolith section according to a scale from 1 (best) to 5 (worst), and the worst nine otoliths (~10%) were later excluded from the analysis.

A subset of 48 randomly selected otoliths was read twice by the same reader to estimate precision using the coefficient of variation (*CV*) method (Campana, 2001). Mean *CV* across all re-read fish was 2.7%, and 10 specimens were later excluded because age estimates differed by more than 5% from the mean. When available, the second reading was always preferred over the first, assuming a learning curve. In total, 102 out of 121 read otoliths were used in the analysis. Precision in increment counts was also assessed between two experienced but independent readers on another otolith subset, which consisted of sprat juveniles caught at various occasions and stages (n=18). The significant linear regression (P<0.001) between the two readings explained 94% of

the overall variability and had a slope of 0.92, which was not significantly different from 1 (95%-confidence = 0.8 – 1.04). The mean CV across all independently read fish was 4.2%.

In the majority of YoY-otoliths, a pronounced shift from weak and indistinct to sharp and well defined increments was typically observed after the innermost 4 increments (see results). This shift was assumed to correspond to the transition from non-daily increment formation during the yolk-sac stage to daily increments deposited after the onset of first-feeding, and only the latter increments were included in the analysis. Therefore, otolith-derived age estimates presented in this study refer to individual ages in days after first feeding (DFF).

Daily somatic growth rates (*SGR*) of YoY-sprat were derived from individually back-calculated lengths-at-age estimated with the “biological intercept method” (Campana, 1990), where the otolith radius at first feeding corresponded to the distance between the core and the 4<sup>th</sup> increment. For the standard length at first feeding a value of 5 mm was assumed, based on Voss *et al.* (2003) who found prey in the guts of 4-6 mm sprat larvae from the Bornholm Basin. The biological intercept method is independent of the slope in the otolith-fish size regression, but assumes linearity in individual otolith-fish size trajectories (Campana 1990).

Because the mean and the variance of increment widths vary with age (Pepin *et al.*, 2001), we used age-detrended otolith data to analyse seasonal patterns in otolith growth of the entire YoY-population. Individual increment widths were standardized to zero mean and unit deviation as in Baumann *et al.* (2003) and represent the daily growth anomaly of a specimen at a given age relative to the population.

### *Hydrodynamic model*

Likely experienced temperatures of YoY-survivors were derived from the Baltic Sea circulation model of Lehmann (1995) and Lehmann and Hinrichsen (2000), which is based upon a free surface Bryan-Cox-Semtner model (Killworth *et al.*, 1991). The model domain encompasses the entire Baltic Sea with a realistic bottom topography. The horizontal resolution is 5 km, a value corresponding to approximately half the internal Rossby radius in the Baltic Sea (Fennel, 1991), which is necessary to fully resolve mesoscale motions (e.g. eddies). 60 vertical levels are specified with a thickness chosen to best represent the different sill depths in the Baltic Sea. The model was initialized in 1979 with mean temperature and salinity fields and forced by actual meteorological data, available at the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping) for a time-series of 24 years (1979-2002). Simulated 3-dimensional velocity fields extracted from the circulation model were then used to derive drift routes of Lagrangian particles seeded into the model domain. Along these trajectories, the model provided temperature data for particles at 6 hour time steps.

Particles were released into the model to simulate the average temperature history of the YoY-population from the day of first feeding (DFF) until catch in October 2002. Important assumptions of the approach include that all survivors caught in and around the Bornholm Basin originated from this area, and that integrated particle drifts were reflective of the average transport pattern experienced by the YoY-cohorts, at least on a broad spatial scale. All particles were released inside the 40m isobath of the Bornholm Basin (Fig. 1), based on average sprat egg distributions (Köster, 1994) that were assumed a proxy for the spatial distribution of first feeding sprat larvae. All drifters were seeded and forced to remain within the 5-10 m depth layer, because feeding sprat larvae predominantly occur in surface waters and appear not to migrate vertically (Voss, 2002; STORE, 2003). Five particle cohorts were released between 31 May (day 151) and 10 July 2002 (day 191), corresponding to the DFF-distribution of YoY-survivors that was back-calculated from otoliths (see results). Each of these 5 larval ‘pulses’ consisted of 618 particles, which were seeded in regular spatial intervals of about 5 km. Depending on the seeding date, drifters were tracked through the model domain for a period of 105-145 days, until all positions were finally recorded on 23 October (day 296). For each release date, likely experienced temperature was estimated as the daily mean across all 618 particles, irrespective of individual horizontal positions in the model domain. The obtained five temperature curves, however, were not significantly different between drifter cohorts 1-3 (released 31 May, 10, and 20 June,  $P=0.145$ ) and 4-5 (released 30 June, 10 July,  $P=0.53$ ) and were therefore pooled. The average daily standard deviation of temperature across all 618 particles was  $1.1^{\circ}\text{C}$ .

Daily temperatures were assigned to daily back-calculated *SGR*'s of individuals according to their age after DFF. All individuals with DFF's prior to 30 June were assigned to temperatures from averaged particle runs 1-3, whereas all other specimens were related to particle simulations 4-5. For example, *SGR* on day 30 of an individual with DFF on 25 June was assigned to temperature on 25 July, taken from averaged particle cohorts 1-3. It should be noted that daily modelled temperatures have the character of an index, which is assumed to reflect the temporal but not the spatial variability in environmental conditions experienced by YoY-sprat from the Bornholm Basin. A back-tracking of individual fish from catch to the day of first feeding in order to resolve the spatial differences was not attempted, given the size and age of YoY-sprat in October 2002 ( $>7.5$  cm TL, see results).

## RESULTS

### *Age, length, and growth of YoY-survivors*

In October 2002, YoY-sprat formed a distinct peak in the length distribution of trawl catches with highest frequencies occurring in the 9 – 9.5 cm TL class (Fig. 3). Age

1+ sprat were clearly recognizable by lengths exceeding 11 cm TL. Abundance of YoY-sprat was high only in southern parts of the Bornholm Basin, in contrast to trawls in northern areas containing very few individuals <11 cm TL (Fig. 3). Because length frequencies of YoY-sprat selected for otolith analysis compared well to catch length distributions (mean±SD TL<sub>oto</sub> = 9.23±0.48 cm, mean±SD TL<sub>trawl</sub> = 9.17±0.46 cm, P = 0.18), the analysed sub-sample was considered representative for YoY-sprat caught in October 2002 (Fig. 3).

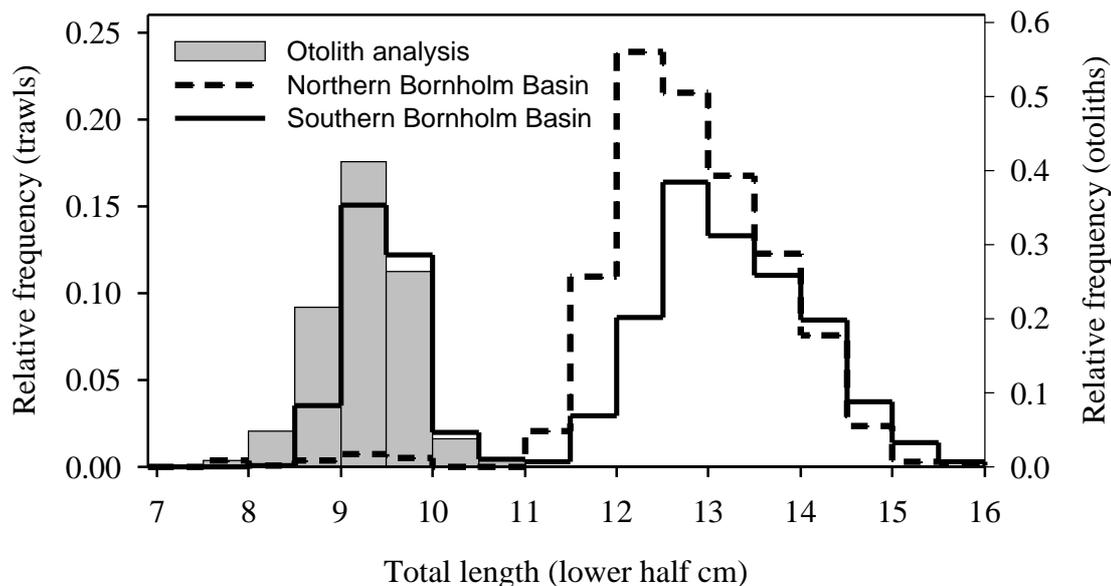


Fig.3: Comparison of sprat length distributions between trawl catches done by the RV "Baltica" in the southern half of the Bornholm Basin (15 hauls, 18 - 23.10.02) and those done by RV "Argos" in the North (3 hauls, 7 - 8.10.02) and of YoY-sprat selected for otolith microstructure analysis.

After grinding and polishing, daily otoliths increments could be identified relatively well (e.g. Fig. 2), although certainty of interpretation differed along the measurement axis. First increments were found at a distance between 5-9  $\mu\text{m}$  from the core (mean±SD = 7.9±1.17  $\mu\text{m}$ ), usually after an iridescent check-mark that possibly corresponded to the hatch day. This check was typically followed by four (range 3-5) weak and indistinct structures, after which a pronounced shift occurred to clear and unambiguous increments that were interpreted as daily rings formed after the onset of exogenous feeding. These increments increased rapidly in width and were broadest between 25-55 days after DFF with mean±SD widths of 7.9±1.25  $\mu\text{m}$ , followed by steadily decreasing increment widths until sampling in October. Mean width±SD of the last 3 full increments prior to catch was 1.6±0.55  $\mu\text{m}$  (Fig. 4).

Mean±SD age of YoY-sprat was 119±14.1 days after DFF corresponding to a mean date of first feeding on 22 June 2002 (Fig. 4). Mean DFF's were not significantly different between individuals sampled in northern and southern areas of the Bornholm Basin (DFF±SD<sub>north</sub> = 24 June±16.5 d, DFF±SD<sub>south</sub> = 21 June±12.1 d, P=0.38). Within the limited age and length range sampled, significant linear relationships (P<0.01,

n=102) were found for age vs. length ( $TL=0.26+61.5 \text{ age}$ ,  $R^2=0.59$ ) and mean somatic vs. mean otolith growth, estimated as the average increase in  $SL$  ( $SG$ ) and otolith radius ( $OG$ ) per day ( $SG_{SL} = 0.12+0.10 \text{ OG}$ ,  $R^2=0.70$ ). Residuals of the latter relationship did not show significant deviations from linearity, indicating an isometric otolith size – fish size relationship.

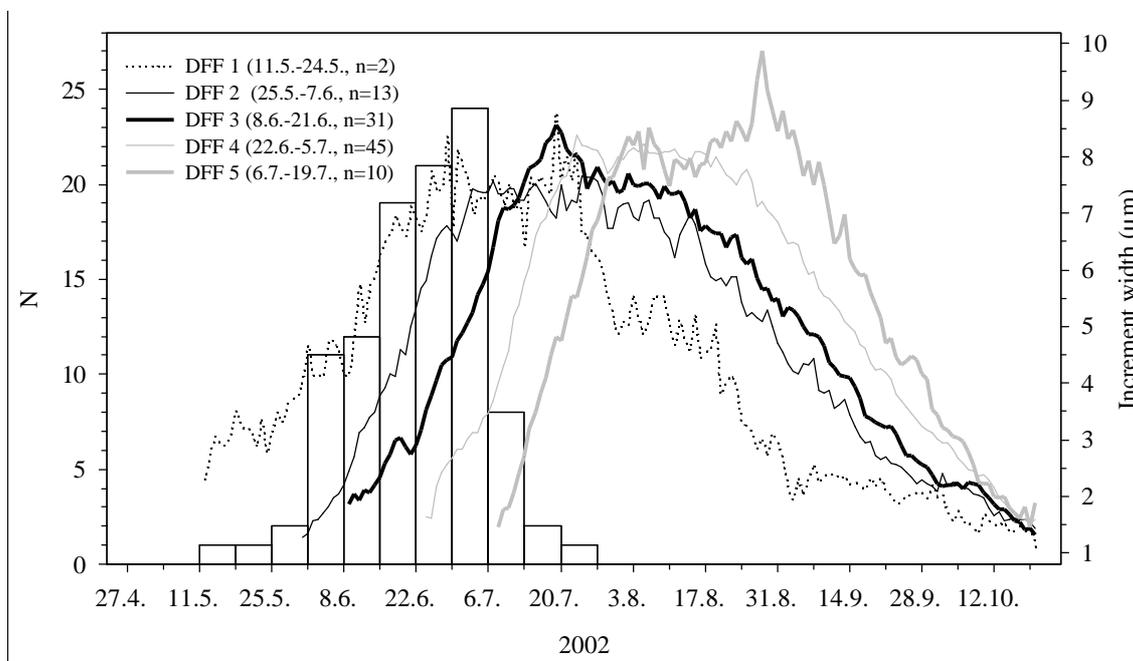


Fig.4: Distribution of back-calculated dates-of-first-feeding (DFF) for YoY-sprat caught in October 2002 in the central Baltic Sea (bars) and mean increment widths of these survivors grouped into 5 fortnightly periods (lines).

When split into 5 cohorts of fortnightly DFF intervals (Fig. 4), YoY-survivors showed markedly different patterns of otolith growth. During the first 25 days after DFF (assumed to correspond to the larval stage), increments of individuals born later in the season increased more rapidly in width than those of earlier born conspecifics. As juveniles, later born YoY's showed more rapidly decreasing increment widths compared to earlier born individuals (Fig. 4). Significant differences in increment width between DFF-cohorts 2 and 5 (25 May – 7 June and 6 July – 19 July, respectively) were found for ages 4 – 27, 42-50, and >74 days after DFF (1-way ANOVA per increment,  $P<0.05$ ). Later born survivors also tended to have greater maximum increment widths than earlier born individuals (Fig. 4).

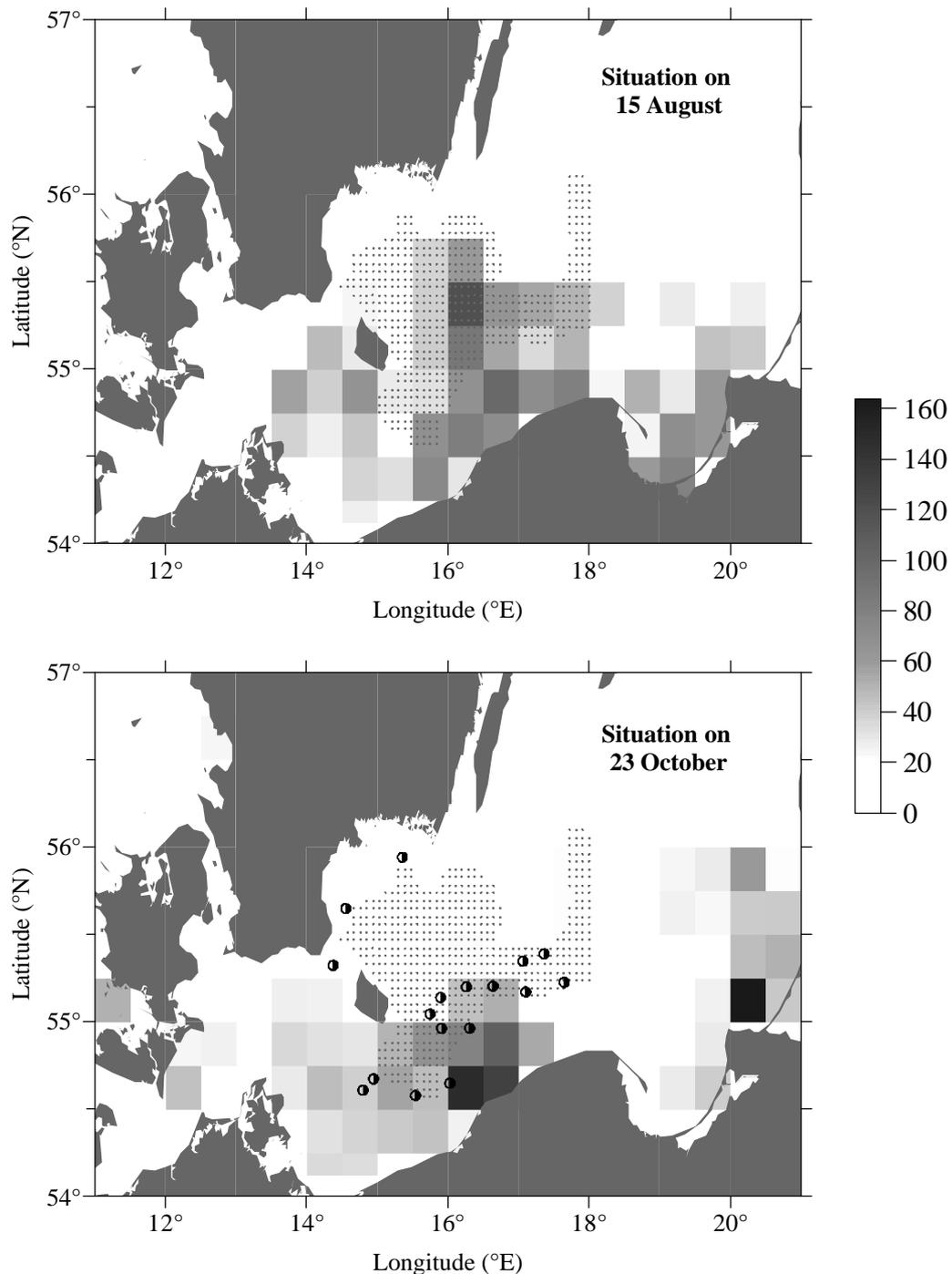


Fig.5: Possible horizontal distribution of sprat larvae and juveniles on a) 15 August and b) 23 October 2002, as inferred from Lagrangian simulations. 5 cohorts of particles were released during the main window of survival (31 May – 10 July 2002). Shading corresponds to the number of particles collected in each 15x15 nautical miles rectangle. Small dots depict particle seeding positions (see also Fig. 1), whereas half-filled circles in the lower panel show YoY sampling sites in October 2002.

Corresponding to the rapid initial increase in increment width, average *SGR* ( $\pm$ SD) across all survivors increased from  $0.23 \pm 0.07$  mm day<sup>-1</sup> on day 1 to  $0.92 \pm 0.17$  mm day<sup>-1</sup> on day 25 after DFF, respectively. Mean *SGR* over the first 25 days after DFF increased significantly from  $0.48$  mm day<sup>-1</sup> for earliest born survivors to  $0.69$  mm day<sup>-1</sup> in the latest DFF-interval (1-way ANOVA, DFF2 vs. DFF5,  $P < 0.05$ ). Highest mean

SGR ( $\pm$ SD) was found on day 29 after DFF with  $0.97\pm 0.19$  mm day<sup>-1</sup>, a value corresponding to an increment width of 8.2  $\mu$ m.

*Otolith growth in relation to temperature*

Drifter positions on 15 August 2002 indicated that most sprat larvae would either have been retained in the spawning area or advected towards the Polish shore, while only minor proportions of larvae would have ended in adjacent basins (Fig. 5a). This general pattern was also apparent after the entire simulation period, although on 23 October a considerable proportion (< 20%) of Bornholm seeded drifters was found in eastern areas of the Gdansk Deep (Fig. 5b). The displacement was strongest (27%) for the first release date (31 May), which would represent only the small fraction of earliest born survivors.

Mean temperatures associated to drifters in 5-10 m varied between 12 – 14 °C in June and increased between 1 – 21 July to values of about 17 °C (Fig. 6). Starting on 22

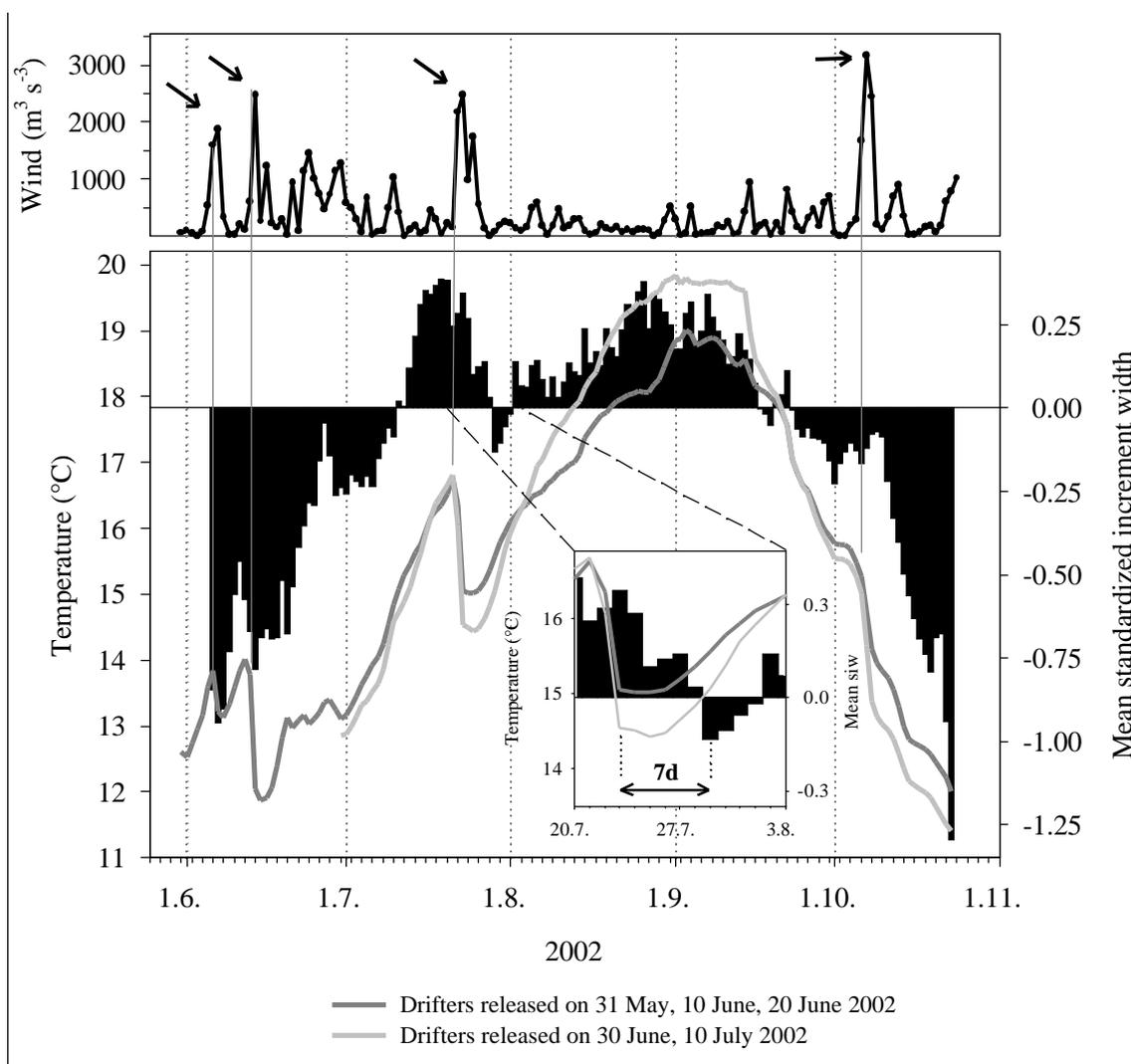


Fig.6: Mean standardized increment widths per date of increment formation (bars) in relation to likely experienced temperature (dark and light gray lines), estimated from Lagrangian particle simulations. Daily winds (black line) over the Bornholm Basin are given in the upper panel with arrows demarking major storm events in summer and autumn 2002. The inlay depicts the period of the sudden temperature drop and the delayed response in otolith growth.

July, temperatures sharply decreased again by 2°C, possibly caused by turbulent mixing due to a storm that was recorded on 22 – 25 July with wind speeds of 10-14 m s<sup>-1</sup> (Fig. 6). After 25 July, temperatures steadily increased again and reached maximum values of 19.0°C (drifter cohorts 1-3) and 19.8°C (drifter cohorts 4-5) during the first week in September. Surface temperatures rapidly declined thereafter to about 12°C on 23 October, the date of the last YoY-sampling in 2002.

The seasonal pattern of detrended otolith growth across the entire YoY population appeared to be closely related to experienced temperature (Fig. 6). Below-average growth, indicated by negative mean standardized increment widths (*SIW*), consistently occurred prior to 12 July and after 24 September 2002, while throughout the intermediate period above-average growth prevailed. However, within this intermediate period YoY otolith growth showed a notable indentation, with mean *SIW*'s starting to decrease on 23 July and a local minimum on 29 July. This rapid and significant (1-way

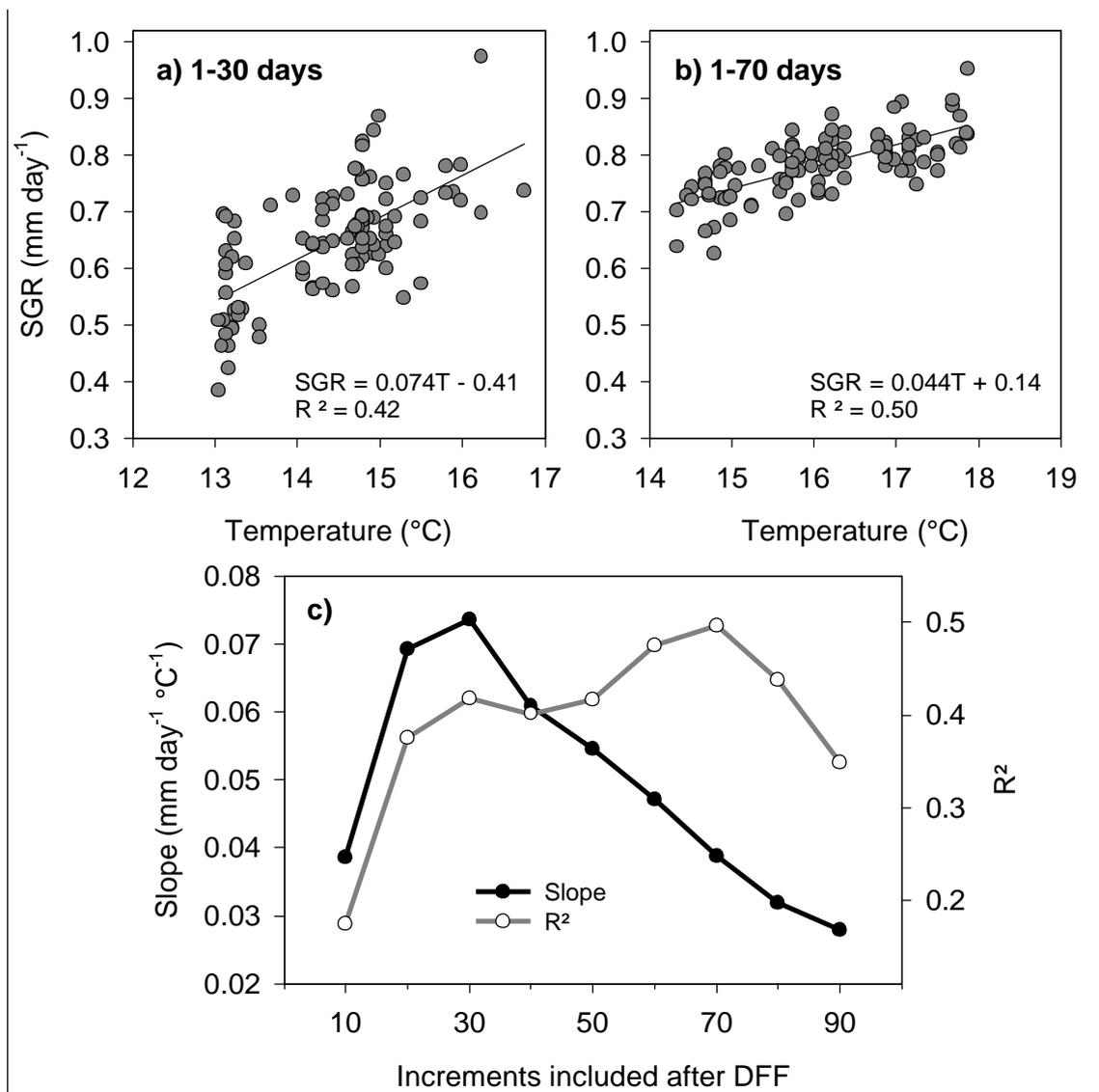


Fig.7: Relationship between temperature and back-calculated somatic growth rate (*SGR*) of YoY-sprat. Experienced temperature and *SGR* were averaged per individual over 30 (a) and 70 days after DFF (b). The lower panel (c) depicts the slope and the coefficient of correlation ( $R^2$ ) of all nine linear regressions, averaging growth over periods of 10 – 90 days post-DFF.

ANOVA, 22 July vs. 29 July,  $P=0.02$ ) change in otolith growth coincided with the observed sharp temperature drop in surface waters caused by the storm event. A time-lag of 7 days was noticed between the local minima of temperature (23 July) and mean *SIW* (29 July, Fig. 6 inlay), suggesting that otolith growth reacted immediately but at a slower rate to abrupt changes in the environment. On 22 July, the majority of YoY-survivors likely had been in the late-larval and early juvenile stage (mean $\pm$ SD age = 29 $\pm$ 12.7 days after DFF). Similar but less pronounced reactions of detrended otolith growth to storm-induced changes in surface temperature were also observed in June and October 2002 (Fig.6). The relationship between temperature ( $T$ , across all particles) and *mean SIW* could be described by a significant quadratic function ( $SIW = -0.02T^2 + 0.79T - 7.08$ ,  $R^2 = 0.75$ ,  $n=145$ ). Although significant, it is important to note that the potential temperature signal in *SIW* was small compared to the overall variability (see also Fig. 8). The significant quadratic relationship between *individual SIW*'s ( $n = 11,751$ ) and temperature explained only 6% of the overall variability.

An alternative approach was to study the cumulative effect of experienced temperature on *SGR*, both averaged per individual over periods of 10, 20, 30, 40, 50, 60, 70, 80, and 90 days after DFF (Fig. 7). Significant linear relationships ( $P<0.001$ ,  $n = 100$ ) between *SGR* vs. temperature were found for all 9 periods, and the explained variance ranged between 17-50%. The slope of the regression was highest after 30 and lowest after 90 days post DFF (0.07 and 0.03 mm day<sup>-1</sup> °C<sup>-1</sup>, respectively), suggesting the strongest influence of temperature during the larval stage of YoY-survivors (Fig. 7c).

## DISCUSSION

The present approach assumed that the analysed YoY-catches in October 2002 were comprised by individuals produced in the Bornholm Basin. Drift simulations generally confirmed this by predicting highest particle concentrations on 23 October in southern areas of the basin, where pelagic trawls were conducted during the hydroacoustic surveys (Fig. 5b). The general drift pattern was also consistent with the very low catches of YoY-sprat in northern areas of the Bornholm Basin. On the other hand, simulations indicated that a considerable fraction of sprat larvae might have drifted eastward into the Gdansk Deep and was therefore underrepresented in this analysis. However, the present findings would only be affected if notable proportions of sprat larvae from other spawning areas had drifted into the study area and mixed with those produced in the Bornholm Basin. This issue has been addressed by Hinrichsen *et al.* (2005), who used Lagrangian simulations to investigate long-term (24 years) mixing probabilities between sprat larvae from the main spawning areas in the Baltic Sea. The results support the present assumption by showing that larvae born in the Gotland Basin and Gdansk Deep generally have a very low probability (~5%) to drift westward into

Bornholm Basin. On the other hand, sprat larvae originating from the adjacent Arkona Basin were found to have a higher potential spatial overlap with individuals produced in the Bornholm Basin (~20%).

#### *Window of survival*

Compared to the average spawning season of Baltic sprat that extends from March to August (Elwertowski, 1960; Karasiova, 2002), the observed DFF-distribution of YoY-survivors was relatively narrow with only 4 individuals having formed first feeding increments prior to June 2002. Since there was clearly only one YoY-peak in the length distributions of trawl catches, and otolith analysis has been shown representative for the present YoY-population (Fig. 3), bias would have occurred only if any older YoY-sprat survived in areas other than the central Baltic Sea. This was not indicated by otolith analyses of YoY-sprat caught in other Baltic areas during parallel surveys (Baumann *et al.*, in press). Sampling bias due to inaccessibility of the very shallow areas (<20m) cannot be ruled out, however, this is likely to have affected both early and late-in-the-season born individuals in the same way. The observed DFF-distribution thus suggests that the YoY-population primarily consisted of individuals born in June/July 2002, and that any sprat larvae produced earlier in the season did not survive until October 2002.

However, the observed first-feeding (DFF) and the actual hatch-date distribution of sprat-survivors are offset by an unknown number of days, since the duration of the yolk-sac stage cannot be determined with confidence by otolith microstructure analysis. For sprat larvae from the North Sea, 6-7 days have been added to the number of counted increments (Ré and Goncalves, 1993), based on rearing experiments under 14-15°C (Alshut, 1988; Shields, 1989). For Baltic sprat, a longer yolk-sac stage should be assumed, given that newly hatched larvae likely start their development under lower temperature conditions in intermediate water layers (Voss, 2002). However, intermediate water temperature in the Bornholm Basin appears to remain relatively constant over the season and in 2002 increased only from 4.7°C in April and 5.2°C in June to 6.5°C in July (45-65m). This suggests that development times would have been rather similar between larvae hatched at different times of the year.

An argument in favour of a potentially selective survival of summer born individuals may come from an evolutionary point of view. Cushing (1990) has proposed that fish in temperate waters have evolved fixed spawning times, with peak spawning matching the average onset of the most favourable conditions for larval survival (e.g. food availability, temperature). For sprat, Karasiova (2002) has published long-term (1947-1999) seasonal means of reproduction effort in an area adjacent to the Bornholm Basin (Gdansk Deep), showing a clear peak in average egg abundance in May and June, which would correspond to larval sprat hatched in June/July. For the Bornholm Basin, seasonal egg abundance was measured in 1999, revealing a clear peak around 1 June. (9

surveys; STORE, 2003). We hypothesize that in June/July environmental conditions are on average most favourable for larval growth and survival, making these summer months the traditional survival window for sprat offspring in the central Baltic Sea. This conclusion has yet to be corroborated by analyses of larval abundance in 2002, but most importantly by laboratory studies that quantify the effect of temperature on the duration of the yolk-sac stage and the formation of first increments in larval Baltic sprat.

#### *Hydrodynamic modelling and YoY-survivors*

The use of Lagrangian simulations has proved a promising way to link growth and environmental histories in YoY-survivors, because it provided temperature fields with a daily resolution and took into account the average drift pattern, to which larvae and juveniles from the Bornholm Basin were potentially exposed. Mean temperatures, however, were probably biased by the temperature histories of about 20% of individuals that likely ended in the Gdansk Deep (Fig. 5b) and became thus unavailable to trawls in the study area. On the other hand, temperature histories between particle simulations 1-3 were not significantly different, indicating negligible differences in experienced temperature between survivors destined for the Bornholm Basin and Gdansk Deep.

In combination with field data, Lagrangian simulations have mostly been carried out to fore- or hindcast likely drift patterns of fish early life stages (Heath and Gallego, 1997; Hinrichsen *et al.*, 1997). The extension of drift simulations beyond the larval stage introduces additional uncertainty because on the level of individuals, older fish are less likely to behave like passively drifting particles. Yet unlike in demersal fish, where juvenile settlement concludes the pelagic phase (e.g. 30 and 65 days for snapper and cod larvae, Nahas *et al.*, 2003; Hinrichsen *et al.*, 2003, respectively), similar constraints are not as readily defined for pelagic species like sprat. The onset of active swimming behaviour or schooling may not necessarily preclude Lagrangian drift studies, if late-larvae or early juveniles keep moving randomly within a water body that is subject to predictable physical forcing (Baumann *et al.*, 2004). Using this approach, Allain *et al.* (2003) inferred likely origins of approximately 100 day old and 80 mm long (Cermeno *et al.*, 2003) juvenile anchovy, *Engraulis encrasicolus*, in the Bay of Biscay. Drift projections will cease to be meaningful after the onset of any active migration, which in YoY-sprat is observed in autumn, when schools mix with the adult population and move into the deep basins (ICES, 2004). We have acknowledged this limitation by adjusting the scope of our modelling exercise; instead of back-calculating historical positions of YoY-individuals we described a spatially integrated scenario that probably reflected the average larval/juvenile drift in summer/autumn 2002.

#### *Back-calculated growth rates and temperature*

Several studies have previously reported somatic growth rates of field collected sprat larvae based on mean age-length relationships. For the North Sea, Valenzuela and

Vargas (2002) found growth rates of  $0.36 - 0.40 \text{ mm day}^{-1}$  over an age range of about 30 days, which is similar to studies by Ré and Goncalves (1993) and Shields (Irish Sea, 1989) reporting values between  $0.37 - 0.46 \text{ mm day}^{-1}$ . A non-linear approach used by Munk (1993) to fit length data over a broader age range, resulted in maximum growth rates of  $0.43$  and  $0.47 \text{ mm day}^{-1}$ , while Dänhardt *et al.* (unpubl. data) found values for Baltic sprat larvae of  $0.39 - 0.46 \text{ mm day}^{-1}$ . The notably higher larval growth rates of YoY-survivors ( $0.48 - 0.69 \text{ mm day}^{-1}$ , first 25 days post-DFF), suggest that only the fastest growing sprat larvae are likely to survive and recruit into the adult population. This would be consistent with the concept of enhanced survival probabilities for faster growing individuals supported by a wealth of field and laboratory studies (e.g. Meekan and Fortier, 1996; Folkvord *et al.*, 1997; Allain *et al.*, 2003; Takasuka *et al.*, 2003; Takahashi and Watanabe, 2004).

Within YoY-sprat, differences in back-calculated growth rates (*SGR*) could largely be attributed to differences in experienced temperature, which is consistent with the general paradigm of temperature as one of the main external factors influencing growth of larval and juvenile fish (Pepin, 1991; Heath, 1992; Sogard, 1997). When integrated over the first 70 days after first feeding, temperature differences explained 50% of the variability in average somatic growth. Due to the relatively narrow range of observed mean growth rates and the rather similar temperatures, the relationships could be described as linear, although over a broader range of conditions a parabolic relationship is to be expected (Campana and Hurley, 1989). According to the slopes of the linear regressions, higher temperatures would lead to considerable size differences. For example, the slope of  $0.07 \text{ mm day}^{-1} \text{ }^{\circ}\text{C}^{-1}$  (30 days post-DFF) indicated a size difference of  $>1\text{cm SL}$  between two fish growing 30 days under temperature differences of  $5^{\circ}\text{C}$ . Importantly, the positive effect of temperature on somatic growth rate appeared to be maximal during the larval stage, but was less pronounced if the larval and juvenile stage were considered together (Fig. 7c).

Despite the demonstrated effects of integrated temperature conditions, age remained the strongest predictor of individual increment widths (and therefore *SGR*). This is summarized by Fig. 8, depicting the general form and the high variability of age- and temperature dependent *SGR*'s in YoY-sprat. Because both the back-calculated *SGR*'s and the modelled temperatures exhibited a high degree of serial correlation (not independent observations), the data were of limited utility to disentangle age- from temperature-effects on individual *SGR*'s. However, the form of the complex relationship is at least partly consistent with the conceptual “age-environment” models published by Heath and Gallego (1997).

Given that food availability also influences larval and juvenile fish growth (Cushing, 1990; Heath, 1992), unexplained variability in individual growth histories could also have come from unresolved differences in YoY-sprat feeding histories. In virtually all laboratory experiments, increased prey rations clearly led to accelerated

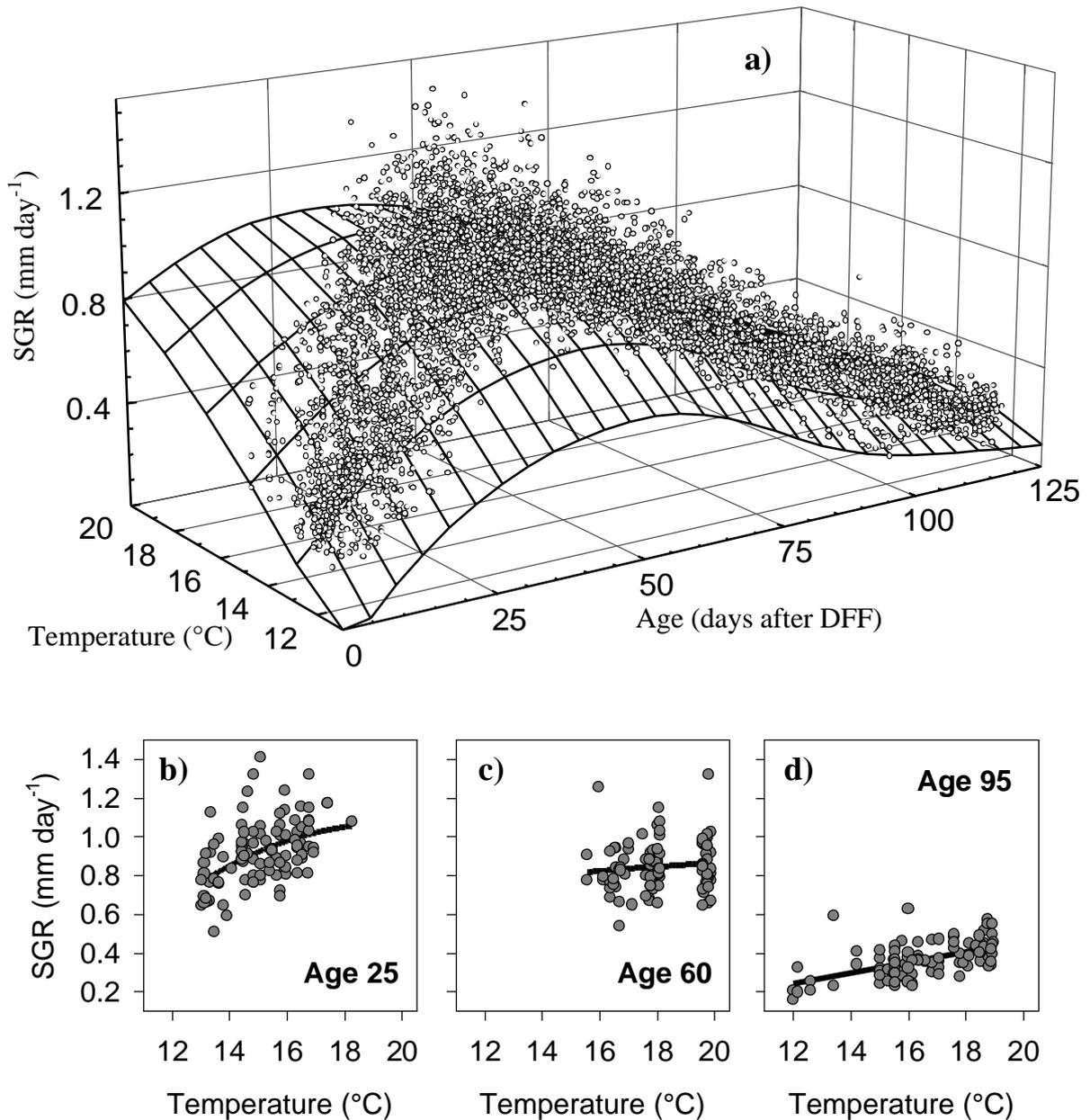


Fig.8: a) 3-d scatterplot and spline-curve representation of back-calculated daily somatic growth rates (*SGR*) of YoY-sprat in relation to age and experienced temperature. The fitted curve was derived by the method of minimized, locally-weighted sum of squares. b-d) 2-dimensional sections through the above 3-d model, showing the relationship between temperature and individual *SGR*'s for three specific ages after DFF.

growth (e.g. Folkvord *et al.*, 1997, Peck *et al.*, 2003, Takahashi and Watanabe, 2004), but in field studies the effect has only occasionally been demonstrated on the population level (e.g. Munk, 1993). Pepin *et al.* (2003) proposed that the influence of prey abundance on growth is coupled to very small spatial and temporal scales, which unfortunately have yet to be adequately sampled or appropriately modelled.

*Short-term temperature variability and otolith growth*

The use of seasonal detrended otolith growth across the entire YoY-sprat population produced new, field based insights how sprat larvae and juveniles reacted to

abrupt temperature changes. Incidentally, we observed a drastic temperature decrease on 22 July 2002, which was likely elicited by a summer storm over the central Baltic Sea. Strong wind events increase turbulence levels that may affect growth directly (Gallego *et al.*, 1996) by enhancing encounter rates between larvae and their prey, while at the same time lowering capture success (MacKenzie and Kiørboe, 2000). However, storms are also able to disrupt the typical summer stratification in the Baltic Sea (Krauss, 1981), thereby mixing colder intermediate with surface water masses at short time scales. Another potential effect of storm-induced water mixing could be a dilution of prey particles in the surface layer. Since atmospheric events act on relatively broad spatial scales, it appears likely that the majority of YoY-sprat would have experienced the consequences, irrespective of their individual position within the area. The observation that detrended otolith growth reacted immediately but less rapidly to the temperature decrease, points to a lagged response of juvenile somatic growth to abrupt changes in the environment. This is generally supported by studies on larvae and juveniles of other species (e.g. Paperno *et al.*, 1997; Molony and Choat, 1990), and by recently conducted experiments on post-larval Baltic sprat, exposed to abruptly changing feeding conditions (Baumann *et al.*, 2005). However, sudden environmental changes may also cause a temporal decoupling of otolith and somatic growth (Barber and Jenkins, 2001; Baumann *et al.*, 2005), thereby leading to a potential misinterpretation of the magnitude of such environmental effects.

This study comprises the first thorough analysis of characteristics in central Baltic YoY-sprat that survived the larval and early juvenile stages up to recruitment in autumn. The combination of otolith microstructure analysis and hydrodynamic modelling was found a promising approach, that revealed the strong influence of temperature on growth of YoY-sprat, both on long- and short-term temporal scales.

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- PAPER 2 -

**TEMPERATURE-INDUCED REGIONAL AND TEMPORAL GROWTH  
DIFFERENCES IN BALTIC YOUNG-OF-THE-YEAR SPRAT, *SPRATTUS*  
*SPRATTUS***

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**ABSTRACT**

We report on spatial and temporal differences in growth patterns of young-of-the-year sprat (YoY), *Sprattus sprattus*, that were sampled in October 2002 synchronously in 4 different regions of the Baltic Sea (i.e. western, central, eastern, north-eastern Baltic). Sagittal otoliths of 427 individuals from 64 sampling sites were analysed for their microstructure to infer the day of first feeding (*DFE*) and the growth history of YoY-survivors. *DFE*-distributions were markedly different between Baltic areas, showing a shift to later mean *DFE*'s and narrower distributions from west to north-east. This was consistent with the shift in mean seasonal spawning effort of Baltic sprat, derived from long-term observations (1973-2002) of sprat egg abundance in these areas. Otolith growth trajectories (i.e. increment widths-at-age) showed a characteristic shape depending on the sampling area, but more importantly on the time of the year the individual started feeding (*DFE*). During the larval stage, individuals from the north-eastern area and those born later in the year had higher growth rates than their earlier born conspecifics, while the pattern was reversed during the juvenile stage. Weekly means of satellite-based sea surface temperature were used to approximate the potential temperature history of YoY-survivors, which significantly influenced the shape of the otolith growth trajectory. We conclude that different *DFE*'s and therefore different temperature histories were primarily responsible for the large-scale spatial growth variability between newly recruited Baltic YoY-sprat in 2002.

**Key words:** Young-of-the-year sprat, otolith microstructure analysis, satellite-based sea surface temperature, growth patterns, day of first feeding, egg abundance

## INTRODUCTION

Sprat, *Sprattus sprattus*, is a small pelagic, zooplanktivorous fish that occurs in most marine waters around Europe. In the Baltic Sea, which comprises the northern limit of its geographical distribution (Muus & Nielsen 1999), sprat has become the most abundant, commercially exploited fish species (ICES<sup>†</sup> 2005a). Sprat is also of key dual importance for the Baltic ecosystem, both as a predator on the zooplankton community (Möllmann & Köster 1999, Köster & Möllmann 2000, Kornilovs et al. 2001) and by being a major prey species itself for Baltic cod, marine birds or mammals (Bagge et al. 1994). Baltic sprat stock abundance and recruitment success have shown large decadal trends, generally ascribed to a regime shift from a cod- to a clupeid-dominated ecosystem (Kornilovs et al. 2001, Köster et al. 2003), whereas the high inter-annual fluctuations of sprat recruitment success remain insufficiently understood (Baumann et al. in press). Prior investigations have confirmed that recruitment strength is mainly determined by differential survival patterns throughout the larval and early juvenile stages of sprat (Köster et al. 2003). Because survival in the field is often coupled to growth (Houde 1989), it is desirable to better understand the processes that influence growth patterns in larval and juvenile Baltic sprat. However, an inherent limitation of growth studies on larvae and early juveniles is that *average* patterns do not reflect the small fraction of individuals that will eventually emerge as survivors of these stages (Sharp, 1987). It may thus be meaningful to obtain samples from successful sprat recruits and investigate their growth histories, which could later be compared to individuals sampled earlier from the population.

Growth histories of sprat survivors are best inferred from otolith microstructure analysis in newly recruited, young-of-the-year (YoY) or 0-group sprat, because until their first winter, sprat are known to form readily discernible, daily increments that correspond in width to daily somatic growth rates and allow a direct back-calculation until the day of first feeding (*DFE*, Baumann et al. in press). In sprat, *DFE*'s comprise the best available proxy for hatch date, because regular increment formation during the yolk-sac stage is considered doubtful (Ré & Gonçalves 1993).

Baltic sprat spawn over an extended period from March to August (Grimm & Herra 1984) and within all major basins, from the Kiel Bight in the western Baltic to the Gulf of Finland in the North-east (Sjöblom & Parmanne 1976, Grauman & Krenkel 1986). Because the Baltic Sea is a very heterogeneous water body (MacKenzie et al. 2002), sprat larvae will likely experience considerable spatial and temporal differences in environmental conditions, depending on *DFE*'s and the region of origin (Nissling et al. 2003, Voss et al. in press). This in turn may lead to spatially and temporally different

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<sup>†</sup> International Council for the Exploration of the Sea ([www.ices.dk](http://www.ices.dk))

growth patterns in sprat survivors, and may also affect the timing and the length of the “window of survival”, i.e. the period when the majority of recruits is produced.

Field studies that attempt to explain variable growth patterns across large spatial scales (e.g. the Baltic Sea) are challenged by the necessity to cover large sampling areas in relatively short periods in order not to confound temporal with spatial variability. Such requirements are best met if multiple research cruises are conducted in parallel. Furthermore, potential differences in growth histories may only be explained by differences in experienced environmental conditions, if appropriate proxies for the environmental past of the studied individuals can be derived. Of the two major external factors influencing larval and juvenile fish growth, i.e. food availability and temperature (Heath 1992), the latter is generally less affected by small-scale variability (i.e. patchiness) and may thus be approximated more readily over the necessary spatial (i.e. Baltic Sea) and temporal (larval to juvenile stages) scales.

To derive temperature-histories of field-caught fish larvae or juveniles, indirect methods such as hydrodynamic circulation models in conjunction with Lagrangian particle simulations have previously been applied (e.g. Hinrichsen et al. 2002, Baumann et al. 2003). Such approaches depend on the reliability of complex flow field estimates and, most importantly, on the inherent assumption that individuals would follow (or be randomly distributed around) the same back-calculated transport patterns as passively drifting particles. This is not justified in Baltic YoY-sprat, which in autumn have already joined adult schools.

Alternatively, appropriate temperature proxies may be derived from satellite-based observations of sea surface temperature (*SST*, e.g. Fowler & Jennings 2003), because feeding sprat larvae are known to predominantly occur in surface waters (Voss et al. in press). Despite the relatively coarse spatial and temporal resolution and unaccounted for larval/juvenile advection, satellite-based *SST*'s are in many ways advantageous over direct temperature measurements or modelling approaches. For example, long-term *SST*-data bases are often well established, readily accessed, and they provide spatially and temporally regular measurements over any desired areal coverage.

Here we used satellite-based *SST*-data to approximate the temperature-histories of YoY-sprat that were caught in October 2002 within four, large regions of the Baltic Sea (Fig. 1). YoY growth histories were inferred from otolith microstructure analysis and tested for systematic differences between Baltic areas and among survivors born at different times of the year 2002. Our main goals were to describe the large-scale spatial variability in YoY-sprat morphology and to attempt and explain it by potential differences in growth due to different experienced temperatures during the larval and juvenile stages of Baltic sprat.

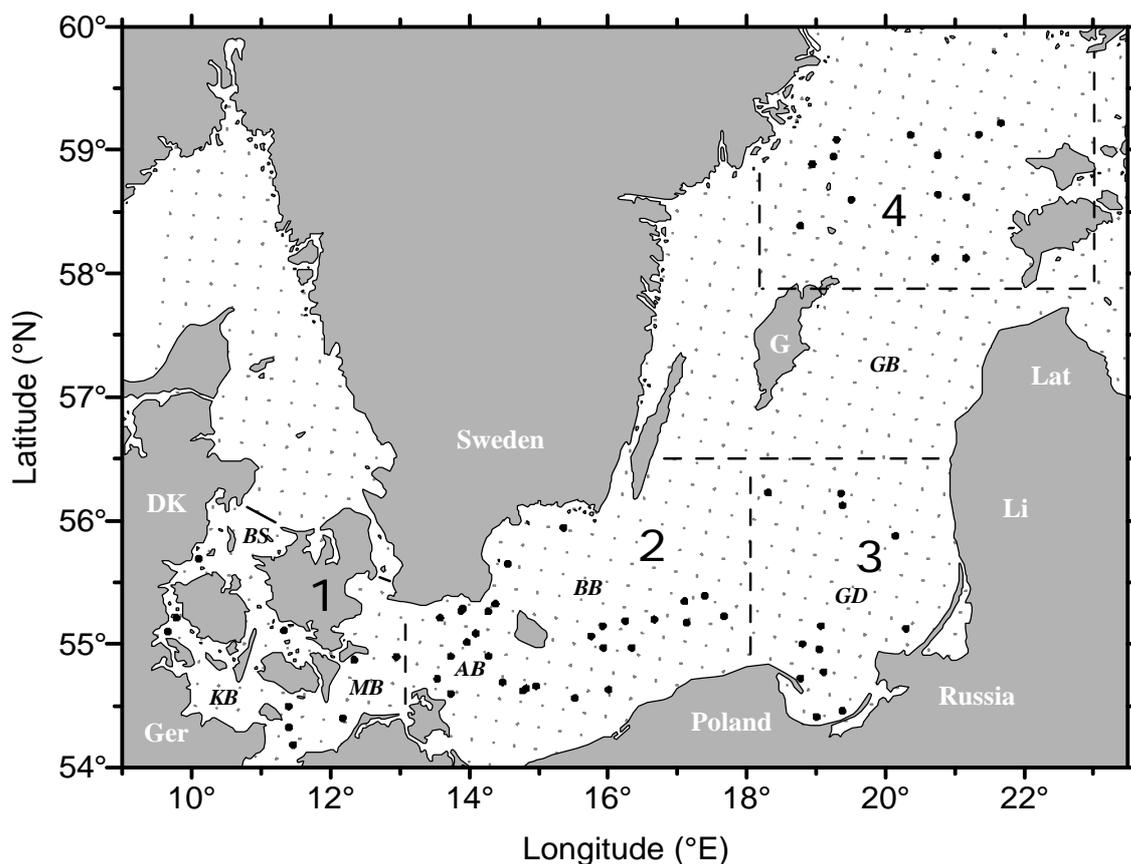


Fig.1: Study area of the Baltic Sea with young-of-the-year (YoY) sprat sampling sites in October 2002 (black dots). Small grey dots depict the grid of satellite-based measurements of weekly sea surface temperature (*SST*), while dashed lines and bold numbers refer to Baltic areas 1 to 4 used in the analysis. AB = Arkona Basin, BB = Bornholm Basin, BS = Belt Seas, DK = Denmark, G = Gotland, GB = Gotland Basin, GD = Gdansk Deep, Ger = Germany, KB = Kiel Bight, MB = Mecklenburg Bight, Lat = Latvia, Li = Lithuania

## MATERIAL AND METHODS

### *Field sampling*

YoY-sprat were sampled in October 2002 during the Baltic International Acoustic Survey (BIAS), conducted annually to yield abundance estimates for pelagic fish stocks. The survey consisted of 4 nearly parallel research cruises, which covered all regions of major sprat stock abundance in the Baltic Sea (Fig. 1, Table 1). The 4 ships deployed different pelagic fishing gears with horizontal and vertical mouth openings of 21 to 90 m and 9 to 28 m, respectively (ICES, 2005b). In order to retain small pelagic fish, the stretched mesh size in the cod end ranged from 12 – 20 mm ( $L_{50}^{\ddagger} = 25 - 40$  mm TL), except for the Swedish vessel that used a 40 mm mesh opening in the cod end ( $L_{50} = 85$  mm TL). The resulting difference in gear selectivity was adjusted for by applying a correction factor for each 5 mm length class, as published by Bethke et al. (1999).

<sup>‡</sup>  $L_{50}$  is the estimated fish length with a 50% chance of being caught by the trawl (ICES 2005b)

Where present in the catch, YoY-sprat always formed a distinct peak in the length frequency distribution and were thus readily distinguished from age 1+ individuals (cut point 95 to 105 mm total length). Between 20 to 50 YoY-sprat per haul were randomly selected and either immediately preserved in 95% ethanol (German, Polish, Swedish samples) or directly processed on board (Russian and Latvian samples). Processing involved length (*TL*, to the nearest mm) and weight measurements (*W*, to the nearest 0.1 g), followed by the extraction of both sagittal otoliths. Since the weights of fresh and preserved specimens were not comparable, only the latter were used in this analysis.

Table 1: Overview of YoY-sprat sampling in October 2002 and otolith microstructure analysis (see Fig. 1 for definition of areas)

Area	Sampling nation	Sampling dates	Size range at capture (TL, mm)	Hauls with YoY-sprat	Otoliths analysed
1	Germany	15 – 24 Oct	67 - 103	10	67
2	Germany, Poland, Sweden	7 – 23 Oct	78 - 105	29	170
3	Latvia, Poland, Russia	20 – 29 Oct	70 – 98	12	111
4	Sweden, Russia	11 – 17 Oct	61 – 92	13	79
Total		7 – 29 Oct	61 - 105	64	427

### *Otolith microstructure analysis*

Otolith microstructure analysis was identical to the methodology described in Baumann et al. (in press). Briefly, sagittal otoliths were mounted individually on microscopic slides with a drop of thermoplastic glue (Crystalbond<sup>®</sup> 509), polished from both sides with a 3 µm lapping film (266x Imperial PSA 3M<sup>®</sup>), and photographed under 400x magnification with a digital camera (Leica<sup>®</sup> DC300). Otolith increments were counted and measured (µm) in multi-frame digital images (ImagePro Plus 4.5.1<sup>®</sup>), which allowed each otolith section to be viewed in 4-7 different focal planes. The measurement axis always went from the core to the post-rostrum of the otolith. A sufficient precision in increment counts was confirmed through re-readings on a subset of otoliths by the same reader (n = 48) and by comparing counts between two experienced but independent readers (n = 18), as reported in Baumann et al. (in press). In total, otoliths of 427 individuals from 64 sampling sites were included in the analysis (Table 1).

To study broad-scale spatial differences between YoY-survivors, we defined four major Baltic areas to which each individual was assigned according to its catch position in October 2002. Area 1 encompassed the western Baltic Sea including the Belt Seas, the Kiel and Mecklenburg Bight (Fig. 1). Area 2 consisted of the two major basins in

the central Baltic, the Arkona and the Bornholm Basin, with northern and southern boundaries defined mostly by Swedish, German, and Polish coastlines (west-east: 13° - 18°E). In the south-eastern Baltic, area 3 represented the Gdansk Deep and southern parts of the Gotland Basin (western and northern boundaries: 18°E and 56.5°N, respectively), while the most north-eastern region, area 4, contained all hauls done north of the Gotland island (18° - 23°E, 58° - 60°N, Fig. 1).

To validate the assumption that the analysed sub-sample was representative of the YoY-sprat population, the YoY-length distribution of the hauls was compared to the one from the otolith sample for each Baltic area. Although there were no significant differences in mean *TL* between field and otolith samples (1-way ANOVA,  $P > 0.05$ ), some of the 5 mm length classes appeared to be under- or overrepresented in our analysis. We corrected for this by assigning to each analysed specimen a weighing factor according to the *TL* class and the Baltic area it was caught in October 2002. Weighing factors ranged between 0.38 (too many otoliths read in a particular length class) and 3.08 (too few otoliths analysed in a length class).

In the majority of YoY-otoliths, a pronounced shift from weak and indistinct to sharp and well defined increments was typically observed after the innermost 4 increments (range 3 to 5). This shift was assumed to correspond to the transition from non-daily increment formation during the yolk-sac stage to daily increments deposited after the onset of first-feeding, and only the latter increments were included in the analysis. Therefore, all otolith-derived age estimates hereafter refer to individual ages in days after first feeding (*DFF*).

Prior to comparing length frequency distributions of YoY-sprat between the 4 Baltic areas, we also adjusted for potential bias introduced by the different sampling periods (Table 1). Since the first haul was done on 7 October 2002, all individual fish lengths were back-calculated to the 6 October 2002 using the biological intercept method (Campana, 1990). The otolith radius at first feeding corresponded to the distance between the core and the 4<sup>th</sup> increment, while for *TL* at first feeding a value of 5 mm was assumed, based on Voss et al. (2003) who found prey in the guts of 4-6 mm sprat larvae from the Bornholm Basin. The biological intercept method is independent of the slope in the otolith-fish size regression, but assumes linearity in individual otolith-fish size trajectories (Campana 1990).

#### *Ichthyoplankton data*

Spatial differences in length and timing of the sprat spawning season were inferred from ichthyoplankton data collected by the Latvian Fish Resources Agency between 1973 – 2002. A vertically operated IKS-80 net with a mouth opening of 0.5 m<sup>2</sup> and a mesh size of 500 µm was regularly deployed during 3 to 6 annual surveys, conducted mainly between March to August. The surveys covered the major sprat spawning grounds in the Baltic Sea, from the Bornholm Basin (corresponding to area 2)

and the Gdansk Deep (area 3) to the northern part of the Gotland Basin (north of 57.5°N, area 4). Unfortunately, seasonal coverage in the single year 2002 was not sufficient to directly compare spawning and survivor patterns. Also, no comparable data exist for area 1. However, to estimate the *average* length and peak of sprat spawning in areas 2 to 4, a 3-parameter Gaussian function of the form

$$N = ae^{\left[-0.5\left(\frac{JD-c}{b}\right)^2\right]} \quad (1)$$

was fitted to the mean number ( $N$ ) of sprat stage 1 eggs ( $n\ m^{-2}$ ) per Julian day ( $JD$ ) from all available years and surveys. The number of days with predicted egg abundances above 10% of the predicted peak abundance (parameter  $a \cdot 10^{-1}$ ) was taken as a rough estimate of the average length of the sprat spawning season in each area.

### *Sea surface temperature*

Data on sea surface temperature ( $SST$ ) in the Baltic Sea were obtained from the “Bundesamt für Seeschifffahrt und Hydrographie” (BSH<sup>§</sup>) for the years 1997 to 2002, and are based on observations of the NOAA 12 & 16 satellites with an initial spatial resolution of 1.1 km. A multi-channel (MC) SST-algorithm was applied to process raw data, which were finally provided as weekly averages of  $SST$  on a regular 20 x 20 km grid (Fig. 1). All grid-points contained within each of the four Baltic areas were later averaged to yield a mean value of  $SST$  per week and area. The mean standard deviation of temperature per area and week (May to October) was rather low and ranged between 0.9 and 1.0 °C.

### *Influence of temperature on otolith growth trajectories*

YoY-sprat were first binned into classes of similar first feeding days ( $DFF$ ). We chose fortnightly intervals starting on 12 May 2002 in order to have sufficient observations per  $DFF$ -interval. For each Baltic area and each 14d  $DFF$ -interval containing more than 3 specimens ( $n = 17$ , Table 2), age-increment width data ( $IW$ ) were then fitted with a non-linear, 5-parameter Weibull function of the form

$$IW = IW_0 + a \left(\frac{c-1}{c}\right)^{\frac{1-c}{c}} \left[ \frac{Age - Age_0}{b} + \left(\frac{c-1}{c}\right)^{\frac{1}{c}} \right]^{c-1} e^{-\left[ \frac{Age - Age_0}{b} + \left(\frac{c-1}{c}\right)^{\frac{1}{c}} \right]^c} + \frac{c-1}{c} \quad (2)$$

with parameters  $a$ ,  $b$ ,  $c$ ,  $IW_0$ , and  $Age_0$  being estimated through iteration (SigmaPlot<sup>®</sup> 9.0). The function appropriately modelled the typical features of the YoY-sprat otolith trajectory, i.e. the initial steep increase, the local maximum and the gradual decrease in increment width. The parameters  $Age_0$ ,  $IW_0+a$ ,  $c$ , and  $b$  corresponded to (i)

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<sup>§</sup> [www.bsh.de/en/Marine%20data/Observations/Sea%20surface%20temperatures/index.jsp](http://www.bsh.de/en/Marine%20data/Observations/Sea%20surface%20temperatures/index.jsp)

the age at peak increment width, (ii) the peak increment width, (iii) the increment width at the first, and (iiii) the age at the second inflection point, respectively.

Table 2: Number of YoY-sprat analysed per area and fortnightly *DFF*-interval in 2002. 5-parameter Weibull-curves were not fitted for intervals containing less than 4 specimens (numbers in brackets).

<i>14d DFF-interval</i>	<i>Area 1</i>	<i>Area 2</i>	<i>Area 3</i>	<i>Area 4</i>
12.5. - 25.5.	(1)	(3)		
26.5. - 8.6.	10	21	(1)	(1)
9.6. - 22.6.	19	46	22	4
23.6. - 6.7.	13	72	45	17
7.7. - 20.7.	11	27	36	37
21.7. - 3.8.	13	(1)	7	19
4.8. - 17.8.				(1)
<b>Total</b>	66 (67)	166 (170)	110 (111)	78 (79)

Within each Baltic area, mean weekly *SST* in 2002 was taken as a proxy for the average temperature history of YoY-sprat populations, assuming that the majority of survivors originated from those broadly defined regions, where they were sampled in October 2002. To test whether the variability in Weibull-parameters (i.e. the shapes of the otolith growth trajectories) could be explained by differences in experienced temperature, *SST* was averaged for each Baltic area over periods of 10, 20, 30, 40, 50, 60, and 70 days starting from the middle of each *DFF*-interval. The different values for each Weibull-parameter comprised independent observations and were subsequently regressed linearly on mean area- and *DFF*-specific *SST* ( $n = 17$  for each of the 7 periods, SPSS<sup>®</sup> 10.0.7).

To test whether significant differences in mean *W*, *TL*, and *DFF* existed between YoY-sprat from different Baltic areas, 1-way ANOVA's were performed, with subsequent LSD (homogeneous variances) or Dunnett-T3 (inhomogeneous variances) post-hoc tests for significant differences between areas (SPSS<sup>®</sup> 10.0.7). To test different pairs of linear regression lines for significant differences in slope and intercept, the method after Zar (1984) was applied, which is implemented in the GraphPad<sup>®</sup> Prism software. For all statistical tests, significance is hereafter reported only for P-levels below 0.05.

## RESULTS

Mean *SST* during the second week in May 2002 ranged between 7.0 to 9.9°C in areas 1-4, increased steadily thereafter until the last week in August (20.3 to 21.8°C),

and decreased sharply again to 6.9 to 10.0°C at the end of October 2002 (Fig. 2). The variability in *SST* between areas was surprisingly low; area differences in mean weekly *SST* only ranged between 0.8 to 3.8°C (mean = 2.2°C). Surface warming was delayed, while autumn cooling was more rapid in area 4 relative to the other Baltic areas. However, between mid-July and the end of August 2002, *SST* was highest in area 4 (Fig. 2), an exceptional situation compared to the previous 5 years 1997-2001.

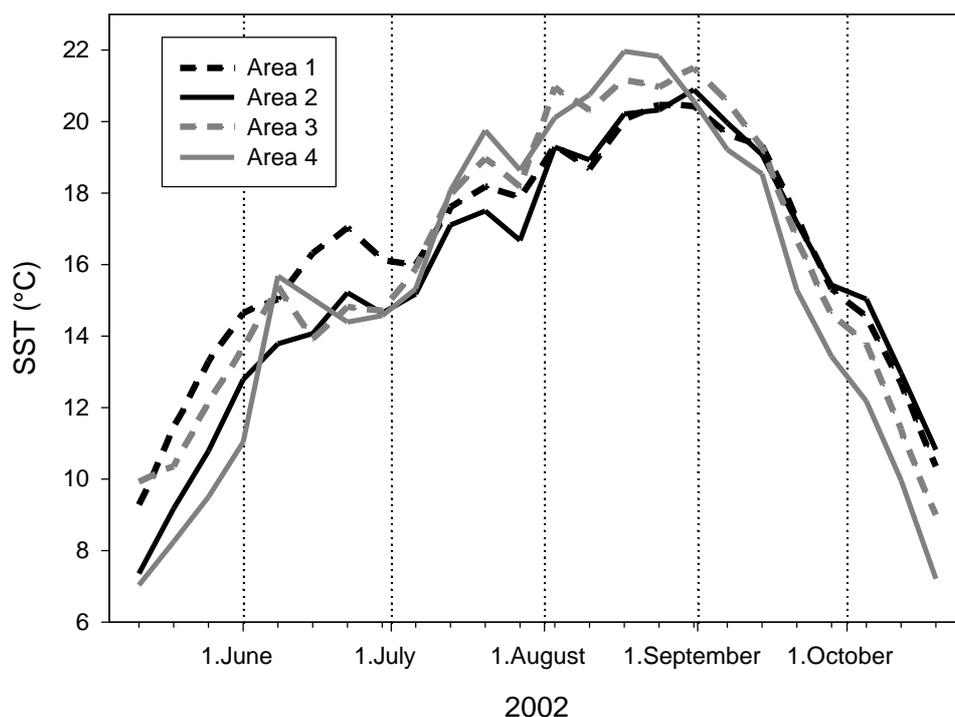


Fig.2: Mean weekly sea surface temperature (*SST*) in Baltic areas 1-4 derived from satellite data

The analysis of YoY-sprat weights, done separately for each 5 mm *TL* class (75 – 95 mm), revealed that individuals in western and central Baltic areas (1 and 2) were significantly heavier than their conspecifics in eastern areas 3 and 4 for all four *TL* classes studied. The relationship between otolith radius (*OR*, in  $\mu\text{m}$ ) and *TL* did not show significant deviations from linearity, neither for pooled ( $TL = 23.01 + 0.104OR$ ,  $r^2 = 0.76$ ,  $n = 426$ ) nor for separately analysed Baltic areas.

Length frequency distributions of YoY-sprat differed considerably between Baltic areas (Fig. 3). Mean *TL* on 6 October was significantly higher in western and central areas 1 and 2 (85.1 mm and 86.9 mm, respectively) than in area 3 (79.8 mm), while individuals in area 4 (73.0 mm) were significantly the smallest YoY-survivors. The broadest and narrowest *TL* distribution was found in area 1 ( $SD = 8.07$  mm) and area 2 ( $SD = 5.23$  mm), respectively, whereas areas 3 and 4 showed intermediate *TL* variability ( $SD = 7.76$  mm and 6.58 mm, respectively). A characteristic shift was also apparent in the *DFE*-distributions, which showed increasing mean *DFE*'s and narrowing distributions from western to north-eastern Baltic areas (Fig. 4). The mean

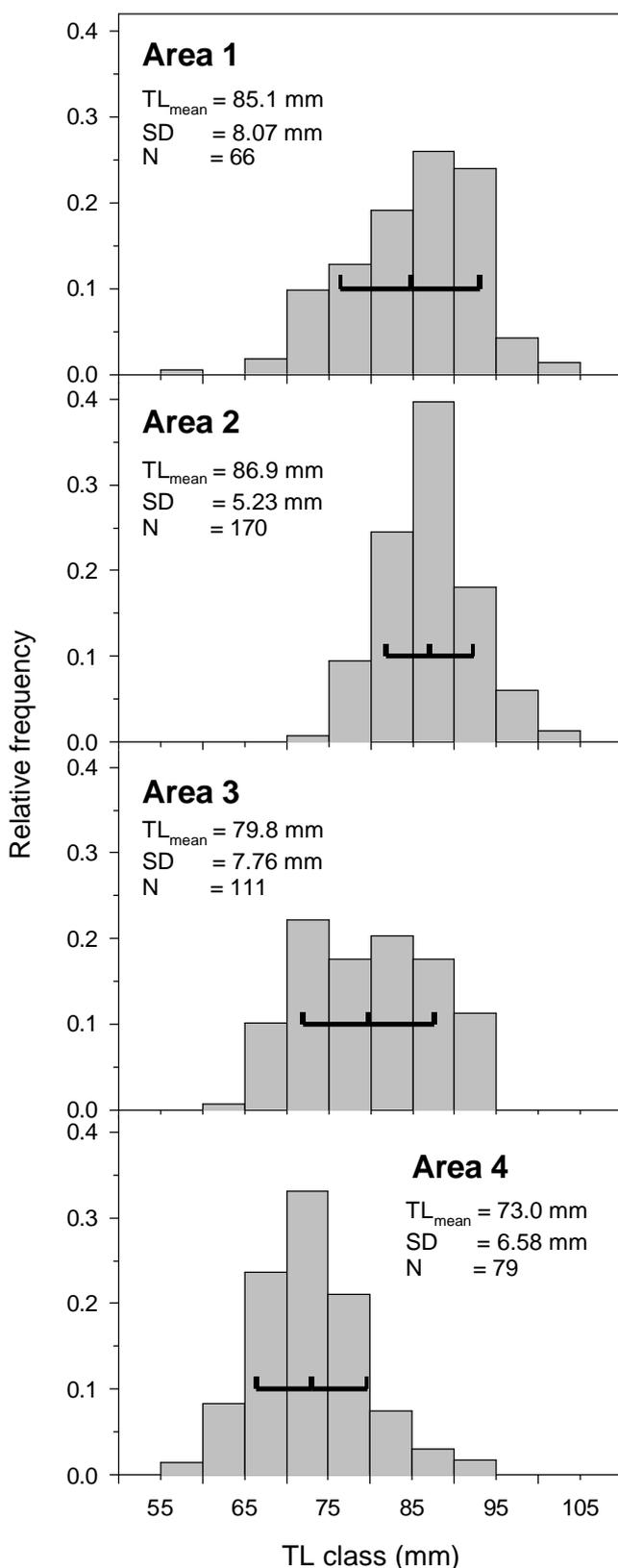


Fig.3: *Sprattus sprattus*. Relative length frequency distribution of YoY-sprat back-calculated to the 6 October 2002 in the 4 different areas of the Baltic Sea. Short black marks = mean  $\pm$  SD.

*DFE* of YoY-sprat in area 4 occurred significantly later than in areas 1 – 2 (19 days) and area 3 (11 days), while individuals in area 3 were significantly younger than those in area 2 (8 days). The main ‘window of survival’ in 2002, here characterised by the difference between the 90<sup>th</sup> – 10<sup>th</sup> percentile of *DFE*’s, narrowed from 58 days in area 1 to 36 days, 31 days, and 27 days in areas 2, 3, and 4, respectively (Fig. 4).

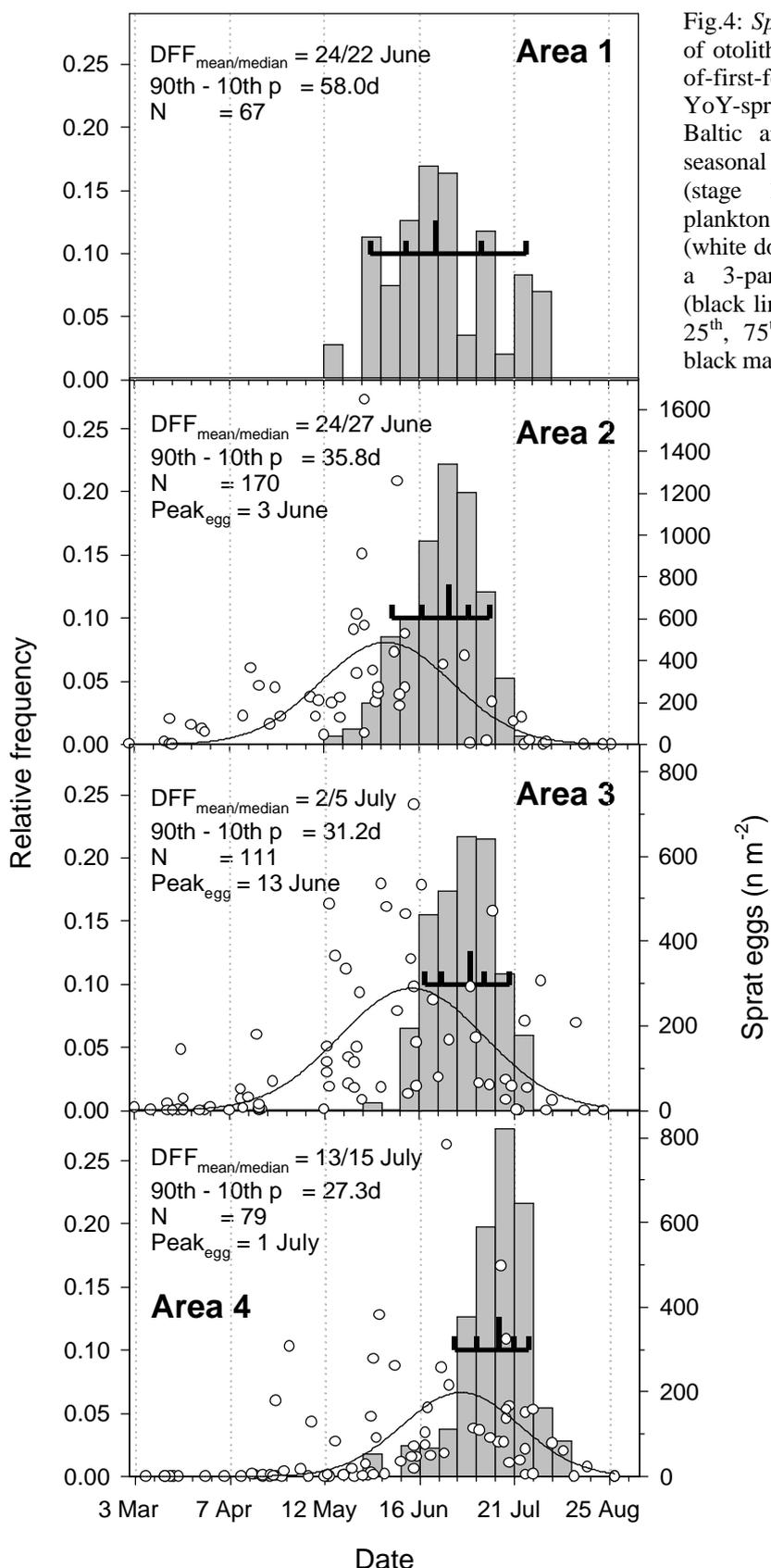


Fig.4: *Sprattus sprattus*. Distributions of otolith based, back-calculated days-of-first-feeding (DFF, grey bars) of YoY-sprat caught in October 2002 in Baltic areas 1-4 in relation to the seasonal abundance of sprat eggs (stage 1) derived from ichthyoplankton hauls between 1973-2002 (white dots). Egg data were fitted with a 3-parameter Gaussian function (black line). Short black marks = 10<sup>th</sup>, 25<sup>th</sup>, 75<sup>th</sup>, and 90<sup>th</sup> percentiles, long black mark = median DFF

Pooled data on sprat egg abundance (1973-2002) were very heterogeneous in all Baltic areas, both in terms of absolute numbers as well as with regard to the time of the year, when eggs appeared in the water column. This was probably due to a combination of high inter-annual variability, spatial patchiness, and the low sampling intensity (only

3-6 surveys per year). Although the 3-parameter Gaussian functions significantly fitted the data in areas 2-4, the curves only explained 37% (areas 2 and 3) and 23% (area 4) of the overall variability in seasonal sprat egg abundance. Mean predicted peak abundance of sprat eggs showed a consistent shift to later dates from area 2 (3 June) and area 3 (13 June) to area 4 (1 July). The longest mean spawning season was found for area 3 with 114 days, followed by area 2 (103 days) and area 4 (92 days, Fig. 4).

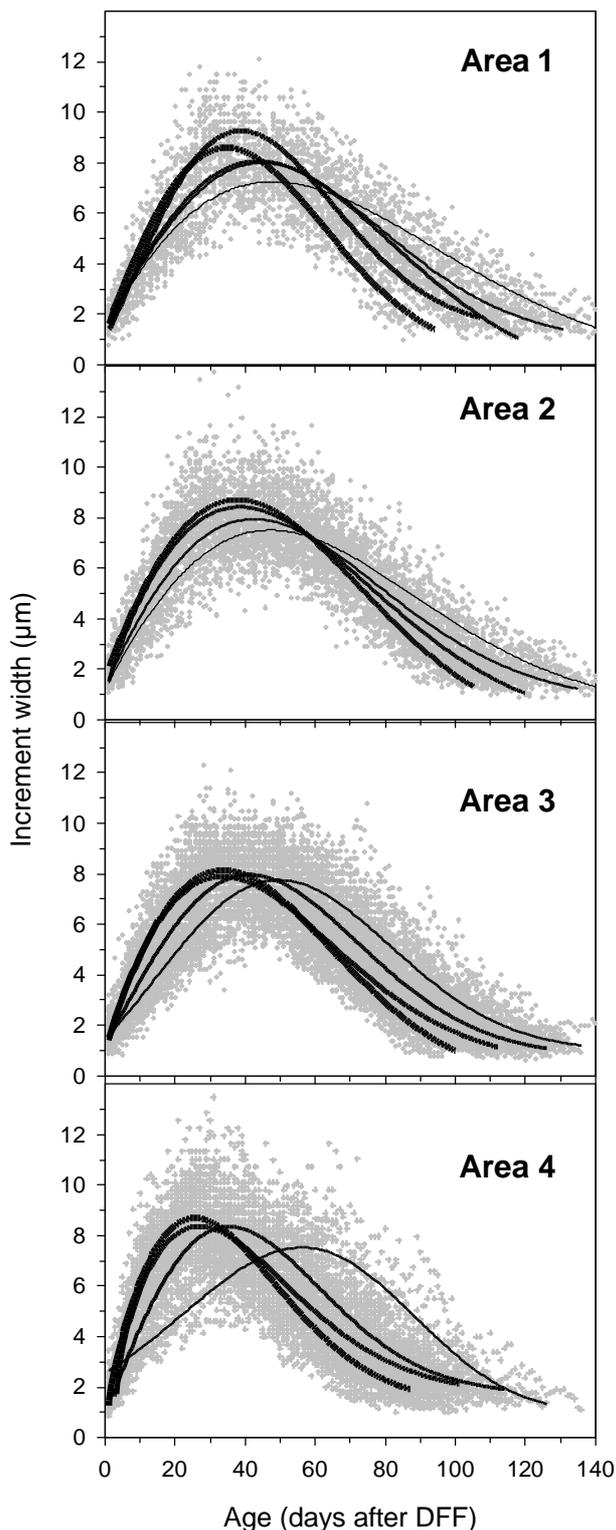


Fig.5: *Sprattus sprattus*. Individual age-increment widths (grey dots) and mean predicted otolith growth trajectories of YoY-sprat (black lines) from the 4 different Baltic areas in 2002. Within each area, data were grouped into fortnightly *DFE*-intervals based upon the back-calculated day of first feeding (*DFE*) and fitted with a Weibull-5-parameter curve. Lines increase in thickness from earliest to latest *DFE*'s (i.e. *DFE*<sub>1</sub>: 26.5.-25.6., *DFE*<sub>2</sub>: 9.6.-22.6., *DFE*<sub>3</sub>: 23.6.-6.7., *DFE*<sub>4</sub>: 7.7.-20.7., and *DFE*<sub>5</sub>: 21.7.-3.8.02)

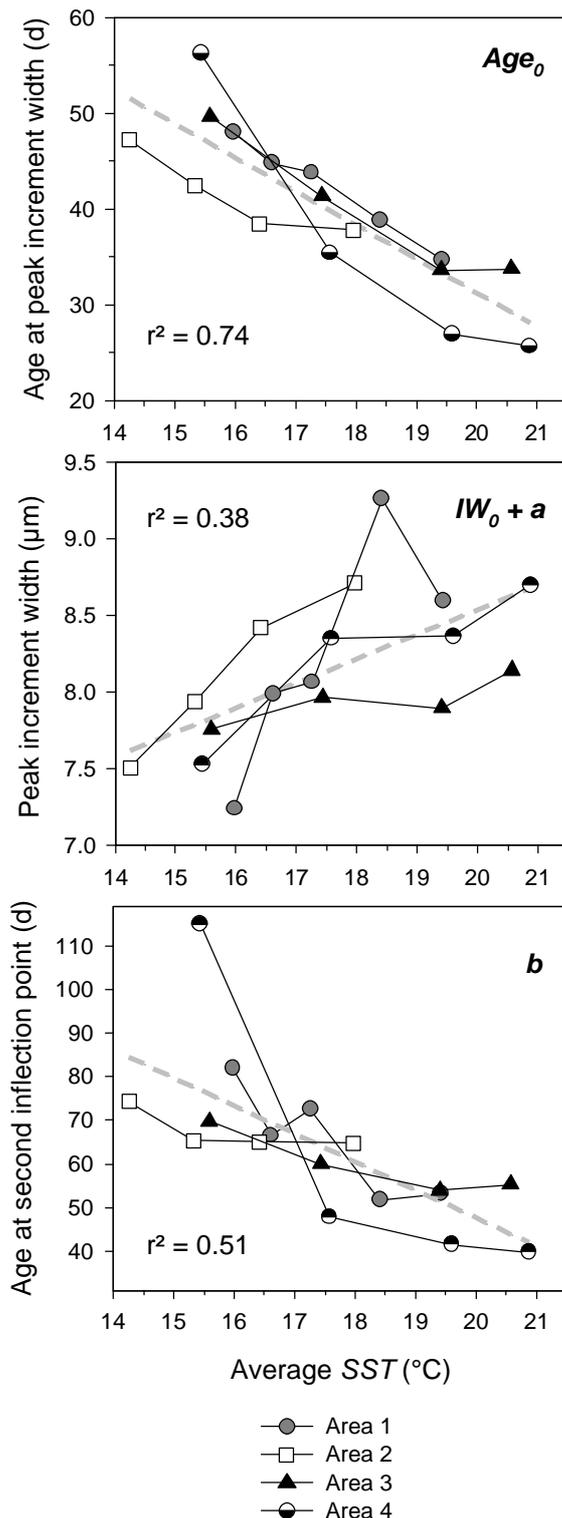


Fig.6: *Sprattus sprattus*. Relationship between Weibull-parameters  $Age_0$  (age at peak increment width),  $IW_0+a$  (peak increment width),  $b$  (age at second inflection point) and average sea surface temperature ( $SST$ ) during the first 30 days after  $DFE$ . Within each Baltic area, between 4-5 Weibull-curves (total  $n = 17$ ) were fitted to age-increment width data, pooled per fortnightly  $DFE$ -interval. Grey dashed lines and  $r^2$ -values refer to significant linear regressions of all data points in each plot.

Despite the expected high variability in individual otolith growth trajectories, increment widths-at-age differed systematically between Baltic areas and between individuals from different  $DFE$ -intervals. This was inferred from significant 5-parameter Weibull-regressions that fitted the data well and explained between 76% and 86% of the overall variability in area- and  $DFE$ -specific otolith trajectories (Fig. 5). Within each area, the initial increase during the larval stage and the gradual decrease in otolith growth rates during the juvenile stage were both notably steeper in individuals born later in the season compared to their earlier born conspecifics (Fig. 5). Within each of the three latest  $DFE$ -intervals, individuals from area 4 appeared to have higher initial otolith growth rates, which were again followed by a steeper decline in increment width relative to YoY-survivors from other Baltic areas.

In total, 17 area- and  $DFE$ -specific Weibull-curves could be fitted (Figs.5 and 6), and the 17 values of each parameter were then linearly regressed on  $SST$ ; the latter averaged over periods of 10 to 70 days. Significant linear relationships were found for all 7 periods, but strongest temperature correlations were observed for parameters  $Age_0$  ( $r^2_{max} = 0.74$ ) >  $b$  ( $r^2_{max} = 0.51$ ) >  $IW_0+a$  ( $r^2_{max} = 0.38$ ) in relation to  $SST_{20}$  and  $SST_{30}$ , suggesting that the temperature experience throughout the first 30 days after  $DFE$  (larval stage) was most influential to the

shape of YoY-sprat otolith trajectories. The increment width at the first inflection point ( $c$ ) was not significantly related to  $SST$ . While age at peak increment width ( $Age_0$ ) and the age at the second inflection point ( $b$ ) were negatively correlated to temperature, predicted peak increment width ( $IW_{0+a}$ ) significantly increased with  $SST$  (Fig. 6, only shown for  $SST_{30}$ ). However, the latter effect was much weaker, thus otolith size at the age of peak increment width ( $OS_{Age_0}$ ,  $\mu\text{m}$ ) also decreased linearly with decreasing  $Age_0$ -values ( $OS_{Age_0} = 61.5 + 4.3Age_0$ ,  $r^2 = 0.93$ ,  $n = 17$ ).

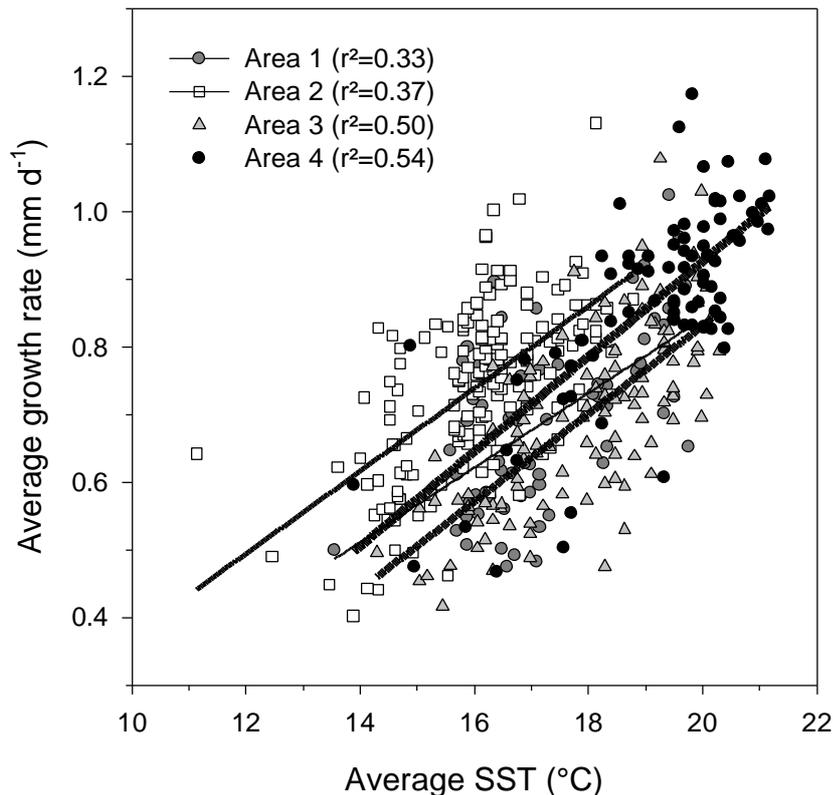


Figure 7: *Sprattus sprattus*. Linear relationships between average, back-calculated somatic growth rate during the larval stage and average SST (~30 days after  $DFE$ ) within each of the four Baltic areas. All relationships were significant on the  $P=0.05$  level. Regression lines increase in thickness from areas 1 to 4.

To test the temperature effect on YoY-growth independently of the Weibull-regressions, mean daily somatic growth rates during the first 30 days after  $DFE$  (biological intercept method) were regressed against the corresponding mean  $SST$ -values. Significant positive relationships between somatic growth rates and temperature were found for all Baltic areas and explained between 33% and 54% of the overall variability (Fig. 7). Slopes increased non-significantly from area 1 to area 4, with a common slope of  $0.063 \text{ mm d}^{-1} \text{ } ^\circ\text{C}^{-1}$ . The regression intercept of area 2 differed significantly from the other areas and indicated that temperature-adjusted larval growth was highest in area 2 followed by areas 4, 1, and 3 (Fig. 7).

## DISCUSSION

### *Temperature-histories based on SST*

Temperature-histories explained remarkably large parts of the spatial and temporal variability in YoY-sprat growth patterns, despite the relatively coarse resolution of satellite-based *SST*'s (weekly and areal means) and our inherent assumption that individuals originated from, and stayed within those Baltic areas, where they were caught as YoY-sprat in October 2002. Because sprat spawning is known to take place in all of these four Baltic areas (Sjöblom & Parmanne 1976, Grauman & Krenkel 1986), *and* we purposely defined only four, but rather large rectangles to allow for some random larval advection, we believe this assumption to be justified. In addition, spatial variability in *SST* was very low compared to seasonal temperature differences, implying only small errors due to individuals originating from nearby regions outside the defined rectangles.

Large-scale larval transport across areas, on the other hand, could have introduced a more serious bias into *SST*-based temperature histories. This issue was addressed recently by Hinrichsen et al. (in press) who used long-term hydrodynamic modelling to estimate the general mixing probabilities of sprat larvae in the Baltic Sea. The authors concluded that a high spatial overlap may only occur between larvae from the Arkona- and Bornholm Basin, which was the main reason for combining these two spawning grounds here. In contrast, estimated mixing probabilities between Bornholm and Gotland Basin larvae were at consistently low levels. Only the Gdansk Deep (area 3) was identified as a region where larvae from neighbouring regions potentially accumulate, including those from eastern parts of the Bornholm Basin (area 2). However, similar Lagrangian simulations by Baumann et al. (in press) revealed that mostly larvae born early in the season 2002 could have been transported far enough into the adjacent Gdansk Deep. The present study, on the other hand, found subtle indications for a partial overlap between central and eastern YoY-sprat. In contrast to areas 1, 2, and 4, the *TL* and *DFE*-distributions in area 3 conspicuously lacked a clear mode (Figs. 3, 4), which could have resulted from mixing two slightly different YoY-groups. This, however, does not invalidate the overall suitability of satellite-based *SST*'s for approximating the temperature history of Baltic YoY-sprat. It is likely that the robust signal already detected with *SST* would have been even more pronounced if the real temperature experience or a closer proxy had been available.

### *Spatial differences between Baltic YoY-sprat*

The finding that sprat recruits in eastern and north-eastern areas were significantly smaller than their conspecifics in central and western parts of the Baltic Sea is consistent with many working reports that studied age-length relationships in Baltic sprat (Lindquist 1971, Aps et al. 1988) or combined these with otolith macrostructure

analyses (Grygiel 1978). For example, Aps et al. (1981) and Shvetsov et al. (1992) measured the innermost otolith growth zone prior to the first winter ring, and concluded that lengths of YoY-sprat decrease from south-western to north-eastern Baltic regions.

Differences in body size could simply result from shifted spawning seasons (Shvetsov et al. 1992, Grygiel 1999). This, however, would expose the offspring to seasonally different environmental conditions and thus likely modify the spatial heterogeneity among survivors (e.g. García et al. 2003). The data presented here first proved that mean spawning effort of sprat is indeed shifted by almost a month from central to north-eastern Baltic spawning grounds. Assuming that sprat reproduction is cued by temperature, like for example in Bay anchovy *Anchoa mitchilli* (Lapolla 2001), this shift is most reasonably explained by the consistently delayed spring warming in north-eastern vs. central Baltic areas. Secondly, the different spawning periods corresponded well to the observed shift in *DFE*-distributions of sprat survivors in 2002, with an offset in mean *DFE*'s between central and north-eastern individuals of 19 days. Assuming spatially and temporally invariable growth patterns, a delay of 19 days could have accounted for a *TL* difference of only 6.7 mm, whereas YoY-survivors in October 2002 differed in mean *TL* by 13.9 mm (area 2 and 4, Fig. 3). Therefore, YoY-sprat growth had to vary substantially between Baltic areas and *DFE*-periods, induced either by different environmental conditions and/or differences in growth capacity between potential subpopulations of Baltic sprat.

#### *Influence of temperature on growth trajectories*

Depending both on the time of first feeding and the Baltic area, YoY-sprat otolith growth patterns showed indeed substantial variability. Within a given area, the initial increase in growth rates (corresponding to the larval stage) was notably steeper in later born individuals, while within a given *DFE*-interval the area-effect consisted of a similar but less pronounced increase in larval growth from western/central to eastern/north-eastern Baltic regions. In both cases, higher larval growth rates were always followed by a steeper decline in growth after the peak, and this similarity indicated that growth trajectories were influenced by a common determinant like temperature, which varied similarly in time and space (Folkvord et al. 2004).

The strong correlations between *SST* and the estimated Weibull-parameters confirmed the key importance of temperature for somatic growth of YoY-sprat, provided that growth-independent temperature effects on otoliths (Huuskonen & Karjalainen 1998) were negligible. The characteristic patterns allowed several further conclusions: (1) the shape of the otolith trajectory was determined mainly by the temperature experience throughout the larval and early juvenile stage, which is consistent with many field (Crecco & Savoy 1985, Baumann et al. in press) and laboratory studies (Otterlei et al. 2002). (2) Sprat larvae born later in the season experienced higher temperatures and therefore had broader peak increments, which they

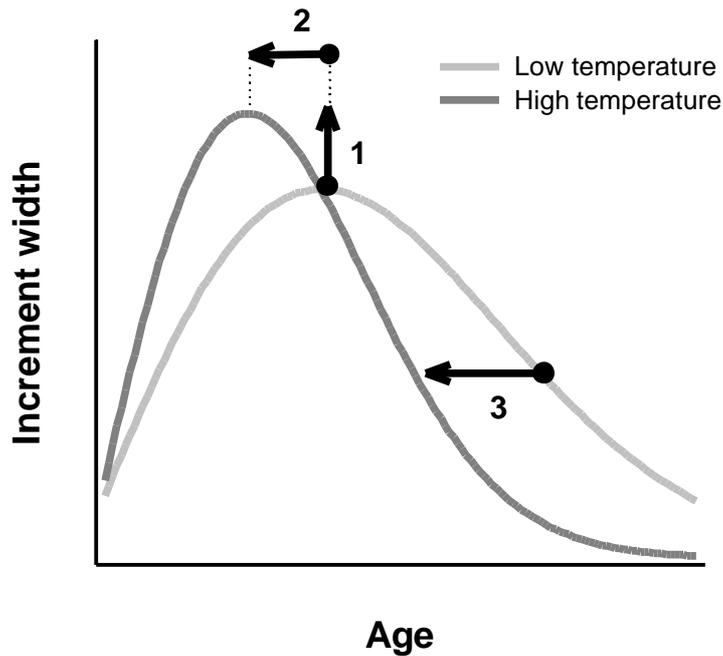


Fig.8: Conceptual diagram illustrating the 3 effects (arrows) of temperature on the shape of the otolith growth trajectory throughout the larval and juvenile stages of sprat (~ first 5 months). Individuals experiencing higher temperatures have broader peak increments (1), which they reach earlier after *DDF* (2), and are also younger at the post-peak inflection point of their otolith trajectory (3).

reached earlier after *DDF* (Fig. 8) and at lower otolith sizes. Thus, fast growing sprat larvae were smaller at the point of maximum growth, although the magnitude of the effect was probably exaggerated, because faster growing individuals often form relatively smaller otoliths (Campana 1990, Baumann et al. 2005). However, temperature-mediated higher growth rates of larvae born later in the season are well documented for temperate fish species (e.g. Rice et al. 1987) and appear positively related to cohort survival (Limburg 1996, Fowler & Jennings 2003). Importantly, the subsequent decline in growth rates occurred independently of the seasonal temperature curves, i.e. increment widths started to decrease well before *SST*'s did at the end of August 2002. This could be due to ontogenetic constraints of otolith and somatic growth, i.e. beyond a certain size or developmental stage (e.g. metamorphosis), sprat juveniles cease to grow faster in length in spite of still rising ambient temperatures. (3) In effect, thus, higher temperatures experienced during the larval stage shortened the period of faster growth, as suggested by the negative relationship between age at the second inflection point (parameter *b*) and temperature (Fig. 8). Hence, the observed trade-off between higher larval, but more rapidly declining juvenile growth rates may have resulted in the remnant *TL* differences between YoY-sprat that were not explained by shifted spawning or *DDF*-distributions. (4) Seasonal temperature variability in 2002 (spring to autumn) was about six times greater than spatial temperature differences between Baltic areas, which is consistent with the strong *DDF* but weaker area-effect on YoY-growth patterns. The lacking correlation between *SST* and increment width at the

first inflection point (parameter  $c$ ) was rather due to inappropriate temperature values, given that the first inflection point was predicted very early after first feeding (1-3 days). Thus, this parameter was probably influenced by temperatures during the yolk-sac stage (Pepin et al. 2001), when sprat larvae in the Baltic Sea still occur at intermediate water depths (Wieland & Zuzarte 1991) and likely experience temperatures that are poorly reflected by *SST*.

The present approach of fitting 5-parameter Weibull-functions to area- and *DFE*-specific increment width-at-age data produced curves similar to those published by Bartsch (2002), who incorporated a temperature-dependent term into logistic growth functions in order to model growth of larval and juvenile mackerel *Scomber scombrus*. In the case of sprat growth trajectories, the use of Weibull-functions was advantageous over the derivative of the logistic formulation, because it allowed for different curvatures and asymmetric inflection points left and right to the growth peak. However, both studies suggest that growth trajectories of fish throughout their first year of life follow similar ontogenetic patterns of increasing larval and decreasing juvenile growth rates, which are modified by ambient temperature conditions (Fig. 8). Over the last 30 years, a wealth of corroborating otolith trajectories has been published for a number of species in different marine systems, although most studies encompassed only parts of the full 0-group pattern (e.g. Meekan & Fortier 1996, Folkvord et al. 1997, Fowler & Jennings 2003, Allain et al. 2003, but see Kurita et al. (2004) for an exception).

In summary, the substantial length differences between north-eastern Baltic YoY-recruits and their conspecifics in central and western regions of the Baltic Sea may have resulted, first, from the temperature-induced delay in spawning activity in area 4, which likely entailed the shifted *DFE*-distribution of YoY-survivors. This in turn led to higher experienced temperatures for individuals in area 4 during the larval and early juvenile stage, and thus elicited higher larval but much lower juvenile growth rates; the latter amplified by the more rapid temperature decline in fall in the north-eastern Baltic. Despite the narrower *DFE*-distribution in area 4, the variability in the observed *TL*'s was comparable to the other Baltic areas, which may be due to the fact that higher experienced temperatures also appear conducive to a higher growth variability (Houde 1989). On the other hand, the narrower *DFE*-distribution just appeared to reflect the shorter mean spawning season of north-eastern Baltic sprat, suggesting that in 2002 the *relative* (in contrast to the absolute) 'survival window' was not substantially smaller than in other Baltic sprat spawning grounds. The question remains, though, whether outstandingly high growth rates of north-eastern Baltic sprat larvae were only a consequence of atypically high summer temperatures in this area in 2002 or whether such a pattern could be generalized. After adjusting for the effects of temperature, larval residual growth rates were highest for YoY-survivors in the central Baltic Sea (area 2, Fig. 7), which could have been due to a number of unresolved factors, most importantly, potential spatial differences in food availability.

Over the last decades, a large body of papers, working reports, and episodic observations has remarked on the obvious existence of a west-east gradient in Baltic sprat morphology (e.g. Grygiel 1978, Aps et al. 1981, Aro 1989), which was fully corroborated by the present study. The consistently greater lengths and weights of sprat individuals in the western and central, compared to the eastern and north-eastern Baltic Sea have stimulated the recurring idea of at least two existing sub-populations of Baltic sprat with different growth characteristics and thus potential implications for the current single-stock management practice (Aps 1991, ICES 2005a). However, the combination of otolith microstructure analysis and satellite-based SST's suggested that most of the regional differences in Baltic YoY-sprat lengths are primarily a consequence of spatial and temporal differences in experienced temperature, thereby highlighting the key role of this environmental factor for growth variability in marine fish.

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**- PAPER 3 -**

**SPRAT RECRUITMENT IN THE BALTIC SEA: THE IMPORTANCE OF  
TEMPERATURE AND TRANSPORT VARIABILITY DURING THE LATE LARVAL  
AND EARLY JUVENILE STAGES**

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**ABSTRACT**

We tested the hypothesis that variable temperature conditions and larval drift patterns significantly influence inter-annual recruitment strength of age 0 sprat, *Sprattus sprattus*, in the Baltic Sea. Temperatures were compiled from the ICES Oceanographic database and analysed per month and depth-stratum, while drift patterns were studied by means of a hydrodynamic circulation model coupled to Lagrangian particle simulations. From the latter, we derived the annual ‘bottom-depth anomaly’ (BDA), an index that likely reflected the variable degree of annual larval transport from the central, deep spawning basins to the shallow coastal areas of the Baltic. BDA’s based on drifter cohorts released late in the season (July) were highly significantly correlated to sprat recruitment success and explained 80% and 75% of the overall variability during the periods 1979-1990 and 1991-2003, respectively. The drift index suggested that years of strong larval displacement towards southern and eastern Baltic coasts corresponded to relative recruitment failure, while retention within the deep basins was linked to relative recruitment success. The strongest correlation between temperature and recruitment occurred during August in surface waters, explaining 73% of the overall variability. The two synergistic approaches allowed to conclude that new year classes of Baltic sprat are predominantly comprised by individuals born late in the season and are determined in strength mainly by processes acting during the late-larval and early juvenile stages. The two proxies could prove valuable for recruitment predictions, although the mechanisms underlying the strong coupling between temperature, drift, and recruitment are not yet fully understood, mainly because of unresolved spatial zooplankton and predation dynamics in the Baltic Sea.

**Key words:** Temperature-recruitment relationship, 3D hydrodynamic circulation model, Lagrangian particle simulations, bottom depth anomaly, MSVPA

## INTRODUCTION

Explaining and predicting recruitment variability are pivotal goals in fisheries science (Sissenwine 1984). For sprat, *Sprattus sprattus*, currently the most abundant, commercially exploited fish species in the Baltic Sea, sustainable management has been challenged by large inter-annual fluctuations in recruitment success, particularly during the last decade (ICES 2005a). Although previous studies found spawning stock size (Köster et al. 2003) and temperature-dependent gonad maturity or egg mortality (MacKenzie and Köster 2004; Köster et al. 2003) to be of significant influence, it has been argued that differential survival patterns throughout the late-larval and early juvenile stages may be more determinant for Baltic sprat recruitment variability (Köster et al. 2003).

While sprat eggs and yolk-sac larvae are found at intermediate water depths in the Baltic, feeding sprat larvae predominantly occur in surface waters (Voss et al. 2003), where variable environmental conditions, such as temperature and food availability, may affect their growth- and therefore survival rates (Houde 1989). In surface waters, sprat larvae would also be particularly susceptible to wind-driven ocean circulation, which may cause retention or advection to areas suitable or unsuitable for survival (Sinclair 1988). Following this rationale, Baumann et al. (2004) used a realistic hydrodynamic circulation model in combination with Lagrangian particle simulations to study 23 years (1979-2001) of larval drift patterns during an average sprat spawning season (April-July). Their “retention index”, defined as the annual proportion of drifters collected within predefined rectangles in- and outside of the Bornholm Basin, a major sprat spawning area (Köster et al. 2001), was significantly related to the number of age 0 sprat recruits in the Central Baltic. The relationship suggested that retention within the deep basin would be beneficial for recruitment, while dispersion and transport to south-eastern Baltic shores would lead to relative recruitment failure. Short-comings of the approach were that (i) the index did not explain the full recruitment time-series but only the most recent 12 years, (ii) that it was restricted to sprat from the Bornholm Basin, and (iii) that it relied on the definition of arbitrary rectangles in the model domain.

Here we present two alternative proxies to explain sprat recruitment variability within the entire Baltic Sea and over the whole, extended time-series of 25 years (1979-2003). The first index was again based on hydrodynamic modelling in conjunction with Lagrangian particle simulations, but instead of final horizontal drifter positions, we considered the bottom depth at the daily position of each tracked particle to be a relative measure of its distance to the shore. The underlying rationale was that years of predominant larval transport into shallow coastal areas should result in anomalously shallow particle distributions. We further investigated potential relationships between sprat recruitment and ambient temperature conditions at various depths and months in

the Baltic Sea, asking where and when during the year such correlations were strongest and thus most determinant for recruitment variability.

## MATERIAL AND METHODS

### *Hydrodynamic circulation model*

A comprehensive description of the hydrodynamic model and the Lagrangian particle-tracking technique has recently been published by Hinrichsen et al. (2005). Briefly, the 3-dimensional, baroclinic circulation model of the Baltic Sea (Lehmann 1995; Lehmann and Hinrichsen 2000) is an adaptation of the free surface Bryan-Cox-Semtner model (Killworth et al. 1991), with a model domain that encompasses the entire Baltic Sea including the Gulf of Bothnia, Gulf of Riga, the Belt Seas, Kattegat, and the Skagerrak with a realistic bottom topography. The horizontal resolution is 5 km, and 60 vertical levels are specified with a thickness chosen to best represent the different sill depths in the Baltic Sea. The model is forced by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI, Norrköping) and river runoff taken from a mean runoff database (Bergström and Carlsson 1994), both for a time-series of 25 years (1979-2003). The 3-dimensional velocity fields extracted from the circulation model were then used to predict Lagrangian drift routes of passive particles seeded into the model domain. Along each particles' drift path, modelled bottom depths (i.e. the water depth at the current position of each particle) were initially stored in 6 hour intervals, but later averaged to obtain daily estimates.

### *Particle releases and indices*

Particles releases were intended to simulate the transport of feeding sprat larvae during an average spawning season (Köster and Möllmann 2000, Karasiova 2002) for each of the 25 years in the Baltic Sea. Initial horizontal drifter positions were based on average sprat egg distributions in the Baltic Sea (Köster 1994, Makarchouk unpublished data), assumed to be a proxy for the spatial distribution of first feeding sprat larvae. The vast majority of particles was released inside the 40 m isobath of the 4 major Baltic spawning grounds Arkona Basin, Bornholm Basin, Gdansk Deep, and Gotland Basin (Fig. 1). All drifters were seeded and forced to remain within the 5-10 m depth layer, because feeding sprat larvae predominantly occur in surface waters and appear not to exhibit clear vertical migration patterns (Voss 2002, Voss et al. in press). Each year, particle cohorts representing batches of first feeding, passively drifting sprat larvae were released on 21 April (day 111<sup>†</sup>) and then every 10 days until 10 July (day 191). Each of

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<sup>†</sup> Dates became shifted by one day in leap years, e.g. Julian day 111 corresponded to the 20<sup>th</sup> of April

these 9 larval ‘pulses’ per year consisted of 2671 particles that were seeded in regular spatial intervals of about 5 km (Fig. 1).

Two different approaches were tested regarding the end of the simulations. First, particles were tracked through the model domain for variable drift periods of 50-130 days, until a common collection date on 28 August (day 240). This arbitrary date was chosen to compromise sufficient drift times for late released larval batches, while avoiding too long drift periods for oldest larvae, because for the latter active swimming becomes likely. In a second approach, drifters were tracked for fixed periods of 50 days, entailing 9 different collection dates (9 June to 28 August).

For an integrated view of annual drift patterns, daily bottom depths were averaged by year and release date across all 2671 particles, regardless of their individual positions in model domain. Then, because we were interested in anomalies rather than absolute values, average daily bottom depths ( $D_{ikl}$ ) were standardized to zero mean and unit deviation across all 25 years modelled (i.e.  $S_{ikl} = (D_{ikl} - m_{kl}) \cdot sd_{kl}^{-1}$ , where  $S_{ikl}$  is the standardized bottom depth of the  $i^{\text{th}}$  year, the  $k^{\text{th}}$  release, and the  $l^{\text{th}}$  day, and  $m$  and  $sd$  are the day- and release-specific mean and standard deviation of bottom depth across all 25 years, respectively). Finally, daily standardized bottom depths were averaged over the considered simulation period; i.e. either over 50 days after release (fixed drift periods) or over release-specific variable drift periods (fixed collection date). Annual, mean standardized bottom depths are hereafter referred to as bottom depth anomalies (*BDA*).

#### *Temperature, recruitment, and larval abundance data*

Temperatures in the Baltic Sea were compiled from the ICES Oceanographic Database<sup>‡</sup>, containing two main data sets of a) surface temperatures (0-10 m) and b) depth-specific CTD and bottle measurements. From the combined data, we selected all available temperatures between 1974-2003 and restricted them further to the area of the major Baltic sprat stock abundance (13-23°E, 53-60°N, ICES 2005b). Data were subsequently aggregated to obtain monthly means per year and 10 m depth-stratum down to a water depth of 70 m (i.e. 0 to <10, 10 to <20, ... 60 to <70 m). Temperature means were derived from on average 223 observations available per month, depth-stratum, and year ( $N_{\text{min-max}} = 1-8063$ ).

Both temperature and *BDA* time-series were tested for correlations to the abundance of age 0 sprat during the 3<sup>d</sup> quarter of each year in the entire Baltic Sea (ICES sub-divisions 22-32). The abundance estimates (1974-2003) were taken from the most recent area-aggregated multi-species virtual population analysis (MSVPA, ICES 2005b), which also provided the updated time-series of sprat spawning stock biomass

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<sup>‡</sup> <http://www.ices.dk/ocean/INDEX.HTM>

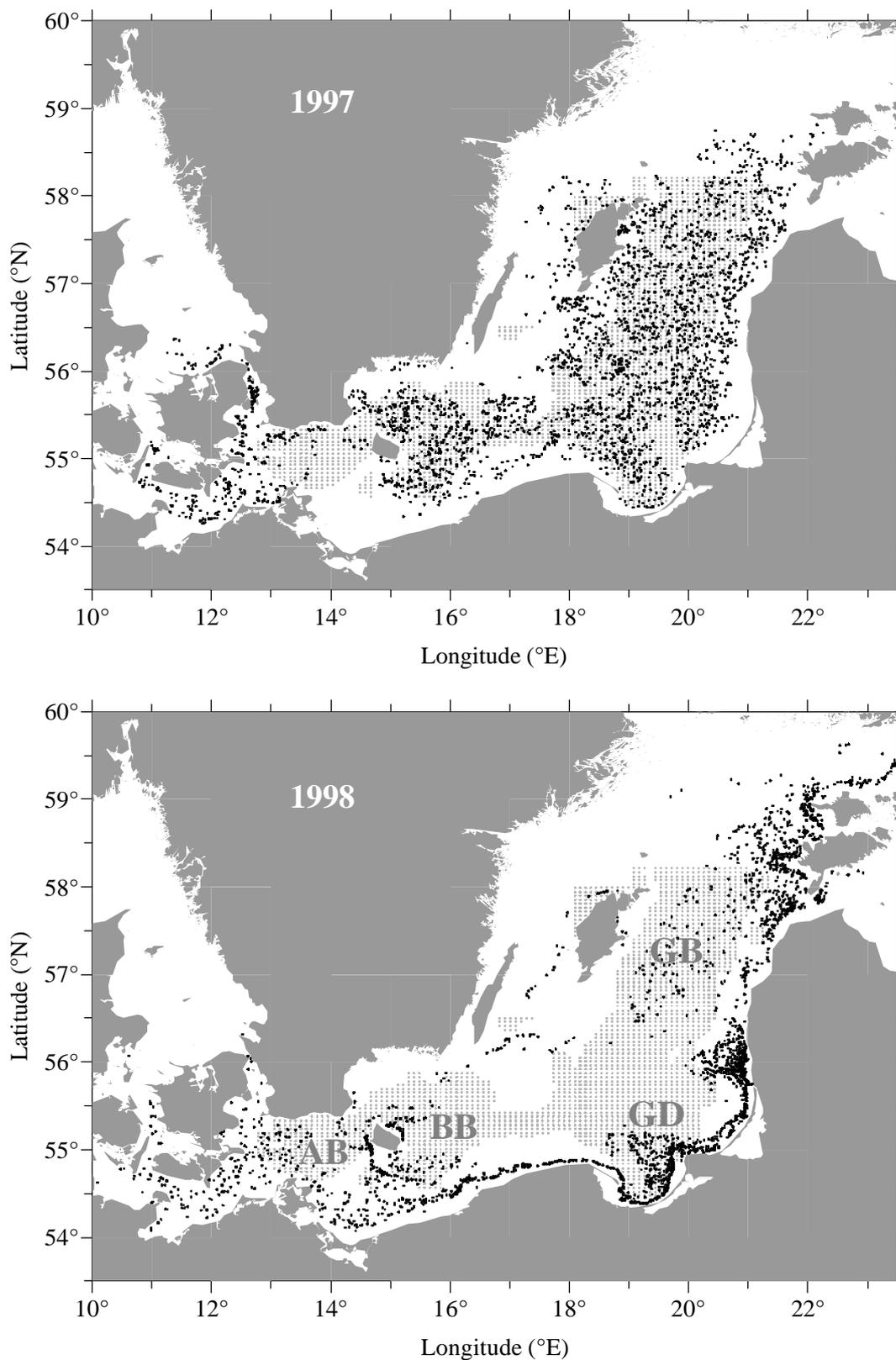


Fig.1: Output example of Lagrangian particle simulations showing initial (small grey dots) and final particle distributions (bigger black dots) in 1997 and 1998, two years with markedly different drift patterns. In both cases, 2671 drifters were released on 10 July (d191) within areas of main sprat spawning effort and tracked for 50 days until 28 August (d240). AB = Arkona Basin, BB = Bornholm Basin, GB = Gotland Basin, GD = Gdansk Deep.

(SSB). Data on larval sprat abundance were available from various ichthyoplankton surveys in the Bornholm Basin, Gdansk Deep, and Gotland Basin between 1979-1999 (stations deeper than 60m), as described by Köster et al. (2003).

Potential temperature- and drift-recruitment relationships were analysed through linear or multiple linear regressions (SPSS<sup>®</sup> 10.0.7), with significant relationships reported for P-levels below 0.05. Cross-correlations between two time-series were assessed using Pearson's bi-variate, two-sided correlation coefficient (SPSS<sup>®</sup> 10.0.7). When testing regressions slopes or intercepts for significant differences, the method after Zar (1984) was applied, which is implemented in the GraphPad<sup>®</sup> Prism 3.0 Software. Durban-Watson statistics were used as a measure of autocorrelation within each time-series.

## RESULTS

### *Transport (BDA) and recruitment*

For virtually all 9 drifter cohorts per year, final particle positions on day 240 (28 August) were indicative of considerable inter-annual differences in Baltic circulation patterns. Two main scenarios could be distinguished: a) years of predominant particle retention within the central deep basins, likely induced by prevailing weak to variable easterly winds in summer (e.g. 1997, Fig. 1), and b) years of large-scale particle

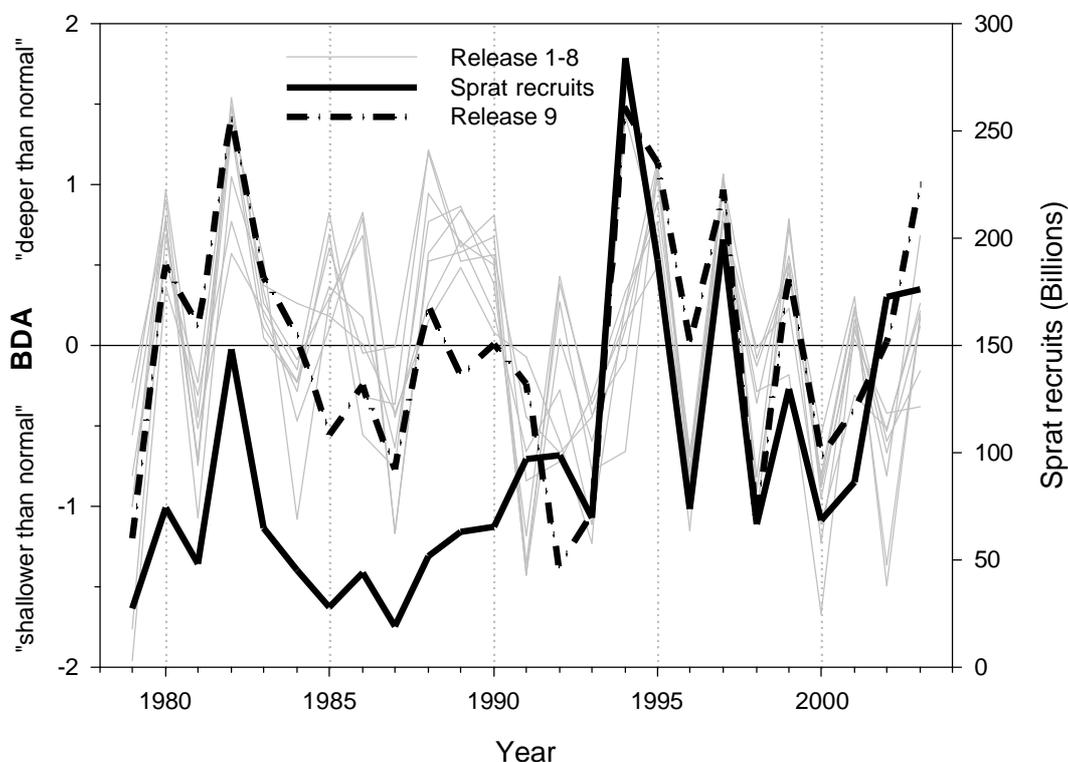


Fig.2: Release-specific bottom-depth anomalies derived from long-term Lagrangian particle simulations. The 9 lines correspond to the 9 different release dates (d111-d191) per year. The thick solid black line shows recruitment strength of 0-group Baltic sprat derived from area- aggregated MSVPA-runs. The best linear relationship was found for  $BDA_9$  ( $r^2=0.50$ , thick, dash-dotted line).

displacement and dense accumulation along southern, south-eastern, and eastern Baltic coastlines, probably as a consequence of prevailing strong to variable westerly winds in summer (e.g. 1998, Fig. 1). Particle displacement towards Swedish coastlines (westward drift) was generally negligible.

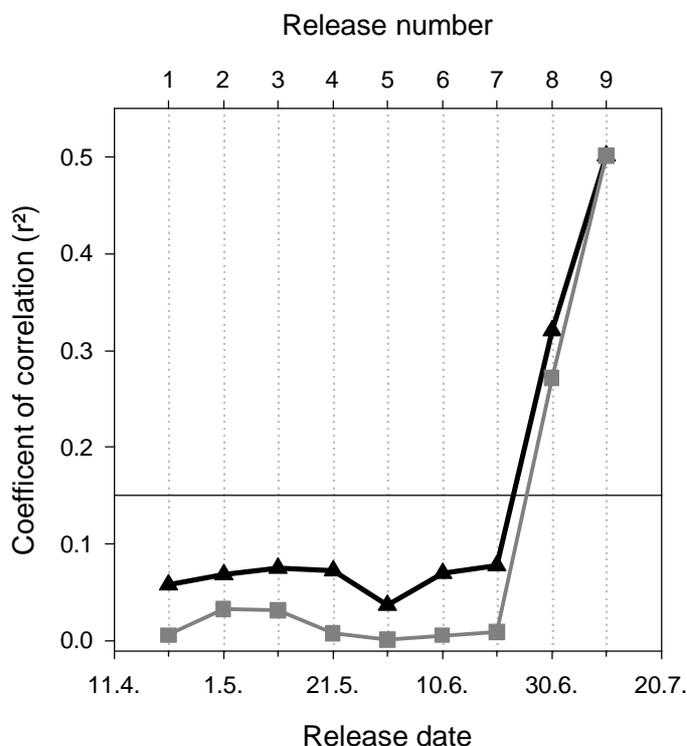


Fig.3: Correlation coefficients of linear regressions of Baltic sprat recruitment success on release-specific *BDA*'s. Grey lines correspond to fixed 50 days drift periods, while black lines correspond to relationships with variable drift times but a common collection date (day 240). Only relationships above  $r^2=0.15$  (thin line) were significant ( $P<0.05$ ).

Release-specific *BDA*'s ( $BDA_{1-9}$ ) reflected these inter-annual differences well, with positive and negative *BDA*'s indicating years when the majority of sprat larvae likely drifted over “deeper than normal” or “shallower than normal” waters, respectively (Fig. 2). Indices derived from variable drift periods (fixed collection on 28 August) were all significantly cross-correlated ( $P < 0.05$ ), in contrast to indices based on fixed 50 days drift periods, where significant cross-correlations did not exceed two subsequent release dates (e.g.  $BDA_3$  was correlated to  $BDA_2$  and  $BDA_{4-5}$  but not  $BDA_{6-9}$ ).

Linear regressions of Baltic sprat age 0 abundance on release-specific *BDA*'s revealed no significant relationships for indices based on early release dates 1-7, whereas  $BDA_8$  and  $BDA_9$  were significantly correlated to recruitment success (Fig. 3). The best correlation was found for  $BDA_9$ , which was based on particles tracked between 10 July and 28 August and explained 50% of the overall sprat recruitment variability (Figs. 3,4). The residuals of this relationship showed a clear decadal pattern: all data points between 1979-1990 laid below the regression line, while all data between 1991-2003 (except 1996) were found above the regression line. In other words, the linear recruitment- $BDA_9$  regression separated the 1980-ies from the 1990-ies (Fig. 4). If both periods were considered separately,  $BDA_9$  explained 80% and 75% of the recruitment

variability between 1979-1990 and 1991-2003, respectively (Fig. 4). The two regression lines had common slopes ( $P = 0.29$ ) but significantly different intercepts ( $P < 0.001$ ).

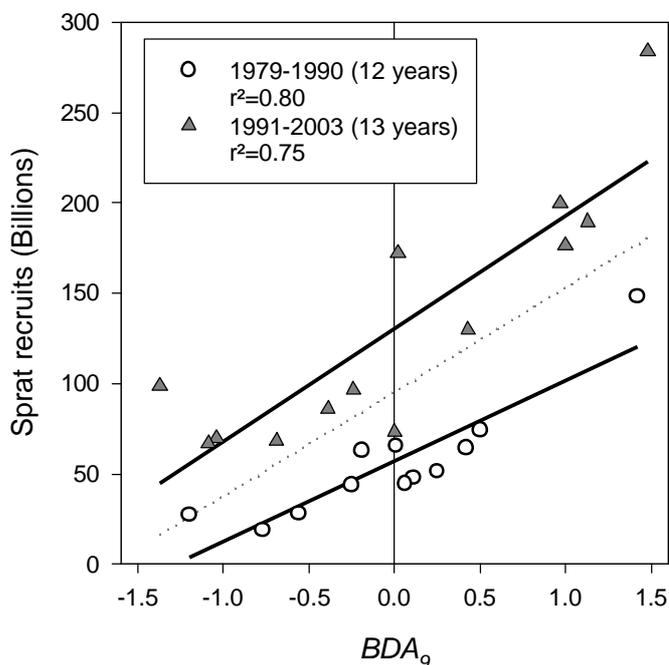


Fig.4: Linear relationships between  $BDA_9$  and age 0-sprat recruitment success in the Baltic Sea for the period 1979-1990 (open circles) and 1991-2003 (grey triangles). Solid regression lines for both periods have significantly different intercepts but non-significant differences in slopes. The dotted line shows the regression line of all data.

#### Temperature and recruitment

Out of the 84 linear regressions (12 months x 7 depth strata), temperature was significantly and positively correlated ( $P < 0.05$ ) to Baltic sprat recruitment success in 31 cases, thereby revealing a remarkable month- and depth-specific pattern (Fig. 5). Significant temperature-recruitment correlations were already observed in January for depths greater 30m, which are bound to reflect pre-spawning processes of the adult stock. February temperatures were uncorrelated to recruitment. Between March and July, significant but loose correlations to recruitment developed mostly in mid-water depths (20-60m,  $r^2_{\max} = 0.21$ ), with April correlations having the broadest depth range. However, from July to August, correlations shifted notably to surface waters, with August temperatures in 0 to 10 m explaining 66% of sprat recruitment variability between 1974-2003 (Fig. 5). The residuals of this regression showed notable yet non-significant signs of non-linearity ( $P = 0.43$ , runs test, GraphPad<sup>®</sup> Prism 3.0) and rather suggested a quadratic fit to the data, which explained 73% of the overall recruitment variability (Fig. 6). A shift in the relationship between decades, as observed for  $BDA$ , was not apparent for temperature. Surface temperatures were still significantly correlated to recruitment strength in September and October ( $r^2_{\max} = 0.22$ ), whereas in November a loose but significant correlation re-appeared in deeper water layers (50-70m,  $r^2_{\max} = 0.20$ , Fig. 5).

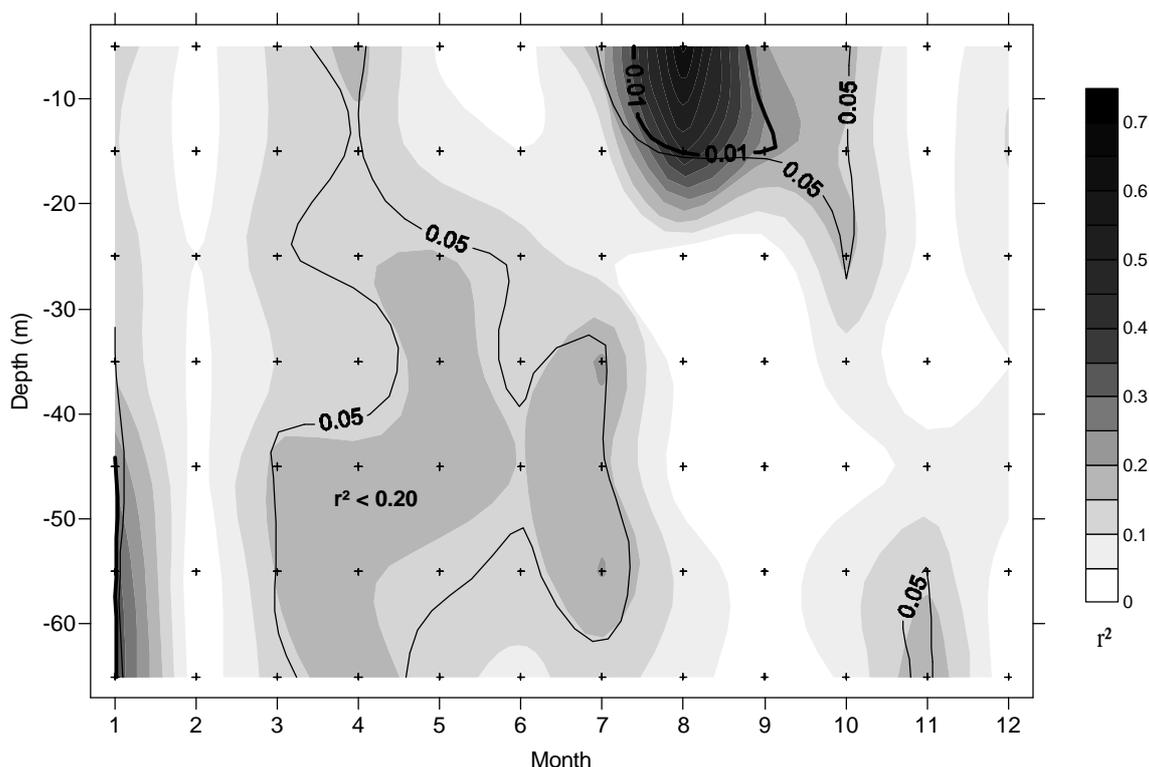


Fig.5: Summarizing the results of sprat age 0 recruitment in the Baltic Sea (1974-2003) regressed linearly on ambient temperature for different depths and months. Shading and isolines correspond to  $r^2$ - and P-values, respectively, while crosses refer to the data grid points used to create the contour plot (Kriging).

*Recruitment models*

The strong cross-correlation between surface temperature in August and  $BDA_0$  ( $P < 0.001$ ,  $r^2 = 0.46$ ) precluded the inclusion of both variables in a common recruitment

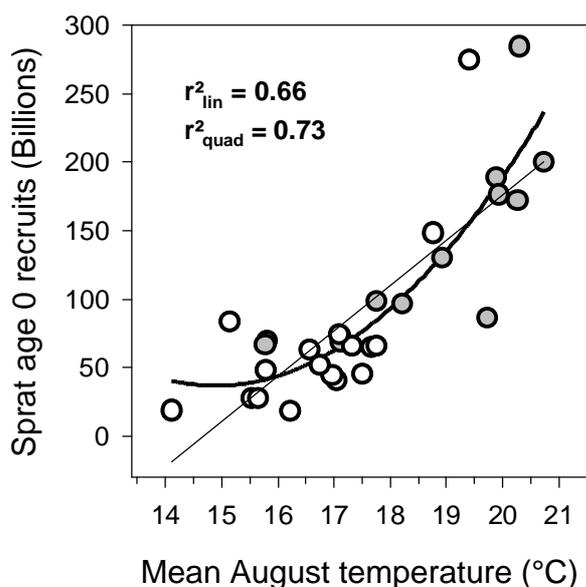


Fig.6: Linear vs. quadratic relationship between mean surface temperature in August (0-10m) and Baltic sprat recruitment success (1974 - 2003). Empty and grey symbols correspond to the periods 1974-1990 and 1991-2003, respectively.

model. We therefore constructed two different models (Table 1), one considering sprat age 0 abundance to be a quadratic function of August temperature (1974-2003), and the other using  $BDA_0$  and spawning stock biomass as independent variables in a multiple linear regression (1979-2003). The SSB time-series was not cross-correlated to  $BDA_0$ , while at the same time showing a corresponding decadal trend with very low biomasses during the 1980-ies (1979-1990) and considerably higher biomasses between 1991-2003. While SSB alone explained 28% of the recruitment variability

Table 1: Parameter estimates, their significance level, and  $r^2$ -values for two recruitment models using  $BDA_9$ +SSB or surface temperature (0-10 m) in August to predict sprat recruitment strength

Dependent variable	Time series	Independent variables	Parameter estimate	$P$	$r^2$	Durbin-Watson
Age 0 sprat abundance (entire Baltic)	1979-2003	Constant	$4.51 \times 10^{10}$	0.003	0.734	1.571
		$BDA_9$	$5.51 \times 10^{10}$	<0.001		
		SSB (entire Baltic)	$5.23 \times 10^4$	<0.001		
	1974-2003	Constant	$1.3 \times 10^{12}$	0.008	0.731	
		Aug temp	$-2 \times 10^{11}$	0.003		
		(Aug temp) <sup>2</sup>	$5.8 \times 10^9$	0.001		

( $P=0.007$ ), the multiple linear regression using both  $BDA_9$  and SSB achieved 73% (Fig 7a), which was identical to the recruitment prediction using August temperature only (73%, Fig. 7b). However, both models predicted different years of sprat recruitment success differently well. While sprat recruitment was considerably underestimated by the linear  $BDA_9$ +SSB model in 1992 and 2002, the quadratic temperature model yielded much closer estimates (Fig. 7). The poor recruitment year 1996 was also much better predicted by the temperature compared to the  $BDA_9$ +SSB model. On the other hand, temperature-based predictions were considerably poorer than the  $BDA_9$ +SSB model in 1982 and 1987, but particularly in 2001. Both models equally underestimated the outstanding recruitment year 1994 (Fig. 7).

## DISCUSSION

### *BDA as a drift proxy*

Bottom depth anomalies have proved a meaningful method to condense and quantify the large amounts of information produced by long-term Lagrangian simulations, and reflected well the variable degree of annual particle transport from the central deep spawning basins of the Baltic Sea to shallower coastal waters (e.g. Figs. 1,2). In addition, averaging daily standardized bottom depths along particle trajectories effectively integrated the drift information over the entire simulation period, which was considered advantageous over the approach by Baumann et al. (2004), who only analysed final horizontal particle positions. This did not affect the key results, though, which were similar for both studies and indicated that years of relative particle retention or coastal displacement corresponded to relative sprat recruitment success or failure, respectively. Both studies were also consistent in finding the strongest correlations to recruitment for particles released late in the season.

However, when moving from particles to living organisms, inferences drawn from Lagrangian simulations rely on the assumption that passive drifter trajectories reflect the average transport patterns of the planktonic species or life-stage studied. In demersal

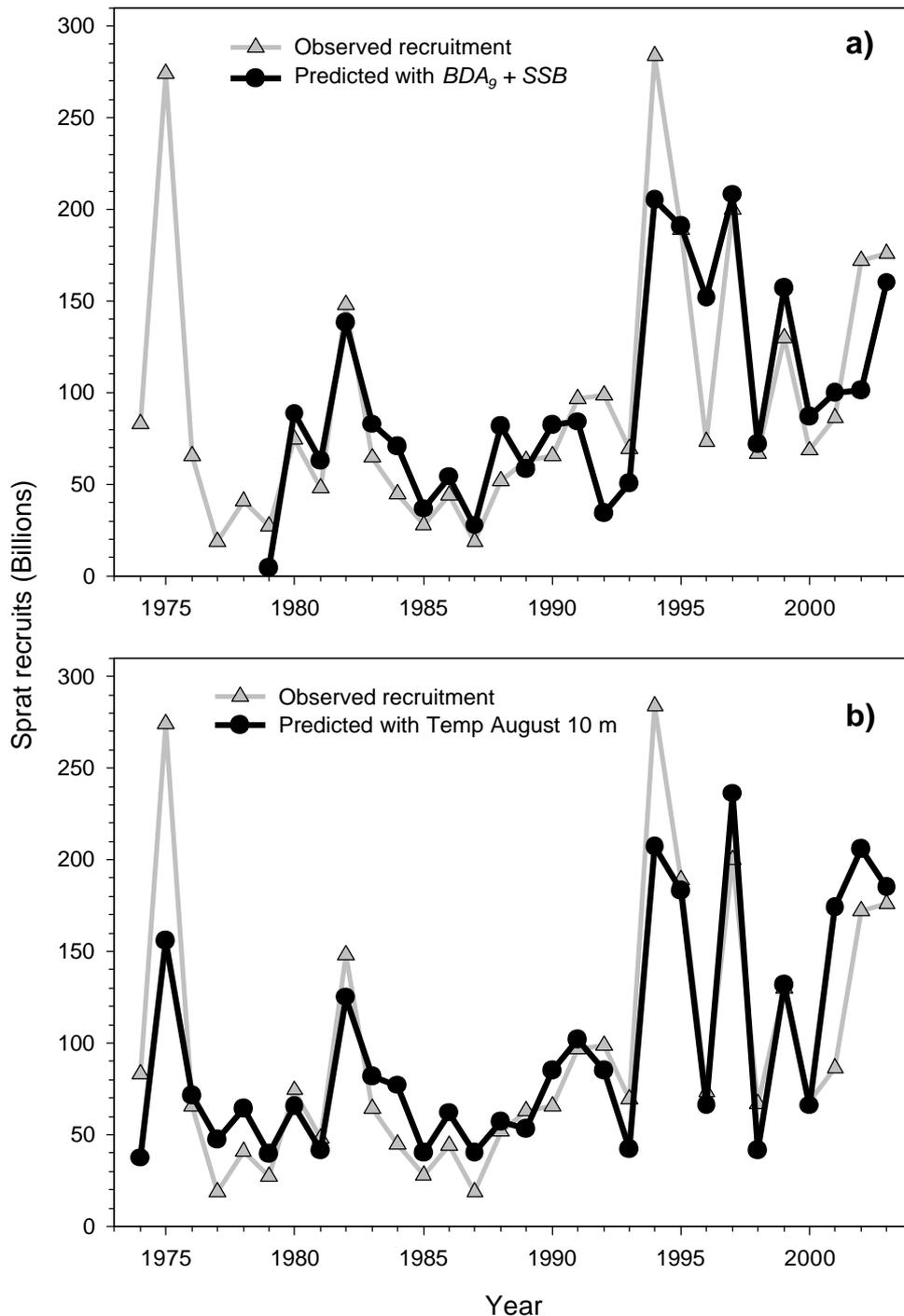


Fig.7: Time-series of observed and predicted recruitment of Baltic age 0-sprat. a) Independent variables used in the multiple linear regression were  $BDA_9$  and SSB, explaining 73% of the variability between 1979-2003. b) Independent variable used in a quadratic regression was mean surface temperature (0-<10m) in August in the Baltic Sea, explaining 75% of recruitment variability between 1974-2003.

fish like cod or flatfish, juvenile settlement concludes the susceptibility to ocean circulation and thus sets a natural limit to drift studies (e.g. 65 days, Hinrichsen et al. 2003). Such a limit is not as readily defined in pelagic species like sprat. The onset of active swimming behaviour or schooling may not necessarily preclude Lagrangian drift simulations, if late-larvae or early juveniles keep moving randomly within a water body

that is subject to predictable physical forcing. For example, Allain *et al.* (2003) successfully used a hydrodynamic model to infer likely origins of approximately 100 day old and 80 mm long (Cermeno *et al.*, 2003) juvenile anchovy, *Engraulis encrasicolus*, in the Bay of Biscay. For the Baltic Sea, Hinrichsen *et al.* (2005) compared average Lagrangian drifter distributions with field data on 0-group sprat abundance, as determined by annual hydroacoustic surveys. They found model and field distributions in generally good accordance, showing the highest mean October abundance of sprat juveniles along the southern and eastern Baltic coasts. The authors also reported that the inclusion of simulated larval vertical migration did not produce contradictory results. It may therefore be justified to assume that average transport patterns of sprat larvae and early juveniles were generally reflected by the present drift model.

Still, longer simulation periods generally increase uncertainty, which could have been a contributory but not the only reason for the apparent lack of correlation between early released particles and recruitment strength, because fixed 50 days and variable drift periods produced identical results. Furthermore, both approaches did not show a gradual but a very sudden shift from non-significant to highly significant *BDA*-recruitment correlations from early (April-June) to late released particles (July), which may reflect the seasonally different contribution of larval production to recruitment. In other words, sprat larvae born early in the season may generally play a negligible role in the recruitment process, while new sprat year classes may predominantly consist of individuals born relatively late in the season. The hypothesis is supported by recent findings of Voss *et al.* (in press), who studied larval sprat survival and condition in relation to food availability in the central Baltic Sea during the season 2002. The authors presented evidence that the late larval stages critically relied on the abundance of larger copepodites and adult copepods, which were scarce in April-May but significantly more abundant in June-July 2002. In addition, Baumann *et al.* (2005a) inferred distributions of days-of-first-feeding (DFF, a proxy for hatch-date) from otolith microstructure analyses in newly recruited 0-group sprat caught in October 2002 in the Baltic Sea. Depending on the Baltic region, DFF-distributions of sprat survivors peaked between the end of June and mid-July 2002, which is consistent with the present conclusion.

If sprat recruitment variability is determined mainly by different survival patterns of larvae born late in the season, what potential mechanisms could cause the observed dependence on circulation variability? Previous studies demonstrating the coupling between recruitment success and advective processes in a number of species and for different marine systems (reviewed e.g. by Sissenwine 1984, Leggett and Deblois 1994) have mostly attributed their results to food availability (e.g. Werner *et al.* 1996, Borja *et al.* 1998, Skogen 2005, Zeldis *et al.* 2005) or feeding success (Crecco and Savoy 1987). For Baltic cod larvae, Hinrichsen *et al.* (2002, 2003) showed that retention *to* but also

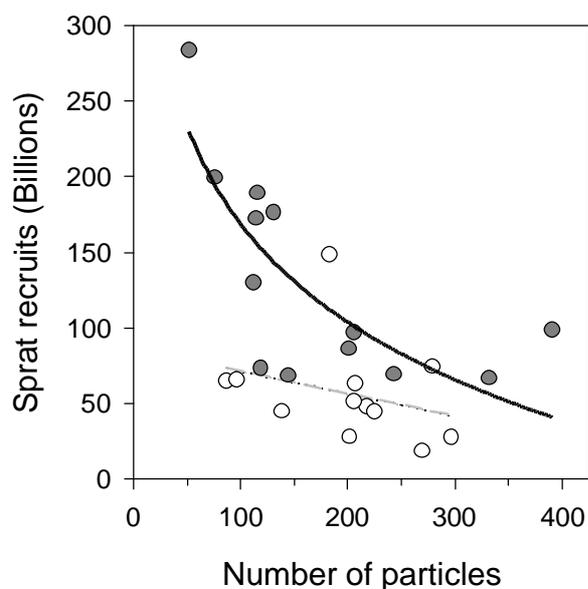


Fig.8: Relationship between sprat recruitment success and the number of Lagrangian drifters (out of 2671) that had at least one "next neighbour" within a 0.5 km radius of their final position. A significant ( $P=0.001$ ) logarithmic relationship was found only for the period 1991-2003 (grey circles). Particles were released on 10 July (release 9) and tracked for 50 days.

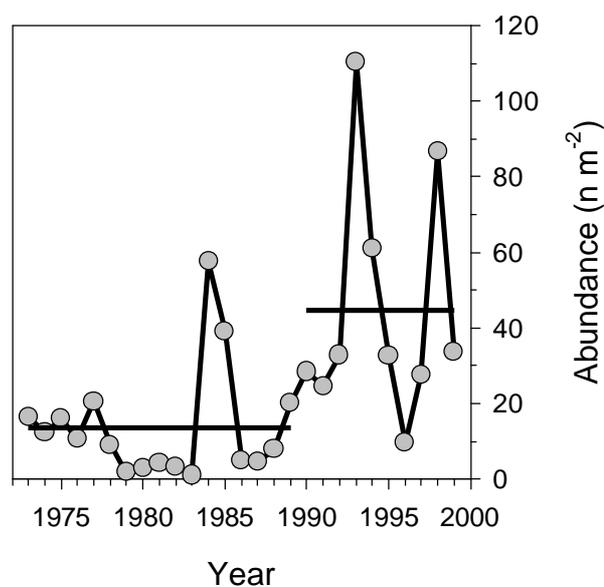


Fig.9: Mean abundance ( $n \cdot m^{-2}$ ) of sprat larvae in the main Baltic spawning grounds Bornholm Basin, Gdansk Deep, and Gotland Basin between May - July. Thick solid lines depict the significantly ( $P < 0.05$ ) different means for the periods 1973-1989 and 1990-1999.

advection *out of* the central Bornholm Basin could have beneficial effects to survival, depending on the abundance of the calanoid copepod *Pseudocalanus elongatus*. For sprat, only general relationships between stock size (Alheit et al. 2005) or 0-group numbers (Kornilovs et al. 2001) and the abundance of the two most important prey species *Acartia* spp. and *Temora* spp. have been reported, but whether spatial differences in zooplankton abundance potentially result in better feeding conditions for larvae retained in the central Baltic basins, still requires investigation. Apart from causing different transport scenarios, variable atmospheric forcing also affects turbulence levels, and the probability that larvae will successfully capture encountered prey items has been shown to decline non-linearly with turbulence (MacKenzie et al. 1994). However, on the population level this mechanism is not unequivocally supported by field studies (MacKenzie 2000), and appears to be of less importance for older larvae and early juveniles, where turbulence levels probably need to be unnaturally high to cause significant detrimental effects on feeding success.

It has also been suggested that density-dependent processes, operating during the late larval/early juvenile stages, may induce significant recruitment variability (Cushing 1974, Leggett and DeBlois 1994). To test this concept on our drift model, we calculated the distance between each particle and its "next neighbour" on 28 August (end of simulation). It was observed that during years of large-scale coastal transport (e.g. 1998, Fig. 1), particles were found in much denser aggregations than during retention years

(e.g. 1997), with particle density being significantly and inversely related to recruitment strength (Fig. 8). The fact that such a relationship was only apparent throughout the last decade, appears to be consistent with the significantly higher mean larval abundance observed between 1991-1999 than during the period 1973-1990 (Fig. 9). In addition, a recent study in the western Baltic Sea compared otolith-based growth rates of sprat recruits caught during the hydroacoustic survey in October 2003 with those of pre-recruits caught at the end of August 2003 in very shallow coastal waters (Baumann submitted). While back-calculated *larval* growth rates were similar between both groups, growth rates of pre-recruits, but not those of successful 0-group sprat, declined sharply just after metamorphosis, possibly caused by competition for limited food resources. However, density-dependent processes cannot be the *only* mechanism underlying the established link between larval/early juvenile transport and recruitment variability, because the effect of *BDA* on recruitment was similarly strong during both the 1980-ies (1979-1990) and the 1990-ies (1991-2003), as suggested by the common slopes of the linear relationships (Fig. 4). The significantly shifted intercepts, on the other hand, appeared to reflect the decadal changes in sprat spawning stock biomass with probable consequences for egg- and larval production.

#### *Temperature and recruitment*

As with transport, studies that prove significant temperature-recruitment correlations are numerous across species and marine systems (e.g. Campana 1996, Fowler and Jennings 2003, Zeldis et al. 2005), but often a multitude of interrelated mechanisms, acting on different life-stages, are proposed to have caused these relationships. Temperature-enhanced growth rates certainly appear to reduce cumulative predatory losses in early larval populations (Pepin 1991, Heath 1992), as formulated by the 'bigger-is-better', the 'stage-duration', or 'growth-selective predation' hypotheses (Takasuka et al. 2004). In many cases, the temperature effect of enhanced survival through higher growth rates is probably augmented by temperature-dependent zooplankton dynamics (Limburg 1996). Van der Veer et al. (2000) even found that temperature favoured recruitment success of newly settled plaice, *Pleuronectes platessa*, in the North Sea by causing increased mortality of crustacean predators - during the last winter. For Baltic sprat, significant temperature effects on recruitment strength may be traced back as far as to the pre-spawning stock because of temperature-dependent gonad development (MacKenzie and Köster 2004), or to the egg and early larval stages, which appear to have a limited tolerance to low mid-water temperatures after severe winters (Köster et al. 2003, Karasiova and Zezera 2000).

The present analysis of month- and depth-specific temperature-recruitment relationships has broadened our perception, when and where temperature-dependent processes are important for recruitment variability. Three main 'cores' of such temperature-recruitment relationships were found (Fig. 5); the first in January and

depths mainly below 50m, which is entirely consistent with MacKenzie and Köster's (op. cit.) findings. The second 'core', encompassing correlations in mid-water depths between March-July fully corroborated the published work (op. cit.) on the temperature-dependence of sprat egg- and early larval mortalities for recruitment. However, the third 'core' has not previously been reported and occurred between July and October in Baltic surface waters, with August relationships having more than three times the explanatory power compared to all temperature correlations earlier in the year. This strongly indicates that in spite of all statistical significance prior to this time, temperature-related survival processes during the late summer months and therefore throughout or after metamorphosis (Baumann et al. 2005a, b) explain most of the recruitment variability in Baltic sprat. We further suggest that finding these significant correlations in August and September *only* in surface waters, could reflect the preferred vertical distribution of pre-recruit sprat late in summer, thus lending independent support for the "surface-assumption" made during our drift simulations.

Although Houde (1992) found survival until metamorphosis to be 45 times lower in marine than in freshwater fish, and consequently suggested that "in marine species larval stage dynamics will have a greater influence on recruitment success", studies concluding just the opposite have become numerous. Bradford (1992) analysed abundance data of fish eggs and larvae compiled from the literature and suggested that "recruitment levels are fixed after the early-larval period", while Leggett and DeBlois (1994) more explicitly proposed that "interannual variability in survival during the juvenile life stage is the most important contributor to recruitment variability". Small pelagic clupeoids appear not to be exceptions to such a concept, as indicated by the present, as well as by recent studies of Wilhelm et al. (2005) on Cape anchovy, *Engraulis encrasicolus*, and Takahashi and Watanabe (2005) on Japanese anchovy, *Engraulis japonicus*.

In the case of post-larval Baltic sprat we need to reconsider the mechanisms responsible for the apparently strong temperature-recruitment relationship. It is noteworthy that all of the established 'temperature-growth-survival' hypotheses for larvae imply size- or growth rate selective predation to ultimately act as the determinant process. Following this rationale, years of high surface temperatures in August would have increased population growth and thus body-size at the end of summer, which then somehow conferred a survival advantage with respect to predation. However, the only major predator of Baltic sprat was assumed to be Baltic cod, *Gadus morhua* (Köster et al. 2003), *before* stocks dramatically declined due to a combination of climate-induced regime shifts and overfishing (Alheit et al. 2005). This has caused an estimated 5-fold decrease in predation mortalities of 0-group sprat from the mid 1970-ies to the early 1990-ies and thereafter (ICES 2005b), which did not affect the persistently strong temperature-recruitment relationship. Whether other Baltic piscivores, particularly in the shallow coastal areas, can significantly prey on 0-group sprat, remains to be

demonstrated. The predation by cod on post-larval and juvenile sprat, however, cannot be regarded as the major mechanism underlying the observed strong coupling between recruitment and late summer surface temperature.

Bigger sizes due to accelerated growth in summer may not necessarily grant immediate survival benefits but could also lead to reduced mortality throughout the subsequent first winter (e.g. Henderson et al. 1988). In her review on size-selective mortality in juvenile fishes, Sogard (1997) compiled laboratory and field evidence to argue that smaller fish have lower energy reserves than bigger con-specifics, which would make them physiologically less tolerant against low temperatures during overwintering. This could be particularly important in a species like sprat, for which the Baltic Sea comprises the northern extreme of its geographical distribution (MacKenzie and Köster 2004). We note that our approach of considering sprat age 0 estimates does not rule out this possibility, because MSVPA's are predominantly driven by catch-at-age data starting at age 1, and are therefore insensitive to potential inter-annual variations in age 0 overwinter mortality. To assess the magnitude of such a potential mechanism, it would be necessary to compare independent abundance time-series of sprat recruits prior and after their first winter.

### *Conclusions*

The strong correlations between long-term data of surface temperature, modelled transport patterns, and sprat recruitment variability demonstrated how tightly atmospheric forcing and recruitment processes are coupled in Baltic Sea. The two synergistic approaches have singled out two highly explanatory recruitment proxies, bottom-depth anomaly and surface temperature in August, which strongly suggested that new sprat year classes are (i) mainly comprised by individuals born late in the season and are (ii) determined in strength by processes acting during the late-larval and early juvenile stages. Both recruitment proxies were highly cross-correlated, indicating that they are different expressions for the same suite of mechanisms responsible for sprat recruitment variability. Both proxies are potentially valuable for improving recruitment predictions, with August surface temperature certainly being the more practicable and easier implemented index. Still, to better understand the mechanisms acting in Baltic sprat recruitment determination, future research needs to shift its focus to the post-larval stages and explicitly consider potential spatial differences in zooplankton dynamics and predation between the central deep spawning basins and the coastal areas of the Baltic Sea.

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**- PAPER 4 -**

**STARVING POST-LARVAL SPRAT, *SPRATTUS SPRATTUS* (LINNAEUS, 1758),  
IN BALTIC COASTAL WATERS: EVIDENCE FROM COMBINED FIELD AND  
LABORATORY OBSERVATIONS IN AUGUST/SEPTEMBER 2003**

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**ABSTRACT**

Recent studies have suggested that the post-larval and early juvenile stages of Baltic sprat play an important role in regulating the strength of new year classes. We compared growth histories, inferred from otolith microstructure analysis, between Baltic sprat early juveniles (26-42 mm total length, *TL*) and age 0 recruits (60-95 mm *TL*), sampled in August in shallow coastal waters and October 2003 in the entire western Baltic Sea (Sub-division 22), respectively. Recent growth rates of sprat juveniles, but not those of similarly old, prospective recruits, had declined very rapidly at the end of August. We suggest that this decline most likely resulted from a severe food deprivation of early juveniles in nearshore waters, given that (1) juveniles and recruits likely experienced similar temperature conditions, (2) that almost all juvenile sprat had empty stomachs on the sampling day, and because (3) field-collected early juveniles responded immediately with increasing growth rates when provided *ad libitum* food rations in the laboratory, while fish kept under zero food conditions showed a similarly rapid growth decline as observed prior to sampling. Starvation of early juvenile fish in the field has not been documented before, but may – at least in the case of Baltic sprat – comprise a density-dependent mechanism operating in coastal nursery areas. The unusually high abundance of age 0 sprat in the western Baltic in 2003 (hydroacoustic estimates) appears to support this concept.

**Key words: Otolith microstructure analysis, starvation, age 0 recruits, laboratory feeding**

## INTRODUCTION

For most marine fish populations, recruitment levels cannot be predicted from the size of the spawning stock alone (Sissenwine, 1984), but depend on annual fluctuations in pre-recruit survival patterns, which appear environmentally regulated (Köster *et al.*, 2003). In order to better understand the nature of such environmental recruitment determinants, it is necessary to obtain samples from the pre-recruit population during all developmental stages and study traits that reflect the environmental changes as well as the survival probability for a given individual or cohort (Miller *et al.*, 1988). Growth rate has been identified as one of the most promising traits for this purpose, because it is generally coupled to survival (Houde, 1997; Takasuka *et al.*, 2004) and influenced by a number of environmental factors, most importantly, by ambient temperature and food availability (Heath, 1992). As an additional advantage, daily somatic growth rates are known to be ‘recorded’ in fish otoliths, thus enabling researchers to infer an individual's growth history from the widths of daily otolith increments (Campana & Jones, 1992).

Otolith microstructure analysis has proved to be a meaningful method to detect short-term changes in growth and selective survival in larval fish (e.g. Hovenkamp *et al.*, 1992; Folkvord *et al.*, 1997; Baumann *et al.*, 2003) or has been used to compare growth rates between successful survivors (e.g. recruits) and larvae that were sampled earlier from the same population (Allain *et al.*, 2003). However, similar approaches have rarely been extended to post-larvae and early juveniles (e.g. Meekan & Fortier, 1996; Takahashi & Watanabe, 2004), not because these intermediate life stages would be less important for recruitment variability, but rather because of a much simpler constraint: accessibility. In contrast to early larvae, individuals close to or just beyond metamorphosis usually escape standard plankton gears (e.g. Bongo, IKMT<sup>†</sup>), while not yet being in the size range that is captured quantitatively by commercial or scientific fishing trawls. The ensuing uncertainties about the spatial distribution, growth and survival patterns of post-larvae and early juveniles have led to a ‘common gap’ in pre-recruit research.

This study investigated growth characteristics of field caught, early juvenile sprat, *Sprattus sprattus* (Fig. 1), a small, pelagic, zooplanktivorous clupeid and a key element of both the Baltic ecosystem (Rudstam *et al.*, 1994; Möllmann & Köster, 1999) and Baltic fisheries (ICES, 2005a). Recent work has suggested that the late larval and early juvenile stages of Baltic sprat play an important role in recruitment determination (Köster *et al.*, 2003; Voss *et al.*, in press; Baumann *et al.*, under review). However, no field studies have explicitly addressed the early juvenile stage of sprat yet, despite their

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<sup>†</sup> Isaacs-Kidd-Midwater-Trawl

potential value for a better understanding of processes responsible for Baltic sprat recruitment variability.

The present work was feasible because in August 2003, dense aggregations of metamorphosing sprat juveniles occurred in very shallow waters (< 5 m) of the Kiel Fjord in the western Baltic Sea (Fig. 2). Specimens could be collected directly from the beach, transferred live into the laboratory and examined in a number of successful experiments on food- and temperature-dependent growth (Peck *et al.*, 2004; 2005; Baumann *et al.*, 2005). This study effectively combined field and laboratory growth histories of sprat juveniles, inferred from otolith microstructure analysis, and compared these with the growth characteristics of newly recruited age 0 sprat sampled in the same area later in October 2003. In this manner, growth differences between early juveniles and recruits were described to gain insights into processes that potentially modify Baltic sprat year-class strength during the late pre-recruit stages.



Fig.1: Early sprat juveniles schooling in the shallow waters of the Kiel Fjord on 28 August 2003. Specimens measured on average 31.4 mm TL (S.D. = 3.0 mm). Photo: D. Stepputtis

## MATERIAL AND METHODS

### *Post-larvae*

On 28 August 2003, nearly 3000 juvenile sprat (Fig. 1) were caught with a dip-net in shallow waters of the Kiel Fjord in the western Baltic Sea (Kiel Strande, Fig. 2). A random sub-sample of 63 specimens was measured immediately for total lengths (*TL*,

nearest mm, Fig. 3), while another 33 individuals were preserved in 4% formaldehyde for stomach content analysis. Gut fullness was judged qualitatively (i.e. full, nearly full, half-full, nearly empty, empty), prey species were identified to the lowest taxonomic level possible, while prey digestion grades were determined on a scale from 1 (prey item complete) to 4 (prey item digested, only mucus remaining). Live specimens were transferred to the laboratory at *in situ* temperature ( $18.0 \pm 0.5^\circ\text{C}$ ) and salinity ( $15.0 \pm 0.5$ ). Seven days after field collection, about 400 individuals were used in a feeding experiment that lasted 22 days and was preceded by a treatment with a fluorescent otolith marker (see Baumann *et al.* 2005). For the present study, we analysed the field growth histories of 51 experimental fish and the laboratory growth histories of those individuals that were reared (i) 22 days under *ad libitum* and (ii) 11 days under zero feeding conditions ( $n=31$ ).

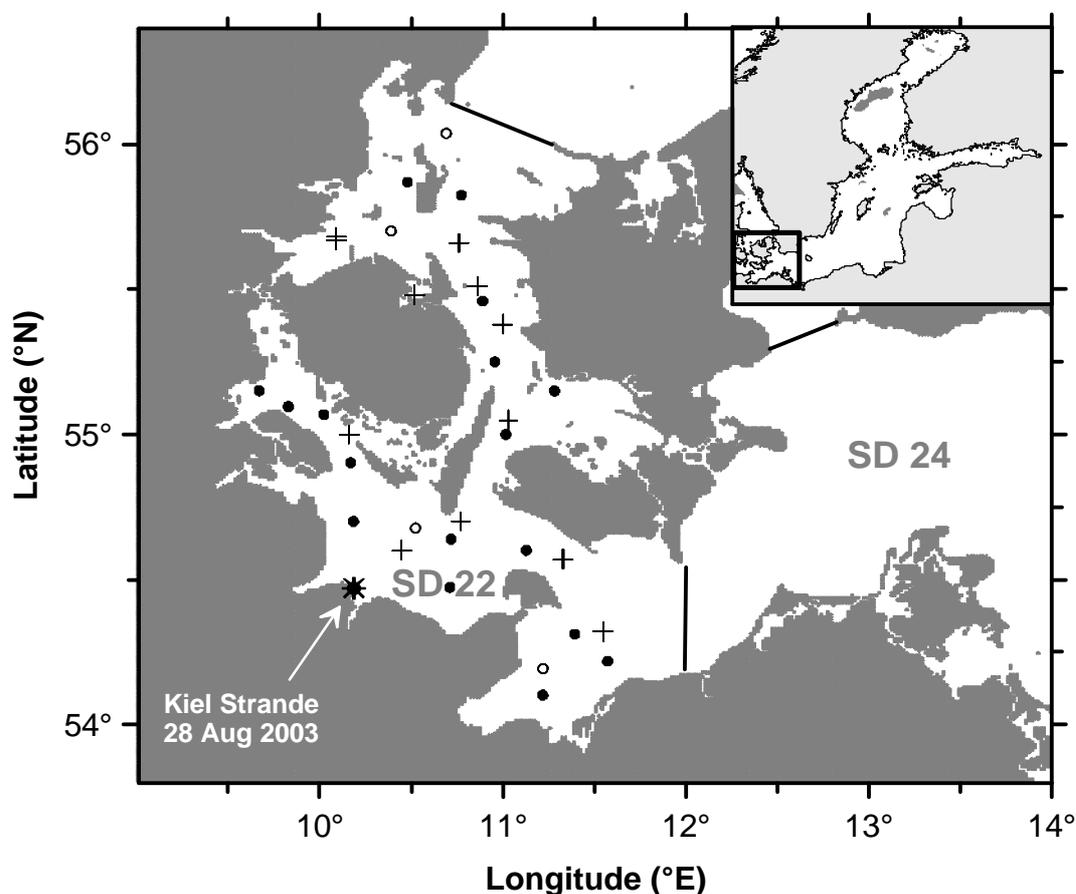


Fig.2: Study area of the western Baltic Sea (ICES sub-division 22, inlay: entire Baltic Sea) with positions of pelagic trawls conducted during the hydroacoustic survey in October 2003 (empty circles refer to hauls void of YoY-sprat). Early juvenile sprat were sampled on 28 August 2003 in the outer Kiel Fjord (Kiel Strande, filled sun). Crosses depict the stations from which temperature measurements were available at the ICES Oceanographic Database.

After termination of the experiment, sagittal otoliths were extracted and mounted individually on microscopic slides with a drop of thermoplastic glue (Crystal Bond<sup>®</sup> 509). Otoliths were then polished from both sides with a 3  $\mu\text{m}$  lapping film (3M<sup>®</sup> 266x

Imperial PSA) until all increments were sufficiently visible along the measurement axis (core to post-rostrum). Polished otoliths were photographed under 400x magnification (Leica<sup>®</sup> DC300), followed by counting and measuring ( $\mu\text{m}$ ) the daily increments with an image analysis program (ImagePro<sup>®</sup> 4.5.1). As reported in Baumann *et al.* (in press, a), the first clear and distinct increments occurred after 3-5 faint (probably non-daily) structures that were assumed to correspond to the yolk-sac stage. Therefore, all otolith-derived age estimates are hereafter given in days after first feeding (*DFF*).

To validate the assumption that growth histories of the experimental fish represented those of the early juveniles encountered in the Kiel Fjord, we compared the *TL*-distribution from the field with the lengths of laboratory individuals back-calculated to the 28 August (Fig. 3). Back-calculations were done with the biological intercept method (Campana, 1990), using 5 mm *TL* as the length intercept for first feeding sprat larvae (Voss *et al.*, 2003) and the distance between the core and the first clear increment as the corresponding initial otolith size. Because both *TL*-distributions were not significantly different (mean  $\pm$  S.D.  $TL_{field} = 31.4 \pm 3.0$  mm,  $TL_{lab} = 31.0 \pm 2.4$  mm, 1-way ANOVA,  $P=0.44$ , SPSS<sup>®</sup> 10.0.7), we concluded that the experimental fish comprised a random sub-sample of the specimens that were present in the Kiel Fjord at the end of August 2003.

### Recruits

Young-of-the-year (YoY) recruits were sampled between 5-14 October 2003 by the RV "Solea" during the annual Baltic International Acoustic Survey (BIAS). The vessel conducted 21 pelagic trawls in ICES sub-division 22 (Fig. 2), using a standard fishing gear with a stretched mesh size of 20 mm in the codend ( $L_{50}^{\ddagger} = 40$  mm). From each haul that contained YoY-sprat ( $n=17$ ), approximately 20 individuals were randomly selected and immediately frozen at  $-20^{\circ}\text{C}$ . In the laboratory, *TL* was measured to the nearest mm, followed by the same extraction, mounting, polishing, and image analysis procedures of sagittal otoliths as described for post-larval sprat. All otoliths were only read once, based on earlier within-reader and across-readers validations published in Baumann *et al.* (in press, a). In total, we included 51 post-larval and 78 YoY-sprat otoliths in the present analysis.

Average temperature conditions experienced by YoY-sprat in July and August 2003 were inferred from mean sea surface temperatures in sub-division 22 (depth = 0-5 m), which were derived from measurements available at the ICES Oceanographic database<sup>§</sup> (Fig. 2). For early juveniles in the Kiel Fjord, daily mean temperatures were

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<sup>‡</sup>  $L_{50}$  is the estimated fish length with a 50% chance of being caught by the trawl (ICES 2005b)

<sup>§</sup> <http://www.ices.dk/ocean/>

obtained from a nearby measurement station (Kiel lighthouse\*\*, 54°30'N, 10°16.5'E, depth = 1.5m).

Annual estimates of YoY-sprat abundance in the Baltic Sea were available from the Baltic Acoustic Database (BAD1), presently covering 14 years of observations (1991-2004).

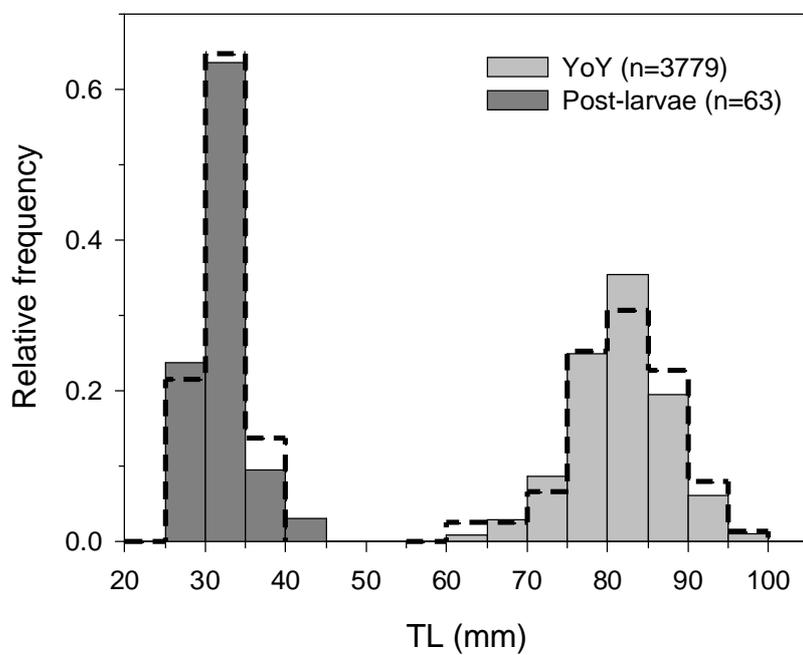


Fig.3: Relative length frequencies of early juvenile and YoY-sprat, sampled on 28 August and 5-14 October 2003, respectively. Dashed lines refer to length frequencies of the random sub-samples for otolith microstructure analysis ( $n_{YoY} = 78$ ,  $n_{Post-larvae} = 51$ ).

Table 1: Stomach contents of 33 post-larval sprat sampled on 28 August 2003 (day) in the Kiel Fjord. Digestion grades were judged on a scale from 1 (fresh) to 4 (fully digested).

Stomach fullness	N	Prey species found	Digestion grade
Empty	19	-	-
Nearly empty	12	Unidentified	4
	1	3 x <i>Centropages hamatus</i>	3-4
Half full	1	3 x <i>Euphausiaceae</i> larvae	2-3

## RESULTS

Out of 33 sprat juveniles that were analysed for their stomach contents, 31 individuals had empty or nearly empty stomachs, while the remaining two contained partly digested copepods, *Centropages hamatus*, and Euphausiacean larvae (Table 1). The mean  $\pm$  S.D. age of early juvenile sprat on 28 August was  $37 \pm 4$  days, whereas YoY-recruits in October were on average  $\pm$  S.D.  $94 \pm 10$  days old. The back-calculated

\*\* <http://www.ifm.uni-kiel.de/fb/fb1/me/kieldata/kieldata-d.html>

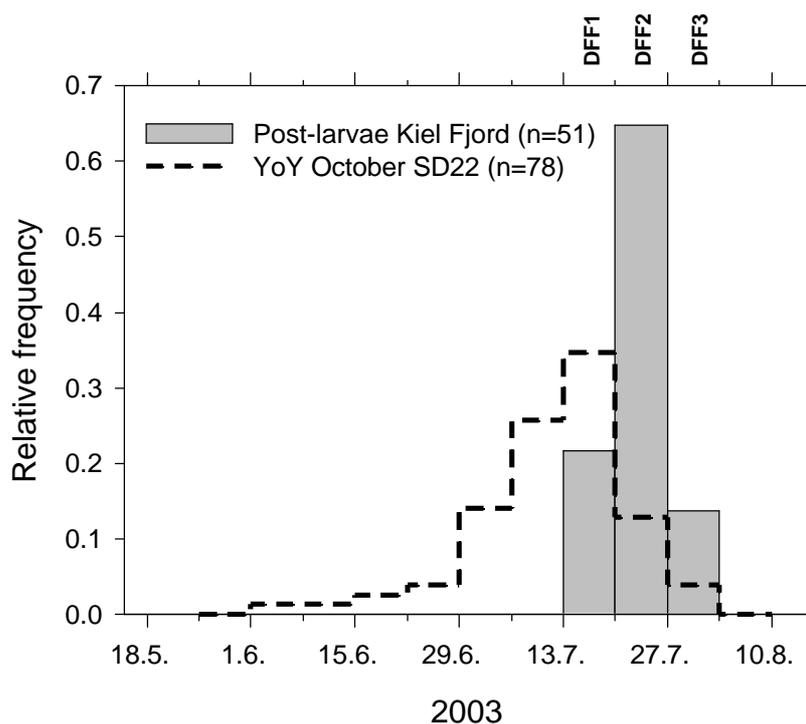


Fig.4: Distributions of back-calculated dates-of-first feeding for early juvenile sprat sampled in August 2003 in the Kiel Fjord and YoY-survivors sampled in October 2003 in the western Baltic Sea. *DDF*1-3 refer to the 3 last weeks in July, when both distributions overlapped.

*DDF*-distribution of early juvenile sprat encompassed only a confined period between 14 July – 1 August 2003 (mean *DDF* = 22 July), in contrast to YoY-survivors that had a much broader distribution (range/mean *DDF* = 6 June - 31 July/11 July 2003, Fig. 4). However, 88% of all YoY-recruits had *DDF*'s in July 2003. Early juvenile and recruit *DDF*-distributions therefore overlapped during the last three weeks in July (*DDF*1-3, Fig. 4). Otolith growth trajectories (i.e. increment width-at-age) of YoY-sprat showed the characteristic pattern of rapidly increasing increment widths until about 25-30 days (larval stage), after which growth rates declined almost linearly until sampling in October 2003. If YoY-survivors were grouped into weekly *DDF*-intervals, individuals in later *DDF*-intervals had notably broader maximum increments that were formed earlier after *DDF*, resulting in a steeper initial growth increase during the larval stage (Fig. 5). The same pattern was also apparent in similarly grouped early juveniles. On average, juvenile sprat increments 1-20 were significantly ( $P < 0.05$ ) narrower than increments of YoY-survivors within the same weekly *DDF*-interval (1-way ANOVA per increment, SPSS<sup>®</sup> 10.0.7). Between age 21-29, however, YoY-increments were not significantly different from those in early juvenile sprat. Significant differences in increment widths ( $P < 0.05$ ) between juveniles and YoY-sprat re-appeared after 30 days of age and increased steadily until sampling, because otolith growth after the broadest increment declined much more rapidly in juveniles compared to YoY-survivors (Fig. 5). On the sampling day, increments of sprat juveniles were on average 3.1  $\mu\text{m}$  and 2.2  $\mu\text{m}$  narrower than those of similarly old YoY-recruits in *DDF*1 and *DDF*2, respectively.

Laboratory residence altered the otolith growth of early sprat juveniles almost immediately. Between August 28 and September 3, when all specimens were

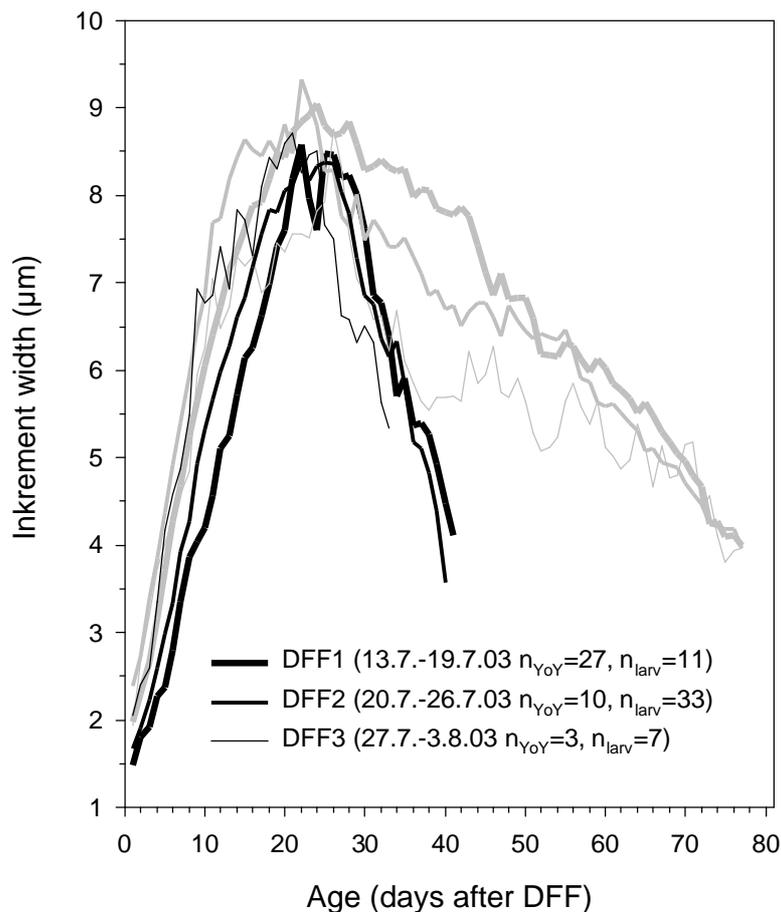


Fig.5: Mean increment widths per age of YoY-sprat sampled in October (grey lines) and early juveniles sampled on 28 August 2003 (black lines). Specimens were grouped into weekly intervals according to their back-calculated day of first feeding (*DFE*1-3). Lines of the same thickness correspond to the same *DFE*-interval. Early *DFE*-intervals (YoY-recruits only) were omitted from the graph.

maintained in 800 l flow-through tanks and fed daily rations of live and frozen food, increment widths did not decrease further but remained approximately constant ( $\sim 4 \mu\text{m}$ , Fig. 6) until the beginning of the feeding trials. Starting on 4 September, specimens fed *ad libitum* rations of live brine shrimp, *Artemia* spp., nauplii promptly responded with increasing increment widths that reached a local maximum after 13 days of the experiment (Fig. 6). Although mean increment widths in *ad libitum* fed juveniles never exceeded those of YoY-survivors, the differences were not significant on the 17<sup>th</sup> and 19<sup>th</sup> day of the experiment (1-way ANOVA per day of increment formation,  $P > 0.05$ , SPSS<sup>®</sup> 10.0.7). In contrast, specimens starved during the experimental period (11 days), showed rapidly decreasing increment widths with a slope similar to the decrease observed prior to sampling (Fig. 6).

From the beginning of July until 16 August, temperatures recorded at the Kiel lighthouse were very similar to mean sea surface temperatures in sub-division 22 (Fig. 6). Maximum temperatures of approximately  $23^{\circ}\text{C}$  were observed between the 8 and 12 August 2003. For the last 12 days prior to the collection of early juveniles, sea surface temperature decreased slightly faster in the entire western Baltic Sea than in the Kiel Fjord (Fig. 6).

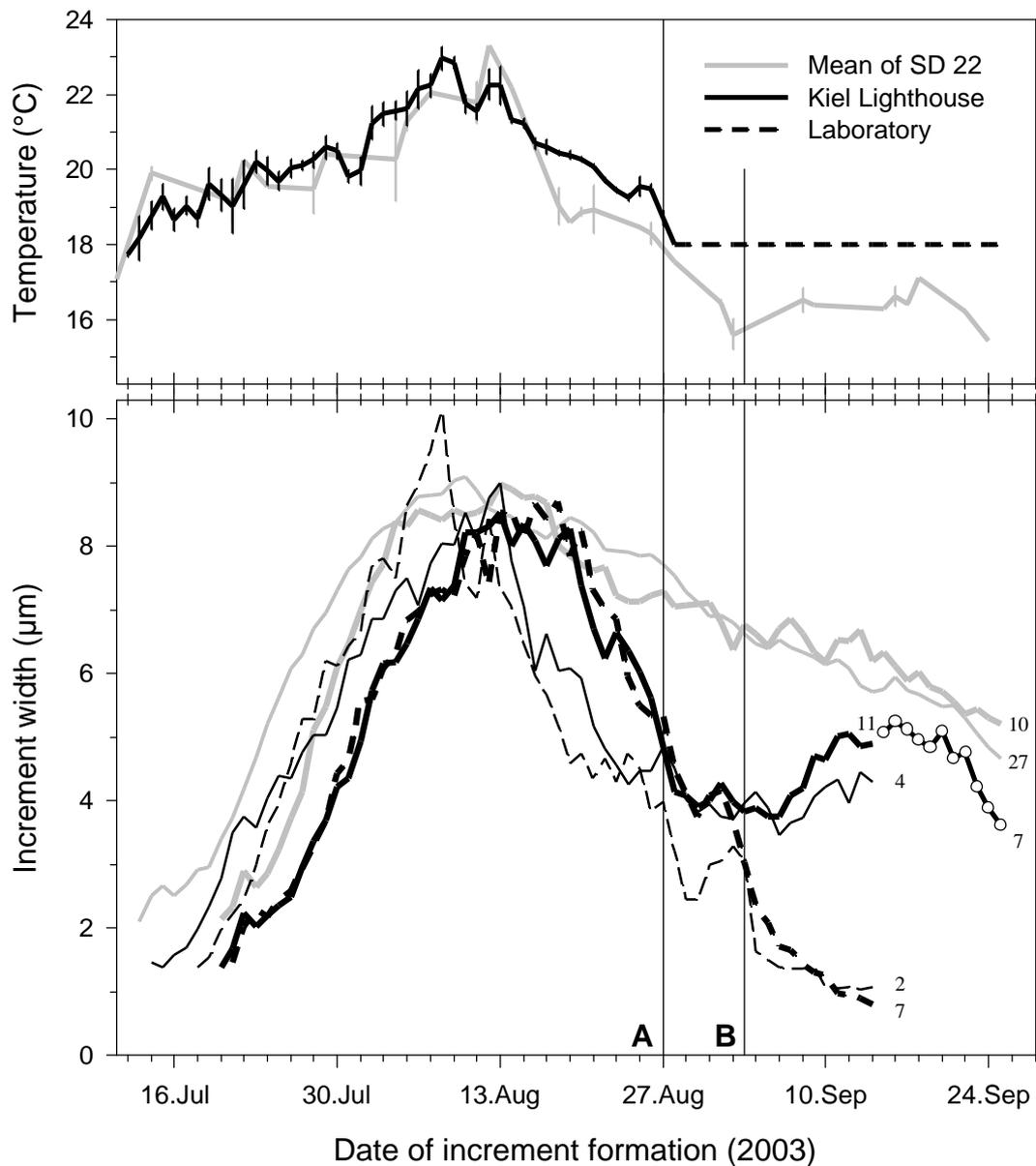


Fig.6: Upper panel: Mean  $\pm$  S.D. sea surface temperature in July and August 2003 in the western Baltic Sea (sub-division 22, grey line) and in the Kiel Fjord (black line). The constant laboratory conditions are shown by the dashed line. Lower panel: Mean increment widths per date of formation for early juvenile (black lines) and YoY-sprat (grey lines) sampled in August and October 2003 in the Kiel Fjord and the western Baltic, respectively. Thin and thick lines correspond to *DDF*-intervals 1 (13.-19.7.03) and 2 (20.-26.7.03), respectively. Solid lines and white circles depict individuals re-fed ad libitum rations, while starving groups are shown by dashed lines. Means were based on the number of individuals given right next to each trajectory. Lines A and B denote the day prior to post-larvae sampling and the start of the feeding trials, respectively.

## DISCUSSION

Growth patterns inferred from otolith increment widths were compared between early juvenile and newly recruited sprat sampled in late August and at the beginning of October, respectively, in the western Baltic Sea. It was assumed that juveniles and recruits originated from the same broadly defined region, which is reasonable because

sprat are known to spawn regularly in the western Baltic (Grauman & Krenkel, 1986; Aro, 1989) and because passive transport from central and eastern Baltic spawning grounds appears to be generally negligible (Hinrichsen *et al.*, 2005). During the first 20 days after *DFE*, YoY-recruits had higher growth rates than juveniles, indicating that a selection for fast growth occurred during the larval stage (e.g. Meekan & Fortier, 1996, Allain *et al.*, 2003). Initial growth rates were higher in younger compared to older recruits *and* juveniles, which appears to be the consequence of higher ambient temperatures experienced by later born individuals (Baumann *et al.*, in press a, b). However, the main observation of this study was that recent growth rates of early juveniles, but not those of similarly old, prospective recruits, had declined very rapidly at the end of August 2003, which we interpret as a result of severe food deprivation in the Kiel Fjord, given the following arguments:

(1) Larval fish growth is predominantly governed by ambient temperature and food availability (Heath, 1992), but the temperatures observed in July and August 2003 in the western Baltic Sea were too homogeneous to induce purely temperature-related growth differences of this magnitude (Baumann *et al.*, in press a, b). In combination with limited prey abundance, however, the slightly higher temperatures on the coast at the end of August could have *accelerated* the starvation process through a higher routine metabolism of sprat juveniles (Houde, 1989).

(2) Almost all specimens that were sampled on 28 August and analysed for their stomach contents had empty or nearly empty stomachs. Given the recent results of Dickmann *et al.* (submitted), who found prey in 81% of all stomachs of sprat larvae caught in July 2002 in the central Baltic Sea (length class: 20 - 25 mm), a much higher feeding incidence was to be expected. The extremely low feeding success of the early juveniles in the Kiel Fjord agrees well with our personal observation of unusually clear waters at the sampling site and the adjacent shallow areas during the end of August. Regrettably, no plankton samples were taken to quantify this subjective impression. However, empty stomachs and clear waters appear at odds with the energy demands imposed by the high rates of otolith and thus somatic growth that usually characterise the early juvenile stage of sprat (Baumann *et al.*, in press a, b).

(3) Laboratory residence and the corresponding growth trajectories of pre-recruit sprat supported the starvation hypothesis. The rapid, pre-sampling growth decline already stopped as individuals were fed an un-quantified, yet unlikely maximal amount of food prior to the beginning of the controlled feeding trials. Within the experiment, *ad libitum* fed specimens showed rapidly increasing growth rates that came close to those observed in similarly old YoY-recruits, thereby indicating a partial growth compensation (Ali *et al.*, 2003) after sub-optimal feeding conditions. In addition, laboratory growth trajectories of starving individuals showed a similarly rapid decline in increment widths as during the pre-sampling period. This seems to particularly emphasize the severity of the food limitation in the field.

In the laboratory, starvation is a well-studied process. A large body of literature shows how *experimentally* induced starvation periods affect growth in larval, juvenile and adult fish, and how this can be detected by various proxies, such as otolith increments (e.g. Maillet & Checkley, 1990; Molony, 1996), condition and histological indices (Suthers, 1998), or changes in RNA:DNA ratios (e.g. Buckley, 1984; Clemmesen & Doan, 1996). It is noteworthy, however, that the common rationale of including starvation treatments in experiments is to provide a reference line to which the effects of other treatments can be compared. In contrast, evidence for truly starving fish in the field is not nearly as ubiquitous (Heath 1992) and seems to be restricted mostly to fish larvae in the transition between endo- and exogenous feeding (e.g. O'Connell, 1980; Chicharo 1998, Grønkjaer *et al.*, 1997). This is because feeding success (Hunter, 1972) and the time to irreversible starvation (point of no return, Blaxter & Hempel, 1963) generally increase very rapidly after first feeding, thus starvation is even less likely to occur during the older larval and early juvenile stages. In fact, the low numbers of larvae usually found starving in the field have led researchers to question the notion of starvation as a major direct source of mortality in larval and juvenile fish (Øiestad, 1985; Leggett & Deblois, 1994). During overwintering, however, starvation appears to cause significant mortality in older juveniles and recruits, particularly in high latitude, freshwater environments (Henderson *et al.*, 1988; Sogard, 1997; Biro *et al.*, 2004).

This study, which is to our knowledge the first account of early juvenile fish starving in the sea, has demonstrated how much effort (and luck) it might take to detect starvation in the field. Only the comparison of daily otolith increments between pre-recruits and recruits (the latter being our reference line) *and* the combination of field and laboratory growth trajectories justified the present conclusion. In addition, those starvation events may only be detectable during rather short periods, given that in 2003 juvenile sprat schools were observed in the Kiel Fjord only between August and the beginning of September (C. Petereit, IfM - GEOMAR, Kiel, personal communication). Very few schools of post-larval sprat were last spotted on 12 September (H. Baumann, personal observation), where groups of garfish, *Belone belone*, and sandeel, *Ammodytes* spp., had been preying voraciously on the remaining individuals. These observations emphasize the role of predation as the ultimate cause of death in the sea, because eventually, “even a sick (or starving) animal dies by being eaten” (Cushing, 1974).

Therefore, it is possible that starvation during the early juvenile stage of Baltic sprat is a more regular and widespread phenomenon than previously acknowledged. For example, Baumann *et al.* (under review) and Hinrichsen *et al.* (2005) have recently modelled the passive transport of feeding sprat larvae from central and eastern Baltic spawning grounds by means of long-term Lagrangian particle simulations (25 years). They found that the high inter-annual variability in the degree of larval transport towards southern and south-eastern Baltic coasts was significantly correlated to Baltic sprat recruitment strength. The results indicated that predominant larval retention within

the deep basins was associated with relative recruitment success, whereas years of strong coastal displacement of sprat larvae corresponded to relative recruitment failure. During weak recruitment years, particles also tended to be more densely aggregated, which was interpreted as a sign for density-dependent effects. Those simulations further suggested that the late larval and early juvenile stages play an important role in determining Baltic sprat year class success. By showing that early juvenile sprat were starving in shallow, coastal waters, the present study appears to offer a plausible mechanism underlying these transport-recruitment correlations. However, it still remains to be demonstrated that starvation events are restricted to the nearshore areas of the Baltic Sea (as implied by the present study) and that sprat juveniles are indeed unable to migrate out of such food depleted coastal environments.

On larger spatial and temporal scales, density-dependent food limitation has already been shown for Baltic clupeid fish stocks. A number of authors investigated condition factors (CF) and weight-at-age data of Baltic herring and sprat, concluding that the pronounced decline in herring and sprat CF's between 1990 – 1998 was attributable to increased pelagic fish abundance and competition for food resources (Raid & Lankov, 1995; Cardinale & Arrhenius, 2000; Cardinale *et al.*, 2002). In addition, Flinkman *et al.* (1998) proposed that adverse changes in the mesoplankton composition could have contributed to the significant decrease in stomach fullness and mesenteric fat in Baltic herring between 1985 and 1991. The present study indicates that density-dependent food limitation may already play a regulatory role during the pre-

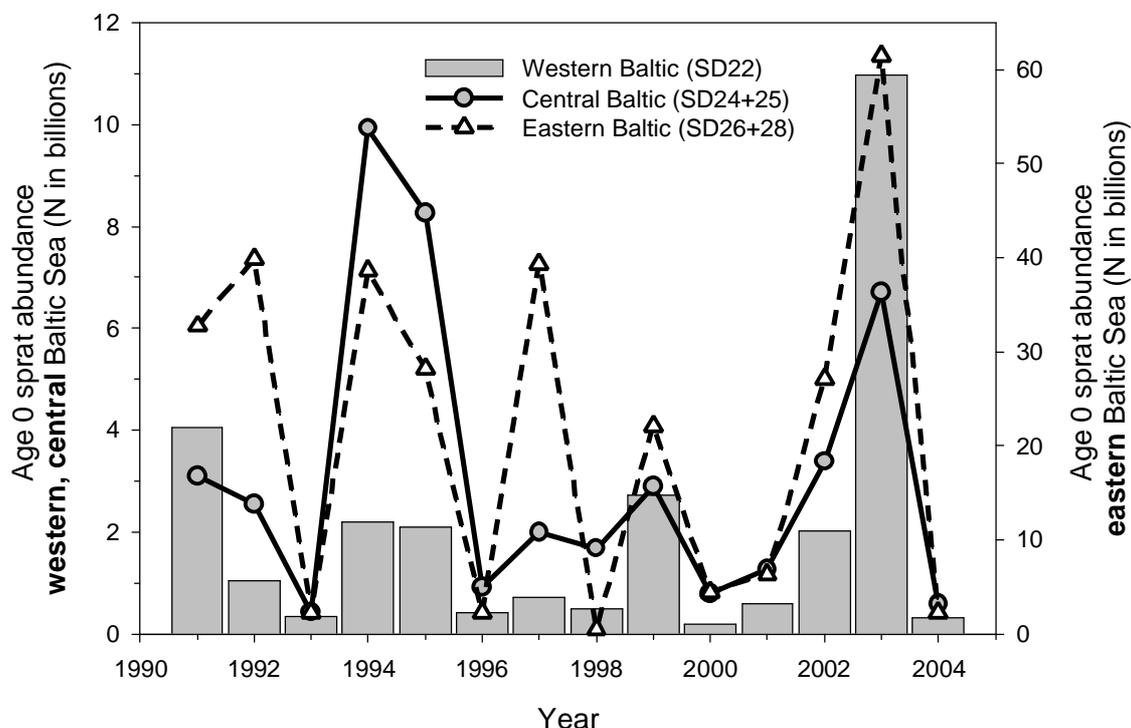


Fig.7: Time-series of hydroacoustic abundance estimates for age 0 sprat in ICES sub-divisions 22 (western Baltic, grey bars), 24-25 (central Baltic, grey circles), and 26+28 (eastern Baltic, white triangles).

recruit stages of Baltic clupeids. While supporting the density-dependence of food limitation, the overall magnitude of early juvenile starvation is questioned by the fact that 2003 was an exceptionally strong recruitment year in the western Baltic Sea (Fig. 7). However, food limitation may have a different impact in central or eastern Baltic areas that are characterized by a different bottom topography, a less complex coastline, and different hydrographical conditions (Winsor *et al.*, 2001).

In conclusion, food limitation during the early juvenile stage of Baltic sprat may comprise a density-dependent mechanism, which might have the potential to modify year class strength. To improve our understanding of Baltic sprat recruitment variability, further studies need to determine the spatial extent and the inter-annual fluctuations of pre-recruit starvation with special emphasis on processes acting in the very shallow coastal areas of the Baltic Sea.

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- PAPER 5 -

**SHORT-TERM DECOUPLING OF OTOLITH AND SOMATIC GROWTH INDUCED BY  
FOOD LEVEL CHANGES IN POST-LARVAL BALTIC SPRAT, *SPRATTUS SPRATTUS***

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**ABSTRACT**

We studied the effects of food level changes on otolith and somatic growth in post-larval Baltic sprat reared initially for a period of 11 days under zero, low, and *ad libitum* feeding conditions. During a subsequent 11d period, feeding regimes were reversed in half of the low and *ad libitum* feeding treatments, and starved fish were re-fed *ad libitum* rations. Somatic growth rates under low and *ad libitum* food rations ranged between 0.15-0.22 mm d<sup>-1</sup> and 0.48-0.63 mm d<sup>-1</sup>, respectively, and led to significant differences in length and weight between feeding regimes. Previously starved fish, however, grew only 0.25-0.28 mm d<sup>-1</sup> under *ad libitum* conditions. During the first period, significant linear relationships were found for otolith vs. length and vs. weight growth across all treatments. After changing feeding regimes, increment widths failed to significantly predict somatic growth for 9 days, after which a significant relationship between otolith and somatic growth became re-established. Recent otolith growth was a good predictor of fish condition after the first, but not after the second period. The results suggest that perturbations in environmental conditions can temporarily decouple otolith from somatic growth in post-larval sprat, which needs to be considered in field studies.

**Key words: Post-larval sprat, otoliths, alizarin, feeding experiment, decoupling of otolith-somatic growth**

## INTRODUCTION

Both in terms of accuracy and temporal resolution, there is currently no better tool for reconstructing past variations in larval fish growth than otolith microstructure analysis. Because the two inherent assumptions, daily periodicity of increment formation and a generally robust otolith-fish size relationship, are commonly met for most species, a wealth of studies has been published over the last three decades on causes and ecological implications of fish growth variability (Jones 1992, Panfili et al. 2002). Almost all studies that back-calculated growth histories have focused on larval and juvenile stages for two reasons: (i) micro-increments are proxies for daily somatic growth and usually become too narrow to be resolved in adult fish otoliths, and (ii) the larval and early juvenile stages are considered 'critical' periods, when growth variability may have profound effects on fluctuations in mortality and recruitment (Hjort 1914, Pepin 1991, Sogard 1997).

Variations in rates of somatic growth result from the interplay of endogenous (e.g. differences in growth potential) and exogenous (e.g. temperature and food abundance) factors (Parma and Deriso 1990). To extract the environmental information potentially contained within otolith increment widths, laboratory experiments are required that can link sequences of unusually broad or narrow otolith increments to changes in somatic growth. Such validations are best if conducted separately for each species and stage (Paperno et al. 1997), since the key exogenous factors affecting somatic growth, temperature and prey availability (Heath 1992), are likely to act species- and stage-specific (Jones 1992). Furthermore, environmental heterogeneity over small spatial and/or temporal scales due, for example, to patchiness of fish prey organisms, may cause different and abruptly changing growth conditions for fish in the field. Therefore, laboratory validations of otolith and somatic growth should attempt to simulate such abrupt changes in environmental conditions, rather than merely examining otoliths of fish growing at different, monotonic feeding levels.

Reconstructions of past somatic growth rates depend on the degree of coupling between otolith and somatic growth. Evidence suggests that, in a number of fish species, extreme temperature (Mosegaard et al. 1988) and feeding conditions (Marshall and Parker 1982), as well as severe ontogenetic shifts (e.g. parr-smolt transition in salmon, Wright et al. 1990) can result in different otolith-fish size relationships for individuals growing at different somatic rates. While such events surely limit our ability to back-calculate lengths-at-age of individual fish, they have not prevented meaningful insights regarding how the environment influences growth and survival of fish cohorts or populations (e.g. Titus and Mosegaard 1991, Meekan and Fortier 1996, Lapolla 2001, Baumann et al. 2003).

In this study, we investigated how otolith growth patterns reflected changes in somatic growth in post-larval Baltic sprat, *Sprattus sprattus*, reared under markedly

different and changing feeding regimes. The sprat is a small, short-lived, zooplanktivorous clupeid (max. length, age = 16 cm, 6 years, Froese and Pauly 2004) that currently comprises the most abundant commercially exploited species in the Baltic Sea (ICES 2003). Despite its ecological (Möllmann and Köster 1999) and commercial importance, the potentially different growth patterns of larval and juvenile sprat under variable feeding regimes have rarely been assessed under controlled laboratory conditions. Such knowledge will aid the interpretation of growth patterns emerging from otolith analysis of field-caught young sprat allowing a better understanding of the processes affecting sprat population dynamics. The three specific goals of this experiment were to determine (i) whether daily periodicity of ring formation was influenced by different and changing feeding conditions, (ii) how these feeding regimes were reflected in otolith increment widths, and (iii) whether abrupt changes in feeding conditions affected the coupling of otolith and somatic growth.

## MATERIAL AND METHODS

Post-larval sprat were caught on 28 August 2003 in the outer Kiel Fjord (54°27'N 10°11'E), which is a part of the Kiel Bight in the Western Baltic Sea. Nearly 3000 fish were collected in very shallow waters with a specialized 2x3 m dip-net that ensured low handling stress. Sprat were acclimated to laboratory conditions (i.e. mean±range salinity = 15.0±0.5‰, temperature = 18.0±0.5°C, light regime 14L:10D) in 800 l flow-through tanks for six days during which they were fed a mixture of frozen copepods, *Cyclops* spp., and live brine shrimp, *Artemia salina*, nauplii. Prior to starting the different feeding trials, approximately 400 fish of similar size were immersed in an alizarin-complexone/seawater solution (50 mg l<sup>-1</sup>, buffered with NaOH) for 18 h to mark their otoliths. Mortality during marking was about 13%.

On 4 September 2003, an initial sample of 21 fish was taken from the alizarin marked sprat and individual standard length (*SL*, nearest 0.1 mm) and wet weight (*W*, nearest 0.1 mg) were measured. From the remaining fish, approximately 40 sprat were randomly loaded into each of 8 tanks (135 l) and reared on newly hatched *Artemia* nauplii for 11 days under zero (starving), low, and *ad libitum* feeding levels. Tanks remained static during the day but were flow-through at night to flush out faeces and all uneaten food, which was collected within 75 µm mesh bags installed at each tank outflow. The *ad libitum* ration was adjusted so that 9-14% of the nauplii were not eaten during the 14 h feeding period. One standard ration size was fed four times and once per day to *ad libitum* and low feeding treatments, respectively.

On the 12<sup>th</sup> day of the experiment, 15 fish per tank were sampled and measured for *SL* and *W* (as above). For the second half of the study, the water volume in the tanks was reduced to 85 l to keep the concentration of fish and food similar to the first period, and feeding levels were changed as follows: One of the two *ad libitum* tanks was

switched to low feeding, one of the two low feeding tanks was provided *ad libitum* rations, and both tanks containing the previously starving fish were provided *ad libitum* rations. The second rearing period also lasted 11 days, after which all remaining fish (13-19 fish per tank) were sampled and also measured for *SL* and *W*. Average daily mortalities throughout the experiment ranged between 0.7-1.4%.

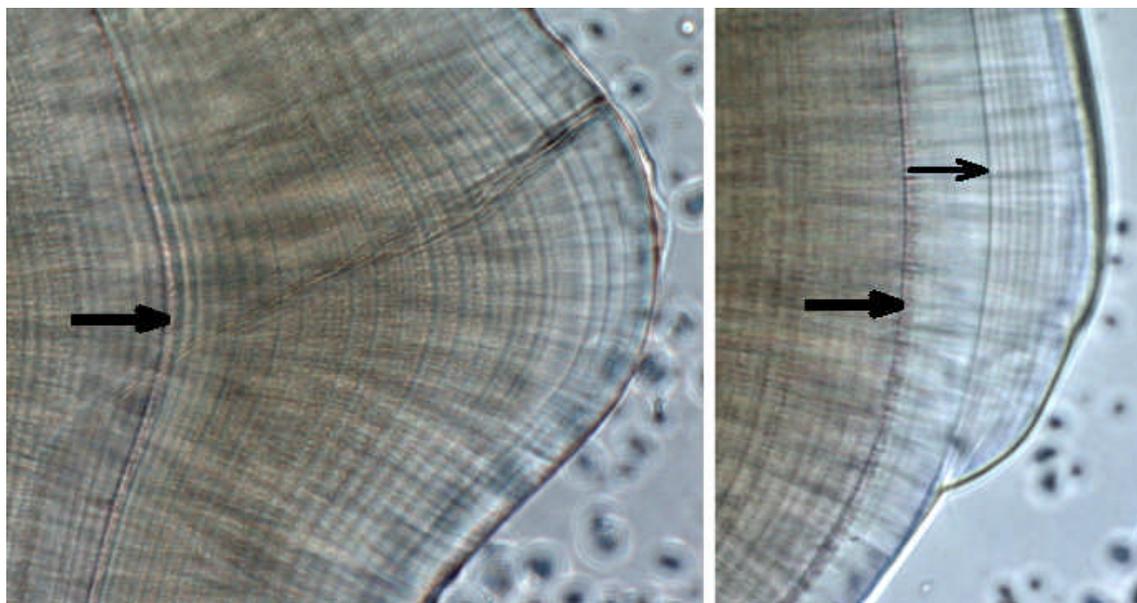


Fig. 1: Two examples of markedly different otolith growth under different feeding regimes (left: 22 days *ad libitum*, right: 11 days starving + 11 days *ad libitum*). The marked increment (alizarin-complexone, bold arrows) corresponds to the day before the start of the feeding trials. In both cases, the same part of the sagittal otolith is shown (post rostrum). In the right image, a second check-mark (thin arrow) corresponds to Day 12 and was probably induced by some mild stress associated with the removal of other fish from the tank.

From the final sample, a total of 10 fish per treatment was randomly selected for otolith microstructure analysis. Both sagittal otoliths were extracted and individually mounted on microscope slides with a drop of Crystal Bond<sup>®</sup> thermoplastic cement. All otoliths were polished from both sides using a 3 $\mu$ m lapping film (3M<sup>®</sup> 266x Imperial PSA). From each individual, the otolith with the most distinct features was chosen for analysis. All increments were measured under 400x magnification along the core-postrostral axis of the otolith using a compound microscope connected to a high resolution digital camera (Leica<sup>®</sup> DC300, 3132 x 2328 pixels) and image analysis system (ImagePro<sup>®</sup> Plus 4.5.1). Otolith readings from individuals starving during the first experimental period were checked under 1000x magnification. The last increment of each otolith was incomplete and removed from the dataset. Fluorescence microscopy was not used because 80% of all alizarin-marked otoliths showed an unambiguous, purple stain under normal transmitted light (Fig.1) corresponding to the increment formed on the day prior to experiment (3 September 2003). In total, we analysed otoliths of 37 individuals within the following treatments: *ad libitum/ad libitum* (n=7), *ad libitum/low food* (n=6), *low food/low food* (n=10), *low food/ad libitum* (n=7), and

starving/*ad libitum* (n=7). Starving/*ad libitum* fish were pooled across tanks, given that there were no significant tank differences in fish length or weight ( $P > 0.05$ ). Otoliths from 13 individuals were either lost through over-polishing or did not show an unambiguous alizarin mark. Fish that died during the experiment were not analysed.

Because there was no statistical evidence to reject the null hypothesis of normality in  $SL$ ,  $W$  and increment width at the  $P = 0.05$  level (Shapiro-Wilk statistic, SPSS<sup>®</sup> version 10.07), 1-way analyses of variance were performed, with subsequent Scheffé (homogeneous variances) or Dunnett-T3 (inhomogeneous variances) post-hoc tests for significant differences between treatment means.

The mean growth rates in  $SL$  ( $G_{SL}$ ,  $\text{mm d}^{-1}$ ) and  $W$  ( $G_W$ ,  $\text{wet mg d}^{-1}$ ) of fish in each tank were calculated based upon individual fish sizes and sampling times. Individual fish  $SL$  and  $W$  data were also used to estimate fish condition

$$C = 100 \cdot W \cdot SL^{-4.2}$$

based on the regression of  $W$  on  $SL$  of sprat sampled during the experiment ( $W = 9.3E-5 \cdot SL^{4.2}$ ,  $r^2 = 0.91$ ,  $P < 0.001$ ,  $n = 202$ ).

## RESULTS

After the first period, sprat in both *ad libitum* treatments were significantly greater in  $SL$  and  $W$  ( $P < 0.05$ ) compared to individuals at low or zero food levels (Fig.2). There were also notable, although insignificant differences in  $G_{SL}$  ( $0.48 \text{ mm d}^{-1}$  and  $0.63 \text{ mm d}^{-1}$ ) between the two *ad libitum* groups. The mean values for  $G_{SL}$  of sprat on low food rations were  $0.15$  and  $0.22 \text{ mm d}^{-1}$ , whereas  $G_{SL}$  in starving individuals was negligible ( $0.02 \text{ mm d}^{-1}$ ). Starving sprat exhibited negative  $G_W$  ( $-0.92 \text{ mg d}^{-1}$ ) and weighed

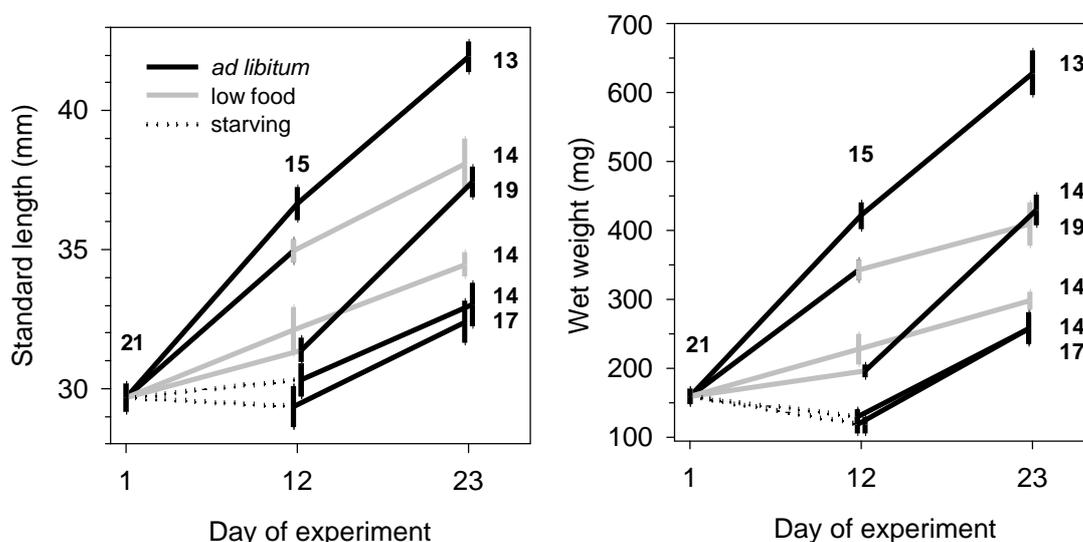


Fig.2: Length ( $SL$ ) and wet weight ( $W$ ) of post larval sprat reared under different and changing food regimes. Average values ( $\pm 1$  s.e.) are shown for fish sampled at the beginning, middle, and end of the experiment.

significantly less ( $P < 0.05$ ) after the first period compared to low feeding treatments (Fig.2).

Changing the feeding regime from *ad libitum* to low during the second period resulted in reduced somatic growth, whereas feeding *ad libitum* rations to previously low food and starving groups elicited accelerated somatic growth (Fig.2). During the second period,  $G_{SL}$  under low food conditions was comparable to the first period and also similar between changed and unchanged treatments ( $0.28 \text{ mm d}^{-1}$  and  $0.22 \text{ mm d}^{-1}$ , respectively).  $G_{SL}$  under *ad libitum* conditions was considerably slower in previously starved fish ( $0.25\text{-}0.28 \text{ mm d}^{-1}$ ) than in previously low fed fish ( $0.55 \text{ mm d}^{-1}$ ) and individuals from the unchanged treatment ( $0.48 \text{ mm d}^{-1}$ ). In the latter group,  $G_{SL}$  was slower during the second period, even though *ad libitum* feeding was maintained. The changes in  $G_W$  followed the same patterns as in  $G_{SL}$  (Fig.2).

The mean ( $\pm$ SD) age of fish sampled for their otoliths was  $70.7 (\pm 3.89)$  days after first increment formation, and there were no significant differences in age among treatments. Otolith microstructure analysis revealed no deviations between the counted and the expected number of rings between the alizarin mark and the otolith edge (e.g. Fig.1). The daily nature of increment formation was further corroborated by two serendipitously induced checkmarks that were frequently observed; one corresponding to the stress associated with field collection and transport (6 days prior to alizarin

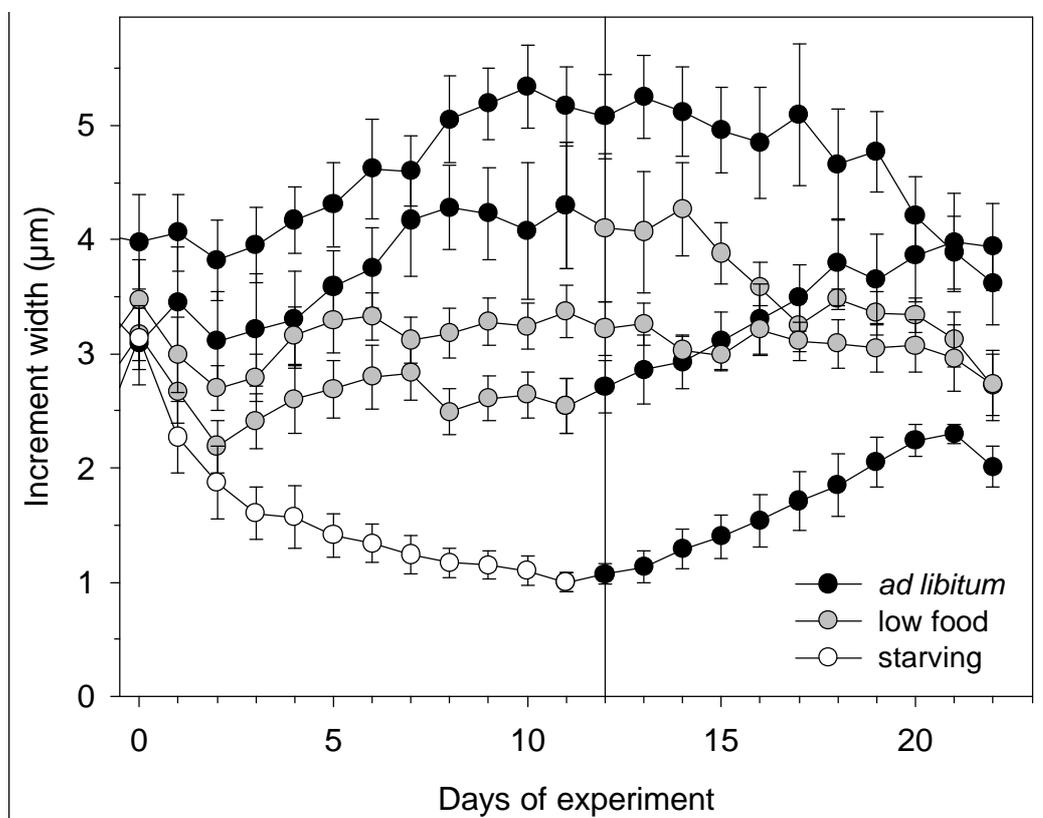


Fig.3: Mean increment widths ( $G_{OT} \pm 1 \text{ s.e.}$ ) of post larval sprat reared under different and changing food regimes. On Day 12 (thin vertical line) feeding levels were changed in three out of five treatments.

marking), and the other with the middle of the experiment, when half the fish in each tank were removed and daily feedings briefly interrupted (Fig.1).

Prior to introducing the different feeding regimes (day 0), there were no significant differences in increment width for fish in all tanks (Fig.3). However, increments were already notably broader in fish that later received 22 days of *ad libitum* food (Fig.3). During the first half of the experiment, increment widths in both *ad libitum* groups increased in a similar way, reaching a maximum average width of 4.3-5.3  $\mu\text{m}$  after 10-11 days. Fish supplied with low food rations showed relatively constant rates of

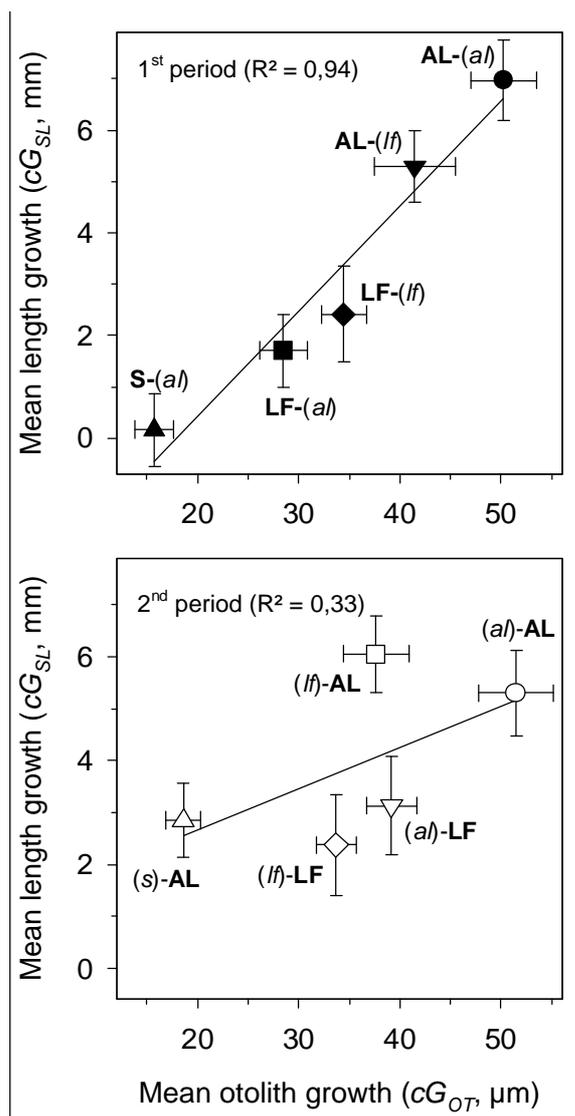


Fig.4: Relationship between average length increase ( $cG_{SL}$ ) and otolith growth ( $cG_{OT}$ ) during the two periods of the experiment. Cumulative  $G_{SL}$  ( $\pm 1$  s.e.) was regressed on the cumulative width of all increments ( $cG_{OT} \pm 1$  s.e.) formed during each 11 day period. Data labels denote the feeding treatment during the actual (capital, bold letters) and the prospective/previous (small, italic letters in brackets) period. AL/al, *ad libitum*; LF/lf, low food; S/s, starving

otolith growth ( $G_{OT}$ ) between 2.5-3.0  $\mu\text{m d}^{-1}$ , whereas  $G_{OT}$  declined rapidly in starving fish where the minimum average increment width was 1.0  $\mu\text{m}$  on day 11. Starting on the 5<sup>th</sup> day of the first period, starving sprat had significantly narrower increments ( $P < 0.05$ ) than all low and *ad libitum* fed fish. On day 11, fish in both low feeding groups also had significantly ( $P < 0.001$ ) narrower increments relative to the faster but not to the slower growing *ad libitum* group.

Changing feeding regimes in starving and low food groups to *ad libitum* rations elicited an immediate increase in average increment width (Fig.3). The  $G_{OT}$  was similar for previously starved and previously low fed fish, indicating no compensatory  $G_{OT}$  in the starving group. On day 21, two days prior to the end of the experiment, re-fed sprat of the former starving group still had significantly narrower mean increment widths than conspecifics in the two other *ad libitum* treatments (Fig.3). Increment widths of fish that were switched from *ad libitum* to low feeding rations remained high for about three days after the change, but declined steadily thereafter (Fig.3). However, this decline is perhaps not fully attributable to reduced feeding, because

increment widths also decreased in fish continuously fed *ad libitum* rations.

The change in feeding regimes affected the relationship between otolith and somatic growth (Fig.4). This was inferred from a different degree of correlation between the average cumulative  $G_{SL}$  ( $cG_{SL}$ , mm 11d<sup>-1</sup>) and  $G_W$  ( $cG_W$ , mg 11d<sup>-1</sup>) and the average cumulative  $G_{OT}$  ( $cG_{OT}$ ,  $\mu$ m 11d<sup>-1</sup>) calculated for each treatment and period. After the first period (days 1-11), the significant linear regression of  $cG_{OT}$  on  $cG_{SL}$  explained 94% of the overall variability ( $P=0.007$ ), and had a negative intercept, predicting positive  $cG_{OT}$  in fish of stagnating  $cG_{SL}$  (Fig.4a). For the second period, however, no significant relationship was found between mean  $cG_{OT}$  and  $cG_{SL}$  ( $r^2=0.33$ ,  $P=0.31$ , Fig.4b).

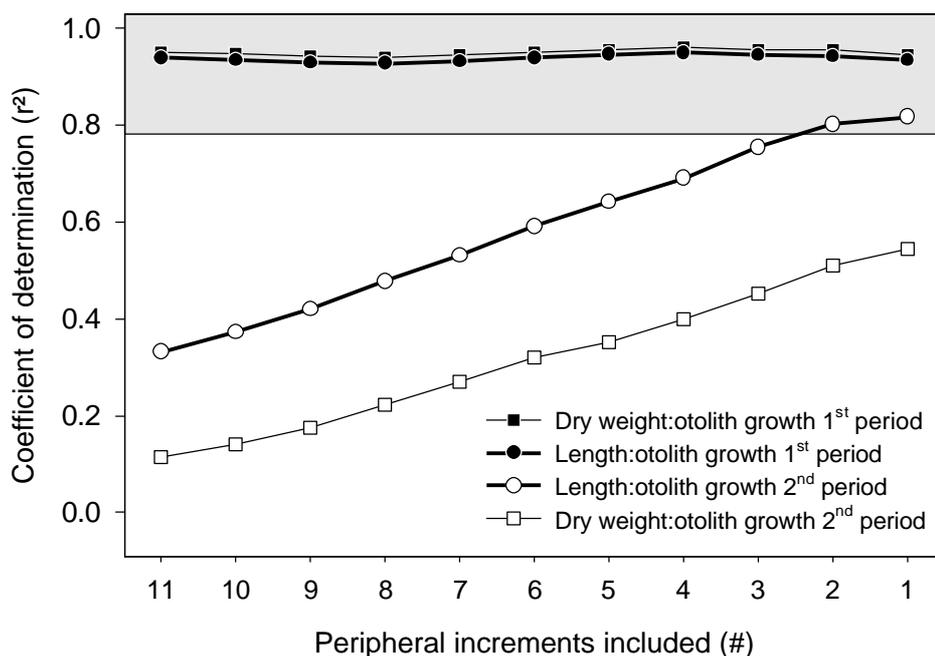


Fig.5: Amount of variability ( $r^2$ -values) explained by different  $cG_{SL}$  vs.  $cG_{OT}$  linear regressions for each of the two periods of the experiment. Because each period lasted 11 days, there were 11 different, cumulative increment widths to predict somatic growth. For example, number 6 on the x-axis refers to the regression done with the cumulative width of the last six increments in each experimental period. Significant linear relationships ( $\alpha = 0.05$ ) have  $r^2$ -values within the grey-shaded area.

To examine the apparent decoupling of otolith and somatic growth, 11 separate linear regressions were calculated for each period by including different subsets of increments to predict the observed  $cG_{SL}$  and  $cG_W$ . Starting with the most peripheral increment in each period, the widths of each of the previous 10 rings were successively added and the new  $cG_{OT}$  regressed on  $cG_{SL}$  and  $cG_W$ . During the first period, the amount of explained variability remained high and significant ( $r^2>0.93$ ,  $P<0.05$ ) and was independent of the number of increments included in  $cG_{OT}$  (Fig.5). During the 2<sup>nd</sup> period, the correlation between otolith and somatic growth was lowest when all increments were included ( $r^2=0.33$  as in Fig.4), but improved steadily as increment widths close to the feeding change were progressively removed from the analysis (Fig.5). Significant linear relationships between  $cG_{OT}$  and  $cG_{SL}$  ( $\alpha = 0.05$ ) occurred

again after 9 days, when only the last two increments of the second period were included. Cumulative  $G_W$ , however, was not significantly related to  $cG_{OT}$  during the second half of the experiment (Fig.5).

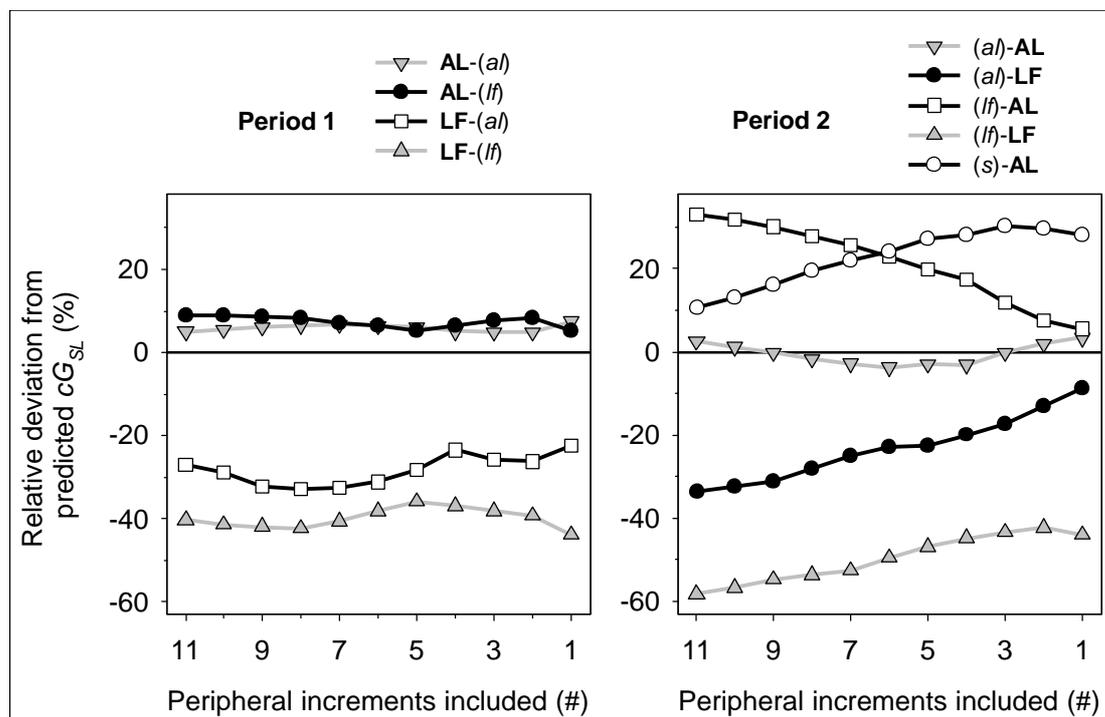


Fig.6: Relative over- and underestimation of  $cG_{SL}$  predicted by the different linear regressions of  $cG_{OT}$  on  $cG_{SL}$  (see text and Fig.5). Negative values, for example, indicate lower  $cG_{SL}$  than predicted from  $cG_{OT}$ . Data labels denote the feeding treatment during the actual (capital, bold letters) and the prospective/previous (small, italic letters in brackets) period. AL/al, ad libitum; LF/lf, low food; S/s, starving.

During the first period, residuals of the 11 regressions (see above) confirmed that the linear relationship consistently over- and underestimated mean  $cG_{SL}$  in low and *ad libitum* food treatments, respectively, independent of the number of included increments (Fig.6). This was also observed in fish within unchanged feeding regimes during the 2<sup>nd</sup> part of the experiment (22 days of low or *ad libitum* food). Over- and underestimation of  $cG_{SL}$  in altered treatments followed the same pattern as in period one, irrespective of the previous feeding regime (i.e.  $cG_{SL}$  in fish changed to low feeding was again overestimated), but the magnitude of over- or underestimation decreased in both cases as fewer peripheral otolith increments were used to predict length growth (Fig.6). Cumulative  $G_{SL}$  of previously starved fish was underestimated but, in contrast to other groups, excluding increments from the otolith growth zone resulted in more deviant residuals (Fig.6).

Recent  $G_{OT}$ , calculated as the cumulative increment width 3 days prior to sampling, significantly predicted fish condition (C) after the first experimental period ( $C=0.0057 \cdot G_{OT}^{0.266}$ ,  $r^2=0.97$ ,  $P=0.002$ ), but again, no correlation was found after the second feeding period (Fig.7). However, mean condition values of previously starved

fish were notably higher than those of all other 2<sup>nd</sup> period treatment groups, indicating a compensatory increase in condition of these re-fed individuals.

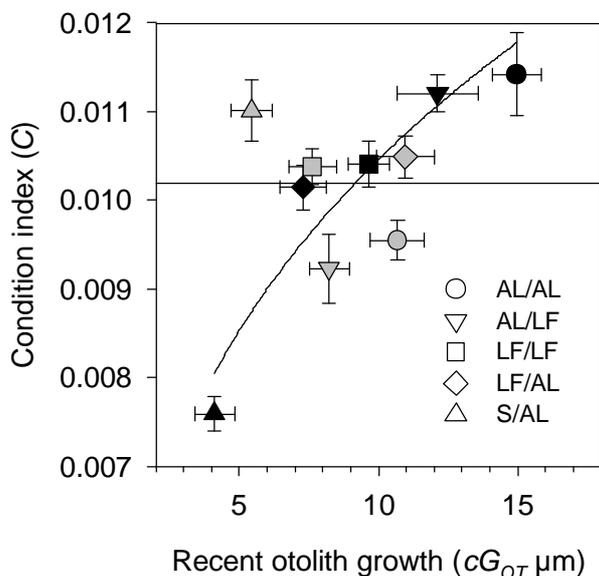


Fig.7: Condition index ( $C \pm 1$  s.e.) in relation to recent otolith growth, calculated as the mean ( $\pm 1$  s.e.) cumulative width ( $cG_{OT}$ ) 3 days before sampling. Black and grey symbols represent the first and second experimental period respectively. A significant relationship was only found for the first period ( $C = 0.0057 \cdot cG_{OT}^{0.266}$ ,  $r^2 = 0.97$ ,  $P = 0.002$ ).

## DISCUSSION

Manipulations of the feeding environment predictably altered somatic growth rates of post-larval Baltic sprat, and both the direction and the timing of these manipulations were well reflected by changes in the otolith microstructure. We found no evidence that different or changing feeding regimes influenced the daily periodicity of increment deposition in post-larval sprat, which has also been found by Shields (1989) and in studies on other fish species (e.g. Jones 1992; Molony 1996). However the effect may be species-specific since less-than-daily ring formation has also been observed in response to poor feeding conditions in herring, *Clupea harengus*, larvae (Folkvord et al. 2000) and juvenile red snapper, *Lutjanus campechanus* (Szedlmayer 1998). The strong linear relationship between otolith and somatic growth, that was apparent after the first period, has generally been confirmed by similar growth-feeding experiments (e.g. Paperno et al. 1997; Takahashi and Watanabe 2004).

However, our data also show systematic deviations from such a general relationship. The negative intercept of the linear regression of length increase as a function of otolith growth (Fig.4) indicates that sprat otoliths keep growing during periods of stagnant growth in length. Slow  $G_{SL}$  induced by low feeding levels clearly led to disproportionately big otoliths, whereas the otolith-somatic growth regression underestimated the length increase of fast growing sprat reared on *ad libitum* rations. Results of the second part of the experiment indicated that the pattern of over- and underestimation in the lengths of slow and fast growing fish remains unchanged irrespective of previous feeding conditions (Fig.6). Similar results have been obtained from otolith microstructural studies on a number of different fish species (e.g. Brothers

1981, Shields 1989, Wright et al. 1990, Campana 1990, Massou et al. 2002, Panfili et al. 2002), a situation that seems to point towards a more complex relationship between otolith and somatic growth than previously acknowledged (Secor and Dean 1989, Mosegaard 1988). After studying otolith-fish size relationships in laboratory-reared whitefish, *Coregonus lavaretus*, Huuskonen and Karjalainen (1998) hypothesized that there were at least two components governing fish otolith growth, one independent and one dependent upon somatic growth, with the first related to maintenance metabolism and the second to feeding-induced growth. This, on the other hand, entails that as long as the ratio between the two components remains constant, otolith growth can be used to predict somatic growth (Dickey and Isely 1997).

Sudden changes in environmental conditions may affect the ratio between growth- and metabolism-related deposition of otolith material. In the present study, the sudden shift in food availability may have caused a differential reaction in maintenance metabolism relative to somatic growth, which was then perceived as a temporal lack of correlation between increment widths and somatic growth. While the direction of the change (i.e. high  $\rightarrow$  low or low  $\rightarrow$  high) was immediately translated into the pattern of otolith growth (as in Paperno et al. 1997), a significant linear relationship between otolith and somatic growth was only re-established after 9 days.

The existence of a time lag between changes in the environment and a significantly different otolith growth has been reported for other fish species and life stages. Pepin et al. (2001) analysed widths of consecutive otolith increments in 3-16 mm larval radiated shanny, *Ulvaria subbifurcata*, noting that serial correlation among increments suggested a time-lag of three days before environmental effects would become detectable. A similarly short delay of 1-3 days was observed by Maillet and Checkley (1989) in 6-20 mm Atlantic menhaden, *Brevoortia tyrannus*, larvae exposed to brief periods of starvation. For 35-40 mm juvenile (120 days post hatch) glass perchlet, *Ambassis vachelli*, Molony and Choat (1990) reported a time-lag of 15 days before starving individuals had significantly narrower increments than fed ones. Similar delays of two and three weeks were also noted in juvenile weakfish *Cynoscion regalis* (Paperno et al. 1997) and chum salmon, *Oncorhynchus tshawytscha* (Neilson and Geen 1985), respectively. Despite different species and approaches, our intermediate value of 9 days obtained for 29-42 mm SL post-larval sprat indicates that the duration of the time lag increases non-linearly with fish size, which is probably a consequence of both the greater energy reserves (Hunter 1976) and reduced growth potentials of bigger fish. The delay in otolith response also likely depends on the severity of the experienced environmental change, as suggested by growth differences between *ad libitum* fed fish during the 2<sup>nd</sup> part of this experiment. After 11 days of *ad libitum* rations, sprat previously provided low food had resumed a mean  $G_{SL}$  comparable to fish in other *ad libitum* treatments, in contrast to those fish where mean  $G_{SL}$  was still lowered due to the previous period of starvation. This lack of compensatory otolith growth was somewhat

unexpected, but paralleled the pattern observed in  $G_{SL}$ . However, the high condition factor of starved/re-fed fish indicated preferential growth in weight as opposed to length. A review of the compensatory growth response in a number of fish species (Ali et al. 2003) suggests that the 11-d re-feeding period in our experiment may not have been long enough to detect compensatory growth in previously starved individuals.

Demonstrating that feeding-related differences in somatic growth rates are imprinted on otoliths is necessary if we are to recognize periods of enhanced or poor feeding in growth histories of field caught fish. Prolonged events of food deprivation, however, may only be seen in juvenile but not in larval otoliths, since early life stages have a much higher vulnerability to starvation (Hunter 1976). Furthermore, as Molony (1996) pointed out, attributing otolith growth patterns to environmental conditions first requires a good understanding of ontogenetically “normal” changes in otolith increment width, otherwise age- and size-related differences in otolith accretion rates will confound any influence of external factors. In our experiment, for example, otolith growth rates in *ad libitum* fed fish first accelerated according to expectation, but decreased later in spite of unchanged feeding levels. Since size-selective mortality was not evident during the experiment, this pattern may reflect ontogenetic limitations of otolith and somatic growth at this body size (Peck et al. in press).

Changes in other environmental factors, most importantly temperature (Pepin 1991, Heath 1992), may affect otolith and somatic growth in a similar way than food availability does. In fact, field studies have frequently demonstrated temperature-effects on larval and juvenile growth (e.g. García et al. 2003, Fowler and Jennings 2003), but feeding-related growth differences appear to be much more difficult to prove in the field than in the laboratory (Baumann et al. 2003). One reason for this might be that food availability, other than temperature, acts on very small spatial and temporal scales, which have yet to be adequately described or sampled (Pepin et al. 2003). Thus, before food related changes in somatic growth can be inferred from otolith microstructure analysis, experienced temperature conditions need to be known.

Given the ubiquitous application of otolith microstructure analysis, laboratory studies comprise a valuable pre-requisite to the meaningful interpretation of growth patterns in field-caught fish. Most of the detailed responses of otolith and somatic growth to different and abruptly changing conditions are likely species- and stage-specific and may also differ between geographical regions. Studies charged with evaluating otoliths of fish having broad ranges in ages and sizes need to take into account the increasingly conservative nature of otolith growth in relation to environmental variability. In the case of the Baltic Sea, the present findings for post-larval sprat bridge the gap between previous research on larvae (Alshut 1988) and larger juveniles (Ustinova 1990) and may therefore increase our understanding about important processes affecting growth and survival of these fish in the sea.

## ACKNOWLEDGEMENTS

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**- PAPER 6 -**

**BALTIC SPRAT LARVAE: COUPLING FOOD AVAILABILITY, LARVAL  
CONDITION AND SURVIVAL**

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**ABSTRACT**

Eggs and larvae of Baltic sprat *Sprattus sprattus* L. were collected during 14 cruises covering the spawning season in 2002 in the Bornholm Basin. Main egg and larval production was recorded in April, with a second small peak in June 2002. The in situ larval abundance was corrected for transport processes by using hydrodynamic model runs. Corrected larval abundance estimates were related to initial larval production to derive an index of larval mortality. This index suggested a much higher survival of summer over spring born sprat larvae, with pronounced differences in survival for larvae > 11 mm. Independent evidence for this survival pattern was gained by measured RNA:DNA ratios in sprat larvae hatched from April-July 2002 and was linked to temporal variability in potential prey abundance. We found higher mean but less variable RNA:DNA ratios in spring- than in summer-born larvae, indicating a strong selection for fast growth in April/May but a less selective environment in June/July. Zooplankton data revealed high naupliar concentrations of *Acartia* spp., a key diet component of sprat, in April/May but very low concentrations of larger prey items like copepodites or adults. In contrast, abundance of larger prey increased considerably in June/July. The results suggest that larger sprat (>11 mm) in April/May 2002 may have been food limited and, therefore, had lower rates of survival, thereby supporting the underlying hypothesis of size-specific, temporally limited 'windows of survival' which are linked to the availability of suitable prey.

**Key words: Baltic Sea, sprat larvae, condition, food availability, mortality, hydrodynamic modelling**

## INTRODUCTION

Natural variations in the abundance of fish stocks can be the result of several factors acting on all life stages. In particular, factors acting on the early life-history stages have been identified to contribute to recruitment variability and hence stock abundance (e.g. Cury & Roy 1989, Fortier & Villeneuve 1996, Köster et al. 2003).

While survival during the egg phase might be critical in some cases (e.g. Köster & Möllmann 2000), emphasis of research has mostly been on the larval stage. Iles & Sinclair (1982) advocated the importance of variable ocean circulation patterns for larval survival. According to the 'member-vagrant' hypothesis (Sinclair & Tremblay 1984) cohort integrity and retention of larvae in areas of favorable environmental conditions would be beneficial for larval survival. Food limitation at the time of first feeding has been suggested as important factor regulating recruitment success as early as 1914 by Hjort who formulated the 'critical period concept'. Cushing (1974) expanded the time period under investigation. In formulating his 'match-mismatch' hypothesis he argued that the temporal coupling or decoupling of the production maxima of fish larvae and their prey organisms are the major source of recruitment variability. However, for species living at the limit of their geographic distribution, the spreading of spawning over a long period of time might be an adaptation to year-to-year variability in environmental conditions (Cushing 1990), and survivors to recruitment must not necessarily stem from peak spawning time. Such potential seasonal variations in larval survival success and their relation to larval prey fields are difficult to investigate, because a sufficient temporal and spatial coverage of the dynamics of larval and zooplankton abundance is needed.

In the Baltic Sea sprat *Sprattus sprattus* L. represents an example of a species occurring at the northern boundary of its geographical distribution (Muus & Nielsen 1999), where the spawning period typically extends from March to August (Elwertowski 1960, Grimm & Herra 1984). Baltic sprat is of high ecological importance (Rudstam et al. 1994, Kornilovs et al. 2001) both as an important prey for top predators (e.g. cod, harbour porpoise) and as a major predator for zooplankton and fish eggs (Arrhenius & Hansson 1993, Bagge et al. 1994, Köster & Schnack 1994, Möllmann & Köster 1999, Köster & Möllmann 2000a,b). It is also presently the most abundant, commercially exploited species in the Baltic Sea (ICES 2004) and its management is challenged by large stock fluctuations mainly caused by a highly variable recruitment success.

Baltic sprat spawning stock biomass is only a poor predictor of recruitment (Köster et al. 2003, MacKenzie & Köster 2004). Recent research has shown that recruitment depends to some degree on temperature conditions influencing gonadal development and egg survival (MacKenzie & Köster 2004). The critical period in the sprat life cycle is, however, the larval and early juvenile stage (Köster et al. 2003).

Mechanisms influencing survival in the larval stage are only poorly understood. Process-oriented investigations are challenged by the long spawning time and the corresponding need to appropriately monitor larval survival and potentially important environmental conditions, such as suitable prey abundance. Survivors might emerge from temporally distinct ‘windows of survival’ which, in the case of food supply, may be determined both by the availability of suitable prey for the first-feeding (i.e. copepod nauplii) and the older larval stages. Sprat larvae generally feed on all developmental stages of copepods, mainly *Acartia* spp. (Voss et al. 2003), but as they grow, the prey field shifts to larger developmental stages (Voss et al. 2003) and food limitation could as well occur due to a temporal mismatch of older copepodite stages and larger sprat larvae.

Sprat spawning is concentrated in the deep basins of the Baltic Sea. In the Bornholm Basin, one of the most important spawning grounds (Köster et al. 2001), the egg distribution is restricted to its central part with sprat eggs occurring in the upper part of the halocline, typically between 45-55m. After hatch sprat larvae migrate to the upper water layers to feed (Voss 2002) and may subsequently be transported away from the spawning grounds. Therefore, direct larval mortality estimates have to account for the temporally highly variable transport potential (Hinrichsen et al. 2003a, b), influencing field-based larval abundance estimates.

In this study, we investigate seasonal variations in the survival success of sprat in different larval size classes during the 2002 spawning season. Our investigations focused on the Bornholm Basin, for which seasonally resolved larval abundance and production values as well as highly resolved zooplankton data were collected. Direct estimates of larval survival up to a specific length were calculated by a combination of field data and hydrodynamic modelling, allowing for a correction of field based abundance values. Additionally, independent information on survival probabilities was gained by an indirect biochemical measure, the RNA:DNA ratio. RNA:DNA ratios have been successfully applied to infer growth, condition and survival probabilities in marine fish larvae under laboratory and field situations (e.g. Buckley 1979, 1984, Clemmesen 1994, Clemmesen et al. 1997).

The underlying hypothesis of our work was that size-specific, temporally limited ‘windows of survival’ exist and that these are linked to the availability of suitable prey.

## **MATERIAL AND METHODS**

### *Seasonal sprat egg and larval abundance*

Sprat eggs and larvae were sampled during 14 cruises to the Bornholm Basin in 2002 (Table 1). During each cruise a standard station grid of 52 stations was covered (Fig. 1). On each station a double oblique Bongo-net haul was performed at 3 knots ship

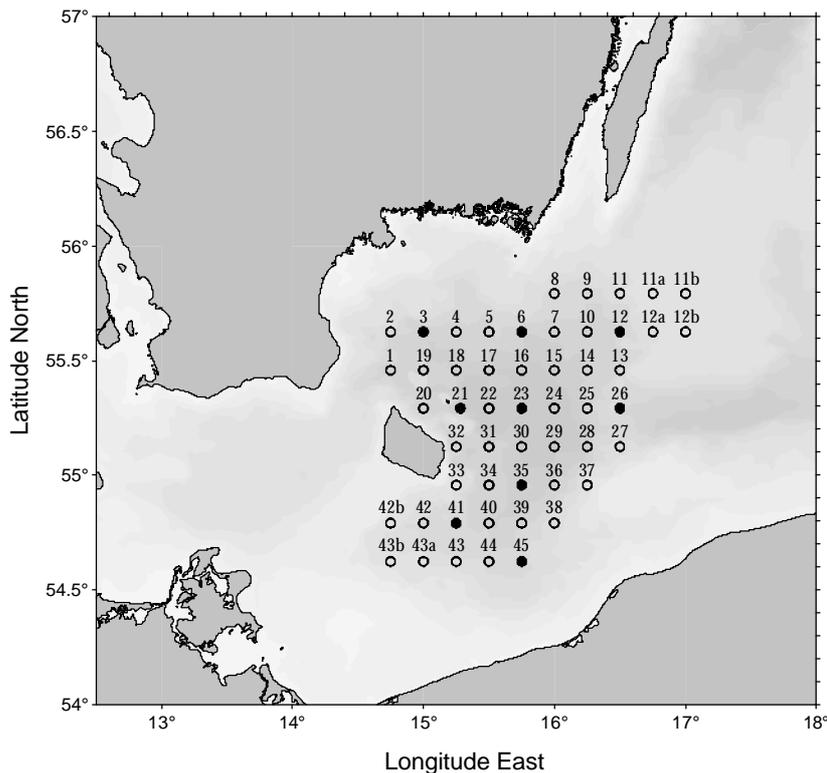


Fig1.: Map of the Bornholm Basin, Baltic Sea. Open circles show standard ichthyoplankton stations, dark circles show stations with additional sampling for larval condition analysis and vertically resolving sampling of zooplankton.

speed. The Bongo (60 cm diameter) was equipped with flowmeters in each of the nets. Sprat eggs and larvae were collected from the 335  $\mu\text{m}$  net. The samples were preserved on board in 4% buffered formaldehyde/seawater solution and were later transferred to formaldehyde-free conservation fluid (Steedman 1976). Fish eggs and larvae were sorted from the samples and staged and measured to the nearest 0.1 mm. At least a subsample of 100 specimen was processed for staging and measuring. The counts were finally standardized to 1  $\text{m}^2$  by the volume of water filtered and the maximum depth of the tow ( $\sim 2$  m above the ground).

Egg staging was performed according to a 4 stage system based on morphological criteria. Stages were chosen according to Thompson et al. (1981) with stages Ia and Ib combined. For all surveys the basin-wide abundance of the different stages of development were calculated by means of objective analysis (Bretherton et al. 1976). The basin-wide egg abundance values per stage of development were then transformed into stage-specific production values by accounting for the stage duration. As stage duration is temperature dependant, ambient temperatures for the egg stages were calculated on a monthly basis, based on temperature profiles and data on the vertical distribution patterns obtained from the research surveys. For sprat eggs the temperature/stage duration relationships from Thompson et al. (1981) were applied. Integration under the daily production curves yielded seasonal production values for the different egg stages.

On a sub-set of stations (see Fig. 1) a random sample of sprat larvae was sorted immediately from the fresh samples and deep-frozen at  $-80^\circ\text{C}$ . These samples were later used for RNA:DNA ratio analyses.

Table. 1. Sampling dates in the Bornholm Basin.

Season	Date	Ichthyo- plankton abundance	Larval length distribution	RNA: DNA	Zoo- plankton	Vertical Distribution of larvae
Winter	18 Mar 02	Yes	-	-	-	-
Spring	05 Apr 02	Yes	-	Yes	Yes	-
Spring	17 Apr 02	Yes	Yes	Yes	Yes	-
Spring	07 May 02	Yes	Yes	Yes	Yes	-
Spring	16 May 02	Yes	Yes	Yes	-	-
Spring	22 May 02	Yes	-	-	-	-
Spring	18 Jun 02	Yes	-	-	Yes	-
Summer	04 Jul 02	Yes	Yes	Yes	-	Yes
Summer	25 Jul 02	Yes	-	Yes	Yes	-
Summer	16 Aug 02	Yes	-	-	-	-
Summer	24 Aug 02	Yes	-	-	-	-
Summer	05 Sep 02	Yes	-	-	-	-
Autumn	05 Oct 02	Yes	-	-	-	-
Autumn	14 Nov 02	Yes	-	-	-	-

### *Feeding environment*

An estimate of prey abundance over the spawning season was calculated by examining the vertical distribution of both the sprat larvae and the zooplankton. The vertical distribution of sprat larvae was examined in June 2002 in the centre of the Bornholm Basin (water depth >80 m) using a towed multinet (5 nets; 0.25 m<sup>2</sup> opening) with a mesh size of 335 µm and equipped with a flowmeter. The nets were towed at a definite depth for ~3 minutes at a speed of 3 knots. Three daytime hauls were combined to determine the vertical distribution in the water column with a resolution of 5 m depth intervals. Sample fixation and analysis in the laboratory were the same as described above for egg and larval abundance sampling.

Vertically resolved (10 m intervals) zooplankton abundance estimates were obtained during 5 cruises (beginning of April, end of April, May, June and July 2002) during which samples were taken by a vertically operated multinet equipped with 50 µm mesh size. The specimens were counted and identified to species and stage of development, e.g. copepods were classified as: (a) nauplii, (b) copepodite stages I-III [C I-III], (c) copepodite stages IV-V [C IV-V], (d) adult males [C VI-m] or adult females [C VI-f]. Stomach content analysis of sprat larvae, covering the spawning season as well as different years, showed that sprat larvae in the Bornholm Basin feed almost exclusively on the different developmental stages of the copepod *Acartia* spp. (Voss et al. 2003). For the 2002 spawning season additional prey items were identified. The

copepods *Centropages hamatus* and *Temora longicornis* were found in smaller proportions in the stomachs (M. Dickmann, Baltic Sea Research Institute Warnemünde, pers. comm.). All other prey types were generally of minor importance. Therefore the potential prey abundance was calculated for two scenarios: sprat larvae fed only on *Acartia* spp. or sprat larvae used *Acartia* spp., *Centropages hamatus* as well as *Temora longicornis* organisms.

Seasonal differences in zooplankton abundance and differences in larval abundance over depth were compared with a Kruskal-Wallis test because, even after transformation, the assumptions of normality of distribution as well as homogeneity of variances were not met.

### ***Larval survival estimates***

Larval ages at length were calculated based on an assumed hatching length of 3 mm and a daily growth rate of 0.4 mm (Shields 1989, Munk 1993, Re & Goncalves 1993, Dulcic 1998, Valenzuela & Vargas 2002, Huwer 2004) and used to assign age-distributions to different size-classes of field caught larvae. For each 1 mm length class (5-<6 mm, 6-<7 mm,...,21-<22 mm) the mean hatching date was back-calculated. Larval production at the assumed hatching date was calculated (based on egg production of egg stage IV and temperature-dependant stage duration, see above) and compared to larval abundance found in the field. This resulted in the definition of an 'abundance-production ratio' (APRA) of larvae for each length class:  $APRA = \ln((N_c / N_h) + 1)$ , where ( $N_c$ ) is the number of larvae caught in the field (in the specific length class) and ( $N_h$ ) is the back-calculated number of larvae hatched (for the specific length class). In this notation high values of the APRA indicate a high survival of larvae up to the specific length class.

To check the sensitivity of the results to the assumed growth rate of 0.4 mm day<sup>-1</sup>, the calculations were repeated for growth rates of 0.2 and 0.6 mm day<sup>-1</sup>. This was also done to account for the seasonal variability of near surface water temperature in the Bornholm Basin.

As larvae, which have originally hatched in the Bornholm Basin, might be advected out of the deep basin and thereby out of the surveyed area, we tried to correct the larval abundance estimates for transport losses before calculating the abundance-production-ratio. The fraction of these 'lost' larvae was calculated for each back-calculated hatching date as a function of drift duration, using the hydrodynamic model described below. Differences in larval survival between sampling dates were tested using Friedman ANOVA and a posteriori Wilcoxon-Wilcox test.

### ***Correction of survival estimates by application of a hydrodynamic model***

The numerical simulations of the Bornholm Basin circulation were performed by application of a three-dimensional (3-D) eddy resolving baroclinic model of the Baltic

Sea (Lehmann 1995). The Baltic Sea Model is based on the free surface Bryan-Cox-Semtner model (Killworth et al. 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan 1969, Semtner 1974, Cox 1984). The Baltic Sea model comprises the whole Baltic with a horizontal resolution of 5 km and 60 vertical levels specified. For the region of the Bornholm Basin this results in a vertical resolution of 3 m layers. A grid size of 5 km and a time step of 5 min were chosen. Within the Bornholm Basin and partly also in adjacent basins the model was initialized with three-dimensional hydrographic data (temperature and salinity) obtained during the research surveys. Outside the observational area, the general features of the Baltic were utilized by incorporation of hydrographic characteristics typical for these regions and time periods obtained from previous model runs. For each depth level of the model, observational data were interpolated onto the model grid by objective analysis (Bretherton et al. 1976). The model was forced for all simulations with actual wind data for the entire Baltic provided by the SMHI (Swedish Meteorological and Hydrological Institute). The model was run for a period of 35 days. A total of 144 drifters were deployed on a regular spaced grid in the area >60 water depth. This area matches the observed distribution of peak egg and larval abundance, as determined from historic surveys (Voss 2002). Drifters were released in 10 m depth, but were allowed to randomly move between 5-15 m depth, simulating the vertical distribution of feeding sprat larvae (Voss 2002). Every 6 hours the fraction of drifters, being distributed outside the 60 m depth isoline (surveyed area), was recorded. This fraction was used to correct the larval abundance estimates.

#### ***Larval condition analysis (RNA:DNA ratio)***

In total 589 larvae have been analysed for RNA:DNA ratio from April (n=236), May (n=168), early July (n=100) and late July 2002 (n=85). Larval sprat samples were freeze dried to constant weight (24 hours, using a Christ Alpha 1-4 freeze-dryer at – 51°C) and were weighed to the nearest 0.0001 mg (Sartorius microbalance SC2). The analysis of the RNA- and DNA content was performed by a modification of Clemmesen (1993) and Belchier et al. (2004). The freeze dried tissues were rehydrated in Tris-SDS-buffer (Tris 0.05M, NaCl 0.01M, EDTA 0.01M, SDS 0.01% ) for 15 min. Cells were disrupted by shaking in a cell-mill with glass beads of different sizes (diameter 2 mm and 0.17-0.34 mm). The resulting homogenate was centrifuged at 6000 rpm at 0°C for 8 min and the supernatant used for the analysis. The amount of nucleic acids (DNA and RNA) was measured fluorometrically in a microtiter fluorescence reader (Labsystems, Fluorescan Ascent) using fluorophor ethidiumbromide. To be able to determine the DNA- content from the sample, a treatment of RNase (Ribonuclease A, Serva) had to be performed prior to the fluorimetric measurement. DNA- and RNA content were calculated as µg DNA or µg RNA per larva. RNA and DNA concentrations were

determined based on calibration curves using Lambda DNA and 16S/23S ribosomal RNA (Boehringer Mannheim).

RNA:DNA values plotted in relation to larval length were analysed using the Signif program described in detail by Evans (2000). This program is useful to analyse distributions where the dependent variable  $y$  can not be expressed as a function of the independent variable  $x$ , and values of  $y$  do not show a constant variance. The approach is to calculate the cumulative probability distributions (CPD) of  $y$  values that are related to a range of  $x$  values. This procedure is repeated along the  $x$  scale and the locally estimated CPD's are expressed by their 10th, 50th and 90th percentile along the  $x$  scale. The scatter is calculated as the difference between 10th and 90th percentile and then compared to 500 data sets in which the assignment of pairs of variables is randomised. An application of this approach for analysing RNA:DNA ratios can be found at Pepin et al. (1999).

## RESULTS

### *Seasonal sprat egg and larval abundance in 2002*

Peak spawning time was in the middle of April, with a mean abundance of egg stage I of 152 n m<sup>-2</sup> (+ 138). A second smaller peak was recorded in June, reaching nearly 29 n m<sup>-2</sup> (+ 45) of the youngest egg stage. Peak larval abundance appeared shortly after peak egg abundance in early May 2002 (45 n m<sup>-2</sup> (+ 40), Fig. 2a). Temperature-dependent egg development times and the spatial distribution of eggs resulted in basin-wide daily egg production values (Fig. 2b), that generally followed the same pattern as the mean abundance. Basin-wide daily egg production of egg stage I reached almost 600 \*10<sup>9</sup> eggs at peak spawning time. For the egg stage IV (close to hatch) production values at the second peak in June reached 37 \*10<sup>9</sup> eggs day<sup>-1</sup>. Additionally the unusual onset of a winter-spawning event of sprat can be seen in November 2002. This special feature was coupled to abnormal high water temperatures and good condition of adult sprat during this time of the year (Kraus et al. 2004).

### *Transport-corrected larval survival estimates*

Advective losses out of the surveyed area generally increased with drift duration (Fig. 3). The specific development of the horizontal distribution patterns was, however, highly variable between the different simulated hatch dates. Mean transport losses after 35 days of drift amounted to 43.6 % (+ 12.6), with a maximum value of 76 % (hatch: 08 June) and a minimum of 26 % (hatch: 29 April). No apparent differences between the start dates were obvious up to a drift duration of 20 days. Afterwards the simulated hatch dates in June revealed higher transport potential out of the area >60 m depth.

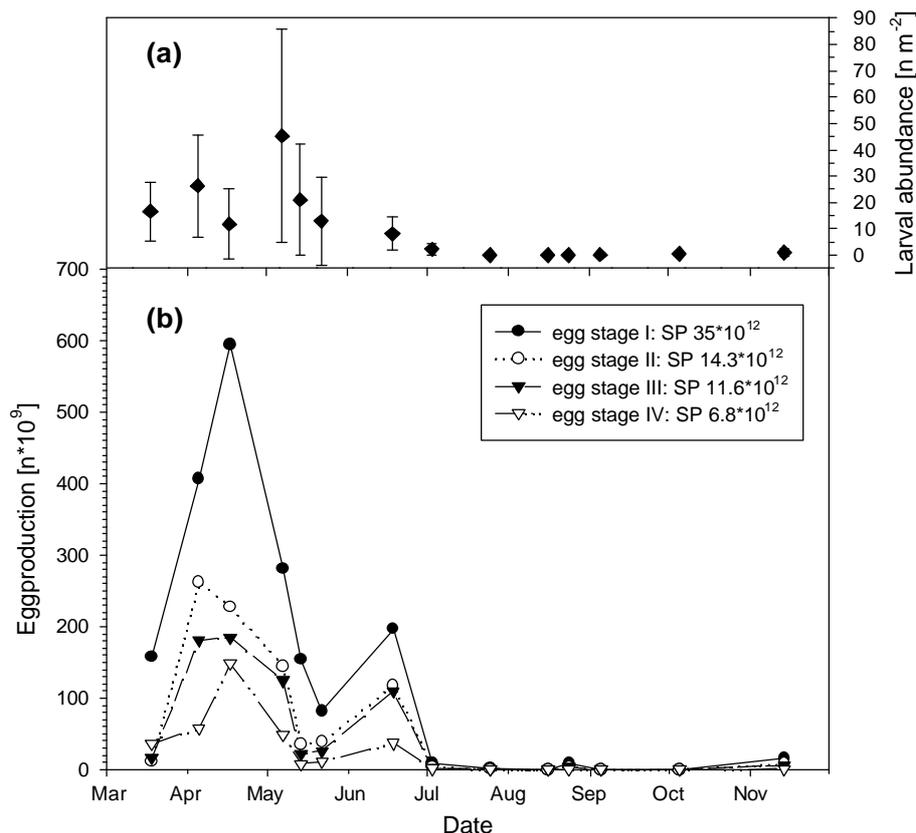


Fig. 2: *Sprattus sprattus*. Seasonal development of early life history stages in the Bornholm Basin during the 2002 spawning season: (a) larval abundance (mean values over a 52 stations standard grid, error bars indicate standard deviation) and (b) Basin-wide daily egg production of different developmental stages. Seasonal production values (SP) of egg stages are given in the legend.

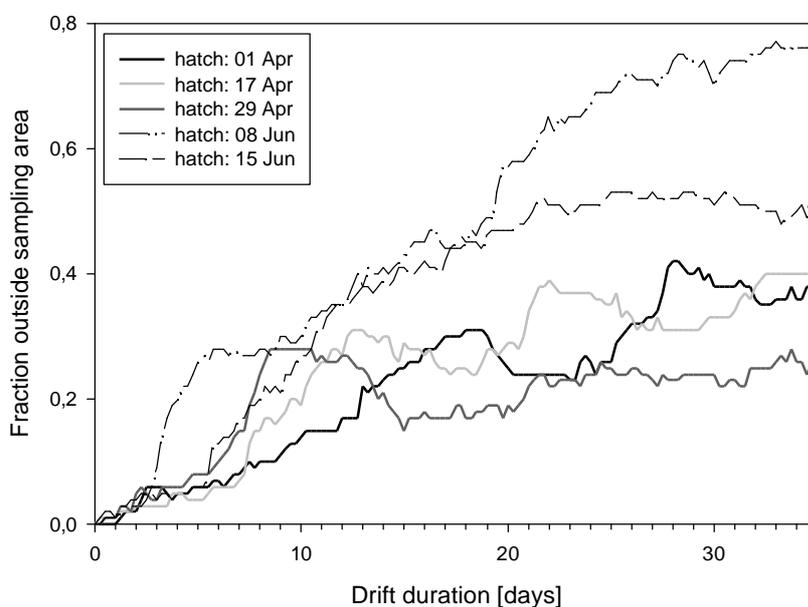


Fig.3: Simulated transport losses of larval drifters out of the surveyed area (>60 m depth). Temporal development for 5 selected hatch dates.

The temporally resolved transport estimates were used to correct larval abundance (Fig. 4) before calculating survival estimates. Corrected larval abundance estimates for each larval size class were higher for assumed slower growth rates, as larval age-at-size

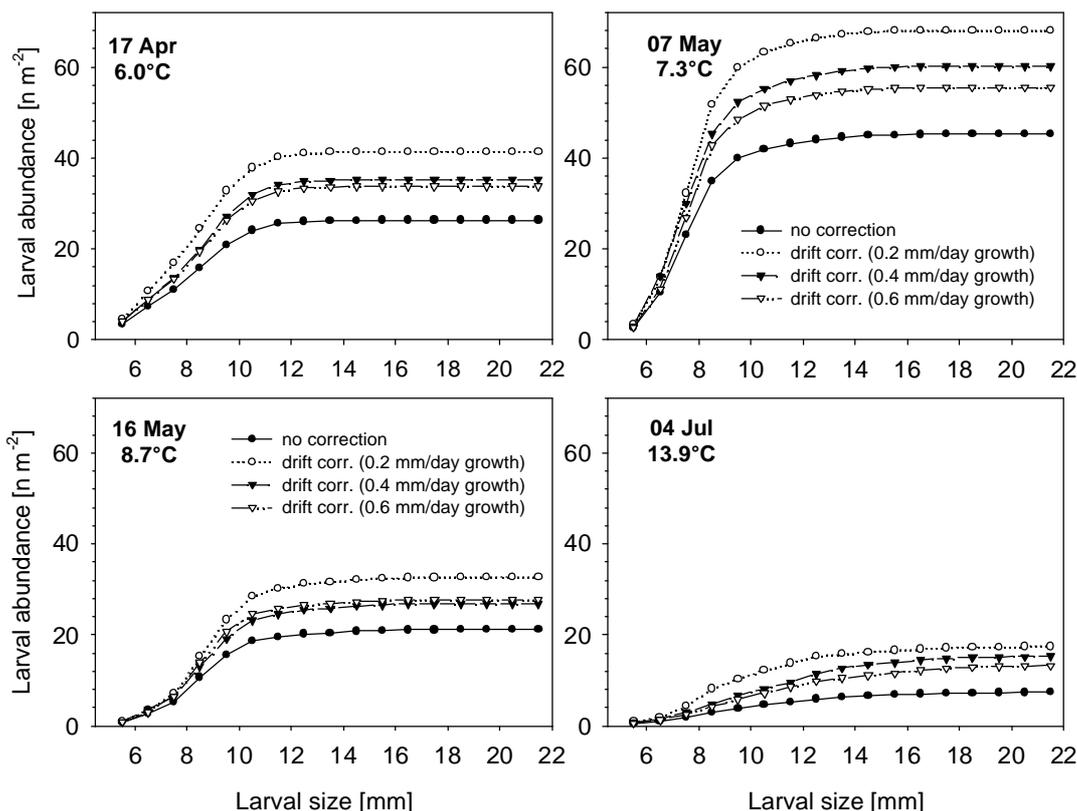


Fig.4: *Sprattus sprattus*. Cumulative larval abundance over size-classes for 4 sampling dates in the Bornholm Basin. Abundance estimates are given without correction and after correcting for transport losses assuming a growth rate of 0.2, 0.4 or 0.6 mm day<sup>-1</sup>.

and hence drift durations were higher. The strongest change in absolute abundance was recorded for larvae caught on 07 May. Assuming a growth rate of 0.2 mm day<sup>-1</sup>, the corrected cumulative abundance value was 22.95 n m<sup>-2</sup> higher compared to the standard assessment without correction (45.20 n m<sup>-2</sup> vs. 68.15 n m<sup>-2</sup>, Fig. 4). The lowest change in absolute abundance was calculated for larvae caught on 04 July (+ 10.07 n m<sup>-2</sup>). Relative changes in cumulative abundance (growth rate of 0.2 mm/day vs. standard) varied between a factor of 1.51 (April) and 2.37 (July).

When assuming a growth rate of 0.4 mm day<sup>-1</sup>, highest values of the abundance-production ratio (APRA), indicative for high survival up to a specific length, were reached for the size-classes between 7-10 mm in the April and May samplings (2.56 - 2.88; Fig. 5). For larvae caught in July, the highest value of the APRA was recorded in the size-class 12-13 mm (2.80). Towards bigger size-classes, the values of the APRA were generally decreasing, as larval abundance decreased with size (Fig. 5). In April and May this decrease was more pronounced, so that values <0.1 were reached for larvae sized 15-16 mm (April) and 17-18 mm (May). Contrary to this, the APRA stayed above 0.5 for the complete investigated size-range for larvae caught in July 2002.

The index revealed no difference in survival up to a larval length of 11 mm between the different sampling dates (Friedman ANOVA, df = 3, n = 6). For larvae >11

mm survival was significantly higher in June (i.e. caught in early July) compared to all other sampling dates (Friedman ANOVA,  $p < 0.001$ ,  $df = 3$ ,  $n = 11$ ).

If growth rates were set to 0.6 mm day<sup>-1</sup>, absolute values of the APRA changed (Fig. 5) but did not affect the result of highest APRA values found in larger, late hatched larvae (July sampling). Again survival was significantly higher for larval sizes >11 mm in July samples compared to all other dates (Friedman ANOVA,  $p < 0.001$ ,  $df = 3$ ,  $n = 11$ ). However, assuming a growth rate of 0.2 mm day<sup>-1</sup> in June/July caused this time period to show a similar pattern to April and May, with survival decreasing rapidly for larger size classes. Given that water temperature in 5-15 m depth was highest in July (13.9°C) compared to April and May (6.0 to 8.7°C), such slow growth rates in July appear unlikely.

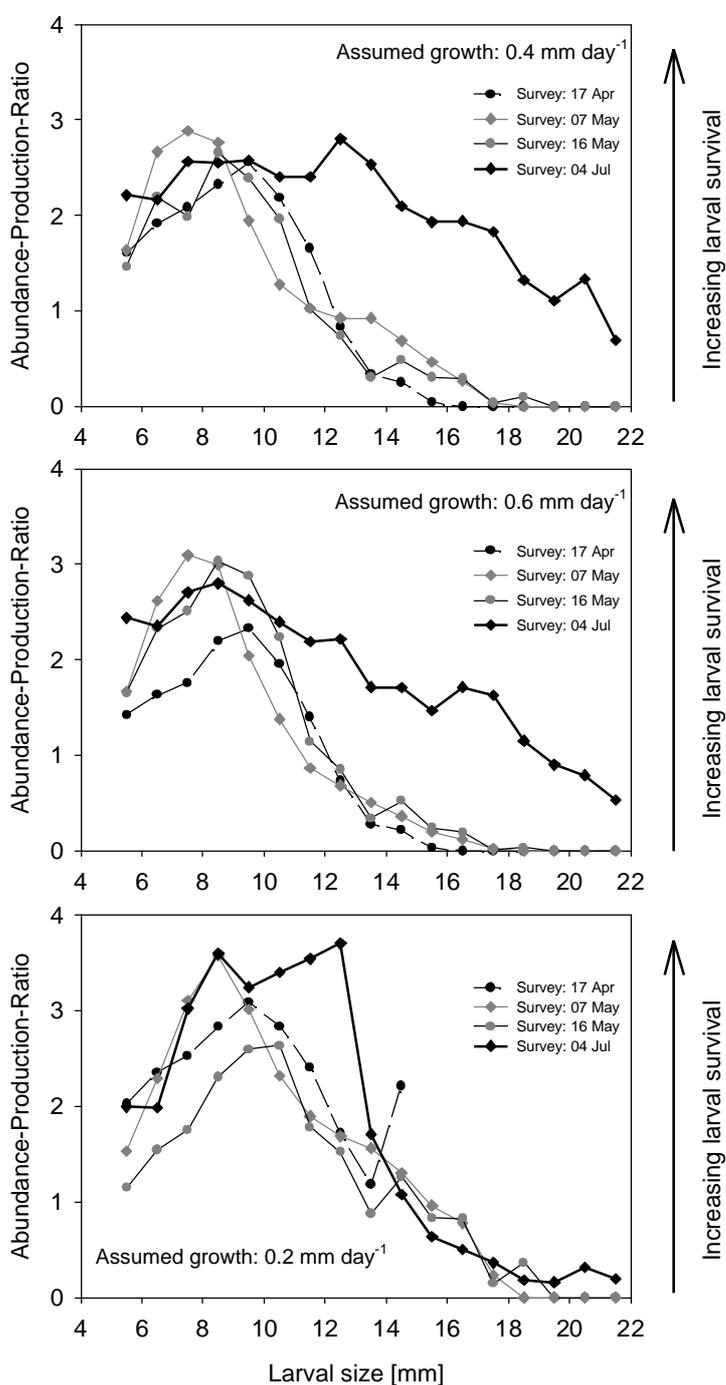


Fig.5: *Sprattus sprattus*. Abundance-production ratio (APRA) indicative for larval survival of different sized sprat larvae under the assumption of growth rates of 0.4, 0.6 or 0.2 mm day<sup>-1</sup>. Sampling dates and mean ambient temperatures are given in the legend.

Condition of larvae in the field

Mean RNA:DNA values generally increased with larval size for all sampling occasions (Fig. 6a-d). While the investigated size range was limited to approx. 13 mm length in April and May, in July also larvae >20 mm length were analysed. Medians were higher in April and May for the size range of 4-13 mm (Fig. 6e). However, the variability of RNA:DNA values was higher in June/July compared to April and May (Fig. 6f). Mean distance between the 10th and 90th percentiles amounted to 1.122 and 1.171 for April and May respectively, while it reached 1.635 and 1.660 in June and July (size range up to 13 mm). The 90th percentiles did not show large differences for the overlapping larval size ranges. The 10th percentile, however, increased to higher values in April and May from approximately 6.5-7 mm larval length on, while it stayed almost

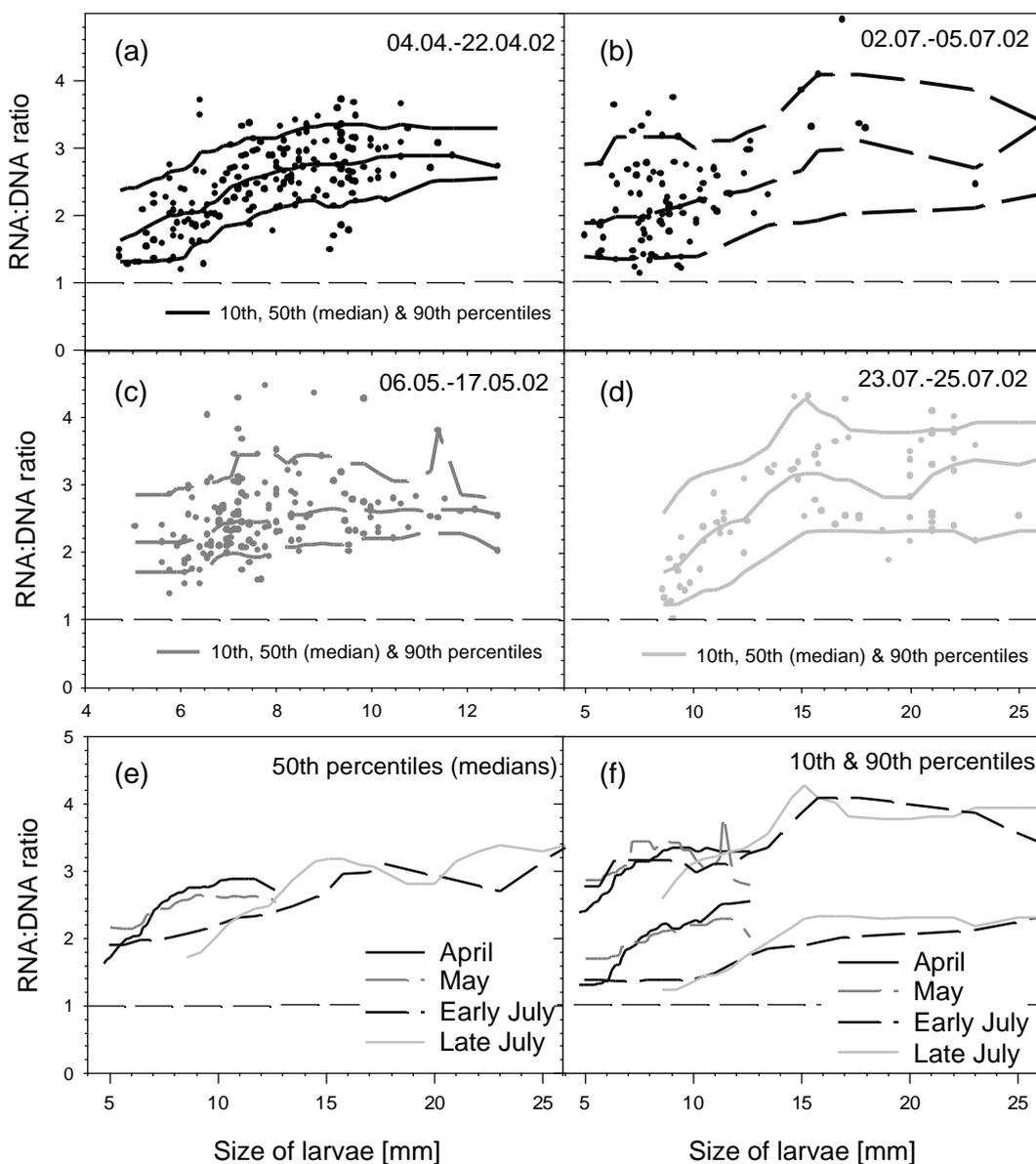


Fig.6: *Sprattus sprattus*. Cumulative probability distributions (CPD) of RNA:DNA content in relation to larval lengths (Evans 2000). Median, 10th and 90th percentiles of the RNA:DNA ratios during 4 cruises in 2002 (a-d). Comparison of medians (e) and 10<sup>th</sup> and 90<sup>th</sup> percentiles (f).

constant on the initial level in June/July. In contrast to June/July, in April and May no larvae were caught with RNA:DNA values indicative for slower growth and/or under-average condition.

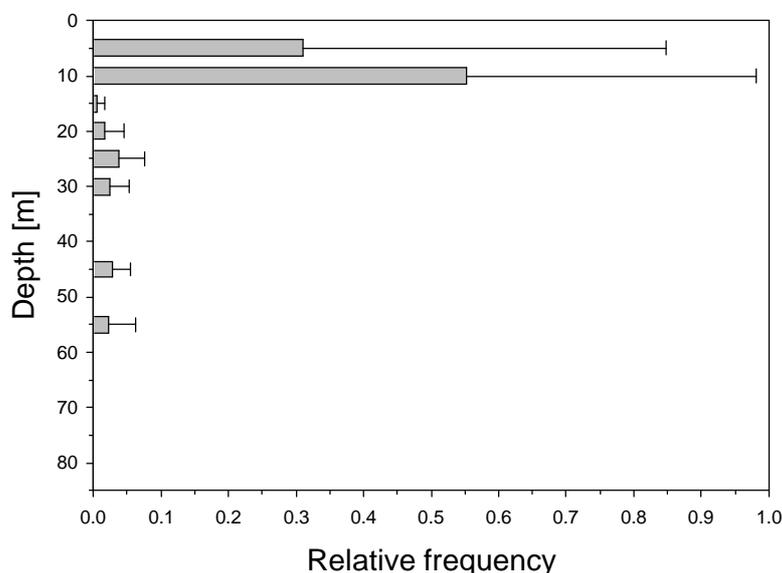


Fig.7: *Sprattus sprattus*. Vertical distribution of larvae >6 mm length in June 2002. Mean values and standard deviation from 3 profiles during day-light hours.

#### *Coupling of condition and survival to prey fields*

The depth range from surface to 30 m depth encompassed almost 95% of the larval distribution. Mean abundance of feeding larvae (>6 mm) was highest in 10 m depth, followed by 5 m depth (Fig. 7). All deeper investigated depth layers showed considerably lower mean values, but statistically significant differences between depths layers could not be detected due to a high variability between samplings (Kruskal-Wallis H-test,  $p = 0.08$ ). We calculated potential prey abundance for the water layer 0-30 m depth from vertically resolving zooplankton samplings. In the first feeding scenario, which is only accounting for *Acartia* spp. as prey, a high abundance of nauplii could be seen in April (Fig. 8a). In mid April *Acartia* spp. nauplii abundance was significantly higher than in May and July, but not different from June (Kruskal-Wallis H-test,  $p < 0.01$ ). The available prey biomass was, however, low in April, as only very small numbers of *Acartia* spp. copepodites and adults could be found. In May and especially June a strong increase in numbers of *Acartia* spp. copepodite stages and adults was recorded (Fig. 8a), resulting in a significantly higher abundance of copepodite stages I-III in June compared to early April or late July (Kruskal-Wallis H-test,  $p < 0.01$ ). The abundance of older developmental stages of *Acartia* spp. (C IV-adult) was also higher in June compared to both April sampling dates.

The general seasonal pattern was very similar for the second feeding scenario (Fig. 8b). When incorporating *Acartia* spp., *Centropages hamatus* as well as *Temora longicornis* organisms as prey, the peak in nauplii abundance in mid April was even

more pronounced. Nauplii abundance in mid April was significantly higher than in early April, May and June (Kruskal-Wallis H-test,  $p < 0.01$ ). Results for copepodite stages I-III as well as for older developmental stages are similar to the first feeding scenario.

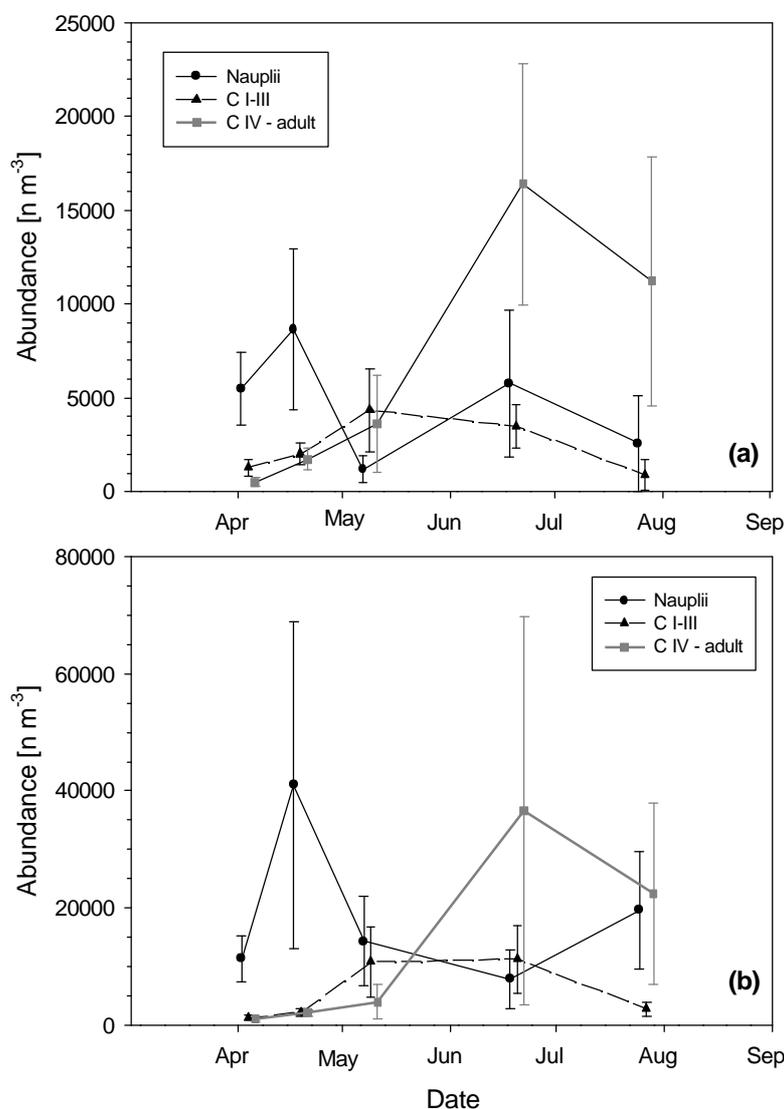


Fig.8: Mean prey abundance and standard deviation for larval sprat in the Bornholm Basin (0-30 m depth): (a) only *Acartia* spp. and (b) *Acartia* spp., *Centropages hamatus* and *Temora longicornes* as prey species.

## DISCUSSION

In Baltic sprat, the larval stage has been shown to be critical for reproductive success, while survival is generally less critical once an individual has reached the juvenile (0-group) phase (Köster et al. 2003). In this study, we found evidence for seasonal variations in sprat larval survival over the spawning season 2002. Especially, the survival of larvae >11 mm, i.e. not related to first feeding success, showed pronounced differences between peak (April) and late (June) spawning time and was linked to prey availability.

Spawning activity of sprat in the Bornholm Basin is usually spread over a long period, i.e. from March to August. Historically the peak spawning time was found around the end of May (A. Makarchouk, Latvian Fisheries Research Agency Riga, pers. comm.), with year-to-year variability depending to a certain extent on the temperature

conditions (Elwertowski 1960, Grimm & Herra 1984). The main spawning peak in April 2002 was early compared to other years, followed, however, by a secondary, smaller peak in June which corresponds better to the historic data. For Baltic cod an overall shift in spawning time has been recorded in the 1990s (Wieland et al. 2000), but corresponding information on sprat is still too scarce to judge if spawning time has generally shifted to earlier months, or if the 2002 season remains an exception.

Our conclusion of higher survival of late spawned larvae was drawn based on abundance to production ratios indicative for relative survival success. Larval abundance has been corrected for transport out of the surveyed area prior to calculation of the ratios using a 3-D hydrodynamic model. Corrections rely on the assumption that modelled drift of passive particles was representative of the average drift of sprat larvae. It is well known that the flow patterns in the Bornholm Basin region are highly complex, being mainly determined by the ephemeral character of wind stress, the baroclinic mass field and the complicated bottom topography (e.g. Lehmann 1995). However, the Baltic Sea model has already been successfully utilized to simulate the drift of larval fish in the Bornholm Basin (Voss et al. 1999, Hinrichsen et al. 2002), including transport correction of abundance estimates for larval cod (Voss et al. 2002), as well as longer term (>35 days) drift simulation of sprat larvae (Baumann et al. 2004). Since the investigated domain was quite large, it was important that the initial distribution of simulated drifters matches the observed larval distribution. In this exercise, simulated drifters were deployed on a regular spaced grid in the area >60 m water depth. Although the horizontal variability in larval abundance was quite high (cf. high standard errors in figure 2), the overall distribution of field caught eggs and larvae as well as drifters matched well.

To be able to determine initial larval production over the spawning season, age-at-length of larvae was calculated based on assumed growth rates. The use of otolith microstructure analysis, currently the best tool for reconstructing past variations in larval fish growth, could have improved the accuracy of growth estimates. Unfortunately, no such samples have been available. However, the range of assumed growth rates of 0.2 - 0.6 mm day<sup>-1</sup> covers well the range of observed growth rates in the field (Shields 1989, Munk 1993, Re & Goncalves 1993, Dulcic 1998, Valenzuela & Vargas 2002, Huwer 2004). Positive anomalies from mean growth rates of 0.4 mm day<sup>-1</sup> were related to higher ambient temperatures. A fact also recorded by Alshut (1988) in laboratory experiments. Therefore, the only inconclusive scenario in our work (lowest growth rates of 0.2 mm day<sup>-1</sup> in July-caught larvae), seems highly unrealistic. All other investigated scenarios point to a critical period in sprat larval survival for larger larvae (>11 mm).

While sufficient nauplii availability has been shown vital for survival of first feeding cod larvae (Hinrichsen et al. 2002), the critical period for larger sprat larvae might be linked to a shift in prey requirements as larvae grow. At a size of 10-12 mm

sprat larvae increasingly depend on older copepodite stages and adults (Voss et al. 2003), while they mainly feed on nauplii at smaller lengths. It appears possible that larval survival in 2002 was critically dependent on a match between high abundance of suitable copepodite and adult stages and larger larvae instead of a match between nauplii and small larvae.

Based on the hypothesis that RNA:DNA values reflect the feeding environment of larvae (Pepin et al. 1999, Evans 2000, Clemmesen et al. 2003), independent evidence was provided for different feeding scenarios during the course of the spawning season 2002. Feeding environment for small, first-feeding larvae was best in April/May, with high abundances of nauplii. On the other hand, the situation was much better for larger sprat larvae in June/July compared to April/May in terms of biomass as well as in terms of stage composition of the prey taxa. Both feeding scenarios were reflected in the condition analysis and the survival probability. Larvae seemed to survive up to large sizes even when showing comparably low RNA:DNA values in July, suggesting a less selective environment at this time. Not only the fast growing, over-average conditioned larvae survived, but slower growing larvae were also successful. In contrast to this, in April and May environmental conditions seemed to strongly select for fast growing larvae. Larvae with lower nutritional condition were removed from the population (i.e. higher mortalities), which was reflected in the rise of the 10% percentile. The majority of survivors in 2002 presumably came from a situation, where the environment was less selective for well-conditioned larger larvae. This is in line with a hypothesis originally proposed by Meekan & Fortier (1996), stating that when larval food supply is abundant, the selective pressure for fast growth is relaxed such that slow-growing larvae survive in larger proportion.

In the present study fish larvae for RNA:DNA analysis were sampled during night and day time and no differentiation according to sampling time was performed. Although Chicharo et al. (1998) seem to demonstrate diel variation in RNA:DNA ratios in *Sardina pilchardus* larvae off the North of Spain with higher RNA:DNA ratios during the night, there is controversy in the literature about the effect. Bailey et al. (1995) found no significant diel effect in *Theragra chalcogramma* larvae. Rooker & Holt (1996) found diel changes in RNA:DNA ratios, with higher values during the daytime. So far no general pattern has been shown, if effects are there they react differently according to species and also according to temperature experienced and not a lot of proof has been shown. In general sudden increase in RNA concentration as a response to increase in food availability is not possible, since this first leads to an increase in RNA activity and later to an increase in RNA number. Therefore RNA:DNA ratios do not reflect the increase in prey availability over a period of hours (Clemmesen 1994, 1996). A diel signal in RNA:DNA ratio can therefore be caused by the effect of size, higher consumption rates, possibly RNA:DNA from the food organisms ingested, vertical distribution patterns and temperature regimes experienced. The authors believe

that the problem of diel periodicity based on an endogenous rhythm still has to be confirmed under controlled conditions and is not a problem for the approach being followed in this study.

Our results suggest that high mean values of RNA:DNA are not always indicative of high survival on the population level. This does not negate the assumption that high RNA:DNA ratios are coupled to fast growth and high survival probability on an individual level. However, on population level, a less selective environment would be indicated by a broader distribution of RNA:DNA values and a lower mean. It becomes obvious, that it is necessary to investigate the distribution of condition factors to correlate the results to survival.

Besides starvation, predation or changes in larval transport might as well determine the survival of early life history stages of fish (predation: Sissenwine 1984, Köster 1994, Köster & Schnack 1994; transport: Iles & Sinclair 1982, Sinclair & Tremblay 1984, Hinrichsen et al. 2002). Adult Baltic herring and sprat strongly prey on fish eggs, including sprat (Köster et al. 2001). Predation on larvae is, however, only of minor importance, as prey and predator are vertically separated. Adult clupeids feed within and below the permanent halocline (Köster & Möllmann 1997), while sprat larvae are distributed near the surface. Also other potential predators on larval sprat (e.g. medusae) have been shown to have a negligible impact (Barz & Hirche 2004). Different transport scenarios might influence larval survival probabilities, due to horizontal differences in levels of primary production, and hence food abundance (Cushing & Walsh 1976, HELCOM 1993, Ochocki et al. 1995) or increased predation risk in shallow water areas, due to higher abundance of e.g. 0-group cod. Time-series analysis of transport potential and sprat recruitment showed indeed a positive correlation between retention in the deep basin and good year-class strength (Baumann et al. 2004), although the underlying processes are not fully understood.

In conclusion, we can state that size-specific, temporally limited ‘windows of survival’ existed during the course of the 2002 spawning season. These were linked to the availability of suitable prey for larger sprat larvae. These results are along the lines of Cushing’s ‘match-mismatch’ hypothesis (1974, 1990), but defining seasonal variability in survival rather than year-to-year variability. Instead of a first-feeding limitation, larval survival in 2002 depended on a match of older sprat larvae and higher concentrations of suitable prey organisms. However, also year-to-year recruitment variability might be influenced by the temporal overlap of larval production and a window of survival, which is itself determined by zooplankton abundance and stage composition.

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- PAPER 7 -

**THE GENERAL DISTRIBUTION PATTERN AND MIXING PROBABILITY OF  
BALTIC SPRAT JUVENILE POPULATIONS**

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**ABSTRACT**

Transport of Baltic sprat *Sprattus sprattus* L. larvae spawned on different spawning grounds was investigated by detailed drift model simulations for the years 1979-2002. Modeling approaches with and without diurnal vertical migration were applied. We used recently collected data on spawning location, vertical distribution and the timing of spawning as input to a particle tracking model. Results of this modeling study enabled the identification of potential nursery grounds for sprat originating from different spawning grounds. On average, westerly winds are prevailing over the Baltic Sea. This leads to on average higher abundance of juvenile sprat along the southern and the eastern coast lines of the Baltic. The horizontal distribution of simulated larval or 0-group sprat is consistent with the observed distribution of 0-group sprat obtained from the hydroacoustic field surveys. In addition, this analysis identifies the potential for advective mixing between juveniles originating from different spawning sites or from the same spawning site throughout the spawning season. High spatial overlap was found between Arkona- and Bornholm Basin larvae hatched at the beginning of the spawning season. Mixing probability of sprat juveniles between Arkona- and Gotland Basin as well as between Bornholm- and Gotland Basin were on relatively low levels.

**Key words: Hydrodynamic modeling, advective mixing, hydroacoustics, sprat nursery grounds, spatial overlap analysis**

## INTRODUCTION

The maintenance of distinct stocks of one species requires that juveniles recruit to their source population and that mixing between stocks is restricted. However, many fish stocks are sedentary as adults but are redistributed as juveniles by currents during their pelagic phases. Many marine species use different locations for spawning, larval development, larval and juvenile feeding, and adult feeding. Their life histories require connections between these spatially disaggregated locations to close the life cycle. Learned behavior might play an important role in maintaining patterns of connectivity or isolation (e.g. Hay et al. 2001). The connectivity between such local populations is likely to be influenced by variable hydrographic and atmospheric forcing conditions (e.g. Hinrichsen et al. 2001), affecting transport and as a consequence survival and subsequent recruitment. Variability in ocean circulation leading to spatio-temporal differences in larval transport may have additionally affected recruitment success of fish stocks, because retention or dispersion of larvae from the spawning grounds to areas suitable or unsuitable for larval survival has been identified as one of the key processes influencing recruitment success in fish stocks (e.g. Werner et al. 1996; Heath and Gallego 1998; Hinrichsen et al. 2002). These transports can be accompanied by advective propagation of passively drifting particles such as eggs and larvae of different origin as well as local populations of a single stock, thus, within the same area lead to mixing of their juveniles. To investigate the influence of circulation patterns on larval and juvenile distributions and variations in recruitment success, detailed numerical flow simulations have yielded insights into movements of marine larvae of certain species in particular systems (e.g. Bartsch et al. 1989; Hinckley et al. 2001). Only the latter approaches provide the opportunity to follow the fate either of cohorts or of individual larvae tracked backward or forward in time through the model domain.

Sprat *Sprattus sprattus* L. play an important role in the Baltic ecosystem. Presently, the fish biomass in the Baltic Sea is dominated by this fish species. Sprat is an important prey species for e.g. cod, and also an important predator on lower trophic levels and cod eggs (Möllmann and Köster 2000). On the other hand, Baltic sprat is at present heavily exploited by the fishery. Although sprat in the Baltic are assessed as a single management unit, there exists some evidence that recruitment varies within and between different stock components and areas of the Baltic Sea (Köster et al. 2003). Three different sprat stocks have been hypothesized in the Baltic (Aro 1989); one inhabits the Belt Seas, the Western Baltic, and the region of the Bornholm Basin, one the Gdansk Deep and the Gotland Deep area and one the Northwestern and Northern Baltic and the Gulf of Finland. The boundaries between the stocks are not very clear and mixing between stocks during feeding and winter periods is apparent (Rechlin 1986).

To investigate long-term (1979-2002) average horizontal distributions of the different juvenile sprat populations in the central Baltic, the present modeling approach

did not focus on individual particle trajectories, but rather on generalized larval drift patterns on the spatial scale of the entire Baltic Sea. We used collected data on spawning location, vertical distribution and the timing of spawning as input to a particle tracking model. First, the results of this exercise were used to identify potential nursery grounds for sprat originating from different spawning grounds. Secondly, our goal was to estimate the overlap between larval sprat either originating from different areas of the Baltic Sea or from the same area but produced at different dates during the spawning period. This analysis allows to determine the potential for advective mixing between different stocks or between different hatching cohorts of the same stock component throughout the spawning season. Furthermore, this analysis also provides information on the temporal stability of nursery areas. In order to examine the implications of larval and juvenile vertical migration behaviour on their horizontal distribution patterns, we have performed additional sensitivity analyses. Finally, results of these modeling studies are compared with horizontal 0-group sprat distributions obtained from hydroacoustic surveys.

## **MATERIAL AND METHODS**

### *Hydrodynamic model and particle tracking*

The hydrodynamic 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 made, necessary to adapt the model to the Baltic Sea can be found in Lehmann (1995) and Lehmann and Hinrichsen (2000a). A detailed analysis of the Baltic Sea circulation has been performed by Lehmann and Hinrichsen (2000b) and by Lehmann et al. (2002).

The model domain comprises the entire Baltic Sea including the Gulf of Bothnia, Gulf of Finland, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km, with 60 vertical levels specified. The thickness of the different levels is chosen to best account for the different sill depths in the Baltic. The Baltic Sea model is driven by atmospheric data provided by the Swedish Meteorological and Hydrological Institute (SMHI: Norrköping, Sweden) and river runoff taken from a mean runoff database (Bergström and Carlsson 1994). The meteorological database covers the whole Baltic Sea drainage basin with a grid of  $1^\circ \times 1^\circ$  squares. Meteorological parameter, such as geostrophic wind, 2-m air temperature, 2-m relative humidity, surface pressure, cloudiness and precipitation are stored with a temporal increment of 3 hours. Prognostic variables of the model are the baroclinic current field, the 3-D temperature, salinity and oxygen distributions, the 2-D surface elevations and the barotropic transport. Physical properties simulated by the hydrodynamic model

agree well with known circulation features and observed physical conditions in the Baltic (for further description see Lehmann 1995; Hinrichsen et al. 1997; Lehmann and Hinrichsen 2000a).

Simulated three-dimensional velocity fields were extracted (at a 6 hours interval) in order to develop a database for a Lagrangian particle tracking exercise for larval sprat. This data set offers the possibility to derive Lagrangian drift routes by calculating the advection of “marked” water particles. Vertical velocities were calculated from the divergence of the horizontal velocity fields. The drifters were allowed to leave the layers where they were launched. The positions of the drifters varied over time as a result of the three-dimensional velocities that they experienced. In order to establish a Lagrangian view of the simulated circulation, drifters can be placed in the modeled flow fields at every location within the model domain. Moreover, the initial launch positions can be chosen independently from the vertical resolution of the model’s grid. Simulated drift routes were obtained from Eulerian flow fields by utilization of a Lagrangian particle-tracking technique. The three-dimensional trajectories of the simulated drifters were computed using a 4th order Runge-Kutta scheme (Hinrichsen et al. 1997).

The hydrodynamic model has been utilized to simulate Baltic sprat larval drift for the time period 1979 to 2002 to obtain mean distributions of Baltic sprat juveniles and their corresponding transport patterns. Each release of drifters consisted of 2671 particles distributed within the main spawning areas of the Central Baltic Sea. Corresponding to the size of the spawning area, 291 drifter started in the Arkona Basin, 636 in the Bornholm Basin and 1744 in the easternmost area representing the Gdansk Deep and the Gotland Basin. The total number of drifters tracked during each year was 24039 (9 releases x 2671 drifters/release). The initial horizontal release locations were derived from mean distribution maps of late egg developmental stages (Makarchouk, pers. comm.), assumed to be a proxy for the distribution of first feeding larvae. Larval drifters were released on a regular spaced grid enclosed by the 40 m isobath representing the main spawning area of the Bornholm Basin, the Gdansk Deep and the Gotland Basin (Fig. 1). Drifters for the western most considered stock component in the Arkona Basin were released inside the 20 m isobath. Drifters, at their release representing first feeding larvae which have finished their initial vertical migration after hatch, were inserted into the modeled flow fields at 10 days intervals and were tracked for certain time periods. The release dates commenced April 21th and ended July 10th, encompassing the spawning period of eastern Baltic sprat. The primary source of information on the timing of spawning was derived from Karasiova (2002) and from unpublished information (Makarchouk pers. comm.). The larvae were allowed to drift for periods of 36-116 days, until all positions were finally recorded on August 15th. This date was chosen to compromise sufficient drift periods for late released larvae as well as avoiding too long drift periods for early released larval batches, because for the latter active swimming behaviour becomes likely. While most of spawning occurs in the

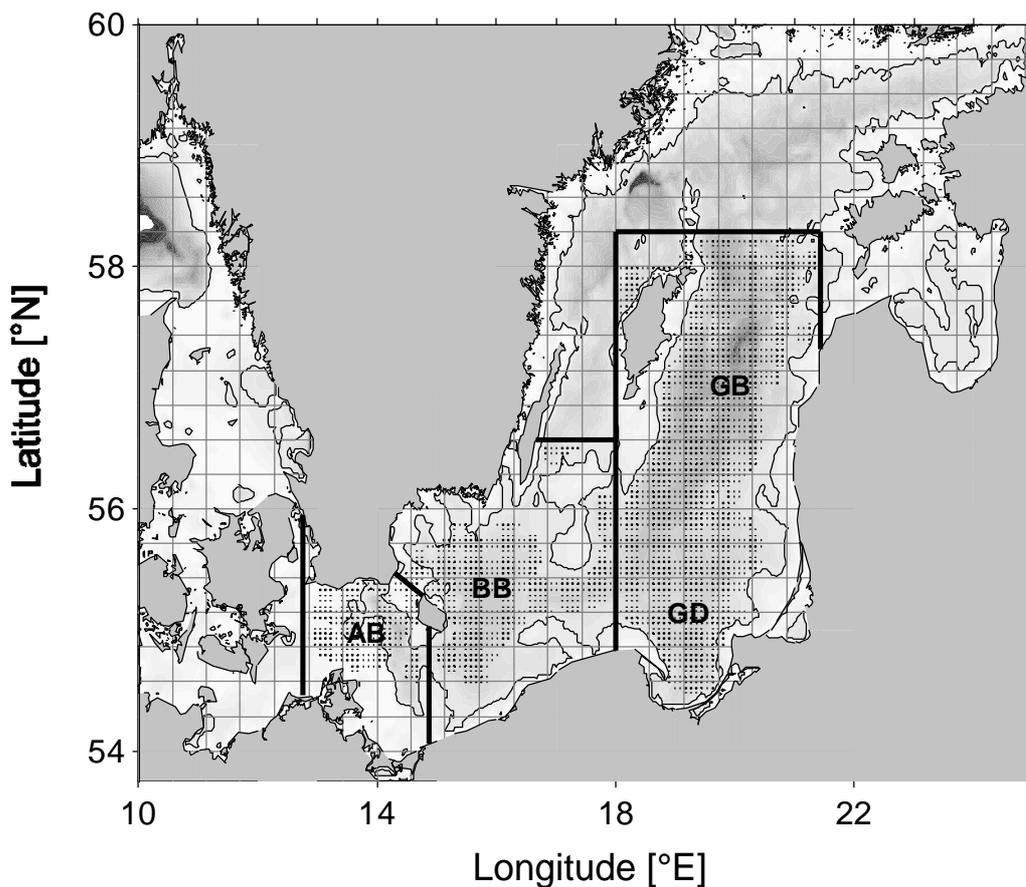


Fig. 1: Horizontal map of the central Baltic Sea, dots show seeding positions of Lagrangian drifters used in the hydrodynamic circulation model, rectangles represent potential areas of larval and juvenile appearance. Rectangles were used for overlap calculations. AB-Arkona Basin, BB-Bornholm Basin, GD-Gdansk Deep, GB-Gotland Basin; thick lines represent sprat spawning areas

deeper part of the basins (Nissling et al. 2003), feeding larvae are mainly found in the upper part of the water column. As a first approximation, Lagrangian drifters were released and forced to remain at depth between 5 and 10 m (depths at which feeding larvae occur after their initial vertical feeding migration). This is in accordance with recent field observations (Voss 2002), showing no influence of daytime on the vertical distribution since the early 1990s.

It was assumed that horizontal swimming is generally of less importance in the context of horizontal flows, but sprat larvae are able to actively change their vertical position in the water column which might significantly alter their drift routes. However, sprat larvae are visual feeders, and their vertical movements are probably associated with a diel feeding periodicity. Evidence for such behaviour is presented by Voss (2002), who observed diel migrations of sprat larvae for the 1980s: larvae concentrated at mid-depths (30-40 m) during day but migrated vertically into upward direction during nighttime. To account for differences in larval transport due to vertical migration, a second model was set up by assigning a simplified behavior to particles: larvae were assumed to be in the depth range of 5-10 m for 12 hours per day and between 30-40 m for the other 12 hours). Small scale variability of vertical larval appearance has been

simulated by assigning each of the larva after every time step a new randomly selected vertical position between 5 to 10 m or between 30 and 40 m, respectively. Although these schemes adopted in the model were highly simplified, the essential features of feeding larval occurrence and behavior are captured well.

Additional sensitivity analyses have been performed to examine the implications of larval and juvenile vertical migration behaviour on their horizontal distribution patterns. Besides our general vertical distribution scenarios, i.e. with and without vertical migration, allowing larvae to stay i) 24 hours between 5 and 10 m depth, and ii) 12 hours between 5 and 10 m depth and 12 hours between 30 and 40 m depth, three additional scenarios were developed. Sensitivity testing was performed assuming that larvae and juveniles have spent iii) 18 hours between 5 and 10 m depth and 6 hours between 30 and 40 m depth, iv) 6 hours between 5 and 10 m depth and 18 hours between 30 and 40 m depth, and v) 24 hours between 30 and 40 m depth. These simplistic diel vertical migration scenarios were applied in 1991, a year for which seasonal variability of meteorological forcing and hence variation in drift patterns was large.

#### *Spatial distribution and overlap analysis*

Horizontal maps of modeled juvenile distributions were constructed by simple integration of larval/juvenile drift endpoints obtained from hydrodynamic model simulations in rectangles (representing quarters of ICES rectangles) of approximately 15x15 nm size covering the main spawning areas as well as the most likely larval and juvenile appearance (Fig. 1). To allow direct relative comparisons of final larval/juvenile distributions between the sub-areas, numbers of drifters found in rectangles were normalized by dividing them with respect to the maximum number of larval/juvenile drift endpoints found in the sub-area.

We applied spatial overlap analysis (Horn 1966), to investigate the relationship between larvae initially released in different areas or within the same area but at different dates during the sprat spawning season. To determine how many larvae of different batch releases in space or time were simultaneously present in the specified sub-areas of the Central Baltic Sea (Fig. 1), a coefficient of overlap (C) was calculated, which is 0 when there is no overlap, and 1 when two distributions are identical:

$$C = 2 \sum_{i=1}^n (A_i \times B_i) / \left( \sum_{i=1}^n A_i^2 + \sum_{i=1}^n B_i^2 \right)$$

where n is the number of statistical rectangles (Fig. 1). Spatial overlap analysis was first applied to study the degree of mixing between larvae initially released within different spawning areas represented by the final distributions A and B. The same approach was then used to describe the spatial overlap of final distributions A and B

between larval drifters that were initially released in the same spawning area but at different dates during the spawning season. This method was used as a descriptive tool to quantitatively assess the importance of overlap between different 0-group sprat populations.

The different predictions of horizontal larvae and juvenile distributions for the model runs in 1991 based on additional vertical migration scenarios were quantitatively compared with spatial overlap analysis.

#### *Hydroacoustic measurements*

Information on spatial distribution patterns of Baltic-sprat-0-group has been collected regularly in the framework of the Baltic International Acoustic Surveys (BIAS). This multi-national and multi-ship survey takes place in October since the beginning of the 1990s (for participating institutes, see Acknowledgements). A detailed description of sampling and data-analysing procedures is given in the 'Manual for the Baltic International Acoustic Survey (BIAS)' (ICES 2001). The data are collected in the

'Baltic Acoustic Database (BAD1)', which contains age-resolved abundance-estimates of herring and sprat for each covered statistical ICES-rectangle, separately for each national sub-survey. For this study, the yearly abundances of sprat-0-group per ICES-rectangle were averaged for the years 1991 to 2002. If in a year a rectangle was covered by more than one single national sub-survey, the values of this rectangle were averaged for this year, before the average over all years was calculated. For comparison to simulated distributions the observational data was normalised.

## **RESULTS**

#### *Simulated horizontal sprat 0-group distribution*

For drifters initially released in the Arkona Basin (Fig. 2a), horizontal distribution maps clearly show higher concentrations of juveniles in the western part of the basin (west of 14°E) at August 15th. Only a low number of particles were transported out of the basin in several directions. Juveniles of Bornholm Basin spawners on average had distributional peaks in the majority of rectangles south and south-east of the Bornholm island (Fig. 2b), with the easternmost peak occurring in the Gdansk Deep. Most of the particles were found in the southeast of the Bornholm Basin as well as in the western and central part of the Gdansk Deep. Potential nursery areas for the easternmost stock component of Baltic sprat were identified in the Gdansk Deep and Gotland Basin. Areas with highest average concentrations of juveniles were found along the Polish-, the Lithuanian- as well as along the Latvian coast lines (Fig. 2c).

Drift patterns and final particle distribution were not similar for the two investigated model scenarios simulating larval sprat advection with and without vertical

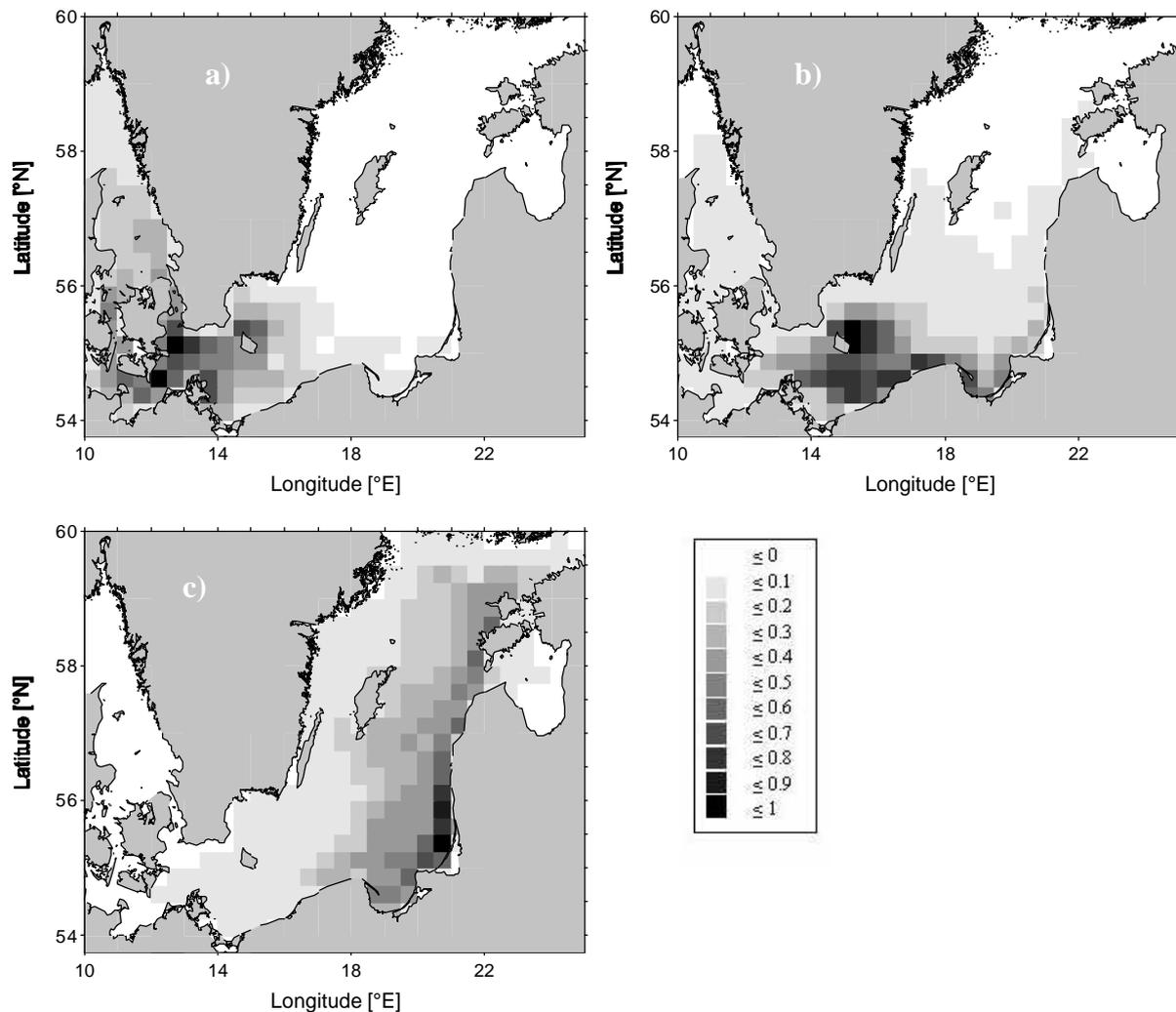


Fig. 2: Final mean distribution (1979-2002) of simulated sprat juveniles at August 15<sup>th</sup> in the whole central Baltic without diurnal vertical migration released in a) the Arkona Basin, b) the Bornholm Basin, and c) the Gotland Basin.

migration. Model outputs showed remarkable differences in the number of particles retained in the deep basins. In general, the model runs including daily vertical migration resulted in higher retention (Fig. 3a-c), because current velocities at mid-depth are lower than in the layers directly below or within the wind-induced mixed layer. This would further decrease the probability of mixing between the different basins. Additionally, compared to the results obtained from model runs without vertical migration, Arkona- and Bornholm Basin spawning products yielded higher particle concentrations within the northern coastal environments. Juveniles initially spawned in the Gdansk Deep and in the Gotland Basin were more widely dispersed over the whole basin if vertical migration was considered, with also higher numbers of particles retained in the deep basin areas.

The combined final distributions of drifters seeded within all three spawning areas of Baltic sprat, indicated clear spatial differences in the average horizontal 0-group distribution (Fig. 4).

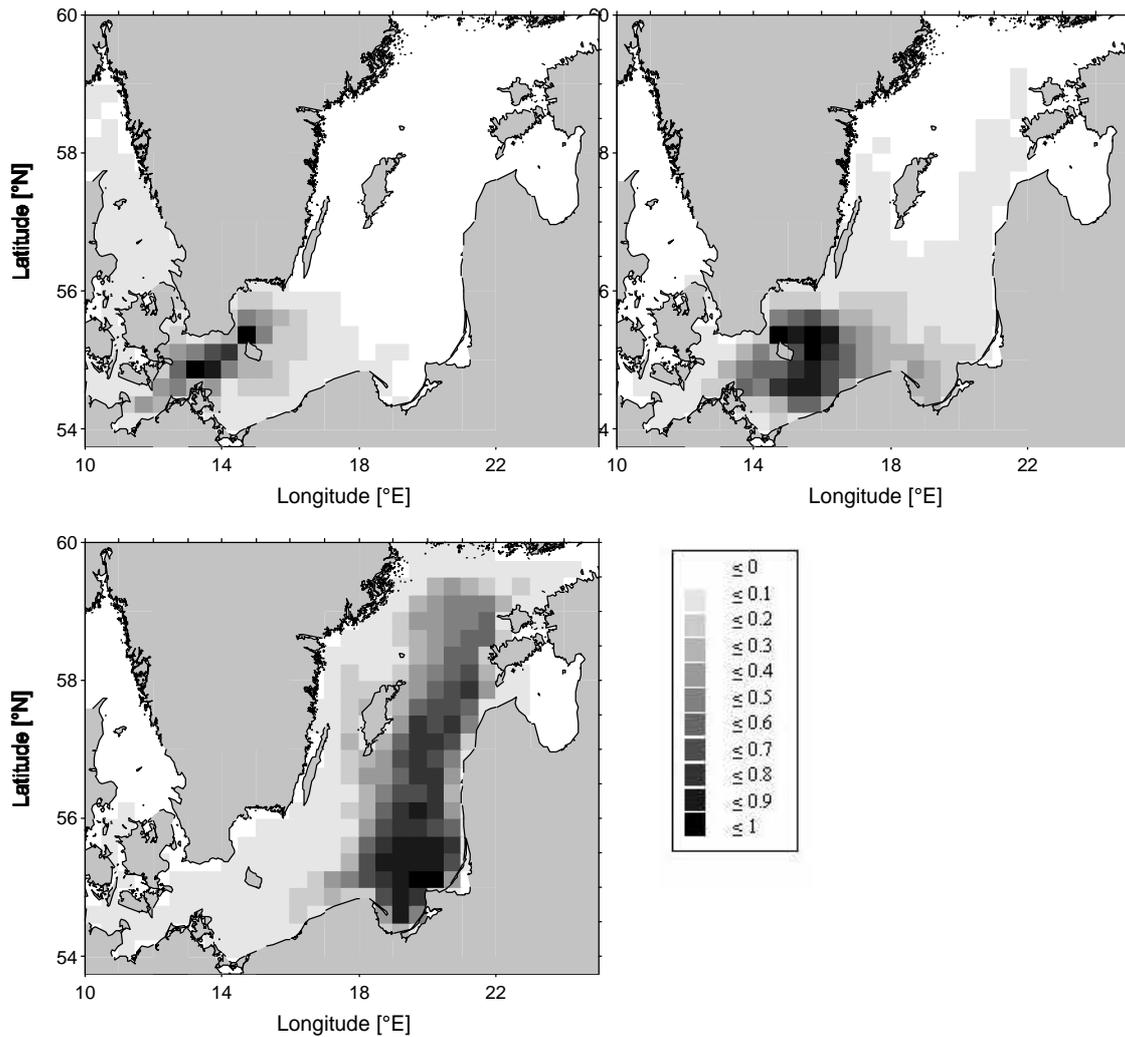


Fig.3: Final mean distribution (1979-2002) of simulated sprat juveniles at August 15<sup>th</sup> in the whole central Baltic with diurnal vertical migration released in a) the Arkona Basin, b) the Bornholm Basin, and c) the Gotland Basin.

As obtained from the results of the long-term model runs, horizontal larval and juvenile distributions indicate higher dispersal of larvae and juveniles the longer the individuals remained in the directly wind-driven sub-surface layer (5 to 10 m). Using the model run from 1991 representing purely passive larval advection (24 hours larval and juvenile appearance in the surface layers) as a reference, the spatial overlap between this baseline scenario and the distribution patterns of the other model runs decreased the longer larvae and juveniles stayed in deeper layers (Table 1).

Table 1: Spatial overlap coefficients of horizontal distributions for larval appearance in the upper layer (24 hours) with horizontal distributions of different vertical migration schemes:

Larval appearance			
5-10 m/ 30-40 m 18h / 6 h	5-10 m/ 30-40m 12h / 12h	5-10 m/ 30-40 m 6h / 18h	5-10 m/ 30-40 m 0h / 24h
0.90	0.63	0.40	0.21

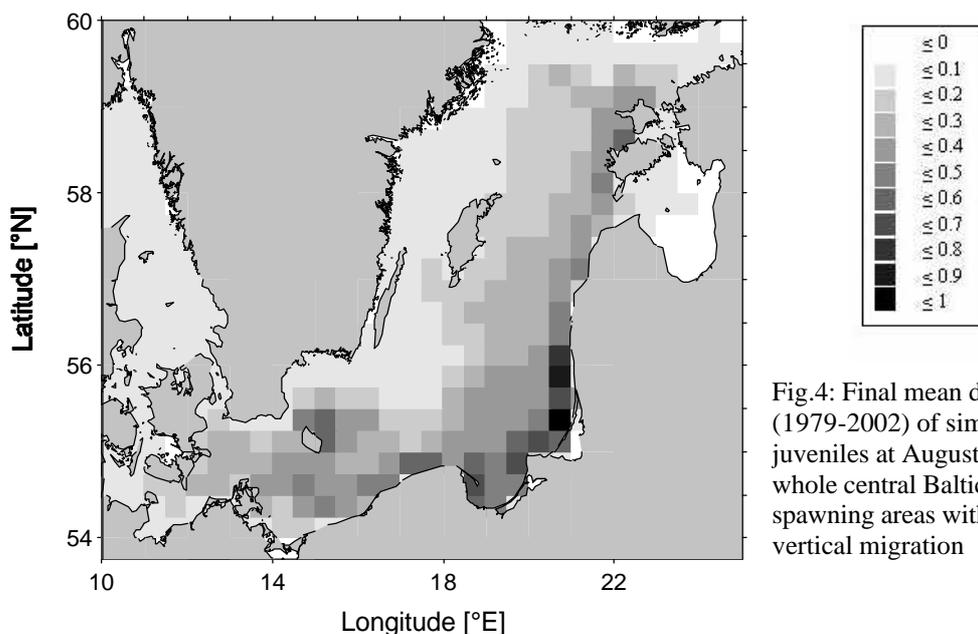


Fig.4: Final mean distribution (1979-2002) of simulated sprat juveniles at August 15<sup>th</sup> in the whole central Baltic released in all spawning areas without diurnal vertical migration

*Comparison between simulated and observed horizontal sprat 0-group distributions*

Similar to Fig. 4, the final distributions of simulated drifters released within all three spawning areas of Baltic sprat between 1991-2002, indicated clear spatial differences in the average simulated horizontal 0-group distribution (Fig. 5). Highest numbers of particles were transported towards the east coast of the central Baltic and directly into the Gdansk Deep, which is consistent with the abundance of 0-group sprat estimated from hydroacoustic surveys between 1991-2002 (Fig. 6). The model results from the runs including vertical diel migration behaviour revealed higher retention in the deeper parts of the basin compared to larval drifters exclusively occurring in the directly wind driven layers. An overlap coefficient of 0.27 was found for a comparison between model predictions and observational data if larvae and juveniles were only allowed to remain between 5 and 10 m depth. A decrease in spatial overlap (0.20) was

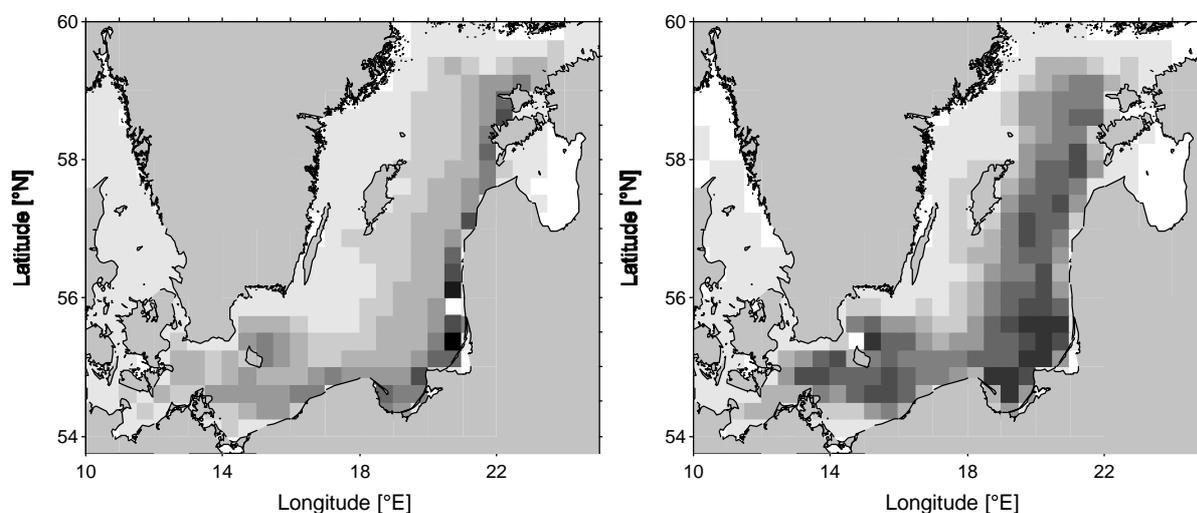


Fig.5: Final mean distribution (1991-2002) of simulated sprat juveniles at August 15<sup>th</sup> in the whole central Baltic released in all spawning areas without diurnal vertical migration a) with and b) without vertical migration (Legend as above).

obtained if diurnal vertical migration was considered. Only low numbers of 0-group sprat were observed in the northern as well as in the western part of the Bornholm Basin. As also predicted by the model simulations, relatively high numbers of sprat larvae were transported away from their original spawning grounds. This resulted in abundance peaks encountered in the southern region of the central Baltic including the coastal areas of the Gdansk Deep as well as the shallower areas of the southeastern Gotland Basin. The potential appearance in the deep central part of the Bornholm Basin suggested by the model was not unequivocally supported by field data. This might be due to a time lag of approximately two months between observations and simulations, resulting either from a further passive drift of juveniles out of the area, or from potentially active redistribution of this stock component.

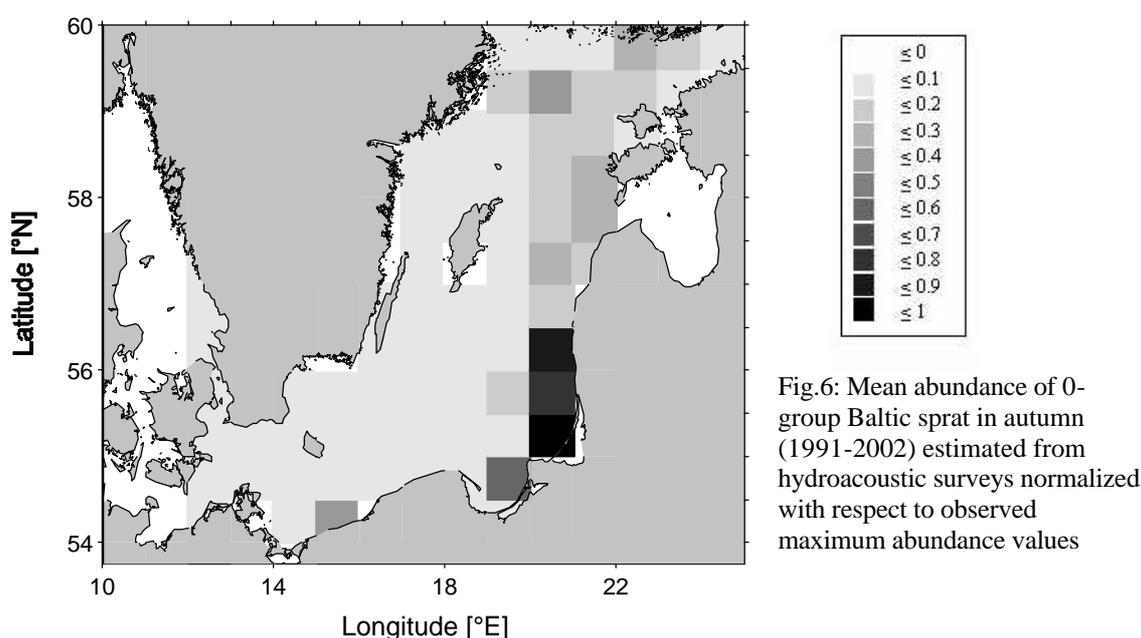


Fig.6: Mean abundance of 0-group Baltic sprat in autumn (1991-2002) estimated from hydroacoustic surveys normalized with respect to observed maximum abundance values

#### *Spatial overlap of different juvenile sprat populations*

Spatial overlap calculation of the simulated distributions of individuals released at different spawning grounds on a particular date provided a measure of the juvenile composition within different areas at that time. The overlap of juvenile sprat starting their drift as first feeding larvae within different spawning grounds of the Baltic was obtained by combining data from all years as well as from all release dates. As shown in Fig. 7a, the spatial overlap between juveniles originating in the Arkona- and Bornholm Basin reflects the relatively high degree of similarity in spatial distribution. Highest probability for spatial overlap of these different juvenile populations can be expected within the Arkona Basin and in the northwestern part of the Bornholm Basin. Both juvenile populations had a relatively high spatial overlap observed late in the season if they originally hatched during the early spawning period with a declining trend towards summer months. Although much smaller in magnitude, the same tendency was obtained if the spatial overlap was calculated for Bornholm- and Gotland Basin spawners (Fig. 7b). Spatial overlap between these juvenile stock components mainly occurred in the

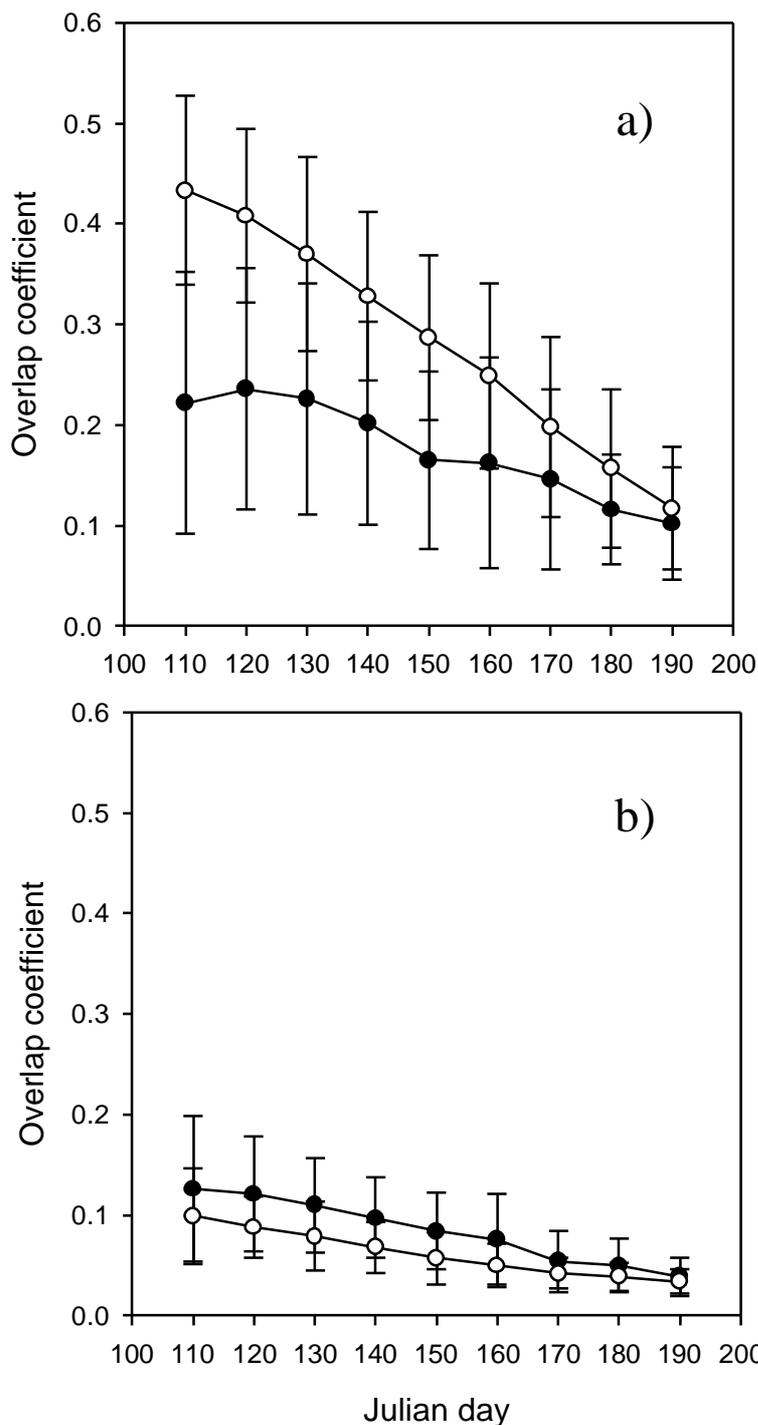


Fig.7: Mean seasonal overlap of simulated juveniles between a) Arkona and Bornholm Basin and b) between Bornholm and Gotland Basin (thick line without and thin line with vertical migration), error bars represent one standard deviation

southern part of the Gdansk Deep and only to a small degree in the eastern part of the Bornholm Basin. Almost no mixing of juveniles originating from the Arkona- and Gotland Basin occurred.

Generally, the model outputs showed remarkable inter-annual differences in the number of particles retained within the Bornholm Basin. On average, however, the results strongly indicate that the western and eastern most stock components of Baltic sprat contribute to the juvenile populations in the area where they were spawned. Taking into account diurnal vertical migration of larvae revealed similar results as for

larvae exclusively being advected within the upper layer. Significantly higher spatial overlap was only found between Arkona- and Bornholm Basin larvae originating from the beginning of the spawning season if diurnal vertical migration was considered. Mixing probability of sprat juveniles between Arkona- and Gotland Basin as well as between Bornholm- and Gotland Basin remained on almost the same low levels as for the simulations not accounting for diurnal vertical migration.

Table2: Overlap (mean and standard deviation) of a) Arkona Basin juveniles b) Bornholm Basin juveniles and c) Gotland Basin juveniles with time lag from 1. through 9. release dates (without vertical migration)

Release								
	2	3	4	5	6	7	8	9
a) Arkona Basin								
0.77/0.09		0.69/0.12	0.64/0.15	0.57/0.15	0.49/0.17	0.44/0.18	0.38/0.16	0.33/0.16
		0.81/0.06	0.78/0.07	0.71/0.08	0.61/0.11	0.55/0.13	0.47/0.12	0.42/0.13
			0.82/0.06	0.76/0.07	0.67/0.10	0.60/0.13	0.52/0.13	0.45/0.13
				0.83/0.05	0.75/0.11	0.68/0.13	0.59/0.13	0.52/0.14
					0.83/0.07	0.76/0.11	0.68/0.10	0.58/0.12
						0.83/0.09	0.74/0.11	0.64/0.11
							0.85/0.09	0.75/0.12
								0.83/0.09
b) Bornholm Basin								
0.90/0.06		0.84/0.11	0.85/0.07	0.81/0.11	0.79/0.13	0.73/0.12	0.69/0.17	0.59/0.20
		0.89/0.08	0.88/0.06	0.84/0.09	0.82/0.10	0.77/0.10	0.71/0.16	0.62/0.20
			0.89/0.09	0.89/0.06	0.86/0.08	0.81/0.10	0.73/0.17	0.65/0.20
				0.90/0.07	0.87/0.10	0.82/0.11	0.76/0.17	0.66/0.20
					0.92/0.04	0.86/0.07	0.78/0.17	0.69/0.20
						0.90/0.06	0.80/0.17	0.70/0.19
							0.87/0.14	0.78/0.16
								0.87/0.08
c) Gotland Basin								
0.91/0.06		0.86/0.09	0.84/0.11	0.82/0.13	0.79/0.15	0.73/0.13	0.70/0.11	0.62/0.14
		0.93/0.03	0.90/0.05	0.88/0.07	0.84/0.08	0.79/0.07	0.75/0.10	0.67/0.14
			0.93/0.03	0.91/0.04	0.86/0.07	0.80/0.08	0.76/0.13	0.68/0.17
				0.94/0.03	0.90/0.06	0.83/0.08	0.77/0.14	0.68/0.18
					0.94/0.03	0.86/0.08	0.79/0.15	0.71/0.19
						0.92/0.06	0.83/0.14	0.75/0.18
							0.90/0.10	0.84/0.12
								0.92/0.05

*Spatio-temporal overlap of juvenile sprat from early to late spawners*

In order to identify whether juveniles spawned at different times of the spawning season within the same spawning area ended up on average in the same nursery grounds or being transported into different regions, we have calculated their spatial overlap. Mixing rates between particles seeded at different times but within the same area

suggested a relatively stable transport pattern of sprat larvae/juveniles from the same population. Overlap indices were smallest for the Arkona Basin (Table 2), whereas the higher spatial overlap for the Bornholm and Gotland Basin indicated larvae/juveniles from these spawning grounds were transported into the same nursery grounds (spatial overlap coefficient: 0.6 – 0.9), independently of their spawning date. Results for model runs including diurnal vertical migration showed the same patterns.

## DISCUSSION

Transport of Baltic sprat larvae spawned on different spawning grounds was investigated by detailed drift model simulations for the years 1979-2002. On average, the combination of field based vertical distribution patterns as well as a simplified diurnal migration behaviour of larval sprat and simulated three-dimensional circulation was clearly capable of generating characteristic patterns of horizontal 0-group distribution in the Baltic. Results of this modeling approach enabled the identification of potential nursery grounds for sprat originating from different spawning grounds. On average, westerly winds are prevailing over the Baltic Sea. This leads to on average higher abundance of juvenile sprat along the southern and the eastern coast lines of the Baltic. This analysis also identifies the potential for advective mixing between juveniles originating from different spawning sites or from the same spawning site throughout the spawning season. High spatial overlap was found between Arkona- and Bornholm Basin larvae hatched at the beginning of the spawning season. Mixing probability of sprat juveniles between Arkona- and Gotland Basin as well as between Bornholm- and Gotland Basin were on relatively low levels.

Results of our analyses are in good accordance with results obtained from numerical studies performed by Lehmann and Hinrichsen (2000a) yielding clear evidence for characteristic persistent circulation patterns which comprise mostly the subbasins of the Baltic Sea with little transport between the basins. The complexity of the flow dynamics in the Baltic Sea is well known and is mainly determined by the ephemeral nature of wind stress, the baroclinic field and the complicated bottom topography (e.g. Lehmann 1995). The transport of larvae and juveniles is primarily determined by the wind-driven circulation of the Baltic Sea. 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 (Krauss and Brüggemann 1991). As obtained from a multi-disciplinary research approach, the simulations for the time period 1979 to 2002 clearly show the effect of atmospheric forcing on the final destination of larval drifters released within different areas of the Baltic (Baumann et al. 2004). The results suggest that during years with a large number of low-pressure systems passing over the Baltic, a high fraction of larvae may be transported to southern and eastern coastal environments of the central Baltic. Conversely, high-pressure

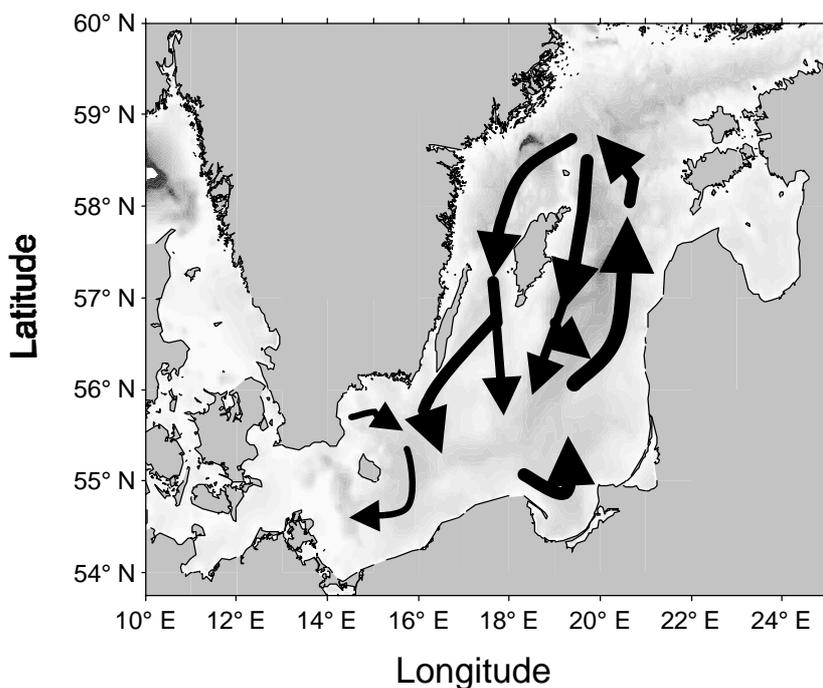


Fig.8: General circulation pattern of the Central Baltic Sea (modified after Lehmann and Hinrichsen, 2000b)

systems over Scandinavia and the eastern Baltic Sea during the spawning season are characterized by weak easterly or northerly winds and correspondingly the larvae might be largely retained within the deepwater region of the spawning areas. On average, however, higher concentrations of juveniles are expected to mainly occur along the southern and the eastern coast lines. As obtained from the numerical study performed by Lehmann and Hinrichsen (1999), the most pronounced circulation structure in the central Baltic Sea is a cyclonic circulation cell comprising the eastern Gotland Basin (Fig. 8). Most of the water is re-circulating in the eastern part, but at the northern tip there is a bifurcation into the western part. This current branch bifurcates again with one branch flowing south into the Bornholm Basin and returning into the Gotland Basin by passing through the Stolpe Trench. The second branch closes the loop into the eastern Gotland Basin. This bifurcating flow patterns are potentially the cause of the low spatial overlap between larvae originating from the Gotland Basin and the other basins. Due to the complex basin-like bottom topography the main part of the water mass circulation comprising the whole Gotland Basin occurs above the permanent halocline (Lehmann et al. 2002). The success of the Baltic Sea model in simulating both the near surface and the middepth circulation of the Baltic Sea was crucial for the identification of basin-scale patterns of Baltic sprat larval drift.

The coefficient of spatial overlap representing larval drifters released within different spawning grounds in the Baltic ranged from 0 to 0.45, suggesting that the hydrodynamic model experiments identified only weak potential for advective exchanges of juveniles between the different sprat spawning areas. The degree of spatial overlap between juveniles released as larvae within different areas of the Baltic is strongly related to atmospheric conditions and hydrographic features that regulate their transports and spatial distributions. Both seasonal and interannual variation in

atmospheric conditions and hydrographic features might have the potential to alter the spatial distribution and the composition of the juvenile populations. However, results of the present study suggest on average only a low probability for advective mixing between different stock components during their early life stages. High transport rates of Bornholm Basin spawning products towards the Arkona Basin earlier in the spawning period resulted from wind events most likely of easterly direction at that time. Although much smaller in size, similar transport patterns from east to west have been obtained for juveniles spawned at the easternmost spawning grounds. The potential for cod early life stages to drift from the western Baltic into the Bornholm Basin and to contribute there to the juvenile population has been shown by Hinrichsen et al. (2001). Here, eastward transport is mainly affected by strong westerly winds, compensating the upper layer Ekman flow by a topographically steered return flow in the central interior of the basins (Krauss and Brügge 1991).

Our model approach does not incorporate horizontal diffusion velocities, because the nature of the circulation in the Baltic and especially in the depth range where sprat larvae mainly occur is for most times during the sprat spawning season to a high degree primarily wind driven. Thus, the current fields are only slightly influenced by small-scale processes not resolved by our hydrodynamic model, which could be parameterized by e.g. horizontal diffusion velocities. In case baroclinic currents become more important, transport and retention is mainly determined by the spatial distribution of the mass field (i.e. temperature and salinity). Horizontal diffusion may have a significant effect on the distribution of larvae and juveniles and consequently on the degree of mixing between areas. However, incorporating diffusion velocities will not reduce the uncertainty in the determination of drift velocities, but it could give a general impression of small scale processes on the variability of the endpoints of larval drift cohorts. On the other hand, such small-scale variability could also be caused by the horizontal swimming ability of larvae.

The suitability of the 3-D hydrodynamic model of the Baltic Sea for examining the circulation and transport of larval sprat is clearly identified in this coupled field and modeling exercise. Information on the distribution of juveniles derived from hydroacoustic surveys in 12 of the 24 years, enabled the direct comparison with simulated distributions. Both, the simulated (August 15th) as well as the observed (October) juvenile distributions show the tendency to be primarily advected towards the southern coast in the Bornholm Basin and towards the east coast in the Gdansk Deep and in the Gotland Basin. Although in relatively good accordance, the simulated distribution was not entirely reflected in the field observations. However, the comparison is restricted by the lack of observed data from shallow coastal zones (Gröhsler et al. 2000). In addition, the observed distribution data are naturally weighted by differences in total reproductive investment between spawning areas, and compared to the modelled distributions at August 15th, the estimation of 0-group sprat using

hydroacoustic measurements was routinely performed in October. Besides this temporal mis-match, spatial mis-match between observations and simulation could be expected. Older larvae or juveniles are able to actively swim and alter their drift routes, thus, they may not entirely behave like passive drifters. Furthermore, the difference between simulated and observed distribution patterns of juvenile sprat could potentially be influenced by variability in temporal and spatial patterns of egg and larval abundance as well as related to variations in growth and mortality.

Our modelling approach is quite simplistic and should be seen as a baseline exercise, to be followed by more comprehensive investigations. Considerable effort has already concentrated on a better understanding of processes potentially responsible for Baltic sprat recruitment variability. A couple of biotic and abiotic variables have been identified to be related to recruitment strength (e.g. Köster et al. 2003; Baumann et al. 2004). Besides water temperature and spawning stock biomass, drift patterns were considered to explain sprat recruitment variability. Intra- and interannual variability of atmospheric forcing conditions resulting in variations of ocean circulation patterns like retention or dispersion from the major spawning grounds in the central Baltic had a strong impact on sprat recruitment (Baumann et al. 2004).

In summary, the initial distinct horizontal distribution patterns of eggs and early larvae as well as the seasonal variability of the circulation patterns provide mechanisms facilitating regionally self-sustaining populations of eastern Baltic sprat, with regions of mixed recruitment in the Arkona Basin and the Gdansk Deep. The potential for genetic differences between fish stock components can only be reflected by long-term average pattern of juvenile distributions if there is evidence for active mixing of different adult stock components. The low population mixing potential in some areas of the central Baltic Sea, however, appears to be sufficient to separate sub-populations and may explain distinct genetic heterogeneity. Further identification of the sprat stocks could be performed by using differences in otolith structure, meristic and morphometrical characters, and growth patterns (e.g. Aps et al. 1981; Ojaveer 1981), but final evidence for a sprat stock separation in the Baltic could only be obtained by genetic population analysis.

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# YOUNG-OF-THE-YEAR BALTIC SPRAT, *SPRATTUS SPRATTUS* L: GROWTH CHARACTERISTICS, TRANSPORT PATTERNS & IMPLICATIONS FOR RECRUITMENT VARIABILITY

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## CONCLUSIONS

The present thesis investigated growth patterns in young-of-the-year Baltic sprat by analysing the complete microstructure of YoY-sprat otoliths. The derived growth histories were linked to temperature, feeding, and advective histories of the individuals, which led to a number of new insights into processes that may regulate survival patterns during the larval and early juvenile stages of Baltic sprat. Importantly, most of the suggested conclusions (Table 1) resulted from multi-disciplinary approaches, i.e. they involved the concerted efforts of fisheries biologists working in the field as well as in the laboratory, of modellers, planktologists, meteorologists, oceanographers, and others. This may emphasise that uni-disciplinary studies are necessary to *describe* a given phenomenon, while the ability to *explain* complex mechanisms operating in the sea may only arise from a combination of synergistic approaches. The notion that multi-disciplinary studies are not some kind of scientific extravagance, but a critical prerequisite to achieve progress in fisheries ecology, has been widely accepted and encouraged (Chambers & Trippel, 1997).

### *Selective survival of central Baltic sprat*

During the 2002 field phase of the German GLOBEC project, multidisciplinary research addressed the question whether successful recruits originated from the entire spawning season of Baltic sprat or whether environmental conditions during a specific “window of survival” were potentially most favourable for sprat offspring. The results of **paper 6** indicated that there were two sprat spawning peaks in 2002 in the central Baltic Sea; a main one in spring (April) and a second, smaller spawning peak in summer (June). This corresponded to a peak in larval appearance in early May 2002, which was consistent with temperature-dependent development times determined in the laboratory (Thompson *et al.*, 1981). Assuming only random larval mortality throughout the season (null-hypothesis), a similar seasonal pattern was to be expected in the back-calculated “day-of-first-feeding”-distributions of successful recruits sampled in October 2002.

## Conclusions

However, this was not indicated by the conducted otolith analyses in **paper 1**, reporting that the vast majority of YoY-recruits apparently originated from June/July, which roughly corresponded to the second peak in sprat reproduction (Fig. 1). Even though the length of the yolk-sac period has yet to be evaluated for temperatures typically experienced by Baltic sprat yolk-sac larvae, the results of **paper 1** and **paper 6** strongly suggested that YoY-recruits in 2002 were predominantly comprised by individuals born relatively late in the season, i.e. in summer rather than spring (Fig. 1). This is consistent with findings of Reglero *et al.* (in press), who first established a relationship between the width of the innermost otolith increments and temperature and inferred then the temporal origin of age 1 Baltic sprat based on known temperature fields. Together thus, **paper 1** and **paper 6** suggested that the “window of survival” for Baltic sprat was considerably narrower in 2002 than the spawning season, likely because environmental conditions in summer were more conducive to larval survival than earlier in the season.

To explore potential mechanisms responsible for the apparent selective survival of summer over spring born sprat larvae, primary attention was given to the two most important environmental determinants of larval growth and survival, temperature and feeding conditions (Heath, 1992). Ambient temperature in surface waters, where feeding sprat larvae predominantly occur (Voss, 2002), increased rapidly in the central Baltic Sea from 5.9°C during the first week in May to 14.1°C in mid-June 2002 (Fig. 1). Therefore, sprat larvae in early May likely experienced temperature conditions close to their lower tolerance limit of 5°C (Nissling *et al.*, 2004), which may have led to increased mortality rates compared to sprat larvae released in June. In addition, larval growth rates generally increase with temperature (Pepin, 1991), therefore, larval cohorts in summer likely grew considerably faster than their spring-born conspecifics. In **paper 1** and **paper 2**, this effect was clearly demonstrated for the larval stage (first 30 days) of successful sprat recruits, which showed an increase in average larval growth rates from 0.48 mm day<sup>-1</sup> for early born survivors to 0.69 mm day<sup>-1</sup> for individuals born late in the season. Larval growth rates of survivors were therefore considerably higher than average growth rates of sprat larvae determined in field studies, indicating that a general selection for fast growth occurs during the early life stages. The linear temperature-growth relationship suggested a considerable increase in average larval growth by 0.07 mm day<sup>-1</sup> *per centigrade* (**paper 1**). Faster larval growth results in larger sizes-at-age, which likely conferred a survival advantage for late born larvae according to the “bigger-is-better” hypothesis and may have also led to lower cumulative mortality rates, because summer-born larvae were growing more rapidly out of the most vulnerable stages (“stage-duration hypothesis”, Leggett & Deblois, 1994). For Japanese anchovy, *Engraulis japonicus*, Takahashi & Watanabe (2004) compared growth rates of recruits and pre-recruits and concluded that a specific growth-threshold appeared to exist, below which pre-recruits had a negligible probability of recruitment. In the case of central Baltic sprat, a similar threshold may have caused the selective survival of faster growing

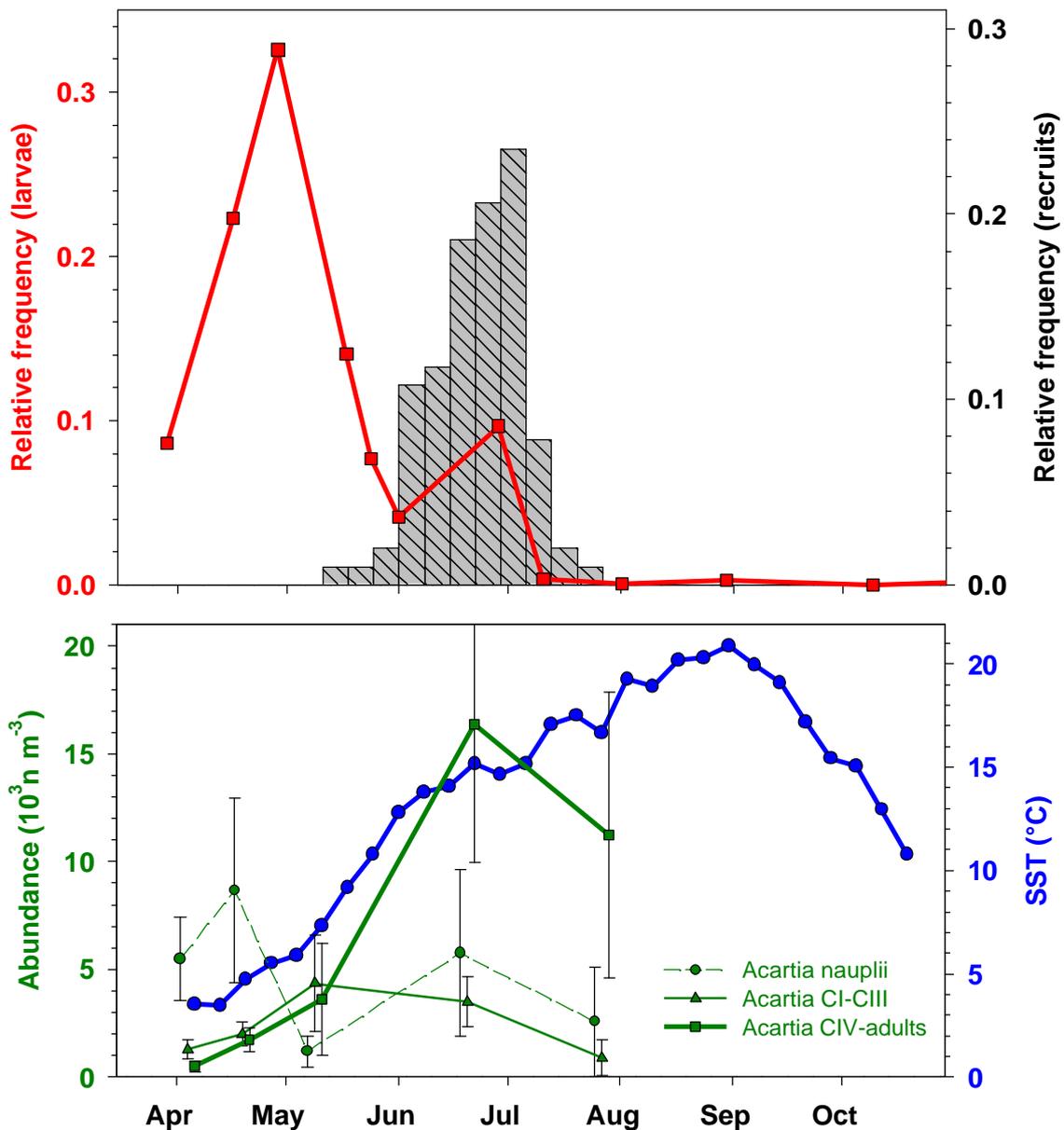


Fig.1: „Window of survival“ for central Baltic sprat in 2002. Upper panel: Seasonal abundance of newly hatched larvae (red line), based on egg stage I abundance in the Bornholm Basin and temperature-dependent development times (Thompson *et al.*, 1981). Grey bars depict the temporal origin of YoY-recruits caught in October 2002, where the “date-of-first-feeding” (*DFE*) was back-calculated from otolith microstructure analysis. Lower panel: Seasonal abundance ( $\pm$ SD) of *Acartia* spp. nauplii, copepodites, and adult copepods in the Bornholm Basin (green lines) and weekly means of sea surface temperature (SST) in this area, derived from satellite measurements.

larvae from June, compared to their slower growing conspecifics present in early May 2002. Similar positive relationships between larval growth and recruitment have been demonstrated for many fish species and marine systems (Campana, 1996; Meekan & Fortier, 1996; Bergenius *et al.*, 2002).

However, increased growth rates due to higher temperatures must be supported by food consumption (Houde, 1989). For Baltic sprat, the findings in **paper 6** indicated that in 2002 prey availability and prey size composition were *both* critical for larval sprat survival. Measurements of the abundance of *Acartia* spp. nauplii, copepodites and

adult copepods (the main food item of larval sprat, Voss *et al.*, 2003) suggested that sprat larvae in spring and summer would have experienced considerably different feeding conditions. Nauplii abundance peaked in spring, when larger copepodites and adult copepods were still scarce in the water column (Fig. 1). Given that RNA:DNA ratios revealed no signs of food limitation in small, first-feeding larvae, neither in spring nor in summer, it was concluded that the important differences in sprat survival rather became established during later larval stages. These late larval stages critically rely on larger prey (Dickmann *et al.*, submitted), e.g. adult copepods, which were highly abundant only in June/July 2002 (Fig. 1).

What therefore determined larval sprat survival in the central Baltic Sea in 2002 could be interpreted as a special, intra-annual ‘match-mismatch’ scenario (Cushing, 1974), because the main effort in sprat spawning apparently failed to match both the most favourable temperature conditions and the seasonal production of larger copepod stages, which appear critical for growth and survival in older larvae (Fig. 1). This would be consistent with results from Köster *et al.* (2003) and the findings in **paper 3**, advocating the general importance of late larval/early juvenile survival patterns for Baltic sprat recruitment variability.

However, from an evolutionary point of view, such spawning patterns appear not to make much sense. Why would any species ‘waste’ most of its reproductive effort? In 2003, seasonal ichthyoplankton samples indicated an even earlier spawning peak of Baltic sprat (R. Voss, unpublished data), which has led to questions concerning the inter-annual variability in the onset and temporal extent of both Baltic sprat spawning and “survival windows”. In other words, is early spawning a typical or atypical behaviour for Baltic sprat? Early investigations conducted in the 1930s and 1950s reported that sprat peak spawning typically occurred between the end of May and July in the western Baltic Sea, but mostly in June (Morawa, 1954). In 1999, central Baltic sprat exhibited a single spawning peak around the beginning of June (STORE, 2003). Karasiova (2002) analysed historical sprat spawning patterns in the Gdansk Deep, another important spawning ground adjacent to the central Baltic Bornholm Basin. She found that during the periods 1947-1955 and 1968-1977, main sprat spawning activity was again centred in June, whereas during the most recent years (1998-1999) a shift to earlier peak spawning (May) was apparent. The even earlier spawning peaks in 2002 and 2003 may therefore point to a recent shift in Baltic sprat spawning patterns, possibly induced by changes in Baltic hydrographical conditions (Karasiova, 2002). During winter months, the pre-spawning sprat stock is known to be distributed mainly in deeper waters, which are characterized by higher temperature and salinity conditions compared to surface and intermediate water layers. Alheit *et al.* (2005) presented a time-series of maximum temperatures observed in the halocline of the Bornholm Basin and found the highest value on record in 2002. Assuming that sprat reproduction is cued by temperature (MacKenzie & Köster, 2004), like for example in Bay anchovy *Anchoa*

*mitchilli* (Lapolla, 2001), such recent trends in temperature conditions potentially altered Baltic sprat spawning patterns, despite the period of most favourable environmental conditions might have remained unchanged. At least in 2002, overall all recruitment strength was relatively low in the central Baltic Sea (ICES sub-division 25, ICES 2005) However, a comprehensive analysis of processes potentially responsible for a shift in Baltic sprat spawning and its importance for recruitment success were beyond the scope of this thesis. Thus, further investigations are recommended, exploring, for example, seasonal patterns in overwintering sprat condition, gonad development and horizontal and vertical stock distribution.

*Spatial and temporal variability of sprat growth in the Baltic Sea*

In **paper 2**, the spatial and temporal differences in growth patterns of YoY-recruits were studied for individuals caught in 4 broadly defined regions of the Baltic Sea (i.e. western, central, eastern, and north-eastern Baltic Sea). Satellite-based measurements of sea surface temperature proved to be useful means to detect the general temperature signal in young-of-the-year growth rates. Apart from the strong influence of age (and body size) on YoY-growth trajectories, this has led to the conclusion that the temperature conditions experienced during the larval stage have the highest potential to alter individual growth trajectories in three different ways: a) higher temperatures lead to higher maximum growth rates at the end of the larval stage, b) these higher growth rates are attained earlier after first feeding and therefore cause a steeper increase in initial growth rates. However, higher larval growth rates were c) consistently associated with a steeper decrease in growth rates during the post-larval stage. This trade-off between higher initial but slower post-larval growth rates may be a reason for the significantly lower lengths of YoY-sprat recruits in north-eastern compared to central Baltic areas. The form of the YoY growth trajectories and its general temperature dependence were in support of many field and modelling studies (e.g. Meekan & Fortier, 1996; Folkvord *et al.*, 1997; Bartsch, 2002; Fowler & Jennings, 2003). In 2002, recruits originating from the north-eastern Baltic Sea were born latest in the season, mainly due to later spawning in this area, thus experienced the highest temperatures, which elicited the highest larval growth rates compared to survivors from western and central Baltic areas. It was concluded that different spawning times, experienced temperatures, and thus growth patterns mainly determine the large-scale spatial size differences of YoY-recruits from different Baltic areas.

*Late-larval/early juvenile stage survival predominately regulates recruitment*

The correlation analyses between temperature/transport and recruitment success in Baltic sprat (**paper 3**) yielded support for Legget & Deblois' (1994) conclusion that in some marine fishes, year class strength is established during the late larval and early juveniles stages. The time-series of month- and depth-specific temperature data enabled

the detection of three main periods during the year, when temperature was significantly correlated to recruitment strength. The first period appeared in January and depths mainly below 50m, which corroborates earlier findings by MacKenzie and Köster (2004), who showed the temperature influence on the pre-spawning sprat stock. A second period (or ‘core’, see **paper 3**) was indicated by significant temperature-recruitment correlations in mid-water depths between March-July, which was consistent with earlier published work on the temperature-dependence of sprat egg- and early larval mortalities for recruitment (Köster *et al.*, 2003; Karasiova & Zezera, 2000). However, the third period has not previously been reported and occurred between July and October in Baltic surface waters, where temperature-recruitment relationships had more than three times the explanatory power compared to all correlations earlier in the year. This strongly indicated that in spite of all statistical significance prior to this time, temperature-related survival processes during the late summer months and therefore throughout or after metamorphosis (**paper 1 & paper 2**) explain most of the recruitment variability in Baltic sprat.

*Environmental variables improve recruitment models*

Considering the late larval and early juvenile stages of Baltic sprat facilitated the development of two highly explanatory recruitment proxies, i.e. August temperature in surface waters and “bottom depth anomaly” (transport index), which are potentially valuable for better recruitment predictions. Both proxies explained more than 70% of the overall recruitment variability in age 0 Baltic sprat abundance between 1974-2003. Prior attempts to include environmental variability into sprat recruitment models resulted in weaker relationships, probably because processes acting late in the year and during post-larval stages have not previously been considered (Köster *et al.*, 2003; MacKenzie & Köster, 2004).

However, the underlying processes responsible for the apparently strong coupling between temperature/recruitment and transport/recruitment are not yet sufficiently understood. The observed positive influence of temperature in late summer on recruitment strength may act through higher population growth rates and thus larger sizes-at-age, which may confer a survival advantage because of reduced predation and starvation mortalities. Yet it is presently questioned, whether predation by the major predator of Baltic sprat, Baltic cod, is a) size-selective enough (Floeter & Temming, 2003) and b) still sufficient to cause significant mortalities at all. Baltic cod stocks declined considerably due to a combination of climate-induced regime shifts and overfishing (Parmanne *et al.*, 1994), which has caused an estimated 5-fold decrease in predation mortalities of 0-group sprat from the mid 1970s to the early 1990s and thereafter (ICES, 2005). Whether other Baltic piscivores, particularly during years of high larval displacement towards Baltic coastal areas (transport index), can significantly prey on 0-group sprat, remains to be demonstrated. In 1997, for example, Patokina &

Feldman (1998) found indications for predation of Baltic herring on small YoY-sprat in the Gotland Basin.

Apart from predation, density-dependent food limitation and overwinter mortalities (Henderson *et al.*, 1988; Sogard, 1997) may contribute to recruitment regulation. In **paper 3**, the derived transport index suggested that a high degree of larval advection towards southern and south-eastern Baltic coasts is associated to relative recruitment failure. In contrast, years of predominant larval retention within the deep spawning basins produced, on average, relatively strong year classes. Processes influencing fish growth and survival in very shallow coastal areas have rarely been studied in the Baltic Sea, but may play an important role in sprat recruitment determination. In **paper 4**, for example, evidence was presented that early juvenile sprat encountered in 2003 on western Baltic coasts were severely food-limited. However, the magnitude and spatial extent of early juvenile sprat food limitation are currently unknown. Particularly in central and eastern Baltic areas, where the majority of the sprat stock is distributed, further studies are recommended to corroborate or falsify the suggested importance of density-dependent food limitation for Baltic sprat recruitment variability.



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## **Description of the individual scientific contributions to the multiple-author papers**

### **Paper 1: “Linking growth- to environmental histories in central Baltic young-of-the-year sprat, *Sprattus sprattus*: an approach based on otolith microstructure analysis and hydrodynamic modelling”**

All analyses, the text writing and graphical presentation were done by Hannes Baumann under the supervision of Prof. Axel Temming. Flow-fields and raw data of the Lagrangian particle simulations were provided by Dr. Hans-Harald Hinrichsen. Other authors were instrumental during field sampling and provided helpful comments to improve earlier versions of the manuscript.

### **Paper 2: “Temperature-induced regional and temporal growth differences in Baltic young-of-the-year sprat, *Sprattus sprattus*”**

All analyses, the text writing and graphical presentation were done by Hannes Baumann under the supervision of Prof. Axel Temming. Data on long-term egg abundance in the Baltic Sea were provided by Andrej Makarchouk. Other authors were instrumental during field sampling and provided helpful comments to improve earlier versions of the manuscript.

### **Paper 3: “Sprat recruitment in the Baltic Sea: the importance of temperature and transport variability during the late larval and early juvenile stages”**

All analyses, the text writing and graphical presentation were done by Hannes Baumann under the supervision of Prof. Axel Temming. Flow-fields and raw data of the Lagrangian particle simulations were provided by Dr. Hans-Harald Hinrichsen. Other authors provided helpful comments to improve earlier versions of the manuscript.

### **Paper 4: “Starving early juvenile sprat, *Sprattus sprattus* L., in Baltic coastal waters: evidence from combined field and laboratory observations in August/September 2003”**

All analyses, the text writing and graphical presentation were done by Hannes Baumann under the supervision of Prof. Axel Temming. Dr. Eberhard Götze & Myron Peck provided the time-series of sprat age 0 abundance in the Baltic and helped to improve earlier versions of the manuscript.

### **Paper 5: “Short-term decoupling of otolith and somatic growth induced by food level changes in post-larval Baltic sprat, *Sprattus sprattus*”**

All analyses, the text writing and graphical presentation were done by Hannes Baumann under the supervision of Dr. Myron Peck & Jens-Peter Herrmann.

### **Paper 6: “Baltic sprat larvae: coupling food availability, larval condition and survival”:**

All analyses, the text writing and graphical presentation were done by Dr. Rudi Voss in close cooperation with Hannes Baumann, Dr. Catriona Clemmesen & Dr. Gerd Kraus. Larval mortalities for corrected with flowfields provided by Dr. Hans-Harald Hinrichsen.

### **Paper 7: “The general distribution pattern and mixing probability of Baltic sprat juvenile populations”**

All analyses, the text writing and graphical presentation were done by Dr. Hans-Harald Hinrichsen in close cooperation with Hannes Baumann, Dr. Gerd Kraus and Dr. Rudi Voss. Sprat age 0 distribution patterns were made available by Daniel Stepputtis.

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