Dietary overlap between the potential competitors herring, sprat and anchovy in the North Sea

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ABSTRACT: European anchovy *Engraulis encrasicolus* increased its abundance and distribution in the North Sea during the mid-1990s and may consume similar zooplankton to and/or compete with other occupants of the North Sea like herring *Clupea harengus* and sprat *Sprattus sprattus*. The diets of adult anchovy, sprat and juvenile herring of comparable sizes, sampled close in time and space, were compared to understand how the 3 species prey on zooplankton and establish whether their diets overlap or not. Anchovy was found to be more generalist, consuming a higher diversity of prey items. Herring was more specialized, with low diversity of food items. Sprat was intermediate between anchovy and herring. The dietary overlap between anchovy and sprat was highest, followed by herring and sprat before anchovy and herring. The mean weight of stomach contents did not differ between species. We conclude that of the 3 species, anchovy is likely to be the least affected by changing plankton communities.

KEY WORDS: Stomach analysis · Generalist · Specialist · Planktivorous fish

INTRODUCTION

The North Sea is a dynamic system and has undergone documented changes in its fish community over the last decades (Daan et al. 2005, Heath 2005, Engelhard et al. 2011). Of interest is the spread of European anchovy *Engraulis encrasicolis* across the North Sea (Armstrong et al. 1999, Beare et al. 2004a) concurrent with the reported pattern of increase in species of southern geographic affinities (Beare et al. 2004b, Perry et al. 2005, ter Hofstede et al. 2010). The ecological interactions involving anchovy in the North Sea are not well understood, likely due to its past restricted distribution and low abundance; although anchovy were present in the Dutch coastal areas of the Oosterschelde and Wadden Sea (Boddeke & Vingerhoed 1996), expansions beyond these

areas were reported to be unusual (Aurich 1950, Beare et al. 2004a). While the effect of the increased anchovy population on higher trophic levels remains unknown, partially due to a lack of predators' stomach data, its potential trophic interactions with lower trophic levels are starting to be addressed.

European anchovy is a confirmed zooplanktivore in both the North and Baltic Seas (Schaber et al. 2010, Raab et al. 2011), just like in other parts of its distribution, e.g. the Bay of Biscay (Plounevez & Champalbert 1999), the Mediterranean (Tudela & Palomera 1995, 1997) and in the Benguela system (van der Lingen et al. 2006). This implies that the North Sea anchovy population may interact with other planktivores such as herring *Clupea harengus* and sprat *Sprattus sprattus*. Herring diet is characterised by various copepods (*Calanus* and *Temora*

species), sandeel larvae (*Ammodytes* spp.), chaetognaths and larvaceans (Hardy 1924, Bainbridge & Forsyth 1972, Daan et al. 1985, Last 1987). Sprat feed mainly on copepods and less on larger planktonic prey (Ellis & Nash 1997, Tičina et al. 2000, Casini et al. 2004, Möllmann et al. 2004) and have a very similar diet to North Sea herring (Silva 1973). Anchovy in the North Sea consume mainly copepods and malacostracans, with other items like fish, chaetognaths, larvaceans, gastropods and cephalopods also being found (Raab et al. 2011), and the species also has a varied diet in the western Baltic Sea (Schaber et al. 2010). Clupeids can eat both fish larvae and eggs (e.g. herring: Huse & Toresen 1996; anchovy: Raab et al. 2011), and anchovy has been observed to be cannibalistic in other systems (Valdés Szeinfeld 1993, Plounevez & Champalbert 2000, Takasuka et al. 2004), though in some instances this may be due to cod-end feeding (suggested by Borme et al. 2009). The interactions between anchovy, herring and sprat may be manifold. In addition to possible competitive interactions, intra-guild predation (Polis & Holt 1992) may also occur, and this is likely to be an important factor in the dynamics of small pelagic fish (Valdés Szeinfeld 1991, Irigoien & de Roos 2011).

Interactions with herring are of particular interest as herring is one of the main commercial species of the North Sea and has suffered low recruitment since 2000, likely due to environmental changes rather than overfishing (Payne et al. 2009, Fässler et al. 2011). North Sea herring has been suggested to have density-dependent growth (Heath et al. 1997, Nash et al. 2009; although see Brunel & Dickey-Collas 2010). Density dependence may be caused by habitat or food limitation of a population. While single-species studies address intra-specific density dependence, inter-specific density dependence may also occur (e.g. as suggested by Casini et al. 2010 between Baltic sprat and herring). The juvenile stage of North Sea herring seems to be the most crucial in determining its growth in later life, thus influencing later reproductive potential since this depends on fish size (Birkeland & Dayton 2005). Therefore, if food limitation occurs at the juvenile herring stage (when the herring are at a similar size and location as anchovy), then, at a later stage, reproduction and stock productivity of herring could be affected by this inter-specific interaction.

Diet studies of North Sea herring, sprat and anchovy are sparse; therefore, comparing diets reported in the literature is suboptimal, since the zooplankton prey of fish can change across time and space (Young et al. 2009). Studies of North Sea herring diet were carried out prior to the anchovy increase (e.g. Hardy 1924, Last 1989) and also before recent changes in the zooplankton community (Beaugrand 2004). The most recent studies of sprat diet come from the Baltic Sea (e.g. Cardinale et al. 2002, Casini et al. 2004) or other systems (e.g. the Adriatic: Tičina et al. 2000). To understand the inter-specific interactions there is a need to compare these clupeids' diets in the same area and at the same time. Anchovy is perceived as a newcomer and few appropriate information sources exist for this species; however, we use a stomach content dataset from the German Bight (SE North Sea) where all 3 species were sampled at the same time.

The aim of this study was to describe and compare the diets of the co-occurring potential competitors anchovy, juvenile herring and sprat, as well as establish the level of dietary overlap between these species.

MATERIALS AND METHODS

Data collection

Anchovy *Engraulis encrasicolus*, herring *Clupea harengus* and sprat *Sprattus sprattus* were sampled in the spring and summer of 2004 as part of the Global Ecosystems Dynamics (GLOBEC, www.globec.org) Germany project. Fish stomachs were extracted onboard and preserved in 4% buffered formaldehyde. For the analysis presented here, only those individuals caught during the same cruises were kept, in an attempt to ensure that all fish were likely to have encountered the same environmental conditions. Since the main interest was the trophic impact of anchovy, we only analysed and compared fish from the cruises where anchovy were caught, and only at stations close to those where anchovy were caught (east of longitude 7° E; Fig. 1). Fish diet changes with size (e.g. Casini et al. 2004); thus, only fish of comparable size (12 to 19 cm) were analysed. The size ranges of fish were 12 to 13 cm for sprat (33 adults), 12 to 15 cm for herring (35 juveniles) and 15 to 19 cm for anchovy (34 adults). This left a relatively small data set originating from May to August 2004. However, it was likely that these fish encountered similar environmental/prey conditions, as factors such as temporal and spatial variation in prey fields and/or size-dependent changes in diet were minimized.

Stomach contents were weighed and prey items identified to the lowest taxonomic and developmen-
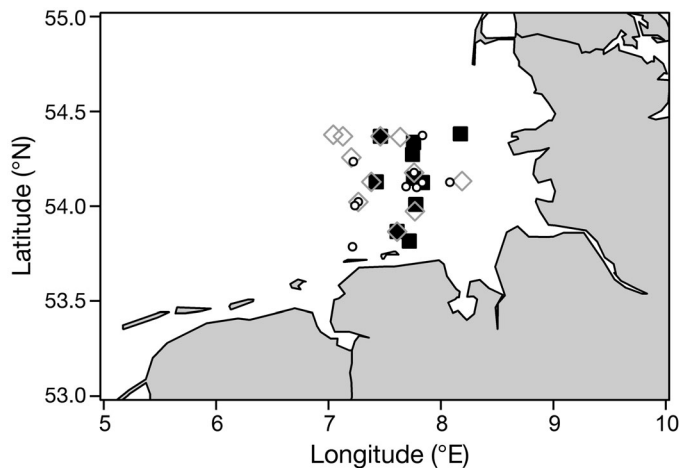
Fig. 1. Sampling stations for anchovy *Engraulis encrasicolus* (■), herring *Clupea harengus* (◇) and sprat *Sprattus sprattus* (o) in the German Bight in late spring/summer 2004

tal stage possible and counted using a binocular microscope when items represented more than half of an identifiable organism. The copepods *Paracalanus* spp. and *Pseudocalanus* spp. were recorded jointly (following the example of the Continuous Plankton Recorder Survey; Warner & Hays 1994) as 'Parapseudocalanus' due to the difficulty in separating these species. An estimate of the volumetric percentage of highly digested items was recorded as these could not be quantified in numbers. We assumed the countable items were also representative for the digested portion of the stomach contents. Counted prey items were grouped into prey categories as often done with stomach analyses (e.g. Möllmann et al. 2004) based on the pooled categorization scheme used in a previous analysis of anchovy diet (Raab et al. 2011). These categories were: *Acartia* spp., *Calanus* spp., *Centropages* spp., chaetognaths, cladocerans, copepods, fish, malacostracans, *Oikopleura* spp., Parapseudocalanus, *Temora* spp. and 'other', which included unidentified items. For each stomach, abundances (numbers), proportions (numerical percentages) and presence–absence of each prey category were calculated providing information on different aspects of the diet. Abundances give information on the absolute quantity of items consumed, proportions tell whether the diet is dominated by certain prey items and presence data simply give information on whether prey composition is the same or not. Abundance and wet weight per individual stomach were corrected for fish size by dividing these 2 variables by the cube of individual fish length (as proxy for fish volume). One anchovy was of unknown length;

therefore, average length of all other anchovies was used for this scaling.

Diet description

The 5 most important categories by abundance (scaled by size), proportions per stomach and frequency of occurrence for each species were extracted. To improve our understanding, the abundance data (scaled by size) were back-translated for a hypothetical 'standard fish' of 14 cm (the average length of all individuals across the species).

Principal components analysis (PCA; described in Legendre & Legendre 1998) was carried out on stomach contents to visualize the differences between species. Proportions were arcsine-transformed ($x' =$ arcsine[$\sqrt{x}$]) before analysis, and PCA was carried out in R (R Development Core Team 2008) using singular value decomposition. Data were centred, and scaling was done only on the abundance data.

Species differences and dietary overlap

Abundance of prey items per stomach and wet weight of stomach contents (in grams and scaled by fish size) were compared between species using the Kruskal-Wallis test. Dietary overlap between species pairs was calculated for each species pair using the Morisita index of similarity. This index is almost independent of sample size (Wolda 1981, Krebs 1999) and only applicable on abundance data. Another commonly used index of dietary overlap is the percentage overlap, also called Schoener's index and the Renkonen measure (Krebs 1999); thus, for comparability with other studies we include this measure as well. Confidence intervals for the overlap indexes were obtained by bootstrapping, using the accelerated bias-correction method (Efron & Tibshirani 1993). Fish caught in the same hauls were also compared for diet similarity (percentage overlap and Morisita index) in order to investigate whether these fish, which had more similar feeding conditions, showed the same results as in the overall analysis. However, the number of hauls in which >1 of the species was caught was very low: 2 hauls with anchovy–herring, 2 hauls with herring–sprat and 1 haul with anchovy–sprat (the latter with only 1 anchovy in it; see Table 1 for details). Therefore, no further statistical analysis was carried out, and only the range of diet overlap was shown as an indication of variability.

Table 1. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Overview of collected samples' origins per species and per species pair: number of cruises, stations, hauls, and time span (dates and time of day) of stomach collection

Species or species pair	Cruises	Stations	Hauls	Dates	Time of day (h)
Anchovy	3	10	10	16 May–10 Aug 2004	6:28 (May)–18:36 (Aug)
Herring	2	11	11	15 May–29 Jun 2004	08:44 (May)–18:05 (May)
Sprat	3	10	10	16 May–16 Aug 2004	08:50 (Jul)–16:03 (Aug)
Anchovy–Herring	2	2	2	16 May 2004	12:30
				27 Jun 2004	09:00
Anchovy–Sprat	1	1	1	1 Jul 2004	12:17
Herring–Sprat	2	2	2	27 Jun 2004	15:55
				18 May 2004	13:05

The average diet breadth as used in the above population-level measures can represent many individuals using the whole breadth or it can represent a range of individuals that are specialized on different parts of the range of items represented (Bolnick et al. 2003). Since many ecological mechanisms occur at an individual level, it is important to understand the diet at an individual level as well; therefore, the numerical percentage was calculated for each individual stomach. Numerical percentages were then sorted in decreasing order and averaged across all stomachs of the same species. The resulting average indicates whether the species consists of individual generalists or individual specialists within the sample population (when considering it relative to the other species). In the latter case, few categories suffice to account for a high percentage of stomach contents in each of the stomachs. In the former case, a relatively larger number of prey categories accounts for the same percentage of stomach contents. The Shannon diversity index of each stomach's content was calculated using the diversity function of the vegan library of statistical software R (R Development Core Team 2008) on prey abundances (scaled by fish size). Mean diversity per stomach was then compared between species by using the Kruskal-Wallis test.

RESULTS

Regardless of measure type (abundance, numerical percentage, or frequency of occurrence), *Temora* spp. was dominant in the stomachs of both anchovy *Engraulis encrasicolus* and sprat *Sprattus sprattus* (Table 2). In an average anchovy stomach, 47% of items were *Temora* spp., and 88% of anchovy stomachs contained this copepod. In the average sprat stomach, 50% of items were *Temora* spp., and *Temora* spp. occurred in 94% of stomachs. A stan-dard size anchovy (14 cm) would contain 79 *Temora* spp., while a standard size sprat would contain 39 *Temora* spp. items. *Centropages* spp. were important in abundance and frequency for anchovy. A 14 cm anchovy would contain 47 *Centropages* spp., and 76% of anchovy stomachs contained *Centropages* spp. *Calanus* spp. were important prey for herring *Clupea harengus*. A 14 cm herring would contain 15 *Calanus* spp., as well as 15 *Temora* spp. items. *Calanus* spp. were more important than *Temora* spp. by proportions (37 and 33%, respectively) and frequency of occurrence (71 and 63%, respectively). The PCA showed different patterns according to whether abundance, proportions or presence–absence was used and explained between 51 and 68% of the dataset's variance with the first 3 dimensions (Table 3). The number of prey items in each anchovy stomach differed from those of herring and sprat (Fig. 2a). The pattern was driven by the categories 'other', *Calanus* spp. and Parapseudocalanus, with anchovy varying most along PC1 (representing 'other') and herring and sprat varying most along PC2 (*Calanus* spp.). Herring was dissimilar from the other 2 species in the proportions of data, with most of the variation explained by the categories *Temora* spp., *Calanus* spp. and malacostracans (Fig. 2b). Prey category composition in stomachs was similar in the 3 species, though anchovy appeared to have a broader range of species in its diet (Fig. 2c).

The total number of items per stomach corrected for fish length differed between species (Fig. 3a; Kruskal-Wallis test, $H = 13.5$; df = 2; p = 0.001). Median abundance per stomach was higher for a 14 cm anchovy (103 items) than for a sprat (67 items) and higher still for a herring (26 items). Stomach content weight did not differ statistically between the 3 fish species (Fig. 3b; Kruskal-Wallis test, $H = 4.5$; df = 2; p = 0.106). Median stomach content weight of a 14 cm fish would be 0.113 g for anchovy, 0.182 g for

Table 2. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Prey categories by abundance, proportion and frequency of occurrence (expressed as percentages) in order of decreasing importance for anchovy, herring and sprat. For abundance, the scaled values back-calculated for a 14 cm fish are given. Parentheses in header line indicate the volumetric percentage of uncountable digested material

Anchovy (+55%)	Percent	Herring (+90%)	Percent	Sprat (+90%)	Percent
Abundance per stomach for a 14 cm fish (SD)					
Temora spp.	79 (94)	*Calanus* spp.	25 (78)	*Temora* spp.	61 (97)
Centropages spp.	47 (92)	*Temora* spp.	17 (40)	*Calanus* spp.	17 (41)
Oikopleura spp.	13 (44)	*Acartia* spp.	5 (22)	Parapseudocalanus	15 (53)
Parapseudocalanus	9 (15)	Malacostracans	5 (8)	Cladocerans	11 (35)
Acartia spp.	9 (17)	Parapseudocalanus	2 (5)	*Centropages* spp.	9 (20)
Other	7 (12)	*Centropages* spp.	0 (1)	*Acartia* spp.	6 (15)
Malacostracans	7 (9)	Copepods	0	Fish	4 (16)
Copepods	6 (13)	*Oikopleura* spp.	0	Malacostracans	2 (5)
Calanus spp.	6 (15)	Other	0	*Oikopleura* spp.	1 (3)
Fish	5 (11)	Chaetognaths	0	Copepods	0 (1)
Cladocerans	3 (6)	Cladocerans	0	Other	0 (1)
Chaetognaths	3 (13)	Fish	0	Chaetognaths	0
Mean proportion per stomach (SD)					
Temora spp.	47 (28)	*Calanus* spp.	37 (40)	*Temora* spp.	50 (34)
Centropages spp.	12 (21)	*Temora* spp.	33 (39)	Cladocerans	16 (27)
Oikopleura spp.	9 (26)	Malacostracans	16 (28)	Parapseudocalanus	9 (21)
Malacostracans	7 (7)	Parapseudocalanus	6 (14)	*Centropages* spp.	8 (15)
Acartia spp.	5 (8)	*Acartia* spp.	5 (18)	*Calanus* spp.	7 (13)
Other	5 (9)	*Centropages* spp.	2 (7)	*Acartia* spp.	6 (12)
Parapseudocalanus	5 (6)	Copepods	0	Fish	2 (8)
Copepods	3 (5)	*Oikopleura* spp.	0	*Oikopleura* spp.	2 (9)
Fish	3 (5)	Other	0	Malacostracans	1 (21)
Calanus spp.	2 (3)	Chaetognaths	0	Other	0 (2)
Chaetognaths	1 (5)	Cladocerans	0	Copepods	0 (1)
Cladocerans	1 (1)	Fish	0	Chaetognaths	0
Frequency of occurrence					
Temora spp.	88	*Calanus* spp.	71	*Temora* spp.	94
Malacostracans	85	*Temora* spp.	63	*Centropages* spp.	58
Centropages spp.	76	Malacostracans	40	Cladocerans	49
Other	76	Parapseudocalanus	23	*Acartia* spp.	36
Copepods	74	*Centropages* spp.	17	*Calanus* spp.	30
Acartia spp.	68	*Acartia* spp.	11	Parapseudocalanus	30
Parapseudocalanus	68	Copepods	3	Malacostracans	21
Fish	62	*Oikopleura* spp.	3	*Oikopleura* spp.	15
Cladocerans	53	Other	3	Copepods	12
Calanus spp.	38	Chaetognaths	0	Fish	12
Oikopleura spp.	29	Cladocerans	0	Other	6
Chaetognaths	21	Fish	0	Chaetognaths	0

Table 3. Results of principal components (PC) analysis on abundance (scaled for fish length), proportions and presence–absence data: proportion of variance explained by the first 3 principal components (expressed as percentage). For each principal component, the prey category representing the highest absolute loading is given

	Variance explained (%)			Categories with highest absolute loading		
	Abund.	Prop.	Pres.–Abs.	Abundance	Proportions	Presence–Absence
PC1	31	38	38	Other: −0.47	*Temora* spp.: −0.75	Copepods: −0.38
PC2	11	19	14	*Calanus* spp.: −0.60	*Calanus* spp.: −0.63	*Calanus* spp.: −0.72
PC3	9	11	10	Parapseudocalanus: −0.51	Malacostracans: −0.88	Malacostracans: −0.48
Total	51	68	62			

herring and 0.082 g for sprat. The median percentage of highly digested items was 55% for anchovy and 90% for both herring and sprat.

Dietary overlap, measured as percent overlap and by the Morisita index, was the highest between anchovy and sprat according to both measures used
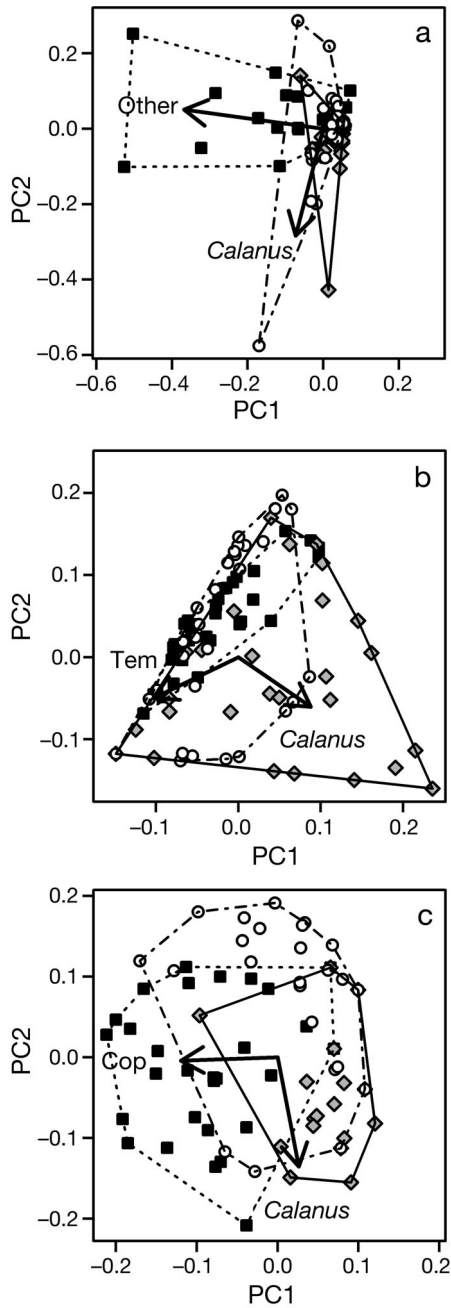

Fig. 2. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Results of principal components (PC) analysis on (a) abundance, (b) proportions and (c) presence–absence of prey categories in the stomachs of anchovy (--■--), herring (–◆–) and sprat (-·o·-). Arrows represent the highest absolute loadings on PC1 and PC2. Tem: *Temora* spp.; cop: copepods

(67.2% and 0.883, respectively) and lowest between anchovy and herring (47.5% and 0.540, respectively). Herring and sprat overlapped by intermediate values (55.9% and 0.734, respectively; Table 4a). The species pairs caught in the same hauls (Table 4b) confirmed that at the within-haul level, anchovy–herring overlap (29.0% and 0.364, respectively) was also lower than herring–sprat (42.4% and 0.525, respectively). The dietary overlap between anchovy and sprat (21.7% and 0.343, respectively) was lower than that of the other 2 species pairs. Anchovy diet was generally more diverse than that of herring and sprat as measured by the Shannon diversity index. Individual variation among the cumulative abundance curves shows that most anchovy stomachs contained many items, while most herring stomachs contained few items of the same prey category (Fig. 4). Among herring, 2 categories on average made up >95% of all prey items, while in sprat and anchovy ca. 3 to 6 categories made up 95% of prey
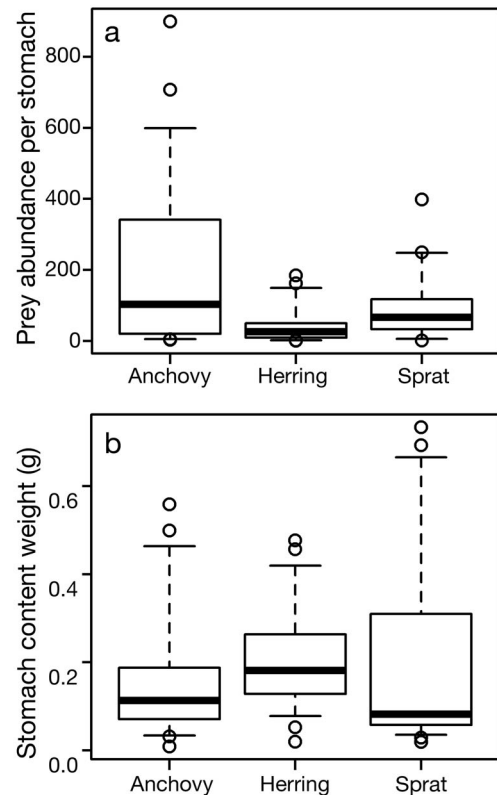

Fig. 3. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Boxplot showing (a) median prey abundance per stomach and (b) median wet weight (g) of stomach contents in anchovy, herring and sprat stomachs back-calculated to a 14 cm standard fish size. Boxes show the medium value (horizontal lines), interquartile range (boxes), 5th and 95th percentiles (whiskers) and outliers (lowest and highest 5 percentiles, circles)

Table 4. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Estimated dietary overlap between the 3 species pairs. Percentage overlap and Morisita's index with (a) 95 % confidence intervals (CI) as estimated by the accelerated bias-correction method or (b) based only on stomachs from the same haul, with the range of resulting dietary overlap values; the number of pairs and stomachs are given.. A: anchovy; H: herring; S: sprat

(a) Species pair	Percentage overlap (95 % CI)	Morisita index (95 % CI)	
Anchovy−Herring	47.5 (42.4−49.1)	0.540 (0.518−0.560)	
Anchovy−Sprat	67.2 (65.9−68.7)	0.883 (0.873−0.906)	
Herring−Sprat	55.9 (50.8−57.5)	0.734 (0.654−0.746)	
(b) Species pair	Percentage overlap (range)	Morisita index (range)	No. of pairs (no. of stomachs)
Anchovy−Herring	29.0 (0−70.7)	0.364 (0−0.862)	9 (6A + 3H)
Anchovy−Sprat	21.7 (20.0−25.1)	0.343 (0.297−0.385)	3 (1A + 3S)
Herring−Sprat	42.4 (12.3−73.5)	0.525 (0.158−0.896)	36 (8H + 8S)

items. Stomach content diversity after correcting for fish length also differed between the 3 species (Fig. 4d; Kruskal-Wallis test, $H = 25.6$; df = 2; p < 0.001), with anchovy having a higher median diversity index (1.17) than sprat (0.74) and herring (0.47).

Because of the particular interest in possible direct feeding on each other of the 3 clupeids (intraguild predation and cannibalism), we explicitly report the 'fish' category (which includes eggs and larvae). Mean abundance of these items per stomach for a 14 cm fish was 5 for anchovy, 3 for sprat and 0 for herring, and the average percentage was 3 for anchovy, 2 for sprat and 0 for herring. A high number of anchovy stomachs contained fish eggs and larvae (21 out of 34 stomachs), which was higher than for sprat and herring (4 out of 33 for sprat; 0 herring out of 35).
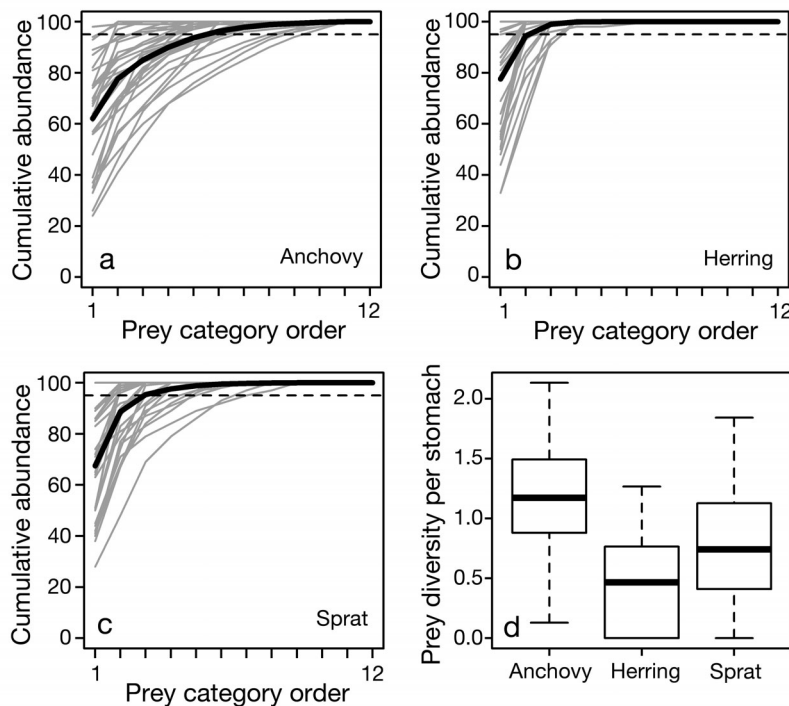

Fig. 4. *Engraulis encrasicolus*, *Clupea harengus* and *Sprattus sprattus*. Diversity in prey items consumed by (a) anchovy, (b) herring and (c) sprat. Cumulative abundance of each individual stomach's prey items (grey) and the average (black) arranged in decreasing order of importance in numerical percentage on the x-axis. Thus, the x-axis can represent different prey categories for different individuals. The 95 % level is indicated by a horizontal dashed line. (d) Boxplot of mean diversity per stomach (details as in Fig. 3)

DISCUSSION

The results suggest that anchovy *Engraulis encrasicolus* is more generalist a planktivore than the other 2 clupeids. Both at the population and at the individual level it consumed a higher number of different prey items than both juvenile herring *Clupea harengus* and sprat *Sprattus sprattus*. While anchovy consumed mainly *Temora* spp. and a number of other items including *Centropages* species, malacostracans, appendicularians and other copepods, juvenile herring was more specialised on *Calanus* and *Temora* species regardless of which measure of importance was used (abundance, numerical percentage or frequency of occurrence). Sprat too showed *Temora* to be their most important prey, but other copepods and cladocerans were also important. The anchovy's generalist diet also explains why the category 'other'

explained much of the variance between stomachs in the multivariate analysis; this was the category that was more abundant and more frequently found in the stomachs of anchovy than in the stomachs of sprat or herring. PCA results from proportions data are more consistent across different categorisation schemes (Raab et al. 2011), suggesting that this may be a more robust measure when semi-arbitrary categorisation schemes are used.

Although there was substantial intra-specific variation in diet, the population level comparison revealed clear differences in diet among the species. Anchovy showed a more diverse diet, whereas sprat and particularly herring showed a more specialised diet. It is well known that predator–prey interactions are affected by the relative size of the predator and prey, but the size dependence may be less prominent in small pelagic fish. It has been found that mean food size (van der Lingen et al. 2009) or wet mass and prey composition (Plounevez & Champalbert 2000, Schaber et al. 2010) do not relate to the size of adult anchovy, nor was any relationship found between anchovy length and maximum prey size: larvae, juveniles and adults fed on the same plankton size classes (Borme et al. 2009). Therefore, we do not expect the higher diversity observed in the anchovy diet to result from the size distribution of fish in our sample. The diet of adult North Sea sprat also seems relatively independent of fish size; they continue consuming medium-sized copepods when herring, in contrast, changes to increasingly larger items (Last 1987).

Percentage overlap between 0.25 and 0.75 is considered to be intermediate (arbitrarily defined in e.g. Pedersen 1999), and thus all species pairs overlap (except the intra-haul anchovy–sprat comparison) and values fall in the 'intermediate' range. The Morisita index is considered more robust than the percentage overlap measure and shows that anchovy and sprat have relatively high dietary overlap. Anchovy–herring had the lowest dietary overlap, which suggests that of the 3 species pairs, this one has the least potential for dietary competition if they are in the same place. The likelihood of anchovy and sprat interacting seems higher. The order of dietary overlap among species pairs does not completely correspond when using intra-haul comparisons compared to all samples. This is because the anchovy–sprat overlap was calculated based on only 1 anchovy stomach which happened to be the one filled with fish larvae, constituting an outlier to the remaining samples. Discounting this species pair, the order of dietary overlap among species pairs remains

the same, with the anchovy–herring still being lower than the herring–sprat overlap. A percentage overlap of 42.3% between herring and sprat was found in the Baltic Sea, and it was highest in spring and summer (Möllmann et al. 2004). Assuming a similar seasonality in feeding by planktivorous clupeids between the North and Baltic Seas, the overlap found in this study would be relatively high compared to other periods of the year since the analysed stomachs came from late spring/summer sampling events. So the impact on trophic interactions or potential competition by anchovy is dependent on whether the food-limited period in its life history is during summer or another time. The details of spatial overlap between these species are not known. Anchovy is distributed throughout the North Sea (in Quarter 3, International Bottom Trawl Data) and sprat is in the southern North Sea (ICES 2011), and both spawn in the German Bight, but appear to separate spatially (Alheit 2007). Most North Sea herring spawn in autumn/winter; therefore, spatial overlap with anchovy and sprat probably occurs when herring is already juvenile and has returned to the eastern North Sea again (ICES 2006). The main feeding time of North Sea herring is from April to June (ICES 2006), and anchovy and sprat spawning activity is also during the sampling time, so if these latter species consume food to cover their increased energetic requirements, the trophic overlap at this time of year is the most relevant to assess. Dietary overlap has been used to suggest trophic competition by several authors (Huse & Toresen 1996, Möllmann et al. 2004), but the former does not necessarily imply the latter (Holt 1987). For trophic competition to occur, there needs to be trophic niche overlap in time and space combined with insufficient food availability through either low food or high consumption by high numbers of consumers. We assumed that the analysed fish did overlap in time and space, they were selected for that reason, but since the spatial scales of feeding ranges and of plankton prey patchiness are unknown, this work could benefit from a study addressing these issues (see e.g. Young et al. 2009). In addition, we assumed that there is an increase in consumption due to an increase in anchovy population. Trophic niche overlap requires more than just co-occurrence. When species co-occur, the criteria used by each species in food selection must also result in similar food being consumed. Although the characteristics of importance to each species' feeding can predict diet quite well (Sibbing & Nagelkerke 2001), these are often unknown. Current work on comparing the feeding morphologies of anchovy sprat and herring in the North Sea

indicates that, although the individual morphological characteristics of the jaw do not differ significantly, the measure of their integrated impact, the filtration area, is significantly larger in anchovy (K. Raab & L. A. J. Nagelkerke unpubl. data). Anchovy (van der Lingen et al. 2006) and herring (Gibson & Ezzi 1990) are known to be able to change from filter feeding to particulate feeding depending on feeding conditions, while it has been suggested that sprat, at least in the Baltic, rely more on particulate feeding (Möllmann et al. 2004) but are also capable of filter feeding. Even when there is dietary overlap, behavioural adaptations for resource partitioning can lead to a low potential for competition (even between similar species like Japanese anchovy *Engraulis japonicus* and Pacific round herring *Etrumeus teres*; Tanaka et al. 2006). Sampling in the same restricted place/time does not necessarily mean that the sampled fish are using the same exact habitat prior to sampling, but it is more likely than if they are caught at a greater distance in time and space. Young herring are known to prey on fish eggs (Last 1989, Segers et al. 2007), on sprat larvae (Last 1987), on *Ammodytes* spp. and on herring itself (Hardy 1924), as well as on plaice and cod eggs (Daan et al. 1985, Ellis & Nash 1997). Sprat also prey on fish eggs (Ellis & Nash 1997), and anchovy can consume fish larvae too (Plounevez & Champalbert 2000, van der Lingen et al. 2006). In this study, anchovy had slightly more fish in their stomachs than sprat. No herring had fish larvae in their stomachs. Sprat, anchovy and sardine larvae are found in the German Bight in June and July (Kanstinger & Peck 2009) and anchovy spawn in May and June. So during the summer they are available to herring, but herring do not consume ichthyoplankton if zooplankton is readily available (Segers et al. 2007). We conclude that direct feeding interactions between all 3 species are possible, but there may be some habitat partitioning which is hidden here by the fact that we specifically chose to analyse the overlapping area. We tried to address this issue by analysing the diets of individual fish caught in the same hauls, but due to very low intra-haul overlap the results are indicative only. However, they confirm the general pattern of anchovy–herring overlap being lower than herring–sprat overlap. No conclusion can be made about anchovy–sprat overlap due to the low sample size (n = 1). More detailed and targeted studies comparing the diet of co-occurring and non-co-occurring populations of these species would offer a way to address this question in the future, as has been done for herring and walleye pollock (see Sturdevant et al. 2001).

The anchovy diet, broad as it is, includes the most important prey items of juvenile herring (*Calanus* and *Temora* species). If these copepods decline, anchovy can continue feeding on other prey. *C. finmarchicus* populations are decreasing in the southern North Sea, while *Temora* species and *C. helgolandicus* have increased between 1958 and 2003 (Pitois & Fox 2006). *C. finmarchicus* is of greater importance by biomass than *C. helgolandicus* in that area, so assuming herring have no preference for either species, the decline would outweigh the increase in its impact on food availability. In the event of a lower abundance of potential prey for herring, it is unclear whether feeding on the second main item (*Temora* spp.) would be sufficient to maintain herring populations, but, given that this species feeds on many copepods in other systems, it seems likely.

Although anchovy stomachs contained slightly more items by abundance, the 3 species compared contained a similar amount of food by wet weight with some overlap (especially between anchovy and sprat). The clearest difference found was the degree of specialization: highest in juvenile herring and lowest in anchovy. Returning to the idea that anchovy may consume the same food as juvenile herring, it seems that, although diets overlap to some extent, anchovy can consume so many more items that it seems unlikely that there would be any particular trophic effect of the new anchovy population on the herring population. This study forms part of a burgeoning body of literature on North Sea anchovy that seems to indicate that its increase is related to habitat changes (Petitgas et al. 2012) rather than strong changes in trophic interactions. Its existence underlines the value of data collection on non-commercial species which may be required for ecological understanding that may become crucial to implementing an ecosystem approach to fisheries.

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