

# Vertically resolved prey selectivity and competition of Baltic herring *Clupea harengus* and sprat *Sprattus sprattus*

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**ABSTRACT:** Prey selectivity of Baltic herring *Clupea harengus* and sprat *Sprattus sprattus* was studied in the Bornholm Basin, Baltic Sea, in June 2001. A total of 165 sprat stomachs (10 to 15 cm total length, TL) and 214 herring stomachs (12 to 30 cm TL) were analysed. The diel vertical distribution of zooplankton prey was analysed by multi-net samples; clupeid distributions were estimated by hydroacoustic measurements. These measurements enabled us to describe the diel feeding rhythm and to estimate vertically resolved selectivity indices for the 2 most important zooplanktivores in the Baltic Sea. Diet composition of herring and sprat were similar (mainly copepods and cladocerans), resulting in strong competition. Possibly to reduce this competition, both species were partly specializing on certain prey species (sprat: *Podon* spp.; herring: *Evadne nordmanni* and *Temora longicornis*) and copepodite stages (sprat: adult [C6] males of *Pseudocalanus acuspes*; herring: C6 females of *P. acuspes*). Sprat and, to some extent, herring exhibited a marked shift in prey preference between day and night. Sprat mainly selected *T. longicornis* during the day and *Podon* spp. during the night, while herring mainly selected *T. longicornis* during the day and *E. nordmanni* during parts of the night. A comparison of the field stomach contents with the estimated gastric evacuation predicted by parameters based on laboratory experiments indicated that sprat fed during the night, while herring did not or only to a minor extent. Comparison of our zooplankton sampling scheme with commonly used sampling designs revealed that investigations which consider both time and stage are needed to fully understand the feeding selectivity dynamics of herring and sprat in the Baltic Sea. However, the objective of a selectivity study should determine the most appropriate zooplankton sampling scheme.

**KEY WORDS:** Selectivity · Competition · Herring · Sprat · Baltic · Diel · Feeding

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## INTRODUCTION

Herring *Clupea harengus* L. and sprat *Sprattus sprattus* L. are the most abundant and commercially important planktivorous fish species in the Baltic Sea. These species are dominant predators on the

crustacean zooplankton and have the potential to control the Baltic Sea zooplankton community (Hansson et al. 1990, Arrhenius & Hansson 1993, Rudstam et al. 1994, Möllmann & Köster 1999, Möllmann et al. 2008). Estimating the potential for top-down control requires knowledge of the feeding ecology, espe-

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cially prey selectivity. For the latter, it is crucial that the actual feeding environment encountered by the predator is reliably known.

In the Baltic Sea, several investigations have been conducted on the selective predation of herring and sprat (Sandström 1980, Hansson et al. 1990, Flinkman et al. 1992, 1998, Arrhenius 1996, Casini et al. 2004). However, most of these studies were conducted in shallow coastal areas of the Baltic. Furthermore, with the exception of Hansson et al. (1990), these studies calculated selectivity indices from zooplankton sampling that integrated most, if not all, of the water column, ignoring the differences in the vertical distribution of various zooplankton species in the Baltic Sea (Hansen et al. 2006). Another shortcoming of earlier studies is the protocol used to identify gut contents and plankton composition, i.e. copepods were frequently not analysed to developmental stage and, thus, estimates of stage-resolved selectivity are generally lacking. This is important as herring and sprat tend to prefer later developmental stages (Möllmann et al. 2004) and prey selectively on adult female copepods and cladocerans that carry conspicuous egg sacs (*Eurytemora affinis* females) or pigmented eggs and embryos (*Bosmina longispina* and *Podon* spp.) (Flinkman et al. 1992). Furthermore, earlier studies were mainly conducted during dusk or at night, when these fish reside in the upper water column and are generally not feeding (Köster & Schnack 1994, Arrhenius 1998). Finally, in the vast majority of studies, prey selectivity was investigated for single months and/or years with no analyses of potential diel cycles in prey selectivity.

We conducted a 48 h *in situ* experiment in a deep Baltic basin to investigate the selective feeding behaviour of herring and sprat. Our study included (1) vertically resolved zooplankton sampling; (2) diel observation of abundance, vertical distribution and stomach contents of the predators (herring and sprat); and (3) stage-resolved analyses of zooplankton caught in net samples and found in fish stomachs. Using these methods, we assessed to what extent traditional techniques yielded reliable estimates of prey selection compared to those applied in this study.

## MATERIALS AND METHODS

The study was carried out in the Bornholm Basin of the southern Baltic Sea (Fig. 1) between 4 and 6 June 2001 using 2 research vessels (RV) 'Walther Herwig III' and 'Alkor' that made measurements in parallel. A triangular transect was sampled over a 48 h period

with the starting point at 55°21'N, 16°00'E. RV 'Walther Herwig III' conducted hydroacoustic measurements and fishing hauls, while the RV 'Alkor' conducted hydrographical measurements, zooplankton-sampling and, additionally, fishing hauls. Hydrographic measurements of temperature, salinity and oxygen were performed after every fishing station with a CTD-probe (type ME-KMS3). Zooplankton was sampled at 3 stations during day and at 3 stations during night.

Hydroacoustic measurements were conducted onboard RV 'Walther Herwig III' with a SIMRAD echosounder EK500 and a hull mounted split beam transducer ES38B, working at a frequency of 38 kHz. The calibration of the acoustic equipment was conducted with the standard copper-sphere method (Foote et al. 1986) at the beginning of the cruise. The basic-settings and the procedure of acoustic measurements, fishery and data processing were applied in accordance with the standards for the Baltic acoustic surveys (ICES 2001). The ship speed during the measurements was 10 knots between fishing stations and approximately 3 knots during trawling. The analysis of the data was performed using the EchoView Software (SonarData 2010). Echo data were integrated in 1 m depth layers and 0.1 nautical mile (n mile) horizontal intervals from 10 m below the surface to 0.5 m above bottom. Integration results were given as nautical area backscattering coefficient (NASC in  $\text{m}^2 \text{ n miles}^{-2}$ ; Huse & Korneliusen 2000).

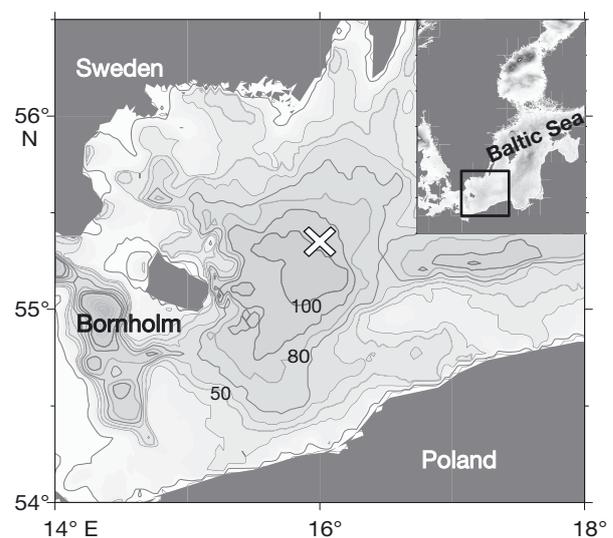


Fig. 1. Bornholm Basin (Baltic Sea). 48 h station from 4 to 6 June 2001, Bornholm Basin 55°21.00'N, 16°00.00'E, marked by white cross

To illustrate the vertical distribution and diel migration, the weighted mean depth of echoes,  $z_c$ , was calculated for every 0.1 n mile horizontal interval:

$$z_c = \frac{\sum_{j=10}^n \text{NASC}_j \times z_j}{\sum_{j=10}^n \text{NASC}_j} \quad (1)$$

where  $j$  is a depth layer of the echo profile,  $n$  is the number of depth layers,  $\text{NASC}_j$  is the NASC of the given depth layer  $j$  and  $z_j$  is the mean depth at depth interval  $j$ .

A total of 15 hauls were performed to identify the species composition of the echoes and for stomach sampling during the 48 h investigation period. A mid-water trawl type PS 205 with a cod-end mesh width of 10 mm was towed for 30 min. The depth of the net was adjusted to visible echoes of the target fish species.

At every station, the mass- and length-distribution of herring and sprat were recorded into 1 cm classes for sprat and 2 cm classes for herring. A total of 3 to 10 fish (per haul and length class) were preserved in 4% di-sodium-tetraborate-buffered formalin-seawater. During stomach analysis, the wet mass of stomach contents was determined. Diet analyses were conducted for 3 fish per sampling time and length class. The contents were analysed using a stereo microscope (magnification 16 to 80 $\times$ ). Each prey item was determined to the lowest possible taxonomic level and copepodites were classified to developmental stages (C1–C5), and adults (C6) to sex in herring and classified to developmental stage groups C1–3 and C4–5 and adults (C6) to sex in sprat. If a stomach contained large numbers of prey, a subsample of 200 identifiable items was analysed. Additionally, the sample was screened for rare taxa and ichthyoplankton. A total of 214 herring and 165 sprat stomachs were analysed. Herring stomach contents were analysed at the Latvian Fisheries Research Institute (LATFRI) in Riga and sprat stomach contents were analysed at the Institute for Hydrobiology and Fisheries Science (IHF), University of Hamburg (Germany). Due to time limitations, copepodites in sprat stomachs were classified to developmental groups (C1–3, C4–5 and C6) only, while the copepodites in herring stomachs were classified to copepodite stages C1–C6 at the sorting center.

### Zooplankton sampling

Vertical distributions were recorded during daytime (12:10, 10:33 and 11:58 h [Coordinated Univer-

sal Time, UTC]) and during nighttime (22:52, 23:34 and 02:45 h). Vertically stratified samples (10 m intervals from surface to 80 m) were obtained using a multiple opening-closing net (Hydro-Bios; www.hydro-bios.de/) with an opening of 0.25 m<sup>2</sup> and a mesh size of 100  $\mu\text{m}$ . Samples were preserved in 4% di-sodium-tetraborate-buffered formalin-seawater solution for later analysis in the laboratory. Mesozooplankton was identified and counted under a binocular microscope on subsamples of not less than 500 individuals per sample. Subsamples were obtained using a Kott-splitter device. Copepods were identified to species, *Pseudocalanus acuspes*, *Temora longicornis*, *Centropages hamatus*, *Oithona similis* and *Acartia* spp. (including *A. bifilosa* and *A. longiremis*). Copepodites were classified to developmental stages (C1–C6), and adults (C6) to sex.

### Selectivity index

Prey selectivity was estimated using the alpha index ( $\alpha_i$ ) developed by Chesson (1978):

$$\alpha_i = \frac{r_i}{n_i} / \sum_{j=1}^k \left( \frac{r_j}{n_j} \right) \quad (2)$$

where  $k$  is the number of prey types,  $r_i$  and  $r_j$  are the proportions of prey type  $i$  or  $j$  in the diet, and  $n_i$  and  $n_j$  are the proportions of prey type  $i$  or  $j$  in the environment. The  $\alpha$ -values are normalized so that:

$$\sum_{i=1}^k \alpha_i = 1.0 \quad (3)$$

with  $\alpha_i = 1 k^{-1}$  denotes unselective (random) feeding,  $\alpha_i > 1 k^{-1}$  denotes that prey species  $i$  is preferred in the diet and  $\alpha_i < 1 k^{-1}$  denotes that prey species  $i$  is avoided in the diet.

For the estimation of selectivity in feeding, the plankton composition 10 m below and above the weighted mean depth of the clupeids was considered as the prey field (Fig. 2). In order to compare our method with the results of earlier studies that evaluated vertically integrated zooplankton sampling, we estimated selectivity simulating integrated plankton samples (day: 41–80 m, night: 0–40 m and day or night: 0–80 m). In order to highlight fluctuations in the selectivity values over the diurnal cycle, we estimated selectivity indices for the copepodite stages of *Temora longicornis* and *Pseudocalanus acuspes* not only over the diel cycle but also pooled for day and night from the average stomach contents. *T. longicornis* and *P. acuspes* were chosen since these 2 species dominate the

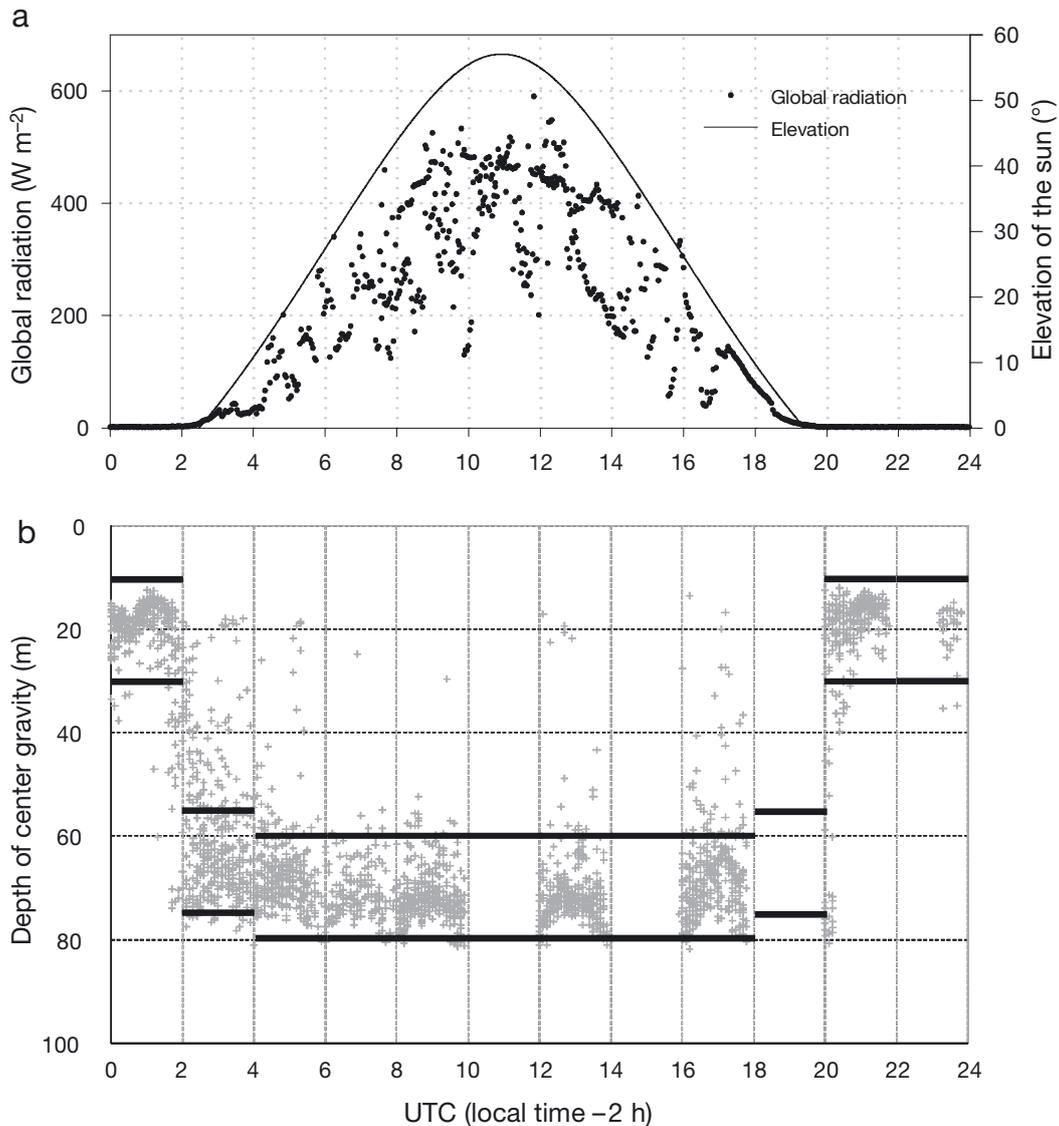


Fig. 2. (a) Measured global radiation (dots) and calculated elevation of the sun (line) on 4 June 2001 at the sampling location. (b) Vertical distribution of fish, represented as weighted mean depth of echo signals at time of day from a 48 h station (4 to 6 June 2001) in the central Bornholm Basin. Each dot represents the weighted mean depth of an echo profile, integrated over 0.1 n miles. Gaps represent times of day that were not covered by hydroacoustics. Black horizontal bars indicate the depth range of the plankton composition that was used for the estimation of prey selectivity

diet of herring and sprat (up to 90%) in the southern and central Baltic (Möllmann & Köster 1999, Casini et al. 2004, Möllmann et al. 2004). The progression of prey selectivity was calculated and displayed in 3 h intervals. In the graphic presentation, the midpoints of these intervals are displayed (01:30, 04:30, ..., 22:30 h). In the analyses, herring was grouped into 2 size classes, small herring (12 to 19.9 cm, mean wet mass [WM] 31.3 g) and large herring (20 to 25.9 cm, mean WM 66.5 g). Previous feeding studies in the Baltic Sea demonstrated that a change in herring diet occurred at approximately

20 cm of total length, after which larger food items like mysids are increasingly found (Casini et al. 2004, Möllmann et al. 2004). Accordingly, we chose this length as a threshold in our study. For sprat, analyses were conducted for one grouped size class (11 to 15.9 cm, mean WM 15.9 g).

We statistically tested for differences between a mean selectivity value and the value for random feeding by testing the null hypothesis that the alpha index is equal to  $1 k^{-1}$  (Rudershausen et al. 2005). For selected prey species, variations between prey selectivity estimation methods (different plankton sam-

pling methods) were analyzed using the Friedman rank sum test and post-hoc test at  $p < 0.05$  significance level. Data were analysed using statistical software R (R version 12.2.0).

### Niche overlap

The niche overlap of herring and sprat was estimated using the percentage overlap index, sometimes referred to as the Renkonen index or Schoener overlap index (Krebs 1999). This measure is calculated as a percentage and is given by

$$P_{jk} \left[ \sum_{i=1}^n (\min p_{ij}, p_{ik}) \right] \times 100 \quad (4)$$

where  $P_{jk}$  is the percentage overlap between species  $j$  and species  $k$ ,  $p_{ij}$  is the proportion resource  $i$  is of the total resources used by species  $j$ ,  $p_{ik}$  is the proportion resource  $i$  is of the total resources used by species  $k$  and  $n$  is the total number of resource states. The percentage overlap was calculated for 3 h intervals over the 24 h period.

## RESULTS

### Hydrography

The mean water depth at the sampling sites was 85 m and the hydrographic depth profile measured was typical for the Bornholm Basin in June (Fig. 3). The temperature was constant at approximately 10°C in the surface layer and decreased between 20 and 55 m to 3.5°C. Between 55 and 80 m, the temperature increased to 7°C. The salinity was constant at 9 psu in the surface layer and decreased slightly to 8 psu at 55 m. Below 55 m, the salinity increased to 17 psu at 80 m. The concentration of dissolved oxygen was about 8 ml l<sup>-1</sup> in the surface layer, decreased to 6 ml l<sup>-1</sup> at 55 m and declined rapidly from the upper limit of the halocline at 55 m to approx. 0 ml l<sup>-1</sup> at 80 m.

### Fish distribution

For linking the diel vertical distribution of the clupeids with the amount of daylight, total global radiation was measured with a ship mounted pyranometre in W m<sup>-2</sup> (Fig. 2). For comparison, the elevation of the sun was computed using the 'Sundi' software (V 1.1), global radiation (W m<sup>-2</sup>) was measured onboard RV

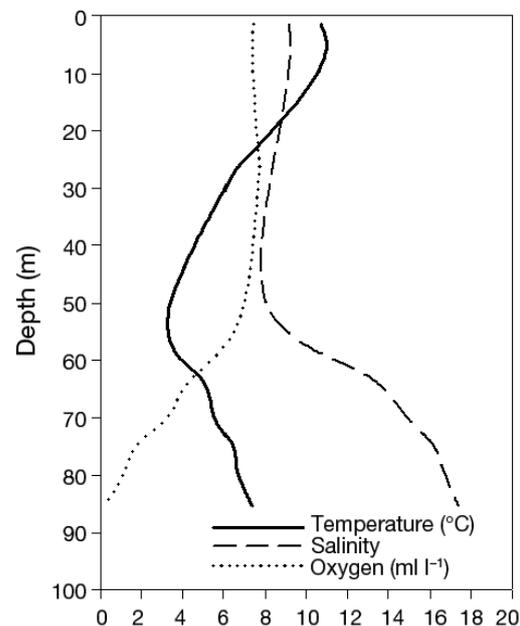


Fig. 3. Vertical profiles of temperature (°C), salinity (psu) and oxygen (ml l<sup>-1</sup>) on 5 June 2001, Bornholm Basin

'Alkor' and recorded at 5 min intervals. Additionally, the elevation of the sun was calculated for location and time of this study using an algorithm ([www.jgiesen.de/SME/tk/index.htm](http://www.jgiesen.de/SME/tk/index.htm)). The measured global radiation was in accordance with the calculated elevation of the sun. Sunrise was at 02:27 h UTC and sunset at 19:23 h UTC.

A distinct diel pattern was evident in the vertical distribution of herring and sprat (Fig. 2b). During daytime, most fish were located between 60 and 80 m depth, below the upper limit of the halocline. Between 18:00 and 21:00 h, both herring and sprat moved up in the water column to the surface layer and, between 22:00 and 02:00 h, were concentrated at 20 m around and above the upper limit of the thermocline. At 02:00 h, the downward movement started and ended at approximately 04:00 h, when fish concentrated between 60 and 80 m again. Due to labour law regulations, measurements were not continuously possible and, therefore, the gaps represent times of the day that were not covered by hydroacoustics. A detailed description of this daily pattern can be found in Stepputtis (2006). On average, 91.8% of all caught fishes were sprat, 4.5% were herring and 3.5% cod *Gadus morhua*. A mean density of 1.74 million fish n miles<sup>-2</sup> was estimated from hydroacoustics, with 1.6 million sprat n miles<sup>-2</sup>, 0.08 million herring n miles<sup>-2</sup> and 0.6 million cod n miles<sup>-2</sup>.

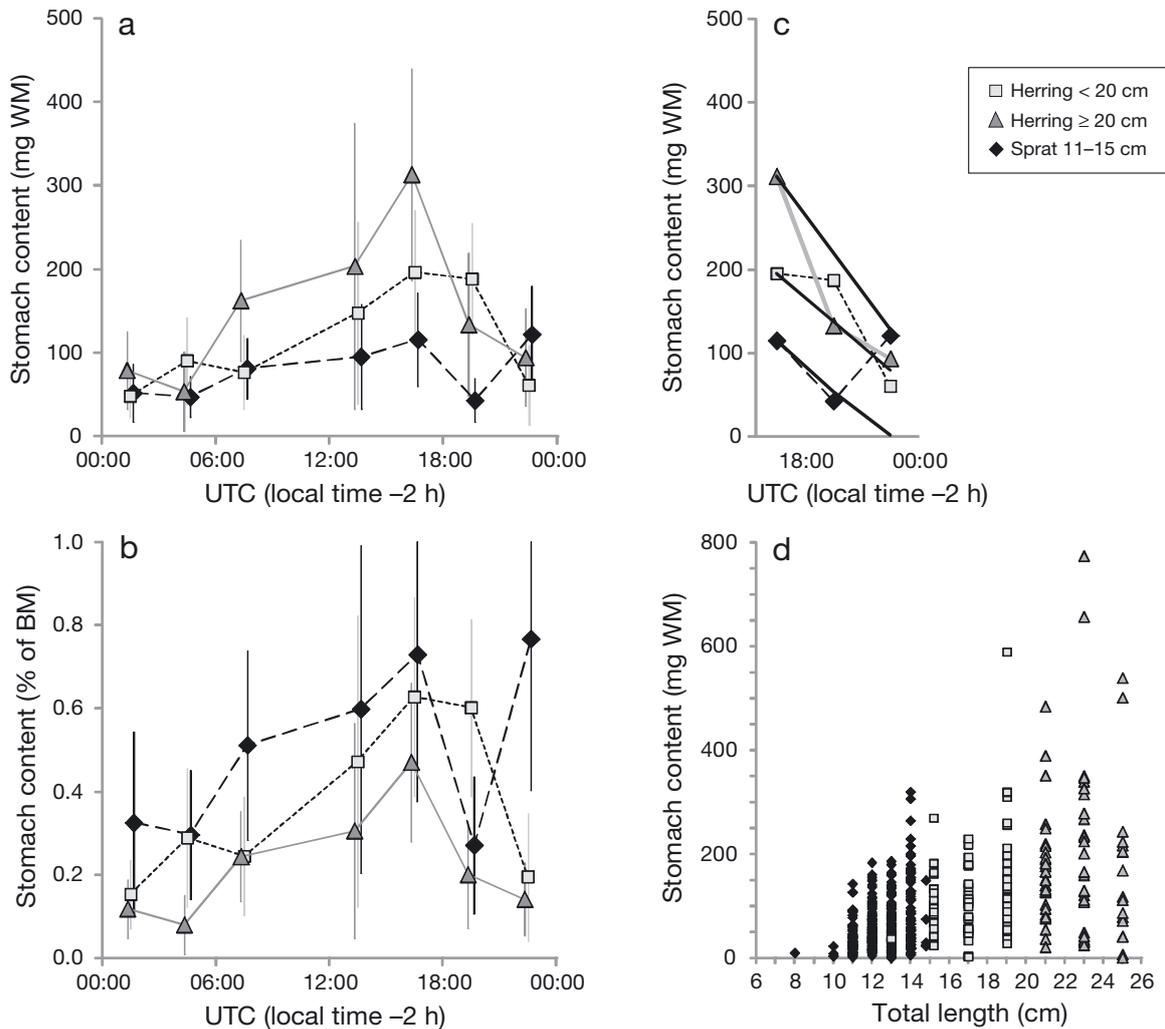


Fig. 4. *Clupea harengus* and *Sprattus sprattus*. (a) Mean ( $\pm$ SD) stomach content of herring and sprat in mg wet mass (WM) over the 24 h period (UTC). Data were pooled over 3 h intervals; data points represent mid-points of these intervals; this applies for (b) and (c) as well. Each point represents the mean of 10 to 38 replicate stomachs. (b) Mean ( $\pm$ SD) relative stomach content (% wet body mass, BM). (c) Theoretical course of gastric evacuation from the time of highest stomach contents at 16:30 h (starting point in graph) until midnight (according to evacuation parameters in Bernreuther et al. 2008, 2009). Black lines indicate stomach content without feeding; grey, dashed and dotted lines indicate stomach content observed in the field. (d) Absolute stomach content (mg WM) versus total length (cm)

### Total stomach content

The mean stomach content increased more or less steadily from the lowest value of 47 mg WM in sprat (11–15.9 cm), 48 mg WM in small herring (12–19.9 cm) and 54 mg WM in large herring (20–25.9 cm) during nighttime hours to a peak value at 16:30 h for both small (196 mg WM) and large herring (313 mg WM) and at 22:30 h for sprat (122 mg WM, Fig. 4a). The highest stomach contents in terms of percent wet body mass (% BM) were 0.77% for sprat at 22:30 h and 0.63 and

0.47% for small and large herring, respectively, at 16:30 h (Fig. 4b). The stomach content in % BM was, with one exception, higher in sprat compared to small herring (Fig. 4b). In similar-sized sprat and herring (15 cm), stomach contents were similar (Fig. 4d). The deviation of the field stomach contents from the theoretical prediction of stomach contents based on parameters derived from gastric evacuation experiments in the laboratory (Bernreuther et al. 2008, 2009) revealed that in contrast to herring, sprat were actively feeding from 19:30 to 22:30 h (Fig. 4c).

Table 1. Mean abundance (ind. m<sup>-3</sup>) from multinet catches over the 24 h investigation period in 10 m intervals. *Acartia* spp. includes *A. bifilosa* and *A. longiremis*, whereas *Podon* spp. includes *P. intermedius*, *P. leuckarti* and *P. polyphenoides*. *Synchaeta* spp. includes *S. monopus* and *S. baltica*. Last column presents the absolute abundance aggregated over the whole water column (0–80 m). Additionally, for copepods *Pseudocalanus acuspes* and *Temora longicornis* the vertically resolved abundance of copepodite stages is presented. C: copepodite stage; f: female; m: male; indet.: undetermined

Species	Depth (m)								
	0–10	11–20	21–30	31–40	41–50	51–60	61–70	71–80	0–80
<b>Copepods</b>									
<i>Acartia</i> spp.	3792	2248	2074	3377	3880	774	613	368	2141
<i>Centropages hamatus</i>	7107	1741	506	1009	1320	1011	390	169	1657
<i>Eurytemora affinis</i>	0	0	0	0	0	13	0	7	3
<i>Oithona similis</i>	30	20	186	883	262	386	2109	1839	714
<i>Pseudocalanus acuspes</i>	2950	2211	3353	4590	3958	3329	2237	1673	3037
C1	555	547	1110	427	414	147	150	96	431
C2	686	512	1102	1150	847	379	197	168	630
C3	1225	802	745	1781	1548	1011	488	320	990
C4	388	251	245	678	658	858	503	426	501
C5	83	58	54	411	284	501	419	447	282
C6f	10	41	87	126	184	388	348	137	165
C6m	3	0	10	17	23	47	132	79	39
<i>Temora longicornis</i>	3003	1407	1338	1059	1794	1093	633	198	1316
C1	328	248	60	20	141	48	60	4	114
C2	503	300	263	51	201	72	67	28	186
C3	495	251	256	72	180	127	93	33	188
C4	574	112	246	194	128	69	82	45	181
C5	518	122	308	254	224	189	53	42	214
C6f	313	149	94	241	437	237	138	27	205
C6m	272	225	111	227	483	351	140	19	229
Copepod indet.	407	185	185	283	229	206	453	168	264
Copepod eggs	32	28	66	87	340	566	379	110	201
Nauplii	4763	3249	1791	1539	3436	1816	1593	371	2320
<b>Cladocerans</b>									
<i>Bosmina l. maritima</i>	72	7	0	7	3	4	0	0	12
<i>Evadne nordmanni</i>	1273	507	218	573	648	171	193	59	455
<i>Podon</i> spp.	95	89	13	0	122	23	10	10	45
<b>Others</b>									
Bivalvia larvae	927	232	15	69	194	34	6	18	187
Fish eggs	0	2	1	0	4	14	7	15	5
<i>Fritillaria borealis</i>	138	34	47	375	446	354	193	78	208
Polychaeta larvae	0	8	8	37	8	33	70	107	34
<i>Synchaeta</i> spp.	942	1317	2015	3563	11812	6400	1083	111	3405

### Food availability

The zooplankton community during the investigation was dominated by the copepods *Acartia* spp. (*A. bifilosa* and *A. longiremis*), *Centropages hamatus*, *Pseudocalanus acuspes*, *Temora longicornis* and unidentified copepod nauplii (Table 1). Additionally, *Synchaeta* spp. were very abundant.

From the surface down to 10 m, *Centropages hamatus* was the most abundant species (7107 ind. m<sup>-3</sup>); its abundance decreased with depth (Table 1, Fig. 5). The cladocerans *Evadne nordmanni* and *Podon* spp. showed highest abundances with 1273 and 122 ind. m<sup>-3</sup> at 0 to 10 m and 41 to

50 m, respectively. Both *Pseudocalanus acuspes* and *Temora longicornis* were present at all depths, but highest abundances were observed at 31 to 40 m with 4590 ind. m<sup>-3</sup> of *P. acuspes* and at 0 to 10 m with 3003 ind. m<sup>-3</sup> of *T. longicornis*. The relative distribution of selected species (Fig. 5) indicates a different vertical distribution between day and night, e.g. *T. longicornis*, *C. hamatus* and *Podon* spp. having a relative abundance of more than 60% in the uppermost layer (0 to 10 m) during nighttime, while the abundance in the same layer during daytime was at 10% for *T. longicornis*, 40% for *C. hamatus* and less than 20% for *Podon* spp.

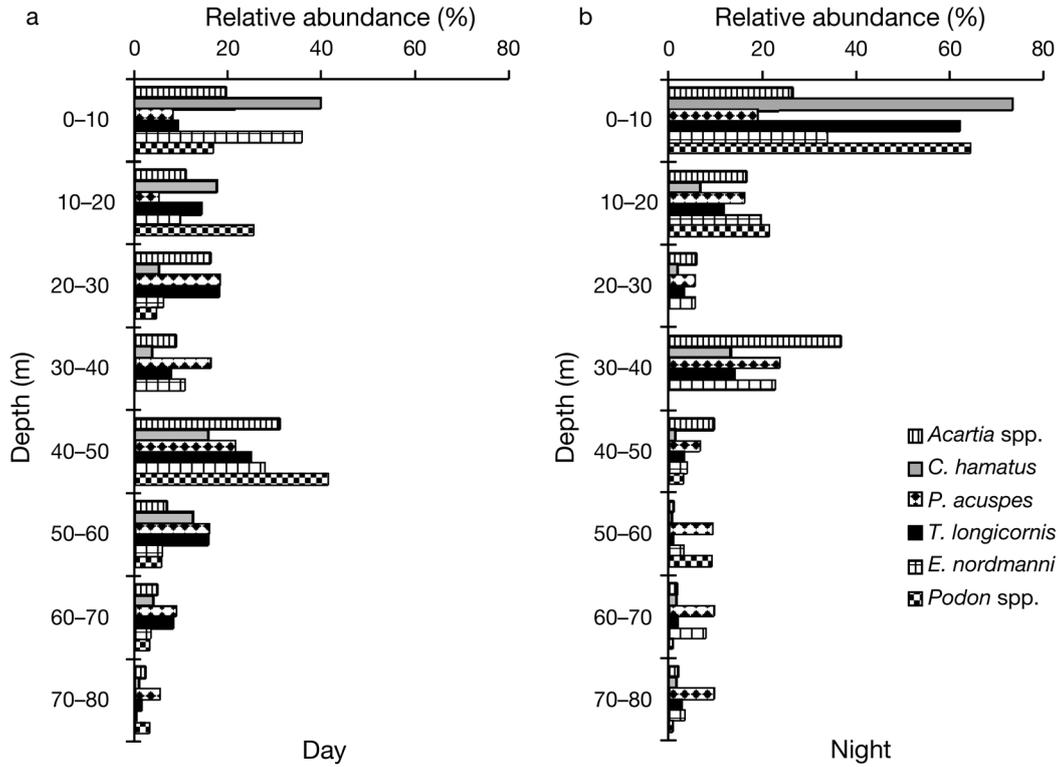


Fig. 5. Relative abundance (%) of the most important prey species from multinet catches presented for (a) day and (b) night. The value per 10 m depth interval and species is relative abundance over the whole water column. *Acartia* spp. includes *A. bifilosa* and *A. longiremis*, whereas *Podon* spp. includes *P. intermedius*, *P. leuckarti* and *P. polyphenoides*. See Table 1 for other species names

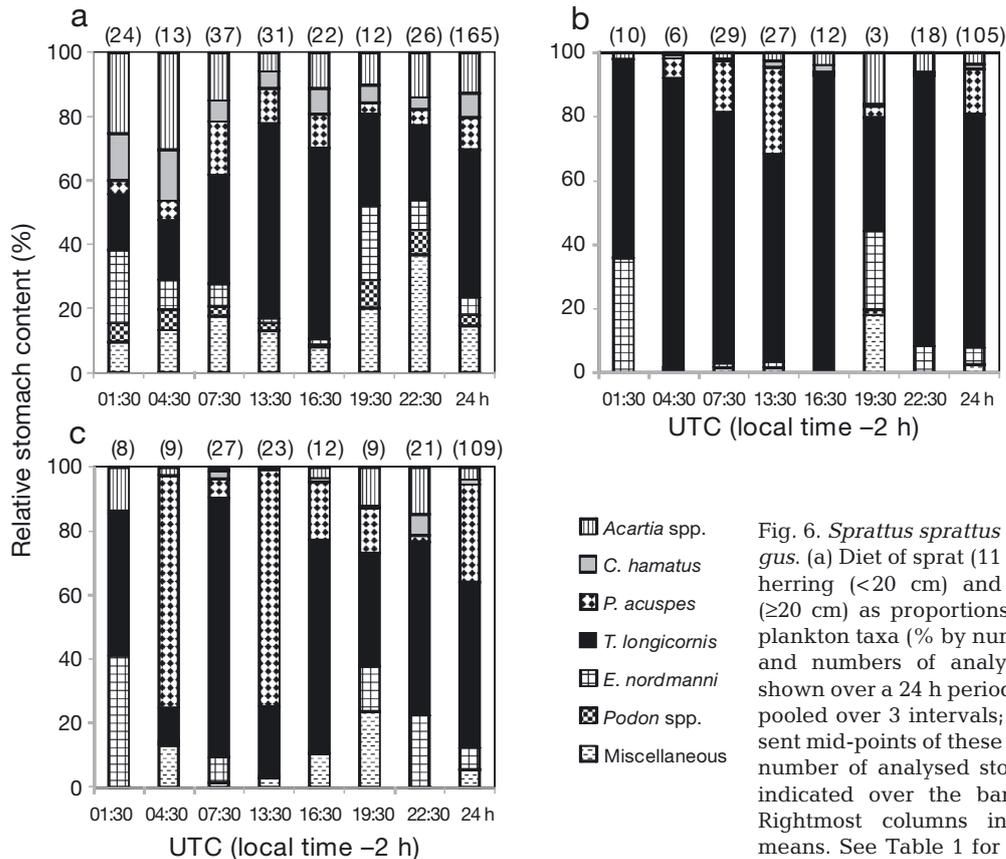


Fig. 6. *Sprattus sprattus* and *Clupea harengus*. (a) Diet of spratt (11 to 15 cm), (b) small herring (<20 cm) and (c) large herring (≥20 cm) as proportions of identified zooplankton taxa (% by numbers). Proportions and numbers of analysed stomachs are shown over a 24 h period (UTC). Date were pooled over 3 intervals; time points represent mid-points of these intervals. The total number of analysed stomachs per time is indicated over the bars in parentheses. Rightmost columns indicate the 24 h means. See Table 1 for full species names

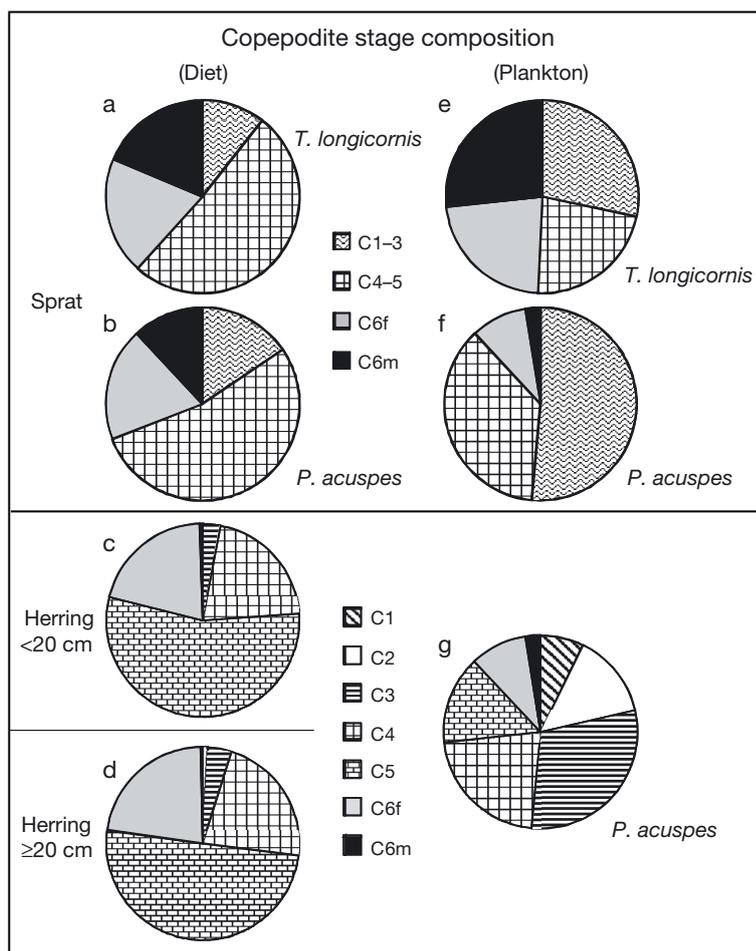


Fig. 7. *Sprattus sprattus* and *Clupea harengus*. Stage-specific copepod diet of sprat (a: *Temora longicornis*; b: *Pseudocalanus acuspes*), small herring (<20 cm, c: *P. acuspes*) and large herring (≥20 cm, d: *P. acuspes*) as proportions of total numbers (%) as well as relative copepodite stage composition of (e) *T. longicornis* and (f,g) *P. acuspes* in plankton catches (41–80 m depth). Data are 24 h means. C1–C6: copepodite stages; f: female; m: male

### Diet composition

The diet of sprat was more diverse compared to herring. The most important prey species for sprat were the copepods *Temora longicornis*, *Pseudocalanus acuspes*, *Acartia* spp. and *Centropages hamatus* and the cladoceran *Evadne nordmanni* (Fig. 6a). During the day, the most important prey species, by numbers, was *T. longicornis*, which made up to 60% of sprat gut contents, while during the night *E. nordmanni* (up to 23%) and *Podon* spp. were also found in large amounts. In *T. longicornis*, mainly older copepodites C4–5, representing 51.1% of all *T. longicornis* copepodites found in the stomachs, and adult (C6) females (19.7%) and males (18.7%) were consumed (Fig. 7a). In *P. acuspes*, the stage composi-

tion was similar with C4–5 representing 53.6% of all *P. acuspes* copepodites found in the stomachs and C6 females and males 18.9 and 12.0%, respectively (Fig. 7b).

The diet of both small (<20 cm) and large (≥20 cm) herring was dominated by *Temora longicornis* (Fig. 6b,c) with stomach contents (by numbers) of up to 93% in the afternoon (16:30 h). Other important prey species were *Pseudocalanus acuspes*, *Evadne nordmanni* and *Acartia* spp. While small herring were predominantly feeding on *T. longicornis*, large herring were additionally feeding intensively on *P. acuspes*. During the night, large amounts of the cladoceran *E. nordmanni* were found in the stomachs of herring. In *P. acuspes*, mainly older copepodites (C5, 55.0 and 50.3% in small and large herring, respectively) and adult (C6) females (20.6 and 22.4%, respectively) were consumed (Fig. 7c,d). Adult (C6) males were only observed in the stomachs in low numbers (0.4 to 0.5%). The plankton samples in both *T. longicornis* and *P. acuspes* were dominated by younger copepodite stages C1–3 (28 and 51%, respectively, Fig. 7e–g), while adult (C6f+m) *T. longicornis* were more common (49%) compared to *P. acuspes* (12%).

The niche overlap (NO) ranged from 20% at 04:30 h to 82.5% at 01:30 h between small and large herring (Fig. 8).

The NOs between sprat and small and large herring were in a similar range, with highest NO of 82% between sprat and large herring at 16:30 h.

### Selective feeding

The copepod *Temora longicornis* and the cladocerans *Evadne nordmanni* and *Podon* spp. were positively selected by sprat (Fig. 9, Table 2). During the middle of the day, we estimated the highest  $\alpha$ -values for *T. longicornis*. This copepod was almost exclusively selected between 12:00 and 18:00 h by sprat (max.  $\alpha$ -value: 0.64). Starting in the evening, sprat showed the highest preference for *Podon* spp. during the night and early morning, with *Podon* spp. being

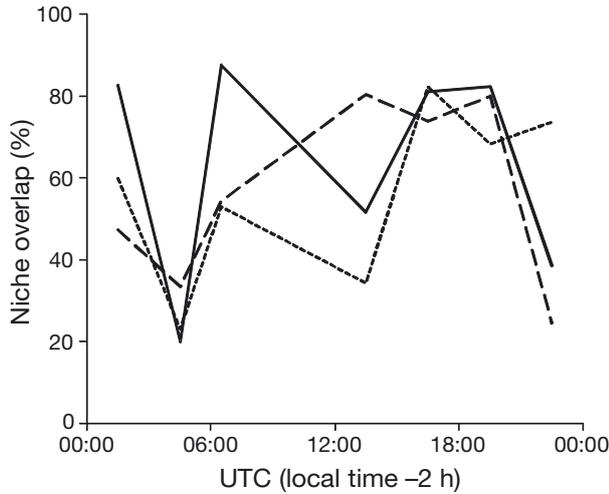


Fig. 8. Niche overlap (%) of the prey species consumed by small herring (<20 cm), large herring (≥20 cm) and sprat over the 24 h period (solid line: small and large herring; long dashed line: sprat and small herring; short dashed line: sprat and large herring). Data were pooled over 3 intervals; data points represent mid-points of these intervals

selected almost exclusively from 18:00 to 00:00 h, with a max.  $\alpha$ -value of 0.83. During the evening and night, sprat negatively selected for *T. longicornis*.

The stage-specific selectivity of *Temora longicornis* copepodites (Fig. 10a) revealed that sprat was positively selecting C4–5 copepodites during the entire investigation period. Adult (C6) females were only positively selected at 13:30 h ( $\alpha$ -value: 0.32), while during the remaining period females were either randomly chosen or negatively selected (Table 3). Sprat were positively selecting *Pseudocalanus acuspes* adult males during almost the entire 24 h period, whereas Stages 1 to 3 were negatively selected through the whole period and adult females were either randomly chosen or negatively selected (Fig. 10a, Table 3).

*Temora longicornis*, *Evadne nordmanni* and *Podon* spp. were the prey species being positively selected for by small and large herring (Fig. 9), with highest selectivity indices for *T. longicornis*. Additionally,

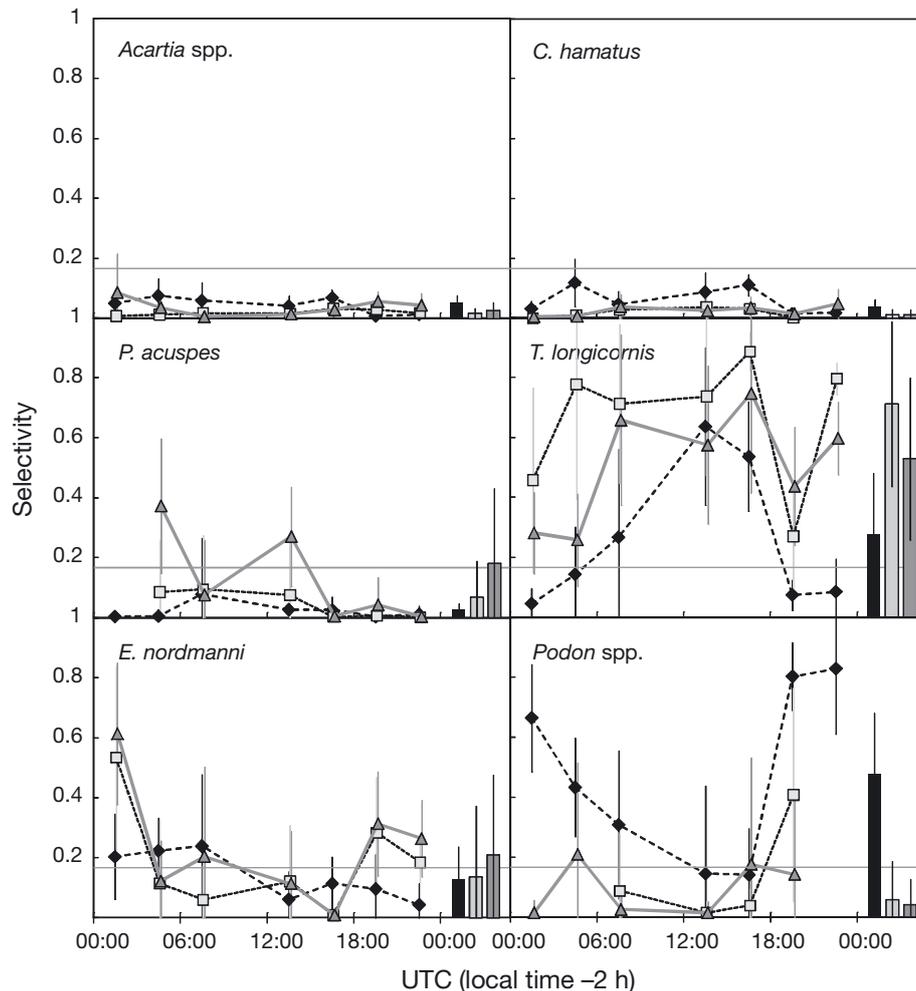


Fig. 9. *Sprattus sprattus* and *Clupea harengus*. Species-specific selectivity (Chesson's  $\alpha$ ,  $\pm$ SD) for important prey species of sprat ( $\blacklozenge$ ), small herring ( $\square$ ) and large herring ( $\blacktriangle$ ). Grey horizontal line indicates  $1 k^{-1}$  (random feeding) for the presented prey species combined. Vertical bars indicate average ( $\pm$ SD) species-specific selectivity estimates for the 24 h period. Data were pooled over 3 h intervals; data points represent mid-points of these intervals. See Table 1 for full species names

Table 2. *Sprattus sprattus* and *Clupea harengus*. Mean prey type selectivity (Chesson's  $\alpha$ ) for sprat, small (<20 cm) and large ( $\geq 20$  cm) herring for different time periods. Values not significantly ( $p > 0.05$ ) different from  $1 k^{-1}$  (0.167) are indicated by 'ns'.  $k$  = random feeding. Data were pooled over 3 h intervals; time points represent mid-points of these intervals. See Table 1 for full species names

Prey	Predator	Time (h, UTC)							
		01:30	04:30	07:30	13:30	16:30	19:30	22:30	24
<i>Acartia</i> spp.	Sprat	0.051	0.076	0.056	0.042	0.069	0.008	0.013	0.051
	Herring <20 cm	0.008	0.013	0.017	0.016	0.032	0.03	0.018	0.017
	Herring $\geq 20$ cm	0.077 <sup>ns</sup>	0.036	0.005	0.013	0.025	0.057	0.044	0.027
<i>C. hamatus</i>	Sprat	0.033	0.109 <sup>ns</sup>	0.048	0.086	0.108	0.014	0.021	0.042
	Herring <20 cm	0.001	0.011	0.029	0.038	0.032	0.004	–	0.013
	Herring $\geq 20$ cm	0.004	0.003	0.03	0.013	0.034	0.008	0.092	0.013
<i>P. acuspes</i>	Sprat	0.004	0.004	0.08	0.027	0.026	0.003	0.012	0.027
	Herring <20 cm	–	0.085 <sup>ns</sup>	0.094	0.075	0.003	0.006	0.001	0.068
	Herring $\geq 20$ cm	–	0.372 <sup>ns</sup>	0.071	0.27	0.004	0.043	0.004	0.181 <sup>ns</sup>
<i>T. longicornis</i>	Sprat	0.063	0.143 <sup>ns</sup>	0.267	0.637	0.536	0.075	0.085	0.276
	Herring <20 cm	0.457	0.777	0.712	0.736	0.886	0.270 <sup>ns</sup>	0.796	0.712
	Herring $\geq 20$ cm	0.281	0.258 <sup>ns</sup>	0.658	0.574	0.747	0.437	0.598	0.528
<i>E. nordmanni</i>	Sprat	0.204 <sup>ns</sup>	0.224 <sup>ns</sup>	0.240 <sup>ns</sup>	0.061	0.115	0.096 <sup>ns</sup>	0.043	0.130 <sup>ns</sup>
	Herring <20 cm	0.534	0.114 <sup>ns</sup>	0.06	0.121 <sup>ns</sup>	0.009	0.283 <sup>ns</sup>	0.185 <sup>ns</sup>	0.136 <sup>ns</sup>
	Herring $\geq 20$ cm	0.614	0.122 <sup>ns</sup>	0.183 <sup>ns</sup>	0.104 <sup>ns</sup>	0.008	0.313	0.263 <sup>ns</sup>	0.210 <sup>ns</sup>
<i>Podon</i> spp.	Sprat	0.664	0.433	0.308	0.146 <sup>ns</sup>	0.142 <sup>ns</sup>	0.803	0.828	0.474
	Herring <20 cm	–	–	0.088	0.015	0.039	0.408 <sup>ns</sup>	–	0.057
	Herring $\geq 20$ cm	0.015	0.209 <sup>ns</sup>	0.026	0.014	0.176 <sup>ns</sup>	0.142 <sup>ns</sup>	–	0.041

Table 3. Mean copepodite stage (or stage group, C1–C6) selectivity (Chesson's  $\alpha$ ) for *Temora longicornis* and *Pseudocalanus acuspes* by sprat and *P. acuspes* by small (<20 cm) and large ( $\geq 20$  cm) herring for different time periods. Data were pooled over 3 h intervals; time points represent mid-points of these intervals. Values not significantly ( $p > 0.05$ ) different from  $1 k^{-1}$  ( $1 k^{-1} = 0.25$  for *P. acuspes* and *T. longicornis* in sprat and  $1 k^{-1} = 0.167$  for *P. acuspes* in herring) are indicated by 'ns'.  $k$  = random feeding; f: female; m: male

Prey	Stage	Time (h, UTC)							
		01:30	04:30	07:30	13:30	16:30	19:30	22:30	24 h
<i>T. longicornis</i> (sprat)	C1–3	0.325 <sup>ns</sup>	0.113	0.159	0.047	0.083	0.077	0.072	0.085
	C4–5	0.439	0.545	0.333	0.357	0.415	0.282 <sup>ns</sup>	0.329	0.38
	C6f	0.154	0.195 <sup>ns</sup>	0.246 <sup>ns</sup>	0.324	0.233 <sup>ns</sup>	0.459 <sup>ns</sup>	0.280 <sup>ns</sup>	0.304
	C6m	0.082	0.146	0.268 <sup>ns</sup>	0.272 <sup>ns</sup>	0.270 <sup>ns</sup>	0.181 <sup>ns</sup>	0.389 <sup>ns</sup>	0.231
<i>P. acuspes</i> (sprat)	C1–3	0.124	0.023	0.035	0.022	0.043	0.017	0.023	0.036
	C4–5	0.576	0.248 <sup>ns</sup>	0.105	0.117	0.107	0.074	0.230 <sup>ns</sup>	0.232 <sup>ns</sup>
	C6f	0.08	0.078 <sup>ns</sup>	0.145	0.202 <sup>ns</sup>	0.105	–	0.216 <sup>ns</sup>	0.242 <sup>ns</sup>
	C6m	0.220 <sup>ns</sup>	0.650 <sup>ns</sup>	0.715	0.662	0.746	0.909	0.531 <sup>ns</sup>	0.49
<i>P. acuspes</i> (herring <20 cm)	C2	–	–	–	0.001	–	–	–	0
	C3	–	0.002	0.028	0.012	0.298 <sup>ns</sup>	0.069	–	0.027
	C4	–	0.157 <sup>ns</sup>	0.209	0.230 <sup>ns</sup>	0.264 <sup>ns</sup>	0.313 <sup>ns</sup>	–	0.170 <sup>ns</sup>
	C5	–	0.447 <sup>ns</sup>	0.413	0.379	0.151 <sup>ns</sup>	0.347 <sup>ns</sup>	–	0.414
	C6f	–	0.320 <sup>ns</sup>	0.35	0.339	0.287 <sup>ns</sup>	0.271 <sup>ns</sup>	–	0.382
	C6m	–	–	–	0.039	–	–	–	0.006
<i>P. acuspes</i> (herring $\geq 20$ cm)	C2	–	–	0.004	0.01	–	–	–	0.002
	C3	–	0.008	0.039	0.043	0.046	0.068	–	0.027
	C4	–	0.099	0.236 <sup>ns</sup>	0.223	0.300 <sup>ns</sup>	0.126 <sup>ns</sup>	0.139 <sup>ns</sup>	0.177 <sup>ns</sup>
	C5	–	0.556	0.391	0.354	0.365	0.61	0.789	0.484
	C6f	–	0.219 <sup>ns</sup>	0.329	0.362	0.289 <sup>ns</sup>	0.197 <sup>ns</sup>	0.072 <sup>ns</sup>	0.294
	C6m	–	0.118 <sup>ns</sup>	–	0.009	–	–	–	0.017

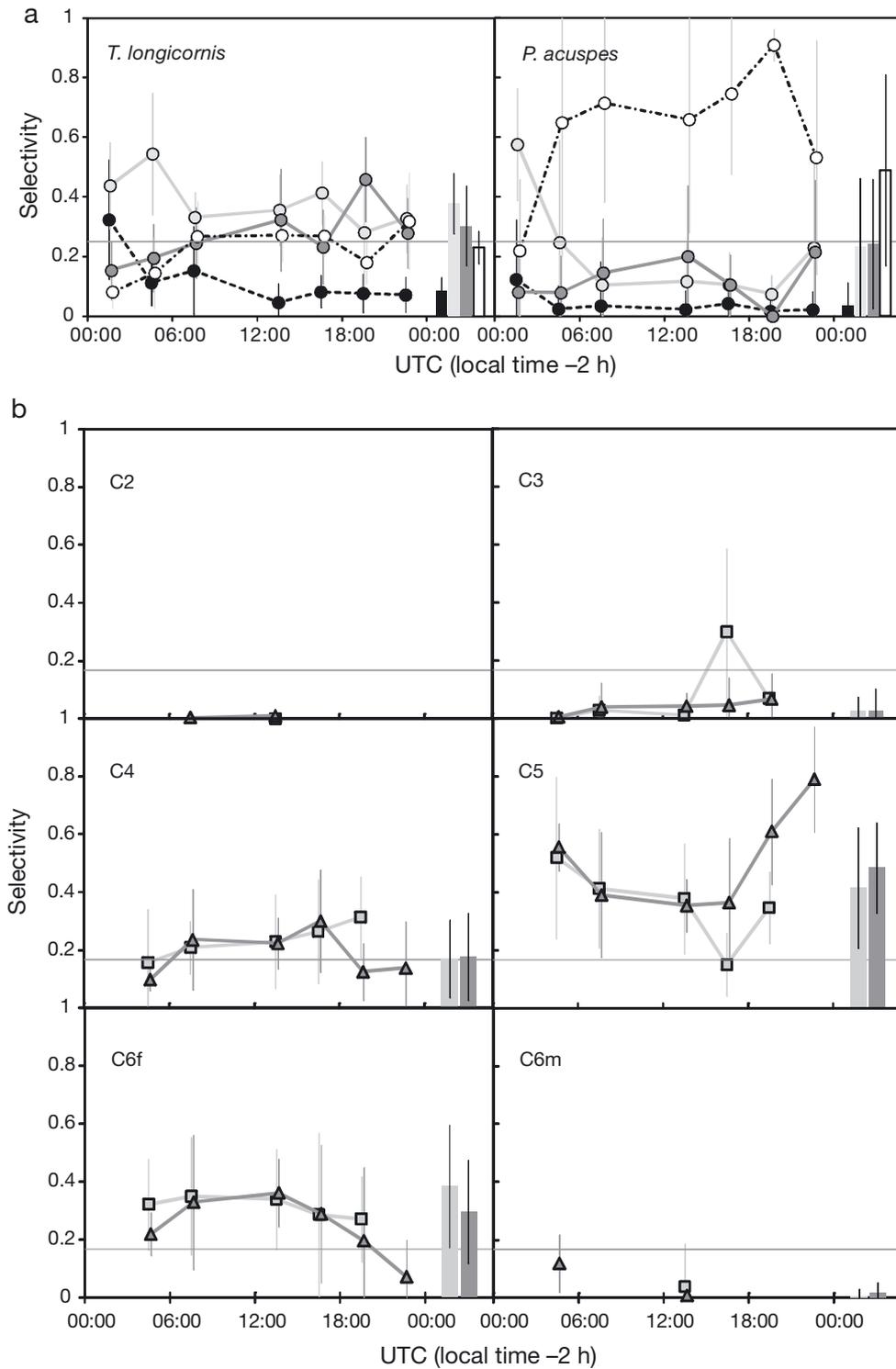


Fig. 10. *Sprattus sprattus* and *Clupea harengus*. (a) Stage-specific selectivity indices (Chesson's  $\alpha$ ,  $\pm$ SD) for *Temora longicornis* and *Pseudocalanus acuspes* in sprat (C1–3: ●; C4–5: ○; C6 females (f): ●; and C6 males (m): ○). Grey horizontal line indicates  $1 k^{-1}$  (random feeding) for stages C1–3 to C6 females (f) and males (m). Vertical bars indicate average stage-specific selectivity estimates for the 24 h period (black: C1–3, medium grey: C4–5, dark grey: C6 females, white: C6 males). (b) Stage-specific selectivity indices (Chesson's  $\alpha$ ,  $\pm$ SD) for *P. acuspes* in small (<20 cm, □) and large ( $\geq$ 20 cm, ▲) herring. Grey horizontal line indicates  $1 k^{-1}$  (random feeding) for copepodite stages C2 to C6 females (f) and males (m). Vertical bars indicate average stage-specific selectivity estimates for the 24 h period (medium grey: herring <20 cm; dark grey: herring  $\geq$ 20 cm). Data were pooled over 3 h intervals; time points represent mid-points of these intervals

Table 4. Friedman rank sum test and post-hoc test for different prey items and copepodite stage groups of *Temora longicornis* in *Sprattus sprattus*. We tested for significant differences in prey selectivity ( $\alpha$ ) between prey selectivity estimation method: A = plankton composition 10 m above and below mean weighted depth of sprat and herring *Clupea harengus* was pooled for the estimation (method used in this manuscript); B = plankton composition was pooled at 0–40 m (night) and 41–80 m (day); C = plankton composition was pooled over the entire water column (0–80 m). Significant differences between methods are indicated by capital letters ( $p < 0.05$ ), and the dashes indicate no significant differences between methods (e.g. 'AB,AC' indicates significant differences in the selectivity indices between Methods A and B and between A and C). Data were pooled over 3 h intervals; time points represent mid-points of these intervals. See Table 1 for full species names

Prey item	Time (h, UTC)						
	01:30	04:30	07:30	13:30	16:30	19:30	22:30
<i>Acartia</i> spp.	AB, AC	AB	AB, BC	AC, BC	AB, BC	AB, AC	AB, AC
<i>C. hamatus</i>	–	AC, BC	AC, BC	AB, AC, BC	AB, AC, BC	AB	AB, AC
<i>P. acuspes</i>	AB, AC	AC	AB, AC, BC	AB, AC, BC	AB, AC, BC	AB	AB, AC, BC
<i>T. longicornis</i>	BC	AC	AB, AC, BC	AC, BC	AB, AC, BC	AB	AB, AC, BC
<i>E. nordmanni</i>	AB, BC	AC	AB, AC, BC	AB, AC, BC	AB, AC, BC	AB	AB, AC, BC
<i>Podon</i> spp.	AB, AC, BC	AC, BC	AC, BC	BC	AC, BC	–	AB, AC
<i>T. longicornis</i>							
C1–3	AB, AC	BC	AB, AC, BC	AB, AC, BC	AB, AC, BC	AB	AB, AC, BC
C4–5	–	–	AB, AC, BC	AB, AC, BC	AB, AC, BC	AB	AB, BC
C6F	AC, BC	BC	AB, BC	AB, AC, BC	AB, AC, BC	AB	AB, AC, BC
C6M	AB, AC	–	AB, BC	AB, AC, BC	AB, AC, BC	–	AB, BC

*Pseudocalanus acuspes* was positively selected by large herring in the early morning (04:30 h) and afternoon (13:30 h). For both size classes of herring, the highest selectivity indices for *T. longicornis* were observed during daytime with  $\alpha$ -values up to 0.89 (small herring) and 0.75 (large herring) (Table 2). The cladocerans *E. nordmanni* and *Podon* spp. were mainly positively selected for during evening or night with highest  $\alpha$ -values of 0.53 and 0.61 for small and large herring, respectively, while they were mainly avoided or randomly chosen during the day (Fig. 9, Table 2).

The stage-specific selectivity of *Pseudocalanus acuspes* copepodites (Fig. 10b, Table 3) indicated that both small and large herring were positively selecting adult females and C5 copepodites during most of the investigation period. Highest  $\alpha$ -values were reached in C5 copepodites with 0.79 at night (22:30 h UTC = 00:30 h local time). C4 were also positively selected during the daytime, but since the results (with one exception) were not significantly different from  $1\text{ k}^{-1}$ , C4 copepodites were consumed randomly. C3 copepodites were negatively selected by small and large herring, with the exception of 16:30 h in large herring, where C3 copepodites were positively selected (Fig. 10b). Males were rarely observed in the stomachs of herring.

A comparison of the selectivity indices estimates of our method (Method A, vertically integrated plankton samples 10 m above and below the weighted mean depth of herring and sprat) and the estimation

by the commonly used methods with vertically integrated plankton samples (Method B, night: 0–40 m, day: 41–80 m and Method C, day and night: 0–80 m) revealed diverging results, depending on the time of the day (Table 4). The prey selectivity indices ( $\alpha$ ) as estimated by Methods A, B and C were not significantly different ( $p \geq 0.05$ ) in only a few instances. Significant differences between all 3 methods were observed in e.g. *Pseudocalanus acuspes*, *Temora longicornis* and *Evadne nordmanni*, as well as in copepodite stages of *T. longicornis* during the mean feeding period (13:30 h and 16:30 h). During other periods (19:30 h), the significant differences were almost entirely between our Method A and Method B (integrated plankton samples; night: 0–40 m, day: 41–80 m).

## DISCUSSION

### Diet composition and competition

This study demonstrated an intensive feeding competition between herring and sprat and indicated possible inter- and intra-specific competition avoidance strategies. The diets of sprat and herring were generally similar in our study. Sprat was exclusively zooplanktivorous and herring was also mainly zooplanktivorous, with few exceptions. Mysids occurred in low numbers in only a few stomachs. This was an expected result in the Baltic Sea, where the 2 top

planktivorous fish, sprat and herring, feed on a limited number of available prey species, and both fish dwell in the same areas and depths during certain periods of the season (Nilsson et al. 2003, Stepputtis 2006, Stepputtis et al. 2011). Previous studies demonstrated that herring typically consume low numbers of mysids in the Baltic basins during summer (especially low in June) and higher numbers are generally consumed during winter (Köster & Schnack 1994, Möllmann & Köster 1999, Möllmann et al. 2004). No phytoplankton was found in the diets of sprat or herring. This is in contrast to anchovy *Engraulis encrasicolus* and sardine *Sardinops sagax* in the Benguela Current ecosystem, and sardine *Sardina pilchardus* off the coast of Portugal and in the North Aegean Sea (Mediterranean Sea), where phytoplankton can play an important role in the diet of both species (van der Lingen 1998, Garrido et al. 2008, Nikolioudakis et al. 2011). Interestingly, a study on the diet composition of anchovy *E. encrasicolus* in the North and Baltic Seas indicated that this species was exclusively zooplanktivorous in these regions, showing a high overlap in the diet with herring and sprat (Raab et al. 2011). The overall diet results of sprat and herring agree with previous studies (Rudstam et al. 1992, 1994, Arrhenius 1996, Szyplula et al. 1997, Möllmann & Köster 1999, Casini et al. 2004, Möllmann et al. 2004). In the diet of small herring (<20 cm), *Temora longicornis* was more important than in the diet of large herring ( $\geq 20$  cm), where *T. longicornis* played an important role at certain periods (03:00 to 06:00 h and 12:00 to 15:00 h UTC); however, in general, *Pseudocalanus acuspes* was the most important prey species. During the day, *T. longicornis* was found in highest amounts in sprat diet, indicating intensive competition for this resource (Casini et al. 2006).

The NO (%), as an indicator of competition, confirms these observations. It varied between 20 and 80% but was usually high (>40%). Both sprat and herring showed a similar diel feeding trend, with highest stomach contents of up to 0.77% BM in sprat and 0.63% BM in small herring. Apparently, neither of the 2 species gained an advantage in terms of higher food intake in the specific feeding situation. Despite the fact that higher mean relative stomach contents have been observed in both sprat (up to 2.8% BM in the Black Sea, Sirotenko & Sorokalit 1979) and herring (up to 4% BM in the Barents Sea, Huse & Toresen 1996), the prey concentration was sufficient for both species to reach average relative stomach contents (Möllmann et al. 2004).

Yet, there are indications that both herring and sprat potentially try to avoid both inter- and intra-

specific competition. While sprat exhibited the most diverse diet, small herring were mainly feeding on *Temora longicornis*, which was also the case in large herring. Large herring were feeding intensively on *Pseudocalanus acuspes* during certain periods only. This resulted in a marked decrease in NO during periods when large herring were feeding on *P. acuspes*. The estimated prey selectivity may be interpreted as possible competition avoidance behavior patterns of herring and sprat. Sprat was either avoiding or randomly feeding on *Evadne nordmanni*, while herring was positively selecting this species at certain times. In turn, sprat was strongly selecting *Podon* spp. for a longer period, while herring, with few exceptions, was avoiding this prey. Additionally, in the morning and evening hours, herring was intensively selecting *T. longicornis*, while sprat was primarily selecting *Podon* spp. We observed this not only at a species level, but interestingly, also at the copepodite stage level. Sandström (1980) and Flinkman et al. (1992) observed in the Baltic Sea that size and visibility of prey were both important factors in the selection of prey by herring and that, in general, the largest food items were preferred. We can confirm this, as our results indicated that mainly older copepodite stages (C4–C6) were positively selected during most investigated periods. However, in *P. acuspes*, sprat was almost entirely selecting male C6, while herring was selecting C5 and female C6 and avoiding male C6.

To our knowledge, this is the first study to describe such diverging feeding behavior of herring and sprat with regard to copepod gender. On the one hand, these observations may suggest that either herring or sprat (or both) tend to specialize their diet to a certain extent in order to reduce inter-specific competition. But, on the other hand, there may be other explanations of the observed differences. The diurnal vertical migrations of small pelagic species like sprat, herring and anchovy are highly variable (Cardinale et al. 2003, Nilsson et al. 2003, Tsagarakis et al. 2012). The differences in stomach contents and selectivity between herring and sprat may partially be explained by differing vertical distributions of both species and different size classes of herring as observed in the Bornholm Basin in autumn (Cardinale et al. 2003), leading to different prey composition and densities experienced. Van der Lingen (1999) hypothesized that the sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* minimize competition in the Benguela Current ecosystem by partitioning food resources

according to prey size. A hypothesis that was supported by studies on the size composition of juvenile *S. sagax* and *E. encrasicolus* schools indicated that *S. sagax* ingested significantly smaller zooplankton prey than *E. encrasicolus* juveniles (Louw et al. 1998). Both anchovies and sardines are able to utilize filter- and particulate feeding (James & Findlay 1989, van der Lingen 1994, Garrido et al. 2007, Costalago et al. 2012) during the day and at night (Tudela & Palomera 1997, Palomera et al. 2007, Borme et al. 2009, Nikolioudakis et al. 2011), enabling them to optimize food intake in a variable and patchy environment.

A competition avoidance behavior as indicated by differing prey size was not observed in this study on herring and sprat. Both species feed mainly on the same stages (sizes) of 2 calanoid copepods in the Baltic Sea, even though herring can potentially also feed on larger prey like mysids, amphipods, polychaetes and fish eggs (Casini et al. 2004, Möllmann et al. 2004). From our 48 h process study, we have indications of predator-specific differences in diet selection with regard to copepod gender and the exploitation of cladocerans. However, it is not clear whether these differences reflect the behavior of herring and sprat or whether they are an indirect effect of vertical predator-prey overlap or are subtle morphological differences.

### Night feeding

It is generally assumed that herring and sprat only feed during daylight hours, including dusk and dawn (Köster & Schnack 1994, Arrhenius 1998, Cardinale et al. 2003, Pliru et al. 2012). To test whether both species were feeding at night despite the temporary decrease in stomach contents, we calculated the expected stomach contents based on gastric evacuation parameters derived from laboratory experiments starting with the peak stomach contents in the evening (Bernreuther et al. 2008, 2009). The herring (small and large) stomach contents decreased with some deviation from those estimated by the gastric evacuation parameters, indicating that they were either not feeding or feeding only to a minor extent (freshly ingested prey items were observed) while in the upper water layers. In contrast, sprat stomach contents increased instead of decreasing (which was predicted by the laboratory-derived parameters), indicating intensive night feeding by sprat. This was further supported by the fact that we observed freshly ingested food items at all times of the day or night.

Our study is the first to demonstrate night feeding of sprat. This result is particularly interesting because in contrast to sprat, our results indicate that herring were not feeding or only to a small extent at night. The ability of herring to employ filter-feeding has been observed and described in laboratory feeding studies (Batty et al. 1986, 1990, Brachvogel et al. 2013). This feeding mode has to this point not been observed in laboratory studies for sprat, where only strict particulate feeding has been observed (Bernreuther et al. 2009, Brachvogel et al. 2013). Analysis of the gill raker morphology of herring confirmed the ability of this species to filter-feed (Gibson 1988). To our knowledge, no similar study has been conducted for sprat. Supposing that the ability to feed by filtering particles out of the water is a prerequisite for night feeding, one may speculate that sprat are able to apply this feeding mode. However, since no study has proven this ability, we rather suggest that the light levels during our study (summertime in the northern hemisphere) were sufficient for particulate feeding, resulting in the observed increase in stomach contents. Ultimately, a morphological study on the feeding apparatus, especially the gill raker morphology, would help to solve the question about the ability or inability of sprat to filter-feed.

### Diel shift in prey preference

We observed a marked shift in the prey preference in sprat and to a lesser extent in herring over the diel cycle. Sprat was primarily selecting *Temora longicornis* during the day and then shifting its preference to the cladoceran *Podon* spp. during the evening, night and early morning. This shift was apparently linked to vertical up- and downward migration during the evening and morning and the fact that sprat dwell in the upper water column during the night. Herring was selecting *T. longicornis* during most of the investigation period, partly shifting to *Evadne nordmanni* during nighttime. Prey shifts are common in fish. Ontogenetic prey shifts are well described for fish species (e.g. Bromley et al. 1997, Mittelbach & Persson 1998, Xue et al. 2005). Diel shifts in the prey composition and feeding intensity have been described in different species, e.g. cod *Gadus morhua* (Adlerstein & Welleman 2000), whiting *Merlangius merlangus* (Rindorf 2003) or congipodid fish *Hypodytes rubripinnis* (Baba & Sano 1987), and are often linked to habitat shifts.

To our knowledge, a diel shift in prey preference has not been described in herring and sprat, and the

explanation for this behavior is not obvious. This shift in preference should not be confused with the commonly known prey switching (Murdoch 1969), where the predator preferentially (disproportionally more) feeds on the most common prey. Both clupeids prey on *Temora longicornis* and to some extent on *Pseudocalanus acuspes* during the day. These 2 copepods are rather large in the Baltic (up to 13 and 14  $\mu\text{g}$  carbon, C; Köster 2003, Hansen et al. 2006) compared to the cladocerans *Evadne nordmanni* and *Podon* spp. (up to 7 and 9  $\mu\text{g}$  C; Köster 2003), which are preferred during the night in the upper water column. Since *T. longicornis* and *P. acuspes* are present in the entire water column and *T. longicornis* even in higher numbers (ind.  $\text{m}^{-3}$ ) in the upper water column, we have to find another explanation for the shift in preference to the smaller and probably energy-poorer cladocerans. In depths between 60 and 80 m, where the 2 clupeids dwell during the daytime, both cladoceran (*E. nordmanni* and *Podon* spp.) were present but negatively selected or randomly chosen. The preference for *Podon* spp. over *T. longicornis* by sprat in the upper water layers may be due to an enhanced response reaction of *T. longicornis*. At depths of 60 to 80 m, the temperature was 4 to 7°C, while the temperature between 10 and 30 m varied between 6 and 10°C. *T. longicornis* is a euryhaline and eurythermal species of marine origin that is adapted to temperate environments (Holste et al. 2009, Dutz et al. 2010). The higher temperature between 10 and 30 m is closer to the optimum temperature for this species (15.0 to 16.6°C; Holste et al. 2009, Dzierzbicka-Glowacka et al. 2011), which may lead to a greater alertness to hydrodynamic signals that result in a rapid and more dynamic escape response. Viitasalo et al. (2001) studied zooplankton escape responses with artificial flow in the laboratory and found that the cladoceran *Bosmina longispina maritima* did not show any escape response, while *T. longicornis* showed a delayed escape response, making both species easy prey. A temperature increase of 2 to 3°C may lead to a more rapid escape response by *T. longicornis*, resulting in the observed preference shift over the diel cycle. Additionally, the visibility of the prey in the upper water column may also play an important role in prey selectivity (Peterson & Ausubel 1984). Evidence of an observed prey preference shift instead of prey switching is given in Table 1, indicating that the cladocerans are definitely not the most common prey items in water column between 10 and 30 m.

The night feeding of sprat and the difference in diet composition between day and night resulting from prey preference shifting underlines the impor-

tance of 24 h investigations. If differences in diet composition and feeding intensity over a diel cycle are not accounted for, this may lead to an underestimation of the predation impact on certain prey species or stages by consumption models based on gastric evacuation (discussed in Haertel & Eckmann 2002). Exact consumption estimations and the impact of predators on the prey populations are especially important in the Baltic Sea. Here, the sprat population can influence the development of *Pseudocalanus acuspes* and *Temora longicornis* (Möllmann & Köster 1999), as well as the egg survival of its most important predator, cod (Voss et al. 2011), and herring growth (Casini et al. 2010). A correct quantification of species interactions is also important for the ecosystem approach to fisheries management (Kempf et al. 2010). However, since this study was conducted in June, when the nights at high latitudes in the northern hemisphere are only a few hours long, this may only be a problem during this time of the year.

Is a vertically, temporarily and prey-stage resolved sampling scheme mandatory in understanding the prey preference of herring and sprat?

Most studies investigating selective feeding of herring and sprat lack a vertically resolved description of the prey field encountered by the predators. The plankton samples used for the estimation of selectivity indices were, with the exception of the investigation of Hansson et al. (1990), not vertically or stage-/sex-resolved (Sandström 1980, Flinkman et al. 1992, Arrhenius 1996, Casini et al. 2004).

A comparison of the results of our temporally (48 h), vertically and copepodite stage-resolved prey selectivity study with commonly used vertically pooled prey distributions (either day: 41–80 m and night: 0–40 m or day and night both 0–80 m) revealed some interesting results. It was only possible to detect the pronounced pattern in species and copepodite stage selectivity with the temporally resolved method. The average selectivity (24 h pooled) for *Podon* spp. by sprat for example, indicated an entirely positive selection. However, our method indicated that *Podon* spp. was randomly consumed during the middle of the day. Additionally, the results of the 24 h-pooled method can be misleading. According to this method, *Temora longicornis* was, in general, positively selected but only at an  $\alpha$ -value of 0.276 (random feeding = 0.167), whereas our method revealed that during the day sprat were almost exclusively selecting *T. longicornis* at high  $\alpha$ -values up to 0.64. Thus, in order to detect fluctuations or changes in the selectivity of herring and sprat, a tem-

porally resolved investigation is necessary. Yet, the temporal resolution of prey selectivity is only important for a detailed understanding of the feeding ecology of herring and sprat. For the quantification of the feeding pressure on the zooplankton, this is of minor interest. Here, the stage-resolving of copepodites is more relevant.

A comparison of grouped and stage-specific selectivity indices revealed the disadvantage of the non-stage-specific index. Grouped values or selectivity estimates underestimated the effect of the predator on the older stages of copepods. Our results demonstrated that sprat and herring were size-selective feeders, which removed older copepodite stages (C5) and reproducing individuals (C6), thereby potentially lowering the production of the zooplankton. Copepods are the main prey items of both sprat and herring in the Baltic Sea (e.g. Shvetsov et al. 1983, Möllmann & Köster 1999, Möllmann et al. 2004, 2008); therefore, our results suggest that the extent of top-down regulation of copepods by clupeids in the Baltic Sea may not be adequately assessed when stage-resolved methods are not employed. This conclusion is strengthened by the findings of Casini et al. (2009), who were able to show that variations in population size of sprat in the Baltic Sea can have implications (through feeding pressure) for ecosystem functioning.

Another aim of our study was to test whether a vertically resolved plankton analysis is mandatory for producing reliable estimates of the prey selectivity of the studied fish species. Estimates of the different methods indicate that the resulting prey selectivity indices are strongly dependent on the plankton sampling scheme. During the main feeding period in the afternoon, we estimated significant differences between all 3 methods. Based on this result, we cannot conclude whether our highly resolved sampling scheme gives generally the most reliable estimates of selectivity. This is rather a matter of scope. Our sampling scheme may be the most appropriate to resolve mechanistically the selection process on a small scale. When comparing the selectivity between night and day, pooling the plankton composition in the lower (during the day) and upper (during the night) water column appears sufficient to understand the prey selectivity of herring and sprat, due to the diel vertical migration of these clupeids in the Baltic Sea (Cardinale et al. 2003, Stepputtis 2006). For a comparison of the selectivity dynamics between different months or years, plankton integrated samples over the entire water column may be sufficient.

## CONCLUSIONS

The generally similar diets of herring and sprat (copepods *Temora longicornis*, *Pseudocalanus acuspes* and *Acartia* spp. along with cladocerans *Evadne nordmanni* and *Podon* spp.) indicated an intense feeding competition. This partly resulted in predator-specific differences in diet selection with regard to copepod gender and the exploitation of cladocerans, with sprat selecting *Podon* spp. during the night and adult (C6) males of *P. acuspes* during the day, and herring selecting *E. nordmanni* during parts of the night and C6 females of *P. acuspes* during the day. This was not only an inter-specific, but also an intra-specific specialization between small (<20 cm) and large ( $\geq 20$  cm) herring.

Estimations of stage-resolved selectivity revealed that sprat and herring were size-selective feeders, which removed older copepodite stages (C5) and reproducing individuals (C6), thereby potentially lowering the production of the zooplankton population.

A comparison of the observed stomach contents with the estimated gastric evacuation contents during the nighttime revealed that sprat was feeding intensively during the night, while herring was apparently not or only to a minor extent.

We observed a marked prey preference shift between day and night mainly in sprat and to a lesser extent in herring. Sprat strongly selected *Temora longicornis* as prey during the day and switched mainly to *Podon* spp. during the night. Small (<20 cm) and large ( $\geq 20$  cm) herring selected *T. longicornis* during most of the investigation period nighttime phases during which *Evadne nordmanni* was selected.

Different plankton sampling schemes, in the majority of cases, produced significantly different estimates, leading to the conclusion that the objective of a study should determine which zooplankton sampling scheme is most appropriate.

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