

Trophic decoupling of mesozooplankton production and the pelagic planktivores sprat *Sprattus sprattus* and herring *Clupea harengus* in the Central Baltic Sea

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ABSTRACT: Quantitative analysis of the predation impact of planktivores on zooplankton is essential for proper understanding of energy flow and trophic coupling in ecosystems. To quantify trophic dynamics between zooplankton and small pelagic fish in the Baltic Sea, we conducted a temporally resolved investigation on the diet, feeding and predation impact of the dominant planktivorous fish species sprat *Sprattus sprattus* L. and herring *Clupea harengus* L. in the Central Baltic Sea (Bornholm Basin). Bi-weekly to monthly coverage between April 2002 and November 2003 included net sampling of copepods, determination of predator stock size using hydro-acoustics and trawl surveys, and extensive stomach content sampling. Herring and sprat were mainly zooplanktivorous, feeding on the calanoid copepods *Temora longicornis*, *Pseudocalanus acuspes* and *Acartia* spp. and, in summer, on the cladocerans *Bosmina* spp. and *Podon* spp. We observed temporally high predation impact of sprat and herring on *T. longicornis* and *P. acuspes* in April and May, when more than the production of these 2 copepod species (copepodite stages C1-6) was consumed (consumption/production [C/P] > 3.5). However, the impact on the population dynamics of both copepods was negligible. Likewise, the impact on *Acartia* spp. was considered negligible (C/P < 0.1). Integrated over the year, utilization of estimated copepod production by both clupeids was comparatively low, with only 18% of the annual production of *T. longicornis* and 36% of the annual production of *P. acuspes* consumed; the production of *Acartia* species (1.4%) and cladocerans (2.3%) was almost completely unused. Use of only 9% of the combined production of copepods and cladocerans indicates poor trophic coupling between mesozooplankton and pelagic planktivores in the Central Baltic Sea.

KEY WORDS: Predation impact · Zooplanktivores · Open pelagic · Consumption versus production · Competition

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INTRODUCTION

According to food chain theory, naturally or anthropogenically induced changes at the top of a food chain can cascade down the food web, eventually influencing the biomass of primary producers (Hair-

stone et al. 1960). Although heavily debated (Chase 2000), these trophic cascades seem to be more prevalent in water than on land (Strong 1992, Polis 1999, Halaj & Wise 2001). In general, zooplanktivorous predators tend to reduce herbivore abundance, but the effect on marine zooplankton has been found to

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be weak (Shurin et al. 2002) or statistically insignificant (Micheli 1999). A few examples of strong cascading effects, restructuring pelagic food webs down to marine plankton, were demonstrated by Daskalov (2002), Frank et al. (2005) and Casini et al. (2008); however, the amount of evidence remains low.

The pelagic ecosystem of the Central Baltic Sea provides an example of an upper trophic level cascade due to the joint effects of overfishing and climate change (Köster et al. 2003). During the early 1990s, the stock of the top predator cod *Gadus morhua* L. collapsed due to climate-induced recruitment failure and high fishing pressure (Köster et al. 2005). The main food item of cod, i.e. sprat *Sprattus sprattus* L., subsequently increased to record levels due to recruitment success and lowered predation pressure (Köster et al. 2003, MacKenzie & Köster 2004, Casini et al. 2009, Eero et al. 2012). Sprat, together with herring *Clupea harengus* L., are the main planktivorous species in the system, preying chiefly on calanoid copepods (Möllmann et al. 2004). Subsequent to the drastic increase in sprat stock size, the dominant calanoid copepods showed different responses in abundance: *Acartia* spp. and *Temora longicornis* increased while *Pseudocalanus acuspes* (formerly often also called *P. elongatus* or *P. minutus elongatus*), decreased (Möllmann et al. 2000, 2003a). Casini et al. (2008) analysed long time-series of cod, clupeid and zooplankton biomass and interpreted the results as a trophic cascade, whereby the increasing clupeid biomass was responsible for the decline in aggregated zooplankton biomass.

The clupeids herring and sprat are size-selective feeders with generally similar diets in the Baltic Sea (Sandström 1980, Bernreuther et al. 2013). They form dense schools and feed on a limited number of available prey species in deeper water during the day, but disperse in the surface layers without feeding activity at night (Köster & Schnack 1994, Cardinale et al. 2003, Stepputtis 2006). Large juveniles and adults feed mainly on older copepodite stages and adult copepods (Flinkman et al. 1992, Arrhenius 1996, Viitasalo et al. 2001, Möllmann & Köster 2002, Bernreuther et al. 2013). The potential for exerting a strong top-down pressure on their prey, and thus controlling the seasonal development of selected species in the Baltic Sea, is high (Rudstam et al. 1992, 1994, Arrhenius & Hansson 1993, Arrhenius 1997, Flinkman et al. 1998, Möllmann & Köster 1999, 2002, Kornilovs et al. 2001). Both clupeids can consume a large amount of the annual production of zooplankton in shallow coastal areas; e.g. ~30 to 70% of the zooplankton production—mostly of cladocerans and *Eurytemora affinis*—was consumed by herring in coastal areas of the

northern Baltic between June and November (Rudstam et al. 1992). Likewise, Arrhenius & Hansson (1993) estimated that herring and sprat consumed between 60 and 80% of the annual zooplankton production, whereas Arrhenius (1997) estimated that young-of-the-year herring alone consumed 30 to 60% of the zooplankton production in the shallow waters of the northern Baltic proper.

Möllmann & Köster (1999, 2002) analysed stomach content data of clupeids from deeper regions of the Gotland basin and found similarly high ratios of consumption to production (C/P) for specific copepod stage-month combinations, mainly in spring for older stages of *P. acuspes* and *T. longicornis*. However, the values varied extremely even between consecutive years for the same predator-prey interactions. The authors concluded that clupeid predation has most likely contributed to declining *P. acuspes* biomass and probably prevented a stronger increase in *T. longicornis* stocks.

While shallow water studies followed the monthly development of plankton populations in parallel to monthly predation, studies in the deeper basins reported only quarterly data, and thus were too coarse to reveal the mechanistic interaction between copepod stage-specific predation and copepod population dynamics. Furthermore, in all these studies copepod production was based on physiological rates estimated for populations from North Atlantic populations.

As a part of the Globec-Germany programme (Renz & Hirche 2006, Renz et al. 2007, Dutz et al. 2010, 2012, Voss et al. 2011, Peck et al. 2012), the present high resolution spatio-temporal investigation was conducted on the predatory effect of sprat and herring on the dynamics of the key copepods *P. acuspes*, *T. longicornis* and *Acartia* spp. in the Bornholm Basin. The area was monitored bi-weekly to monthly between April 2002 and November 2003, and the study included spatially resolved net sampling of copepods, on-board egg production experiments, stomach sampling and abundance estimation of both clupeids using hydroacoustics and trawl catches. The specific aim of this work was to quantify seasonal variations in the stage-specific consumption of copepods by sprat and herring, and to assess the predation impact of both clupeids on the population dynamics of the dominant calanoid copepod species. The central hypothesis was that clupeids exert a similar controlling influence on *P. acuspes* and *T. longicornis* in the deep basins as suggested by Casini et al. (2008) and as demonstrated for shallow water populations of cladocerans and *E. affinis* by Rudstam et al. (1992).

MATERIALS AND METHODS

Sampling and laboratory analyses

Systematic hydrography and zooplankton surveys were conducted with the German research vessels (RVs) 'Alkor', 'Heincke' and 'A. v. Humboldt' from April 2002 to November 2003 in the Bornholm Basin (BB), (Central Baltic Sea, ICES subdivision 25; Fig. 1, see Table 1). Vertical profiles of conductivity, temperature, depth and oxygen concentration (CTD- O_2) were collected during day and night on a grid of 45 stations. On each survey, between 7 and 9 stations were sampled for zooplankton, in most instances

during daytime using a vertically towed Multinet (Hydrobios; 0.25 m² mouth opening, 50 μ m mesh size), taking separate samples at 10 m depth intervals (Fig. 1). Samples were immediately preserved in a 4% borax-buffered formaldehyde seawater solution. In the laboratory, mesozooplankton was identified and counted under a binocular microscope on subsamples of not less than 500 ind. sample⁻¹. Copepods were identified under the microscope to the lowest taxonomic level, determining their discrete developmental stage, i.e. nauplii (N1–6), copepodites 1–5 (C1–C5) and adults (C6). Copepod abundance was calculated as the monthly mean of the vertically integrated abundances at each sampling station.

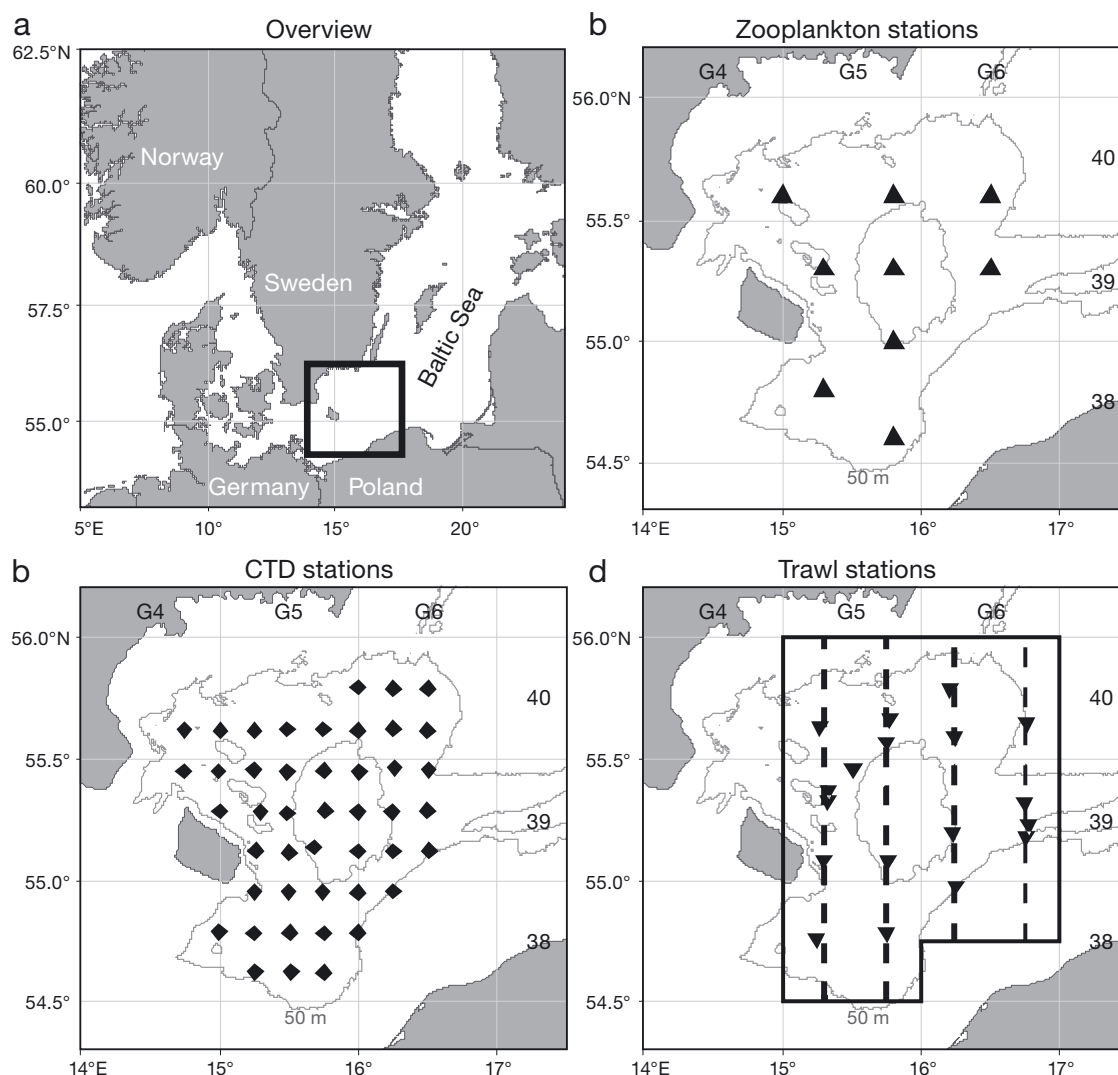


Fig. 1. (a) Study area (Bornholm Basin) in the Baltic Sea, (b) zooplankton sampling stations, (c) CTD stations and (d) pelagic trawl stations with hydroacoustic transects (dashed line). The labelling at the margins of each map indicates the ICES statistical rectangle coding system (ICES 1977) of latitudinal rows (0.5° wide) and longitudinal columns (1° wide); accordingly, the northeast corner of our study area is designated 40G6. The polygon in the trawl station map surrounds the exact area of investigation

We used hydroacoustic recordings in combination with pelagic trawling on 4 transects in the BB with the German RVs 'Alkor' and 'Walther Herwig III' to estimate the spatio-temporal occurrence of planktivorous fish (Fig. 1). Acoustic measurements were conducted during the daytime feeding period of Baltic sprat and herring (Köster & Schnack 1994, Cardinale et al. 2003). Echosounders (EK 500 and EK60; Simrad) were used on RVs 'Walther Herwig III' and 'Alkor', respectively. Calibration of the echosounders was performed using the standard copper-sphere method (Foote et al. 1986). The procedure and settings of the acoustic measurements as well as data processing were conducted according to the 'Manual for the Baltic International Acoustic Survey' (ICES 2001). Echo-data were integrated as 'nautical area backscattering coefficient' (NASC; in $\text{m}^2 \text{nm}^{-2}$) from 10 m below the surface to 0.5 m above the bottom. We performed standard 30 min pelagic trawling during daytime (10 to 20 hauls per survey; see Table 1) with a Kombitrawl (Engel trawls; www.engelnetze.com) on the hydroacoustic transects, targeting observed schools of pelagic fish. The total catch and length distribution of sprat and herring were recorded after each haul. Stock sizes of herring and sprat were computed for ICES rectangles (ICES 1977). The total abundances of herring in sprat in the BB were estimated by summarizing the numbers of the sampled rectangles (Fig. 1).

We collected stomachs of the clupeids for feeding analyses according to a length-stratified sampling scheme, using 1 cm length-classes for sprat and 2 cm length-classes for herring. When available, contents of 3 stomachs per length-class were analyzed per trawl station, summing to a total of 3058 herring and 3466 sprat stomachs (see Table 1). The total stomach content (in g wet mass; g_{WM}) was measured as the difference between the full and empty stomach and weighed with the total catch. Stomach fullness (SF) was estimated as $SF = (SC \times BM^{-1}) \times 100$, where SC is the stomach content and BM is the fish body mass in g_{WM} . Identifiable food items were identified to species level and copepods to developmental stages as described for the zooplankton samples. When the sample size was too large, a subsample of at least 100 identifiable prey items was analysed. Additionally, the sample was screened for rare taxa and ichthyoplankton. For a better overview, herring and sprat were each grouped into 2 size classes: small (12 to 19 cm total length, TL) and large (20 to 29 cm TL) herring and small (7 to 10 cm TL) and large (11 to 15 cm TL) sprat. Previous feeding studies in the Baltic Sea demonstrated that a change in herring diet occurred

at approximately 20 cm TL, after which larger food items like mysids were increasingly found (Casini et al. 2004, Möllmann et al. 2004). Accordingly, we chose this length as a threshold in parts of our study for herring.

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:

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

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.

Predator consumption

We estimated mean daily rations (DR) in g_{WM} per length class of herring and month using an exponential model of gastric evacuation (Tyler 1970, Persson 1979) that incorporated ambient temperature as a variable (Temming 1995, Möllmann & Köster 1999, Köster & Möllmann 2000): $DR_H = R' \times S \times D \times e^{(A \times T)} + S_t - S_0$, where R' is a food type constant (0.084 for herring), S is the average stomach content (in g_{WM}), D is the duration of the feeding period, A is a temperature coefficient (0.129 for herring), T is the ambient temperature ($^{\circ}\text{C}$), and S_t and S_0 are the average stomach contents (in g_{WM}) at the end and the beginning of the feeding period, respectively. Values for S_t (144 and 110% of S for sprat and herring, respectively) and S_0 (57 and 48% of S for sprat and herring, respectively) were estimated from 24 h fisheries, and represent mean relative deviations from the average stomach content during daytime, 2 h before and after the food ingestion stopped and commenced, i.e. sunset and sunrise (Köster 1994, Möllmann & Köster 2002). Laboratory studies have demonstrated that the gastric evacuation of sprat is best described with a general gastric evacuation model (Jones 1974, Temming & Andersen 1994, Bernreuther et al. 2009). For sprat, we used a version that incorporates ambient temperature and predator weight as variables (Temming 1995, Bernreuther et al. 2009): $DR_S = R'' \times e^{(A \times T)} \times (1 - [1 + e^{-A1(T - T50)}]^{-1}) \times S^B \times D \times W^C + S_t - S_0$, where R'' is a food type constant (0.018), $A1$ (0.078) and $T50$ (23.99) are additional parameters, B

(0.668) is a shape parameter (no units) of the gastric evacuation, W is the average fish mass (g dry mass) and C is a mass coefficient (0.503). Values for R' , R'' , A , $A1$, $T50$ and C were derived from Bernreuther et al. (2008, 2009) and Temming (1995). The ambient temperature used for consumption estimates was calculated at the depth of the center of mass of herring and sprat observed during daytime.

The prey species-specific DR (in g_{WM}) of feeding on *Pseudocalanus acuspes*, *Temora longicornis*, *Acartia* spp. and the cladocerans for each length class of sprat and herring were derived by multiplying the relative proportion (in numbers) of grouped copepod stages (C1–3, C4–5 and C6) in the stomachs by the average DR of each length class of fish. For the DR of the cladocerans, all identified and unidentified species were grouped into 'cladocerans'. We estimated the total consumption rates of herring and sprat by multiplying the individual DR with total abundance of these species in the BB. For a comparison with prey production rates, these were scaled to values per m^2 ($1.9 \times 10^{10} m^{-2}$ for the study area; Stepputtis 2006). Consumed wet mass was converted to carbon, assuming the carbon content (C) to be 12 % of the wet mass (Köster 2003).

Prey biomass and production

Daily secondary production was calculated for the dominant copepod species in the BB. Assuming similar somatic and reproductive growth rates, steady state conditions and isochronal development of copepodites (Runge & Roff 2000), mean secondary carbon production m^{-2} was estimated using egg production measurements for *P. acuspes* (Renz et al. 2007), *Acartia* spp. (J. Dutz et al. unpubl. data) and *T. longicornis* (Dutz et al. 2012). The rate at which a stage is entered or left is constant, and production depends on the biomass in each stage (Rigler & Downing 1984, Kimmerer 1987, see also Runge & Roff 2000). This allows for calculation of stage-specific production. The estimated production does not take stage-specific mortality into account, and therefore represents gross production. Egg production of the different species was converted into carbon-specific production rates using size of eggs and/or carbon conversion factors for eggs and females (Kjørboe et al. 1985, Dam & Lopes 2003, Köster 2003, Renz et al. 2007). Mean copepod biomass was estimated from multinet hauls and converted into biomass using carbon conversion factors for stage-resolved copepods (*Acartia* spp.: 0.37 to 3.44 $\mu g C$

ind. $^{-1}$; *P. acuspes*: 0.53 to 7.12 $\mu g C$ ind. $^{-1}$; *T. longicornis*: 0.38 to 5.61 $\mu g C$ ind. $^{-1}$; Köster 2003). Stage-specific daily production (in $C m^{-2}$) was then calculated by multiplying mean stage-specific copepod biomass and carbon-specific production rates. The biomass of cladocerans was roughly estimated from the numbers of individuals times an average carbon content of 2 $\mu g C$ ind. $^{-1}$ (Köster 2003). Production to biomass ratios by season were taken from Johansson et al. (2004).

For an assessment of the magnitude of the consumption (in $mg C m^{-2} d^{-1}$) by herring and sprat in comparison to the production (in $mg C m^{-2} d^{-1}$) and biomass (in $mg C m^{-2}$) of *T. longicornis*, *P. acuspes* and *Acartia* spp., we estimated the predation impact as the ratio of prey consumption to prey production (C/P) and the ratio of prey consumption to prey biomass (C/B).

RESULTS

Stomach fullness and daily ration

Low numbers of empty stomachs were observed over the entire investigation period for both clupeids, implying that sprat and herring were actively feeding during the whole year. The largest number of empty stomachs in sprat was observed in January 2003 (24 %; Table 1), and in herring in March 2003 (17 %; Table 1). No empty stomachs (in either clupeid) were observed in August 2002 or in April, May, July and August 2003 (Table 1).

SF of small and large sprat was rather constant from April to November and September 2002, respectively. SF varied between 0.24 and 0.33 % of the body mass (BM) in small sprat and between 0.21 and 0.35 % in large sprat from April to September, with a slight decrease in August (0.18 %; Fig. 2a,b). Lowest values were observed in January 2003 with 0.07 and 0.06 % BM in small and large sprat, respectively. For herring, lowest SF was observed in March 2003, with values of 0.12 % BM in small herring and 0.06 % BM in large herring (Fig. 2c,d). SF increased subsequently in both species, with the highest levels of 0.42 to 0.68 % BM reached in May to August 2003. A second peak in SF was observed in large herring, with 0.51 % BM in November 2003 (Fig. 2d).

The DRs (in % wet BM) of herring and sprat followed a seasonal cycle (Fig. 3). The rations increased steadily from 0.4 and 0.5 % in small and large herring and 1.3 and 1.0 % in small and large sprat in April to higher rations in June and July, when the highest

Table 1. Survey dates in the Bornholm Basin between April 2002 and December 2003, with numbers of CTD stations, zooplankton multinet stations, pelagic trawl hauls, and herring and sprat stomachs analyzed per cruise, and percentage of empty stomachs; 89% of sprat stomachs and 87% of herring stomachs were sampled at depths greater than 50 m (max.: 100 m)

Survey dates	CTD stations	Zooplankton multinet stations	Pelagic trawl hauls	Herring stomachs		Sprat stomachs	
				Analyzed	% empty	Analyzed	% empty
02–30 Apr 2002	45	9	19	225	9.8	340	0
05–24 May 2002	45	9	15	218	0.9	254	0.4
11–23 Jun 2002	45	9	15	196	0	203	2.0
22 Jul–07 Aug 2002	45	9	20	257	0	186	1.6
12–21 Aug 2002	45	9	12	39	0	86	0
03–13 Sep 2002	45	9	12	218	17.4	175	0
11–29 Nov 2002	45	9	15	294	16.4	270	2.2
13–24 Jan 2003	45	9	13	272	4.4	257	23.7
03–22 Mar 2003	45	9	18	248	9.7	319	6.3
17–28 Apr 2003	45	9	17	264	0	306	0
15 May–03 Jun 2003	45	9	19	316	0	416	0
01–19 Jul 2003	45	2	19	155	0	293	0
07–18 Aug 2003	45	3	10	118	0	116	0
24 Nov–05 Dec 2003	45	1	12	239	3	245	1.2
				Σ 3058	$\bar{\varnothing}$ 5.0	Σ 3466	$\bar{\varnothing}$ 2.8

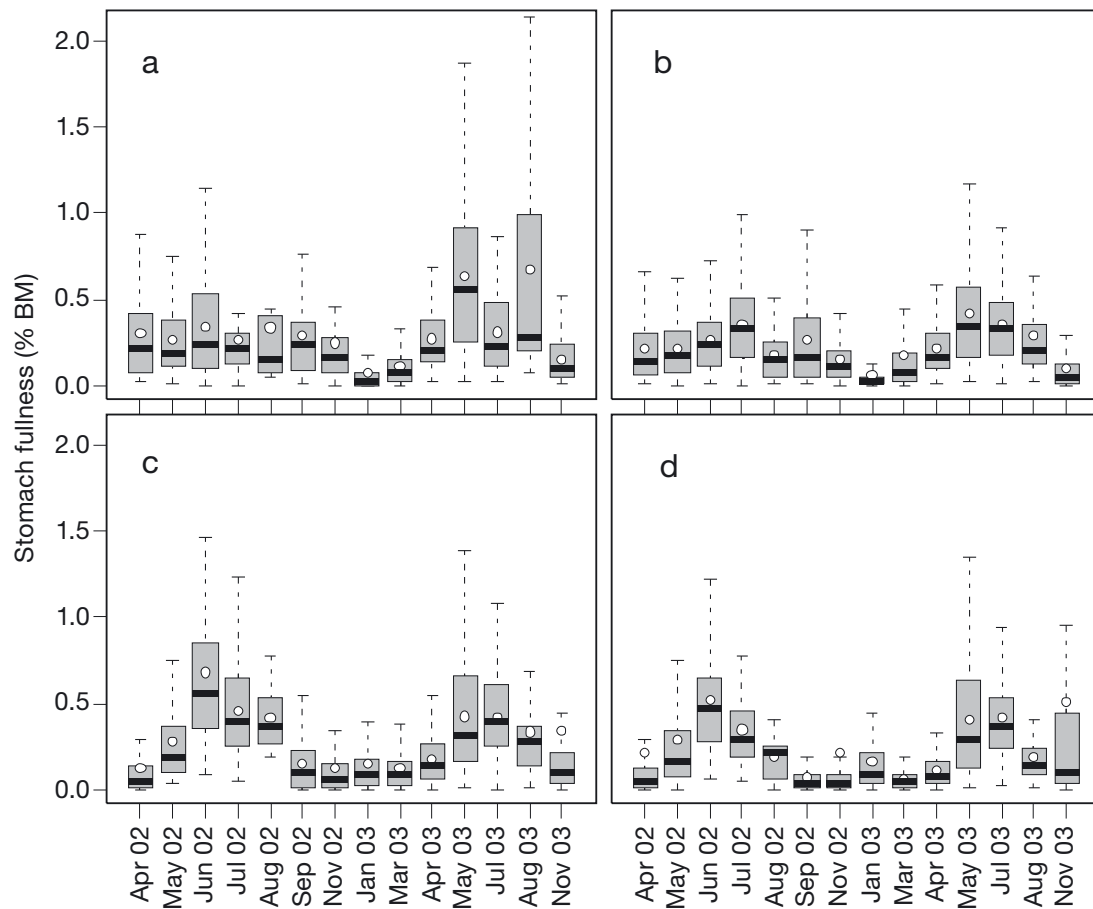


Fig. 2. Seasonal variation in average stomach content in % wet body mass (BM) in (a) small sprat (7 to 10 cm total length, TL), (b) large sprat (11 to 15 cm TL), (c) small herring (12/13 to 18/19 cm TL) and (d) large herring (20/21 to 28/29 cm TL). Black lines: medians; white circles: means; boxes: 1st to 3rd quartile (interquartile range, IQR); whiskers: extremes (>1.5 IQR)

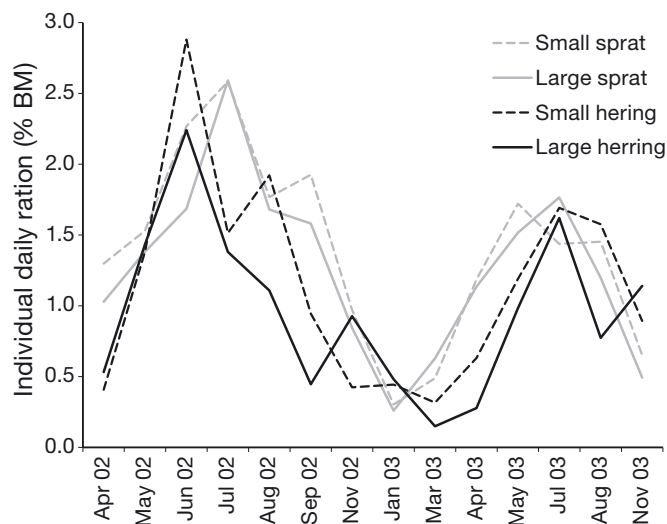


Fig. 3. Mean individual daily ration (% wet body mass) per month by size groups small and large sprat and small and large herring

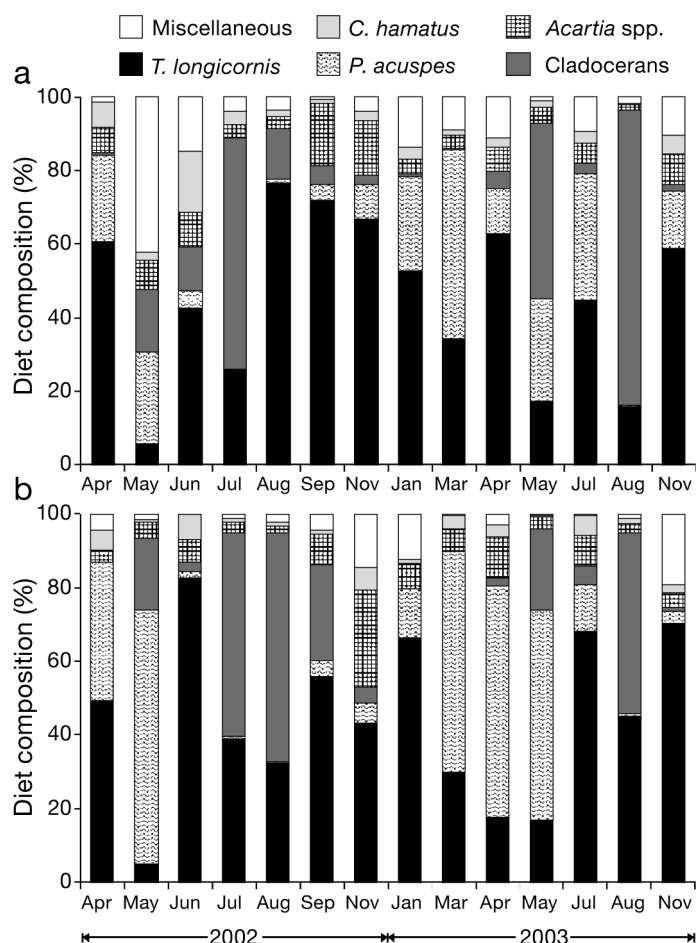


Fig. 4. Seasonal development of the diet composition (% by numbers) for (a) sprat and (b) herring

values were 2.9% in small herring, 2.2% in large herring and a value of 2.6% was estimated for both size groups of sprat. The DRs subsequently declined to reach lowest levels in January and March (<0.3 to 0.7%) in both species. The rations increased again in March and April to reach highest levels May to August 2003 of 1.6 to 1.8% BM.

Diet composition

The most important prey in numbers for both herring and sprat was the calanoid copepod *Temora longicornis*, followed by *Pseudocalanus acuspes* (Fig. 4a,b). *T. longicornis* represented between 40 and 70% of stomach contents of sprat in most sampled months, while it dominated the diet of herring (>43% relative contribution) in 7 of 14 analysed months. *P. acuspes* was the most important prey species for sprat in March 2003 with 51% of stomach contents, and for herring in May 2002 and March to May 2003, with >57%. The other 2 calanoid copepods, *Centropages hamatus* and *Acartia* spp. (including *A. bifilosa* and *A. longiremis*), represented only a minor percentage of the stomach contents in both herring and sprat, with a highest relative contribution to the diet of herring in November 2002 at 27% (Fig. 4b).

The cladocerans *Podon* spp. (including *P. intermedius* and *P. leuckarti*), *Pleopsis polyphaemoides*, *Bosmina* spp. and *Evadne nordmanni* were the most numerous prey items in sprat stomachs in July 2002 (63%) and May (48%) and August (80%) 2003, while the diet of herring consisted of 55 to 62% of cladocerans in July and August 2002 (mainly *Bosmina* spp.) and 49% cladocerans in August 2003. Larger prey species were only observed in the stomachs of herring in November 2002 and 2003, when mysids accounted for 1.3 and 4.4% of the diet.

There was a clear trend towards later copepodite stages (C4–5) and adults (C6) in the diet composition of herring and sprat. The 2 most important calanoid copepods were *T. longicornis* and *P. acuspes* (Fig. 5). For *T. longicornis*, the largest relative amounts of adults (C6) were consumed by sprat in April 2002 and 2003 (80 and 72%, respectively) (Fig. 5a). C1–3 were generally of minor importance for sprat and herring with a maximum relative amount of 24 to 28% of all copepodite stages consumed in May 2002. In *P. acuspes* we observed a seasonal trend. Mainly adults and C4–5 were consumed from April to July by sprat (Fig. 5c). From August onwards throughout winter months, C1–3 were consumed, while the amount of adults found in the stomachs reached lowest numbers

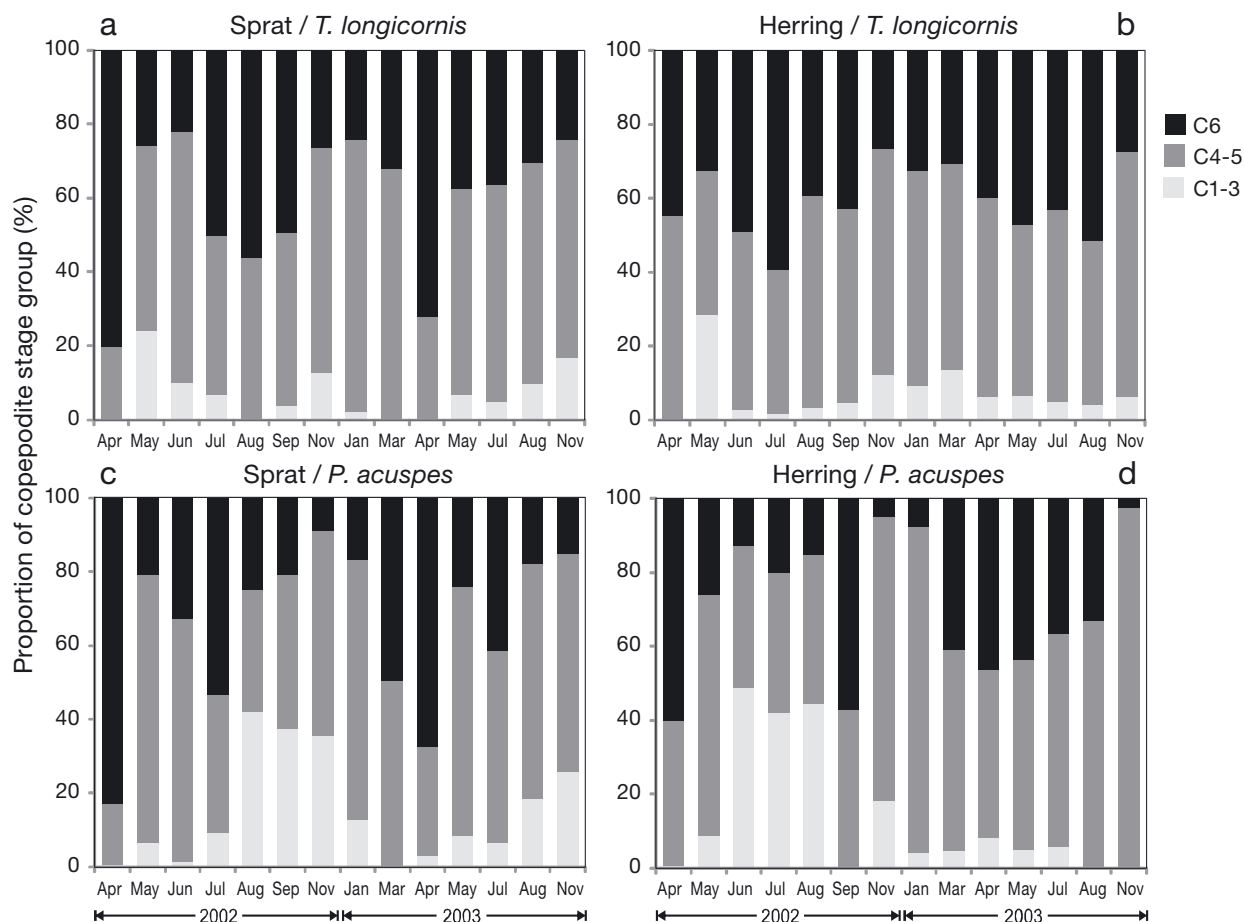


Fig. 5. Seasonal development of the proportion of copepodite stage groups for (a,b) *Temora longicornis* and (c,d) *Pseudocalanus acuspes* in the diet of sprat (a,c) and herring (b,d)

in both years in November (9 and 15 %, respectively). In herring, 42 to 49 % of the consumed *P. acuspes* in June, July and August 2002 were copepodite stages C1–3 (Fig. 5d).

Niche overlap

The intensity of the niche overlap (as a measure of similarity in diets) between herring and sprat estimated from the prey-specific diet composition varied between 43 and 86 %. The lowest value was observed in April 2003 and the highest was observed in March 2003.

Consumption estimates

The combined consumption of sprat and herring of the different groups of development stages of *T. longicornis* varied between $<0.001 \text{ mg C m}^{-2} \text{ d}^{-1}$ for

C1–3 and $18 \text{ mg C m}^{-2} \text{ d}^{-1}$ for C6 in April 2002 (Fig. 6a). Consumption of C1–3 was always $<0.2 \text{ mg C m}^{-2} \text{ d}^{-1}$, and the consumption of C4–5 and C6 varied mainly between 1 and $7 \text{ mg C m}^{-2} \text{ d}^{-1}$. Consumption of the different stage groups of *P. acuspes* varied mainly between 0.5 and $5 \text{ mg C m}^{-2} \text{ d}^{-1}$, with a maximum of $19 \text{ mg C m}^{-2} \text{ d}^{-1}$ for C4–5 in May 2003 and $16 \text{ mg C m}^{-2} \text{ d}^{-1}$ in April 2002. The consumption of *Acartia* spp. was generally low, varying between 0.01 and $1 \text{ mg C m}^{-2} \text{ d}^{-1}$ with a maximum of $1.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ in May 2002 (C4–5).

The highest consumption rates for the combined stages were observed in *T. longicornis* in April 2002 with $20 \text{ mg C m}^{-2} \text{ d}^{-1}$, and in *P. acuspes* during May in both years at 22 and $25 \text{ mg C m}^{-2} \text{ d}^{-1}$, respectively (lines in Fig. 6a). Both *Acartia* spp. and the cladocerans (all observed species combined) were consumed to a much lesser extent, with highest values of $2.7 \text{ mg C m}^{-2} \text{ d}^{-1}$ for *Acartia* spp. in May 2002 and $4.9 \text{ mg C m}^{-2} \text{ d}^{-1}$ for cladocerans in May 2003 (not presented in Fig. 6).

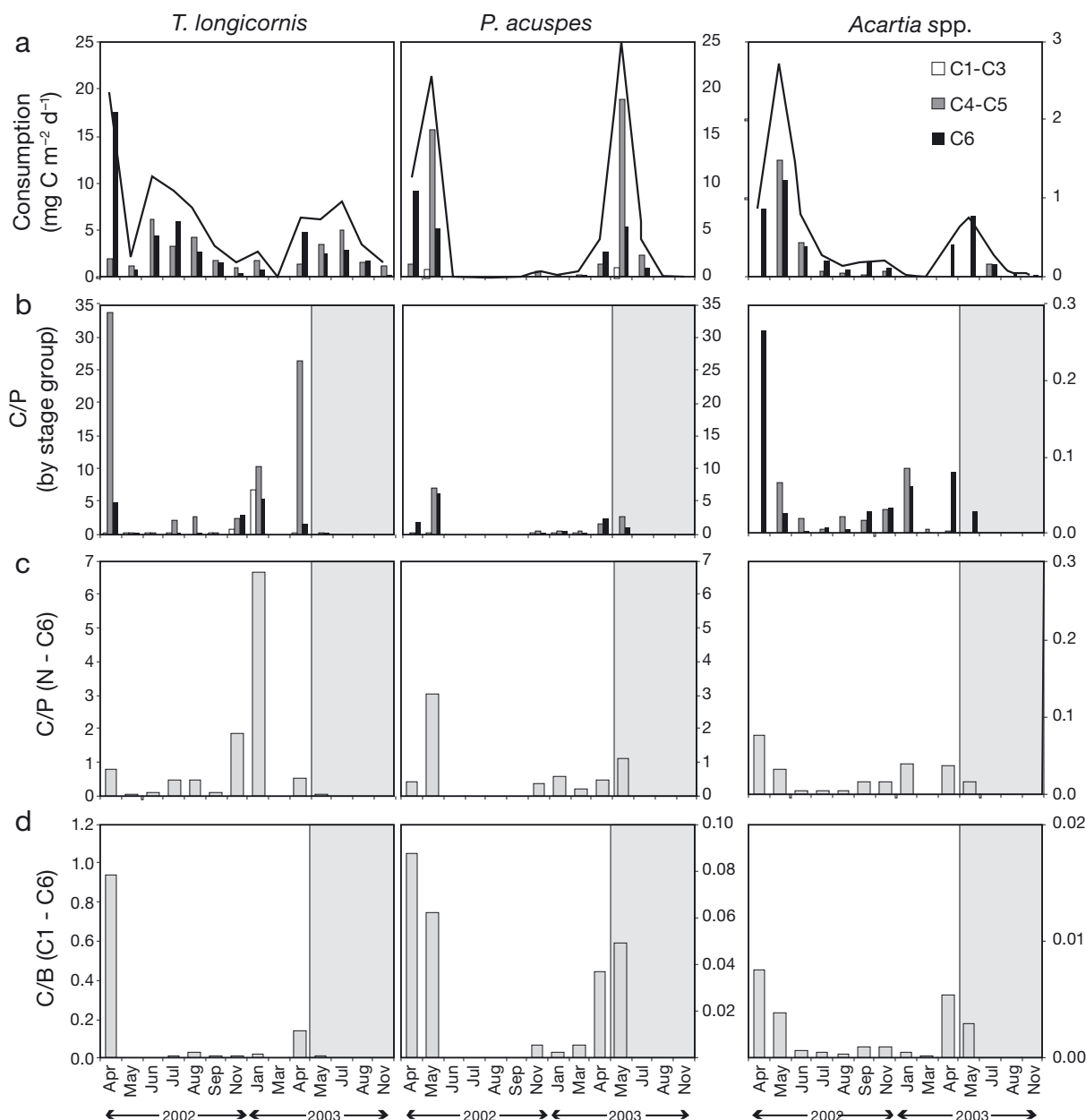


Fig. 6. (a) Sprat and herring consumption of *Temora longicornis*, *Pseudocalanus acuspis* and *Acartia* spp. by copepodite stage groups (C1–3, C4–5, C6; in mg C m⁻² d⁻¹) (lines indicate consumption rates for combined stages C1–6); (b) ratio between consumption and production (C/P) by copepodite stage groups; (c) C/P ratio of the nauplii and copepodite stages N–C6; (d) ratio between consumption and biomass (C/B) of C1–6, presented by month and combined for herring and sprat. Grey boxes: biomass and production values for May and August 2003 are uncertain and should be treated as such; for July and November 2003 we have no biomass and production values

Total consumption of the dominant copepods by the clupeids in the entire BB was highest in April and May 2002, with 410 t C d⁻¹ of *T. longicornis*, 391 t C d⁻¹ of *P. acuspis*, and only 57 t C d⁻¹ of *Acartia* spp. (Fig. 7). Consumption of cladocerans was highest in July and August 2002, at 79 and 69 t C d⁻¹, respectively. The majority of the clupeids in the BB were

sprat, with highest numbers of approximately 5.7×10^{10} in comparison to herring numbers of 6.2×10^8 in April 2002. The numbers of sprat decreased towards the summer, while the numbers of herring in the BB increased during the same period. However, the numbers of sprat were constantly higher than herring numbers during our study (Fig. 7).

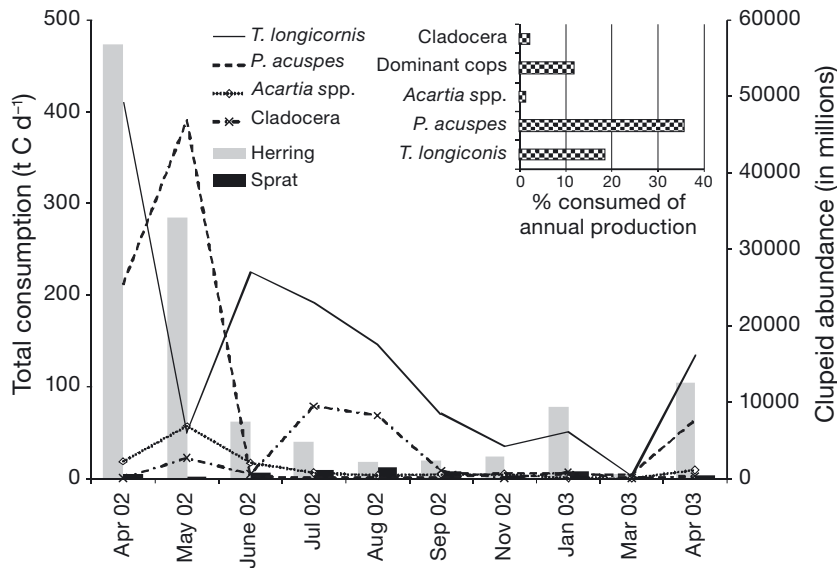


Fig. 7. Total consumption (in t C d^{-1}) of calanoid copepods *Temora longicornis*, *Pseudocalanus acuspes* and *Acartia* spp. and cladocerans (*Podon* spp., *Pleopsis polyphaemoides*, *Bosmina* spp. and *Evadne nordmanni*) for each investigated month from April 2002 to April 2003 by the clupeids herring and sprat as estimated for the entire Bornholm Basin (BB) versus herring and sprat abundance (in millions) per month. Embedded graph indicates utilization (in %) of the annual production of the 3 copepods (dominant copepods) by the clupeids in the BB

Predation impact on mesozooplankton

We observed clear differences in the predation impact of the clupeids feeding on *T. longicornis*, *P. acuspes* and *Acartia* spp. When comparing the copepodite production with the consumption of these stages, highest C/P ratios were estimated for C4 and C5 of *T. longicornis* in April 2002 ($C/P = 34$) and 2003 ($C/P = 26$), respectively (Fig. 6b). The predation impact was lower on adult (C6) *T. longicornis* with highest C/P ratios of around 5 in April 2002 and January 2003. A considerable impact on stages C1–3 was only estimated for January 2003 when the C/P ratio was 6.6. In *P. acuspes*, the predation impact was in general lower compared to *T. longicornis*; the highest impact was estimated for adults (C6) and stages C4–5 in May 2002 with C/P ratios of 6.1 and 7.1, respectively. With the exception of April and May 2003, when ratios of 1.1 to 2.7 were observed for stages C4–6, the predation impact was rather low. The C/P ratios for *Acartia* spp. were much lower compared to *T. longicornis* and *P. acuspes* with the highest value of 0.27 for C6 in April 2002.

The highest predation impact (i.e. C/P) on all developmental stages combined (nauplii and copepodites) was 6.7 for *T. longicornis* in January 2003

and 3.0 for *P. acuspes* in May 2002, while the C/P ratios for *Acartia* spp. were constantly below 0.08 (Fig. 6c).

For an assessment of the predation impact on the prey biomass of the most important calanoid copepods, we also estimated the ratio between the consumption and biomass (Fig. 6d). For *P. acuspes* and *Acartia* spp. the impact was very low with C/B ratios <0.09 . With the exception of April in both studied years, the values for *T. longicornis* were also low (<0.03), whereas in April 2002 the clupeids almost consumed the entire biomass of the copepodite stages C1–6, indicated by a ratio of 0.94.

When integrated over the year, utilization of *T. longicornis* production by both clupeids was comparatively low. Only 18% of the annual production (all stages) was consumed, while 36% of the annual *P. acuspes* production was consumed (Fig. 7). The production of *Acartia* species (1.4%) and cladocerans (2.3%) was almost completely unused by fish predators. The annual utilization of the 3 dominant copepod species (*T. longicornis*, *P. acuspes* and *Acartia* spp.) combined by clupeids amounted to only 12%. Including cladocerans, only 9.2% of the whole mesozooplankton production was utilized.

DISCUSSION

Bornholm Basin as a feeding ground

In general, the proportion of feeding fish was high in the Central Baltic Sea (CBS) and the majority of the clupeids residing in the BB were actively feeding throughout the year, although the average numbers of prey items in sprat and herring stomachs was relatively low from January to April (<100 in sprat). Similar high numbers of feeding sprat were observed by Shvetsov et al. (1983) in the eastern and southeastern part of the Baltic Sea. In a more recent study, Dzieduch (2011) observed a number of empty herring stomachs in the southern BB in September equal to 20%, which is very close to our value of 17.4% for the same month. These numbers are quite low compared to De Silva (1973), who observed that 50 to 60% of the sampled sprat and herring off the Scottish west

coast had empty stomachs from November to January. The results of the study of Last (1987) from the English east coast indicated that in the winter months <25% of the sampled sprat were feeding, in some months all sprat ceased feeding, and <50% of the sampled herring had fed. An analyses of mature spring-spawning herring feeding in the Norwegian Sea indicated a large inter-annual variation (between 2005 and 2010) in the feeding intensity during spring and summer (Bachiller et al. 2016), with the amount of empty stomachs varying from 0 to 60% (Prokopchuk 2009, Bachiller et al. 2016).

SF of herring and sprat was similar or slightly lower than previous observations from the Baltic Sea basins (Möllmann et al. 2004, Möllmann & Köster 1999). In our study, average monthly SF of herring never exceeded 0.7% BM, and was mainly below 0.5% BM, while in sprat the average SF per month rarely exceeded 0.5% BM. Higher average SF (up to 2.8% BM) in sprat was observed in coastal areas of the Black Sea for Mediterranean sprat *Sprattus sprattus phalericus* by Sirotenko & Sorokalit (1979), and up to an average of 4% BM in May in the Belgian part of the North Sea by Van Ginderdeuren et al. (2014). In herring, distinctly higher values were observed in the Barents Sea (Huse & Toresen 1996), where herring in early summer exhibited a SF of 0.7 to 4% BM (depending on body length, with smaller herring having a higher stomach fullness), in the Norwegian Sea in May with >1% BM (Bachiller et al. 2016) and in the Belgian part of the North Sea in June and July with on average >1% BM (Van Ginderdeuren et al. 2014).

These results lead to the question of whether herring and sprat feed more intensively in certain regions (e.g. coastal areas) or if these differences were due to temporal (i.e. decadal) changes. The BB is considered a major feeding ground for herring (Parmanne et al. 1994) and sprat (Aro 1989). Based on the SF we are not able to fully consent to this conclusion, because the SF fullness did not show higher values compared to the neighboring basins.

Our DR estimates for herring (0.8 to 2.9% BM in summer; 0.4 to 1.1% BM in winter) and sprat (1.2 to 2.6% BM in summer; 0.3 to 1.0% BM in winter) are partially higher than the estimates from an extensive food consumption study in the CBS by Möllmann & Köster (1999), with DR estimates of 0.1 to 1.5% BM in summer and 0.1 to 0.5% BM in winter/spring for herring and 0.5 to 1.6% BM in summer and 0.28 to 0.8% BM in winter/spring for sprat. Certainly, higher DRs (3.6 to 17% BM) have been estimated both in the Baltic and North Seas, but they stem from juvenile fish that generally have higher relative rations com-

pared to adults and/or from coastal areas (Arrhenius & Hansson 1994, Maes et al. 2005). Still, this could give us a hint about those areas in which feeding might be more intensive as, for instance, coastal zones of the Baltic Sea. For calculation of the daily food intake by individual herring and sprat, we used a gastric evacuation model approach, which has been shown to yield lower estimates than alternative bioenergetics modelling (Hansson et al. 1996, Möllmann & Köster 1999, Maes et al. 2005). Due to a lack of detailed physiological studies conducted on herring and sprat, most of the bioenergetics models previously constructed for these species (e.g. Stewart & Binkowski 1986, Rudstam 1988, Arrhenius 1995, Utne et al. 2012, Frisk et al. 2015) suffer from lack of experimental evidence and subsequent 'species-borrowing' (Ney 1993) of parameters. Consequently, we consider our estimates more robust but rather conservative and a potential underestimate of true consumption by clupeid fish (Möllmann & Köster 2002). Based on the SF and the DRs, we conclude that the BB serves as a feeding ground for sprat as well as herring as long as they reside there. However, comparison with values from other regions of the North Atlantic suggests that both clupeids feed more intensively in other areas of the Baltic, like coastal zones.

Diet composition and niche overlap

Both herring and sprat are mainly zooplanktivorous. Their most important prey species over the annual cycle were the 2 calanoid copepods *Temora longicornis* and *Pseudocalanus acuspes* along with the cladocerans *Bosmina* spp., *Podon* spp. and *Pleop-sis polyphaemoides* in summer. This observation is typical for the Central and Southern Baltic Sea, where sprat and herring mainly prey on *P. acuspes* in winter and spring. *P. acuspes* is in its main reproductive period between March and May, and biomass strongly increases to peak values in July (Möllmann et al. 2002, 2004, Renz et al. 2007). Afterwards, the clupeids tend to switch to feeding on *T. longicornis* for the rest of the year (Szypula et al. 1997, Möllmann & Köster 1999, Casini et al. 2004, Möllmann et al. 2004). Both sprat and herring mainly preyed on C4–5 and adults (C6) of *T. longicornis* and *P. acuspes*, an observation that was confirmed by a stage-resolved selection study by Bernreuther et al. (2013) in June in the BB, showing that both sprat and herring preferentially feed on these stages. From late summer to winter, C4 and C3 were also consumed. The observation of Möllmann & Köster (2002) that herring were

forced to switch from consuming mainly C5/C6 of *P. acuspes* and *T. longicornis* to C2 of *T. longicornis* due to competition with an increased sprat stock in the Gotland Basin cannot be confirmed by our results from the BB. The proportion of C1 and C2 in the diet of both clupeids was negligible. Although the results of previous diet studies in the CBS are generally consistent with our observations, a notable deviation from this seasonal pattern was observed in our study. Both herring and sprat were already intensively feeding on *T. longicornis*, especially adults (C6), in spring (April 2002). This is surprising because a preferential consumption of late copepodites/adults of *P. acuspes* would have been expected from their vertical overlap during the feeding time of sprat (and herring). In April, the majority of sprat (~99% of all pelagic fishes in the BB in April 2002 were sprat; Stepputtis 2006) concentrates in deeper areas below 60 m (Stepputtis 2006). The weighted mean depth (WMD) of late copepodites and adults of *P. acuspes* in April 2002 in the BB was approximately 50 to 85 m (Renz & Hirche 2006), much closer to the distribution of the majority of sprat than the WMD of late copepodites and adults of *T. longicornis* (approx. 30 m; Dutz et al. 2010). Additionally, the abundance (ind. m⁻²) of *P. acuspes* was 2 to 5 times higher than that of *T. longicornis* (Renz & Hirche 2006, Dutz et al. 2010). Moreover, it was demonstrated in a 48 h *in situ* experiment in the BB in June by Bernreuther et al. (2013) that sprat were actively selecting mainly adult males of *P. acuspes*. Hence, an explanation for this feeding behaviour is not clear, especially since both males and females of *P. acuspes* had a higher mass than *T. longicornis* adults (Köster 2003). Nevertheless, we are able to exclude a sampling artefact, since sprat was also feeding intensively on *T. longicornis* in April 2003, during which time the WMD of the species was even shallower (<30 m).

The high percentage of cladocerans in the diet of sprat and herring in summer was due to the fact that cladocerans are generally at their seasonal peak in abundance in summer in the upper water layers, where they benefit from direct access to phytoplankton (Möllmann et al. 2002, Schulz et al. 2012). Furthermore, cladocerans show weak escape responses (Viitasalo et al. 2001) and are captured with greater success than copepods by visual-feeding planktivores (Drenner et al. 1978, Bernreuther et al. 2013), which seems to be energetically beneficial for predators (Higginson & Ruxton 2015).

The observed niche overlap (50 to 80%) indicated a high similarity in the diets, which was higher than observed by Möllmann et al. (2004) in the previous

decade (1996 to 1999) in the neighbouring Gotland Basin and Gdansk Deep. In addition, the small number of prey species available in the Baltic Sea (Postel 1996) suggests a potential for strong competition for food resources between herring and sprat in the BB. However, it is unclear if the resources in common are limiting (Wilson et al. 2006). High prey densities may cause a high diet overlap between species since there is no need to partition the available resources (Pianka 1982, Bachiller & Irigoien 2015). Yet an increase in the consumption of Mysidacea by herring in November (2002 and 2003) was the only indication of possible resource partitioning, which might not be needed by herring and sprat in the BB. In the first place, the stock sizes of both herring and sprat in the Baltic may explain the lack of need to resource partitioning. The combined stock sizes were average during our study period compared to historical data (ICES 2017) and about half the size (in tonnes) compared to the maxima in 1974 and 1995. In the second place, migration patterns may counteract the competitive effects. Most sprat use to leave the BB after spawning in May and June (Stepputtis 2006), whereas adult herring migrate back after spawning in late winter and early spring to the open Baltic and the BB for feeding, where they stay from July to December (Aro 1989). Spring-spawning herring are in poor condition after spawning, when they migrate to their feeding areas in deep Baltic basins to refill their energy stores (Möllmann et al. 2003b). By the time the herring arrive in the BB, the sprat population has already been feeding intensively on adult *P. acuspes* and *T. longicornis*, as indicated by the high proportion of C6 in the diet, eventually reducing an important part of the adult copepods. However, the migration of the majority of sprat out of the BB in May and June could possibly outweigh the negative effects of this selective feeding by sprat.

Predation impact on mesozooplankton

The comparison of DR with copepod production and copepod biomass provides a clear indication for a temporary, short but intense predation pressure by herring and sprat on the stocks of *T. longicornis* and *P. acuspes*.

The predation pressure on older copepodites (C4–5) and adult *T. longicornis* was particularly high during winter and spring, when copepod stocks still were low (Dutz et al. 2012). In both years, clupeid consumption exceeded the specific production of C4–5 and C6 and potentially contributed to keep the spring stock at a

low level. Furthermore, predation on C6 stages on a single day in April was sufficient to eliminate almost the entire biomass of adult *T. longicornis* ($C/B = 0.91$). A likewise high predation impact in spring on older stages of *T. longicornis* was reported for the Gotland Basin (Möllmann & Köster 2002).

However, despite the high predation impact on the production and biomass of *T. longicornis*, the stock dynamics were apparently not negatively affected, since abundance of C4–5 and adults increased dramatically from April to May (Dutz et al. 2010) and in May production of C4–5 had already exceeded by far the consumption of the clupeids. The most likely explanation for this mismatch of observations is a net import of C4–5 and adult stages from adjacent areas of the BB. The absence of a significant predatory control of the *T. longicornis* population is also confirmed from the analysis of time-series (Rudstam et al. 1994) showing a simultaneous increase of the sprat and the copepod populations in the 1990s (Möllmann et al. 2005).

Our results also indicated high predation pressure by the clupeids on *P. acuspes*, especially in May 2002, but also to a lesser extent in May 2003, when considerably more than the full production of copepodite stages C4–5 and adults was consumed ($C/P = 7.1$ in 2002 and $C/P = 2.7$ in 2003), according to previous observations in the Gotland Basin (Möllmann & Köster 2002).

The decrease of the stock of *Pseudocalanus* sp. during the 1990s has been related also to a decreasing trend in salinity (Dippner et al. 2000, Möllmann et al. 2003a). An investigation of the seasonal and spatial distribution of *P. acuspes* further indicated that low salinities may force later copepodites and adults of this copepod into deeper water layers (Renz & Hirche 2006), where low oxygen levels potentially influence survival of the offspring (Schmidt et al. 2003). Our results indicate that besides suffering from a bottom-up effect, i.e. a detrimental physical environment, the older stages of this copepod were at least temporarily controlled from the top-down. However, the biomass of C4–5 and adult stages of *P. acuspes* increased steadily after the May predation to reach maximum values in June to August 2002 (Renz & Hirche 2006). This can be explained with the main reproduction period of *P. acuspes* in early spring (Renz et al. 2007), which leads to maximum numbers of nauplii in March and April. In May, when the old generation of adults is decimated by clupeid predation along with the stock of C4–5 stages this new cohort survives as C1–3 stages, which are consumed by the clupeids to a minor degree. This finding contrasts with the re-

sults of a study of Casini et al. (2008) on the systemic relevance of the top-down control by sprat. The authors showed for the open Baltic Sea that the cod stock decrease, as the main predator of sprat, cascaded down the food web, directly affecting its main prey, sprat, and indirectly zooplankton and phytoplankton. The zooplankton biomass at the community level was mainly regulated by sprat predation (Casini et al. 2008). Our results indicate that the predation impact of herring and sprat, at least at the stock sizes observed during our study period, was seasonally off-set and not strong enough to regulate the zooplankton dynamics in the BB.

The predation impact on *Acartia* spp. was even lower, where the C/B -ratios were negligible with values below 0.01. The reason behind the low predation pressure is a very limited vertical predator–prey overlap. While *Acartia* spp. preferentially inhabit the upper 30 m of the water column (Möllmann & Köster 2002, Hansen et al. 2006), clupeid fish generally feed during daylight in deeper areas (Cardinale et al. 2003, Bernreuther et al. 2013). The smaller fraction of *Acartia* spp. in the diet of both herring and sprat may be explained by the brief encounter of the copepods during the diurnal vertical migrations of the clupeids during dusk and dawn (Köster & Schnack 1994).

That the highest predation pressure by herring and sprat on *T. longicornis* and *P. acuspes* occurs in spring (April and May) appears to be contradictory to other studies in the Baltic (Arrhenius & Hansson 1993, Rudstam et al. 1994), an estuary of the North Sea (Maes et al. 2005) and freshwater ecology (Kitchell & Carpenter 1993), where the decline of the zooplankton populations in late summer and autumn were mainly attributed to intense planktivory during these seasons. Our observations in late summer and autumn with low or negligible C/P ratios are in line with the observations of Möllmann & Köster (2002), who also observed negligible ratios in the CBS indicating a limited influence of sprat predation on the seasonal dynamics of these copepods in the deep Baltic basins.

When viewed from a system perspective, the ecotrophic efficiency of the BB is rather low. The utilization of only 9% of the combined production of copepods and cladocerans indicates an overall poor trophic coupling between mesozooplankton and pelagic planktivores in the CBS. These utilization rates can be compared to estimates of the ecotrophic efficiencies from ECOPATH models for the Baltic, which were estimated to be as high as 76% for mesozooplankton (Harvey et al. 2003) or equal to 35% for *Acartia* spp., 46% for *T. longicornis* and 51% for *P.*

acuspes (Tomczak et al. 2012). These generally much higher values are estimated within ECOPATH to be sufficiently large to balance the flows between trophic levels up to the commercial catches of the whole system. The discrepancy with our lower values can most likely be explained by the difference in the regional reference. While our values refer to a deep basin, the ECOPATH model estimates refer to the total system including shallower regions, and suggest that in other regions the coupling must be much tighter than in the central basins. However, most of the data sets on plankton and fish stomachs collected so far have a strong focus on the deep basins, while the shallow parts (which appear to be more relevant for trophic coupling), are probably understudied and should be further investigated. The low trophic coupling in the deep basins between zooplanktivorous fish and zooplankton has some important ecosystem implications for the Baltic ecosystem. Relatively low predation pressure on mesozooplankton may lead to an increase in predation on phytoplankton, which in turn could counteract intense algal blooms resulting from eutrophication and high temperature (Finni et al. 2001). If not preyed upon, the majority of the zooplankton production sinks to the bottom and contributes to the oxygen problems of these deep regions (Dzierzbicka-Glowacka et al. 2011, Tang et al. 2014). On the other hand, there appears to be an unutilized niche in this system that may pose a risk by enabling the establishment of a potential invader with fitting eco-physiological properties.

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