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Sven Klimpel · Annett Seehagen · Harry W. Palm

# Metazoan parasites and feeding behaviour of four small-sized fish species from the central North Sea

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**Abstract** The metazoan parasites and stomach contents of the small-sized demersal fishes *Agonus cataphractus*, *Buglossidium luteum*, *Callionymus lyra* and *Rhinonemus cimbrius* were studied and analysed. The fishes were captured using various sampling gears at 12 stations in the central North Sea. A total of 16 metazoan parasite species were isolated: six adult Digenea, three larval and adult Cestoda, four larval and adult Nematoda and three larval and adult Crustacea. With nine parasites species each, *A. cataphractus* and *R. cimbrius* harboured the highest parasite diversity, while *B. luteum* and *C. lyra* hosted only six and five parasite species, respectively. Eighteen new hosts and four new locality records were established. No Myxozoa, Monogenea or Acanthocephala were found. Most of the detected parasites showed a wide geographical range and a low host-specificity. The composition of the parasite fauna differed between the fish species, in accordance with their different feeding behaviours. The diet of bentho-pelagic feeders (*A. cataphractus*, *R. cimbrius*) was more diverse in comparison with the more specialised benthic feeders (*C. lyra*, *B. luteum*). This correlated with the lower diversity of heteroxenic parasites within both small-sized benthic fish species.

S. Klimpel (✉) · A. Seehagen
Marine Pathology Group, Department of Fisheries Biology,
Institut für Meereskunde an der Universität Kiel,
Düsternbrooker Weg 20, 24105 Kiel, Germany
E-mail: sklimpel@ifm.uni-kiel.de
Tel.: +49-431-6004580
Fax: +49-431-6001671

S. Klimpel · H. W. Palm
Institut für Zoomorphologie, Zellbiologie und Parasitologie,
Heinrich-Heine-Universität Düsseldorf,
Universitätsstraße 1, 40225 Düsseldorf, Germany

H. W. Palm
Faculty of Fisheries and Marine Science, Bogor Agricultural
University, Campus IPB Darmaga,
16680 Bogor, Indonesia

## Introduction

Parasites are an essential part of each aquatic community. Their presence becomes evident after a massive development, causing diseases and sometimes even leading to the mass mortality of infested hosts. Such events are often combined with biotic or abiotic changes in the environment (Möller 1987). There is increasing evidence that parasites are an important element of marine biodiversity (Mariaux 1996; Palm et al. 1999; Klimpel et al. 2001). In fisheries biology, parasitological studies have increasing importance, because parasites may serve as natural markers for the identification of fish stocks (MacKenzie 1983; Williams et al. 1992). Moreover, parasites can help to analyse the diet of fish species, serving as biological indicators of the prey species and their origin (Campbell et al. 1980; Palm et al. 1998). Whereas stomach analyses may provide detailed information on the immediate trophic relationship at the time of sampling, parasitological studies make it possible to infer previous trophic interactions, thus integrating short-term variability in the food web to make wider relationships more apparent. Helminths are particularly useful for such studies, because the different stages in their life cycle are passed through the marine food web until they reach their definitive host (Campbell et al. 1980). Finally, parasites provide information on habitats and trophic status of the studied fish species within the marine ecosystem.

Small fish species are frequent food items for piscivorous fish. Predatory fish largely acquire and accumulate parasites by ingesting small fish species that are infested and serve as carriers (Lile 1998). Parasitological studies, however, mainly focus on commercial fish species. In *Gadus morhua* L., 1758 and *Clupea harengus* L., 1758, for instance, the number of parasite species determined to date attains 123 and 80, respectively (Arthur and Arai 1984; Hemmingsen and MacKenzie 1993). Moreover, there is also an increasing interest in the patterns of parasite distribution within non-commercial fish species. Palm et al. (1999) demonstrated that the small-sized fish species *Gasterosteus aculeatus* L., 1758, *Gobius niger* L., 1758, *Pomatoschistus microps* (Krøyer, 1838), *P. minutus* (Pallas, 1770) and *Pungitius pungitius* (L., 1758) from the North Sea harbour a great parasite diversity (41, 22, 30, 33, 32 species, respectively), most of them having a low host-specificity.

The diversity of parasites is dependent on the specific feeding behaviour of hosts, the availability of intermediate and final hosts, depth distribution and host migrations (Rhode 1984; Kennedy et al. 1986; Poulin 1995). Similarities in diet and habitat of potential host species may result in similar parasite faunas (Polyanski 1966). In contrast, hosts with different food preferences may have large differences in their parasite faunas (Polyanski 1961). The aim of the present study is to investigate the parasite fauna of hitherto little-studied small-sized fish species in the central North Sea. The result is intended to clarify their role within the marine food web and illustrate their feeding ecology and parasite diversity.

## Materials and methods

A total of 70 specimens each of *Agonus cataphractus* (total length 12.9–17.4 cm, total weight 21.2–59.7 g), *Buglossidium luteum* (total length 7.9–11.8 cm, total weight 5.2–20.0 g), *Callionymus lyra* (total length 10.5–21.8 cm, total weight 8.7–59.4 g) and *Rhinonemus cimbrius* (total length 14.2–22.5 cm, total weight 13.2–62.7 g) were collected on board of the German research vessel FFK Solea. The fishes were caught in the central North Sea (53°48′ to 54°43′N, 06°29′ to 08°08′E) between 2 January and 12 February 1999 by bottom trawls at a water depth of 16–44 m.

All fish specimens were deep-frozen and later studied in the laboratory. Ectoparasite infestation was examined while the fish was still in a partly frozen state. Skin, fins, eyes, nasal capsules, gills and the buccal and branchial cavities were studied for metazoan parasites. While the body cavity, internal organs and digestive tract were examined under a stereomicroscope, the gall bladder was removed and studied using phase-contrast microscopy. Belly flaps and musculature were examined using a candling table. Additionally, a subsample of 35 specimens per species of *A. cataphractus*, *B. luteum*, *C. lyra* and *R. cimbrius* were examined for stomach contents, which were then sorted and prey items were identified to the lowest possible taxon. The frequency of occurrence ($F$) of prey items in non-empty stomachs was recorded and calculated in accordance with Hyslop (1980).

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 and Cestoda were stained with acetic carmin, dehydrated, cleared with eugenol or creosote and then mounted in Canada balsam. Crustacea were dehydrated in a gradated ethanol series and transferred into Canada balsam.

Parasite identification literature included original descriptions by Bray and Gibson (1986), Gibson and Bray (1986) and Køie (1976, 1978, 1979, 1992, 1995) for Digenea, Dollfus (1942) and Khalil et al. (1994) for Cestoda, Køie (1993, 2000, 2001) and Moravec (1987) for Nematoda and Kabata (1979, 1992) for Crustacea. Parasitological terms (prevalence, intensity, mean intensity) were used in accordance with Bush et al. (1997). The diversity of metazoan parasite faunas of each fish species was estimated using the Shannon diversity index ($H'$) and the evenness index ($J'$) of Pielou (Magurran 1988). Correlations were analysed by Spearman's rank correlation coefficient. Differences in numbers of different parasite species between the four small-sized fish species were tested for statistical significance by the Kruskal–Wallis test.

## Results

### *Agonus cataphractus* (L., 1758)

Nine parasite species were found in or on *A. cataphractus*: three Digenea, two Cestoda and four Nematoda (Table 1). The digenean trematodes *Brachyphallus crenatus*, *Derogenes varicus* and *Hemiurus communis* were present as adults and were located in the stomach. Two larval cestodes were identified: *Bothriocephalus scorpii* and *Solex pleuronectis* (Tetraphyllidea indet.). They were located in the pyloric caeca and the intestine. Among the nematodes, *Hysterothylacium aduncum* was found as third and fourth stage larvae (L3/L4) and *Ascarophis arctica*, *Capillaria gracilis*, *Cucullanus heterochrous* and *H. aduncum* were found as adults. The adult nematodes were found in the stomach, pyloric caeca and the intestine, while the larvae were located exclusively in the body cavity. The present findings of *B. crenatus*, *H. communis*, *S. pleuronectis*, *B. scorpii*, *C. heterochrous*, *A. arctica* and *C. gracilis* represent new host records; and the finding of *A. arctica* represents a new locality for the central North Sea.

### *Buglossidium luteum* (Risso, 1810)

Six different parasite species were detected in or on *B. luteum*: two Digenea, two Nematoda and two Crustacea (Table 1). *D. varicus* and *Podocotyle atomon* were present as adults. *D. varicus* was located in the stomach, while *P. atomon* was found in the intestine. *C. heterochrous* and *H. aduncum* were present as adult stages and *H. aduncum* was also found as L3 and L4 larvae. The adult nematodes were encountered in the digestive tract; and the larval stages were encysted in the body cavity. The crustacean parasite *Bomolochus* sp. and copepodite stages of *Lernaeocera branchialis* were located on the gills. The present findings of *D. varicus*, *P. atomon*, *C. heterochrous*, *H. aduncum*, *Bomolochus* sp. and *L. branchialis* represent new host records; and *Bomolochus* sp. represents a new locality record.

### *Callionymus lyra* (L., 1758)

*C. lyra* had a total of five parasite species: three Digenea and two Nematoda (Table 1). The digenean trematodes *D. varicus*, *P. atomon* and *Zoogonoides viviparus* were found as adults. *D. varicus* was exclusively located in the stomach, *P. atomon* and *Z. viviparus* only in the intestine. The fishes were also infested by the adult nematodes *Capillaria gracilis* and *H. aduncum* and by L3 and L4 stages of *H. aduncum*. The adult nematodes were present in the digestive tract and the larval stages were encysted in the body cavity. The present findings of *P. atomon*, *C. gracilis* and *H. aduncum* represent new host records.

**Table 1** Prevalence (*P*) and mean intensity (*mI*) of infestation of four small-sized fish species from the central North Sea

| Parasite species | Adult/Larva | *Agonus cataphractus* | | *Buglossidium luteum* | | *Callionymus lyra* | | *Rhinonemus cimbrius* | |
|---|---|---|---|---|---|---|---|---|---|
| | | P (%) | mI (range) | P (%) | mI (range) | P (%) | mI (range) | P (%) | mI (range) |
| Digenea | | | | | | | | | |
| *Brachyphallus crenatus* (Rudolphi, 1776) | Adult | 27.1 | 2.5 (1–4) | | | | | 21.4 | 1.7 (1–3) |
| *Derogenes varicus* (Müller, 1780) | Adult | 45.7 | 2.4 (1–4) | 21.4 | 1.1 (1–2) | 24.3 | 1.1 (1–2) | 68.6 | 2.0 (1–4) |
| *Hemiurus communis* (Odhner, 1905) | Adult | 15.7 | 1.7 (1–3) | | | | | 12.9 | 1.1 (1–2) |
| *Podocotyle atomon* (Rudolphi, 1802) | Adult | | | 18.6 | 1.5 (1–3) | 31.4 | 2.5 (1–5) | | |
| *Stephanostomum caducum* (Looss, 1901) | Adult | | | | | | | 41.4 | 3.0 (1–4) |
| *Zoogonoides viviparus* (Olsson, 1868) | Adult | | | | | 64.3 | 14.3 (2–64) | | |
| Cestoda | | | | | | | | | |
| *Bothriocephalus scorpii* (Müller, 1776) | Adult/Larva | 15.7 | 1.8 (1–3) | | | | | 31.4 | 2.3 (1–4) |
| *Lacistorhynchus tenuis* (van Beneden, 1858) | Larva | | | | | | | 1.4 | 1.0 (1) |
| *Scolex pleuronectis* (Müller, 1788) | Larva | 64.3 | 5.6 (1–10) | | | | | | |
| Nematoda | | | | | | | | | |
| *Ascarophis arctica* Polyanski, 1952 | Adult | 68.6 | 5.2 (1–14) | | | | | | |
| *Capillaria gracilis* (Bellingham, 1840) | Adult | 55.7 | 2.6 (1–6) | | | 15.7 | 1.2 (1–2) | 50.0 | 3.4 (1–6) |
| *Cucullanus heterochrous* Rudolphi, 1802 | Adult | 18.6 | 1.5 (1–5) | 14.3 | 1.0 (1) | | | | |
| *Hysterothylacium aduncum* (Rudolphi, 1802) | Adult/Larva | 100.0 | 10.0 (3–21) | 74.3 | 4.2 (1–7) | 67.1 | 1.5 (1–3) | 100.0 | 8.5 (2–15) |
| Crustacea | | | | | | | | | |
| *Taeniacanthus onosi* (Scott, 1902) | Adult | | | | | | | 58.6 | 3.5 (1–7) |
| *Bomolochus* sp. von Nordmann, 1832 | Adult | | | 24.3 | 1.1 (1–2) | | | | |
| *Lernaeocera branchialis* (Linnaeus, 1776) | Larva | | | 14.3 | 1.2 (1–2) | | | | |

**Table 2** Frequency of occurrence (*F*) of the prey items identified in the stomach of four small-sized fish species from the central North Sea

| Food taxon | *Agonus cataphractus* *F* (%) | *Buglossidium luteum* *F* (%) | *Callionymus lyra* *F* (%) | *Rhinonemus cimbrius* *F* (%) |
|---|---|---|---|---|
| Polychaeta | 11.4 | 6.7 | 20.0 | 22.9 |
| *Pectinaria* sp. | 2.9 | | | 8.6 |
| Gastropoda | 14.3 | 6.7 | 11.4 | 8.6 |
| Bivalvia | 8.6 | 16.7 | 5.7 | 5.7 |
| Ostracoda | | 6.7 | | |
| Copepoda | 17.1 | | | |
| Mysidacea | | | | 11.4 |
| Cumacea | | 63.3 | | 20.0 |
| Amphipoda | 28.6 | 23.3 | | 37.1 |
| Gammaridea | 45.7 | 46.7 | 17.1 | 62.9 |
| Hyperiidae | 20.0 | | | 11.4 |
| Euphausiacea | 11.4 | | | 22.9 |
| Decapoda | 8.6 | | | 34.3 |
| *Crangon crangon* | 68.6 | | | 42.9 |
| *Pagurus bernhardus* | 5.7 | | | 20.0 |
| *Carcinus maenas* | 2.9 | | | 5.7 |
| Ophiuroidea | | 50.0 | 5.7 | |
| *Ophiura* spp. | | | 65.7 | |
| Echinoidea | | | 14.3 | |
| Gobiidae | 5.7 | | | 34.3 |
| Number of stomachs with content | 35 | 30 | 35 | 35 |
| Number of empty stomachs | 0 | 5 | 0 | 0 |

### *Rhinonemus cimbrius* (L., 1758)

A total of nine parasite species were found in or on *R. cimbrius*: four Digenea, two Cestoda, two Nematoda and one Crustacea (Table 1). *B. crenatus*, *D. varicus*, *H. communis* and *Stephanostomum caducum* were present as adults. *B. crenatus*, *D. varicus* and *H. communis* were found exclusively in the stomach and *S. caducum* was located in the pyloric caeca and the intestine. The cestodes were represented by a larval stage of *Lacistorhynchus tenuis* and adult stages of *B. scorpii*. *L. tenuis* was located in the body cavity and *B. scorpii* in the pyloric caeca. The nematodes *C. gracilis* and *H. aduncum* were present as adults and within the digestive tract. The only nematode larvae (L3/L4) belonged to *H. aduncum* and were encysted in the body cavity. Adults of the crustacean species *Taeniacanthus onosi* were located exclusively on the gills. The present findings

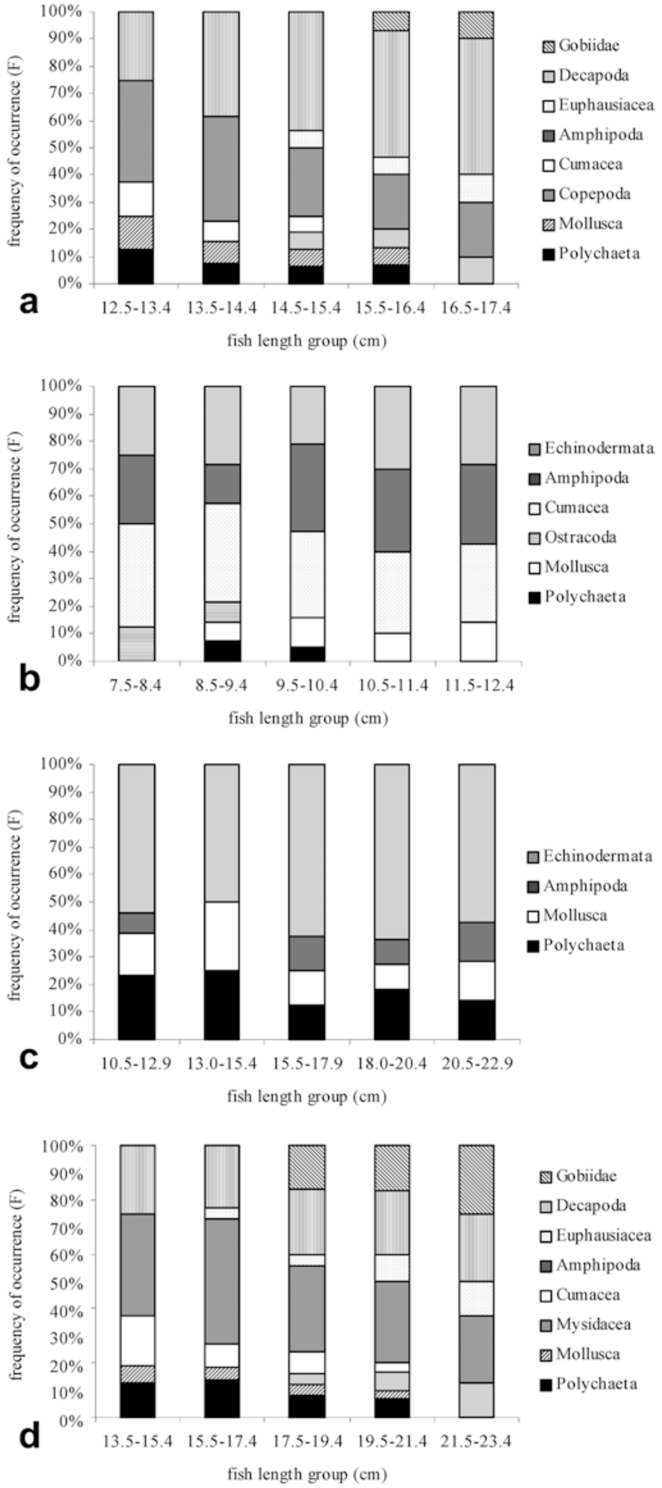

**Fig. 1a–d** The food composition of *Agonus cataphractus*, *Rhinonemus cimbrius*, *Buglossidium luteum* and *Callionymus lyra*. The food composition of *A. cataphractus* (**a**) and *R. cimbrius* (**d**) depends on the total fish length. With increasing total fish length, the contribution of the Polychaeta and Amphipoda decreases, while Decapoda, Euphausiacea, Copepoda and Gobiidae increase. The composition of the food items within *B. luteum* (**b**) and *C. lyra* (**c**) is not dependent on the total fish length, with all prey items being present within the different length classes

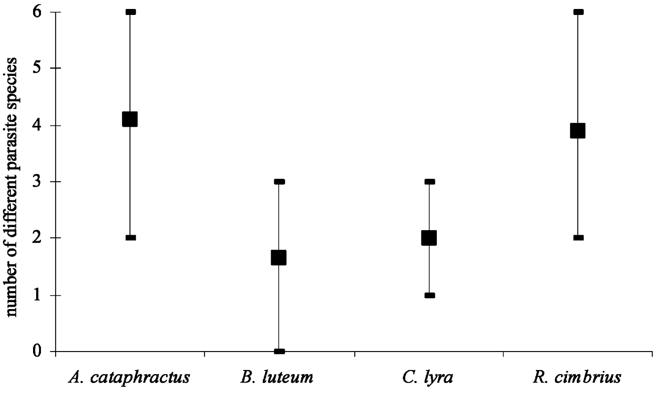

**Fig. 2** Parasite diversity. *A. cataphractus* and *R. cimbrius* usually harbour 2–6 different parasite species (mean 4.1 and 3.9, respectively), whereas *B. luteum* and *C. lyra* are mostly infested with 1–3 species (mean 1.7 and 2.0, respectively)

of *L. tenuis* and *B. scorpii* represent new host records; and the findings of *C. gracilis* and *T. onosi* represent new locality records.

## Feeding ecology

The food of *A. cataphractus* consisted mainly of Crustacea, Polychaeta, Mollusca and fish (Table 2). The Crustacea were dominated by Decapoda [mainly *Crangon crangon* (L., 1758)], Amphipoda (mostly Gammaridea and Hyperiidae), Copepoda and Euphausiacea. The fish belonged almost exclusively to the Gobiidae.

The food of *B. luteum* consisted of small Crustacea, Echinodermata, Mollusca and Polychaeta (Table 2). The Crustacea were dominated by Cumacea and small Amphipoda (mostly Gammaridea). The Mollusca were dominated by Bivalvia; and the Echinodermata belonged almost exclusively to the Ophiuroidea.

The main food of *C. lyra* were Echinodermata and, to a much lesser extent, Polychaeta and Crustacea (Table 2). The Echinodermata were dominated by Ophiuroidea (the main food genus was *Ophiura*) and Echinoidea. The Crustacea were almost exclusively small Gammaridea.

The food of *R. cimbrius* consisted mostly of Crustacea, fish, Polychaeta and Mollusca (Table 2). The Crustacea were mainly Amphipoda (mostly Gammaridea and Hyperiidae), Decapoda [the main food species were *C. crangon* and *Pagurus bernhardus* (L., 1758)], Euphausiacea and Cumacea. The fish belonged almost exclusively to the Gobiidae.

The food composition of *A. cataphractus* and *R. cimbrius* depended on the total fish length. With increasing total fish length (Fig. 1), the contribution of the Polychaeta and Amphipoda decreased, while Decapoda, Euphausiacea, Copepoda and Gobiidae increased. The composition of the food items within *B. luteum* and

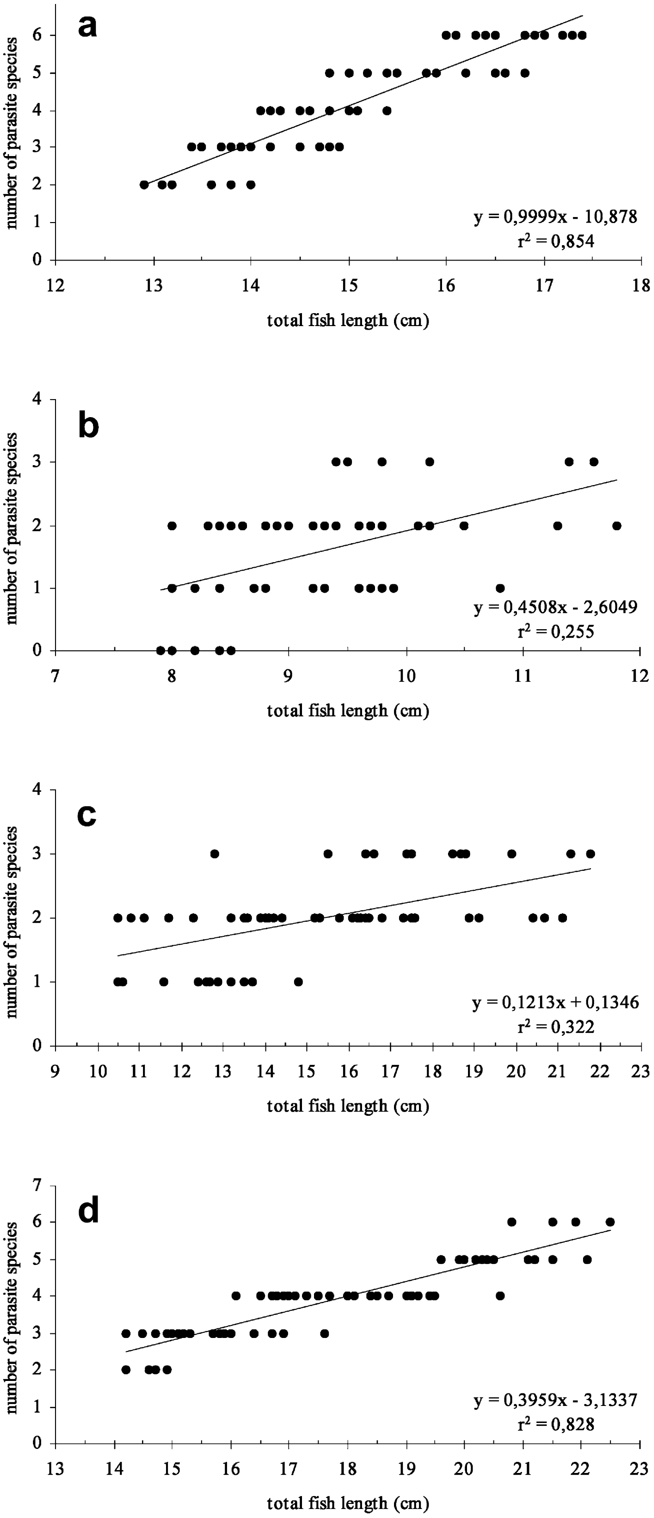

**Fig. 3a–d** The number of parasite species rises with increasing total fish length (see Results for details). (**a**) *A. cataphractus*, (**b**) *B. luteum*, (**c**) *C. lyra*, (**d**) *R. cimbrius*

*C. lyra* was not dependent on the total fish length, with all prey items being present within the different length classes (Fig. 1).

### Parasite diversity

*A. cataphractus* and *R. cimbrius* usually harboured 2–6 different parasite species (mean 4.1 and 3.9, respectively), whereas *B. luteum* and *C. lyra* were mostly infested with 1–3 species (mean 1.7 and 2.0, respectively; Fig. 2).

The number of parasite species rose with increasing total fish length (Fig. 3). This significant correlation was strong in *A. cataphractus* ($n = 70$, $r^2 = 0.854$, $P < 0.01$) and *R. cimbrius* ($n = 70$, $r^2 = 0.828$, $P < 0.01$), but weak in *B. luteum* ($n = 70$, $r^2 = 0.255$, $P < 0.01$) and *C. lyra* ($n = 70$, $r^2 = 0.322$, $P < 0.01$). The Shannon diversity index was relatively high in *A. cataphractus* ($H' = 1.574$, $J' = 0.716$) and *R. cimbrius* ($H' = 1.514$, $J' = 0.689$), but lower in *B. luteum* ($H' = 0.982$, $J' = 0.548$) and *C. lyra* ($H' = 0.731$, $J' = 0.454$).

## Discussion

The analysed North Sea fishes were parasitised by numerous parasites that are defined as generalists, i.e. unspecialised parasites that infest fishes regardless of the host species (Lile 1998; Marcogliese 2002). *Agonus cataphractus* and *Rhinonemus cimbrius* were the most heavily infested fishes and usually hosted 2–6 parasite species. Furthermore, there was a significant correlation between the number of parasite species and the total fish length of *A. cataphractus* and *R. cimbrius*. The fishes acquire and accumulate parasite species through preying upon infected intermediate and transport hosts (Lile 1998). Benthic invertebrates (e.g. Polychaeta, Crustacea) are the principal food of the smaller specimens of *A. cataphractus* and *R. cimbrius*, whereas the larger specimens feed mostly on fish and crustaceans. This demonstrates an important shift towards a piscivorous and crustacean-feeding behaviour during growth. Because of the increasing number and change in prey organisms, both species demonstrate an increasing parasite load with increasing total fish length. In contrast to *A. cataphractus* and *R. cimbrius*, the number of different parasite species in *Buglossidium luteum* and *Callionymus lyra* was lower, being 1–3. Both fish species feed exclusively on small benthic invertebrates and, therefore, are infested directly from the benthic intermediate hosts. Because there is no change in feeding behaviour with increasing total fish length, the infestation of *B. luteum* and *C. lyra* was probably directly dependent on the availability of the first intermediate host and not on the fish size. The parasite diversity was higher in *A. cataphractus* and *R. cimbrius*, while essentially lower values were tallied for *B. luteum* and *C. lyra*. These results clearly reflect the indicator function of fish parasites for the feeding behaviour of their hosts.

All four fish species were infested with *Derogenes varicus* and *Hysterothylacium aduncum*. These two parasite species are among the most common in marine fishes of the northern hemisphere (Køie 1979, 1993) and have been recorded from many different fish species along the German coast (Palm et al. 1999). The first intermediate host of *D. varicus* in the study area is the prosobranch, *Natica* spp. (Køie 1979), while *H. aduncum* has several planktonic and benthic invertebrates as first intermediate hosts (Marcogliese 1996; Jackson et al. 1997). The latter may also serve as second intermediate hosts to both *D. varicus* and *H. aduncum* (e.g. Øresland 1986; Køie 1993). The infestation of the fishes studied with both parasite species is therefore linked to the availability of the first intermediate host and the low host-specificity of the parasites with regard to their second intermediate host.

The nematode *Capillaria gracilis* was found in three of the fish species and did not occur in *B. luteum*. The life cycle of this parasite was recently described by Køie (2001), who showed experimentally that Annelida and Gobiidae are its first and second intermediate hosts. *A. cataphractus* and *R. cimbrius* were presumably infested with *C. gracilis* by feeding on various gobiids that serve as vectors. The lower infestation of *C. lyra* with *C. gracilis* indicates this fish species preys infrequently on Annelida. The nematode *Cucullanus heterochrous* detected in *A. cataphractus* and *B. luteum* typically infests flatfishes of the family Pleuronectidae (Palm et al. 1999). Gibson (1972) suggested that *C. heterochrous* might have an indirect development. However, Køie (2000) demonstrated experimentally that its intermediate hosts are various species of Polychaeta which are preyed upon by the fish species within the present study. The coexistence of the various parasite species is caused by the uptake of prey organisms that serve as intermediate hosts. The high similarity of infestation rates and the similar number of parasite species in *A. cataphractus* and *R. cimbrius* indicate that both species have an active food-searching behaviour and a variable diet, thus increasing their chance of becoming infested.

*A. cataphractus* feeds bentho-pelagically, as indicated by the presence of the Digenea, *Brachyphallus crenatus* and *Hemiururs communis*. Both parasite species have snails of the genus *Retusa* as first intermediate hosts (Køie 1992, 1995); and field studies have detected metacercaria of both species in several planktonic invertebrates as second intermediate hosts (Gibson and Bray 1986; Køie 1992, 1995). *B. crenatus* and *H. communis* have been found in a variety of final hosts in the north-east Atlantic (Gibson and Bray 1986; Palm et al. 1999), indicating a low host-specificity. Large numbers of the nematode *Ascarophis arctica* were only found in *A. cataphractus*. Its life cycle is unknown, but several species of benthic Crustacea may serve as first intermediate hosts. Benthic Decapoda and Amphipoda, known as intermediate hosts of other *Ascarophis* species (Uspenskaya 1953; Appy 1981; Jackson et al. 1997), belong to the regular diet of *A. cataphractus*.

*C. lyra* feeds selectively on benthic invertebrates and consequently has fewer parasite species than *A. cataphractus* and *R. cimbrius*. Its specialised diet explains the high infestation with the trematode *Zoogonoides viviparus* and the relatively low infestation with *H. aduncum*. The first intermediate host of *Z. viviparus* is the Common whelk, *Buccinum undatum* L., 1758. Polychaeta and Echinodermata (particularly those of the genus *Ophiura*) are the second intermediate hosts (Køie 1976). *C. lyra* preys mostly upon Echinodermata and Polychaeta within the study area, enabling transfer of the parasite. The life cycle of *Podocotyle atomon* was described by Hunninen and Cable (1943) and repeated experimentally by Køie (1981). The main first intermediate host is the snail *Littorina saxatilis* (Olivi, 1792). The cercariae encyst in various benthic Amphipoda which serve as second intermediate hosts (Køie 1981). The presence of *P. atomon* in *C. lyra* indicates that it may also feed on benthic Crustacea, as was demonstrated in the present study. The parasite species and infestation rates of *B. luteum* reflect the small size of the analysed fishes. Analysis of the stomach contents showed that *B. luteum* mostly feeds on Cumacea, small Amphipoda, Mollusca and Echinodermata. Most benthic Crustacea are probably too large to be prey organisms. The special scope of benthic organisms in the diet of *B. luteum* and *C. lyra* and their selectivity on prey that is not commonly utilised by other fishes is reflected in the large number of *P. atomon* and *Z. viviparus*. For the first time, a parasitic copepod species of the family Bomolochidae, genus *Bomolochus*, was found on the gills of *B. luteum*. After Kabata (1992), the North Sea fauna contains only *Bomolochus soleae* as a crustacean parasite species of *Solea solea* (L., 1758). As a second crustacean species, copepodite stages of *Lernaeocera branchialis* were also found on *B. luteum*. This species typically infests fish of the family Gadidae (Palm et al. 1999). Thirteen intermediate hosts have been recorded so far in the literature, eight of them flatfishes (Kabata 1992). In the North Sea, intermediate hosts are usually *Platichthys flesus* (L., 1758) and *Microstomus kitt* (Walbaum, 1792) (Kabata 1992). In general, specimens of *B. luteum* live offshore on sandy bottoms, but small numbers of juveniles migrate infrequently to inshore waters in summer (Nottage and Perkins 1983), where presumably the infection with *L. branchialis* take place. However, *B. luteum* probably plays a less important role in the life cycle of *L. branchialis*, which is typically a coastal parasite species (Templeman et al. 1976).

*R. cimbrius* is characterised by its parasites and their infestation rates, which are typical of a species predatory on Crustacea and fishes. This is demonstrated by the presence of *B. crenatus*, *Stephanostomum caducum* and *Bothriocephalus scorpii*. Experiments have shown that *S. caducum* uses the prosobranch *Natica alderi* (Forbes, 1838) as first and Gobiidae as second intermediate hosts (Køie 1978). The latter are frequently preyed upon by *R. cimbrius*. The first intermediate hosts of *B. scorpii* are copepods and various fish species are obligatory secondary hosts (Palm et al. 1999). *R. cimbrius* presumably is infected with adult *B. scorpii* via Gobiidae, since only these are capable of developing into adult cestodes. With

*Taeniacanthus onosi*, one copepod species was found to infest *R. cimbrius*. This parasite species was previously recorded only from *Ciliata mustela* (L., 1758) and *R. cimbrius* collected in northern British waters (Kabata 1979). *T. onosi* shows a high degree of host-specificity and is therefore a typical crustacean parasite of *R. cimbrius*.

The present study fills a gap in our knowledge on the parasite composition of four different small-sized fish species in the central North Sea. Several new host and locality records are established.

A combination of different factors, especially the feeding ecology and habitat preferences of the hosts, can be seen as the reason for the observed infestation patterns. Also, small-sized fish species with a wide range of prey organisms, such as *A. cataphractus* and *R. cimbrius*, can harbour a diverse parasite fauna, mainly consisting of species with a low host-specificity. They either have a generalist feeding behaviour and eat various invertebrates, or they feed on other fish species. Small-sized fishes, such as *B. luteum* and *C. lyra*, harbour a relatively poor parasite fauna, reflecting their specialised feeding behaviour and local range of distribution. It is concluded that the observed parasite fauna provides important insights into the trophic relationship of their fish hosts.

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