

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

OCEANOLOGIA, 51 (1), 2009.
pp. 117–138.

© 2009, by Institute of
Oceanology PAS.

KEYWORDS

Food competition
Small pelagics
Habitat preference
Co-existence
Food overlap

RÜDIGER VOSS^{1,*}
MIRIAM DICKMANN²
JÖRN O. SCHMIDT³

¹ Sustainable Fishery, Department of Economics,
University of Kiel,
Wilhelm-Seelig Platz 1, D–24118 Kiel, Germany;
voss@economics.uni-kiel.de

*corresponding author

² Baltic Sea Research Institute Warnemünde,
Seestrasse 15, D–18119 Warnemünde, Germany

³ Leibniz Institute of Marine Sciences,
University of Kiel,
Düsternbrooker Weg 20, D–24105 Kiel, Germany

Received 25 August 2008, revised 9 January 2009, accepted 13 January 2009.

Abstract

The abundance of the sardine in the North Sea suddenly increased after 1995. Since 2002, the sardine has been spawning regularly in the German Bight, and all its life stages can be found in the area. The larval feeding ecology of two small pelagic clupeiform species with very similar life histories was investigated, the particular aim being to determine signs of food overlap. The distribution and feeding of sprat and sardine larvae were investigated during late spring 2003 on two transects

* This work was conducted within the framework of the GLOBEC Germany project, with financial support from BMBF (03F0320C).

covering a wide range of environmental conditions in the German Bight. Larvae co-occurred at all the stations investigated. Sprat and sardine larvae shared a wide range of prey types. Gut fullness and feeding success were similar in both species; however, potential food competition is avoided to some extent by different habitat preferences.

1. Introduction

Small pelagic fish comprise important ecological links between plankton production and higher, piscivorous trophic levels (Bakun 2006); these fish are of substantial economic importance. Their management is, however, challenged by a highly variable recruitment success and hence large stock fluctuations. In particular, factors acting on the early life-history stages have been identified as contributing variability in recruitment and stock abundance (e.g. Cury & Roy 1989, Fortier & Villeneuve 1996, Köster et al. 2003). Among the processes suggested as influencing egg and larval survival are predation (Sissenwine 1984, Köster & Möllmann 2000), variable ocean circulation patterns (e.g. Iles & Sinclair 1982) and food limitation. Food limitation at the time of first feeding was suggested as an important factor regulating recruitment success as early as 1914 by Hjort, who formulated the ‘critical period concept’. In putting forward the ‘match-mismatch’ hypothesis Cushing (1974) argued that the temporal coupling or decoupling of the production maxima of fish larvae and their prey organisms are the major source of recruitment variability. The ‘stage duration hypothesis’ (Houde 1987) states that larval growth rate is another important factor influencing larval mortality. Favourable feeding conditions increase larval growth rates; consequently, larvae can better overcome critical life stages. Body size of both predator and prey is linked directly to foraging success, and the relationship between prey and predator size determines the outcome of species interaction (Scharf et al. 2000). During larval development mouth size increases and prey-searching ability improves, with mean prey size increasing in parallel (Sabatés & 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.

Several studies assume that abiotic environmental parameters have a significant effect on larval feeding success and survival (e.g. Nakata et al. 1994, Dower et al. 2002). Whereas temperature and oxygen may influence larval mortality directly, other parameters, e.g. turbulence, may influence larval survival indirectly as a result of their impact on plankton production and concentration (MacKenzie et al. 1994, Solow 2002). Frontal systems often provide zones of high food availability for fish larvae or other

planktivorous predators (Munk 1993, Morgan et al. 2005) owing 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 for evaluating the environmental effect on survival and recruitment. However, starvation mortality is determined not only by prey abundance, but also by the abundance and skills of other predators competing for the same source of prey.

In the North Sea, the sprat (*Sprattus sprattus* L.) is the dominant small pelagic fish species. The 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 the sprat in the North Sea (Aurich 1941, Daan et al. 1990). In the German Bight, young life stages appear to aggregate temporarily because of the area's retention character (Bartsch & Knust 1994). In the area itself spawning of sprat peaks from May to July (Alheit et al. 1987); at this time, larvae are released into a highly productive system (Tillmann et al. 2000). The shallow German Bight (20–40 m depth) has a complex and spatially variable hydrography owing to the influence of seasonal warming, river discharge and (semidiurnal) tidal mixing. This results in the formation of hydrographic fronts. The recruitment level and spawning stock of the sprat have shown strong variations in recent years (ICES 2007).

The sardine (*Sardina pilchardus* W.) is traditionally an important commercial fish species in the coastal waters off Portugal and northern Spain (Robles et al. 1992). The distribution areas are the North Atlantic, the Mediterranean, the Adriatic and the Black Sea (Muus & Nielsen 1999), and the main spawning grounds are along the coasts of Portugal and northern Spain as well as along the English Channel. Like the sprat, the sardine is a batch spawner with peak spawning from April to May on the coast of Spain (Chícharo 1998). The latter occurred episodically in the German Bight during the periods 1948–52, 1958–60 (Aurich 1953, Postuma 1978) and 1990–94 (Corten & van de Kamp 1996). Based on results of the International Bottom Trawl Survey of ICES, Beare et al. (2004) showed that the abundance of sardines in the North Sea increased suddenly after 1995. The GLOBEC Germany project demonstrated that sardines have been spawning in the German Bight since 2002 (J. Alheit, personal communication). All life stages were found in the area: eggs, larvae, juveniles and adults.

The recent invasion of sardines into the North Sea raises a highly interesting question: What are the feeding habits of these two small pelagic

clupeiform species with very similar life histories (Hunter & Alheit 1995)? Such information is needed in order to predict potential future recruitment scenarios and to assess how these species can co-exist in the same area.

Our hypotheses were that sprat and sardine larvae caught in the German Bight used different prey items, and that their spatial distributions did not overlap. To test these hypotheses, the distribution and feeding of sprat and sardine larvae during late spring 2003 were investigated on two transects covering a wide range of environmental conditions in the German Bight.

2. Material and methods

2.1. Sampling

Sampling took place during June 2003 on two perpendicular transects (T1, T2) in the German Bight (Figure 1). Vertically resolved larval samples were collected on each transect. At T1 only 5 of 7 stations were used for gut content analysis; on T2 all four stations could be used. Additionally, profiles of conductivity, temperature and depth (CTD) were recorded at each station, including measurements of chlorophyll *a* distribution.

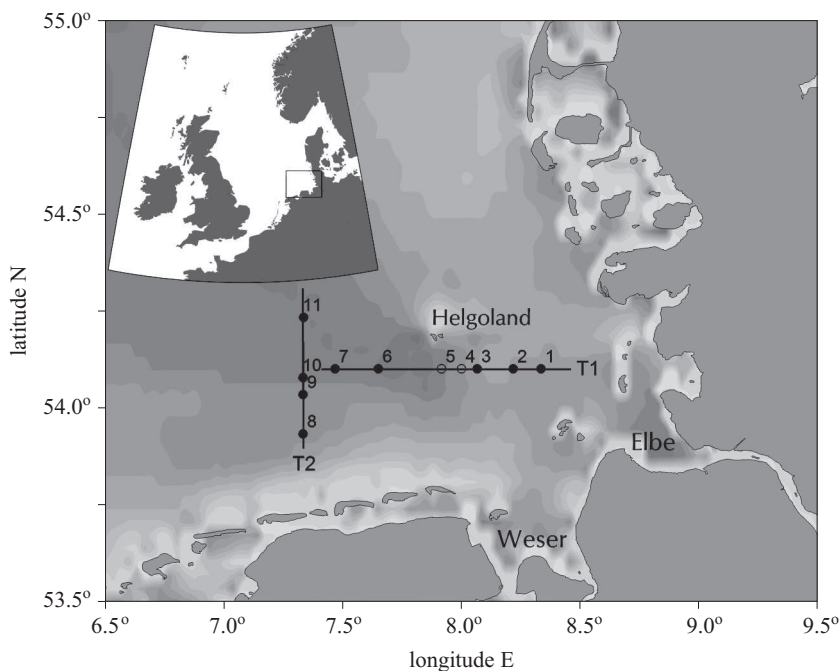


Figure 1. Map of the investigation area in the German Bight showing transect 1 (T1, stations 1–7) and transect 2 (T2, stations 8–11). Full circles: plankton and CTD; open circles: CTD

Because sardine and sprat larvae feed only during daylight (Voss et al. 2003, Dickmann et al. 2007), larvae were only sampled during daytime with a towed multinet (mouth opening 0.5 m², 335 μ m mesh size). In mixed water columns samples were taken at each station at the surface, near the bottom and at the depth of the chlorophyll peak, if this had formed. At stratified stations larvae were sampled above, within and below the thermocline. Abundances ($n \times m^{-3}$) were recorded using information on filtered volumes.

The zooplankton prey field was recorded in parallel to the sampling of fish larvae at each station. Vertical hauls were performed with a small multinet (mouth opening 0.25 m², 50 μ m mesh size) deployed in 5 m steps down to 35 m. Abundances ($n \times m^{-3}$) of zooplankton species were calculated. All samples were preserved in a 4% borax buffered formaldehyde solution for later laboratory analyses.

2.2. Laboratory analyses

In the laboratory, the standard length (SL) of 270 sprat and 451 sardine larvae was measured to the nearest 10 μ m. The entire alimentary canal of each individual larva was removed, opened and the gut contents analysed under a stereomicroscope. The analyses were conducted by first counting the intact individuals and afterwards checking for the remains of individuals in a more advanced stage of digestion (e.g. mandibles). Where possible, all prey particles were identified to species level. Five copepod stages were resolved, including nauplii (N), early copepodites (C1–3), late copepodites (C4–5) and adults (C6). Nauplii of *Pseudocalanus* spp., *Paracalanus* spp., and *Calanus* spp. were pooled as ‘Clausocalanoid nauplii’. All diatoms, ciliates and other unidentifiable small cells and microplankton remains were grouped together as ‘microplankton’. The ‘other plankton’ group contained mainly copepod eggs and bivalve larvae as well as synchaeta and polychaeta. Zooplankton samples were also analysed under a stereomicroscope, and the same sorting protocol was applied as for the larval gut contents. The length and width of prey items in larval guts and from plankton samples were measured to the nearest 10 μ m. The dry weight of all copepod stages was calculated by applying the estimates of Hernroth (Hernroth ed. 1985) and Mauchline (1998), while that of synchaeta was calculated by applying the estimates given by Hernroth (1985) and Mullin (1969). The dry weight of copepod eggs was taken from Kiørboe & Sabatini (1994), that of bivalve larvae and polychaete larvae from Nickolaus (unpubl. data). The dry weight of microplankton, diatoms and ciliates was calculated on the basis of estimates taken from Pelegrí et al. (1999). No correction was applied for length changes resulting from the preservation of fish larvae or zooplankton.

2.3. Data analyses

To describe the dietary composition of sprat and sardine larvae the frequency of occurrence $F(\%)$ of each food item in all the guts of each species (excluding empty guts) was computed, as was the percentage dry weight of each food item $W(\%)$ as $F(\%) = 100n_i N^{-1}$ and $W(\%) = 100S_i S_t^{-1}$, where n_i is the number of larvae with prey type i in their guts, N the total number of analysed guts, S_i the mass of prey type i and S_t the total gut content mass. To determine feeding trends both indices in ‘Costello graphics’ (Costello 1990) were used.

The food overlap of sprat and sardine larvae was calculated using Schoener’s index (Schoener 1968), $D = 1 - 0.5 \sum |P_{sprat,i} - P_{sardine,i}|$, where $P_{sprat,i}$ and $P_{sardine,i}$ are the respective proportions for sprat and sardine for the i^{th} prey item. A range between 0.25 and 0.74 was considered moderate, whereas values > 0.74 were defined as indicating substantial overlap (Pedersen 1999).

To analyse prey selectivity, the mean prey abundance of all zooplankton sampling stations was compared with the abundance in the larval guts. Selectivity values were calculated only for the main prey items, i.e. developmental stages of the copepods *Pseudo-/Paracalanus* spp., *Acartia* spp. and *Temora longicornis*. In order to compare similar size ranges and to obtain sufficient numbers of larvae with enough food items to calculate selectivity indices, the larvae were grouped into three size classes (< 8.5 mm, $8.5 - < 14.5$ mm, $14.5 - 18.5$ mm). 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.

The Kruskal-Wallis rank sum test was used to test for differences in gut fullness between sprat larval size classes, and the Mann-Whitney U-test was applied to test for differences in gut fullness between species and between sardine larval size classes.

To investigate size-related trends in sardine larvae feeding, the relationship between log-prey and larval length as well as trophic niche breadth was studied. For the prey-size to larval-size relationship, the mean of the logarithmic prey lengths in each larval size class was estimated. Niche breadth was computed as the standard deviation of the mean logarithmic prey size in each predator size class (Pearre 1986). 1 mm larval size classes were chosen so as to obtain the maximum number of predator size classes containing 3 or more prey entries.

Owing to the low number of possible prey length measurements, mean log-transformed prey length and niche breadth were calculated only for

the sardine larvae and compared with literature values for the Baltic sprat (Dickmann et al. 2007).

3. Results

3.1. Physical environment and larval distribution

Co-occurring sprat and sardine larvae were found at all stations and in all the investigated depth layers (Figures 2, 3).

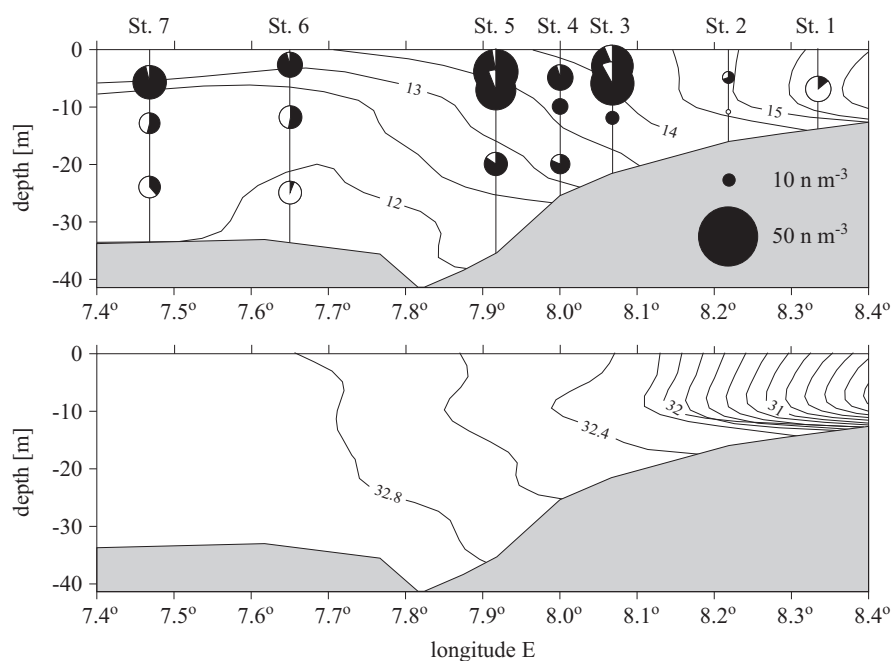


Figure 2. Hydrography of transect 1 (T1). Temperature (top) and salinity (bottom); black lines indicate sampling stations, pie charts illustrate the abundance and composition of fish larvae at the sampling depths; white – proportion of sprat larvae, black – proportion of sardine larvae

A total of 270 sprat and 451 sardine larvae were investigated for dietary composition along both transects (Table 1). The Mann-Whitney U-test showed a significantly higher mean larval length for both larval species on T1 compared to T2 ($p < 0.0001$ for sprat larvae, $p < 0.005$ for sardine larvae). Further sprat larvae were significantly larger than sardine larvae on both transects (T1: $p < 0.0001$, T2: $p < 0.005$).

River discharge, indicated by higher temperatures and lower salinities, was conspicuous at both coastal stations of T1 (Figure 2), where a higher

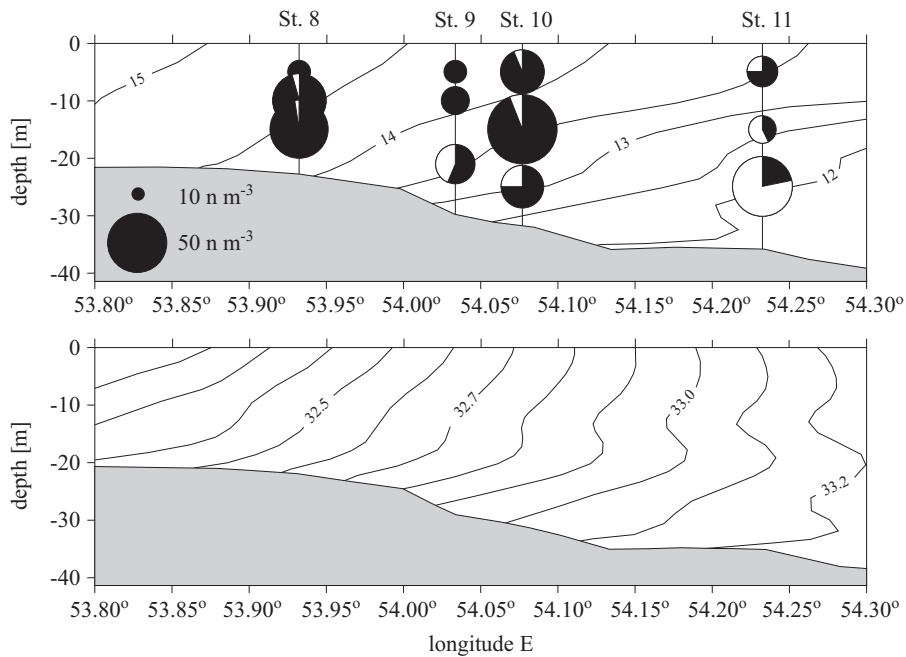


Figure 3. Hydrography of transect 2 (T2). Temperature (top) and salinity (bottom); black lines indicate sampling stations, pie charts illustrate the abundance and composition of fish larvae at the sampling depths; white – proportion of sprat larvae, black – proportion of sardine larvae

Table 1. Sampling locations and basic larval data. Ne – number of larvae examined, %NL – proportion of feeding larvae, m SL – mean standard length with standard deviation

Transect	Station	Ne	Ne	%NL	%NL	m SL	m SL
		Sprat	Sardine	Sprat	Sardine	Sprat	Sardine
T1	1	2	1	0	100.0	4.6 ± 1.6	5.3
	2	5	16	80.0	50.0	11.1 ± 3.6	9.6 ± 2.3
	3	14	47	64.3	61.7	9.9 ± 3.7	8.5 ± 2.9
	6	32	34	53.1	29.4	9.8 ± 3.4	7.7 ± 2.3
	7	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	7.5 ± 2.8
T2	8	24	42	41.7	38.1	7.2 ± 2.0	7.2 ± 2.0
	9	30	81	43.3	32.1	6.6 ± 2.2	6.0 ± 1.7
	10	32	83	31.3	24.1	7.1 ± 2.0	6.8 ± 1.8
	11	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	6.7 ± 2.2

Table 2. Dietary composition of sprat and sardine larvae. N – numbers of prey items in the guts, %N – proportion of prey types in numbers, DW – dry weight [μg] of prey in the guts, %DW – proportion of prey types in weight

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
C1–3	A13	10	5.8	6.5	4.7	3	1.0	2.0	1.7
C4–5	A45	1	0.6	1.6	1.1	0	0.0	0.0	0.0
C6	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
C1–3	T13	2	1.2	1.6	1.1	0	0.0	0.0	0.0
C4–5	T45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C6	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
<i>Pseudo-/Paracalanus</i> spp.									
Clausocalanoid Nauplii	CLN	65	38.0	22.7	16.4	110	37.9	38.3	33.8
C1–3	P13	2	1.2	4.6	3.3	0	0.0	0.0	0.0
C4–5	P45	3	1.8	18.8	13.6	0	0.0	0.0	0.0
C6	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
C1–3	C13	1	0.6	0.8	0.6	0	0.0	0.0	0.0
C4–5	C45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C6	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
C1–3	O13	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C4–5	O45	0	0.0	0.0	0.0	0	0.0	0.0	0.0
C6	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	–	–

proportion of sprat larvae was found. Further offshore, temperature decreased and exhibited stratification, whereas at the same time salinity increased. In this stratified area sardine larvae tended to remain in the upper, warmer water layers, while sprat larvae stayed in the deeper, colder water layers.

At station T2 sprat larvae were most abundant in the stratified, cooler waters farther offshore. Sardines were most abundant at the warmer, mixed-water station closest to the coast (Figure 3).

3.2. Dietary composition

General diets. The general dietary composition of both species was similar (Table 2). Clausocalanoid nauplii were the most important prey, followed by unidentified copepods. The proportion of older developmental stages (copepodites and adult copepods) was relatively high in this group. *Acartia* spp., *Temora longicornis* and *Oithona* spp. made up similar shares in the dietary composition of sardine larvae. While sardine larvae fed almost exclusively on copepod nauplii, sprat larvae ingested a larger number of copepodite and adult stages (Table 2). However, it has to be noted that the underlying larval size-distributions were different, i.e. the inclusion of large sardine larvae might have changed the picture.

Size-specific feeding. With increasing size of sprat larvae, a trend towards larger prey items was obvious. Clausocalanoid nauplii were by far the most important prey item for small sprat larvae (3.5–<8.5 mm) followed by the group of unidentified copepods (Figure 4). In the 8.5–<14.5 mm length class clausocalanoid nauplii were the most frequently occurring prey, while unidentified copepods dominated by weight. *Pseudo-/Paracalanus* C4–5

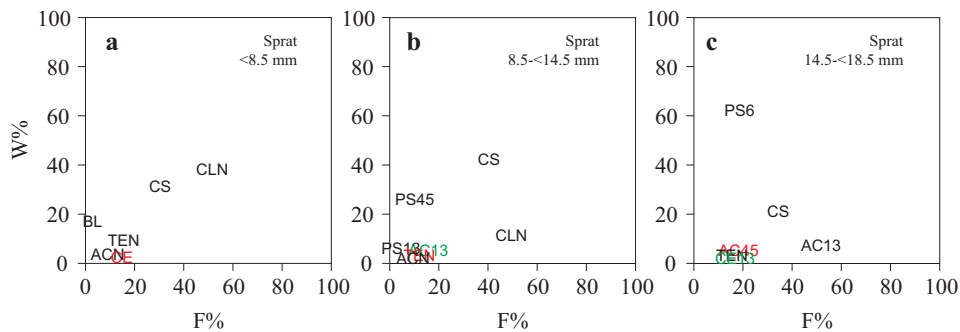


Figure 4. *Sprattus sprattus*. Dietary composition of larvae. (a) <8.5 mm, (b) 8.5–14.5 mm, (c) 14.5–<18.5 mm; W% – percentage of dry weight of each food item in the gut, F% – frequency of occurrence of each food item in the gut; only prey groups with proportions >2% are shown; for abbreviations, see Table 2

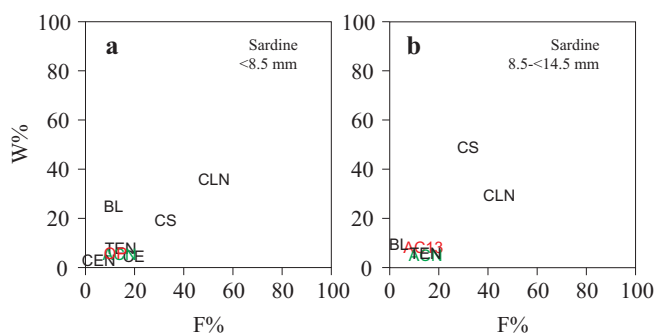


Figure 5. *Sardina pilchardus*. Dietary composition of larvae. (a) < 8.5 mm, (b) 8.5 – < 14.5 mm; W% – percentage of dry weight of each food item in the gut, F% – frequency of occurrence of each food item in the gut; only prey groups with proportions > 2% are shown; for abbreviations, see Table 2

ranked second in terms of weight, but occurred only in small numbers. In the largest length class (14.5 – < 18.5 mm) *Acartia* spp. C1–3 (numbers) and *Pseudo-/Paracalanus* C6 (weight) were the most important prey groups.

In the diet of sardine larvae clausocalanoid and unidentified copepod stages were the most important prey types for larvae up to 14.5 mm in length (Figure 5). Sardine larvae < 8.5 mm preyed mostly on clausocalanoid nauplii, while unidentified copepod stages dominated the diet of larger sardines.

3.3. Food overlap

Values of food overlap were moderate to high at all stations. A substantial food overlap – according to the definition of Pedersen (1999) – was found for 2 stations, one on each transect (Table 3). For station 1 no overlap was calculated, as no feeding sprat larvae were found there. Food overlap between different size classes was always moderate to high (Table 4). There was substantial overlap in the < 8.5 mm size class on both transects. On transect 2 sprat larvae < 8.5 mm additionally showed considerable overlap with sardine larvae of the 8.5 – < 14.5 mm length class, the overlap being

Table 3. Food overlap values of sprat and sardine larvae (Schoener, 1968). Values > 0.74 indicate considerable overlap

Station	T1				T2			
	2	3	6	7	8	9	10	11
Overlap	0.62	0.74	0.67	0.72	0.58	0.81	0.67	0.56

Table 4. Food overlap values between different size classes of sprat and sardine larvae

			Sardine	
			< 8.5 mm	8.5 – < 14.5 mm
T1	Sprat	< 8.5 mm	0.81	0.56
		8.5 – < 14.5 mm	0.60	0.63
T2	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

mainly within the group of unidentified copepods. Hence, while there is overlap in prey size, there is no proof of a substantial overlap at the species level.

3.4. Selectivity

Small and medium-sized sprat larvae (< 14.5 mm) showed significantly positive selectivity values for clausocalanoid nauplii (Figure 6). Larvae > 14.5 mm significantly selected for *Acartia* spp. C1–3, *T. longicornis* C1–3 and *Pseudo-/Paracalanus* adults. Small and medium-sized sardine larvae also significantly favoured clausocalanoid nauplii. *Pseudo-/Paracalanus* C1–3 and *Acartia* spp. C1–3 were avoided by sardine larvae < 8.5 mm. For no other prey groups were statistically significant selection values found.

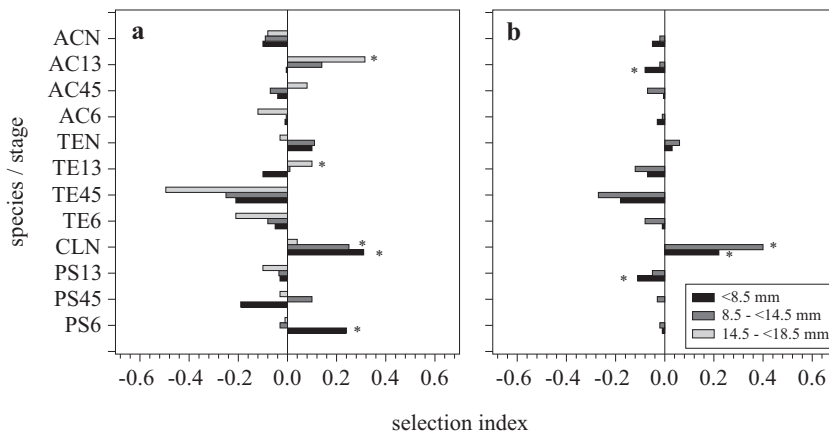


Figure 6. *Sprattus sprattus* (a) and *Sardina pilchardus* (b). Selective feeding of larval size classes (Index C, Pearre jr. 1982). * indicates significant selective feeding at the 5% level; for abbreviations, see Table 2

3.5. Feeding success

The Mann-Whitney U-test also revealed no significant differences in the index of gut fullness (numbers or weight) between sprat and sardine larvae, either on T1 (numbers: $p=0.37$ and weight: $p=0.07$) or on T2 (numbers: $p=0.70$ and weight: $p=0.98$). Furthermore, no significant differences in gut fullness were found between sprat and sardine larval size classes (sprat: Kruskal-Wallis rank sum test, $p=0.67$; sardine: Mann-Whitney U-test, $p=0.5$). However, the Mann-Whitney U-test showed significant differences in gut fullness in terms of weight between transects for both species ($p < 0.0005$ for sprat larvae and $p < 0.005$ for sardine larvae), indicating variability between the transects.

3.6. Predator-prey relationship of sardine larvae

A slight increase in prey length with larval length, though not significant, was observed. The logarithmic mean size of prey also showed a slight increase with sardine length, but was not significantly correlated ($p < 0.1$, Figure 7). Trophic niche breadth was independent of larval size, too, and did not change over the investigated size range. Interspecific comparison of the 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.

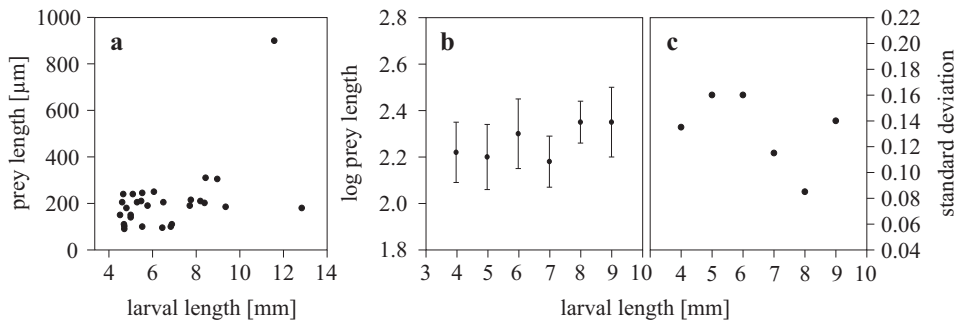


Figure 7. *Sardina pilchardus*. Predator-prey size relationships. (a) untransformed raw data, (b) log-mean prey length, (c) trophic niche breadth

4. Discussion

A comprehensive study of the feeding ecology of sprat and sardine larvae was carried out in the German Bight. Sardine larvae had not been observed for several decades in the German Bight. Some evidence exists that in recent years the abundance of the sardine and other predominately southern species

has increased in the northern North Sea (e.g. Beare et al. 2004). This has opened the way for potential food competition between the larvae of these two clupeid species.

4.1. Zooplankton and larval distribution in relation to the physical environment

Although only moderate changes in temperature and salinity were found on both transects, the water bodies of frontal systems (mixed, transition, stratified) were clearly distinguishable. Several studies have found a relationship between the physical environment in frontal systems and biological patterns (e.g. Munk 1993, Rissik & Suthers 1996). Because of the anticipated high chlorophyll *a* values and primary production at the front (e.g. Pingree et al. 1975, 1978, Pedersen 1994, Danovaro et al. 2000), a higher zooplankton density would be expected there than in adjacent waters (e.g. le Fèvre 1986). Aggregation of phyto- and zooplankton would be assumed to cause higher abundances of predators in frontal systems (Morgan et al. 2005). In the present study higher chlorophyll *a* values were not observed at the frontal stations (M. Dickmann, pers. comm.), and there was accordingly no aggregation of larvae at the frontal zones. Furthermore, no difference in feeding success between the stations was recorded. Sardine larvae displayed a preference for warmer, highly saline water, whereas sprat larvae tended to stay in colder water with a lower salinity. However, more data would be needed to resolve habitat participation in relation to ambient physical conditions.

4.2. Dietary composition

Copepod stages were identified as the most important food source for sprat and sardine larvae in the German Bight. This is in accordance with previous studies in different regions (e.g. Last 1980, Conway et al. 1991, 1994, Kurts & Matsuura 2001, Voss et al. 2003). Clausocalanoid nauplii dominated the gut contents of sprat and sardine larvae in the < 14.5 mm size class and were positively selected by both species. Jiang & Paffenhöfer (2004) suggested that continuous swimmers like the nauplii of *Paracalanus quasimodo* should be positively selected, because of their lower sensitivity to hydrodynamic signals and their inefficiency in remotely detecting predators, as compared to nauplii that move in a ‘jump – sink pattern’ (Titelman & Kiørboe 2003, Jiang & Paffenhöfer 2004). This effect could have contributed to the observed high selection of clausocalanoid nauplii by both species. Sprat larvae in the larger size classes preyed selectively on copepodites of *Acartia* spp. and *T. longicornis* as well as on adult copepods of *Pseudo-/Paracalanus* spp. Checkley jr. (1982) assumed that

adult *Pseudocalanus* spp. should be positively selected by herring larvae – because these copepods are unable to accelerate rapidly, they cannot make a quick escape from a predator. Furthermore, Viitasalo et al. (2001) observed that adult *Pseudocalanus elongates* exhibit a weak escape response and a small sensitivity to hydrodynamic signals. *Acartia* spp. perform a weak escape jump with a small escape distance (Viitasalo et al. 2001), which is positively related to a predator's success of attack (e.g. Caparroy 2000). Both the poor alertness of *Pseudocalanus* spp. and the very weak escape response of both copepod species could have contributed to the observed selection of these prey types. However, selectivity estimates may be biased if zooplankton samples do not reflect the zooplankton abundances where the larvae were feeding (Arrhenius 1996). The small-scale patchiness of larvae and prey distribution in a turbulent environment makes it difficult to relate larval feeding to the food environment (e.g. MacKenzie et al. 1990, Pepin 2004). In the present study larvae and zooplankton were sampled at the same stations and in the same depth range; nevertheless, selectivity indices were probably influenced by the integration of all stations. This integration over a large number of samples was necessary, however, owing to the generally low numbers of feeding larvae and ingested prey items.

4.3. Predator and prey-size related feeding

Capture success increases with larval development (Houde & Scheckter 1980) because older larvae move at 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 the number of ingested prey organisms in different fish species (Sabatés & Saiz 2000, Viñas & Santos 2000, Cass-Calay 2003). In contrast, Kurtz & Matsuura (2001) observed a constant decline in the proportion of feeding Brazilian sardine (*Sardinella brasiliensis*) larvae with larval size. This result, unexpected for fish larvae in general, was confirmed by Conway et al. (1991), who found a decrease in gut fullness in small (<10 mm) to medium-sized (10–15 mm) sardine larvae. In the present study, the difference in feeding success of different-sized sardine larvae was not significant.

For sprat larvae this study found only a slight, non-significant increase in feeding success over the complete size range of larvae investigated (3.5–18.5 mm). This is in accordance with results reported for Baltic sprat larvae <15.5 mm long (Dickmann et al. 2007). However, for Baltic sprat larvae >15.5 mm in length a pronounced increase in the number of prey items in the guts was observed that was not found in the North Sea. The feeding success of small, first-feeding larvae in the North Sea

was substantially higher compared to the Baltic (Dickmann et al. 2007), indicating that this larval stage is probably less critical in the North Sea than in the Baltic.

As the feeding success of both species was not significantly different over the entire investigated size range, no obvious competitive advantage could be determined for either of the species.

Previous studies (e.g. Last 1980, Conway et al. 1994, Sabatés & Saiz 2000, Voss et al. 2003) showed that the size of prey ingested by the larvae of several fish species increases throughout larval development because of their improving ability to cope with larger prey (Last 1980). The same significant correlation was found for sprat larvae in the German Bight. For sardine larvae, a greater weight of unidentified copepodite stages between the small and medium size classes indicates a similar trend. This is in agreement with Conway et al. (1994), who reported an elevated proportion of copepodites in the guts of sardine > 15 mm, and with Nakata (1998), who reported the preference of the Japanese sardine (*Sardinops melanostictus*) > 20 mm for adult copepods.

Feeding theory predicts that, under food-limited conditions, the niche breadth of larval fish should increase owing to the ingestion of a wider range of prey sizes (Werner & Hall 1974, Bartell 1982, Reiss et al. 2005). However, several studies have found no significant relationship between niche breadth and larval size (e.g. Pearre jr. 1986, Munk 1992, Reiss et al. 2005). Pepin & Penney (1997) reported an increase in niche breadth with larval growth for 6 out of 11 species investigated, whereas Scharf et al. (2000) observed a decrease in the breadth of relative prey sizes for several investigated fish species. The niche breadth of sardine larvae in 2003 exhibited no correlation with larval length; this result led to the inference that there was no food limitation. However, the restricted size distribution of larvae and the limited temporal coverage of sampling preclude more general conclusions.

In comparison, the niche breadth of Baltic sprat larvae was observed to increase linearly until a length of c. 16 mm (Dickmann et al. 2007). Beyond that length, larger larvae had a narrower and highly variable niche breadth. This pattern was explained by a combination of larval growth and the seasonal plankton cycle. The results of Dickmann et al. (2007) showed that any evaluation of the relationship between larval size and niche breadth has to take the taxonomic and size composition of the prey field into consideration. In the German Bight nauplii were by far the most abundant meso-zooplankton group. It is assumed that small sardine larvae are limited to small food items, i.e. nauplii, by their poor swimming ability and small mouth size. This has resulted in a restricted size range of prey items and consequently a small niche breadth. Larger larvae did not increase their

niche breadth; they may have been restricted by the nauplii-dominated food supply in the field. Despite the low abundances of larger food items during this study, sprat and sardine larvae exhibited feeding incidences comparable with those found in other studies (Conway et al. 1994, Kurts & Matsuura 2001, Voss et al. 2003), similar growth (Huwer 2004) and good nutritional condition (Holtappels 2004).

5. Conclusions

Aurich (1953) suggested that the northward shift in the distribution of the sardine into the North Sea observed in the late 1940s had been caused by a higher sea surface temperature (SST) and changes in the current system. Although Aurich (1953) related the spread of sardines at that time to climate variability, the recent influence of global warming has to be considered as well. According to expert knowledge a further increase in water temperatures in the North Sea can be expected (IPCC 2007), bringing with it a further improvement in living conditions for sardines.

The food overlap analysis confirmed that sprat and sardine larvae share a wide range of prey types (Conway et al. 1994, Kurts & Matsuura 2001, Voss et al. 2003). Competition for food is possible and gut fullness and feeding success were similar in both species. However, direct competition seemed to be avoided to some extent as a result of different preferences in ambient conditions. Co-existence therefore seems likely in the future.

6. Acknowledgements

We thank all those involved in sampling and analysing the material, especially the crews of the research vessels 'Alkor' and 'Heincke' and all the participants of the GLOBEC Germany project.

References

- Alheit J., Wahl E., Cihangir B., 1987, *Distribution, abundance, development rates, production and mortality of sprat eggs*, ICES CM 1987/H:45.
- Arrhenius F., 1996, *Diet composition and food selectivity of 0-group herring (*Clupea harengus* L.) and sprat (*Sprattus sprattus* (L.)) in the northern Baltic Sea*, ICES J. Mar. Sci., 53 (4), 701–712.
- Aurich H. J., 1941, *Die Verbreitung der pelagischen Fischbrut in der südlichen Nordsee während der Frühjahrsfahrten 1926–1937 der Deutschen Forschungsschiffe Poseidon und Makrele*, Helgol. Wiss. Meeresunters., 2 (2), 184–225.
- Aurich H. J., 1953, *Verbreitung und Laichverhältnisse von Sardelle und Sardine in der südöstlichen Nordsee und ihre Veränderungen als Folge der Klimaänderung*, Helgol. Wiss. Meeresunters., 4 (3), 175–204.

- Bakun A., 2006, *Wasp-waist populations and marine ecosystem dynamics: Navigating the 'predator pit' topographies*, Prog. Oceanogr., 68 (2–4), 271–288.
- Bartell S. M., 1982, *Influence of prey abundance on size-selective predation by bluegills*, T. Am. Fish. Soc., 111 (4), 453–461.
- Bartsch J., Knust R., 1994, *Simulating the dispersion of vertically migrating sprat larvae (*Sprattus sprattus* (L.)) in the German Bight with a circulation and transport model system*, Fish. Oceanogr., 3 (2), 92–105.
- Beare D., Burns F., Jones E., Peach K., Portilla E., Greig T., McKenzie E., Reid D., 2004, *An increase in the abundance of anchovies and sardines in the north-western North Sea since 1995*, Glob. Change Biol., 10 (7), 1209–1213.
- Caparroy P., Thygesen U. H., Visser A. W., 2000, *Modelling the attack success of planktonic predators: patterns and mechanisms of prey size selectivity*, J. Plankton Res., 22 (10), 1871–1900.
- Cass-Calay S. L., 2003, *The feeding ecology of larval Pacific hake (*Merluccius productus*) in the California Current region: an updated approach using a combined OPC/MOCNESS to estimate prey biovolume*, Fish. Oceanogr., 12 (1), 34–48.
- Checkley jr. D. M., 1982, *Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages*, Mar. Ecol.-Prog. Ser., 9, 245–253.
- Chícharo M. A., 1998, *Nutritional condition and starvation in *Sardina pilchardus* (L.) larvae off southern Portugal compared with some environmental factors*, J. Exp. Mar. Biol. Ecol., 225 (1), 123–137.
- Conway D. V. P., Coombs S. H., Fernández de Puelles M. L., Tranter P. R. G., 1994, *Feeding of larval sardine, *Sardina pilchardus* (Walbaum), off the north coast of Spain*, Bol. Inst. Esp. Oceanogr., 10 (2), 165–175.
- Conway D. V. P., Tranter P. R. G., Fernández de Puelles M. L., Coombs S. H., 1991, *Feeding of larval sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* Walbaum)*, ICES CM 1991/L:76.
- Corten A., van de Kamp G., 1996, *Variation in the abundance of southern fish species in the southern North Sea in relation to hydrography and wind*, ICES J. Mar. Sci., 53 (6), 1113–1119.
- Costello M. J., 1990, *Predator feeding strategy and prey importance: a new graphical analysis*, J. Fish. Biol., 36 (2), 261–263.
- Cury P., Roy C., 1989, *Optimal environmental window and pelagic fish recruitment success in upwelling areas*, Can. J. Fish. Aquat. Sci., 46 (4), 670–680.
- Cushing D. H., 1974, *The natural regulation of fish populations*, [in:] *Sea fisheries research*, F. R. Harden Jones (ed.), Paul Elek, London, 399–412.
- Daan N., Bromley P. J., Hislop J. R. G., Nielsen N. A., 1990, *Ecology of North Sea fish*, Neth. J. Sea Res., 26 (2–4), 343–386.
- Danovaro R., Gambi C., Manini E., Fabiano M., 2000, *Meiofauna response to a dynamic river plume front*, Mar. Biol., 137 (2), 359–370.

- Dickmann M., Möllmann C., Voss R., 2007, *Feeding ecology of Central Baltic sprat *Sprattus sprattus* larvae in relation to zooplankton dynamics: implications for survival*, Mar. Ecol.-Prog. Ser., 342, 277–289.
- Dower J.F., Pepin P., Leggett W.C., 2002, *Using patch studies to link mesoscale patterns of feeding and growth in larval fish to environmental variability*, Fish. Oceanogr., 11 (4), 219–232.
- Le Fèvre J., 1986, *Aspects of the biology of frontal systems*, Adv. Mar. Biol., 23, 163–299.
- Fortier L., Villeneuve A., 1996, *Cannibalism and predation on fish larvae by larvae of Atlantic mackerel, *Scomber scombrus*: trophodynamics and potential impact on recruitment*, Fish. B.-NOAA, 94 (2), 268–281.
- Hernroth L. (ed.), 1985, *Recommendations on methods for marine biological studies in the Baltic Sea. Mesozooplankton biomass assessment*, Baltic Mar. Biol. Publ. No. 10, 1–32.
- Hjort J., 1914, *Fluctuation in the great fisheries of northern Europe*, Rapp. P.-V. Réun. Cons. Perm. Int. Explor. Mer, 20, 1–228.
- Holtappels M., 2004, *The nutritional condition of sprat and sardine larvae in the frontal systems of the German Bight*, B.Sc. thesis, Instit. Ostseeforschung, Warnemünde, 1–87.
- Houde E. D., 1987, *Fish early life dynamics and recruitment variability*, Am. Fish. Soc. Symp. Ser., 2, 17–29.
- Houde E. D., Schekter R. C., 1980, *Feeding by marine fish larvae: developmental and functional responses*, Environ. Biol. Fish., 5 (4), 315–334.
- Hunter J.R., 1981, *Feeding Ecology and Predation of Marine Fish Larvae*, [in:] *Marine fish larvae: morphology, ecology, and relations to fisheries*, R. Lasker (ed.), Washington Press, Seattle, 33–77.
- Hunter J.R., Alheit J., 1995, *International GLOBEC Small Pelagic Fishes and Climate Change Program*, GLOBEC Rep. No. 8, 72 pp.
- Huwer B., 2004, *Larval growth of *Sardina pilchardus* and *Sprattus sprattus* in relation to frontal systems in the German Bight*, B.Sc. thesis, Univ. Kiel, 1–109.
- ICES, 2007, *Report of the Herring Assessment Working Group south of 62°N (HAWG)*, ICES CM 2007/ACFM:11.
- Iles T.D., Sinclair M., 1982, *Atlantic herring: stock discreteness and abundance*, Science, 215 (4533), 627–633.
- IPCC – Intergovernmental Panel on Climate Change, 2007, *The physical science basis, Contribution of Working Group I to the Fourth Assessment Report*, (available at <http://www.ipcc.ch/ipccreports/ar4-syr.htm>).
- Jiang H., Paffenhöfer G.A., 2004, *Relation of behaviour of copepod juveniles to potential predation by omnivorous copepods: an empirical-modeling study*, Mar. Ecol.-Prog. Ser., 278, 225–239.

- Kjørboe T., Sabatini M., 1994, *Reproductive and life cycle strategies in egg-carrying cyclopoid and free-spawning calanoid copepods*, J. Plankton Res., 16 (10), 1353–1366.
- Köster F. W., Möllmann C., 2000, *Trophodynamic control by clupeid predators on recruitment success in Baltic cod*, ICES J. Mar. Sci., 57 (2), 310–323.
- Köster F. W., Schnack D., Möllmann C., 2003, *Scientific knowledge of biological processes potentially useful in fish stock predictions*, Sci. Mar., 67 (Suppl. 1), 101–127.
- Kurtz F. W., Matsuura Y., 2001, *Food and feeding ecology of Brazilian sardine (*Sardinella brasiliensis*) larvae from the south-eastern Brazilian Bight*, Rev. Bras. Oceanogr., 49 (1–2), 61–74.
- Last J. M., 1980, *The food of twenty species of fish larvae in the west-central North Sea*, Fish. Res. Tech. Rep., MAFF Direct. Fish. Res., Lowestoft, 60, 1–44.
- MacKenzie B. R., Leggett W. C., Peters R. H., 1990, *Estimating larval fish ingestion rates: can laboratory derived values be reliably extrapolated to the wild?*, Mar. Ecol.-Prog. Ser., 67, 209–225.
- MacKenzie B. R., Miller T. J., Cyr S., Leggett W. C., 1994, *Evidence for a domeshaped relationship between turbulence and larval fish ingestion rates*, Limnol. Oceanogr., 39 (8), 1790–1799.
- Mauchline J., 1998, *The biology of calanoid copepods*, Adv. Mar. Biol., 33, 1–710.
- Morgan C. A., de Robertis A., Zabel R. W., 2005, *Columbia River plume fronts, I. Hydrography, zooplankton distribution, and community composition*, Mar. Ecol.-Prog. Ser., 299, 19–31.
- Mullin M. M., 1969, *Production of zooplankton in the ocean: the present status and problems (RV)*, Oceanogr. Mar. Biol. Ann. Rev., 7, 293–314.
- Munk P., 1992, *Foraging behaviour and prey size spectra of larval herring *Clupea harengus**, Mar. Ecol.-Prog. Ser., 80, 149–158.
- Munk P., 1993, *Differential growth of larval sprat *Sprattus sprattus* across a tidal front in the eastern North Sea*, Mar. Ecol.-Prog. Ser., 99, 17–29.
- Munk P., 1997, *Prey size spectra of gadoid fish larvae, their relation to larval size and type of prey*, Ann. Int. Symp. Fish. Soc. Brit. Isles (Galway, Ireland), 1–34.
- Muus B. J., Nielsen J. G., 1999, *Sea fish*, Blackwell Science, Oxford, 1–340.
- Nakata K., 1988, *Alimentary tract contents and feeding conditions of ocean-caught post larval Japanese sardine, *Sardinops melanostictus**, Bull. Tokai. Reg. Fish. Res. Lab., 126, 11–24.
- Nakata K., Hada A., Matsukawa Y., 1994, *Variation in food abundance for Japanese sardine larvae related to the Kuroshio meander*, Fish. Oceanogr., 3 (1), 39–49.
- Pearre jr. S., 1982, *Estimating prey preference by predators: uses of various indices, and a proposal of another based on χ^2* , Can. J. Fish. Aquat. Sci., 39 (6), 914–923.

- Pearre jr. S., 1986, *Ratio-based trophic niche breadths of fish, the Sheldon spectrum, and size-efficiency hypothesis*, Mar. Ecol.-Prog. Ser., 27, 299–314.
- Pedersen F.B., 1994, *The oceanographic and biological tidal cycle succession in shallow sea fronts in the North Sea and the English Channel*, Estuar. Coast. Shelf. Sci., 38 (3), 249–269.
- Pedersen J., 1999, *Diet comparison between pelagic and demersal whiting in the North Sea*, J. Fish Biol., 55 (5), 1096–1113.
- Pelegrí S. P., Dolan J., Rassoulzadegan F., 1999, *Use of high temperature catalytic oxidation (HTCO) to measure carbon content of microorganisms*, Aquat. Microb. Ecol., 16 (3), 273–280.
- Pepin P., 2004, *Early life history studies of prey-predator interactions: quantifying the stochastic individual responses to environmental variability*, Can. J. Fish. Aquat. Sci., 61 (4), 659–671.
- Pepin P., Penney R. W., 1997, *Patterns of prey size and taxonomic composition in larval fish: are there general size-dependent models?*, J. Fish Biol., 51 (sA), 84–100.
- Pingree R. D., Holligan P. M., Mardell G. T., 1978, *The effects of vertical stability of phytoplankton distributions in the summer on the northwest European Shelf*, Deep-Sea Res. Pt. II, 25 (11), 1011–1028.
- Pingree R. D., Pugh P. R., Holligan P. M., Forster G. R., 1975, *Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel*, Nature, 258 (5537), 672–677.
- Postuma K. H., 1978, *Immigration of southern fish into the North Sea*, Rapp. P.-V. Reun. Cons. Int. Explor. Mer., 172, 225–229.
- Reiss C., McLaren I., Avendaño P., Taggart C., 2005, *Feeding ecology of silver hake larvae on the Western Bank, Scotian Shelf, and comparison with Atlantic Cod*, J. Fish Biol., 66 (30), 703–720.
- Rissik D., Suthers I. M., 1996, *Feeding in a larval fish assemblage: the nutritional significance of an estuarine plume front*, Mar. Biol., 125 (2), 233–240.
- Robles R., Porteiro C., Cabanas J. M., 1992, *The stock of Atlanto-Iberian sardine: possible causes of variability*, Rapp. P.-V. Reun. Cons. Int. Explor. Mer., 195, 418–423.
- Sabatés A., Saiz E., 2000, *Intra- and interspecific variability in prey size and niche breadth of myctophiform fish larvae*, Mar. Ecol.-Prog. Ser., 201, 261–271.
- Scharf F. S., Juanes F., Rountree R. A., 2000, *Predator size-prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth*, Mar. Ecol.-Prog. Ser., 208, 229–248.
- Schoener T. W., 1968, *The Anolis lizards of Bimini: resource partitioning in a complex fauna*, Ecology, 49 (4), 704–726.
- Sissenwine M. P., 1984, *Why do fish populations vary?*, [in:] *Exploitation of marine communities*, R. M. May (ed.), Springer-Verlag, Berlin, 59–94.
- Solow A. R., 2002, *Fisheries recruitment and the North Atlantic Oscillation*, Fish. Res., 54 (2), 295–297.

- Tillmann U., Hesse K.-J., Colijn F., 2000, *Planktonic primary production in the German Wadden Sea*, J. Plankton Res., 22 (7), 1253–1276.
- Titelman J., Kjørboe T., 2003, *Predator avoidance by nauplii*, Mar. Ecol.-Prog. Ser., 247, 137–149.
- Viitasalo M., Flinkman J., Viherluoto M., 2001, *Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions*, Mar. Ecol.-Prog. Ser., 216, 191–200.
- Viñas M. D., Santos B. A., 2000, *First-feeding of hake (*Merluccius hubbsi*) larvae and prey availability in the north Patagonian spawning area – comparison with anchovy*, Arch. Fish. Mar. Res., 48 (3), 242–254.
- Voss R., Køster F. W., Dickmann M., 2003, *Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm basin, Baltic Sea*, Fish. Res., 63 (1), 97–111.
- Werner E. E., Hall D. J., 1974, *Optimal foraging and size-selection of prey by the bluegill sunfish (*Lepomis macrochirus*)*, Ecology, 55 (5), 1042–1052.