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Parasite communities of four fish species in the Wadden Sea and the role of fish discarded by the shrimp fisheries in parasite transmission

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ABSTRACT: Parasites were observed in medium- and small-sized fish taken from the discards of a commercial shrimper during seven different cruises in the tidal channels of the North Frisian Wadden Sea (Süderaue, North Sea) from April to September 1991. In total, 442 fish comprising four species *(Sprattus sprattus, Hyperoplus lanceolatus, Ammodytes tobianus, Pomatoschistus minutus)* were investigated. The parasite fauna consisted of 22 species. The parasite community structure of the 4 hosts was compared. The diet of the hosts seemed to be the main factor determining the structure of the parasite community. Other factors could not be assessed. Eight species of parasites occurred as larval stages. This indicated that fish were intermediate or paratenic hosts in their life cycle. The nematode *Hysterothylacium* sp. (Anisakidae) and the digenean *Cryptocotyle lingua* (Heterophyidea) were the dominant parasites, reaching their highest prevalence and density in sprat and sand eel. Sprat and sand eel play a very important role in parasite transmission to predacious fish and seabirds.

INTRODUCTION

Publications on fish parasites in the North Sea are numerous, but to date have mainly dealt with single species (taxa) of parasites or with hosts which are relevant to fisheries, such as flatfish or gadoids (Køie, 1983, 1984; for references see Möller & Anders, 1986). This paper focusses on parasites of medium- and small-sized fish species, which so far have not been paid much attention, i.e. goby [*Pomatoschistus minutus* (Pallas, 1770)], sand eel [*Ammodytes tobianus* Linnaeus, 1758 and *Hyperoplus lanceolatus* (Le Sauvage, 1824)] and sprat [*Sprattus sprattus* (Linnaeus, 1758)]. These species play an important role in the food web of the coastal areas of the North Sea (Hartwig & Söhl, 1975; Kühl & Kuipers, 1978; Bailey & Bakken, 1990). They may be of importance for parasites that infest several different components of marine food chains in their life cycle. This is the case for a number of helminth species. Relationships of this kind have been studied in detail in the Baltic Sea (Zander, 1988; Zander & Döring, 1989, Zander et al., 1993) and in

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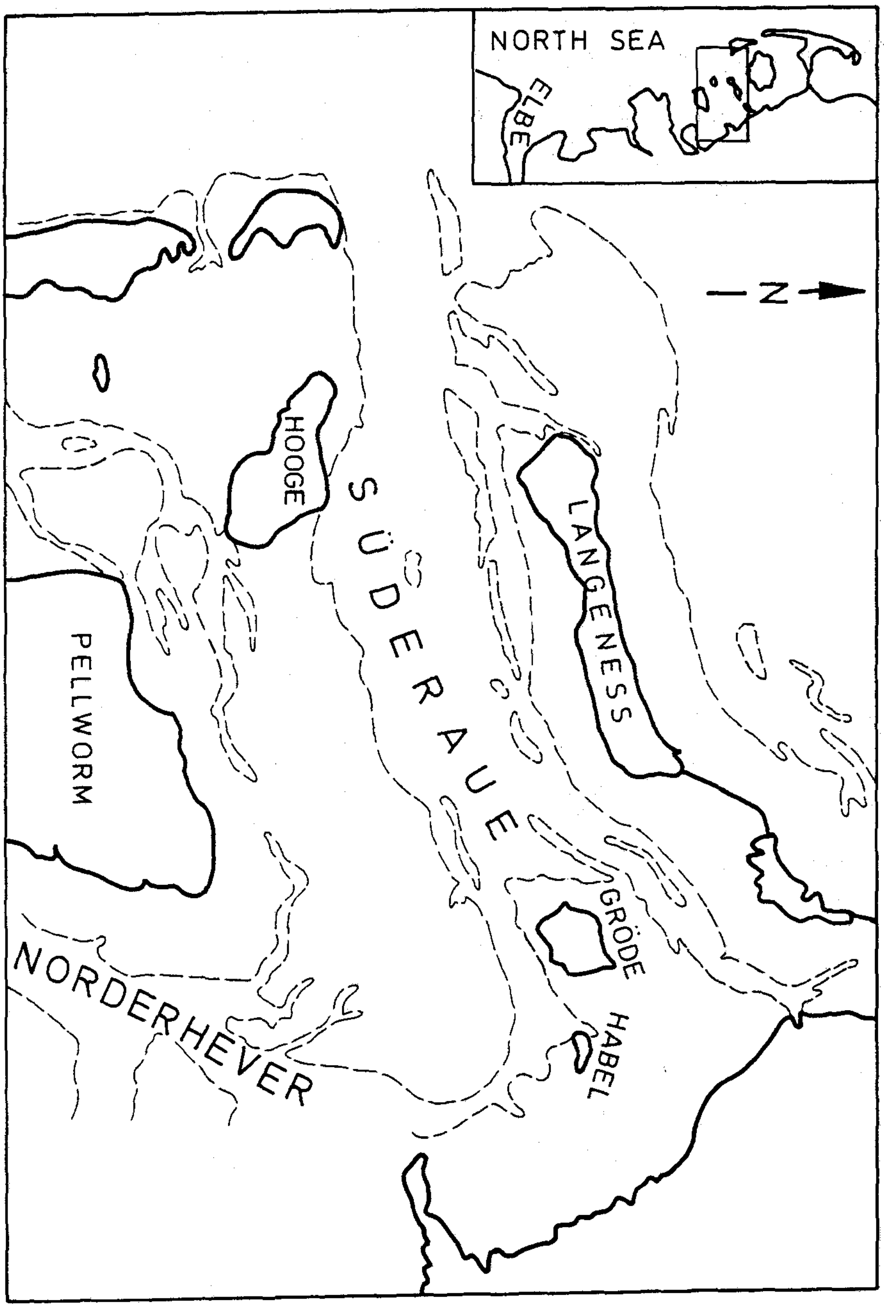

Fig. 1. Research area in the North Frisian Wadden Sea (eastern North Sea)

the Schlei fjord (Zander & Westphal, 1991). In the North Sea, the parasite fauna of gobies (Hamerlynck et al., 1989) and of sprat (Reimer, pers. comm.) have been investigated. Reports on parasites of sand eels in the North Sea are rare (Sprehn, 1960).

The objectives of this study are: (1) to contribute to the inventory of the parasite fauna of the above-mentioned hosts, including the analysis of the community structure; (2) to assess the four fish species as intermediate hosts for parasites that infest a number of final hosts.

The overlapping parasite fauna of the fish species was also studied with regard to similarities in habitat structure of the hosts as well as their role in the food web and differences in autecology. The discards of fishing vessels provide an important food resource for seabirds (Furness, 1987; Berghahn & Rösner, 1992). Fisheries might thereby promote a number of parasite species to completion of their life cycles in shorter time periods, i.e. in higher numbers or in other words, in higher densities as compared to pristine conditions. Particular attention was paid to the role of medium- and small-sized fish as intermediate hosts for helminths, which have to reach top predators such as fish, sea mammals, and seabirds.

STUDY AREA AND METHODS

Fish samples were taken from the by-catch of a commercial shrimper during seven different day cruises in the subtidal area "Süderaue" between the islands Langeness, Oland, Gröde, and Hooge (Fig. 1) from April to September 1991. The vessel was equipped with two commercial beam trawls (widths 7.8 m); rollers were attached to the ground rope; mesh sizes in the cod end were 11 mm. In total, 442 fish comprising four species were randomly selected from the by-catch: *Sprattus sprattus, Ammodytes tobianus, Hyperoplus lanceolatus, Pomatoschistus minutus.* Most specimens were fixed in buffered seawater formalin (5 %). Food organisms from their stomach contents were determined and were subjected to frequency analyses (% of specimens of a fish species containing these food items) in order to identify potential intermediate hosts. All helminths were transferred to an alcohol-glycerol mixture (Reichenow et al., 1969). Small nematodes and Digenea were placed in glycerol prior to examination under a light microscope; larger specimens of anisakids were cleared in 100 % lactic acid (Berland, 1961; Hartwich, 1975). Anisakid larvae were determined to the genus level according to Berland (1989). Infested organs were defined as "microhabitats" after Rohde (1982).

Besides prevalence [%] (Rohde, 1982), parasitic burden (all parasites per examined hosts) and abundance (parasites of species "i" per examined hosts of species "h"), the following indices were used:

(1) Relative frequency [%]:

$$\text{Relative frequency} = \frac{n_i \cdot 100}{n_{all}}$$

(n_i = number of parasite individuals of species "i"; n_{all} = number of all parasite individuals of a host species)

(2) Shannon-Wiener-Index:

$$Hs = -\sum_{i=1}^{s} (p_i \cdot \ln p_i)$$

(Hs = diversity index; p_i = relative frequency of species "i"; s = number of species in the community)
(3) Eveness (Streit, 1980):

$$E = Hs/\ln S$$

(S = number of species of the community)

Prevalence [%] and relative frequency [%] (dominance) were subjected to similarity analysis according to Renkonen in order to compare the parasite fauna of host species:
(4) RI [%] = $pr_1 + pr_2 \ldots + pr_n$
(RI = Renkonen index; pr [%] = minor common values for prevalences or relative frequencies [one] of two compared host species regarding infestations by parasite species 1 to "n")
The Jaccard-Index [%] was employed in order to compare mutual parasite species (Streit, 1980):

$$J = \frac{p_{hc} \cdot 100}{p_{h1,\,2}}$$

(P_{hc} = number of common parasite species of two compared host species; $P_{h1,2}$ = number of all parasite species of two compared host species)

RESULTS

Length and food of hosts

Most sprat and lesser sand eel were one year old, the former ranging from 90 to 120 mm, the latter from 145 to 175 mm in length. Both species preferred calanoid copepods and cypris larvae (Balanoidea) as food items (Table 1). In contrast, greater sand eel (mostly between 215 and 230 mm long) fed mainly on lesser sand eels and to a lesser extent on polychaetes and copepods. Sand gobies (mainly 0- and I-group) were predominantly between 50 and 80 mm long and fed preferably on *Crangon crangon* (Linnaeus, 1758) and gammarids.

Parasite burden of hosts

In total, 9433 parasites were detected in 22 different species or higher taxa. The highest mean burden of 88 parasites per host was found in lesser sand eel. Gobies carried by far the lowest burden, i.e. 0.7 parasites per specimen (Table 2). The infestation rate was 100 % in lesser sand eel, 87 % in sprat, 70 % in greater sand eel, and 25 % in goby. Most fish were infested with several parasite species (Fig. 2), in particular sprat and lesser sand eel; more than 50 % of the latter two species carried 2 to 6 parasite species per host. In gobies, less than 1 % of the specimens contained more than 2 parasite species. The full taxonomy of the following species is given in Table 3.

Highest prevalences among Digenea were achieved by *Brachyphallus crenatus* and *Cryptocotyle lingua* in *Ammodytes tobianus* (Table 3). *Brachyphallus* also occurred in the other 3 fish species in relatively high prevalences. It was, however, most abundant in *Ammodytes*, with densities of more than 84 parasites per host (Table 4). Other hemiuroids like *Hemiurus communis* and *Hemiurus luehei* were more prevalent in *Ammodytes* than in other hosts, but in the other fish species they were not as frequent as *Brachyphallus*.

Table 1. Percent frequency of occurrence of different food items in sprat *Sprattus sprattus* (*S. spr.*), lesser sand eel *Ammodytes tobianus* (*A. tob.*), greater sand eel *Hyperoplus lanceolatus* (*H. lan.*), and sand goby *Pomatoschistus minutus* (*P. min.*)

Number of specimens	*S. spr.* 159	*A. tob.* 54	*H. lan.* 39	*P. min.* 194
CRUSTACEA				
Crangon		8.3		68.3
Gammarids		6.7		39.0
Mysids	17.1			8.3
Copepods	73.4	91.7	12.5	
Balanids				11.8
Cypris larvae	37.7	53.3	2.1	27.7
Nauplius larvae	11.5	13.7		
POLYCHAETA				
Several species	4.5		14.2	14.4
Larvae (plankton)		30.0		
MOLLUSCA				
Hydrobia				5.8
TELEOSTEI				
Sand eels			46.0	
Gobies			1.7	4.4
OTHERS	2.1	5.2	9.7	5.7

Table 2. Parasitic burden and ecological indices of the helminth communities of sprat (*S. spr.*), lesser sand eel (*A. tob.*), greater sand eel (*H. lan.*), and sand goby (*P. min.*). Hs = diversity index; E = evenness

	S. spr.	*A. tob.*	*H. lan.*	*P. min.*
Number of examined hosts	159	54	39	194
Infested by parasites [%]	87	100	70	25
Parasitic burden	26.9	87.7	7.0	0.7
Number of helminth species	13	7	6	13
Hs (helminth only)	0.95	0.20	1.32	2.03
E (helminth only)	0.37	0.10	0.74	0.79

Cryptocotyle lingua had higher infestation rates in sand eel than in sprat, but densities were greater in the latter (Tables 3 and 4). In one extreme case, 629 metacercariae were found in a single fish. Very high prevalences and densities were determined for the nematode *Hysterothylacium* sp., particularly in sprat. In gobies and greater sand eels this nematode showed the highest prevalence of all parasites, although densities were lower than in sprat.

Remarkably high prevalences were found for the parasitic copepods *Lernaeenicus sprattae* and *L. encrasicoli* in sprat. Almost one-fifth of the investigated sprat were infested (Table 3).

The findings concerning *Microphallus primas* and the two tetraphyllids deserve

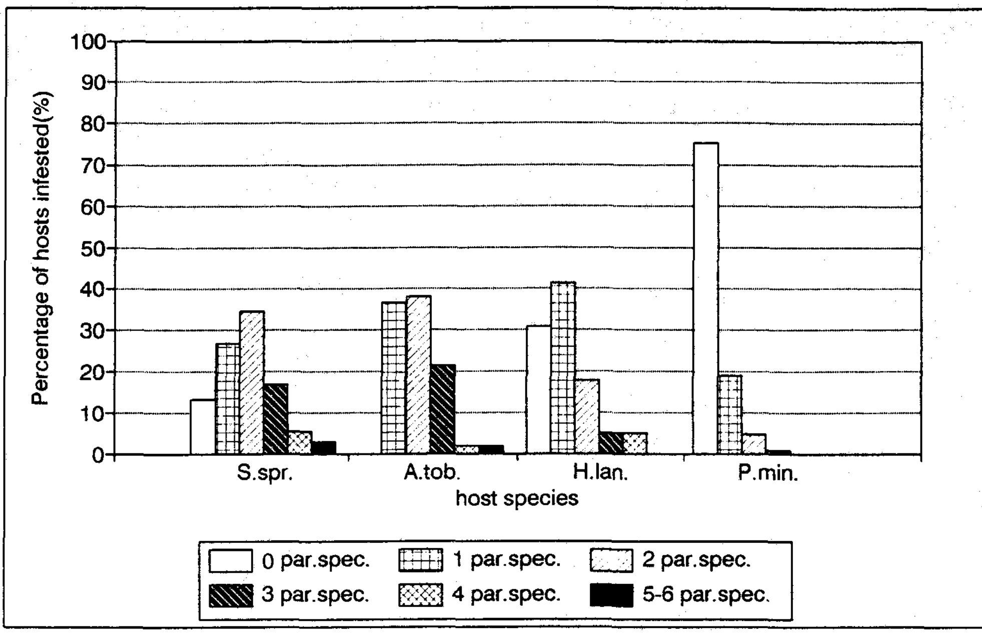

Fig. 2. Prevalences of parasite species (par. spec.) occurring in sprat *Sprattus sprattus* (S. spr.), lesser sand eel *Ammodytes tobianus* (A. tob.), greater sand eel *Hyperoplus lanceolatus* (H. lan.), and sand goby *Pomatoschistus minutus* (P. min.)

special attention. Generally, metacercariae of microphallids can be found in crustaceans. In this study, cysts as well as free metacercariae were observed in the gut of gobies. Two types of tetraphyllids were present which were referred to as *Scolex pleuronectis* "type a" and "type b". "Type a" larvae are about 140 µm long with 4 bothrids (20–25 µm) which centre around a suction disk. "Type b" is characterized by 175-µm long larvae with inverted scolices.

Structure of the helminth community

The role of the different parasites within the population of their hosts can be described by the abundance (Table 4) in combination with the diversity index and evenness. Ectoparasitic copepods are excluded from the following considerations. The parasite community of sprat consists of 13 helminth species and is unbalanced, as indicated by both low diversity and low evenness. *Cryptocotyle lingua* and *Hysterothylacium* sp. were dominant, whereas all other parasites only occurred in low densities. Seven species (5 Digenea and 2 nematodes) were detected in lesser sand eel. Low diversity and low evenness pointed to a one-sided species composition. *Brachyphallus crenatus* was extremely abundant and thereby far dominant. With regard to prevalence, parasites like *Cryptocotyle, Hemiurus* sp. and *Hysterothylacium* were important as well. However, they occurred in much lower densities (Tables 3 and 4). *Cryptocotyle, Brachyphallus* and *Hysterothylacium* also dominated the more balanced parasite community of greater sand eels (7 helminth spp.), in which only two other Digenea and

Table 3. Prevalence [%] and developmental stage of parasites in sprat (*S. spr.*), lesser sand eel (*A. tob.*), greater sand eel (*H. lan.*), and sand goby (*P. min.*). Cyst = metacercarie encysted; f. metacer. = free metacercarie, not encysted; L3, L4 = 3rd and 4th larval stage; pleroc. = plerocercoid

	S. spr.	*A. tob.*	*H. lanc.*	*P. min.*	Stage
DIGENEA					
Brachyphallus crenatus (Rudolphi, 1802)	6.9	96.3	20.5	0.5	adult
Hemiurus communis Odhner, 1905	8.8	22.2	10.3	0.5	adult
Hemiurus luehei Odhner, 1905	5.6	20.4			adult
Derogenes varicus (Müller, 1784)	1.9	3.7		2.1	adult
Lecithaster gibbosus (Rudolphi, 1802)	3.1			2.6	adult
Cryptocotyle lingua (Creplin, 1825)	23.3	35.2	28.2		cyst
Podocotyle atomon (Rudolphi, 1802)				0.5	adult
Pronomrymna ventricosa (Rudolphi, 1819)	6.9				adult
Steringotrema pagelli (Van Beneden, 1871)				0.5	adult
Microphallus primas (Jägerskjöld, 1908)				1.0	f. metacer.
MONOGENEA					
Mazocraes sp. (Van Beneden, 1870)	0.6				adult
EUCESTODA					
Bothriocephalus scorpii (Müller, 1776)				5.2	pleroc.
Scolex pleuronectis "a" Müller, 1788	3.1		7.7		pleroc.
Scolex pleuronectis "b"	5.0				pleroc.
NEMATODA					
Hysterothylacium sp.	73.0	9.3	41.0	8.8	L3, L4
Contracaecum sp.	6.3	5.6		0.5	L3, L4
Cucullanus heterochrous Rudolphi, 1802				3.6	adult
Cucullanus minutus (Rudolphi, 1819)				0.5	adult
Cosmocephalus obvelatus (Creplin, 1825)	2.5		5.2	0.5	L3
PARASITIC COPEPODA					
Lernaeenicus sprattae (Sowerby, 1804)	18.9				adult
Lernaeenicus encrasicoli (Turton, 1807)	18.9				adult
Lernaeocera minuta (T. Scott, 1900)				3.6	adult

Table 4. Abundances of parasites and preferred target organ (microhabitat) in the four fish species. See legend to Table 3

	S. spr.	*A. tob.*	*H. lanc.*	*P. min.*	Preferred organ
DIGENEA					
Brachyphallus crenatus	0.15	84.48	2.44	0.01	stomach
Hemiurus communis	0.13	1.20	0.28	0.01	stomach
Hemiurus luehei	0.12	0.17			stomach
Derogenes varicus	0.04	0.11		0.03	stomach
Lecithaster gibbosus	0.05			0.03	intestines
Cryptocotyle lingua	12.68	1.44	2.67		skin
Podocotyle atomon				0.01	intestines
Pronomrymna ventricosa	0.41				pyl. caecae
Steringotrema pagelli				0.20	intestines
Microphallus primas				0.13	stom., intest.
MONOGENEA					
Mazocraes sp.	0.01				gill
EUCESTODA					
Bothriocephalus scorpii				0.08	stomach
Scolex pleuronectis "a"	<0.01		0.02		stom., intest.
Scolex pleuronectis "b"	0.01				int., pylorus
NEMATODA					
Hysterothylacium sp.	12.40	0.22	1.46	0.10	body cavity
Contracaecum sp.	0.18	0.06		0.01	body cavity
Cucullanus heterochrous				0.04	intestines
Cucullanus minutus				0.03	stomach
Cosmocephalus obvelatus	0.04		0.05	0.01	body cavity
PARASITIC COPEPODA					
Lernaeenicus sprattae	0.29				eye
Lernaeenicus encrasicoli	0.30				body muscle
Lernaeocera minuta				0.05	gill

Cosmocephalus obvelatus were members. In contrast, the helminth fauna of sand gobies was most diverse, consisting of 13 species. Its parasite community can be regarded as balanced, since it had the highest evenness among the four fish species studied (Table 2). Although Digenea, like *Steringotrema pagelli* and *Microphallus primas*, were not important with regard to prevalence (Table 3), they were most abundant followed by *Hysterothylacium* and *Bothriocephalus scorpii* (Table 4).

Species composition of the parasites in the four host species

The greatest degree of conformity in parasite species composition (Fig. 3) and in prevalences was between sprat and the two species of sand eel. The similarity in relative abundance of the helminth species was greatest between sprat and greater sand eel as well as between the two sand eel species. It was lowest between sand eels and gobies. Striking differences were noted in various combinations of hosts, between sprat and sand eels, for example, and between sand goby and the other 3 hosts.

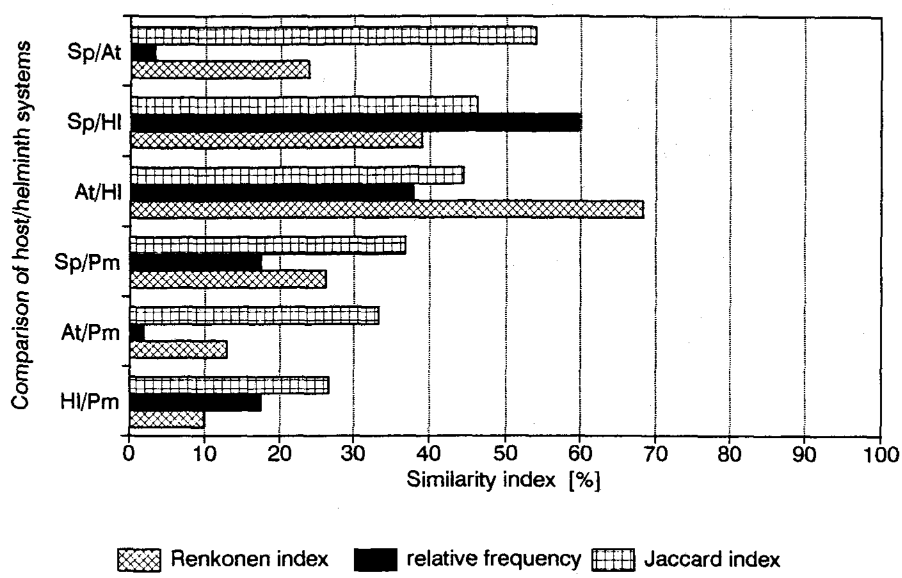

Fig. 3. Comparison of the parasite fauna of the 4 hosts. Sp = helminth fauna of *Sprattus sprattus*; At = do. of *Ammodytes tobianus*, Hl = do. of *Hyperoplus lanceolatus*; Pm = do. of *Pomatoschistus minutus*

Potential of medium- and small-sized fish to act as transmitters of parasites

Infested fish specimens were grouped according to their potential to act as intermediate or transport hosts for final hosts (Fig. 4) as follows:

(1) Final host for parasites: hosts infested with adult, fertile parasites (cf. Table 3).

(2) Intermediate host: all hosts infested with larval stages of parasites using the host as intermediate host in their life-history.

(2a) Infectious for seabirds or sea mammals: *Cryptocotyle lingua, Microphallus primas, Contracaecum* sp., *Cosmocephalus obvelatus* (so-called "allogenous parasites").

(2b) Infectious for predatory fish: *Bothriocephalus scorpii, Scolex pleuronectis* (two different types), *Hysterothylacium* sp.

Among the 22 parasite species and higher taxa, 8 species and almost 50 % of all parasite specimens occurred as larvae or juveniles. Three quarters of the sprat were found to be serving as intermediate hosts for different parasites; of these parasites almost one-third were potentially infectious for birds and mammals (Fig. 4). Sand eel carried a considerable portion of intermediate stages of bird parasites. In lesser sand eel, this fraction amounted to 40 %. Gobies played only a minor role as intermediate hosts. Only 2 % were potential transmitters of bird parasites.

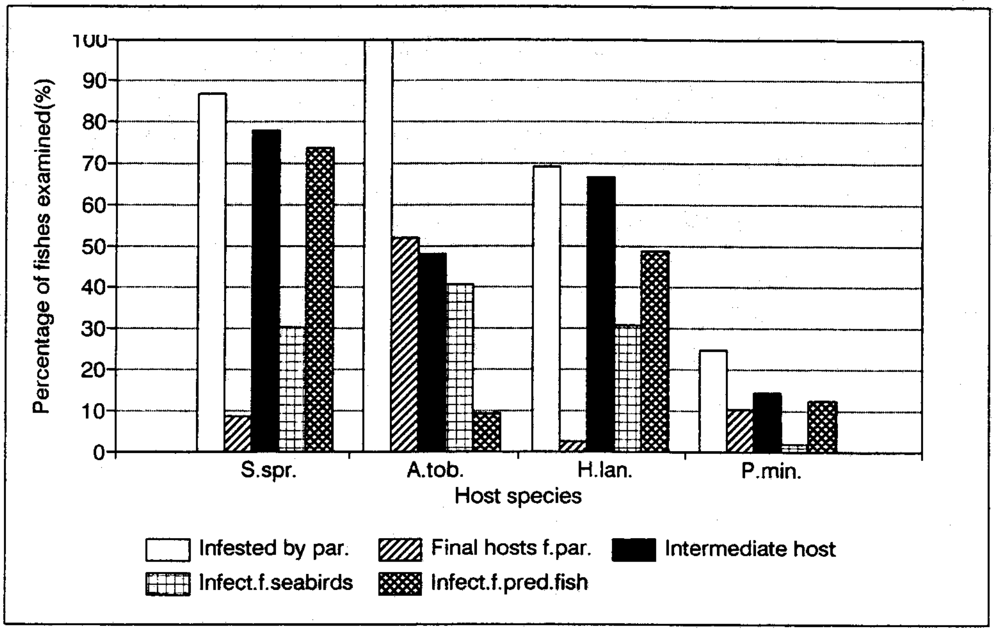

Fig. 4. Potential fraction of the 4 fish species which can act as intermediate or transport hosts for infestation of final hosts. *S. spr.* = *Sprattus sprattus*; *A. tob.* = *Ammodytes tobianus*; *H. lan.* = *Hyperoplus lanceolatus*; *P. min.* = *Pomatoschistus minutus*

DISCUSSION

Spectrum of parasite species

Among the Digenea, the cosmopolitan Hemiurata were dominant. This group is indicative of the feeding habits of the corresponding fish (Reimer, 1970), as the second intermediate hosts are mostly planktonic copepods. This might explain the higher infestation with *Brachyphallus crenatus* and *Hemiurus communis* in lesser sand eel which prefer planktonic copepods as food items. *Lecithaster gibbosus* and *Derogenes varicus* appeared in sprat, lesser sand eel and sand goby in relatively low densities (Table 4). Køie (1979, 1989) has identified many hosts for these parasites in a number of marine areas. The occurrence of a parasite may depend on various factors such as density, food quality and migration patterns of the host (Esch et al., 1989). The presumable primary hosts of *Derogenes* and *Lecithaster*, the snails *Natica* sp. and *Odostomia* sp., are not at all common in the Wadden Sea (Wolff & Dankers, 1981) in contrast to *Littorina* spp., which are the primary hosts of *Cryptocotyle lingua* and *Podocotyle atomon*. The silty areas of the highly dynamic Wadden Sea can be considered less suitable for *P. atomon*, since its cercariae move like inchworms on the bottom (Reimer, 1970). In any case, the infestation rates in sand gobies are extremely low compared to those recorded in other studies. Zander et al. (1993) found infestation rates in the Baltic Sea close to 30 %. Werding (1969) detected only low numbers of larval *P. atomon* in *Littorina littorea*. *Littorina saxatilis* is known to be the main primary host of this trematode in the southern North Sea (Gibson & Bray, 1979). *L. saxatilis* is common on hard bottoms in the upper intertidal. The crawling cercariae are well-adapted to these conditions (James, 1971). *L. saxatilis* as well as *L. littorea* can act as first intermediate host for *Cryptocotyle lingua* and are highly infested in some places, according to Werding (1969) and Lauckner (1984). From spring to autumn, masses of cercariae are released, driven by temperature and other factors (Sindermann & Farrin, 1962). The cercariae of *Cryptocotyle* are distinctly positively phototactic (Chapman, 1974). Thus, the lower densities in sand eel as compared to sprat might be related to the nocturnal activity of sand eel. Infestation rates with this sort of metacercariae may also be linked to fish migrations, as pointed out by Gorman & Moring (1982) for gunell *(Pholis gunellus)* along rocky sea shores. Perhaps this is the reason for the absence of *Cryptocotyle* in gobies in this study, since sand gobies most likely inhabit deeper waters at the border of the Wadden Sea in early summer (Fonds, 1973), while the other species were infested in the Wadden Sea proper (Groenewold, 1992). Furthermore, *C. lingua* has a preference for pelagic fish (Sinderman & Farrin, 1962). The main hosts of *Steringotrema pagelli* in the North Sea are dab *(Limanda limanda)* and lemon sole *(Microstomus kitt)* according to Køie (1980). *Steringotrema pagelli* has also been shown to occur in plaice *(Pleuronectes platessa)* in the southern North Sea (under the synonym: *Steringotrema cluthense*; Odhner, 1911). Gobies are not mentioned as hosts. The finding in this study was either accidental or related to the benthic behaviour of sand gobies, which this species has in common with the other hosts mentioned above. First intermediate hosts of *Steringotrema pagelli* are the bivalves *Nucula nitidosa* and *N. nucleus* which dominate the subtidal bottom in some areas of the North Sea (Salzwedel et al., 1985). It is not clear whether a second intermediate host is involved (Køie, 1980). The life cycle of *Pronoprymna ventricosa* is completely unknown. This Digenea has been found in the pyloric appendices and in the midgut of clupeids (Bray & Gibson, 1980), which was also supported by this study. Much information concerning hosts of the two fellostomid species has been compiled from warmer regions (Bray & Gibson, 1980). In the Mediterranean Sea, *Steringotrema pagelli* has often been detected in *Atherina* sp. The distribution centre of *Pronoprymna ventricosa* is the Mediterranean Sea (in *Engraulis* sp.), the Black Sea, the Sea of Asov and also the Red Sea. At higher latitudes hosts were sprat, alice shad *(Alosa alosa)* and twaite shad *(A. fallax)* along the Belgium coast and in the Irish Sea.

Microphallus primas uses additional paratenic hosts. The second intermediate host of this microphallid are shore crabs *(Carcinus maenas)* or gammarids such as *Gammarus salinus* and *G. locusta*. However, free metacercariae of *Microphallus primas* and another microphallid – *Maritrema subdolum* – have also been found in the gut of *Pholis gunellus* (Reimer, 1963). This pathway offers the opportunity for the parasite to infest birds which feed exclusively on fish. It remains an open question whether infestations of sand gobies, as detected in this study, can be considered an exception or the rule. The life cycle of *Microphallus primas* was retraced in the laboratory by Saville & Irwin (1991) employing in ovo cultivation. The main primary is *Hydrobia ulvae*, which occurs in the Wadden Sea in masses and is the first intermediate host for other microphallids, as well.

An extended life cycle is also known for the nematode *Cosmocephalus obvelatus*. As in microphallids, no further development takes place in the fish. However, adaptation of *Cosmocephalus* is much more advanced, since the nematode actively invades the coelom of its transport host (Plötz, 1982a).

Differently developed stages of plerocercoids of the eucestode *Bothriocephalus scorpii* have been reported. According to Markowski (1935b), who elucidated the life cycle, *Myoxocephalus scorpius* besides *Scophthalmus maximus* is an important final host. The "father lasher" is widely distributed in the Wadden Sea (Dankers & De Veen, 1978).

The tetraphyllid larvae, which have been referred to as *Scolex pleuronectis* in this study, have been described for many fish species. They occur mainly and most abundantly in clupeids (Reimer, 1970). Sand eels are not mentioned in the list presented by Williams (1968). However, the findings in greater sand eel reported here cannot be considered unusual, since copepods are common intermediate hosts. Final hosts for all tetraphyllids are elasmobranchs. In the Wadden Sea proper, the most likely target species would be *Raja clavata*. This species, however, has become extremely rare in this area (Berghahn, 1990).

No species identification was possible for the frequently found specimens of *Hysterothylacium* sp. The genus *Hysterothylacium* has a world-wide distribution and is one of the most abundant nematodes in fish (Möller & Anders, 1986). In particular, 3 species have been described most frequently (Berland, 1961), which, however, could have been confused with one another (Soleim & Berland, 1983): *Hysterothylacium aduncum*, *H. gadi* and *H. auctum*.

Contracaecum sp. could also not be determined to the species level, which would have revealed the final host. *Contracaecum osculatum*, for example, is a cosmopolitan nematode of diverse seals (Pinnipedia), (Valtonen et al., 1988; Fagerholm, 1989). The larval stages have been identified with the help of in vitro cultivation (McClelland & Ronald, 1974), but the life cycle remains unclear. Diverse copepod species (*Tisbe furcata*, *Amphiascus similis*) were experimentally infested (Davey, 1969). Fagerhom (1988) clarified the identity of *Contracaecum osculatum* larvae in cod (*Gadus morhua*), which is heavily infested with this parasite in the Baltic. Descriptions of the larval stages of *Contracaecum* species, which have birds as final hosts, were provided by Huizinga (1966) and Deardorff & Overstreet (1980). The life cycle of *Contracaecum spiculigerum* (syn.: *C. rudolphi*) was clarified by Huizinga. Along the west coast of North America, *Myoxocephalus octodecimspinosus* and *Pseudopleuronectes americanus* are intermediate hosts (Deardorff & Overstreet, 1980). Another marine species is *Contracaecum variegatum*, the larvae of which have not been described (Hartwich, 1975). In conclusion, all 3 species may occur as parasites in the investigated fish species.

Infestation rates of *Lerneocera minuta* (Tables 3 and 4) were close to those reported by Mann (1964), who detected this parasitic copepod in 3–5 % of the gobies from the by-catch of shrimpers. Petersen (1992), however, noted considerable regional differences in prevalence. Apart from *Hysterothylacium* and *Cryptocotyle*, *Lernaeenicus sprattae* and *L. encrasicoli* were the most abundant parasites in sprat (18.9 %). In the Oslo fjord, Schram (1987) found much lower prevalences: 4.3 % for *L. sprattae* and only 0.4 % for *L. encrasicoli*.

Structure of the helminth community

With respect to dominance, the different helminth species play a variable role within the parasite fauna of the 4 fish species investigated (Table 4). In particular, the very unbalanced helminth community of *Ammodytes* made it clear that a single species – *Brachyphallus crenatus* – can be completely dominant. According to Hanski (1982), Holmes (1989) classifies parasites of a community with regard to their prevalence in core, secondary and satellite species. Core species are characterized by more than 60 % prevalence and a positive correlation between prevalence and density. In this study, only *Brachyphallus crenatus* in lesser sand eel *Ammodytes*, and *Hysterothylacium* sp. in sprat fall into this category (Table 4). Only if seasonal differences in infestation rates are considered, is this also true for *Cryptocotyle* and *H. luehei* in *Ammodytes* (Groenewold, 1992). This result corresponds also to the situation of the goby guild of Lübeck Bight (Zander et al., 1993). Secondary species achieve prevalences between 40 % and 60 %, whereas satellite species stay below 40 %. It was striking that, besides *Brachyphallus*, only two species within the community played a major role, all of which had 4 or at least 3 of the fish species as intermediate host, namely *Hysterothylacium* and *Cryptocotyle*. Both are not very specific with regard to their second intermediate host (Berland, 1961; Reimer, 1963). Hemiuroids can also be considered to be generalists (Gibson & Bray, 1979). The highest numbers of *Brachyphallus* in lesser sand eel may result from accumulation due to selective feeding on planktonic copepods which are the second intermediate hosts. Similar conditions were found for *Podocotyle atomon* and *Hysterothylacium* sp. in *Zoarces viviparus* (Zander, 1991). In contrast, *Pronoprymna ventricosa* has almost exclusively been detected in other clupeids (Bray & Gibson, 1980).

The composition of the parasite fauna of different host fishes is highly dependent on the area of the sea (Rohde, 1982). For example, in gobies from brackish waters in the Baltic, typical freshwater parasites were numerous (Markowski, 1935a; Koter, 1962; Zander & Döring, 1989; Zander et al., 1993). In this study, however, these were not important, since salinity was always above S = 26 ‰. Moreover, Acanthocephala were not present, which were frequently detected in the Baltic Sea (Markowski, 1935a; Zander & Döring, 1989; Zander et al., 1993), in particular in the Schlei Fjord (Zander & Westphal, 1991; Kesting, 1992). It should be critically noted that differences in spatial distribution of parasites on a small scale can be considerable as demonstrated by Petersen (1992) for sand goby in the Wadden Sea.

The comparison between the 4 host/helminth systems (Fig. 4) provides further information concerning factors which shape the structure of the helminth fauna. The fairly great differences between benthic sand gobies, on the one hand, and sand eels or sprat, on the other, give reason to conclude that the food composition of host fishes and the resulting uptake of intermediate hosts is of paramount importance for the composition and the structure of parasite communities. However, the great similarity between the 2 sand eel species with their quite different food items (Table 1) reveals that other factors are also important. These are, in particular, habitat and behaviour of hosts (activity rhythm, migration) as well as the more difficult to record requirements of parasites concerning their microhabitats.

Importance of small-sized fish as intermediate hosts for parasites

It is possible that the catchability of fish infested with parasites is increased (Anders & Möller, 1991). Moreover, infestation with parasites, such as *Lernaeenicus* in sprat, might make them more accessible to potential predators. However, in view of the role of parasites in small-sized fish from the by-catch of shrimpers, special attention should be paid to the fact that a considerable amount of discards is removed by seabirds or other predators (Berghahn & Rösner, 1992). This aspect has also been stressed by Plötz (1982b), who found high intensities of *Cosmocephalus* in offal from fisheries around Helgoland Island.

Many investigations have pointed out the important role of smaller-sized fish in the food web. Gobies can contribute more than 20 % (in number) to the food items of seals (Sievers, 1989). Together with sand eel, gobies can represent a considerable share in the food of herring gulls *(Larus argentatus)*, kittywakes *(Rissa tridactyla)* or other seabirds (Hartwig & Söhl, 1975; Vauk & Jokele, 1975; Dornboos, 1984). Goby (Zijlstra, 1978; Zander & Döring, 1989), sand eel (Reay, 1970), and sprat (Bailey & Bakken, 1990) are common prey for bigger fishes. Many of these predators are also final hosts for helminth species found in this study. According to Lick (1991), 27 % of the seals in the Wadden Sea are infested with *Contracaecum osculatum*. In the Kattegat-Skagerrak region, infestation rates were up to 20 % (Lunneryd, 1991). High rates of infestation with *Contracaecum variegatum, C. rudolphii* and *Cosmocephalus obvelatus* were detected in herring gull and great black-backed gull *(Larus marinus)* around Helgoland Island (Plötz, 1979). Sixty-five percent of the herring gulls in the southern North Sea are infested with *Cryptocotyle lingua* (Loos-Frank, 1971). The infestation rate in nestlings of black-headed gulls *(Larus ridibundus)* by *Microphallus primas, Cosmocephalus, Contracecum variegatum* and *Cryptocotyle* reached 43 to 53 % in prevalence on Wangerooge Island (Lorch et al., 1982).

It remains unclear whether the discards from shrimpers have any effect on the structure of the parasite fauna. Referring to the results of his long-term studies, Lauckner (1990) assumes that the high densities of seabirds (i.e. final hosts) in Königshafen, a small bay on Sylt island, lead to an increase in the density of the corresponding parasites, which consequently affects the species composition and population dynamics of many intermediate hosts. The infestation pressure caused by final hosts may also have an impact on diverse medium and small-sized fish species, e.g. an increase in mortality of fish larvae may be caused by parasites such as *Cryptocotyle* (Rosenthal, 1967; Lauckner, 1984). In any case, it is evident from the high degree of parasite transmission found in this study how efficiently final hosts might be reached by helminth species via the discards of shrimpers. Berghahn (1990) calculated the potential intake of shrimping discards by herring gulls in the North Frisian Wadden Sea in June (raising of nestlings) as amounting to 17.9 tons.

It should be noted that the conditions for parasites with 2 or 3 hosts in their life cycle are optimal in the Wadden Sea due to the high densities of all intermediate hosts, short infestation pathways and infestation times as well as high encounter rates of intermediate and final hosts. It will be difficult to disentangle these factors from the impact of the shrimp fishery. Even if zero-use areas were provided for comparative studies, the pronounced migratory behaviour of the intermediate hosts, medium and small-sized fish, would most probably mask the potential differences from the fishing grounds.

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