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Parasite communities and feeding ecology of the European sprat (*Sprattus sprattus* L.) over its range of distribution

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Abstract The metazoan parasite fauna and feeding ecology of 165 *Sprattus sprattus* (L., 1758) was studied from different geographic regions (Baltic Sea, North Sea, English Channel, Bay of Biscay, Mediterranean Sea). A total of 13 metazoan parasite species were identified including six Digenea, one Monogenea, two Cestoda, two Nematoda and two Crustacea. Didymozoidae indet., *Lecithocladium excisum* and Bomolochidae indet. represent new host records. The parasite species richness differed according to regions and ranged between 3 and 10. The most species-rich parasite fauna was recorded for sprats from the Bay of Biscay (North Atlantic), and the fishes from the Baltic Sea contained the lowest number of parasite species. More closely connected geographical regions, the North Sea, English Channel and Bay of Biscay, showed more similar parasite component communities compared with more distant regions. From the examined stomachs of *S. sprattus*, a total of 11 different prey items were identified, including Mollusca, Annelida, Crustacea and Tunicata. The highest number of prey organisms belonged to the crustaceans. The variety of prey items in the stomach was reflected by the parasite community differences and parasite species richness from the different regions. The feeding ecology of the fish at the sampled localities was responsible for the observed parasite composition and, secondarily, the zoogeographical distribution of the parasites, questioning the use of the recorded sprat parasites as biological indicators for environmental conditions and change.

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Introduction

Fish parasites are an integral part of every ecosystem and play an important role for the health of marine organisms. In 14,500 marine fishes, there is an estimate of 43,200 metazoan parasites (Klimpel et al. 2009). The biodiversity of fish parasites has been studied by several authors and published in parasite–host and host–parasite checklists. These checklists reflect the parasite fauna in different geographical regions, such as German waters (Palm et al. 1999), Canada (Margolis and Arthur 1979), USA (Love and Moser 1983) and in the deep sea (Klimpel et al. 2009). Fish parasites are also useful tools as biological indicators, e.g. for fish stock separation (MacKenzie 1983), host migration behaviour (Arthur and Albert 1993), environmental pollution, environmental change, bacterial biomass and heavy metal contamination (e.g. Palm and Dobberstein 1999; Sures 2008; Palm and Rückert 2009; Kleinertz 2010; Palm 2011; Palm et al. 2011).

The European sprat (*Sprattus sprattus*) is a small pelagic and schooling clupeid fish species and is commercially exploited and of high economic interest (Möllmann et al.

2004). Sprats are widely distributed in the shelf waters of Europe and North Africa, ranging from Morocco to Norway, including the Mediterranean, Black Sea and Baltic Sea (Limborg et al. 2009). Three subspecies can be morphometrically differentiated based on small differences in the number of postpelvic scutes with *S. sprattus sprattus* distributed in the northeast Atlantic Ocean and the North Sea, *S. sprattus balticus* in the Baltic Sea and *S. sprattus phalericus* in the Mediterranean, Adriatic Sea and Black Sea (e.g. Dailianis et al. 2008). Sprats tolerate temperatures between ~4°C and 18°C, but the upper temperature limit is not yet clearly defined. Sprats undertake extensive and large migrations, and because of their great salinity and temperature tolerance, this species has successfully colonised a wide range of environments (Cardinale et al. 2002). They are short-living with a general upper age limit of 5 years and a length of 12–16 cm (Fiedler 1991). Adult sprats feed exclusively on zooplankton such as copepods, amphipods and euphausiids. They represent an important link between predators of higher trophic levels (e.g. seabirds, piscivorous fishes) and zooplankton (Cardinale et al. 2002, 2003), thus being important for the transmission of fish helminths into larger host.

To date, parasitological studies of *S. sprattus* predominantly were carried out in the North Sea and the Baltic Sea (e.g. Palm et al. 1999), whilst data from the Atlantic and the Mediterranean Sea are mostly missing. The aim of the study was to describe the parasite component communities and feeding ecology of the European sprat (*S. sprattus* L.) over its range of distribution. Our results imply the possible use of sprat parasites as biological indicators for sprat migrations, but not indicating environmental change.

Materials and methods

Sample collection

Fishes were collected from July 2005 to April 2006 on board the German research vessels Walther Herwig and Alkor between 24- and 74-m water depths. A total of 165 *S. sprattus* (European sprat) were studied, including 35 specimens from the Baltic Sea (B, 54° N–15° E), 32 from the North Sea (SN, 55° N–006° E), 28 from the English Channel (EK, 50° N–001° E), 35 from the Bay of Biscay (A, 47° N–002°–003° W) and 35 specimens from the Mediterranean Sea (M, 45° N–13° E). They were frozen immediately after catch for subsequent examination in the laboratory. Prior to examination, each fish (specimen) was defrosted at 0–1°C. Morphometrical data including the head length (HL), standard length (SL), total weight (TW) and slaughter weight (SW) were recorded to the nearest 0.1 cm and 0.1 g, respectively (see Table 1).

Parasitological examination

The eyes, skin, fins, gills, nostrils and buccal cavity of each fish were examined for ectoparasites. The body cavity was opened to examine the liver, stomach, pyloric caeca, intestine and gonads microscopically for endoparasites. The isolated parasites were fixed in 4% borax-buffered formalin and preserved in 70% ethanol/5% glycerine. For identification purposes, Nematoda were dehydrated in a gradated ethanol series and transferred to 100% glycerine (Riemann 1988). Digenea, Monogenea and Cestoda were stained with acetic carmine, dehydrated, cleared with eugenol or creosote and mounted in Canada balsam. Crustacea were dehydrated and transferred into Canada balsam. Parasite identification literature included original descriptions. The parasitological terms follow Bush et al. (1997).

Stomach content analysis

The stomach contents were sorted and prey items were identified to the lowest possible taxon and grouped into taxonomic categories. In order to determine the relative importance of food items, the numerical percentage of prey (*N*%), the weight percentage of prey (*W*%) and the frequency of occurrence (*F*%) were determined (Hyslop 1980; Klimpel et al. 2003). Using these three indices, the index of relative importance, IRI (Pinkas et al. 1971), was calculated. The importance of a specific prey item increases with higher values for *N*, *W*, *F* and IRI.

Table 1 HL, SL, TW and SW, and sex of examined *S. sprattus* from the different regions

Locality	*n*	HL (cm)	SL (cm)	TW (g)	SW (g)	m	f	n.I
Baltic sea (B)	35	2.4 (1.9–2.9)	10.2 (7.4–11.7)	10.6 (3.5–17.7)	8.9 (2.8–14.2)	14	20	1
North Sea (SN)	32	2.2 (2.0–2.4)	9.9 (8.6–10.7)	12.3 (7.8–15.8)	10.9 (7.2–13.2)	11	17	4
English Channel (EK)	28	2.1 (1.8–2.3)	9.5 (8.2–10.2)	8.7 (5.6–10.9)	7.6 (4.9–9.6)	12	16	–
Biscaya (A)	35	2.1 (1.7–2.6)	9.0 (7.3–11.8)	8.6 (4.1–19.3)	7.2 (3.7–14.3)	8	27	–
Mediterranean Sea (M)	35	2.6 (2.1–2.9)	11.1 (8.7–12.2)	16.4 (7.0–21.5)	14.5 (6.3–18.5)	22	13	–

HL head length, *SL* standard length, *TW* total weight, *SW* slaughter weight, *m* male, *f* female, *n.I.* sex not identified

Species richness and diversity

The diversity of the metazoan parasite fauna and stomach content was estimated using the Shannon–Wiener diversity index (H') and the evenness index (E) of Pielou (Magurran 1988):

$$H' = H_s = -\sum_{i=1}^{s} p_i \ln p_i \qquad E = H_s / \ln s$$

where H' is the diversity index, p_i the proportion of the individual species to the total, and s is the total number of species in the community (species richness).

According to Palm and Rückert (2009) and Palm et al. (2011), the ratio of ectoparasites to endoparasites was calculated as [Ec/En ratio (R) = No. of ectoparasite species/No. of endoparasite species].

Statistics

Multivariate statistical analyses were conducted with the Primer programme (release 6, Primer-E Ltd. 6.1.11). Prior to the analyses, the parasite community data were square root-transformed to avoid an overvaluation of rare species. A similarity matrix was constructed using the Bray–Curtis similarity measure. One-way analyses of similarity were applied to figure out the differences in community structure of parasite species composition between stations (routine ANOSIM, values close to 1 indicate high differences and close to 0 indicate high similarity between species compositions). Routine SIMPER analyses was applied to test which parasite species contributed most to show differences between stations. SIMPER analysis was used to determine which species was most responsible for the differences seen between sites with Bray–Curtis analysis (according to Bell and Barnes 2003).

Results

The analyses of 165 *S. sprattus* from the representative regions revealed the highest parasite species number (Table 2) in the Bay of Biscay compared with the lowest in the Baltic Sea (also see the relative percentage of each parasite phylum in each sample in Fig. 1). This difference could be shown additionally on the community level for this regions (ANOSIM: R=0.943, p=0.05; average dissimilarity, 97.17%). A total of 13 different parasite species/taxa were identified, and most parasites were isolated from sprats from more than one geographical region. The more closely connected localities North Sea, English Channel and Bay of Biscay demonstrated an obvious correlation in species diversity of parasites and prey items (Fig. 2a, b). The real parasite number might be even higher, considering tetraphyllidean cestodes being composite of different species. Two digenean parasites species (Didymozoidae indet. and *Lecithocladium excisum*) and a crustacean species, belonging to the Bomolochidae, were recorded for the first time from *S. sprattus.*

Parasite fauna and regional distribution

There were obvious differences in the relative proportion of parasite phyla over the range of distribution (composition of parasite phyla) of *S. sprattus* from the more closely connected regions North Sea (SN), English Channel (EK) and Bay of Biscay (A) compared with the samples from the Mediterranean (M) and Baltic Sea (B) (Fig. 1a). Additionally, this could be observed on the community level as well (pairwise test ANOSIM: A vs. EK, R = 0.249; A vs. B, R=0.993; A vs. M, R=0.334; A vs. SN, R=0.39; EK vs. B, R=0.99; EK vs. M, R=0.283; EK vs. SN, R=0.543; B vs. M, R=0.99; B vs. SN, R=0.99; M vs. SN, R=0.646, all values between p=0.01 and 0.05). For more details on the infestation rates and sites of all isolated parasite species from the investigated sprats, see Table 2.

Most parasite species were found in/on *S. sprattus* from the Bay of Biscay (ten), followed by the amount of parasites in the North Sea (eight) and in the Mediterranean Sea (six). Sprats from the English Channel and the Baltic Sea harboured three or four parasite species, respectively. The nematode *Hysterothylacium aduncum* was the most predominant parasite species (Table 2) and contributed the most to show differences regarding SIMPER (29.3–100% contribution) at all locations. This species infested fish in all the studied regions, with prevalences between 5.7% and 100% (Table 2). *Anisakis* sp. occurred only in the North Sea and the Bay of Biscay (SIMPER, 5.2–7.6%). Digeneans were also abundant in all the studied regions, with prevalences between 2.9% and 96.9%. For example, *Derogenes varicus* occurred in four of five stations in the North Sea (34.4% prevalence), English Channel (46.4% prevalence), Mediterranean Sea (57.1% prevalence) and Bay of Biscay (60.0% prevalence; SIMPER, 7.3–27.9%). *Pseudanthocotyloides heterocotyle* (Monogenea) and larval tetraphyllidean cestodes (*Scolex pleuronectis*) were only isolated from sprats in the North Sea, English Channel and Bay of Biscay, with prevalences of 7.1–22.9% and 2.9–7.1%, respectively (Table 2). The crustacean *Lernaeenicus sprattae* was only isolated from sprats from the North Sea, whilst Bomolochidae indet. occurred in the Bay of Biscay and the Mediterranean Sea, with prevalences of 5.7% and 6.3% (Table 2). The diversity index (Shannon–Wiener) ranged from 0.2 in sprats from English Channel and up to 1.0 in sprats from the Bay of Biscay (evenness index = 0.44) and Baltic Sea. The high evenness index of sprats from the Baltic Sea is caused by a low number of parasite species

Table 2 Metazoan parasites in/on *S. sprattus* from five geographical locations

Parasite species	Stage	Site[a]	Locality														
			Baltic Sea (B)			North Sea (SN)			English Channel (EK)			Biscaya (A)			Mediterranean Sea (M)		
			P (%)	mI (I)	*A*	*P* (%)	mI (I)	*A*	*P* (%)	mI (I)	*A*	*P* (%)	mI (I)	*A*	*P* (%)	mI (I)	*A*
Digenea			–	–	–	96.9	10.8 (1–63)	–	46.4	2.1 (1–5)		85.7	6.1 (1–16)	–	91.4	5.9 (1–23)	
Brachyphallus crenatus	a	st	–	–	–	–	–	–	–	–	–	–	–	–	2.9	1.0 (1)	0.03
Derogenes varicus	l, a	st	–	–	–	34.4	1.6 (1–4)	0.56	46.4	2.1 (1–5)	0.86	60.0	6.5 (1–16)	3.89	57.1	3.5 (1–23)	2.00
Didymozoidae indet.	l	bv/isy	–	–	–	–	–	–	–	–	–	5.7	2.0 (1)	0.03	80.0	3.8 (1–15)	3.06
Hemiurus luehei	a	st	2.9	2.0 (2)	0.03	96.9	10.7 (1–63)	9.97	–	–	–	25.7	2.4 (1–10)	0.63	2.9	1.0 (1)	0.03
Lecithaster confusus	a	in, pc	–	–	–	6.3	4.0 (3–5)	0.25	–	–	–	25.7	2.4 (1–7)	0.63	–	–	–
Lecithocladium excisum	a	st	–	–	–	–	–	–	–	–	–	2.9	1.0 (1)	0.03	–	–	–
Monogenea			–	–	–	12.5	1.0 (1)	–	7.1	1.0 (1)		22.9	1.6 (1–4)		–	–	–
Pseudanthocotyloides heterocotyle	a	g	–	–	–	12.5	1.0 (1)	0.19	7.1	1.0 (1)	0.07	22.9	1.6 (1–4)	0.37	–	–	–
Cestoda			–	–	–	6.3	2.0 (2)		7.1	1.0 (1)		2.9	1.0 (1)	–	–	–	–
Scolex pleuronectis		in	–	–	–	6.3	2.0 (2)	0.06	7.1	1.0 (1)	0.14	2.9	1.0 (1)	0.03	–	–	–
Cestoda indet.	l		2.9	1.0 (1)	0.03							–	–	–	–	–	–
Nematoda			–	–	–	100	19.8 (1–118)	–	100	29.8 (4–85)		97.1	13.7 (1–54)	–	100	23.0 (1–70)	
Anisakis simplex	l	bc, in, pc	–	–	–	6.3	1.5 (1–2)	0.09	–	–	–	25.7	1.4 (1–2)	0.37	–	–	–
Hysterothylacium aduncum	l	bc, in, pc	5.7	1.0 (1)	0.06	100	19.6 (2–118)	20.41	100	29.8 (4–85)	25.39	97.1	13.3 (1–54)	12.9	100	23.0 (1–70)	23.00
Crustacea			–	–	–	6.3	1.0 (1)	–	–	–	–	5.7	1.0 (1)	–	5.7	1.0 (1)	–
Bomolochidae indet.	a	g	–	–	–	–	–	–	–	–	–	5.7	1.0 (1)	0.06	5.7	1.0 (1)	0.06
Lernaeenicus sprattae	a	ey	–	–	–	6.3	1.0 (1)	0.06	–	–	–	–	–	–	–	–	–
Ectoparasite species				0			2			1			2			1	
Endopsrasite species				2			6			3			8			5	
Ratio				0.0			0.3			0.3			0.3			0.2	

a adult, *l* larval, *P* prevalence (in per cent), *mI* mean intensity, *I* intensity, *A* mean Abundance, *st* stomach, *bv/isy* blood vessels/intravascular system, *in* intestine, *pc* pyloric caeca, *g* gills, *bc* body cavity, *ey* eyes

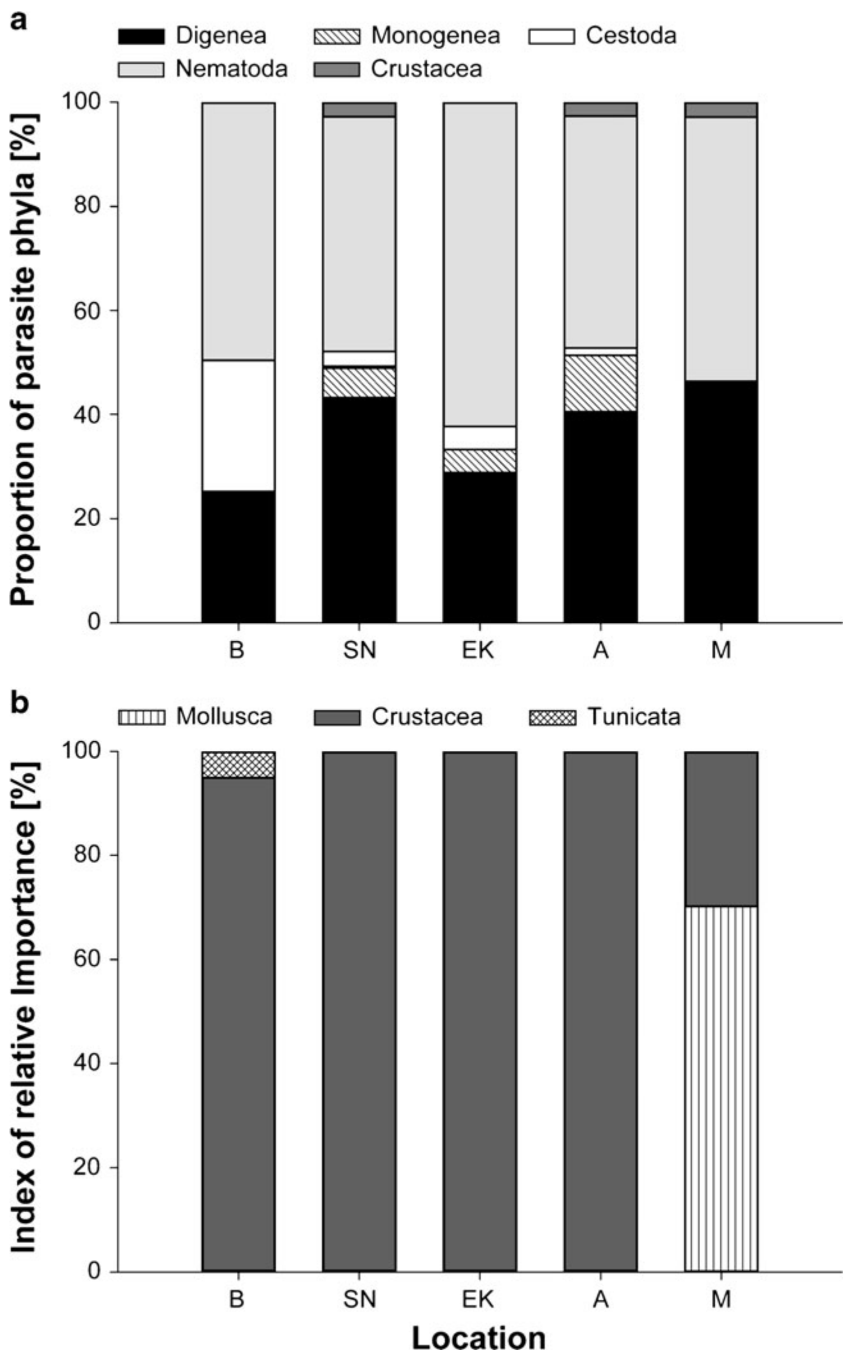

Fig. 1 **a** Parasite fauna (proportion of parasite phyla based on prevalence data, expressed as relative percentage). **b** Prey items (IRI in per cent) of *S. sprattus* from five geographical regions: *B* Baltic Sea, *SN* North Sea, *EK* English Channel, *A* Bay of Biscay, *M* Mediterranean Sea

that are represented by only a few specimens (very high evenness index, 0.95; Fig. 2a). The ectoparasite/endoparasite ratio ranged from 0 to 0.3 (Table 2).

Feeding ecology

The prey analyses showed that *S. sprattus* mainly fed on crustaceans, such as copepods (calanoid and harpacticoid), euphausiids, decapods and amphipods, whilst ostracods and cumaceans were secondary prey items (Fig. 1b and Table 3). Molluscs (bivalves), annelids (polychaets) and tunicates (thaliaceans) also played a secondary role, reflecting the pelagic feeding behaviour of sprats. The food of *S. sprattus* consisted of four (Baltic Sea and North Sea), five (English Channel), eight (Bay of Biscay) and six (Mediterranean Sea) different prey items, respectively (Table 3). The most diverse food composition, mainly of crustaceans, was found in the Bay of Biscay followed by the Mediterranean Sea. The most frequent prey items of sprats from the Baltic Sea were harpacticoid copepods and thaliaceans. The most important prey items in the North Sea and the English Channel were calanoid copepods, whilst the food composition in the Bay of

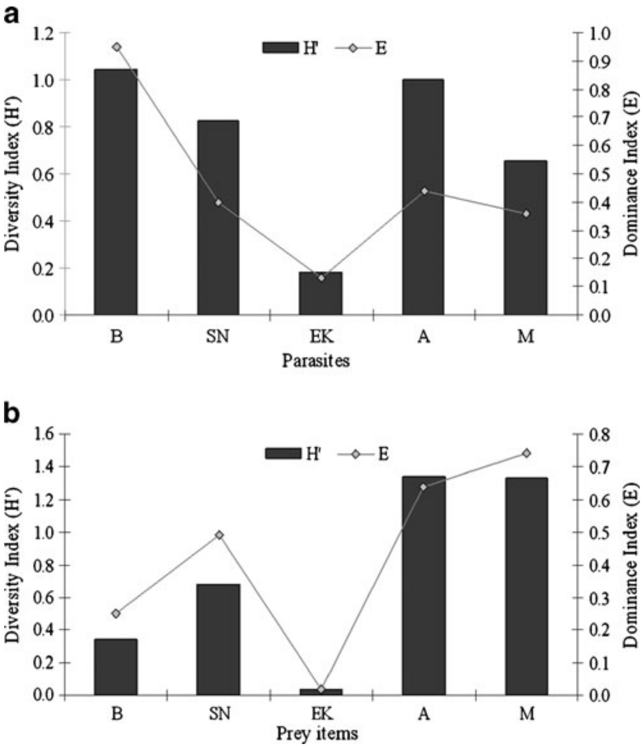

Fig. 2 Shannon–Wiener Index (H') and evenness (E): Parasites (**a**) and prey items (**b**) from the locations: *B* Baltic Sea, *SN* North Sea, *EK* English Channel, *A* Bay of Biscay, *M* Mediterranean Sea

Biscay was dominated by euphausiids and calanoid copepods. The most important prey items in the Mediterranean Sea were calanoid and harpacticoid copepods, bivalves and euphausiids (Table 3). The diversity index for the prey items ranged from 0.04 in sprats from the English Channel (evenness index = 0.02) up to 1.34 in sprats from the Bay of Biscay (evenness index = 0.64), whilst those from the Mediterranean (evenness index = 0.74) was 1.33 (Fig. 2b).

Discussion

The present study is the first large-scale investigation of European sprat (*S. sprattus*) parasites covering a wide geographical distribution of this fish species. A total of 13 parasite species and 11 different prey items were identified. The species diversity and abundance differed in the sprats that were obtained from the five different regions.

Parasite fauna

As demonstrated by Klimpel et al. (2008) for the striped red mullet (*Mullus surmuletus*), the parasite fauna of European sprats is also characterized by digeneans, nematodes and crustaceans, whilst monogeneans, cestodes and acanthocephalans are scarce or missing. The most common were the core species (species with prevalences above 60–100%) *H. aduncum*, being highly abundant and most important numerically in all the studied regions except the Baltic Sea, followed by *Hemiurus luehei*, Didymozoidae indet. and *D. varicus* (digenean trematodes). Parasitological studies of *S. sprattus* so far included the North Sea and Baltic Sea (e.g. Palm et al. 1999), whilst data from the Atlantic and Mediterranean Sea are still missing. According to previous studies, a total of 19 different parasite species have been recorded from the North Sea compared with only seven species from the Baltic Sea (e.g. Palm et al. 1999). Five parasites had an overlapping range of distribution, and a single parasite record originated from the Black Sea (Dimitrov et al. 1999). Our results demonstrate less parasite species richness than recorded earlier, however in a similar range as observed for *S. sprattus* from the North Sea by Groenewold (1992) and Groenewold et al. (1996) (14 species vs. 13 in the present study).

The nematode *H. aduncum* and the digeneans *H. luehei* and *D. varicus* appeared in much higher numbers than recorded by earlier authors. Though being the most prevalent and less host-specific nematode species in the North Atlantic that is able to infect various teleosts and invertebrates as intermediate (calanoid copepods and euphausiids) or final hosts (Køie 1993; Marcogliese 1996; Berland 1998; Klimpel and Rückert 2005; Klimpel et al. 2007), only Fischer (1955) so far recorded this parasite from sprats from the Baltic Sea at unknown infestation rates. *H. aduncum* was highly abundant within the present study, reaching prevalences of 100% and intensities of 118 in the North Sea, and the lowest infection rates in the Baltic Sea (5.7%, Table 2). Similarly, *H. luehei* reached a prevalence of infection of 96.9% within the present study and *D. varicus* a prevalence of 34.4–60.0% compared with the low infestation rates of 0.6% by Reimer (1978) and 1.9% by Groenewold et al. (1996).

Having three parasite species in the Baltic Sea compared with eight in the North Sea, four in the English Channel, ten in the Bay of Biscay and six in the mid-Mediterranean, it seems that the northwestern and southern regions are more parasite-rich than the East. However, according to Williams et al. (1992) and Arthur (1997), the parasite species composition of fish reflects the differences in the food source, feeding preferences and habitats. There is an obvious correlation between the heteroxenous parasite fauna diversity and the observed diversity of prey items in the fish (as intermediate hosts or possible parasite transmitters, see Dzikowski et al. 2003; see Fig. 2). Figure 2a, b illustrates the relationship between the parasite diversity in sprats at the sampled localities and the observed diversity of prey items in the stomachs. Consequently, the differences in parasite species richness in *S. sprattus* over its range of distribution (see Table 2) from the Mediterranean to the Baltic Sea must be caused by the differences in prey item

Table 3 Frequency of occurrence (*F*), numerical percentage of prey (*N*), weight percentage of prey (*W*, all in per cent) and IRI of the food items identified from the stomach contents of *S. sprattus* from five geographical locations

Prey groups	Locality																			
	Baltic Sea [B]				North Sea (SN)				English Channel (EK)				Biscaya (A)				Mediterranean Sea ([M)			
	F (%)	*N* (%)	*W* (%)	IRI	*F* (%)	*N* (%)	*W* (%)	IRI	*F* (%)	*N* (%)	*W* (%)	IRI	*F* (%)	*N* (%)	*W* (%)	IRI	*F* (%)	*N* (%)	*W* (%)	IRI
Mollusca	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	96.9	22.9	10.6	3246.9
Bivalvia	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	96.9	22.9	10.6	3246.9
Annelida	–	–	–	–	18.8	0.3	0.2	8.9	–	–	–	–	–	–	–	–	6.3	1.1	1.6	1.9
Polychaeta	–	–	–	–	18.8	0.3	0.2	8.9	–	–	–	–	–	–	–	–	6.3	1.1	1.6	1.9
Crustacea	100	92.7	91.5	18407.7	100	99.7	99.8	19952.8	100	100	100	20000.0	229.4	99.9	100	45842.4	100	76.0	87.8	1378.2
Ostracoda	–	–	–	–	–	–	–	–	4.0	0.1	0.4	1.8	–	–	–	–	–	–	–	–
Copepoda (calanoid)	14.3	0.7	2.0	39.7	93.8	72.7	77.5	14081.4	4.0	0.1	0.8	3.4	32.4	36.6	16.1	1707.9	100	23.5	28.1	5162.8
Copepoda (harpacticoid)	95.2	91.3	88.0	17074.2	100	24.8	16.1	4091.9	88.0	99.5	96.9	17279.6	38.2	32.3	8.7	159.5	100	43.0	31.3	7428.6
Euphausiacea	14.3	0.6	1.4	28.8	–	–	–	–	–	–	–	–	97.1	23.9	71.9	9301.1	65.6	9.5	28.4	2485.0
Decapoda	–	–	–	–	34.4	2.2	6.2	289.0	–	–	–	–	11.8	0.6	1.8	27.4	–	–	–	–
Cumacea	–	–	–	–	–	–	–	–	4.0	0.1	0.4	1.8	5.9	0.2	0.3	3.2	–	–	–	–
Amphipoda	–	–	–	–	–	–	–	–	12.0	0.3	1.0	22.6	20.6	2.7	0.7	9.7	–	–	–	–
Crustacea indet.	–	–	–	–	–	–	–	–	–	–	–	–	23.5	3.5	0.4	91.7	–	–	–	–
Tunicata	61.9	7.4	8.6	985.7	–	–	–	–	–	–	–	–	2.9	0.1	0.02	0.5	3.1	0.3	0.3	1.8
Thaliacea	61.9	7.4	8.6	985.7	–	–	–	–	–	–	–	–	2.9	0.1	0.02	0.5	3.1	0.3	0.3	1.8

availability and food composition, possibly depending on regional habitat conditions at the sampled localities.

Transmission pathways

Within the present study, the predominant species in the Mediterranean was the nematode *H. aduncum*, which was abundant at all studied localities (except in the Baltic Sea region with low prevalences), as well as the digenea Didymozoidae indet., which additionally occurred in sprats from the Bay of Biscay with lower infestation rates. Digenea of the family Didymozoidae in general use gastropods as first intermediate hosts, planktonic invertebrates (cirripedia, polychaets) as second, and small or piscivorous teleosts (Nikolaeva 1965; Køie and Lester 1985) as final hosts. The digenea *Brachyphallus crenatus* appeared only in Mediterranean sprats, but this species has been recorded already from 21 different fish species from the North Sea and the Baltic Sea (Palm et al. 1999). Køie (1992) suggested an arctic–boreal distribution for this parasite and identified bivalvia as first intermediate hosts, copepods as second and teleosts as the final hosts.

The monogenean *P. heterocotyle* with a direct life cycle was recorded for the first time from the Bay of Biscay and also the English Channel and the North Sea, distinguishing these from the Mediterranean and Baltic Sea. The digenean *H. luehei* was the most abundant trematode parasite species in the North Sea together with the nematode *H. aduncum*. *H. aduncum* was highly abundant and numerically most important within four of five locations, except in the Bay of Biscay, followed by one of the most common and least host-specific digenean, *D. varicus*. *H. luehei* is one of the most common parasites in clupeid and salmonid fishes along the Atlantic coast line, the Baltic Sea and the Mediterranean Sea (Gibson and Bray 1986; Tolonen and Karlsbakk 2003). Køie (1990) and Palm et al. (1999) recorded *H. luehei* in ten different final hosts, among them *S. sprattus*. Reimer (1978) observed *H. luehei* with prevalences of 29.7% in the North Sea and 18.0% in the Baltic Sea. Bivalves are used as first intermediate hosts, calanoid copepods as second, and planktivorous clupeids, piscivore salmonids and gadids (Køie 1990) as final hosts. Calanoid copepods were highly abundant in the investigated stomachs in the North Sea and the Bay of Biscay, a possible reason for the high intensity of *H. luehei* especially in the North Sea. The Digenea *D. varicus* utilizes calanoid and harpacticoid copepods as intermediate hosts (Køie 1979), both identified in the stomach content analyses (Table 3).

The zoonotic and therefore economically and commercially important fish parasitic nematode *Anisakis* sp. was isolated from the North Sea and Bay of Biscay samples. This can be referred to the lack of cetacean final hosts in the other localities (Strømnes and Andersen 2000; Abollo et al. 2001a, b; Klimpel et al. 2004). Gibson et al. (1998) and Herreras et al. (1997) already recorded adult *Anisakis* sp. in six different cetacean species from the North Sea. Different crustaceans (copepods, euphausiids) serve as first intermediate host and teleosts and cephalopods as second and paratenic hosts (Klimpel and Palm 2011). The larval cestode *S. pleuronectis* showed a similar distribution to *Anisakis simplex* and also occurred in the English Channel. Marcogliese (1995) reported copepods and chaetognaths as possible first intermediate hosts; the adults infect elasmobranchs and holocephalans.

The stomach content analysis of the studied *S. sprattus* identified 11 different prey items belonging to the Mollusca, Annelida, Crustacea and Tunicata. Especially the crustaceans play the most important role as intermediate hosts for fish parasites (Marcogliese 2002), being important transmitters for cestodes, nematodes and also acanthocephalans. The highest diversity of prey items was observed in sprats from the Bay of Biscay and the Mediterranean Sea, consisting mainly of crustaceans such as calanoid and harpacticoid copepods, euphausiids, decapods, cumaceans, amphipods and thunicates (thaliaceans; in the Bay of Biscay). In the Mediterranean Sea, also the crustaceans were of major importance (highest IRI values), with calanoid and harpacticoid copepods, euphausids, molluscs (bivalvia) and annelids (polychaets; Table 3). With the exception of the Baltic Sea, the number of different prey items reflects the evenness and diversity of the parasite component community. Crustaceans are important drivers of parasite life cycles in the sea, consequently supporting parasite transmission at the sampled localities.

Possible influence of abiotic factors

The zooplankton diversity and species distribution, thus the possible parasite transmission into the sprats, depends on abiotic factors at the different sampling sites, e.g. salinity and season. The open surface water of the Baltic Sea has a low salinity of 6.0–8.0‰ in the central part (Rheinheimer 1995). In the North Sea, salinity values reach around 35.0‰ (in the northern part) and decreases to the southern part to values of 32.0–34.0‰, more or less similar to the salinity of the surface water in the western English Channel with <35‰ (Kelly-Gerreyn et al. 2006). Lazure et al. (2006) demonstrated salinities of 30.0‰ (in late winter or spring) up to 35.0‰ (in summer) for the Bay of Biscay. Their observations demonstrated significant differences in salinity concentrations over time for the Bay of Biscay. The salinity of the Mediterranean Sea has a mean value of about 39.0‰, with increasing values from the East (36‰) to the West (39‰; Rother 1993). Consequently, salinity might have caused the different diversity and abundance of fish parasites in sprats, with the lowest salinity (Baltic Sea) and the highest salinity (Mediterranean Sea) being correlated with the lowest diversity of sprat parasites. This would imply that the highest parasite diversity is found in the centre of the sprat distribution, or possibly also the most beneficial conditions for a successful parasite transmission and completion of the life cycle.

Another influencing factor might be the condition factor of the studied clupeids that is also dependent on the surrounding salinity. Physiologically stressed fish might have a reduced feed intake, also reducing parasite transmission load. On the other hand, such fish will be easier preyed upon by other predators of the higher trophic levels (e.g. seabirds; Cardinale et al. 2002, 2003), resulting in a faster transmission rate and completion of the parasite life cycles. According to our observation, the condition factors of the sprats were different in the studied regions, with the lowest condition factor (0.98) in the Baltic Sea and the highest in the North Sea (1.25). Interestingly, the condition factor of sprats from the Mediterranean Sea was also high (1.17), reflecting the diversity of prey items that were recorded in the stomachs of these fish (vs. English Channel, 1.01; Bay of Biscay, 1.07). Groenewold et al. (1996) stated that the diet of sprats seems to be the main reason for determining the structure of the parasite community. This is in accordance with Williams et al. (1992) and Arthur (1997) who stated that the parasite species composition of fish reflects distinct differences in the feed source, feeding preferences and habitats.

A correlation between the season and the parasite fauna has not been discussed in the available literature for sprats, and also our data are not sufficient. According to Casini et al. (2006), there is inter-annual variation in the condition of sprats, caused by factors such as salinity and temperature. Similarly, a different size of sprats results in a different feeding behaviour and, consequently, parasite transmission rates. Earlier parasitological studies of sprats focused on fishes from the North Sea and the Baltic Sea (see above), and the parasite load of sprats for the Baltic region within the present study is fairly low in contrast to these previous investigations. Until 2006, there were no data available on sprat parasites from the Atlantic and the Mediterranean region. Consequently, comparisons to detect long-term changes in the parasite composition cannot be made.

Metazoan parasites from *S. sprattus* as biological indicators

According to Williams et al. (1992) and Arthur (1997), the parasite fauna of a host species reflects its diet and characterizes the feeding ecology of the host. The present study demonstrates that the parasite fauna of sprats over the sampled range of distribution directly reflects the diversity of prey items in the stomach, which is closely linked to the abiotic conditions of the environment at the sampled localities. Fish parasites can be used for a wide range of applications, e.g. as biological indicators for environmental change (Vidal-Martínez et al. 2010; Palm 2011) and pollution (Sasal et al. 2007). Applying the methodology by Palm and Rückert (2009), Palm et al. (2011) suggested that demersal groupers could be used as biomarkers to monitor environmental change in tropical habitats. This contrasts fish parasites of pelagic clupeids such as *Clupea harengus* and the scombrid *Scomber scombrus* that have been earlier used as biological indicators for stock separation in the North Sea (MacKenzie 1985, 1987, 1990). The close correlation of food and parasite diversity in sprats over its range of distribution demonstrates that these parasites might be useful for stock migration and separation as well, if separate sprat populations feed in one region and later on migrate into another. However, the different infection levels of low host-specific and widely distributed parasite species within the present study demonstrate that the feeding behaviour in the pelagic realm and the migration patterns result in the observed parasite community. Thus, high swimming speeds and a wide range of sprat distribution seem to eliminate this pelagic fish as potential candidates to monitor environmental conditions and change.

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