

**Feeding ecology of sprat (*Sprattus sprattus* L.) and
sardine (*Sardina pilchardus* W.) larvae in the Baltic
Sea and in the North Sea**

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I Introduction

Year-class strength of fish populations is widely accepted to be determined by factors acting on the early life-history stages (e.g. Gulland 1965, Myers & Cadigan 1993, Leggett & de Blois 1994). Egg and larval stage mortality rates are high and often less than 1% of fish larvae survive until they reach the juvenile stage (Hjort 1914, Houde 1989). In the egg and yolk-sac stage predation is possibly the largest source of mortality, as these stages are independent from accessibility of suitable prey items in the field (Hunter 1981). In the Baltic Sea egg predation could cause strong variations in recruitment (Köster & Möllmann 2000, Neuenfeldt & Köster 2000), while direct evidence is scarce for other regions (Bailey & Houde 1989).

In the last century research focussed mainly on fish larvae and several hypotheses suggested a causal link between larval feeding, survival and subsequently recruitment. The “Critical Period Hypothesis” (Hjort 1914) linked larval survival to food abundance during transition from the yolk-sac stage to exogenous feeding. The “Match-mismatch Hypothesis” (Cushing 1990) relaxed the emphasis on a special larval period and pointed to the general importance of temporal overlap between the production and development of larvae and suitable prey. He suggested that the temporal coupling or decoupling of production maxima of fish larvae and prey organisms is the main source of recruitment variability. The “Stage duration hypothesis” (Houde 1987) indicated that larval growth rate is another important factor contributing to recruitment variability, because early life stages are more vulnerable to predation than later developmental stages. Favourable feeding conditions increase larval growth rate and consequently they can easier overcome critical early life stages (Cushing 1975). Further body size of both prey and predator is linked directly to foraging success. The relationship between prey- and predator size determines the outcome of species interactions (Scharf et al. 2000). During larval development mouth size and prey-searching ability increase and in parallel mean prey size increases (Sabatés and Saiz 2000). In larval fish, the prey-niche breadth has been calculated to remain generally constant (e.g. Pearre jr. 1986, Munk 1992, 1997) or to increase (Pepin & Penney 1997) with increasing larval size.

However, for species showing a prolonged spawning period as sprat, new larval cohorts develop into a continuously changing prey field. Consequently knowledge on seasonal trends in the feeding ecology, i.e. feeding success and gut fullness, diet composition and

selectivity, in relation to the food supply is a prerequisite to understand the processes affecting the subsequent year-class-strength of adult fish (Last 1980, Arrhenius 1996).

Cushing (1972) has shown that timing and intensity of the seasonal cycle of plankton production depends also on abiotic factors. Further several studies assume that environmental parameters have a significant effect on larval survival (e.g. Nakata et al. 1994, Dower et al. 2002). Whereas temperature and oxygen may influence larval and egg mortality directly, other parameters such as e.g. North Atlantic Oscillation (NAO) and turbulence influences larval survival indirectly due to their impact on plankton production and concentration (Solow 2002, MacKenzie et al. 1994). In this consequence, shelf sea areas, frontal systems and river plumes are important regions of biological activity and production (e.g. Cowan & Shaw 2002). Frontal systems often provide zones of high food availability for fish larvae or other planktivorous predators (Morgan et al. 2005) due to high primary production and chlorophyll-*a* values (e.g. Pingree et al. 1975, 1978, Pedersen 1994, Danovaro et al. 2000) as well as aggregation of zooplankton (e.g. le Fèvre 1986). Therefore the identification of feeding parameters related to the physical environment is of paramount importance to evaluate the environmental effect on survival and recruitment.

The present study investigated seasonal trends in feeding ecology of Baltic sprat larvae as well as the influence of the physical environment on the feeding ecology of sprat and sardine larvae in the German Bight.

The main distribution area of the planktivore sprat (*Sprattus sprattus* L.) is the Northeast Atlantic, including the North Sea as well as the Baltic Sea (Muus & Nielsen 1999). In the Baltic, sprat is presently the dominating commercial fish stock (Köster et al. 2003a). Beside the Gotland Basin and Gdansk Deep the Bornholm Basin is one of the major spawning grounds for this batch spawner in the Baltic (Köster et al. 2001). The spawning period extends usually from March/April to August/September (Wieland et al. 2000). The recruitment level has generally increased since the mid-1980s (Parmanne et al. 1994), but year class strength and stock level is presently highly variable (Köster et al. 2003a). The stock development of sprat is closely linked to cod (*Gadus morhua* L.) abundance due to strong species interactions. A decrease of cod abundance since the mid 1980s reduced the predation pressure on sprat and in combination with low fishing mortality and mainly high reproductive success of sprat, stock size of sprat increase during the last decade (Köster et al. 2001). High reproduction success is linked to higher temperature conditions during gonads, egg, larval and early juvenile development (MacKenzie & Köster 2004, Baumann et al. 2005). Further higher temperature in spring during the last decade had a positive

effect on the population dynamics of *Acartia* spp. and *Temora longicornis* (Möllmann et al. 2000), which are suggested to be the preferred food items for sprat (Voss et al. 2003). Köster et al. (2003b) suggested that favourable food supply of the last years was a major impact factor for sprat larval recruitment success.

The inner German Bight, the British coast from Scotland to the English Channel and the northwest coast of Jutland are identified as the three main spawning areas for sprat in the North Sea (Aurich 1941). In the German Bight peak spawning is observed generally from May to July (Alheit 1987). The recruitment level of sprat has increased in the early 70s, with considerable lower recruitment level afterwards. Since 1996 egg abundance increased (v. Westernhagen et al. 2002) and a positive development of the standing stock were observed in the last years (Dornheim & Wegner 1998). High egg and larval abundances are associated with tidal fronts in the German Bight (Valenzuela et al. 1991, Munk 1991, 1993). Further larval abundance and growth rate are related to chlorophyll peaks and enhanced food supply in the fronts (Valenzuela et al. 1991, Munk 1993). This indicates that areas near tidal fronts offer favourable conditions for early life-stages of sprat (Munk 1993).

Sardine (*Sardina pilchardus* W.) is an important commercial fish species in the coastal waters of Portugal and northern Spain (Robles et al. 1992). Distribution areas are the North Atlantic until west off Iceland, the Mediterranean, the Adriatic and the Black Sea (Muus & Nielsen 1999). Main spawning grounds are along the coast of Portugal and northern Spain as well as along the English Channel. Like sprat, sardine is a batch spawner with peak spawning from April to May at the coast of Spain (Chícharo 1998). Sardine occurred episodically in the German Bight during the periods 1948-1952, 1958-1960 (Aurich 1953, Postuma 1978) and 1990-1994 (Corten & van de Kamp 1996). The enhanced seasonal migration from the English Channel into the German Bight should be caused by higher temperatures (Aurich 1953, Corten & van de Kamp 1996) and southerly winds (Corten & van de Kamp 1996). Positive temperature anomalies since 1988 in the North Sea (Becker & Pauly 1996, Corten & van de Kamp 1996, Reid et al. 2001) have led to a regularly appearance of sardine larvae in the German Bight, where recruitment success related to the environmental conditions is unknown.

II Aim of the PhD thesis

The present PhD thesis is a contribution to the German-GLOBEC project. The aim of the project was to investigate the trophic interactions between zooplankton and fish under the influence of physical processes. This study presents gut content data of more than 2900 sprat and sardine larvae to investigate the trophic interactions with their zooplankton prey. It highlights details of the feeding ecology of sprat larvae, which is essential for survival and consequently stock recruitment. The investigations were conducted in the Baltic and the North Sea, two shelf seas with very different hydrographical conditions. To study the feeding ecology of sprat larvae the taxonomic as well as predator- and prey size dependent trends in feeding were followed in relation to the zooplankton composition.

In the Bornholm Basin monthly resolved larval abundance and gut content data as well as temporal and spatial highly resolved zooplankton data were collected. The goal was to investigate feeding ecology in relation to seasonal changing zooplankton prey field (Chapter V: **“Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics - implications for survival”**). Trends in gut fullness, feeding success, diet composition, prey selection and niche breadth are described, to identify critical periods for sprat larval survival.

A second aim was to investigate the influence of frontal systems on the feeding ecology of sprat larvae (Chapter VI): **“Feeding ecology of sprat (*Sprattus Sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae on two frontal systems in the German Bight – a comparison”**. To this end larval abundance and gut content data as well as zooplankton data were collected on two transects covering different frontal systems in the German Bight. The intention was to evaluate implications for their survival and the possible link between survival and different hydrographical structures. Further the unusual appearance of sardine larvae in the North Sea offered the opportunity to compare their feeding ecology with that of sprat. The amplitude of food overlap is calculated between both species and mechanisms were discussed to avoid possible food competition.

Besides different hydrographical conditions in the Baltic and North Sea, both areas show also differences in plankton composition. Data of the Chapter V and Chapter VI were used to compare larval feeding success, gut fullness, diet composition and selectivity between both study areas. The influence of hydrographical conditions and effects of the different food supply on feeding ecology, survival and recruitment of sprat larvae were compared

between the areas (Chapter VII: **“Comparison of sprat (*Sprattus Sprattus* L.) larval feeding ecology between the Baltic Sea and the North Sea”**).

III Study area

Baltic Sea

The brackish Baltic Sea is characterised by several basins (Fig. III.1) i.e Arkona Basin, Bornholm Basin, Gdansk Basin, Gotland Basin, Farö Deep, Bothnian Sea and Bothnian Bay, which are separated by sills (Krauss 2001).

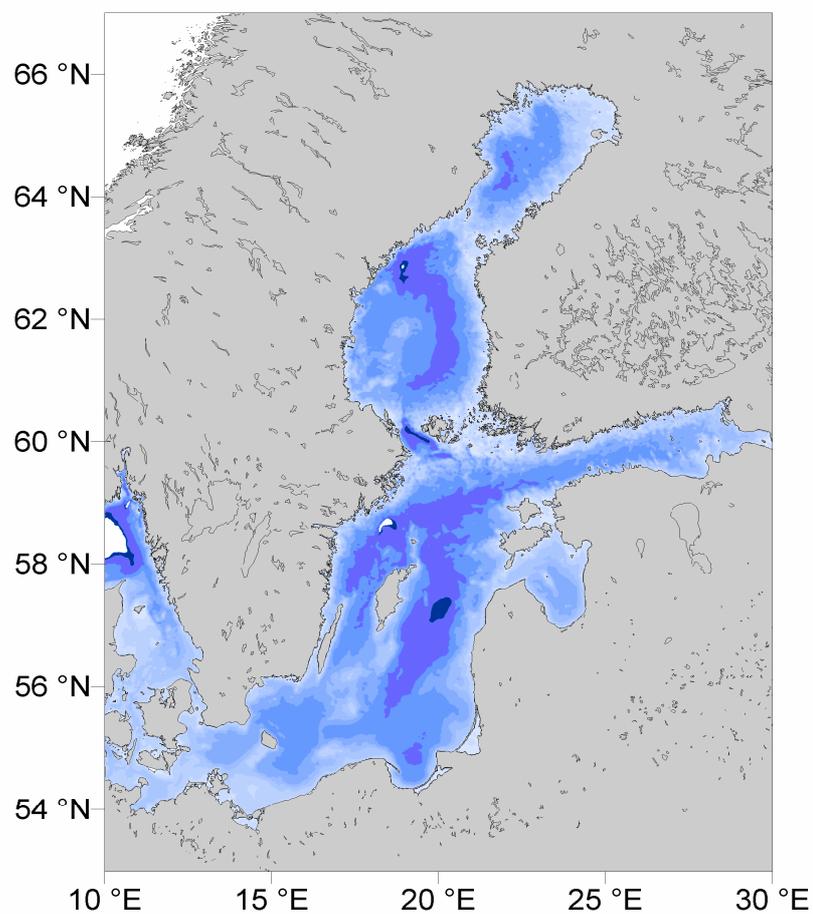


Fig.III.1: Scheme of the Baltic Sea

The water exchange with the North Sea takes place through the shallow Kattegatt and the Danish Straits. Due to the large freshwater supply from the rivers a gradient in salinity exists from 30-34 psu in the Kattegatt to 8 psu in the central and western part and to about 4 psu in the eastern and northern parts of the Baltic Sea (Krauss 2001).

A permanent halocline between 60 and 80 m depth (Matthäus 1995) separates less saline, but oxygen rich surface water from deeper waters of higher salinity (Fig III.2). While the upper layer is mixed in winter, the deep water is only renewed by so called 'Major Baltic Inflows' (MBI, Schinke & Matthäus 1998). During such inflows highly saline and oxygen rich water from the North Sea flows along the sea floor and accumulates in the adjacent deeper basins. In addition to the halocline a thermocline develops in summer and separates a 20 - 30 m warm surface layer from a cooler intermediate water body. Both clines represent natural boundaries for several species. For instance the marine copepod *Pseudocalanus* sp. prefers the deeper water layers with higher salinity, while *Acartia bifilosa* and cladocerans can be found almost exclusively in the surface layer.

North Sea

The North Sea is a part of the northwest European shelf (Fig. III.2). The German Bight is a shallow area in the southern North Sea with water depths between 20 - 40 m. The area is characterised by the Elbe River glacial valley and is strongly affected by the fresh water outflow from the rivers Elbe and Weser leading to a complex vertical structure of the water column (Otto et al. 1990).

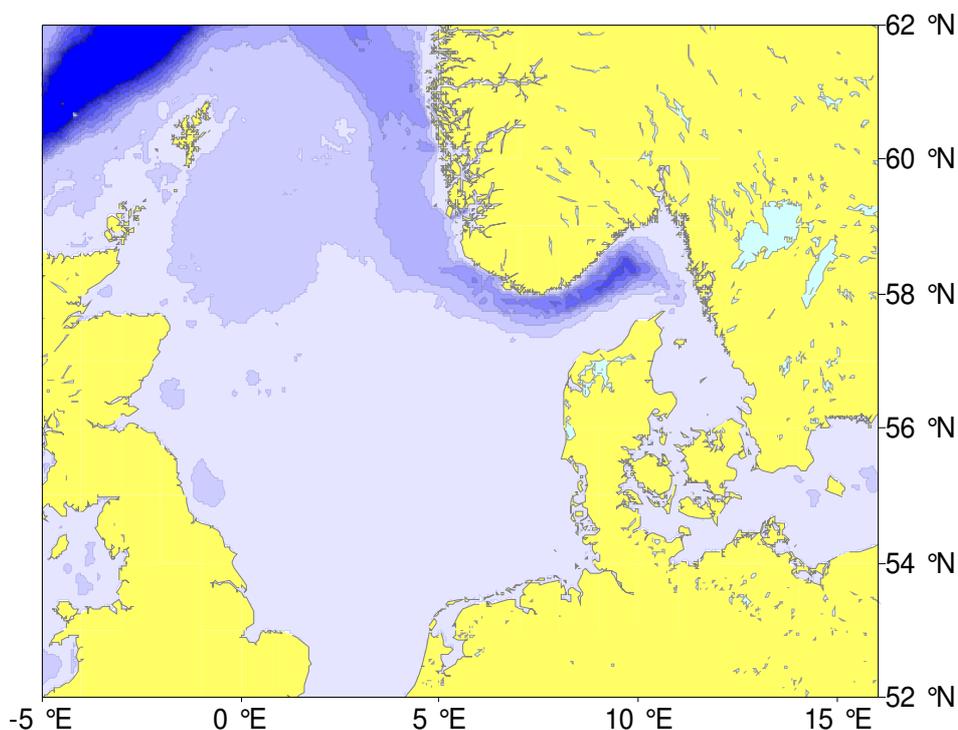


Fig. III.2: Scheme of the North Sea

The main current signal is generated by semidiurnal tides (Budéus 1989) and river discharge causes a persistent horizontal density gradient throughout the year. In combination with tidal mixing, heat input and strong winds three different types of fronts can be found in the German Bight (Krause et al. 1986, Budéus 1989, Fig. III.3):

(1) During easterly and south-easterly winds offshore transport of surface water is replaced by upwelling of North Sea bottom water in the Old Elbe Valley (Krause et al. 1986, Dippner 1995); (2) river plume fronts (RPF) are characteristic for the eastern part of the German Bight and are generated mainly as a result of river discharge from Elbe and Weser, and (3) tidal mixing fronts (TMF) are commonly established in summer north to the East-Frisian coast and separate stratified waters from vertically mixed water bodies (Budéus 1989).

Exact location and characteristic of fronts in the German Bight depends in general on surface heating, tidal stream velocity and water depth (Simpson & Hunter 1974).

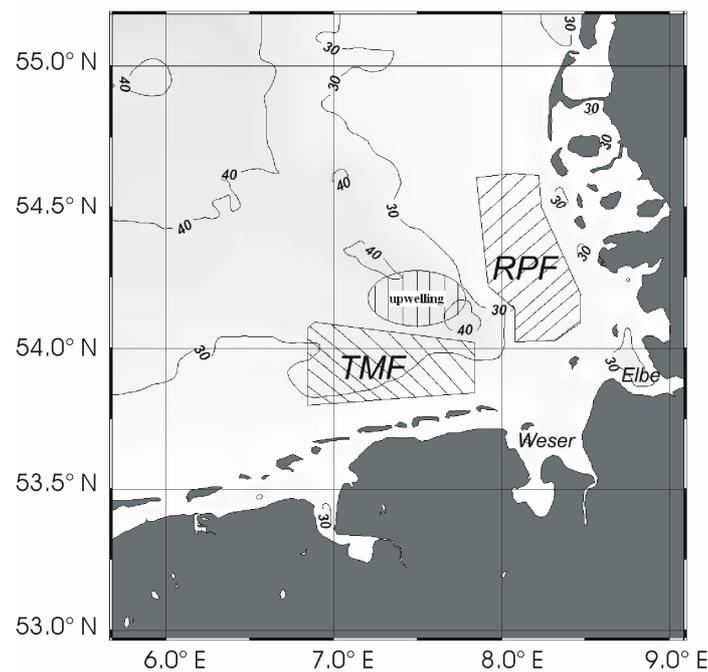


Fig. III.3: Overview of the three fronts in the German Bight: Areas with predominant occurrence of tidal mixing fronts (TMF), river plume fronts (RPF) and upwelling fronts (according to Holtappels 2004, Krause et al. 1986)

Tidal mixing front (TMF)

The effect of tidal mixing decreases in offshore direction and at a certain distance from the coast seasonal heat input leads to a stratified water column. The position of a TMF is related to the depth and the surface tidal current amplitude (Budéus 1989). Five different water bodies can be distinguished (Fig. III.4), (1) the mixed water column on the inshore side, (2) the transition zone (front) and at the stratified area, (3) a surface layer, (4) a thermocline and (5) a bottom layer (Valenzuela et al. 1991). The lifetime of a TMF ranges from half a tidal cycle to several months in the German Bight (Krause et al. 1986, Mohrholz unpubl. data).

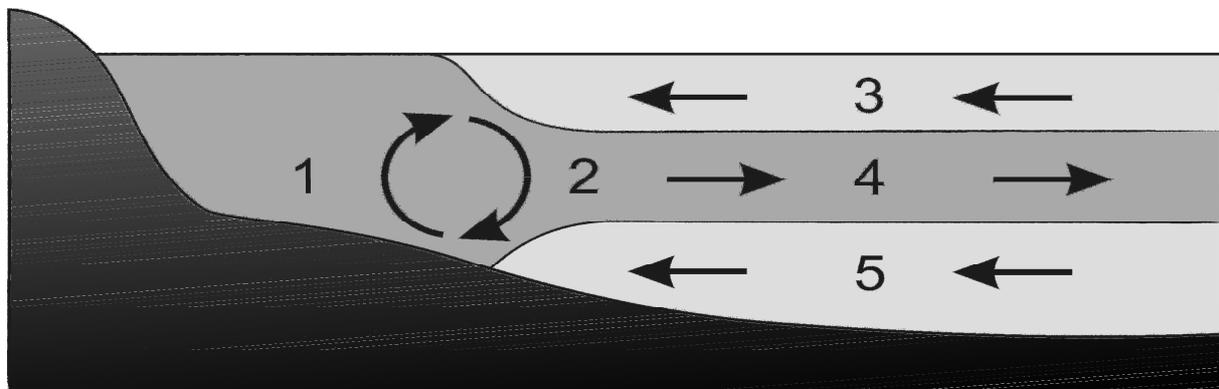


Fig. III.4: Scheme of a tidal mixing front (TMF) in the German Bight. Numbers indicate the different parts of a TMF front: (1) mixed water column on the inshore side, (2) transition zone (front), (3) surface layer, (4) thermocline and (5) bottom layer (modified, according to Bakun & Parrish 1991)

River plume front (RPF)

The permanent RPFs exist where the freshwater river outflow overlays the marine waters of higher density (Fig. III.5). Hence a gradient in temperature and salinity emerges from the coast to offshore areas. The location of RPFs is highly variable in the German Bight due to changes in tidal currents and river outflow. With the river discharge a large amount of nutrients is washed out into the sea, which may cause enhanced primary production in this area.

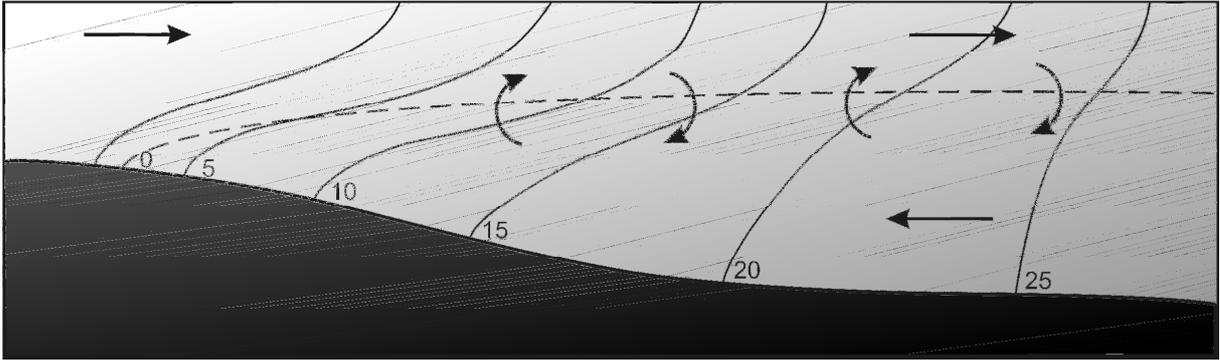


Fig. III.5: Scheme of a river plume front in the German Bight with isolines of salinity (thin lines) and residual currents (arrows). Numbers indicate velocity of horizontal currents of the bottom layer (modified, according to Huwer 2004)

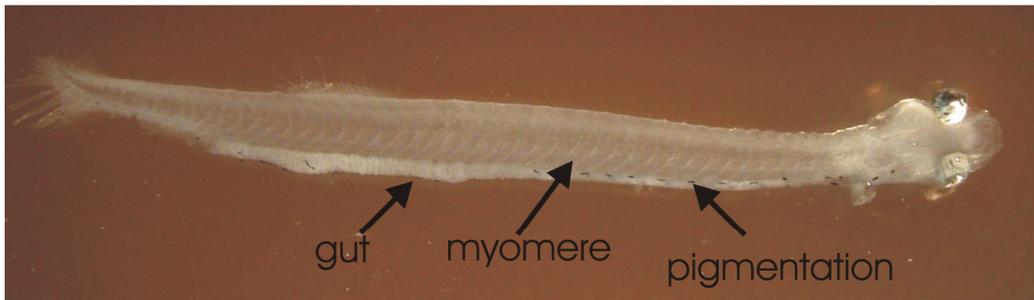
IV Material and Methods

Laboratory analyses

In the laboratory, the standard length (SL) of 2084 individual sprat larvae from the Baltic Sea and 270 sprat larvae as well as 451 sardine larvae from the North Sea was measured to the nearest 10 μm .

Both species have an elongated larval form and a straight gut (Fig. IV.1). Identification of larvae based on the identification key of Halbeisen (1988) and comments of H-C. John (pers. comm. Hamburg, Germany) and was only possible by counting myomeres and by comparing pigmentation. While sprat larvae have 35-38 myomeres sardine larvae show 40-42 (all numbers relate to preanal counts from the first neck myomere to the anus).

a)



b)



Fig. IV.1: Photo of (a) sprat larva and (b) sardine larva

The whole alimentary channel of each individual larva was removed with a sharp needle, opened and the gut contents analysed using a stereo-microscope. If possible, all prey items were identified to species level. Five copepod stages were resolved including nauplii (N), early copepodites (C1-3), late copepodites (C4-5) and adults (C6). In the North Sea nauplii

of *Pseudocalanus* spp., *Paracalanus* spp., and *Calanus* spp. were pooled to “clausocalanoid nauplii”, in the Baltic nauplii of *Pseudocalanus* sp. were named in the same way in the charts although only consisting of one species. The same method was applied to copepod stages C1-6 of *Pseudocalanus* sp. and *Paracalanus* spp., which were grouped to Pseudo/Paracalanus.

All, diatoms, ciliates, other unidentifiable small cells and microplankton remains were grouped together as “microplankton”. The “other plankton” group in the Baltic Sea contained mainly copepod eggs, bivalve larvae, synchaeta, polychaeta and some remains of zooplankton, while in the North Sea this group contained only remains of zooplankton.

Zooplankton samples were as well analysed under a stereo-microscope following the same sorting protocol as for larval gut contents. Length and width of prey items in larval guts and from plankton samples were measured to the nearest 10 μm . Dry weight of the different prey items was calculated applying estimates of Hernroth (1985) and Mauchline (1998) for copepod stages and cladocerans. Dry weights of the other zooplankton species were taken from various sources (Tab. IV.1). Neither for larval nor for prey items length correction was applied due to preservation.

Tab. IV.1: References used for dry weight estimation

Prey type	Literature
Synchaeta spp.	Henroth 1985
Copepod eggs	Kiørboe & Sabatini 1994
Bivalve larvae	Nickolaus unpubl. data
Polychaeta larvae	Nickolaus unpubl. data
Microplankton	Pelegrí et al. 1999

Data analyses

The gut fullness was calculated as the average number of prey items in larval guts, weighted according to the length-frequency distribution. The feeding success was calculated as the percentage of all analysed larvae containing food and simple regression analysis was performed to evaluate the relationship between feeding success and larval length.

For the description of the diet composition of sprat larvae the frequency of occurrence $F(\%)$ of each food item in all guts (excluding empty guts) and the percentage of dry weight of each food item $W(\%)$ as $F(\%) = 100n_i N^{-1}$ and $W(\%) = 100S_i S_i^{-1}$, were computed,

where n_i is the number of larvae with prey type i in their guts, N is the total number of analysed guts, S_i is the mass of prey type i and S_t is the total mass of gut contents. For the determination of feeding trends both indices were used in “Costello graphics” (Costello 1990). For the statistical analysis of diet composition R x C contingency table analysis were used to test for independence between food categories and predator characteristics (Legendre & Legendre 1998). This technique is able to identify the source of variation in the diet composition (Crow 1982, Cortés 1997). Thereby a high number of cells with expected frequencies <5 should be avoided (Sokal & Rohlf 1995).

For the analysis of taxonomic prey selectivity, the mean prey abundance of all zooplankton sampling stations was compared in the Baltic Sea in the depth where sprat larvae occurred (0 – 20 m) with the abundance in the larval guts. In the North Sea, the mean prey abundance of all zooplankton sampling stations of the whole water column was compared with the abundance in the larval guts. In the “Costello graphics” and in the selectivity plots the same abbreviations for the prey types were used (Tab. IV.2).

Prey type	Abbreviation
<i>Acartia</i> spp. nauplii	ACN
<i>Acartia</i> spp. C1-3	AC13
<i>Acartia</i> spp. C4-5	AC45
<i>Acartia</i> spp. C6	AC6
<i>T. longicornis</i> nauplii	TEN
<i>T. longicornis</i> C1-3	TE13
<i>T. longicornis</i> C4-5	TE45
<i>T. longicornis</i> C6	TE6
<i>C. hamatus</i> nauplii	CEN
<i>C. hamatus</i> C1-3	CE13
<i>C. hamatus</i> C4-5	CE45
<i>C. hamatus</i> C6	CE6
Clausocalanoid nauplii	CLN
Pseudo/Paracalanus C1-3	PS13
Pseudo/Paracalanus C4-5	PS45
Pseudo/Paracalanus C6	PS6
Unident. copepod stages	CS
Cladocerans	CLA
Bivalve larvae	BL
Copepod eggs	CE
“Other plankton”	OP
Microplankton	MP

Tab. IV.2: Abbreviations used in the “Costello graphics” and in the selectivity plots.

The index C (Pearre jr. 1982) was used to describe the feeding selectivity. C varies from -1 to 1, whereby -1 indicates avoidance and +1 shows absolute preference for a certain prey type. Significance was calculated using the χ^2 -Test. Selectivity values were calculated only for the main prey items, i.e. in the Baltic Sea developmental stages of the copepods *Acartia*

spp., *Temora longicornis*, *Centropages hamatus* and *Pseudocalanus* sp., as well as for cladocerans and in the North Sea developmental stages of the copepods Pseudo/Paracalanus, *Acartia* spp. and *Temora longicornis*.

For the prey-size to larval-size relationship the mean of the log-transformed prey lengths was estimated for each larval size class. Niche breadth was computed as the standard deviation of the mean logarithmic prey size in each predator size class (Pearre jr. 1986). To get the maximum number of predator size classes containing not less than three prey entries 0.5 mm larval size classes were chosen.

V Feeding ecology of Central Baltic sprat (*Sprattus sprattus* L.) larvae in relation to zooplankton dynamics – implication for survival

Introduction

Correlation studies of the spawning stock biomass, production of different egg stages, as well as larval and 0-group abundance of sprat in the Baltic Sea have demonstrated that the larval and early juvenile stages are critical for the survival of a sprat year-class (Köster et al. 2003b). Information is scarce about the impact of larval feeding behaviour influencing the recruitment levels in sprat larvae in the Baltic Sea. Historical gut content analyses revealed Baltic sprat larvae to have a very restricted prey spectrum and to be sensitive to food limitation (Wosnitza 1974, Graumann et al. 1989). However, Voss et al. (2003), concluded that due to a larger niche breadth of sprat larvae, compared to cod (*Gadus morhua*), sprat larvae should be able to cope better with a changing prey field, but no information on seasonal changes in the prey field, both with respect to size and taxonomic composition, was given. In the present chapter larval diet composition of sprat and selective feeding were investigated in relation to the seasonal population dynamics of their zooplanktonic prey in the Central Baltic Sea. Predator- and prey size-dependent trends in feeding ecology of sprat larvae were followed to identify mechanisms leading to variability in larval survival. The underlying hypothesis of the 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

Sampling

We sampled sprat larvae during 13 cruises between March and November 2002 with the German research vessels RV ALKOR, RV HEINCKE, RV PENK and RV A. v. HUMBOLDT on a grid of 48 stations in the Bornholm Basin of the Central Baltic Sea

(Fig. V.1, Tab. V.1). Larvae were collected with a Bongo-sampler (60 cm diameter) using nets with 335 μm and 500 μm mesh sizes in double-oblique hauls from the surface to 5 m above the sea floor. Larval abundance and larval length were measured for larvae collected on all cruises. Larval abundance during the season ($\text{Ind.}\cdot\text{m}^{-2}$) was calculated using information on filtered water volume and depth. Because of their better condition, all larvae from 335 μm nets were used for gut content analyses, substituted by larvae from 500 μm , if sufficient numbers were not available from the smaller mesh size.

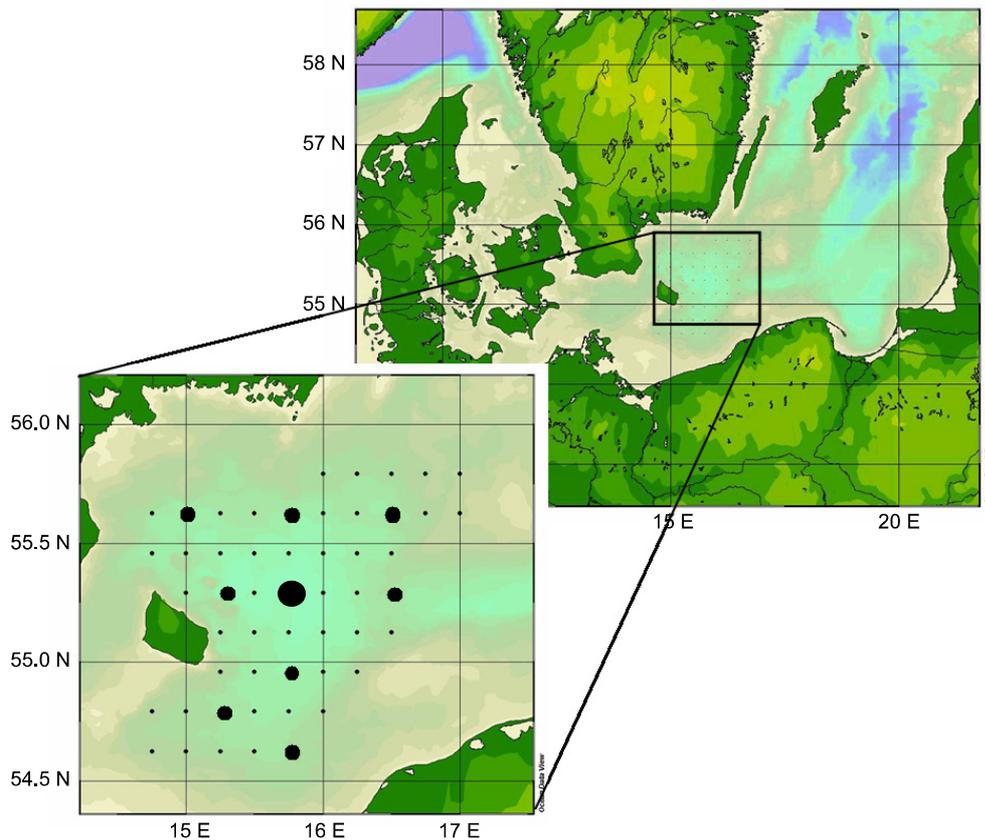


Fig. V.1: Map of the Baltic Sea with an inlet showing the study site, the Bornholm Basin. Small dots - larval sampling grid, medium dots - stations with additional zooplankton sampling and large dot - station with additional vertical sampling

Gut contents were investigated for larvae collected on seven cruises (Tab. V.1). As feeding of sprat larvae occurs only during daylight (Voss et al. 2003), we used only larvae from daylight samples.

Tab. V.1: Sampling information; Ns - Number of larval sample stations, Ne - Number of larvae analysed for gut contents

Sampling Date	Vessel	Ns	Ne
17-19 Mar 2002	R/V A. v. Humboldt	8	439
03-06 Apr 2002	R/V Alkor	4	52
17-19 Apr 2002	R/V Penk	21	-
06-11 May 2002	R/V Heincke	45	-
23-28 May 2002	R/V A. v. Humboldt	21	740
18-22 Jun 2002	R/V Alkor	11	596
02-05 Jul 2002	R/V Alkor	35	-
23-28 Jul 2002	R/V Alkor	36	232
13-18 Aug 2002	R/V Heincke	48	-
23-27 Aug 2002	R/V Alkor	26	-
04-08 Sep 2002	R/V Alkor	44	-
02-10 Oct 2002	R/V A. v. Humboldt	5	14
12-16 Nov 2002	R/V Heincke	6	11

We recorded the vertical distribution of sprat larvae in May 2002 on a permanent station (Fig. V.1) using a towed Multinet (mouth opening of 0.5 m², 335 µm mesh size) deployed in 5 m steps from the surface to 80 m. Abundance of vertical distribution (Ind.*m⁻³) was recorded from 3 vertical profiles using recorded filtered volumes.

We recorded the zooplankton prey field in parallel to the sampling of sprat larvae on nine stations of the grid (Fig. V.1). To this end vertical hauls were performed with a Multinet (mouth opening of 0.25 m², 50 µm mesh size) deployed in 10 m steps from a maximum depth of 80 m. Using information about the filtered water volumes, abundances (Ind.*m⁻³) of zooplankton species were calculated. All samples were preserved in a 4% borax buffered formaldehyde seawater solution for laboratory analyses.

Data analyses

We tested for differences in gut fullness among months and predator size using the Kruskal-Wallis rank sum test. For the determination of feeding trends between months and larval size classes (<5.5 mm, 5.5 - <10.5 mm, 10.5 - <15.5 mm, 15.5 - <20.5 mm, 20.5 - <25.5 mm) we used frequency of occurrence $F(\%)$ and the percentage of dry weight of each food item $W(\%)$ in “Costello graphics” (Costello 1990). To compare similar size ranges and to get sufficient numbers of larvae with sufficient food items to calculate selectivity indices, the larvae were grouped into the same size classes as used for the “Costello graphics”. To investigate size-related trends in feeding of sprat larvae, we studied the relationship between maximum, mean and minimum log-transformed-prey and

larval length as well as trophic niche breadth. We applied linear and non-linear regression analyses to study the different relationships.

Results

Seasonal development of abundance and length of sprat larvae

We found considerable abundances of sprat larvae between March and July and low abundances of larvae again in October and November (Fig. V.2).

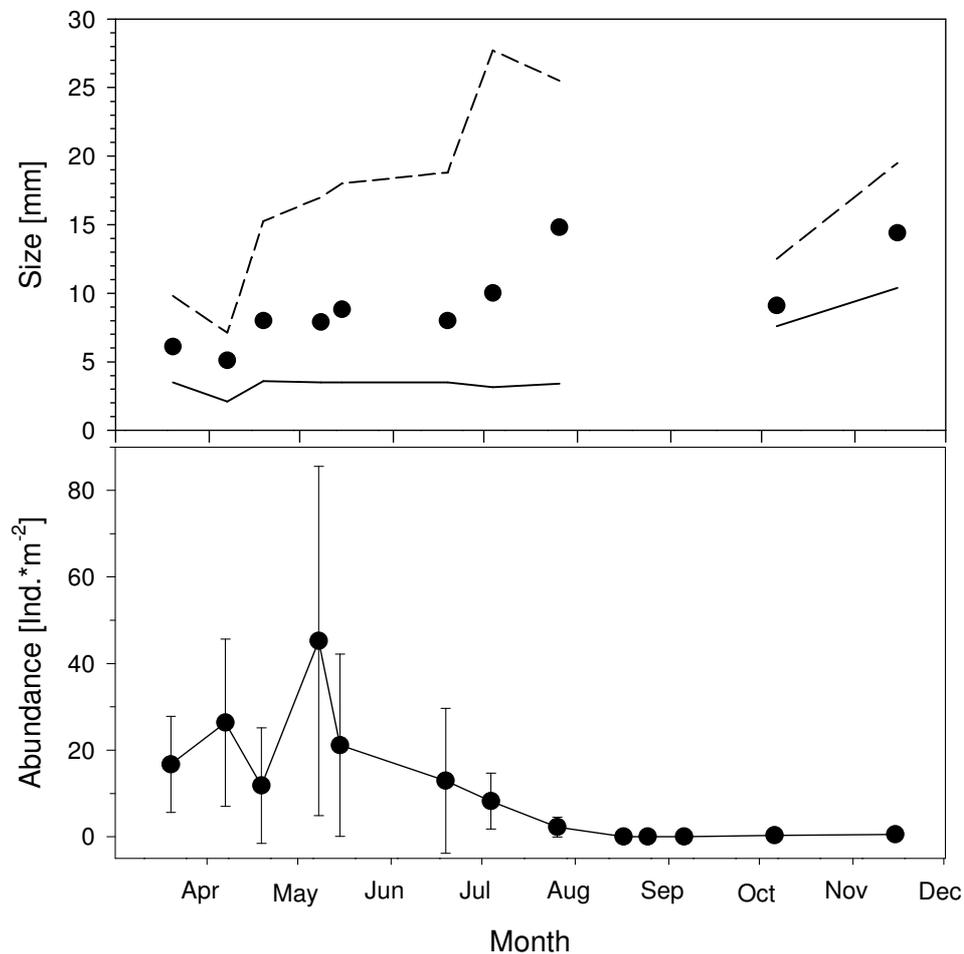


Fig. V.2: Seasonal development of (a) sprat larval length (dashed line - maximum length, solid line - minimum length, black dots - mean length) and (b) mean larval abundance (error bars represent \pm s.d.)

Due to their occurrence, we investigated the feeding ecology of Baltic sprat larvae only for months where considerable abundances of feeding larvae were available, i.e. March to July. Abundance increased towards a peak in early May after an intermediate minimum in late April. From late May onwards, the abundance of sprat larvae decreased, and sprat disappeared from the plankton in August. Mean and maximum larval length increased constantly from March to July, while the minimum lengths remained constant (Fig. V.2).

Vertical distribution of sprat larvae

We investigated the vertical distribution of sprat larvae during peak sprat larval abundance in May 2002 (Fig. V.3). The observed vertical distribution reflects the typical ontogenetic vertical migration behaviour of Baltic sprat larvae. Baltic sprat eggs are neutrally buoyant in high salinity deep waters, where also the larvae hatch. Consequently we observed a peak of recently hatched small individuals in 55 m depth. After hatching larvae migrated into the food-rich surface waters and consequently medium-sized and large larvae were found in the upper 20 m. We observed the maximum abundances in 10 m depth, where also a secondary peak of small larvae was found.

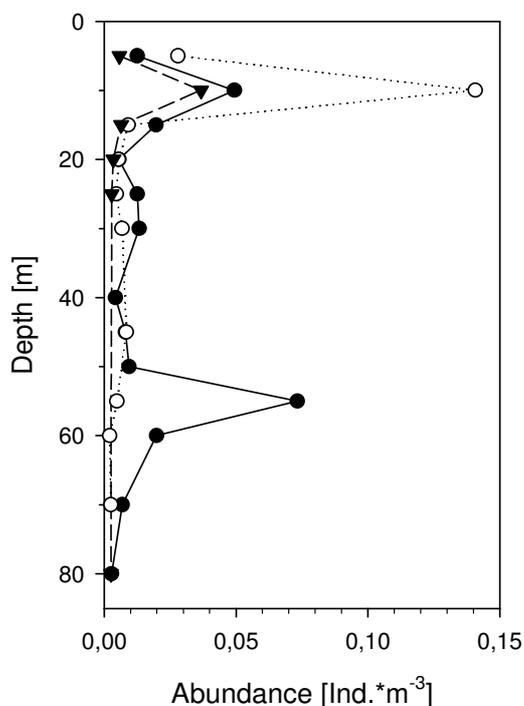


Fig.V.3: Vertical distribution of sprat larvae in May 2002 (black dots - small larvae, white dots - medium larvae, triangles - large larvae)

Prey availability

According to the vertical distribution, we defined the zooplankton community in the upper 20 m to represent the prey field for feeding sprat larvae. The prey availability consisted of the copepods *Acartia* spp., *Temora longicornis*, *Centropages hamatus* and *Pseudocalanus* sp. as well as cladocerans (Fig. V.4).

Nauplii of all species dominated the prey field in April and May. Highest abundances were observed for *T. longicornis*, which peaked in April, and *Acartia* spp., which peaked in May. In May maximum abundance of C1-3 and C4-5 were observed as well, with *T. longicornis* being the most abundant, followed by *Acartia* spp. and *C. hamatus*. From June onwards, adults (C6) of *Acartia* spp. and *T. longicornis* generally dominated the copepod community while in July and August cladocerans were by far the most abundant zooplankton group.

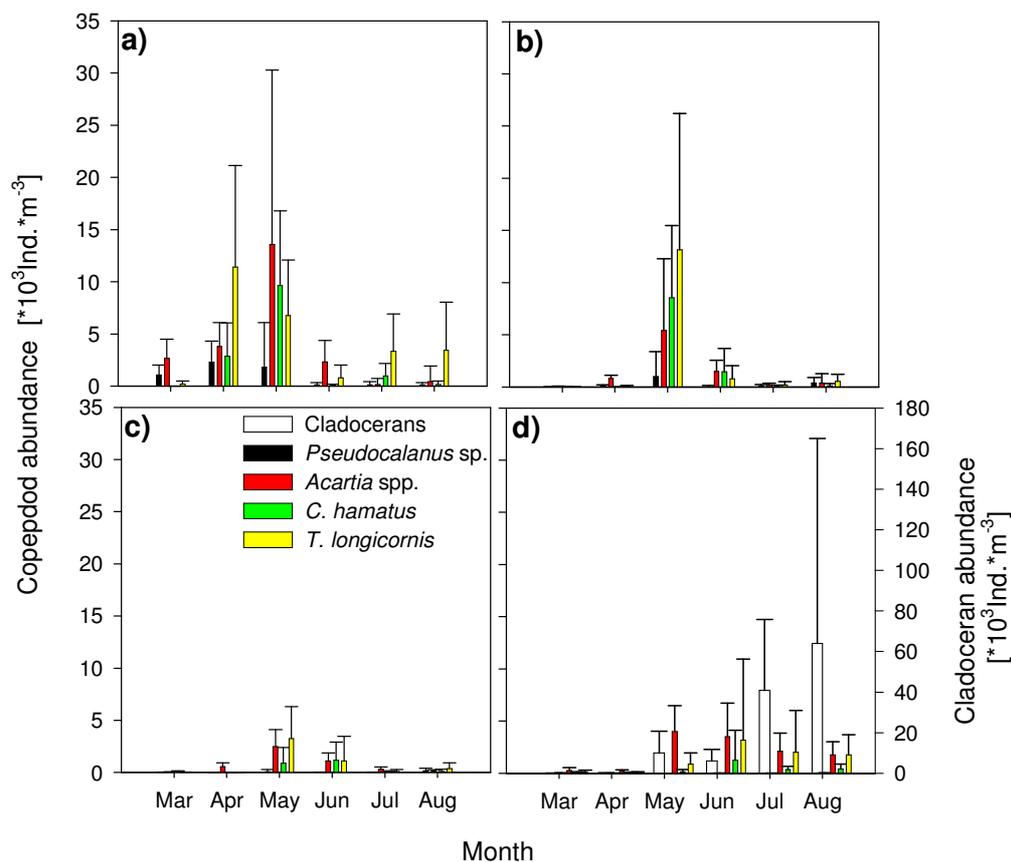


Fig. V.4: Seasonal development of larval sprat prey availability: (a) nauplii, (b) copepodite stages C1-3, (c) copepodite stages C4-5, (d) adult copepods and cladocerans (error bars represent \pm s.d.)

Beside the taxonomic composition we characterized the prey field by computing the mean size of the prey items available to sprat larvae (Fig. V.5). The mean size of the individual

items in the plankton was more than doubled from April to June and remained constant thereafter.

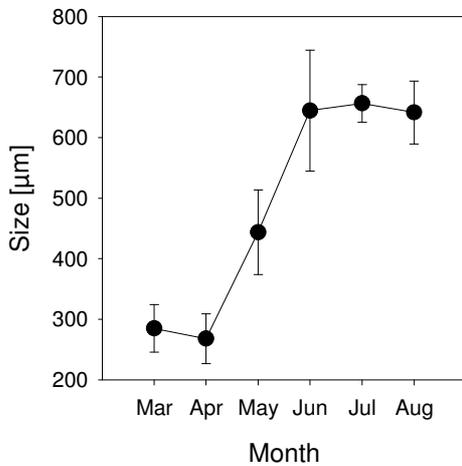


Fig. V.5: Seasonal development of the mean prey length in the plankton (error bars represent \pm s.d)

Diet composition

At the beginning of the sprat spawning season (in March and April), sprat larval guts contained almost exclusively microplankton (not shown). In May, nauplii of *T. longicornis*, *C. hamatus* and *Acartia* spp. dominated the diet (Fig. V.6).

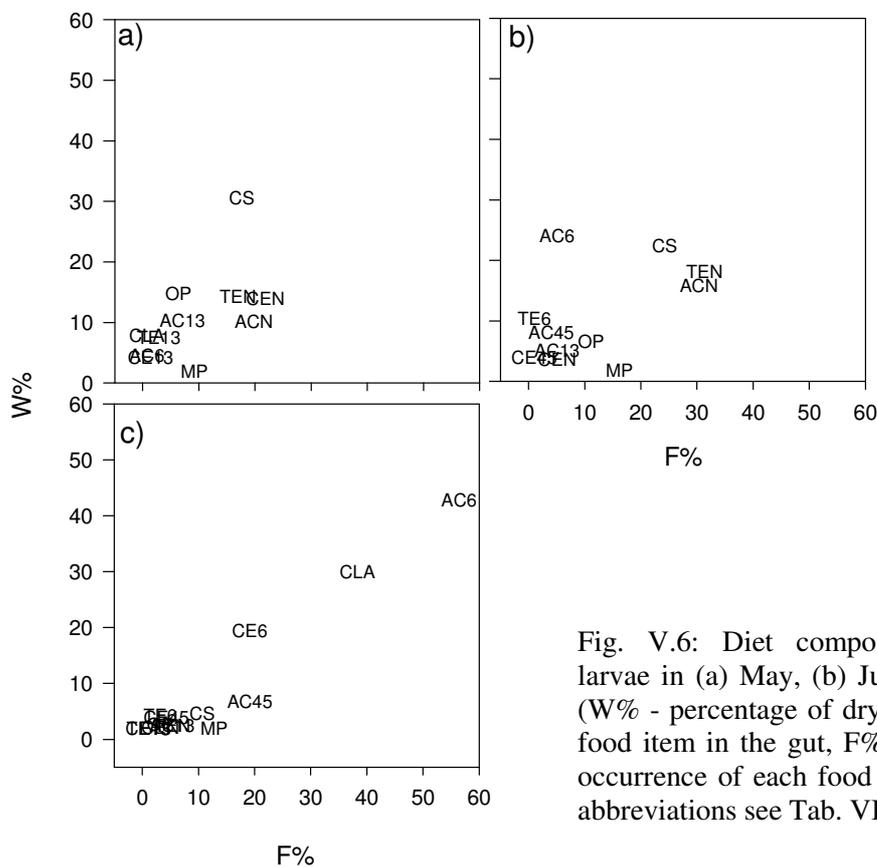


Fig. V.6: Diet composition of sprat larvae in (a) May, (b) June and (c) July (W% - percentage of dry weight of each food item in the gut, F% - frequency of occurrence of each food item in the gut, abbreviations see Tab. VI.2)

Further the group “other plankton” and early copepodites of *Acartia* spp. were of importance in May. In June unidentified nauplii as well as nauplii of *T. longicornis* and *Acartia* spp., were the most frequently occurring prey items, while adults of *Acartia* spp. dominated in weight. From July onwards adults of *Acartia* spp. and *C. hamatus*, cladocerans as well C4-5 of *Acartia* spp. were the dominating prey items. The seasonal progression of the sprat larval diet from smaller to larger prey items was also visible when the diet composition among different size classes was compared (Fig. V.7).

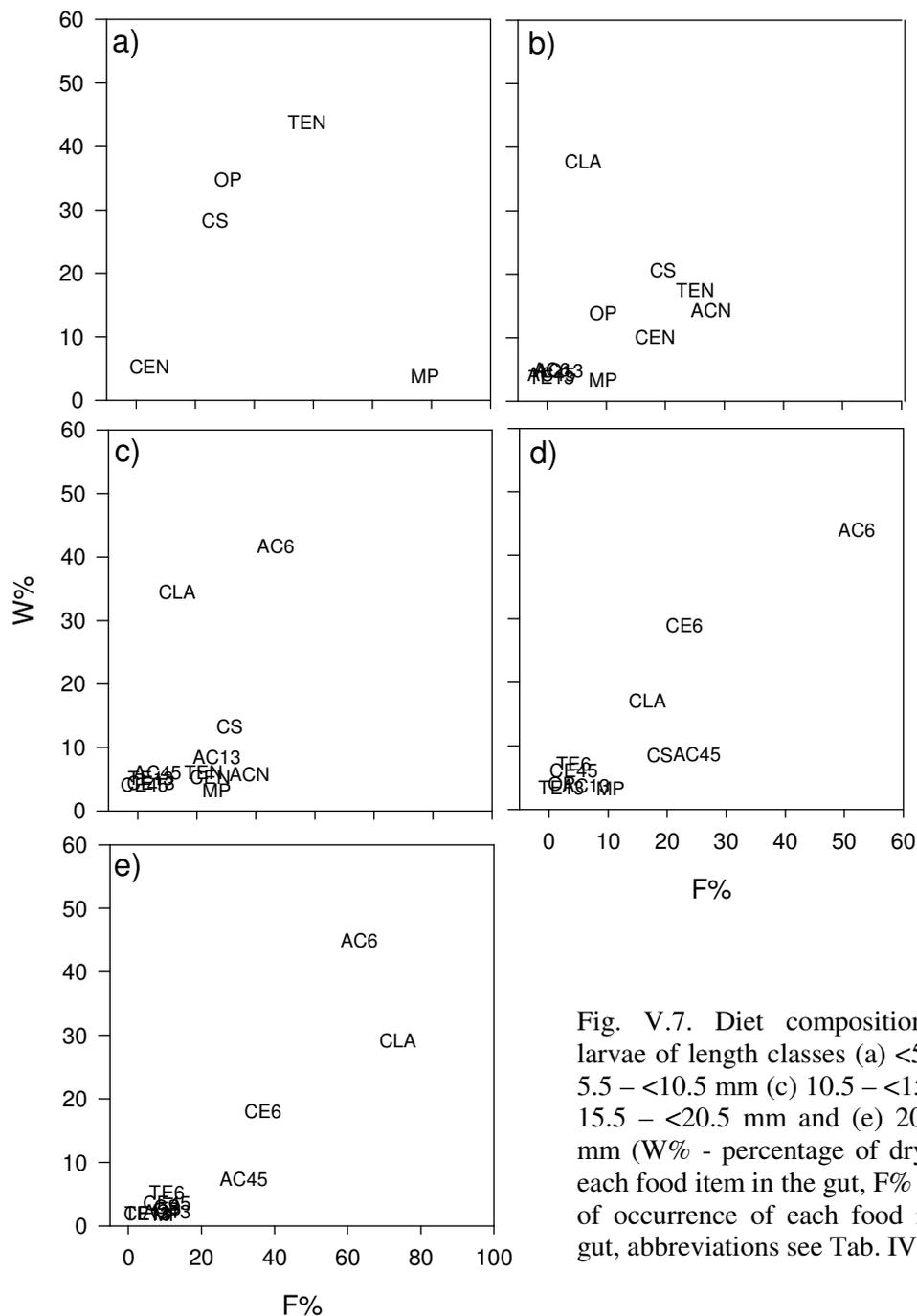


Fig. V.7. Diet composition of sprat larvae of length classes (a) <5.5 mm (b) 5.5 – <10.5 mm (c) 10.5 – <15.5 mm, (d) 15.5 – <20.5 mm and (e) 20.5 – <25.5 mm (W% - percentage of dry weight of each food item in the gut, F% - frequency of occurrence of each food item in the gut, abbreviations see Tab. IV.2)

We found the smallest feeding larvae (<5.5 mm) to prey mainly on microplankton and *T. longicornis* nauplii. For 5.5 - <10.5 mm larvae, copepod nauplii (mainly of *T. longicornis* and *Acartia* spp.) dominated the gut contents while the gut contents of 10.5 - <15.5 mm larvae contained mostly *Acartia* spp. C6 and cladocerans. In general, the largest sprat larvae (15.5 - <25.5 mm) preyed upon C6 of *Acartia* spp. and *C. hamatus*, cladocerans and C4-5 of *Acartia* spp.

We used contingency table analysis for a statistical evaluation of differences in diet among months and size-classes of larval sprat. We excluded March and April from the analysis of temporal differences because, in these months, mainly microplankton and “other plankton” occurred in the guts. Comparing the diet in May, June and July we derived a total χ^2 -value that indicated a highly significant difference ($\chi^2 = 452.48$, $df = 18$, $p < 0.0001$) in the occurrence of prey types. Among prey types, the main source of variation was in *Acartia* spp. ($\chi^2 = 144.34$) and among months from July ($\chi^2 = 229.68$). The contingency table analysis of the difference between size-classes showed a significant total χ^2 -value as well ($\chi^2 = 451.95$, $df = 27$, $p < 0.0001$). Most of the variation in prey types derived again from *Acartia* spp. ($\chi^2 = 144.17$), whereas for size-classes the highest variability was observed for 5.5 - <10.5 mm long larvae ($\chi^2 = 137.26$).

Selective feeding

We calculated selectivity indices for different larval sizes and prey items for May, June and July, when sufficient numbers of filled guts for a wide range of larval sizes were available (Fig. V.8). We found differences in selective feeding between larval size classes and month. In all months, the smallest larvae (≤ 10.5 mm) significantly selected nauplii of *Acartia* spp., *C. hamatus* and *T. longicornis*. With increasing size (10.5 - <20.5 mm), larvae selected significantly developmental stages of *Acartia* spp. in May and June, and additionally adult *C. hamatus* in July. The largest larvae (20.5 - <25.5 mm), observed only in July, also selected *Acartia* spp. life-stages and as well as C6 of *C. hamatus*. In all months, a negative selection was calculated for developmental stages of *Pseudo/Paracalanus* sp., *T. longicornis* and cladocerans.

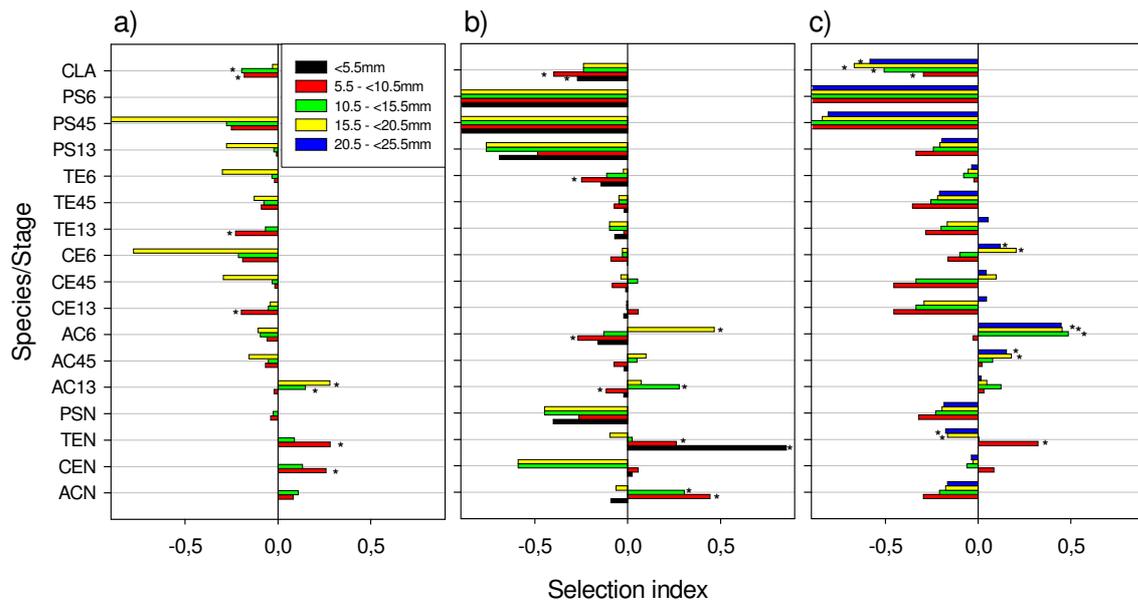


Fig. V.8: Selective feeding of sprat larvae (Index C) in (a) May, (b) June and (c) July (* indicates significant selective feeding at the 5% level, abbreviations see Tab. IV.2)

Gut fullness and feeding success

Gut fullness in terms of numbers increased until July with a smaller intermediate peak in April (Fig. V.9). Gut fullness in terms of weight increased constantly from low levels throughout a large part of the season to a very pronounced peak in July. We observed both indices of gut fullness to increase with larval length, displaying a pronounced increase to the largest length group (Fig. V.9). The Kruskal-Wallis-rank sum test showed significant differences in gut fullness between months ($\chi^2 = 125.53$, $p < 0.001$ for prey numbers and $\chi^2 = 129.39$, $p < 0.001$ for prey weight) and predator sizes ($\chi^2 = 217.01$, $p < 0.001$ for prey numbers and $\chi^2 = 219.52$, $p < 0.01$ for prey weight).

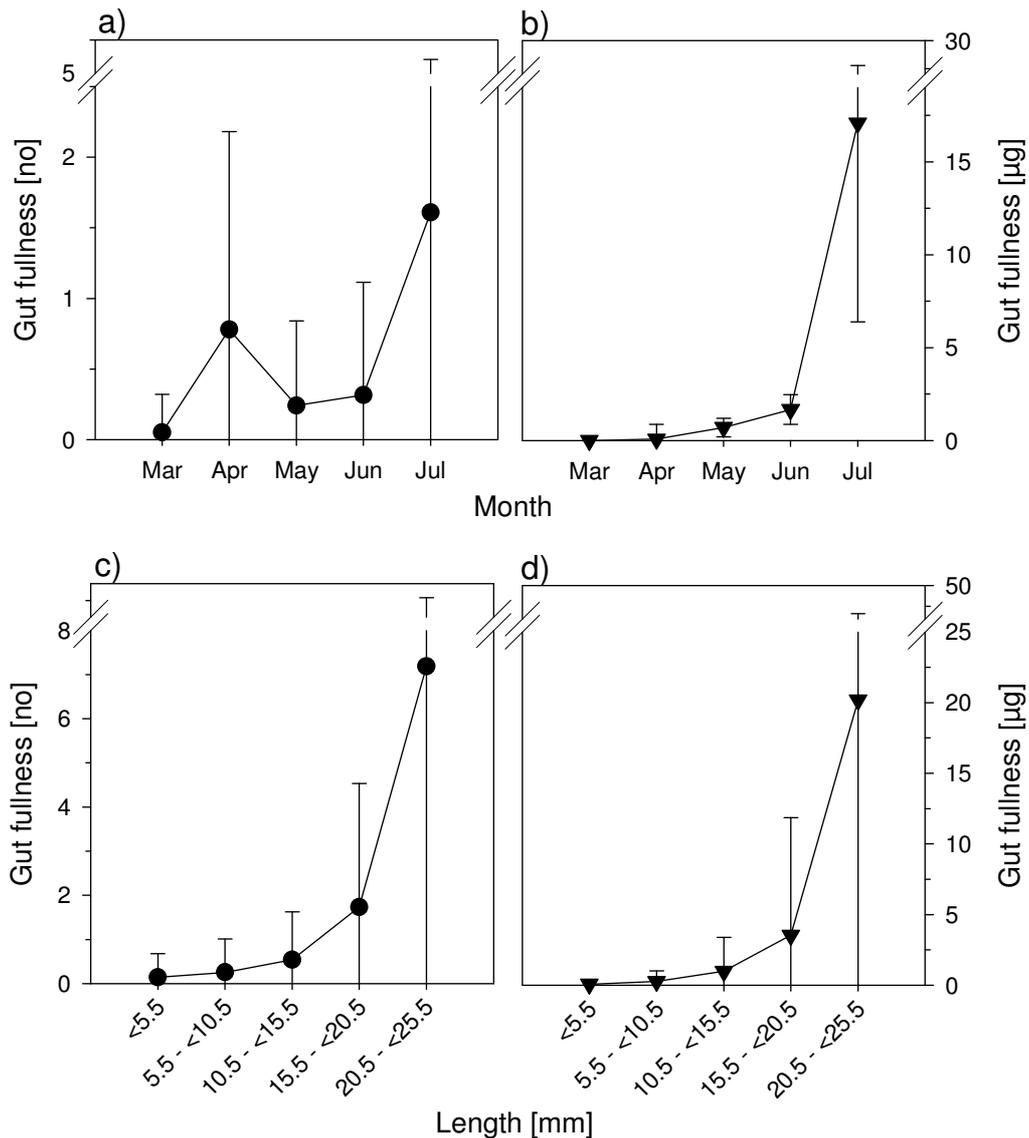


Fig. V.9: Seasonal (a, b) and size-dependent (c, d) development of larval gut fullness (dots - gut fullness in terms of numbers, triangles - gut fullness in terms of weight; error bars represent \pm s.d.)

We evaluated feeding success on a monthly basis. Almost no feeding larvae were found in March, indicating that feeding started generally in April (not shown). From May onwards the share of feeding larvae was significantly ($p < 0.01$) related to larval length (Fig. V.10). While the regression model explained a large part of the variability in the data in May, more variable relationships were found for June and July.

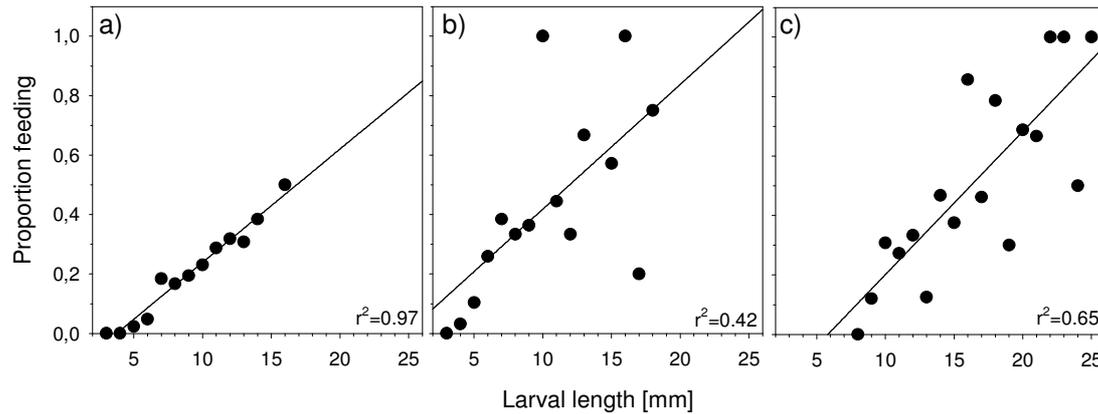


Fig. V.10: Relationships between larval feeding success and larval length in (a) May, (b) June and (c) July

Predator-prey size relationships and trophic niche breadth

The mean log-length of ingested prey increased with larval size up to a plateau at 16 mm (Fig. V.11). A non-linear regression analysis revealed a highly significant relationship ($r^2 = 0.85$, $p < 0.01$). Maximum prey length also increased to a plateau, in this case at 13 mm. Minimum log-prey length remained constant to 12 mm SL, increasing afterwards. Non-linear regression analyses revealed a highly significant relationship for both maximum ($r^2 = 0.94$, $p < 0.01$) and minimum log-prey length ($r^2 = 0.58$, $p < 0.01$).

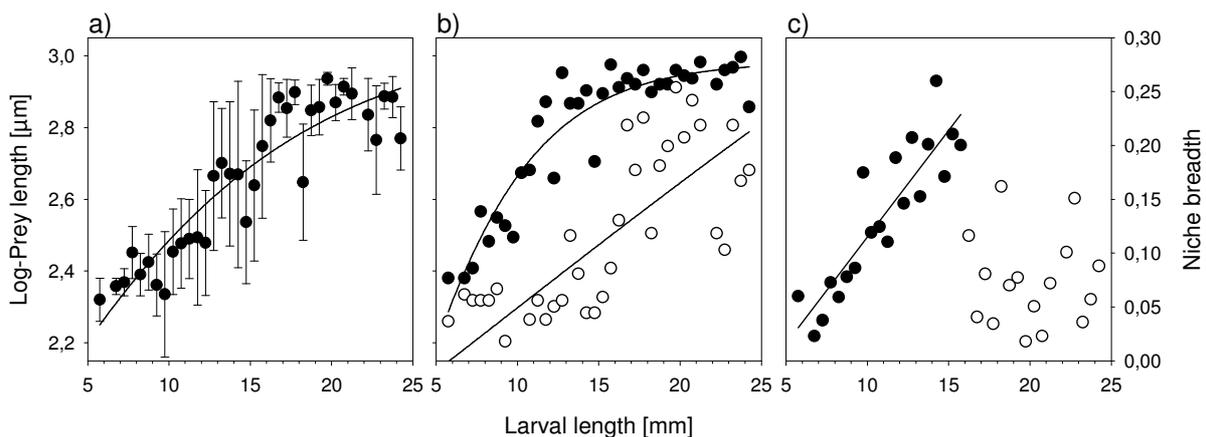


Fig. V.11: Relationships between larval length and a) log mean prey length, b) log maximum and minimum prey length (black dots - maximum prey length, white dots - minimum prey length) and c) niche breadth

Niche breadth also increased linearly with increasing length to 16 mm, ($r^2 = 0.79$, $p < 0.01$) but was unrelated to larval length for larger larvae. Larger larvae showed on average a smaller niche breadth, however with a considerable variability.

Discussion

We performed a comprehensive study of the feeding ecology of larval Baltic sprat with the goal to identify critical periods for larval survival with respect to prey availability. To this end we followed taxonomic as well as predator- and prey size-dependent trends in feeding and prey selection of sprat larvae in relation to the seasonal population dynamics of their zooplanktonic prey.

Diet composition and selective feeding

In this study, copepods and cladocerans were the most important food source for sprat larvae. This is in agreement with earlier studies on sprat larval diet composition in the Baltic (Wosnitza 1974, Graumann et al. 1989, Arrhenius 1996, Voss et al. 2003) as well as in the Irish Sea and North Sea (Last 1980, Conway et al. 1991, Coombs et al. 1992).

Contrary to an earlier study (Voss et al. 2003), we observed considerable amounts of microplankton in the guts of small first-feeding larvae (<10.5 mm). A reason for this may be that most of the microplankton are fragile and non-loricate species and can easily be decomposed without digestive residue in the larval guts, thus remaining undetected (Stoecker & Govoni 1984, Fukami et al. 1999). Several other studies suggest that fish larvae start feeding on diatoms and/or “protozoan-like cells”, including flagellates and ciliates (e.g. Last 1978a,b, Last 1980, Conway et al. 1991, Fukami et al. 1999). Last (1978a) assumed that protozoa and diatoms could be an important prey for the first-feeding larvae. Further, Stoecker & Govoni (1984) suggested that ciliates might have a supplemental nutritional role for these larvae when nauplii concentration was low. The swimming ability of small larvae is relatively poor and small larvae may be unable to catch fast swimming zooplanktonic prey (Checkley jr. 1982, Hunt von Herbing & Gallager 2000). Protozoa move more slowly than nauplii and are thus easily caught by first-feeding larvae (Stoecker & Govoni 1984). Furthermore, feeding on microplankton might serve as trial food to establish the feeding behaviour of larval fish (Stoecker & Govoni 1984). We

observed a peak of first-feeding larvae in 10 m depth, where dinoflagellates and other microzooplankton were abundant at the beginning of the sprat spawning season (Beusekom, Alfred-Wegener-Institute, Sylt pers. com.). We thus conclude that microplankton can be an important food source for first-feeding Baltic sprat larvae, although the nutritional value of these items remains unknown.

The diet composition of Baltic sprat larvae displayed a clear seasonal trend related to the increase in average predator size. In accordance with the composition of available prey, larval sprat initially fed on nauplii in May, when most of the larvae were small. Later in the season, with increasing body size, larvae gradually switch to larger prey items, especially adult copepods of *Acartia* spp., as well as *Centropages hamatus* and cladocerans. These trends in sprat larval diets were, to a large degree, explainable by selective feeding. Sprat larvae appear to be highly selective and showed the same temporal and predator-size dependent trend from nauplii early in the season to later stages of *Acartia* spp. and *C. hamatus* in summer.

Developmental stages of *Acartia* spp. dominated the gut contents and were positively selected by Baltic sprat larvae. However, Checkley jr. (1982) assumed that adult *Acartia* spp. should be negatively selected by herring larvae, because of their ability to escape due to the greater burst speed compared to other copepods such as *Pseudocalanus* sp. and *Oithona* sp. Further, Viitasalo et al. 2001 found that larger copepodites and adults of *Acartia* spp. show a high alertness to hydrodynamic signals, which should also act to reduce their vulnerability to predation. But Viitasalo et al. (2001) also observed that *Acartia* spp. performs only weak escape jumps with small escape distances, attributes positively related to predator attack success (e.g. Caparroy 2000). This might have contributed to the observed high selection of *Acartia* spp., which was confirmed by other studies in the Baltic Sea investigating food preferences of larvae and 0-group sprat (Arrhenius 1996, Voss et al. 2003).

Cladocerans were the main prey for the largest sprat larvae in terms of numbers, although selection indices for this taxonomic group were strongly negative. We explain this apparent contradiction by the extremely large population sizes of cladocerans in summer that allow sprat larvae to feed on cladocerans unrestrictedly. We assume that feeding incidence of the larvae is too low to reflect the extremely high availability of cladocerans in their gut contents. Similar findings were reported by Nip et al. (2003), investigating larval black seabream (*Acanthopagrus schlegeli*) feeding on copepods.

Selectivity estimates can generally be biased by a spatio-temporal mismatch between the sampling of predators and prey. In the study, zooplankton abundance and larval diets were not compared on a station-by-station basis. Rather, selection indices were calculated by integrating gut contents and food availability over all sampled stations from one survey. This integration over a large number of samples was necessary due to the generally low numbers of feeding larvae and ingested prey items. Further, we assumed the feeding environment of the larvae to be represented by the upper 20 m water column, because most of the larvae were found in this water layer. These integrated samples represent an average prey concentration over a broad scale relative to the larva's feeding ambit (Pepin 2004). Some evidence exists that copepods are aggregated in fine-scale layers (Fernández de Puelles et al. 1996, Gallager et al. 2004) associated to hydrographical discontinuities, where high prey abundances are found as well (Munk 1995, Munk et al. 1999). Our sampling did not allow resolving the fine-scale distribution of the prey, but we believe that such distribution patterns have a strong influence on observed selection indices. Future investigations of the fine scale distribution of copepods and larvae with continuous samplers (e.g. Longhurst-Hardy-Plankton-Recorder, Video-Plankton-Recorder) might give an answer whether the positive selection indices for *Acartia* spp. are 1) merely are an artefact of small-scale predator-prey overlap that is not resolved by traditional net sampling, or 2) a real selection due to a higher capture success compared to other copepod species.

Predator and prey size related feeding trends

With larval development prey attack ability and therefore capture success increase (Houde & Schekter 1980). Furthermore the higher cruising speed of older larvae positively affects the frequency of prey encounter (Hunter 1981). Consequently, several studies observed positive relationships between body size and number of prey items ingested (Sabatés & Saiz 2000, Viñas & Santos 2000, Cass-Calay 2003, Reiss et al. 2005). In the present study, we also found feeding success and gut fullness to be strongly positive related to larval length. We observed only a slight increase in the number of prey items in the guts of the smaller size classes (<15.5 mm) and a pronounced increase in larger larvae (>15.5 mm). The very low feeding success of small, first-feeding larvae indicates a critical period during this larval stage. Furthermore, this result supports the hypothesis that, given natural

prey densities, these small fish larvae cannot afford to actively choose amongst several simultaneously available prey items (Browman 2005).

Our analysis of taxonomic diet composition and selective feeding of Baltic sprat larvae showed that with increasing larval size the diet changed to larger food items, i.e. later developmental stages of copepods as well as cladocerans. Consequently we found an increase in the mean size of the ingested prey up to 16 mm larval length, remaining constant afterwards. This relationship between larval development and the incorporation of larger prey is consistent with results from earlier investigations (e.g. Arthur 1976, Last 1978a,b, 1980, Coombs et al. 1992, Arrhenius 1996, Pepin & Penney 1997, Voss et al. 2003).

Feeding theory predicts that, under food-limited conditions, the niche breadth of larval fish should increase due to the ingestion of a wider range of prey sizes (Werner & Hall 1974, Bartell 1982, Reiss et al. 2005). However, several studies found no significant relationship between niche breadth and larval size (e.g. Pearre jr. 1986, Munk 1992, Reiss et al. 2005). Pepin and Penney (1997) observed an increase in niche breadth with larval growth for 6 out of 11 species investigated, while Scharf et al. (2000) observed a decrease in breadth of relative prey sizes for several investigated fish species. For Baltic sprat, we observed the niche breadth of sprat larvae to linearly increase until a length of ca. 16 mm. Afterwards the relationship broke down and larger larvae had a lower and highly variable niche breadth. We explain this pattern by a combination of larval growth and the seasonal plankton cycle. In the beginning of the season sprat larvae are small and thus limited to small food items, i.e. nauplii, which are prevailing in the plankton. Consequently small larvae displayed a small niche breadth. Larval growth in the spring allows larger prey items to be utilized and coincides with the appearance of larger prey in the plankton. Nonetheless, larvae targeted smaller prey items thus increasing their niche breadth. In July most of the larvae were in the largest size class and in parallel mainly larger prey items were available in the plankton. Consequently these larvae displayed again a smaller niche breadth. The results show that when evaluating the relationship between larval size and niche breadth, the taxonomic and size composition of the prey field has to be considered. This is especially true when investigating this relationship for species with a prolonged spawning time during which the zooplankton community changes. E.g. Voss et al. (2003) estimated a constant niche breadth with larval size for Baltic sprat. However, when considering the present findings, the same pattern of an increase in the niche breadth until a certain size (14 mm) and a decrease afterwards appears (Fig. 6 in Voss et al. (2003)).

Implications of observed feeding trends for sprat larval survival

The temporal- and size-dependent trends in Baltic sprat larval feeding ecology observed in the present study allow to identify potentially critical periods during larval development. Our results suggest that first-feeding sprat larvae (<10.5 mm) are prone to the danger of food-limitation in all months. This conclusion is based on the observations that sprat larvae 1) experienced a very low feeding success, and 2) rapidly increased their niche breadth with increasing body size. This implies that even if sprat larvae are born into the spring nauplii production peak, they most probably suffer high mortalities. In contrast, we found the largest larvae (>16.0 mm), which occur mainly during summer, not to be strongly food-limited. The main argument for this assumption is their high feeding success. In summer obviously a sufficient standing stock of larger zooplankton is available to the larvae.

Our results indicate that medium-sized sprat larvae (10.5 - 16.5 mm) are the life-stage which has the potential to cause most of the inter-annual variability in sprat larval survival as opposed to first-feeding larvae (that always suffer food limitation) and the largest larvae (that infrequently suffer food limitation). We base this hypothesis on the maximum trophic niche breadth we found for this part of the larval sprat population, pointing towards the need to incorporate all available prey types in the diet not to be prone to starvation. We further conclude that there a temporally-limited 'window of survival' for this larval stage exists, depending on the prey field they encounter. Larvae born too early in the season (April/May), despite profiting from high nauplii abundances for first-feeding larvae, suffer from the restricted size-spectrum of the zooplankton available as they grow. In contrast, larvae born too late in the season (July) will suffer from the low nauplii availability. There exists however a transition period where larvae encounter both enough nauplii for first-feeding and later copepodite stages for their further growth. Hence, we hypothesise, that the match of larval production relative to the period where the broadest size-spectrum of zooplankton is available, determines larval survival.

This hypothesis is supported in a parallel study by Voss et al. (2005) investigating seasonal variability in sprat larval condition and survival in the same year. In their study larvae >11 mm displayed a higher survival when born in June compared to April, which they attribute to the difference in the composition of the available prey. Further support is found in a study by Baumann et al. (2005) investigating spatio-temporal patterns in growth of Baltic young-of-the-year sprat based on otolith microstructure analysis and hydrodynamic modelling. This study revealed that surviving sprat larvae from the Bornholm Basin in

2002 were born in summer, supporting the present results of the best food availability in terms of size during this season.

Finally, our study confirmed the outstanding importance of the copepod *Acartia* spp. for the nutrition of sprat larvae (Voss et al. 2003) and a comparison of prey fields between May and June/July suggests that also cladocerans might be important for larval survival. High *Acartia* spp. abundance supports (1) the supply of first-feeding larvae with nauplii and (2) the availability of later copepodite stages for larger sprat larvae. The temperature-induced increase in *Acartia* spp. during the 1990s (Möllmann et al. 2000, 2003) may thus be a likely reason for the high recruitment level of Baltic sprat and consequently the strong increase in stock size during this decade (Köster et al. 2003a). Thus this study points towards the importance of climate-induced changes in the physical environment for the structure and functioning of marine ecosystems.

VI Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in relation to frontal systems in the German Bight

Introduction

High concentrations of sprat eggs and larvae are related to tidal fronts in the North Sea indicating that these areas may offer favourable conditions for sprat larvae (Valenzuela 1991, Munk 1993). Information in the German Bight is sparse to what extent frontal systems affect larval feeding ecology and consequently their survival. In the present chapter the influence of frontal systems on the feeding ecology of sprat and sardine larvae was investigated to evaluate implications for their survival in relation to such structures. The underlying hypothesis of the study was that differences in feeding ecology of fish larvae are related to the availability of suitable prey, which is linked to hydrographical structures. Further the exceptional appearance of sardine larvae offers the opportunity to compare their feeding ecology with sprat larvae and to investigate the amplitude of food overlap as well as mechanisms to avoid possible food competition.

Material and Methods

Sampling

Sampling took place during one cruise with RV ALKOR in June 2003 on two transects crossing a tidal mixing front (TMF) and a river plume front (RPF), respectively, in the German Bight (Fig. VI.1). Larval samples were collected on five stations of the RPF transect and on four stations along the TMF transect (Fig. VI.1). On each transect three additional CTD stations and FluoroProbe measurements were taken to record temperature, salinity and chlorophyll-*a*.

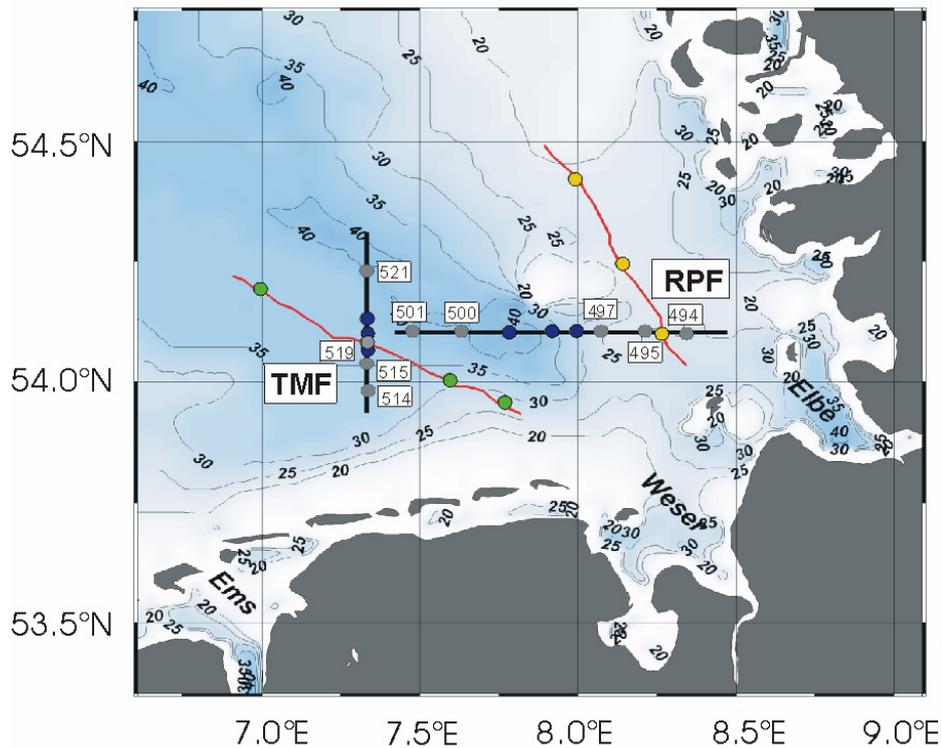


Fig. VI.1: Study area with both fronts, sampling transects and stations: TMF - Tidal mixing Front (green dots), RPF - River Plume Front (orange dots), Grey dots - larval sampling stations, blue dots - additional CTD stations, numbers - station numbers, (modified according to Holtappels 2004)

Sampling of larvae was performed during daytime with a towed Multinet (mouth opening 0.5 m^2 , $335 \mu\text{m}$ mesh size). In mixed water columns samples were taken at the surface, near the bottom and – if existing – in the depth of the chlorophyll peak. In stratified water columns larvae were sampled above, within and below the thermocline. On the shallow station 494 only one sample was taken at 7 m. All samples were preserved in 4% buffered formalin seawater solution.

The zooplankton prey field was sampled at larval sampling stations with a vertically towed Multinet ($55 \mu\text{m}$ mesh size, mouth opening 0.25 m^2) in 5 m steps from surface to a maximum of 35 m. Abundances of larvae ($\text{Ind.} \cdot \text{m}^{-3}$) and zooplankton ($\text{Ind.} \cdot \text{m}^{-3}$) were calculated using information on filtered volume. For zooplankton abundance only the potential prey species were used which were also found in the guts.

Data analyses

For both transects the temperature, salinity and chlorophyll-*a* values from the CTD- and FluoroProbe-stations were plotted in profiles over the whole transect to show the physical conditions during the sampling procedure. On each temperature profile abundances and composition of the fish larvae were displayed as pie charts in every sampling depth.

Zooplankton data were provided by Hindrichs and Alheit (unpubl. data 2004). Simple regression analyses were performed to evaluate the relationship between larval abundances and zooplankton abundance. The Kruskal-Wallis rank sum test was used for testing differences in gut fullness among stations and sprat larval size classes. The Mann-Whitney U-test was applied to test differences in gut fullness between species and between transects, respectively, as well as sardine larval size classes. Further simple regression analyses were used to evaluate the relationship between gut fullness and zooplankton abundance.

The diet composition at the different stations of both transects were described with simple bar charts. In these charts the copepod stages C1-6 of each prey species were pooled to reduce prey categories. For the description of the diet composition in different size classes (< 8.5 mm, 8.5 - <14.5 mm, 14.5 – 18.5 mm) the frequency of occurrence $F(\%)$ and the percentage of dry weight of each food item $W(\%)$ were used in “Costello graphics” (Costello, 1990).

Food overlap of sprat and sardine larvae was calculated using Schoener’s index (Schoener 1968), as $D = 1 - 0.5 \sum |P_{x,i} - P_{y,i}|$, where $P_{x,i}$ and $P_{y,i}$ are the proportions for predator type x and y , respectively, for the i th prey item. The range between 0.25 and 0.74 was considered as moderate (Pedersen 1999). D above 0.74 was defined arbitrarily to indicate high overlap.

To compare similar size ranges and to get sufficient numbers of larvae with sufficient food items to calculate selectivity indices, the larvae were grouped into the same size classes as used in the “Costello graphics”.

The relationship between prey and larval length was studied to investigate the size-related trends in feeding of both species. Due to the low number of possible prey length measurements mean log-transformed-prey length and niche breadth were calculated only for the sardine larvae.

Results

Physical environment and larval distribution

Tidal Mixing Front (TMF)

Fig. VI.2 shows the hydrographic situation on the sampling transect, crossing the tidal mixing front (TMF) from south to north. In the temperature profile a clear change from a stratified area to a mixed water column was obvious.

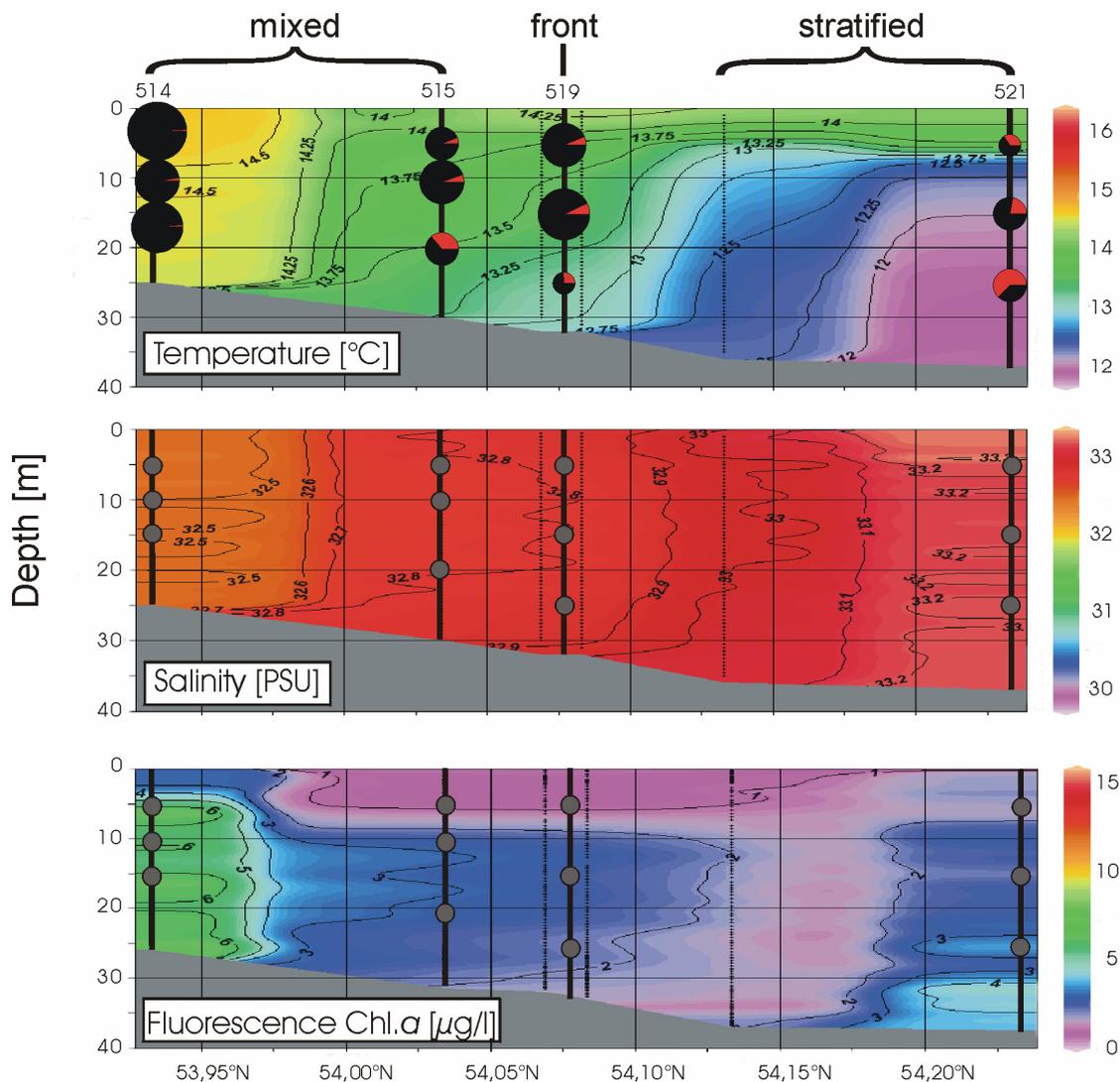


Fig. VI.2: Hydrography of the transect crossing the tidal mixing front (TMF). Solid black lines - sample stations, dotted lines - additional CTD and Fluoroprobe stations, pie charts illustrate abundance and composition of fish larvae at the sampling depths, red - proportion of sprat larvae, black - proportion of sardine larvae; grey dots - larval sampling depths (modified according to Holtappels 2004)

The salinity profile was less pronounced as the temperature profile and showed only small variations along the sampling transect. The chlorophyll-*a* profile exhibited low values at

the surface and higher values in the deeper layers. In all profiles a water mass was observed near the coast with higher temperature and chlorophyll-*a* values and lower salinity compared to the adjacent water mass (Fig. VI.2).

Sprat larval abundance was low on the whole transect and did not change considerably between the stations (Fig. VI.2). Sardine larvae contributed highest abundances at station 514 with highest chlorophyll-*a* values. Further offshore in the stratified area of the TMF transect (station 521) sardine larvae were almost absent from the water column. While sprat larvae tended to stay in colder water, sardine showed a tendency for warmer water.

River Plume Front (RPF)

In Fig. VI.3 the hydrographical situation along the river plume front (RPF) is mapped from east to west.

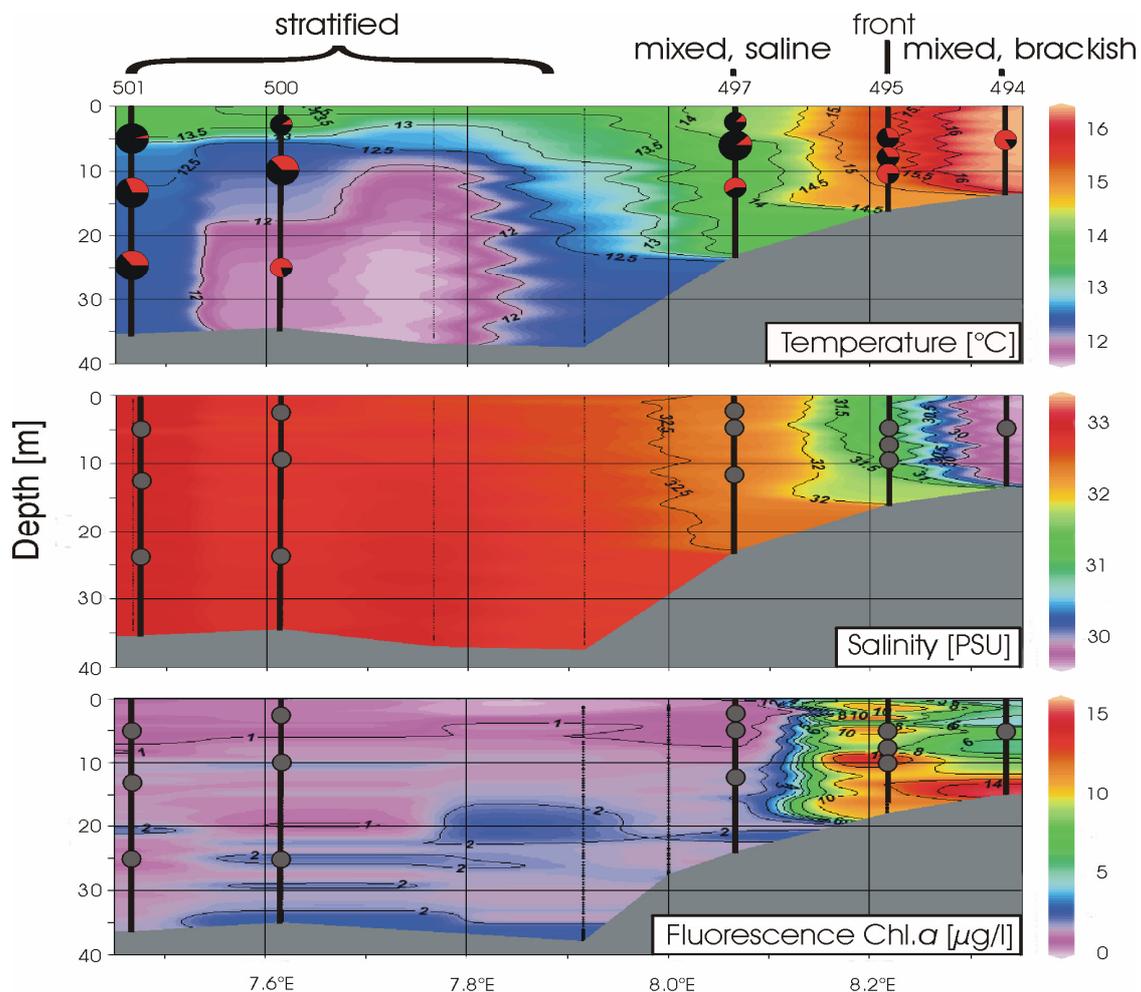


Fig. VI.3: Hydrography of the transect crossing the river plume front (RPF). Solid black lines - sample stations, dotted lines - additional CTD and Fluoroprobe stations; pie charts illustrate abundance and composition of fish larvae at the sampling depths, red - proportion of sprat larvae, black - proportion of sardine larvae; grey dots - larval sampling depths (modified according to Holtappels 2004)

The stations 500 and 501 belong not direct to the system of the RPF, but to a stratified area near the RPF. The river discharge was clearly visible because of its higher chlorophyll-*a* and temperature values as well as because of the lower salinity compared with the adjacent water mass. Further offshore temperature decreased and showed a stratification, while salinity increased. Chlorophyll-*a* values decrease rapidly between station 495 and 497 to about $1 \mu\text{g l}^{-1}$ chl-*a* in the water. While abundances of sardine larvae were much lower on the RPF transect than on the TMF transect, sprat larvae occurred in similar abundances. At station 494 sprat larvae abundance was higher than abundance of sardine. Further offshore sardine tended to stay in the upper, warmer water layer, while sprat larvae stayed rather deeper, in the colder water layer.

Zooplankton composition

On the TMF transect *Acartia* spp. and clausocalanoid nauplii dominate the copepod composition at all stations (Fig. VI.4). At station 514 copepod eggs show the highest abundance of the TMF front and dominate the zooplankton composition at this station.

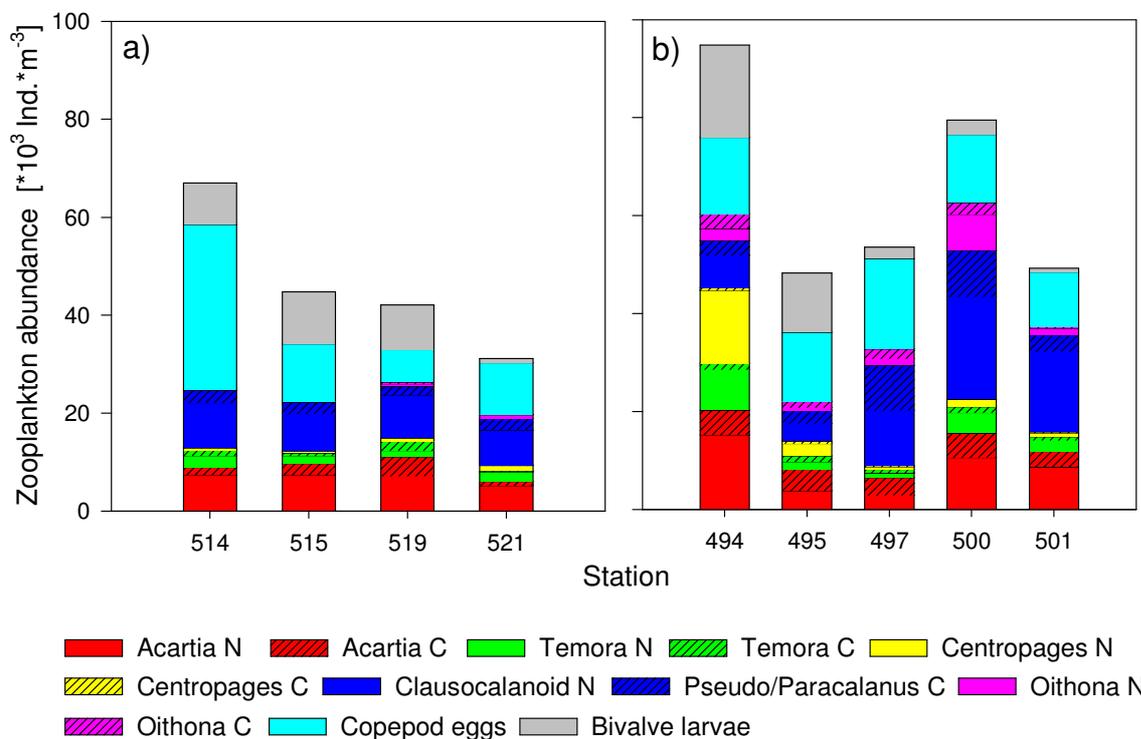


Fig. VI.4: Zooplankton composition at the stations of (a) TMF transect and (b) RPF transect. N - nauplii of the copepod species, C - all copepodite stages (C1-6) of the copepod species

On the RPF transect distinct changes were observed in the zooplankton abundance and composition. The abundances of copepod stages were higher on this transect than on the

TMF transect. While the share of clausocalanoid nauplii increased further offshore, the share of *Centropages* spp. nauplii decreased.

Abundance of both fish species was not correlated to the zooplankton abundance (Fig. VI.5), though on the TMF transect sardines abundance decreased with decreasing zooplankton abundance. However, at station 494 with the highest zooplankton abundance, sardines showed lowest abundance and sprat larvae were also found in low abundance.

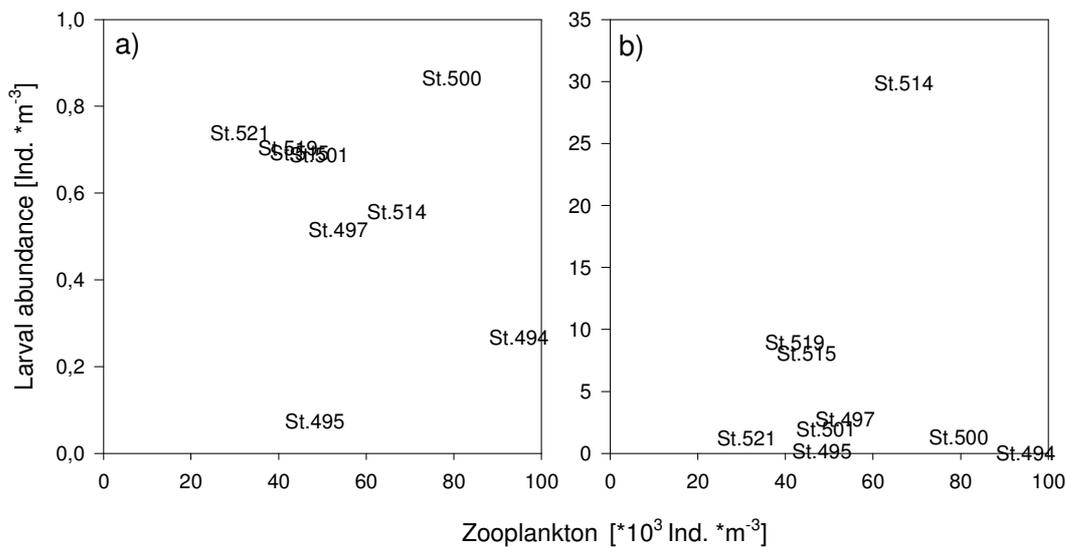


Fig. VI.5: Larval abundance in relation to zooplankton abundance. Stations are marked by their number. (a) sprat, (b) sardine

Gut fullness and feeding success

In total 270 sprat and 451 sardine larvae were investigated for diet composition along both transects in the North Sea (Tab. VI.1). Mean feeding success of both species was higher on the RPF transect. Mann & Whitney U-test showed a significant higher mean larval length for both larval species ($U = 5147.5$, $p < 0.0001$ for sprat larvae and $U = 18188.5$, $p < 0.005$ for sardine larvae) on the RPF than on the TMF. Further sprat larvae were on both transects significantly larger than sardine larvae ($U = 19287.0$, $p < 0.005$ on the TMF front and $U = 4441.0$, $p < 0.0001$ on the RPF).

Tab. VI.1: Sampling locations and basic larval data. N_e - Number of larvae examined, % N_L - Proportion of feeding larvae, m SL - mean standard length with standard deviation

Transect	Station	Water column	N_e		% N_L		m SL	
			Sprat	Sardine	Sprat	Sardine	Sprat	Sardine
TMF	514	Mixed	24	42	41.7	38.1	7.2 ± 2.0	7.2 ± 2.0
	515	Mixed	30	81	43.3	32.1	6.6 ± 2.2	6.0 ± 1.7
	519	Front	32	83	31.3	24.1	7.1 ± 2.0	6.8 ± 1.8
	521	Stratified	96	77	17.7	18.2	8.5 ± 3.4	7.0 ± 2.9
	Total			182	283	27.5	26.9	7.7 ± 2.9
RPF	494	Mixed, brackish	2	1	0	100.0	4.6 ± 1.6	5.3
	495	Front	5	16	80.0	50.0	11.1 ± 3.6	9.6 ± 2.3
	497	Mixed, saline	14	47	64.3	61.7	9.9 ± 3.7	8.5 ± 2.9
	500	Stratified	32	34	53.1	29.4	9.8 ± 3.4	7.7 ± 2.3
	501	Stratified	35	70	51.4	30.0	9.5 ± 3.6	6.3 ± 2.6
	Total			88	168	54.5	41.1	9.7 ± 3.6

Gut fullness of sprat and sardine in terms of numbers and weights peaked on the TMF transect at station 515 (Fig. VI.6).

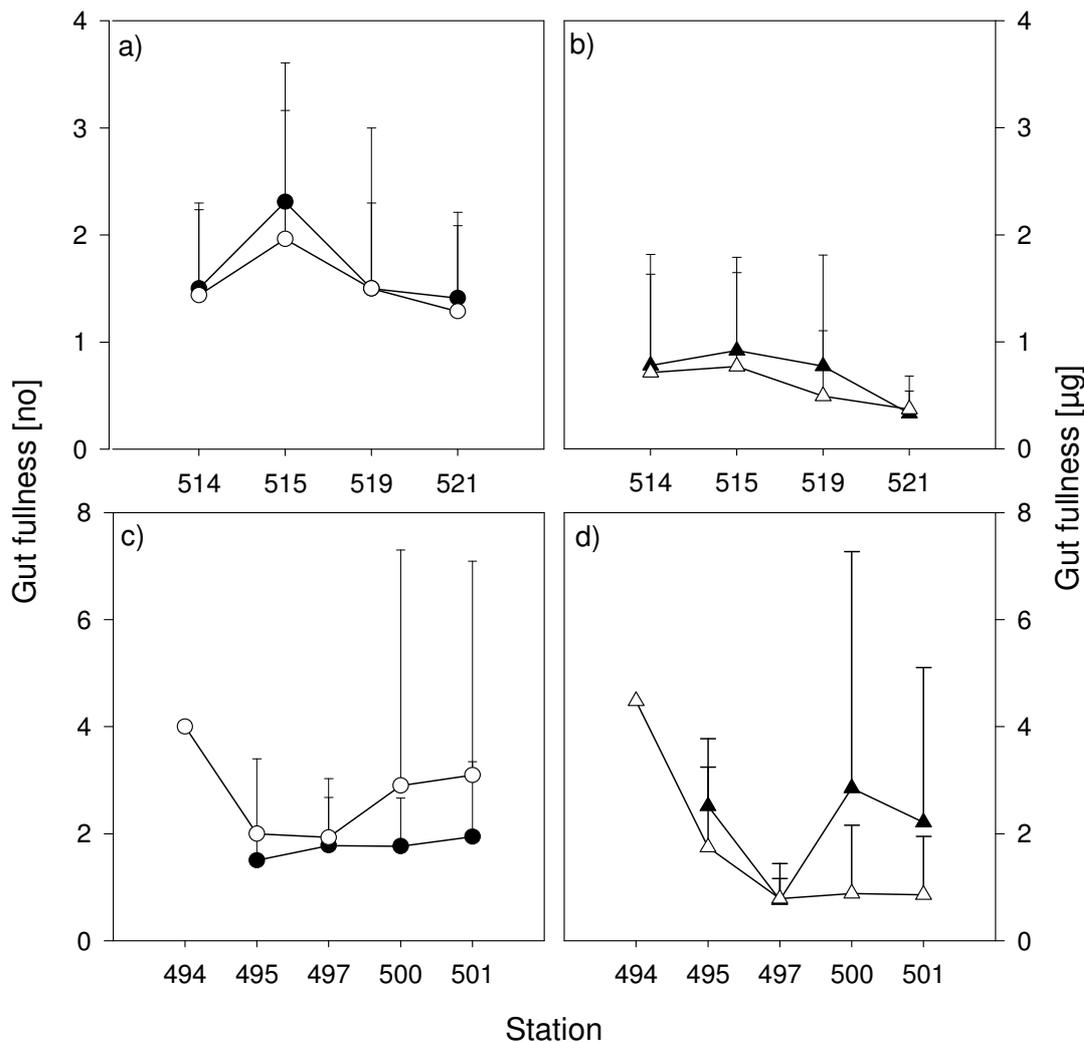


Fig. VI.6: Gut fullness of sprat (black dots and triangles) and sardine (white dots and triangles) larvae on the stations of (a, b) the TMF transect and of (c, d) the RPF transect

Lowest indices for gut fullness were found at station 521 for both fish species. On the RPF sardine larvae showed highest gut fullness in both indices at station 494, while sprat larvae exhibited higher gut fullness in terms of numbers at station 500 and 501 in terms of weight (Fig. VI.6).

However, Kruskal-Wallis rank sum test showed no significant differences in both indices of gut fullness between stations on the TMF and on the RPF transect, respectively, for both species (Tab. VI.2).

Tab. VI.2: Statistical values of the Kruskal-Wallis-Test to test the differences in gut fullness between the stations

		Numbers		Weight	
		H value	p	H value	p
TMF	Sprat	6.47	0.09	5.23	0.15
	Sardine	6.38	0.09	6.71	0.08
RPF	Sprat	0.11	0.99	2.63	0.45
	Sardine	3.84	0.43	4.30	0.30

Further Mann & Whitney U-test showed no significant differences in both indices of gut fullness between sprat and sardine neither on the TMF ($U = 1822.5$, $p = 0.70$ in terms of number and $U = 1895.5$, $p = 0.98$ in terms of weight) nor on the RPF ($U = 1494.0$, $p = 0.37$ in terms of number and $U = 1328.0$, $p = 0.07$ in term of weight). Even so Mann & Whitney U-test showed significant differences in gut fullness in terms of weight between TMF and RPF for both species ($U = 700.5$, $p < 0.0005$ for sprat larvae and $U = 1894.0$, $p < 0.005$ for sardine larvae). While Mann & Whitney U-test showed significant differences in gut fullness in terms of numbers for sardine larvae ($U = 2099.0$, $p < 0.5$), no significant differences were found in gut fullness in terms of numbers for sprat larvae ($U = 1117.5$, $p = 0.56$).

Gut fullness increased with sprat larval length (Tab. VI.3), even though the Kruskal-Wallis rank sum test showed no significant differences in gut fullness between sprat larval size classes ($H = 0.787$, $p = 0.67$). For the sardine larvae Mann & Whitney U-test showed also no significant differences between the size classes ($U = 1506.5$, $p = 0.5$).

Larval length class	Gut fullness
Sprat 3.5 – <8.5 mm	1.7 ± 1.0
Sprat 8.5 - <14.5 mm	1.8 ± 1.2
Sprat 14.5 - <18.5 mm	2.0 ± 1.2
Sardine 4.5 - <8.5 mm	2.1 ± 2.4
Sardine 8.5 - <14.5 mm	1.8 ± 1.2

Tab. VI.3: Gut fullness (in terms of numbers) of different larval size classes

Gut fullness of the sprat larvae was not correlated with the zooplankton abundance (Fig. VI.7). For sardine larvae a significant correlation was found (Fig. VI.7, $r^2 = 0.55$, $p < 0.05$). Though it has to be taken into account that the gut fullness at station 494 was based on one larva, only. However, when removing station 494 from the regression, the correlation becomes insignificant.

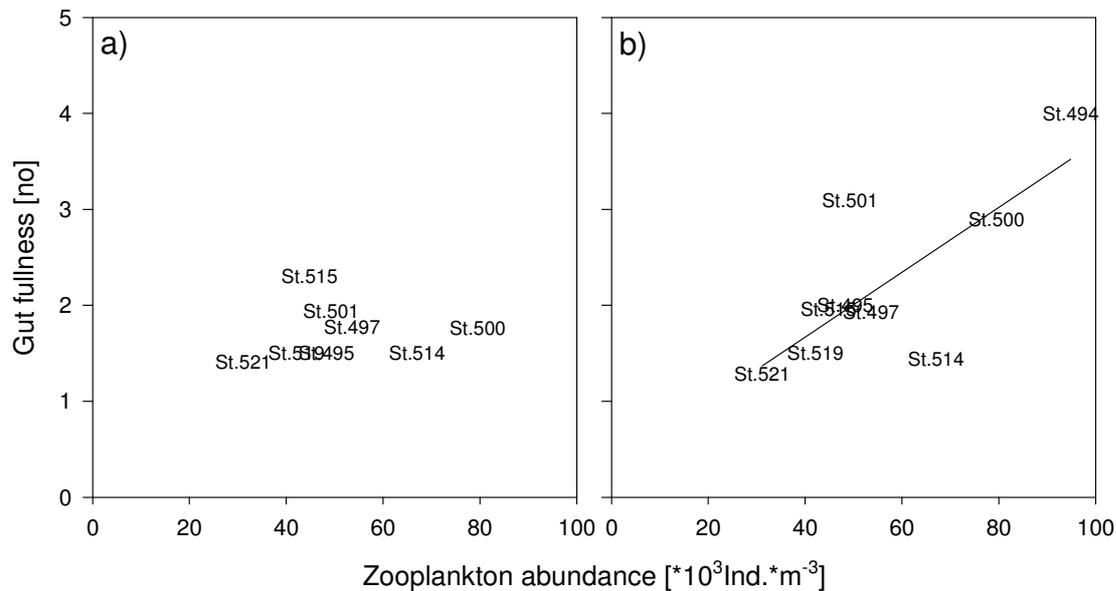


Fig. VI.7: Gut fullness of (a) sprat and (b) sardine in relation to zooplankton abundance. Stations are marked by their numbers.

General diet

Overall, clausocalanoid nauplii were the most important prey for both species in terms of numbers and weight followed by the group of unidentified copepods (Tab. VI.4). The relative large weight for the latter group indicated, that the proportion of copepodites and adult copepods was relative high in this group. *Acartia* spp., *Temora longicornis* and *Oithona* spp. made up similar shares in the diet composition of the sardine larvae and have the same order in terms of numbers as copepod eggs and bivalve larvae. While sardine larvae fed almost exclusively on nauplii, sprat larvae ingested a higher amount of copepodites and adult copepods (Tab. VI.4).

Tab. VI.4: Diet composition of sprat and sardine larvae. N - Numbers of prey types in the guts, %N - proportion of prey types in numbers, DW - Dry weight [μg] of prey types in the guts, %DW - proportion of prey types in weights

Prey type	Abbr.	Sprat				Sardine			
		N	%N	DW	%DW	N	%N	DW	%DW
<i>Acartia</i> spp.									
Nauplii	AN	8	4.7	2.1	1.5	21	7.2	2.5	4.8
C 1-3	A13	10	5.8	6.5	4.7	3	1.0	2.0	1.7
C 4-5	A45	1	0.6	1.6	1.1	0	0.0	0.0	0.0
C 6	A6	0	0.0	0.0	0.0	0	0.0	0.0	0.0
Total		19	11.1	10.2	7.3	24	8.2	4.5	6.5
<i>Temora longicornis</i>									
Nauplii	TN	15	8.8	5.9	4.3	19	6.6	7.4	6.5
C 1-3	T13	2	1.2	1.6	1.1	0	0.0	0.0	0.0
C 4-5	T45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C 6	T6	0	0.0	0.0	0.0	0	0.0	0.0	0.0
Total		17	10.0	7.5	5.4	19	6.6	7.4	6.5
Pseudo/Paracalanus spp.									
Clausocalanoid Nauplii	CLN	65	38.0	22.7	16.4	110	37.9	38.3	33.8
C 1-3	P13	2	1.2	4.6	3.3	0	0.0	0.0	0.0
C 4-5	P45	3	1.8	18.8	13.6	0	0.0	0.0	0.0
C 6	P6	2	1.2	18.6	13.5	0	0.0	0.0	0.0
Total		72	42.2	64.7	46.8	110	37.9	38.3	33.8
<i>Centropages</i> spp.									
Nauplii	CN	2	1.2	0.7	0.5	4	1.4	1.3	1.1
C 1-3	C13	1	0.6	0.8	0.6	0	0.0	0.0	0.0
C 4-5	C45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C 6	C6	0	0.0	0.0	0.0	0	0.0	0.0	0.0
Total		3	1.8	1.5	1.1	4	1.4	1.3	1.1
<i>Oithona</i> spp.									
Nauplii	ON	3	1.8	0.5	0.4	23	7.9	4.0	3.5
C 1-3	O13	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C 4-5	O45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C 6	O6	0	0.0	0.0	0.0	0	0.0	0.0	0.0
Total		3	1.8	0.5	0.4	23	7.9	4.0	3.5
Unidentified copepods	CS	37	21.6	48.5	35.1	56	19.3	29.3	25.8
Copepod eggs	CE	12	7.0	1.0	0.8	26	9.0	2.2	1.9
Bivalve larvae	BL	4	2.3	4.5	3.2	21	7.3	23.5	20.7
Unidentified microplankton	MP	3	1.8	<0.1	<0.1	5	1.7	<0.1	<0.1
Other plankton	OP	1	0.6	-	-	2	0.7	-	-

Diet along transects

High numbers of clausocalanoid nauplii were observed in the guts of both species at almost all stations (Fig. VI.8). *Temora longicornis* and copepod eggs could also take in a considerable share of the diet of sprat larvae. For sprat larvae a higher share of copepodites was found compared to the sardine larvae.

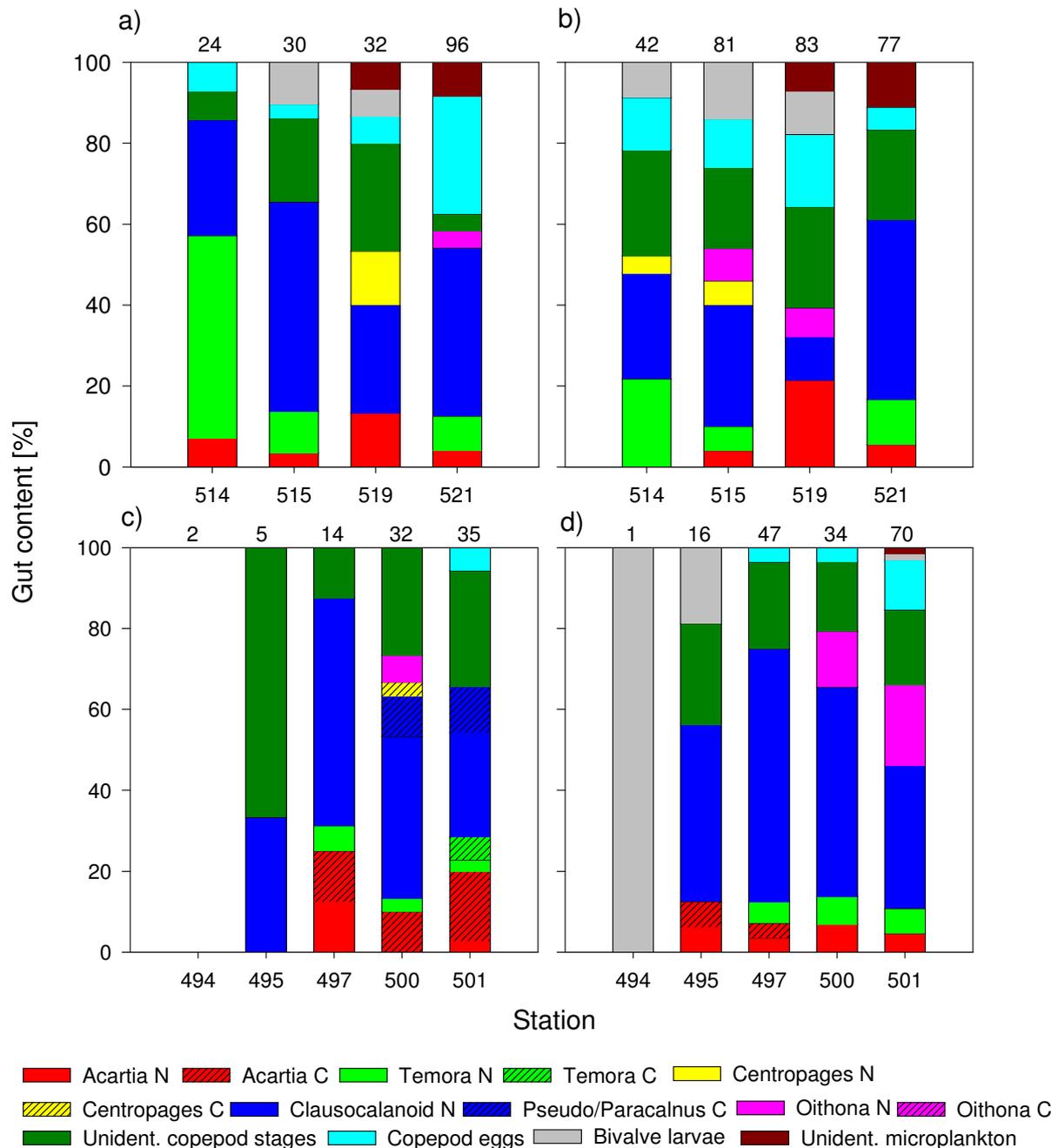


Fig. VI.8: Diet composition of (a) sprat larvae and (b) sardine larvae at the stations of the TMF transect and (c) sprat larvae and (d) sardine larvae at the stations of the RPF transect. Numbers above the bars display the number of examined larvae at the station

Comparing the diet of sprat larvae at the TMF a total χ^2 -value was derived that indicated a significant difference ($\chi^2 = 50.25$, $df = 24$, $p < 0.01$) between the stations. Among prey types, the main source of variation came from nauplii of *T. longicornis* ($\chi^2 = 15.18$) and among stations from station 514 ($\chi^2 = 15.00$). The diet of sprat larvae at the RPF transect showed no significant differences between the stations. The contingency table analysis of the difference between sardines' diet on stations at the TMF transect showed a significant total χ^2 -value ($\chi^2 = 39.49$, $df = 24$, $p < 0.05$). Most of the variation in prey types came from

nauplii of *Acartia* spp. ($\chi^2 = 9.79$), whereas for stations the highest variability was observed for station 519 ($\chi^2 = 15.26$). Comparing the diet of sardine larvae at the RPF (excluding station 494) a total χ^2 -value was derived that indicated a significant difference ($\chi^2 = 51.92$, $df = 24$, $p < 0.001$) between the stations as well. The highest variability was observed for station 495 ($\chi^2 = 23.48$) and among prey types the main source of variation came from bivalve larvae ($\chi^2 = 19.98$). The diet of sprat and sardine larvae at the TMF transect was not significantly different. Contrarily the contingency table analysis of the differences between sprat and sardine diet at the RPF transect showed a significant χ^2 -value ($\chi^2 = 44.59$, $df = 11$, $p < 0.001$).

Changes in food composition and feeding success with larval size

Clausocalanoid nauplii were by far the most important prey item in the guts of the smallest sprat larvae (3.5 - <8.5 mm) in terms of numbers and weight followed by unidentified copepod stages (Fig. VI.9).

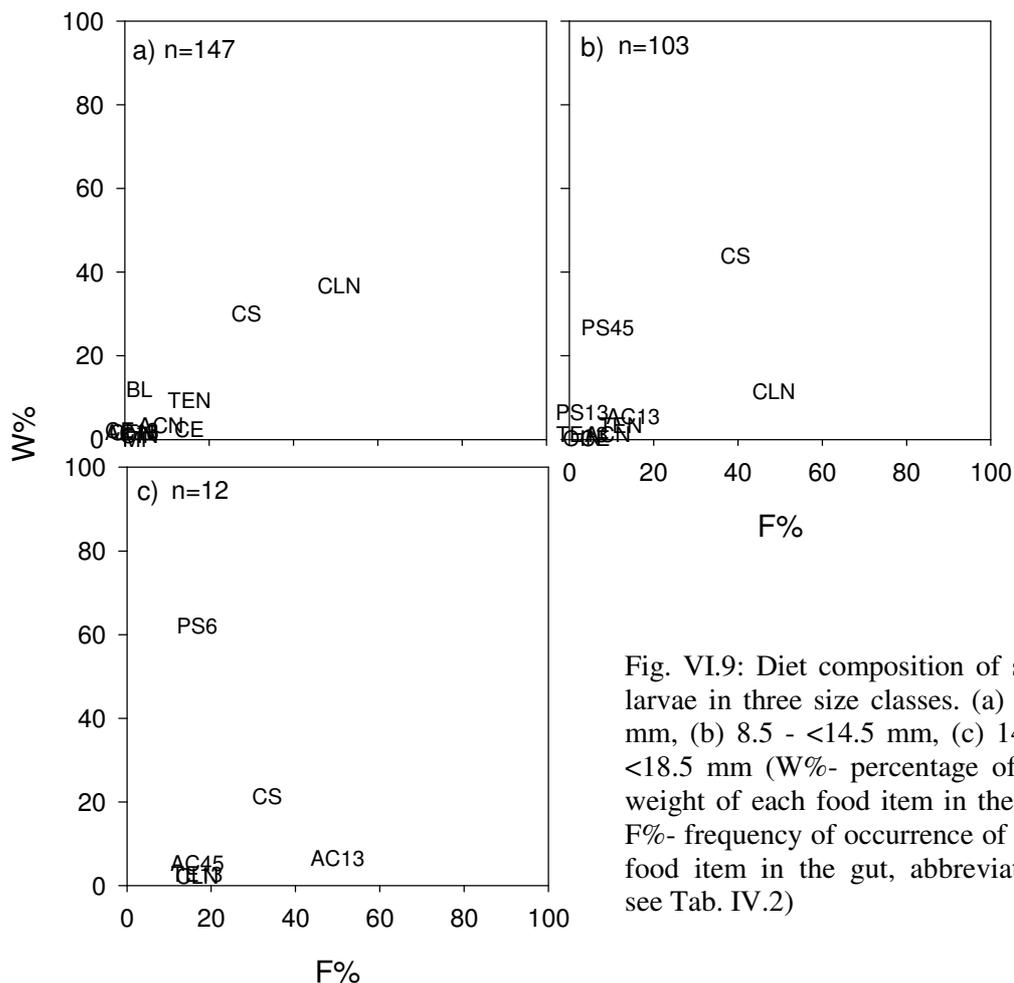


Fig. VI.9: Diet composition of sprat larvae in three size classes. (a) <8.5 mm, (b) 8.5 - <14.5 mm, (c) 14.5 - <18.5 mm (W%- percentage of dry weight of each food item in the gut, F%- frequency of occurrence of each food item in the gut, abbreviations see Tab. IV.2)

In the length class 8.5 - <14.5 mm again clausocalanoid nauplii were the most frequently occurring prey in the diet composition, while unidentified copepod stages dominated in weight. Pseudo/Paracalanus C4-5 was also important in terms of weights for sprat larvae diet in this length class, but occurred only in small numbers.

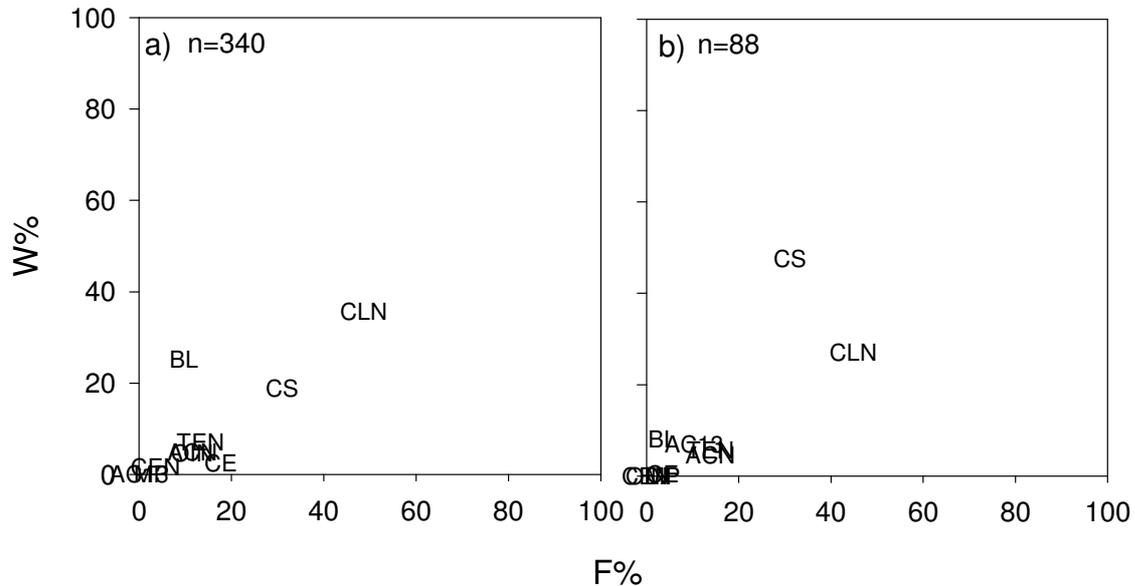


Fig. VI.10: Diet composition of sardine larvae in two size classes. (a) <8.5mm, (b) 8.5- <14.5mm (W% - percentage of dry weight of each food item in the gut, F% - frequency of occurrence of each food item in the gut, abbreviations see Tab. IV.2)

In the largest length class (14.5 - <18.5 mm) larvae fed mainly on *Acartia* spp. C1-3, but Pseudo/Paracalanus C6 dominated in terms of weight. With increasing larval size a slight trend to larger copepod stages was obvious.

In the diet composition of sardine larvae clausocalanoid and unidentified copepod stages were the most important prey types in both size classes (Fig. VI.10). Small sardine larvae preyed mostly on clausocalanoid nauplii. Unidentified copepod stages dominated the diet of the large sardine larvae in terms of weights.

Feeding success in 1mm size classes was evaluated for sprat and sardine larvae with data from both transects (Fig. VI.11). A slight trend to increasing feeding success with larvae length was observed for both species.

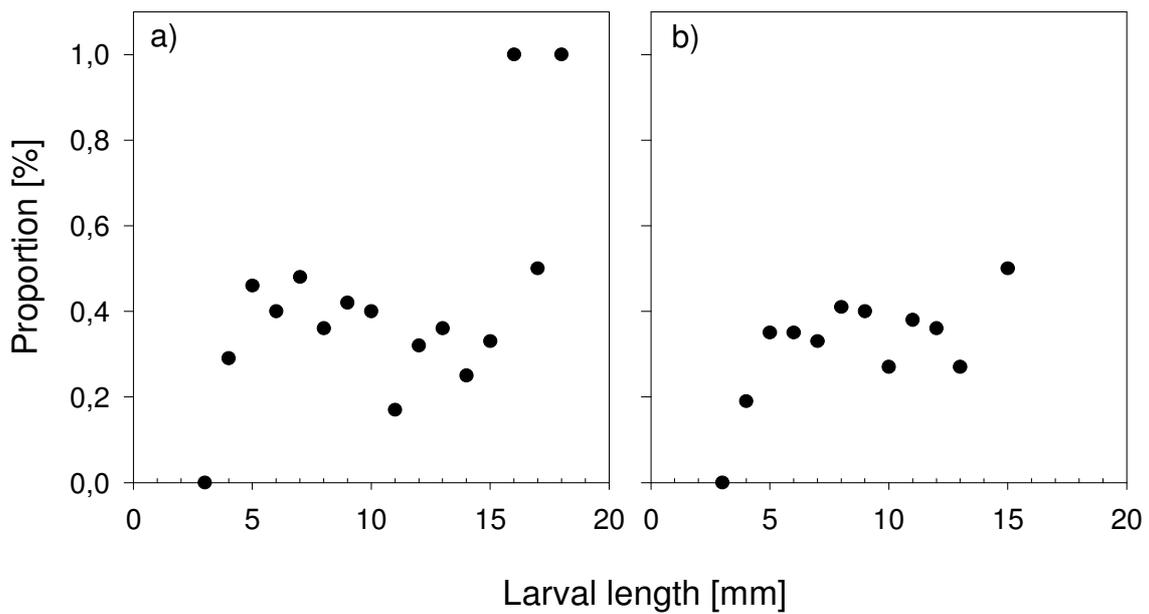


Fig. VI.11: Feeding success for sprat and sardine larvae in relation to the larval length (a) sprat ($r^2=0.32$, $p=0.22$), (b) sardine larvae ($r^2=0.40$, $p=0.28$)

Food overlap

Food overlap between the two fish species was calculated to investigate to which extent the species shared a number of abundant prey types. Values were moderate to high for all combinations of stations. A significant food overlap was found between sprat and sardine larvae at station 515 of the TMF and station 497 of the RPF (Tab. VI.5).

Tab. VI.5: Food overlap sprat vs. sardine between stations a) within the TMF transect and b) within the RFP transect. Significantly high values are in bold

		Sardine			
		514	515	519	521
Sprat	514	0.62	-	-	-
	515	-	0.74	-	-
	519	-	-	0.67	-
	521	-	-	-	0.72

		Sardine			
		495	497	500	501
Sprat	495	0.58	-	-	-
	497	-	0.81	-	-
	500	-	-	0.67	-
	501	-	-	-	0.56

Food overlap between different size classes was always moderate to high (Tab. VI.6). Significant high food overlap between sprat and sardine larvae of the <8.5 mm size class was observed on both transects (Tab. VI.6). On the RPF transect sprat larvae in the size class <8.5 mm showed significantly high overlap with class sardine larvae in the 8.5- <14.5 mm size class.

Tab. VI.6: Food overlap between species in different size classes. Significantly high values are in bold. (a) TMF transect, (b) RPF transect

a)

		Sardine	
		<8.5 mm	8.5 - <14.5 mm
Sprat	<8.5 mm	0.81	0.56
	8.5 - <14.5 mm	0.60	0.63

b)

		Sardine	
		<8.5 mm	8.5 - <14.5 mm
Sprat	<8.5 mm	0.78	0.77
	8.5 - <14.5 mm	0.68	0.69
	14.5 - <18.5 mm	0.37	0.42

Selectivity

Selectivity indices were calculated for different larval size classes and the different main prey types for both species (Fig. VI.12). Smaller sprat larvae (<14.5 mm) showed significantly positive selectivity values for clausocalanoid nauplii. The same was calculated for *Acartia* spp. and *T. longicornis* C1-3 by larvae of 8.5 – <14.5 mm size and for Pseudo/Paracalanus C6 by larvae of >14.5 mm. A change in selectivity feeding with increasing larval length was found from smaller to larger prey items.

Sardine larvae of both size classes favoured significantly clausocalanoid nauplii only. Consequently a change in selectivity feeding from smaller to larger prey items was not observed.

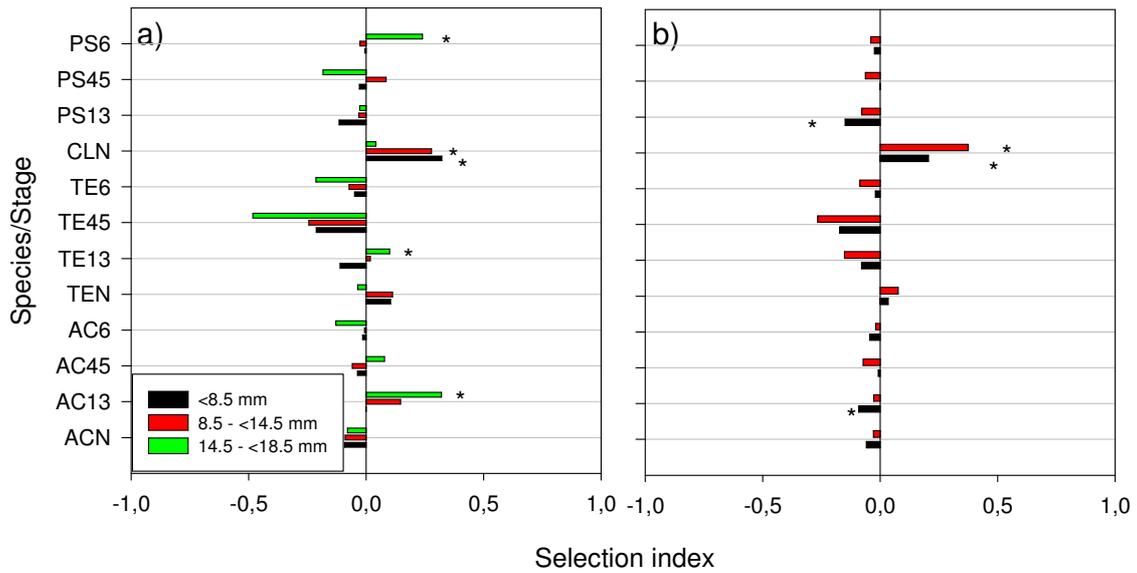


Fig. VI.12: Selective feeding of (a) sprat and (b) sardine larvae (Index C). (* indicates significant selective feeding at the 5% level, abbreviations see Tab. IV.2)

Prey-Predator relationship

Both species exhibited a variable relationship between prey size and predator size (Fig. VI.13).

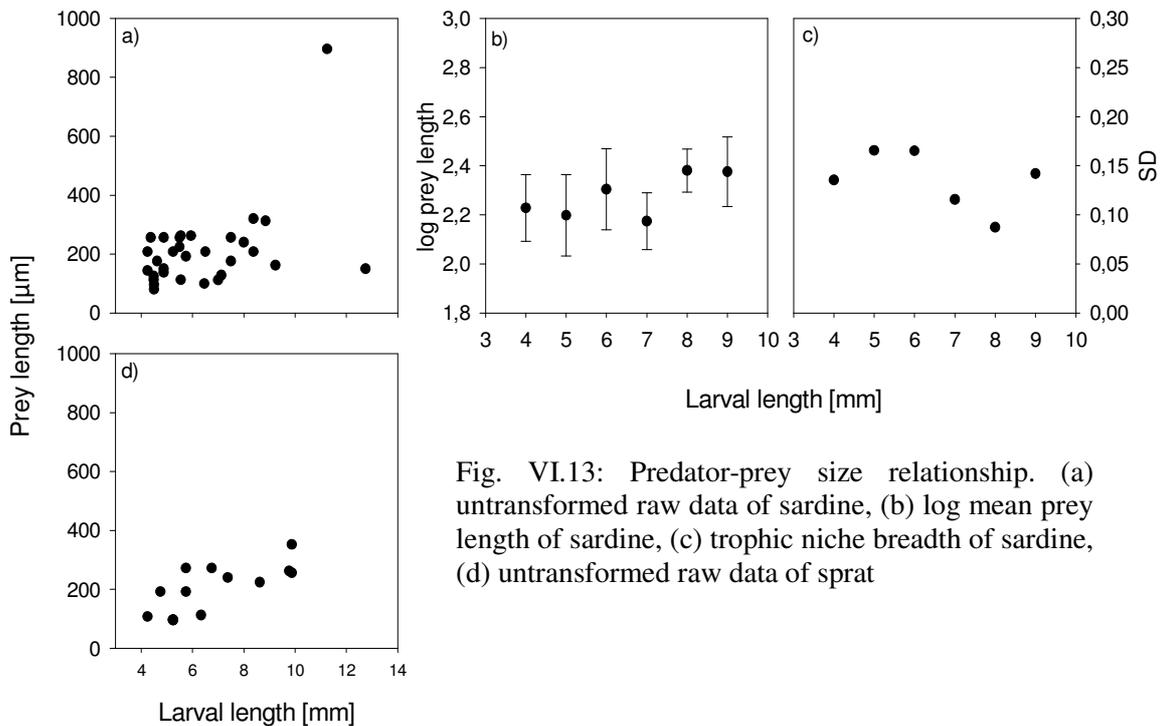


Fig. VI.13: Predator-prey size relationship. (a) untransformed raw data of sardine, (b) log mean prey length of sardine, (c) trophic niche breadth of sardine, (d) untransformed raw data of sprat

A slight increase in prey size with larval development even though not significant was observed for sprat larvae. The logarithmic mean size of prey showed a slight increase with sardine length, but was not significantly correlated with length ($p > 0.1$, Fig. VI.13.b). Niche breadth was independent of larval size, too, and did not change up to a larval length of 10 mm (Fig. VI.13.c). Inter-specific comparison of logarithmic mean size of prey and niche breadth was not possible due to the low sample number of prey size measurements from the guts of sprat larvae.

Discussion

A comprehensive study of feeding ecology of sprat and sardine larvae in the German Bight in relation to frontal systems was carried out. To this end zooplankton and larval distribution as well as larval diet composition and prey selectivity were studied.

Sardine larvae had not been observed for several decades in the German Bight. Some evidence exists that in the last years abundance of sardine and other predominately southern species increased in the northern North Sea (e.g. Beare et al. 2004). This correlates with positive temperature anomalies and southerly winds over The Netherlands (Corten & van de Kamp 1996, Beare et al. 2004). Already Aurich (1953) suggested that a shift in the distribution of the sardine was caused by changes in hydrography, due to changes in Sea surface temperature (SST) and currents.

Zooplankton and larval distribution in relation to the physical environment

Both frontal systems were located as expected parallel to the southern edge of the Elbe River glacial valley (TMF) and along the North Frisian Islands (RPF). Although only moderate changes in temperature and salinity were found on both transects, the distinct different water bodies of frontal systems could be distinguished. Several studies found a relationship between the physical environment in frontal systems and biological patterns (e.g. Munk 1993, Rissik & Suthers 1996). Due to anticipated high chlorophyll-*a* values and primary production in the tidal front (e.g. Pingree et al. 1975, 1978, Danovaro et al. 2000, Pedersen 1994), higher zooplankton density would be expected than in adjacent waters (e.g. le Fèvre 1986). In the present study higher chlorophyll-*a* values were not observed at the frontal station on the TMF transect, but at a station with a mixed water column. A storm occurred three days prior to sampling in the area of the TMF transect. This might

have caused a transport of chlorophyll-rich water, observed 12 km westward from the transect (Mohrholz pers. comm. Institut für Ostseeforschung, Rostock). This observed chlorophyll-*a* peak coincided with maximum zooplankton density on this transect. Probably the zooplankton was also transported in this chlorophyll-*a* rich water mass due to the storm. On the RPF transect maximum zooplankton density coincided with high chlorophyll-*a* values near the river discharge. The results are in accordance with earlier findings from Valenzuela et al. (1991) carried out close to the same observation site. Aggregation of zooplankton is assumed to cause higher abundances of predators in frontal systems (Morgan et al. 2005). Whereas the by far highest abundance of sardine larvae was found in the zooplankton peak on the TMF transect, sprat larvae showed lowest abundance at this station. On the RPF the high food supply near the coast did not coincide with high fish larval abundance. However, sardine larvae showed a tendency for warmer water with high salinity, while sprat larvae tended to stay in colder water with lower salinity.

Diet composition

In the present study copepod stages were the most important food for sprat and sardine larvae in the German Bight. This is confirming with previous studies of sprat and sardine larvae in different regions (e.g. Last 1980, Conway et al. 1991, 1994, Kurts & Matsuura 2001, Voss et al. 2003). In the present study clausocalanoid nauplii dominated the diet composition in terms of numbers and weights of both fish species. Further Pseudo/Paracalanus C6 and *Acartia* spp. copepodite stages were important prey items for larger sprat larvae (>14.5 mm). Conway (1991) described a strong increase of Pseudo/Paracalanus copepodites stages in the guts of sprat and sardine larvae >15.0 mm in the Irish Sea and near the coast of northern Spain, respectively. Feeding sardine larvae >15.0 mm were not found in the present study; consequently no conclusion of possible taxonomic changes in their diet composition could be done.

The trend in the fish larval diet was to a large degree explainable by selective feeding. Clausocalanoid nauplii dominated the gut contents of sprat and sardine larvae in the size class <14.5 mm and were positively selected by both species. Jiang & Paffenhöfer (2004) suggested that continuous swimmers like nauplii of *Paracalanus quasimodo* should be positively selected, because of their lower sensitivity to hydrodynamic signals and their infectivity in remotely detecting predators compared to nauplii that move in a “jump – sink

pattern” (Titelman & Kiørboe 2003, Jiang & Paffenhöfer 2004). This effect might have contributed to the observed high selection of clausocalanoid nauplii by both fish species. Sprat larvae in the larger size classes preyed on copepodites of *Acartia* spp. and *Temora longicornis* as well as for adult copepods of Pseudo/Paracalanus and showed a preference for these prey types as well. Checkley jr. (1982) assumed that adult *Pseudocalanus* spp. should be positively selected by herring larvae, because of their low ability to escape due to a small burst speed. Viitasalo et al. (2001) observed that adult *Pseudocalanus elongatus* shows a weak escape response and a small sensitivity to hydrodynamic signals. Both weak escape response and small sensitivity to signals should enhance their vulnerability to predation as well. Further Viitasalo et al. (2001) observed that *Acartia* spp. performs a weak escape jump with a small escape distance, which is positively related to attack success of a predator (e.g. Caparroy 2000). Both the weak alertness of *Pseudocalanus* spp. and the very weak escape response of both copepod species might have contributed to the observed selection of these prey types.

However, selectivity estimates can be biased if the zooplankton samples do not reflect the zooplankton abundances where the larvae had been feeding (Arrhenius 1996). Small scale patchiness of larvae and prey distribution in a turbulent environment makes it difficult to relate larval feeding to food environment (e.g. MacKenzie et al. 1990). In the present study larvae and zooplankton were sampled on the same stations, but nevertheless, selectivity indices are probably influenced by integrating all stations. This integration over a large number of samples was necessary due to in general low numbers of feeding larvae and ingested prey items.

Food overlap was calculated between both species with regard to the diet composition of different developmental stages. The results confirmed that sprat and sardine larvae share a wide range of prey types. Competition for food was possible, but gut fullness and feeding success were similar in both species as demonstrated in other areas (Kurts & Matsuura 2001, Conway et al. 1994, Voss et al. 2003). Further direct competition seemed to be avoided by different vertical distribution of the species. In the German Bight a marginal share of starved sprat and sardine larvae was found (Holtappels 2004) and growth rates indicated regular growth for both species (Huer 2004) at all stations. It is assumed that larval survival was not affected by food competition.

Predator and prey size related feeding

Capture success increases with larval development (Houde & Scheckter 1980), because older larvae exhibit a higher cruising speed, which has a positive effect on the frequency of larval prey encounter (Hunter 1981). Consequently several studies reported a positive relationship between larval size and number of ingested prey organisms for different fish species (Sabatés & Saiz 2000, Viñas & Santos 2000, Cass-Calay 2003). In the present study sprat larvae showed a slight, but not significant, increase in the number of prey items with increasing size. In contrast, smaller sardine larvae (<8.5 mm) exhibited higher gut fullness than medium sized sardine larvae (8.5 - <14.5 mm). However, this difference was not significant. This is confirming the results of Conway et al. (1991) who found a decrease in gut fullness from sardine larvae <10 mm to medium larvae of 10-15 mm, but an increase in gut fullness between medium larvae and larger larvae (>15 mm). However, significant higher gut fullness in terms of weight of both species on the RPF coincided with significant larger mean size of larvae on this transect.

Conway et al. (1994) found an increase in feeding success with larval development, but Kurtz & Matsuura (2001) observed a constant decline in proportion of feeding Brazilian sardine (*Sardinella brasiliensis*) larvae with larval size. In the present study a slight, but non-significant increase could be recognised for both species.

The results on diet composition and selectivity of sprat larvae showed that with increasing larval size the diet changes to larger copepod stages. From several previous studies (e.g. Last 1980, Conway et al. 1994, Sabatés & Saiz 2000 Voss et al. 2003) it is known that in several fish larvae the size of ingested prey increased throughout larval development, because they become able to cope with larger prey (Last 1980). For sprat larvae in the German Bight the same significant correlation was found. The lack of feeding sardine larvae >15 mm allowed no conclusion about the possible change in the diet composition of this size class, but the increased weight of unidentified copepodite stages between small and medium size classes indicates that the proportion of copepodites increased with larval length. This is in agreement with Conway (1994), who reported an increased share of copepodites in the guts of sardine >15 mm. Further Japanese sardine (*Sardinops melanostictus*) >20 mm is known to prefer adult copepods (Nakata 1988).

Niche breadth of sardine larvae exhibited no correlation with larval length in the present study. In the literature information about the relationships between niche breadth and larval size differ from a decrease to an increase of niche breadth with larval length (e.g. Pearre jr. 1986, Munk 1992, Reiss et al. 2005, Pepin and Penney 1997, Scharf et al. 2000). The

results of Chapter V show that when evaluating the relationship between larval size and niche breadth, the zooplankton composition in the field has to be considered. In the German Bight nauplii clearly dominated the zooplankton composition. It is assumed that small sardine larvae are limited by their low swimming ability and small mouth size to small food items i.e. nauplii and displayed consequently a small niche breadth. Larger larvae did not increase niche breadth as they were possibly restricted by the naupliar dominated food supply in the field. Despite low abundances of larger food items during this study, sprat and sardine larvae exhibited feeding incidences comparable to other studies (Kurts & Matsuura 2001, Conway et al. 1994, Voss et al. 2003) and similar growth (Huwer 2004) as well as good nutritional condition (Holtappels 2004). Consequently survival of fish larvae did not seem to be critically affected by the limited food supply. However, results of Chapter V indicate that medium-sized larvae may suffer from a restricted size-spectrum of zooplankton available when they grow.

Feeding in relation to frontal systems

Feeding theory predicts that growth and consequently survival should be improved in frontal systems due to higher food density (e.g. Buckley et al. 1987, Grimes & Finucane 1991, Johnson & Dropkin 1995, Kiørboe & Munk 1986). In the present study neither feeding success nor gut fullness of sprat larvae was related to the enhanced food supply in the environment. For sardine larvae a significant correlation between gut fullness and zooplankton abundance was found only, when including data of gut fullness at station 494 which was based on one larva. Gut fullness did not differ significantly between the stations in the present study. Conway et al. (1994) found a weak relationship between feeding success of sardine larvae and zooplankton abundance. Munk (1995) investigated foraging behaviour of larval cod (*Gadus morhua*) influenced by prey density and found a relationship between attack rate and prey density, but no significant correlation between prey abundance and the number of prey items in the larval guts. Sprat larvae are able to migrate between different layers of the water column in the frontal system of the German Bight to avoid offshore transport (Valenzuela et al. 1991) leading to different food supply during the day. However, gut fullness might be biased by sampling at different times of day, because sardine and sprat larvae exhibited distinct diurnal feeding patterns (Conway 1994, Kurtz & Matsuura 2001, Voss et al. 2003).

Huwer (2004) investigated growth of sprat and sardine larvae from the same survey as the present study and found a tendency (mostly non-significant) to higher growth rates for both species further offshore of the same TMF transect. Holtappels (2004) noted starving larvae only at mixed station 514 and measured highest nutritional conditions at the stratified station 521. Differences in nutritional condition between the stations differ greatly between the species and the length classes. However, growth rate and nutritional condition showed no correlation with the zooplankton abundance (Holtappels 2004, Huwer 2004).

It was not possible to find any compelling evidence that the environmental conditions in the German Bight significantly altered the feeding ecology, as other have observed (Coombs et al. 1991, Nakata et al. 1994). E.g. Grimes and Finucane (1991) found significant differences in feeding ecology of larval and juvenile fish in frontal waters of the Mississippi River plume front. This frontal system was described as a distinct and persistent system over a long time. Contrary to this area the German Bight is a physically dynamic system and fronts are highly variable and their location and strength can change within a few hours (Mohrholz pers. comm., Institut für Ostseeforschung, Rostock). This recorded high variability of the system and the probable migration of fish larvae between different water masses are likely the main reasons for the small differences in gut fullness, feeding success and diet composition. However, feeding ecology indicate favourable conditions for survival of both species in the whole German Bight.

VII Comparison of sprat (*Sprattus sprattus* L.) larval feeding ecology between the Baltic Sea and the North Sea

Introduction

While in Chapter V the seasonal and developmental changes in the larval feeding ecology were investigated in the Bornholm Basin, Baltic Sea, in Chapter VI the aim was to study the larval feeding ecology in relation to frontal systems in the German Bight, North Sea. In the present chapter the feeding ecology of larval sprat between the Bornholm Basin and the German Bight is compared as both systems show considerably environmental differences and plankton composition as well as population dynamics vary between these areas. Hence, different food supply is available for sprat larvae. In the Bornholm Basin *Acartia* spp. is the most common copepod in the water layers where sprat larvae mainly occur. Additionally *Temora longicornis* and *Centropages hamatus* are found in considerable numbers in the same depth. *Pseudocalanus* sp. is mainly observed in the deeper water layers (>30 m), where usually no feeding sprat larvae are found.

In the German Bight the *Pseudocalanus* spp. group is the predominant copepod group. Accessorily *Acartia* spp., *Centropages* spp. and *T. longicornis* are also found in high numbers (Fransz et al. 1991).

The differences in food supply between the study areas cause different larval feeding success, diet composition and selective feeding. In the present chapter differences in feeding ecology were evaluated with regard to the influence on larval survival and subsequent recruitment.

Methodical aspects

Gut content data from 596 sprat larvae collected in the Baltic in June 2002 (Chapter V) and from 270 larvae sampled in June 2003 in the North Sea (Chapter VI) were drawn on to compare sprat larvae feeding ecology. From the Baltic the data set from June 2002 was chosen as the larvae showed a comparable broad size range as in June 2003 in the North Sea. This is a prerequisite for a comparative trial on the feeding ecology of the same

species in two different environments. Horizontal differences were neglected and data integrated over all stations from one area.

The frequency distributions of larval sprat size were displayed by histograms. The Mann-Whitney U-test was performed to test differences in larval mean size between Baltic and North Sea sprat larvae.

The zooplankton prey field was described by simple bar charts. Copepod stages C1-6 of each species were pooled to reduce prey categories. In “Costello graphics” (Costello 1990) diet composition in four size classes (<5.5 mm, 5.5 - <10.5 mm, 10.5 - <15.5 mm, 15.5 - <20.5 mm) were compared between both areas. The abbreviations for the prey types in the guts were the same as used in the previous chapters (Tab. IV.2).

Selectivity values were calculated only for the main prey items i.e. the developmental stages of the copepods *Acartia* spp., *Temora longicornis*, *Centropages* spp. as well as Pseudo/Paracalanus. For the calculation the same larval size classes were used as for the “Costello graphics”.

The G-test of independence was applied to test the differences in feeding success between Baltic and North Sea sprat. The Kruskal-Wallis rank sum test was performed to test differences in gut fullness between larval size classes. Further the Mann-Whitney U-test was applied to test for differences in gut fullness between Baltic and North Sea sprat larvae. The prey- predator length relationship was investigated in a simple scatter chart.

Results and discussion

Larval size distribution

Sprat larvae of both areas comprised a similar size range, but their frequency distribution differed between the areas. Mean larval size of North Sea sprat was 8.4 ± 3.3 mm and significantly higher ($U = 49210.5$; $p < 0.00001$) than the mean size of 6.4 ± 2.5 mm in the Baltic Sea. Proportion of larvae >7.0 mm was considerable smaller in the Baltic Sea than in the North Sea (Fig. VII.1). In the Baltic Sea most larvae were between 4.0 to 6.0 mm in size and a pronounced peak of 5.0 mm larvae was observed. In the North Sea observed size frequency of 6.0 mm larvae was highest, but only a slight decrease in frequency of larger length classes was observed.

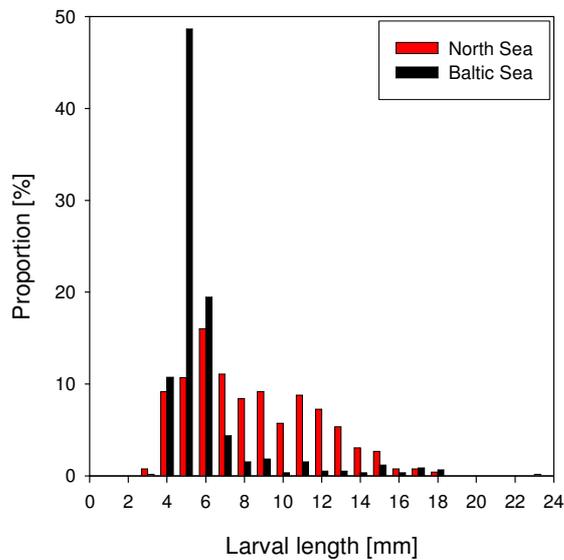


Fig. VII.1: Frequency distribution of larval size in the North Sea and the Baltic Sea

In the Baltic Sea the main spawning time was in April 2002 and the subsequent peak of sprat larval production was observed in May, whereas in the North Sea peak spawning generally occurs from May to July (Alheit 1987). Hence, a pronounced peak of small larvae (4 - 6 mm) would rather be expected in the North Sea than in the Baltic Sea. The higher frequency of larger larvae in the North Sea might be an indication of favourable conditions and lower mortality rates for early born larvae in this area. The very low frequency of larger larvae in the Baltic Sea might instead indicate a high mortality of first-feeding larvae. This theory is supported by observation that survivors in the Baltic Sea did not stem from the peak spawning in April but hatched in June 2002 (see also Chapter V, Baumann et al. 2005). Another reason for the very low frequency of larger larvae might be enhanced transport out of the studied area in the Bornholm Basin.

Due to these differences in the size distribution the diet composition, selectivity, feeding success and gut fullness were compared in different size classes between both areas.

Prey availability

While in the North Sea total zooplankton abundance in the field was considerable higher than in the Baltic Sea, the total biomass is higher in the Baltic Sea (Fig. VII.2). This effect is mainly caused by a higher proportion of copepodites and adult copepods as well as cladocerans in the Baltic Sea when compared to the North Sea.

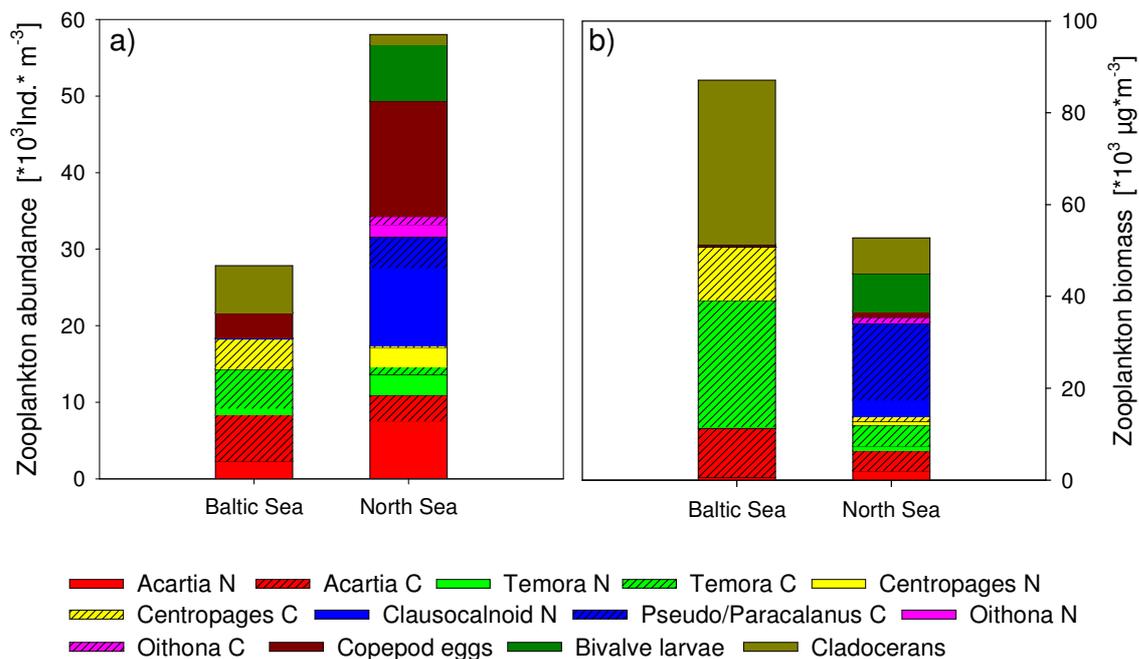


Fig. VII.2: Zooplankton composition at both study areas; Baltic: June 2002, North Sea: June 2003; (a) abundance and (b) biomass

In the Baltic Sea developmental stages of *Temora longicornis* and *Acartia* spp. as well as cladocerans were available in highest numbers, while copepod stages C1-6 of *T. longicornis* and cladocerans dominated the biomass. In the North Sea copepod eggs and developmental stages of *Acartia* spp. as well as Pseudo/Paracalanus (including clausocalanoid nauplii) were most important in the zooplankton composition in terms of numbers, while C1-6 of Pseudo/Paracalanus dominated in terms of weight.

For fish larvae it is important that sufficient numbers of suitable prey in an appropriate size are available in the field (Munk 1993). Hence, abundance of prey items in the field should be of major importance for larval feeding ecology. Especially for small larvae with poor swimming ability and a low attack success (Hunt von Herbing & Gallanger 2000, Houde & Scheckter 1980) it is likely important to encounter suitable prey quite often. The North Sea exhibited higher nauplii abundance, the preferred prey of small larvae (Chapter V + VI), hence, feeding conditions in particular for small larvae should be better in this area compared to the Baltic Sea. With larval development prey attack ability and therefore capture success increase (Houde & Scheckter 1980). Larger larvae exhibited a higher cruising speed and include larger copepodites and adult copepods in their diet. Consequently higher zooplankton biomass in the Baltic Sea might be better for larger larvae.

With increasing body size larvae become able to cope with larger prey (Last 1980) and consequently medium-sized larvae (10.5 - <15.5 mm) in the Baltic Sea larvae preyed upon copepod stages of *Acartia* spp. and *Centropages hamatus*, while in the North Sea Pseudo/Paracalanus was of importance in the gut contents. Nonetheless, larvae targeted smaller prey items also; hence nauplii (i.e. in the Baltic Sea *Acartia* spp. and in the North Sea clausocalanoid nauplii) were the most frequently occurring prey in the guts in both areas.

Gut contents of the largest larvae (15.5 – 20.5 mm) in the Baltic Sea contained mostly adult *Acartia* spp., while the gut content in the North Sea was dominated by copepodites of *Acartia* spp. However, including the developmental stages of Pseudo/Paracalanus resulted in a broader food spectrum being available for the sprat larvae in the North Sea. Similar to *T. longicornis* and *C. hamatus* in the Baltic Sea, Pseudo/Paracalanus formed an important part of the diet of the medium and large larvae in the North Sea. The predator-size dependent trend from nauplii to later stages of *Acartia* spp. in sprat larval diets was, to a large degree, explainable by selective feeding in both areas.

Small larvae (<10.5 mm) in the Baltic significantly selected nauplii of *Acartia* spp. and *T. longicornis*, while sprat larvae in the North Sea selected clausocalanoid nauplii (Fig. VII.4). The gut content of small larvae reflected different zooplankton compositions in terms of numbers in both areas. This supports the hypothesis that these small fish larvae cannot afford to actively choose amongst several simultaneously available prey items (Browman 2005). In larger length classes sprat larvae appear to be more selective. In both areas larger larvae selected significantly developmental stages of *Acartia* spp., though copepod stages of *T. longicornis* in the Baltic Sea and Pseudo/Paracalanus in the North Sea also were available in considerable numbers in the field.

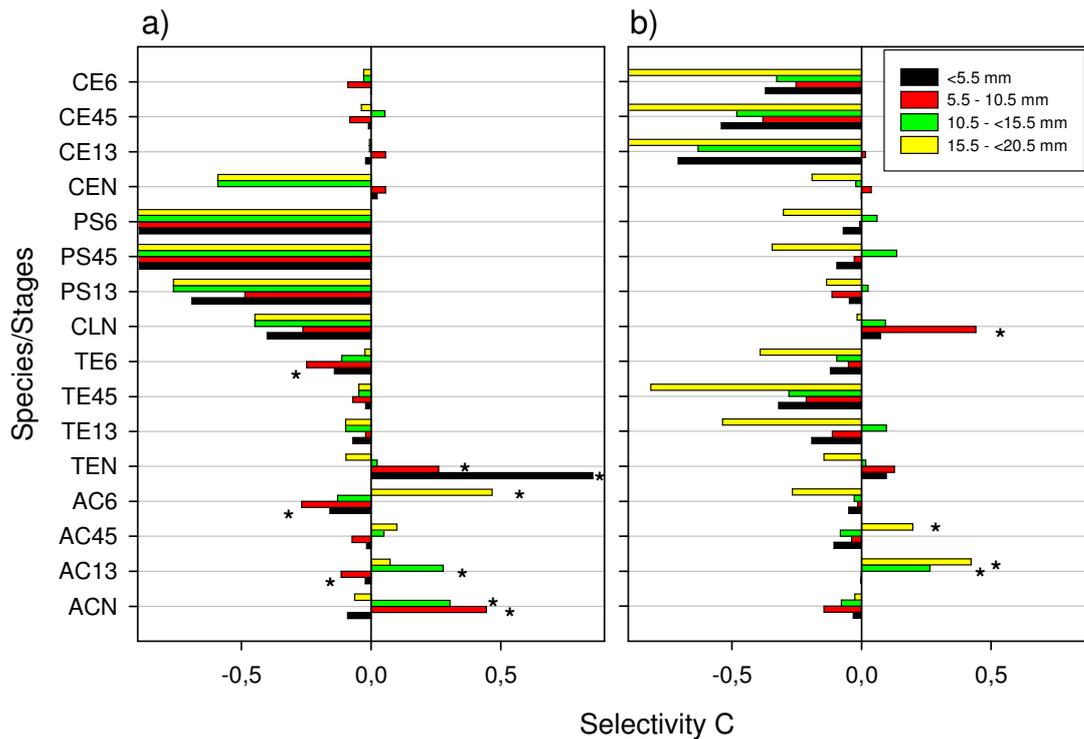


Fig. VII.4: Selective feeding of sprat larvae (Index C) (a) Baltic Sea; (b) North Sea. * indicates significant selective feeding at the 5% level

However, as mentioned in the previous chapters selectivity values can be biased by (i) integrating all samples of one area, (ii) the small sample size in the larger length classes or (iii) micro- to meso-scale variability not resolved by the sampling strategy. (For a detailed discussion see Chapters V+VI.)

Feeding success and gut fullness

Only in the Baltic Sea the share of feeding larvae was significantly related to larval size (Fig. VII.5; $r^2 = 0.42$; $p < 0.01$, see also Chapter V). In the North Sea shares of first-feeding larvae (4 and 5 mm) were significantly higher ($G = 85.86$ and $G = 20.39$, respectively, $p < 0.001$) than in the Baltic Sea. Feeding success of the larger length classes (>10 mm) was generally highly variable.

Results in Chapter V suggest that first-feeding sprat larvae are generally prone to the danger of food-limitation, due to their small feeding success. It was assumed that even if sprat larvae are born into the Baltic nauplii production peak, they most probably suffer from food-limitation. The result in the present chapter implies that high nauplii abundance in the field can increase feeding success of first-feeding larvae and consequently decrease

the danger of food-limitation. Kiørboe & Munk (1986) found an increase in attack rate with higher prey density for all larval length classes. Therefore the feeding success should increase with higher prey density at constant attack success of fish larvae. This effect may be more important for small larvae with very small attack ability (Houde & Scheckter 1980). Another reason for the higher feeding success of first - feeding larvae in the North Sea might be the low sensitivity to hydrodynamic signals of clausocalanoid nauplii (Titelman & Kiørboe 2003, Jiang & Paffenhöfer 2004). As mentioned in Chapter VI clausocalanoid nauplii are rather ineffective in remotely detecting predators (Titelman & Kiørboe 2003, Jiang & Paffenhöfer 2004) and might be easy to catch for first-feeding larvae leading to a higher feeding success in the North Sea. In the Baltic Sea clausocalanoid nauplii were available for sprat larvae only in very low numbers and larvae cannot benefit from this prey.

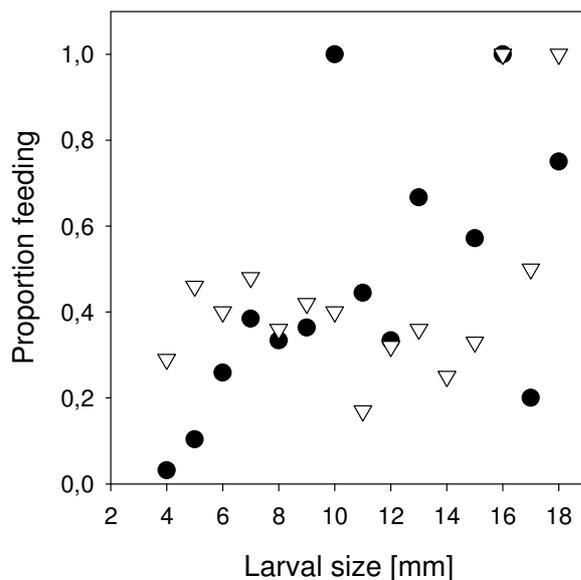


Fig. VII.5: Relationship between larval feeding success and larval length (black dots - larvae in the Baltic Sea, white triangles - larvae in the North Sea)

In the North Sea and in the Baltic Sea gut fullness in terms of numbers and weight was observed to increase with larval length and displayed a peak in the length group 15.5 - <20.5 mm in both areas (Fig. VII.6). Kruskal-Wallis rank sum test showed significant differences in gut fullness between predator sizes in the Baltic Sea for both indices ($H = 67.8$, $p < 0.001$ for prey numbers and $H = 78.1$, $p < 0.001$ for prey weight) and in the North Sea for gut fullness in terms of weight, only ($H = 5.9$, $p = 0.117$ for prey numbers and $H = 9.2$, $p < 0.05$ for prey weight).

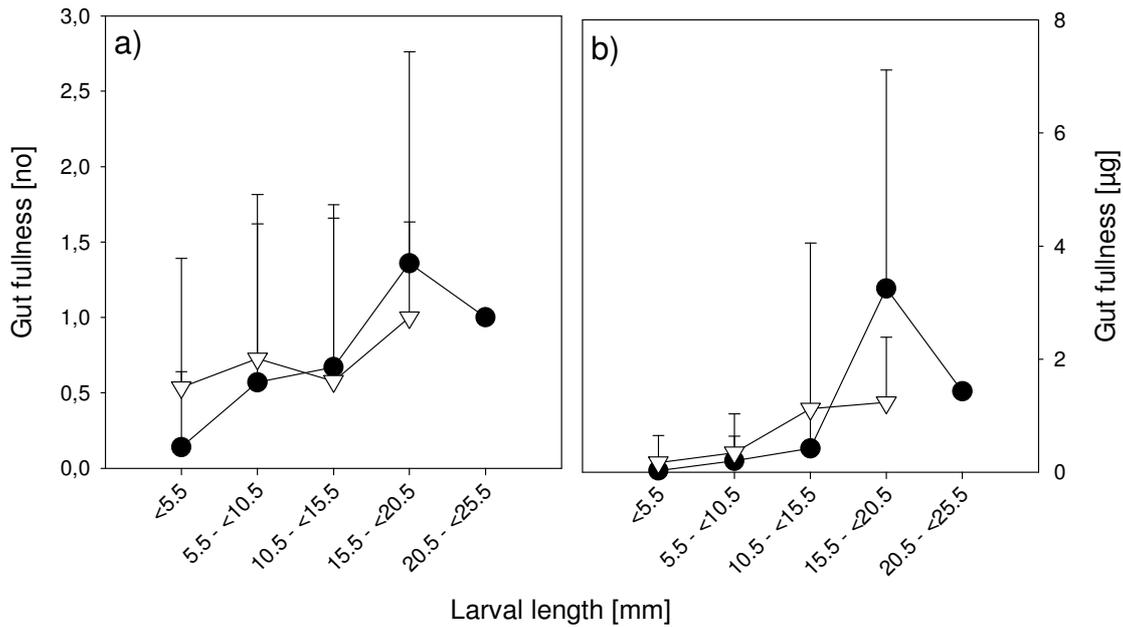


Fig. VII.6: Size-dependent development of larval gut fullness; (a) in numbers, (b) in weight. (black dots - gut fullness of sprat larvae in the Baltic Sea, white triangles - gut fullness of sprat larvae in the North Sea; error bars represent \pm s.d.)

Mann & Whitney U-test showed significant higher gut fullness in both indices for the smallest larvae (<5.5 mm) in the North Sea than in the Baltic Sea ($U = 6874.5$, $p < 0.001$ for prey numbers and $U = 6963.5$, $p < 0.005$ for prey weight). Further significant difference was found between the gut fullness in terms of weight between the 5.5 - <10.5 mm larvae in the North Sea and in the Baltic Sea ($U = 9190.5$, $p < 0.05$ for prey weight). In Chapter VI no correlation was found between gut fullness and zooplankton abundance in the field. But as stated earlier the German Bight is a highly variable ecosystem, which made it difficult to find relationship between feeding ecology and environmental conditions. Munk (1993) assumed that gut fullness is correlated with abundance of preferred prey types. The higher abundance of nauplii, the main food for first-feeding larvae, in the North Sea might have led to the observed differences in gut fullness. Further gut fullness of first-feeding larvae might be enhanced as well due to the above mentioned high abundance of easy catchable clausocalanoid nauplii in the North Sea. In both areas it was possible to measure prey size for a few prey items only, because most of them were damaged. The prey size of ingested prey increased with larval size in both areas (Fig. VII.7). While prey size was significantly correlated with larval size in the Baltic Sea ($r^2 = 0.90$; $p < 0.001$), it was not in the North Sea (see also Chapter VI). Ingested prey tended to be larger in size within the same larval length in the North Sea than in the Baltic.

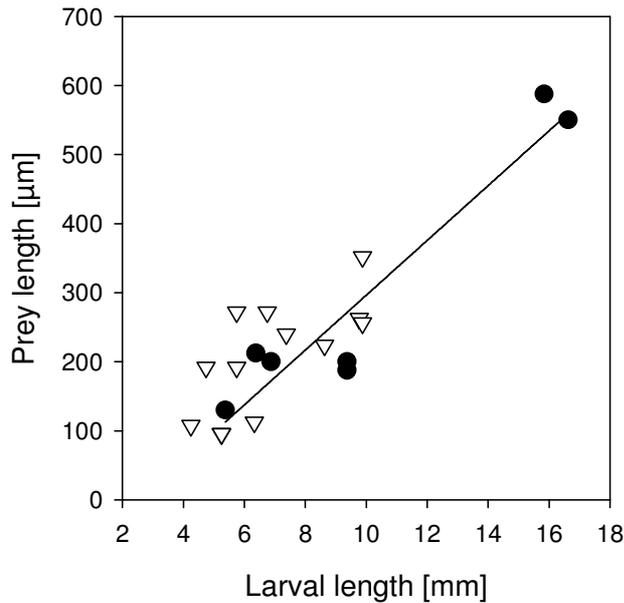


Fig. VII.7: Prey-predator-size relationship. (black dots - Baltic Sea, white triangles - North Sea, black line - regression of the Baltic Sea data)

Conclusion

Results of higher feeding success, gut fullness as well as prey-predator size relationship of first-feeding larvae in the North Sea imply that larval phase of first-feeding is not as critical as in the Baltic Sea. High numbers of clausocalanoid nauplii in the field may be an important factor for survival and subsequent recruitment of the sprat larvae in the North Sea.

In Chapter V it was assumed that for medium-sized larvae the change-over to bigger prey items is essential for survival and therefore availability of bigger prey items in the environment is critical. In the Baltic Sea higher numbers of copepodites and adult copepods were observed in the field than in the North Sea, hence in the North Sea medium-sized larvae might suffer from the restricted size-spectrum of the zooplankton available when they grow. Therefore this larval phase might be even more critical in the North Sea than in the Baltic Sea. However, despite low abundances of larger food items in June 2003, medium and large sprat larvae exhibited feeding incidences comparable to Baltic sprat. Further studies of larval growth (Huwer 2004) and nutritional condition (Holtappels 2004) found only a very small share of starving larvae in the same area. The probably higher turbulence in the North Sea might be responsible for comparable feeding success of these larvae in both areas, because turbulence can increase prey encounter rates and attack success (e.g. Rothschild & Osborn 1988, MacKenzie et al. 1994). Further the

average size of ingested prey is significantly positive related to turbulence (Dower et al. 1998, Reiss et al. 2002).

Finally, in both areas *Acartia* spp. is important for the nutrition of sprat larvae. As mentioned in Chapter V the temperature-induced increase of *Acartia* spp. in the Baltic Sea during the 1990s (Möllmann et al. 2000, 2003) may thus be a likely reason for the presently high recruitment level. In the North Sea Beaugrand & Ibanez (2004) found changes in the calanoid copepod composition and abundance due to climate induced changes in the hydrography since the late 1980s. The so called “warm - biological episodic event” (Edwards et al. 2002) induced favourable conditions for “shelf-sea species” as *Pseudocalanus* spp. and *Acartia* spp, although the latter one is reported to be a cold-temerated species. (Beaugrand et al. 2002). This increase in *Acartia* spp. and *Pseudocalanus* spp. in the North Sea may thus have a positive effect on the sprat larval survival and subsequent recruitment in the next years.

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IX Summary

Detailed knowledge of fish larval feeding ecology is necessary to understand the processes affecting the subsequent year-class-strength of the adult fish. The aim of this PhD-thesis was to study feeding ecology of larval sprat (*Sprattus sprattus* L.) in the Bornholm Basin (Central Baltic Sea) and in the German Bight (Southern North Sea). Further, the unexpected appearance of sardine (*Sardine pilchardus* W.) larvae in the German Bight offered the opportunity to investigate their feeding ecology beyond their known distribution and to compare feeding ecology of sprat and sardine larvae.

In the Bornholm Basin (Chapter V) seasonally-resolved larval abundance and gut content data as well as zooplankton data were collected with the goal to identify mechanisms leading to variability in larval survival. The results show sprat larvae to feed progressively on larger food items as they grow during the season, depending on the size and composition of available prey. Small larvae preyed mainly upon nauplii of the copepods *Acartia* spp., *Temora longicornis* and *Centropages hamatus*, whereas larger larvae consumed mainly copepodite stages of *Acartia* spp. and cladocerans. Trends in sprat larval diets were, to a large degree, explained by selective feeding. Feeding success and gut fullness increased linearly with body size. The trophic niche breadth increased with body size as well. However, niche breadth decreased markedly at predator sizes > 16 mm due to a restricted size spectrum of prey available for larger sprat larvae. This highlights the need to consider the structure of the actual food supply in further studies when predator size to niche breadth relationships is evaluated. Moreover, the results suggest that first-feeding larvae of Baltic sprat are always food-limited, while larger larvae are not. It was hypothesised that the medium-sized sprat larvae in the Baltic Sea are the life-stage which has the potential to cause most of the inter-annual variability in sprat larval survival, dependent on a match/mismatch between larval production and the timing with the planktonic cycle.

In the German Bight (Chapter VI), the influence of frontal systems on the feeding ecology of sprat and sardine larvae was investigated. Frontal zones often provide high food availability for fish larvae and therefore survival of larvae might be enhanced there. Identification of feeding parameters related to the physical environment is necessary to evaluate the effect of frontal systems on survival and recruitment of fish larvae. In the German Bight sprat and sardine larvae were sampled on two transects crossing a tidal mixing front (TMF) and a river plume front (RPF). The amplitude of food overlap between

sprat and sardine larvae was investigated to evaluate mechanisms which avoid possible food competition.

The results show that the abundance of both fish species was not correlated to zooplankton abundance, but depended more on the physical conditions at the stations. While sardine dominated in waters with higher temperatures and salinities, sprat was predominantly found in colder and less saline water bodies. On the RPF transect, both larval species showed a larger mean length and also a higher mean feeding success than on the TMF transect. Clausocalanoid nauplii dominated the gut contents of small sprat and sardine larvae and were positively selected by both species. Sprat larvae in the larger size classes preyed on copepodites of *Acartia* spp. and *Temora longicornis* as well as on adults of Pseudo/Paracalanus and also showed a preference for these prey types. The results confirmed that sprat and sardine larvae share a wide range of prey types. This indicates food competition, however, gut fullness and feeding success were similar in both species as was demonstrated in other areas. The mean size of prey as well as trophic niche breadth did not change with length of sardine larvae. It is assumed that small sardine larvae, as observed for sprat larvae (see Chapter V), are limited by their low swimming ability and small mouth size to small food items, predominantly nauplii, and consequently displayed a small niche breadth. Larger sardine larvae did not increase their niche breadth as they were possibly restricted by the naupliar dominated food supply in the field. In the present study neither feeding success nor gut fullness of sprat larvae was related to the enhanced food supply in the environment. For sardine larvae a significant correlation between gut fullness and zooplankton abundance was only found, when data at station 494 based on one larva were included. Furthermore, it was not possible to find any significant relationship between the environmental conditions in the German Bight and the feeding ecology. It is hypothesised that the physical variability in the German Bight is too high to find clear relationships between larval feeding ecology and hydrographical environment with the effort of this study.

The feeding ecology of larval sprat was compared between the Bornholm Basin and the German Bight (Chapter VII) as both areas vary considerably in their hydrographical conditions. For the comparison, gut content data from the Baltic in June 2002 (Chapter V) and data from North Sea in June 2003 (Chapter VI) were used.

Feeding success and gut fullness of first-feeding larvae were higher in the North Sea than in the Baltic Sea, while feeding success as well as gut fullness of the larger length classes differed not significantly between both areas. It is assumed that first-feeding larvae were

able to catch clausocalanoid nauplii easier than other nauplii, and that a high abundance of the former might be responsible for the observed higher feeding success and gut fullness of sprat larvae in the North Sea. These results combined with the results of the predator-prey size relationship of first-feeding larvae in the North Sea imply that this larval phase is not as critical here as it is in the Baltic Sea. Lower abundances of copepodites and adult copepods in the North Sea indicate that medium-sized larvae might suffer from the restricted size-spectrum of the zooplankton available for them during their growth. Therefore, this larval phase might be more critical in the North Sea than in the Baltic Sea.

X Zusammenfassung

Detaillierte Kenntnisse über die Nahrungsökologie von Fischlarven sind notwendig, um die Prozesse, die die folgende Jahresklassenstärke der erwachsenen Fische bestimmen, zu verstehen. Ziel dieser Doktorarbeit war es, die Nahrungsökologie der Sprottlarven (*Sprattus sprattus* L.) im Bornholm Becken (zentrale Ostsee) und in der Deutschen Bucht (südliche Nordsee) zu untersuchen. Des Weiteren war es durch das unerwartete Auftreten von Sardinenlarven (*Sardina pilchardus* W.) in der Deutschen Bucht möglich, deren Nahrungsökologie abseits ihrer bekannten Verteilung zu untersuchen und mit der Sprotte zu vergleichen.

Im Bornholm Becken (Kapitel V) sind zeitlich aufgelöste Daten über Larvendichten, den Darmfüllungsgrad der Larven sowie über Zooplanktondichten und Zusammensetzung aufgenommen worden mit dem Ziel die Mechanismen zu identifizieren, die zu einer Variabilität in dem Überleben der Larven führen. Die Ergebnisse zeigen, dass Sprottlarven im Verlauf des saisonalen Wachstums kontinuierlich größere Nahrungspartikel fraßen, in Abhängigkeit von der Größe und der Zusammensetzung der vorhandenen Beute. Kleine Larven fraßen hauptsächlich Nauplien von *Acartia* spp. *Temora longicornis* und *Centropages hamatus*, wohingegen größere Larven hauptsächlich Copepoditstadien von *Acartia* spp. und Cladoceren gefressen haben. Die Änderung in der Nahrung der Sprottlarven kann durch ein großes Maß an selektivem Fraß erklärt werden. Es zeigte sich, dass der Anteil fressender Larven und der Grad der Darmfüllung linear mit der Körpergröße stieg. Ebenso stieg die trophische Nischenbreite mit der Körpergröße. Allerdings sinkt letztere merklich mit einer Größe der Räuber > 16 mm durch ein begrenztes Größenspektrum, der für die Sprottlarven verfügbaren Beute. Deswegen ist es bei zukünftigen Untersuchungen wichtig, die Struktur des aktuellen Nahrungsangebotes zu beachten, wenn das Verhältnis der Größe des Räubers zu seiner Nischenbreite beurteilt werden soll. Ferner deuteten die Ergebnisse darauf hin, dass Sprottlarven im ersten Fressstadium in der Ostsee immer Futter limitiert sind, während größere Larven es nicht sind. Es wurde die Hypothese aufgestellt, dass Larven mit einer mittleren Größe in der Ostsee jenes Lebensstadium darstellen, dass das größte Potential hat, die jährliche Schwankungen im Überleben der Sprottlarven zu verursachen und dieses von einer Übereinstimmung zwischen Larvenproduktion und dem Status des Planktonzyklus abhängt.

In der Deutschen Bucht (Kapitel VI) wurde der Einfluss von Frontsystemen auf die Nahrungsökologie von Sprott- und Sardinenlarven untersucht. Frontbereiche bieten oft hohe Nahrungsverfügbarkeit für Fischlarven und daher könnte es dort zu einem erhöhten Überleben der Larven kommen. Die Identifikation von Fraßparametern in Beziehung zur physikalischen Umwelt ist notwendig um den Effekt von Frontsystemen auf das Überleben und die Rekrutierung von Fischlarven zu beurteilen. In der Deutschen Bucht wurden Sprott- und Sardinenlarven auf zwei Transekten, die jeweils eine Tidenfront (TF) und eine Flusswasserfront (FWF) kreuzten, gesammelt. Es wurde die Größe der Überschneidung des Nahrungsspektrums zwischen Sprotte und Sardine untersucht, um die Mechanismen zu beurteilen, die zu einer Vermeidung von möglicher Nahrungskonkurrenz führen.

Die Ergebnisse zeigten, dass die Dichte beider Fischarten nicht mit der Zooplanktondichte korreliert war, sondern stärker von den physikalischen Gegebenheiten an den Stationen abhing. Während Sardinen in Wasserkörpern mit höherer Temperatur und Salinität dominierten, wurde Sprotten vorherrschend in kälteren und salzärmeren Wasserkörpern gefunden. Auf der FWF war sowohl die mittlere Länge beider Larvenarten größer als auf der TF, als auch der Anteil fressender Sprotten. Clausocalanoide Nauplien dominierten den Darminhalt von kleinen Sprott- und Sardinenlarven und wurden von beiden Arten positiv selektiert. Sprottlarven in der größeren Längensklasse fraßen sowohl Copepodite von *Acartia* spp. und *Temora longicornis* als auch ausgewachsene Copepoden von Pseudo/Paracalanus und zeigten auch eine Präferenz für diese Beutetiere. Die Ergebnisse bestätigten, dass sich das Beutespektrum von Sprott- und Sardinenlarven stark überschneidet. Dies lässt auf eine Konkurrenz um Nahrung schließen, jedoch waren der Darmfüllungsgrad und der Anteil fressender Larven bei beiden Arten ähnlich hoch wie es für andere Regionen beschrieben worden ist. Die mittlere Größe der Beute veränderte sich nicht mit der Länge der Sardinenlarven, das gleiche gilt für die trophische Nischenbreite. Es wird vermutet, dass Sardinenlarven durch ihre eingeschränkte Schwimffähigkeit und ihren kleinen Maulgröße, ähnlich wie Sprottlarven (Kapitel V), auf kleine Nahrungspartikel vorwiegend Nauplien beschränkt sind und deswegen eine kleine trophische Nischenbreite aufweisen. Größere Sardinenlarven erhöhen ihre trophische Nischenbreite nicht, weil sie möglicherweise durch das Nauplien dominierte Nahrungsangebot eingeschränkt waren. In der vorliegenden Studie stand weder der Anteil fressender Larven noch der Darmfüllungsgrad der Sprottlarven in Beziehung zu dem erhöhten Nahrungsangebot. Für Sardinenlarven fand sich nur eine signifikante Korrelation zwischen dem Darmfüllungsgrad und der Zooplanktondichte, wenn die Daten der Darmfüllung auf

Station 494, die nur auf einer Larve basierten, miteinbezogen wurden. Darüber hinaus ließ sich kein signifikanter Zusammenhang zwischen den Umweltbedingungen in der Deutschen Bucht und der Nahrungsökologie der Fischlarven finden. Es wurde die Hypothese aufgestellt, dass die physikalische Variabilität in der Deutschen Bucht zu hoch ist, um mit Untersuchungen in diesem Umfang klare Beziehungen zwischen der Nahrungsökologie der Larven und der hydrographischen Umwelt aufzudecken.

Die Nahrungsökologie der Sprottlarven im Bornholmbecken wurde mit der Nahrungsökologie der Sprottlarven in der Deutschen Bucht verglichen (Kapitel VII), zwei Seegebiete, die sich deutlich in ihren hydrografischen Konditionen unterscheiden. Für den Vergleich wurden die Darminhalte der Larven aus der Ostsee im Juni 2002 und aus der Nordsee im Juni 2003 benutzt. In der Nordsee war der Anteil der fressenden Larven und der Darmfüllungsgrad bei den Larven im ersten Fressstadium größer als in der Ostsee, wohingegen größere Larven keinen signifikanten Unterschied im Anteil fressender Larven und im Darmfüllungsgrad aufweisen. Es wurde vermutet, dass clausocalanoide Nauplien für Larven im ersten Fressstadium leichter zu fangen sind als andere Nauplien und dass deren hohe Dichte in der Nordsee möglicherweise zu einem höheren Anteil an fressenden Larven und zu einer höheren Darmfüllungsgrad führte. Diese Ergebnisse sowie die Ergebnisse aus der Räuber-Beute-Größenbeziehung implizierten, dass das erste Fressstadium für die Sprotte in der Nordsee nicht so kritisch ist wie für die Sprotten in der Ostsee. Die geringeren Anzahlen von Copepoditen und erwachsenen Copepoden in der Nordsee ließ vermuten, dass Larven mit einer mittleren Größe in der Nordsee gegebenenfalls am eingeschränkten Größenspektrum des verfügbaren Zooplanktons leiden, wenn sie wachsen. Daher war dieses Larven-Stadium eventuell kritischer in der Nordsee als in der Ostsee.

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