Parasite fauna of Antarctic *Macrourus whitsoni* (Gadiformes: Macrouridae) in comparison with closely related macrourids

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**Abstract**

**Background:** The extreme, isolated environment within the Antarctic Convergence has fuelled the evolution of a highly endemic fauna with unique adaptations. One species known from this area is the Whitson’s grenadier *Macrourus whitsoni* (Regan, 1913). While closely related species occurring in the Northern Hemisphere were targets of a variety of studies, knowledge on *M. whitsoni* is scarce, including not only its ecology but also its parasite fauna. Parasites, an often overlooked but important component of every ecosystem, can provide important insights into host ecology, including feeding habits, food web interactions and distribution patterns. The aim of our study was to increase the currently limited knowledge on the ecology of *M. whitsoni* and its parasite life-cycles.

**Methods:** In this study, parasite fauna and stomach content of 50 specimens of *M. whitsoni* were sampled off Elephant and King George Islands. Fish samples were morphological, food ecological and parasitological examined and parasites morphological and partly molecular identified. To evaluate the findings, results were compared with other macrourid species.

**Results:** The parasite fauna of *M. whitsoni* revealed 9 genera and 17 species. Stomach content analysis indicated Amphipoda and Mysida as the primary food source. Considering the parasites of *M. whitsoni*, the highest diversity was found within the Digenea, while prevalence was highest for the Acanthocephala and Nematoda. The diverse parasite fauna of *M. whitsoni* together with the stomach content analysis, suggests a benthopelagic mode of life. Furthermore, an extensive evaluation of the parasite fauna of species of the Macrourinae was conducted, which is probably the most thorough one yet, to compare the findings with closely related host fish species. A similarity analysis revealed a strong connection between the parasite fauna composition and geographical distribution, with a clear separation between the parasite faunas in fishes sampled in the Pacific and the Atlantic Oceans.

**Conclusions:** Due to the isolated habitat within the Antarctic Conversion, the parasite fauna of *M. whitsoni* differs clearly from those of closely related and closely occurring species of the genus *Macrourus*. Our study revealed an endemically dominated parasite fauna, with parasites often host-specific to *M. whitsoni*. The comparison with the faunas of other species of the Macrourinae revealed a largely endemic parasite fauna, which emphasizes again the isolated character of the Antarctic shelf regions.

**Keywords:** Antarctica, Feeding behaviour, Macrourinae, *Macrourus whitsoni*, Grenadier fish, Parasites, Digenea, Nematoda

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Background
The Macrouridae is, with over 300 species, the dominant benthiopelagic deep-sea fish family in terms of species as well as biomass [1–3]. Macrourids occur primarily at the continental slopes in depths between 200 and 2000 m. Some species can also be found in the abyssal plains and only a few inhabit the meso- and bathypelagic zones of the oceans. Macrourids are absent in high Arctic waters [1, 3, 4]. The feeding ecology of macrourids is highly diverse, depending on species, size, depth and the nature of the seabed [2]. Most species feed near the bottom, where they search for prey in the sediments, or hunt bentthic Crustacea; only few prey on fish, cephalopods and euphausiids in the water column [2].

The family Macrouridae consists of four subfamilies: Bathygadinae, Macrouroidinae, Macrourinae and Trachyrincinae. While the species richness for three subfamilies is relatively low, the Macrourinae contains 28 genera and over 270 species, including the commercially exploited genera Coryphaenoides and Macrourus [2, 5]. Within the genus Coryphaenoides, species exhibit a cosmopolitan distribution, except in Antarctic waters. Within the genus Macrourus four out of five species (M. caml, M. carinatus, M. holotrachys, M. whitsoni) occur only in the southern hemisphere and one, M. berglax, in the North Atlantic [3, 5, 6]. While species of the North Atlantic have been the targets of a variety of studies (e.g. Coryphaenoides rupestris or Macrourus berglax), other macrourids are not as well studied. This is especially true for the Southern Ocean, where species such as Macrourus whitsoni and M. caml commonly occur within the Antarctic Convergence (except for Falkland Islands) [5].

Studies of fishes often focus on feeding habits. Combined, with their parasite fauna (e.g. parasite diversity and infection rates), these studies allow a better understanding of the host’s ecology and can help to elucidate the roles of different groups within food webs [7, 8]. For instance, metazoan parasites, especially helminths, have evolved complex life-cycles, including several hosts among different trophic levels, and are therefore deeply embedded within food webs [8]. Encircled by the Antarctic Convergence causing geographical and seasonal isolation, the Antarctic is a unique ecosystem, home to a multitude of endemic species that are forming a relatively simple food web consisting of phytoplanktonic primary producers, zooplanktonic primary consumers and a series of predators (e.g. fish, whales, seals, seabirds, detritivores) [9]. Here, parasite fauna and infection patterns of the Whitson’s grenadier, M. whitsoni, were assessed and combined with stomach content analysis in an effort to increase our currently limited knowledge of the ecology and parasite life-cycles relevant to this host. Data were then used to compare the parasite fauna of M. whitsoni with other closely related species within the genera Coryphaenoides and Macrourus; this should help produce a more comprehensive picture of the parasite fauna and the global role of the genera Macrourus and Coryphaenoides in oceanic food webs.

Methods
Sample collection
Macrourus whitsoni were sampled in March and April 2012 during the research cruise ANT XXVIII/4 on board of the German RV Polarstern in waters off King George and Elephant Island, Antarctica. Sampling was conducted with a bottom trawl at depths of 420.1 to 479.1 m with a towing time of 30 min and a speed of 2.8–4.1 kn (nautical miles/ hour). A total of 50 specimens of M. whitsoni were caught and stored at -40 °C immediately after capture for subsequent examination at the Institute of Ecology, Evolution and Diversity, Goethe University, Frankfurt, Germany. Prior to examination, each specimen was thawed and taxonomically identified using Gon & Heemstra [10].

Morphological and parasitological examination
Total length (TL), preanal length (PAL), total weight (TW) and carcass weight (CW) were measured to the nearest 0.1 cm or 0.1 g, respectively. First, the eyes, fins, skin, gills as well as the nasal, buccal and branchial cavities were inspected for ectoparasites. Afterwards, the body cavity was opened and the internal organs, i.e. the liver, stomach, pyloric caeca, intestine and gonads, were dissected and checked for endoparasites using a stereomicroscope (Olympus SZ 61, at magnifications of 6.7–45). Stomach contents were removed for content analyses (see below). Parasites were isolated and host tissue was removed. Digenean, monogenean, cestode and acanthocephalan parasites were fixed in 4 % borax buffered formalin, preserved in 70 % ethanol (with 4 % glycerol) and morphologically identified using the existing keys and original descriptions [11–16]. Nematode specimens were directly preserved in absolute ethanol for subsequent molecular identification (see Additional file 1).

Stomach content analyses
Food items were separated and identified to the lowest possible taxonomic level and grouped into taxonomic categories (e.g. subphylum). The dry weight of full and empty stomachs as well as the dry weight of the different food items and groups were recorded to the nearest 0.001 g. Frequency of occurrence (F in %), numerical percentage of prey (N in %) and the weight percentage of prey (W in %) were calculated following Hyslop [17]. The index of relative importance (IRI) was calculated based on these data [18].
**Data analyses**

Statistical analyses were performed using the software Graphpad Prism v5.01. Parasitological and ecological terminology follow Bush et al. [19]: prevalence (P) defined as the relative number of fish infected with a specific parasite; intensity (I) as the number of individuals of a particular parasite species in a single infected host (given as a range); and mean intensity (MI) as the average intensity of a particular parasite species among the infected specimens of a particular host species.

**Metadata analysis**

The data on the metazoan parasite fauna previously reported from the different macrourid species was collected by means of a search in Google Scholar and cross-checked with the references in the Web of Knowledge. For the search, the names of all known species of *Macrourus* and *Coryphaenoides*, along with the keywords “parasite”, “Digenea”, “Monogenea”, “Cestoda”, “Nematoda”, “Acanthocephala” and “Crustacea”, were used. Species names were checked using the World Register of Marine Species (www.marinespecies.org). Only unambiguous records were included. In addition to original publications, Klimpel et al. [20] was also utilized. Parasite species richness was calculated for each fish species and its correlation with the number of publications assessed. For a comparison of the parasite faunas in the different fish species, Bray-Curtis similarities were calculated using presence/absence data for the parasite species; based on these data, hierarchical cluster analysis was performed with the Primer 6 software [21].

Tables list species identified to the species level. Numbers of taxa are given as well, i.e. reflecting identification to order, class, family, genera or species level. However, these taxa counts are most likely an overestimation as unidentified specimens from different studies may have been counted as different taxa although they could be the same. Thus, only parasite unambiguously identified to the species level were used for Bray-Curtis calculations.

**Results**

**Host biometric data and parasite infection data**

The mean TL and PAL of the 50 examined specimens of *Macrourus whitsoni* was 23.14 cm (± standard deviation, SD, 5.0 cm), normality test: $P = 0.74$) and 7.7 (± 1.7 cm SD), respectively; the mean TW was 67.2 g (± 34.9 g SD) and CW = 50.9 g (± 27.7 g SD). Of the 50 examined fish, 43 (P = 84.0 %) were infected with a total of seven genera and ten species of parasite, consisting of 219 individual specimens (Table 1). Digeneans infecting the gastrointestinal tract, had the highest diversity, with a total of

| Table 1 | Parasite fauna of *Macrourus whitsoni*. Parasites of *M. whitsoni* (n = 43) sampled in Antarctica (off Elephant and King George Islands). Species marked as unidentified were clearly recognised as distinct species. Shown are the site in host, prevalence (P in %), mean intensity (MI) and range for intensity (I) |
| --- | --- | --- | --- | --- |
| **Parasite** | **Life-cycle stage** | **Site in host** | **P (%)** | **MI (I)*** |
| Monogenea | A | G | 44.0 | 1.9 (1–4) |
| *Macruricola clavipes* | A | G | 44.0 | 1.9 (1–4) |
| Unidentified monogenean | A | G | 2.0 | 1.0 (1) |
| Digenea | A | In, P | 28.0 | 2.2 (1–7) |
| *Paralepidapedon dubium* | A | P | 2.0 | 4.0 (4) |
| *Paralepidapedon avii* | A | P, In | 2.0 | 1.0 (1) |
| *Paralepidapedon antarctica* | A | P | 2.0 | 1.0 (1) |
| *Lepidapedon brayi* | A | P | 4.0 | 1.0 (1) |
| *Lepidapedon ninae* | A | P | 2.0 | 1.0 (1) |
| *Gonocerca phycidis* | A | St | 2.0 | 1.0 (1) |
| Unidentified digenean* | A | In, P, St | 52.0 | 1.6 (1–7) |
| Nematoda | L | L, St | 52.0 | 1.6 (1–6) |
| *Pseudoterranova decipiens* | E | L | 14.0 | 1.1 (1–2) |
| Unidentified nematode | L | L, St | 42.0 | 1.7 (1–5) |
| Cestoda | A | I | 2.0 | 1.0 (1) |
| *Parabothriocephalus johnstoni* | A | I | 2.0 | 1.0 (1) |
| Acanthocephala | L | Bc | 64.0 | 3.2 (1–13) |
| *Corynosoma bulbosum* | L | Bc | 64.0 | 3.2 (1–13) |

*Abbreviations: A adult, L larva, G gills, In intestine, L liver, P pyloric caeca, St stomach

*Presumably five different species
11 species. Macruricotreyle claviceps was the only identified species of monogenean parasitizing the gills of \textit{M. whitsoni}. Larval specimens of the acanthocephalan \textit{Corynosoma bulbosum} were found in the visceral cavity. The nematode \textit{Pseudoterranova decipiens} E [22] (GenBank: KX378173, KX378174; reference accession number: KF017610.1 [23]), identified by molecular analysis, constitutes a new host record for \textit{M. whitsoni}.

**Stomach content analyses**

The stomach content analyses revealed that 92.3 % of the stomachs contained food items belonging to the Crustacea. Overall three food items, i.e., belonging to the Amphipoda, Isopoda and Mysida, were identified. The most frequent preys were amphipods (F = 30.8 %, IRI = 628.32) followed by mysids (F = 12.8 %, IRI = 256). Isopods were less frequent (Table 2). Due to the advanced state of digestion of most food items, identification to a lower taxonomic level was often not possible.

**Comparison of parasites reported from \textit{Macrourus} spp. and \textit{Coryphaenoides} spp.**

The search on Google Scholar resulted in 72 publications. In the search, only macrourid species with an already documented parasite fauna were included. The numbers of parasite taxa and publications were highly correlated (Spearman’s rank correlation \( r = 0.862, P < 0.001 \)) (Fig. 1). A total of 169 different metazoan parasite taxa were found among the 24 fish species included in the search, with 82 (48.5 %) parasite taxa being recorded only from one host species (Table 3). A total of 97 taxa (66 identified plus 31 unidentified species) were found reported for the four \textit{Macrourus} spp. The greatest parasite diversity was found in \textit{M. berglax} with 50 taxa (34 species) and in \textit{M. carinatus} with 29 taxa (22 spp.) (Table 3, Additional file 2: Table S1). Within the genus \textit{Coryphaenoides} containing 19 species, a total of 101 different parasite taxa (68 spp.) were recorded. \textit{Coryphaenoides ruber} and \textit{C. armatus}, both Atlantic species, had the most diverse parasite faunas, with 30 and 25 different taxa, respectively; whereas parasite numbers for species of \textit{Coryphaenoides} inhabiting the Pacific ranged between 3–8 species. Overall, the most diverse parasite groups were the Digenea with 78 taxa (57 spp.) followed by the Nematoda with 27 taxa (16 spp.). The Acanthocephala had the lowest diversity with only 7 taxa (5 spp.). Highest numbers of fish hosts were recorded for parasites known to have low host specificity (generalist parasites), e.g. \textit{Glonemicirrus macrouri} in nine, and \textit{Gonocerca haedrichi} in seven fish species. Detailed information on the parasite taxa found only in one species or shared among different fish species can be found in Additional file 2: Table S1 [6, 13, 14, 20, 23–97].

The hierarchical cluster analysis based on Bray-Curtis similarity matrix revealed one cluster for species sampled in the Atlantic (plus two species from the North Pacific) (Fig. 2). This main cluster is subdivided into three subclusters. Thus, seven species of \textit{Coryphaenoides} clustered together with \textit{Macrourus} spp. In the Atlantic cluster within the genus \textit{Macrourus}, the species \textit{M. carinatus} and \textit{M. holotrachys} exhibited the greatest similarity (45.4 %). These were followed by \textit{M. holotrachys} and \textit{M. whitsoni} (similarity of 35.9 %) and \textit{M. carinatus} and \textit{M. whitsoni} (similarity of 24.5 %). Overall, \textit{M. berglax} shared the lowest similarities with the three other \textit{Macrourus} species (19.1 % with \textit{M. carinatus}, 8.8 % with \textit{M. whitsoni} and 6.3 % with \textit{M. holotrachys}, respectively), but revealed the greatest similarity with \textit{C. rupestris} (genus \textit{Coryphaenoides}) (42.2 %). Among the species of \textit{Coryphaenoides}, the parasite faunas in \textit{C. armatus} and \textit{C. carapinus} were identified as being most similar (similarity of 52.4 %). Apart from the main cluster, two smaller clusters of \textit{Coryphaenoides} spp. from Pacific waters were found. Here, \textit{C. filifer} and \textit{C. serrulatus} had the highest similarity (42.8 %). \textit{Coryphaenoides acrolepis} showed the most pronounced similarity patterns with \textit{C. longifilis} (15.4 %) with which it formed a cluster, whereas \textit{Coryphaenoides serrulatus} and \textit{C. subattractus}, occurring in the same waters had a similarity of 36.4 % in their parasite fauna. \textit{Coryphaenoides delsolari} and \textit{C. striatus}, did not fit to either of the clusters and showed no similarity with the other species.

**Discussion**

As suggested by Polyanskii [98], parasites in higher, Nordic latitudes are often generalists, an assumption that was later on extended upon parasites from Antarctic waters [99]. However, most parasites in the Antarctic and sub-Antarctic regions are endemic and for many of them, fish serve as final hosts [100]. The aim of this study was to investigate the parasite fauna and diet of
Macrourus whitsoni from the Antarctic region and to compare it with closely related species within the subfamily Macrourinae. Sixteen different metazoan parasite species were found in the 50 specimens of M. whitsoni examined. Although a total number of 25 metazoan parasites are known so far from M. whitsoni (Additional file 2: Table S1) mainly from studies in the Weddell Sea and off King George Island [49], the numbers found here still suggest that M. whitsoni is one of the most diversely parasitized deep-sea fish species. In comparison, only six parasite species are known for Gymnodraco acuticeps (Bathydraconidae) occurring in the same region [101–103]. The parasite fauna of M. whitsoni found in our study consists of taxa with high host specificity and a restricted distribution and is, to our current knowledge, host-specific either for Macrourus spp. or only M. whitsoni. However, some generalist parasites with cosmopolitan distribution were also found. Our literature data search revealed that macrourid species, at least those that are well-studied, have diverse parasite faunas, that might be ascribed to a high biomass of benthic organisms and therefore a high number of potential intermediate hosts in the deep-sea habitats [20, 26]. The parasite fauna of M. whitsoni consists to a large extent of species only known from Antarctic waters, with some of these parasite species using M. whitsoni as their only definitive host [13, 49, 50]. Most of these endemic species are digeneans, also the most diverse group found in this study, with all six identified species maturing in M. whitsoni. Digeneans are considered as the most species-rich parasite group in the waters off King George and Elephant Islands, with most of them maturing in teleosts ([49, 50, 100], this study). Forty-five species of digenean are known from these waters, belonging to the superfamilies Hemiuroidea and Allocreadioidea [50, 100]. Of these, 30 appear to be endemic to Antarctic waters while four are known to be cosmopolitan or bipolar [104]. Only Gonocerca phycidis has a cosmopolitan distribution with a broad host and depth ranges [20, 49], whereas the other species found in our study (Lepidapedon brayi, L. ninae, Paralepidapedon avii, P. antarctica and P. dubium) are only known from M. whitsoni so far [13, 100]. Thus, they might be endemic to Antarctic waters with distinct host specificity for M. whitsoni as suggested previously [49]. Some digeneans, presumably five species, could not be identified, due to their poor condition. Only one nematode, Pseudoterranova decipiens E
could be identified. Pseudoterranova decipiens E can be characterized as a species with low intermediate host specificity in Antarctic waters; its distribution and abundance generally depend on seal populations within the area [105, 106]. Although this parasite is widely distributed in Antarctic waters and known to occur in other fish intermediate hosts in these waters [107], it has not been found in M. whitsoni before [13, 49, 106]. Thus, it should be considered a new host record. The presence of this parasite indicates demersal feeding behaviour of M. whitsoni, as, contrary to other nematode larvae such as Anisakis spp. or Contracaecum radiatum, larvae of P. decipiens are unable to swim and therefore sink to the ground to follow a benthic life-cycle [106, 108]. Within the Acanthocephala, Corynosoma bullosum was the only recorded species in our samples of M. whitsoni. This is not surprising as C. bulbosum is one of the few species that are typically found on the open-sea shelf, while most acanthocephalans in Antarctic waters are abundant in inshore regions [12] and likely to be absent from deep sea-fish like M. whitsoni. Generally, C. bulbosum has a circumpolar distribution in the Antarctic and possesses, together with other members of its genus, a relatively complex life-cycle, including Amphipoda, e.g. Bovallia gigantean and Waldeckia obesa as first intermediate host [109, 110]. Apart from M. whitsoni, other fish species, e.g. Chaenocephalus aceratus or Dissostichus eleginoides, can serve as paratenic hosts for this parasite, whereas seals, e.g. Mirounga leonine or Leptonychotes weddellii serve as definitive hosts [12, 111–113]. Confirming earlier findings from the Weddell Sea and off King George Island by Walter et al. [49], the only species of monogenean found in the samples was Macruricotyle clavipes. The Monogenea, as known so far, parasitize only the Macrouridae, mostly Macrourus spp. (M. clavipes, M. holotrichys) in Antarctic and sub-Antarctic waters [49]. Among the cestodes, one adult specimen of Parabothriocephalus johnstoni was found in one individual of M. whitsoni. This cestode species seems to be endemic to Antarctic waters and is so far only known from M. whitsoni [49, 101].

| Table 3 Species richness of the major parasite groups in Coryphaenoides spp. and Macrourus spp. Data represent the total number and the number of distinct taxa (Unique) based on the review of the literature |
|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                | Mono | Dige | Cest | Nema | Acan | Crus | Total | Unique |
| C. acrolepis  | 1    | 5    | 0    | 1    | 0    | 0    | 7    | 2    |
| C. armatus    | 1    | 12   | 2    | 6    | 0    | 4    | 25   | 7    |
| C. brevibarbis| 1    | 1    | 1    | 0    | 0    | 1    | 4    | 0    |
| C. carapinus  | 1    | 11   | 2    | 5    | 1    | 2    | 22   | 4    |
| C. carminifer | 0    | 10   | 0    | 0    | 0    | 0    | 10   | 0    |
| C. delsolari  | 0    | 0    | 0    | 0    | 0    | 1    | 1    | 1    |
| C. filifer    | 0    | 5    | 0    | 0    | 0    | 1    | 6    | 1    |
| C. guentheri  | 0    | 2    | 0    | 0    | 0    | 0    | 2    | 1    |
| C. leptolepis | 0    | 8    | 1    | 0    | 0    | 1    | 11   | 1    |
| C. longifilis | 0    | 2    | 0    | 0    | 0    | 0    | 7    | 3    |
| C. marginatus | 0    | 3    | 0    | 0    | 0    | 3    | 6    | 2    |
| C. mediterraneus| 0   | 8   | 2    | 8    | 0    | 1    | 19   | 4    |
| C. mexicanus  | 0    | 2    | 0    | 0    | 0    | 0    | 2    | 0    |
| C. nasutus    | 0    | 0    | 0    | 0    | 0    | 4    | 4    | 2    |
| C. profundicolus| 0  | 1    | 0    | 0    | 0    | 0    | 1    | 0    |
| C. rupestris  | 1    | 14   | 5    | 6    | 1    | 3    | 30   | 4    |
| C. serrulatus | 4    | 5    | 0    | 0    | 0    | 1    | 10   | 3    |
| C. striatulus | 0    | 9    | 1    | 0    | 0    | 0    | 10   | 1    |
| C. subserrulatus| 2   | 0   | 0    | 0    | 0    | 1    | 3    | 1    |
| C. zaniophorus| 1    | 3    | 0    | 0    | 0    | 0    | 4    | 1    |
| M. berglax    | 3    | 16   | 10   | 11   | 3    | 7    | 50   | 19   |
| M. carinatus  | 2    | 10   | 5    | 8    | 2    | 2    | 29   | 7    |
| M. holotrichys| 4    | 8    | 0    | 0    | 1    | 6    | 19   | 5    |
| M. whitsoni   | 2    | 10   | 4    | 4    | 2    | 3    | 25   | 13   |
| different taxa| 14   | 78   | 18   | 27   | 7    | 25   | 169  | 82   |

Abbreviations: Mono Monogenea, Dige Digenea, Cest Cestoda, Nema Nematoda, Acan Acanthocephala, Crus Crustacea
Trophic studies on *M. whitsoni* are scarce, but it seems that Amphipoda and Euphausiacea are most likely the main preys throughout its life history ([106]; this study). Teleosts, however, were not of importance, although they are reported in the diet of different *Macrourus* spp. from the Ross Sea slope [114]. One explanation might be an ontogenetic shift in diet when reaching a specific size, thus, fish as prey items might only occur in specimens over TL of 30 cm, which was the maximum length sampled here. These dietary patterns are in accordance with other trophic studies from Antarctic waters where amphipods were recognized as the main food source for many fish species [115]. Crustaceans are important intermediate hosts, especially for nematodes and acanthocephalans, but usually show low infection rates (e.g. *Corynosoma bullosum* showed a prevalence of 0.49 % in the amphipod *Bovallia gigantea* and 0.08 % in *Waldecka obesa* in the Admiralty Bay and *Corynosoma pseudohamanni* was found with a prevalence of 0.56 % in the amphipod *Cheirimedon femonratus* off South Shetland Islands [109, 116, 117]. Therefore, fish preying on crustaceans, such as *M. whitsoni*, are often only lightly infected (Nematoda: P = 52.0 %, MI = 1.65; Acanthocephala: P = 64.0 %, MI = 3.22), while piscivorous fish such as *Dissostichus eleginoides*, an important predator of *M. whitsoni* [118], can be heavily infected [111].

Using presence/absence data for parasite fauna composition and the Bray-Curtis similarity index, macrourid species clustered in one main cluster with species from the Atlantic (and two from the Pacific) and two smaller clusters, including species solely from Pacific waters. This pattern may be explained by the fact that species occurring closely or in the same waters would share more parasite species than species living further apart or in different ocean basins. Considering species in the Atlantic cluster, three subclusters were distinguished. One of these three clusters consisted of one species from the North Atlantic (*Coryphaenoides guentheri*), two species from Caribbean waters (*C. mexicanus* and *C. zaniophorus*), one species occurring in the Caribbean as well as Pacific waters off Middle America (*C. carminifer*) and two species from the Pacific (*C.
marginatus and C. nasutus). The clustering of species solely inhabiting the Pacific with those from the Atlantic might be affected by sampling bias (low sampling effort in the Pacific overall) and an increase of sampling might reveal closer similarities with other species from the Pacific. However, the two Pacific species (C. marginatus and C. nasutus) clustered together with species from the Caribbean and Panama waters and not with other Atlantic species, indicating that distance might play a role for similarity in parasite species. In the case of cosmopolitan fish species, e.g. C. armatus, parasite fauna showed greater similarities with those of fish species from the Atlantic than from the Pacific. However, this might only reflect a sampling bias as most of the studies on these species have taken place in the Atlantic (e.g. C. armatus: [57, 58]; C. carapinus: [57, 67]). Species from the Antarctic and sub-Antarctic regions showed greater similarities of their parasite faunas with species from Atlantic rather than Pacific waters. Between both Macrourus spp. inhabiting the sub-Antarctic and temperate waters around the Antarctic Convergence (M. carinatus: circumpolar; M. holotrachys: off the South American coast) [3, 5], the literature data revealed a parasite fauna with only 41.7 % similarity, whereas a more similar fauna in closely related species, occurring in the same marine geographic locality would be expected. One explanation for this dissimilarity might be their different feeding habits. Macrourus carinatus forages in the pelagic realm at depths shallower than 900 m while M. holotrachys feeds in the demersal zone at depths deeper than 1000 m [119]. Thus, their niches and potential parasite intermediate hosts do not overlap. Similar spatial partitioning can be expected in other regions where closely related macrourids occur (e.g. M. caml and M. whitsoni). Despite their close geographical distribution, the parasite fauna of M. whitsoni differs from that of M. carinatus and M. holotrachys. The reason might be found in the hydrographic characteristics of the Antarctic Convergence, which functions as a barrier for most animals, including fish, with M. whitsoni occurring within and M. carinatus and M. holotrachys outside of this barrier. While marine mammals (e.g. cetaceans, pinnipeds) can overcome this barrier and with them their parasites (e.g. different nematodes), for teleosts and their affiliated parasites, e.g. most digeneans, this is not possible. This explains the high percentage of animals being unique and endemic within this border [120]. Due to its isolated location geographically, oceanographically, bathymetrically and thermally, the Antarctic shelf is highly valuable for studying evolutionary mechanisms and can be compared to ancient rift lakes (e.g. Lake Tanganyika) with endemic species flocks [121]. To extend our knowledge and to test whether the same pronounced endemic patterns occur in other fish species inhabiting this unique ecosystem, further studies are underway.

Conclusions

The study helped to shed light on the remote and isolated Antarctic realm, with a focus on the ecology of Macrourus whitsoni and its diverse parasite fauna. The comparison with closely related species of Coryphaenoides and Macrourus helped to emphasize the endemically dominated parasite fauna within the Antarctic Convergence. We hope that our findings may not only help generating knowledge on the isolation patterns of Macrourus whitsoni, but also stimulate further research on other deep-sea fish species in this unique environment.

Additional files

| Additional file 1: | PCR amplification and species identification. (DOCX 16 kb) |
| Additional file 2: | Table S1. Parasite taxa in species of Coryphaenoides and Macrourus based on literature data. (DOCX 57 kb) |

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Availability of data and materials

The dataset supporting the conclusions of this article is included within the article and its Additional files. The sequences for Pseudoterranova decipiens E [22] are submitted in the GenBank database under the accession numbers KX378173 and KX378174.

Authors’ contributions

JM, JK, TK designed the study. JM, JK conducted the analyses. JM, JK, SK, RK, TK wrote the manuscript. All authors read and approved the final manuscript.

Competing interests

The authors declare that they have no competing interests.

Consent for publication

Not applicable.

Ethics approval and consent to participate

Approval of our present study by a review board institution or ethics committee was not necessary because all fish were caught during a regular research cruise on board of the RV Polarstern. No living animals were used. All fish were expertly killed according to the German Animal Protection Law (Tierschutzverordnung § 13).

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References

1. Marshall NB. Systematic and biological studies of the macrourid fishes (Anacanthini-Teleostii). Deep Sea Res Oceanogr Abstr. 1965;12:299–322.
2. McLellan T. Feeding strategies of the macrourids. Deep Sea Res. 1977;24:
   1019–26.
3. Cohen DM, Inada T, Ishiwatari T, Scialabba N. Gadiform Fishes of the World (Order Gadiformes). An Annotated and Illustrated Catalogue of Codes, Hakes, Grenadiers and Gadiform Fishes Known to Date. FAO; 1990.
4. Massuti E, Morales-Nin B, Stefanescu C. Distribution and biology of five
gnadiad fish (Pisces: Macruridae) from the upper and middle slope of the
north-western Mediterranean. Deep Sea Res Part I Oceanogr Res Pap. 1995;42:
307–30.
5. Froese R, Pauly D. FishBase. World Wide Web Electron. Publ. www.fishbase.
org. 2015.
6. Palm HW, Klimpel S. Metazoan fish parasites of Macrourus berglax, 1801 and other macrourid fishes of the North Atlantic: Invasion of the deep sea from the continental shelf. Deep Sea Res Part II Top Stud Oceanogr. 2008;55:236–42.
7. Hemmingsen W, Mackenzie K. The parasite fauna of the Atlantic cod, Gadus
morhua L. Adv Mar Biol. 2001;401–80.
8. Parker GA, Chubb JC, Ball MA, Roberts GN. Evolution of complex life cycles
in helmidt parasites. Nature. 2003;425:480–4.
9. Griffiths HJ. Antarctic marine biodiversity - what do we know about the
distribution of life in the Southern Ocean? PLoS One. 2010;5:e1683.
10. Gon O, Heemstra PC. Fishes of the southern ocean. JLB Smith Institute
of Ichthyology Grahamstown; 1990.
11. Zdzitowicki K. Occurrence of digenans in open sea fishes off the South
Shetland Islands and South Georgia, and a list of fish digenans in the
Antarctic. Pol Polar Res. 1991;12:55–72.
12. Zdzitowicki K. Antarctic acanthocephala. Koenigstein: Koeltz Scientific
Books; 1991.
13. Zdziwtowicki K, Cielecka D. Digenea of fishes of the Weddell Sea. I. Parases of Macrourous whitoni (Gadiformes, Macruridae). Acta Parasitol. 1997;42:23–30.
14. Rocka A. Zdziwtowicki K. Cestodes in fishes of the Weddell Sea. Acta
Parasitol. 1998;43:64–70.
15. Rocka A. Nematodes of the Antarctic fishes. Pol Polar Res. 2004;25:135–52.
16. Sokolov SG, Gordievsky II. New data on trematodes (Plathelmintes, Trematoda)
of fishes in the Ross Sea (Antarctic). Invert Zool. 2013;10(3):255–67.
17. Hystop EJ. Stomach contents analysis - a review of methods and their application. J Fish Biol. 1980;17:411–29.
18. Pinkas L, Olphrant MS, Herson ILK. Food habits study. Fish Bull. 1971;1255–10.
19. Bush AO, Lafferty KD, Lotz JM, Shostak AW. Parasitology meets ecology on
its own terms: Margolis et al. revisited. J Parasitol. 1997;83:575–8.
20. Klimpel S, Palm HW, Kellermanns E, Rückert S. Fish parasites in the
north-western Mediterranean. Deep Sea Res Part Oceanogr Res Pap. 1995;42:
307–30.
21. Bullini L, Arduino P, Cianchi R, Nascetti G, Dall'Amello, M, Mazzucco M, Paglii P, Orechia P, Plottz J, Berland B, Smith JW, Brayt J. Genetic and ecological research on Anisakis endoparasites of fish and marine mammals in the
Antarctic and Arctic-boreal regions. In: Battaglia B, Valenca J, Walton DWH, editors. Antarctic Communities: Species, Structure and Survival. Cambridge: Cambridge University Press; 1997. p. 39–44.
22. Timi JT, Paolelli M, Cimaruta R, Lanfranchi AL, Arcos AJ, Garbin L, et al. Molecular identification, morphological characterization and new insights into the ecology of larval Pseudotrematodea cattani in fishes from the
Argentine coast with its differentiation from the Antarctic species, P. decipiens sp. E (Nematoda: Anisakidae). Vet Parasitol. 2014;199:59–72.
23. Kaba T, Z new genus and species of trematode parasitic in Macrourus fabrici (Sondeval), a deep-sea fish. Proc Zool Soc Lond Wiley Online Library. 1961.
24. Zdzitowicki AV. Nematodes of some Macrourinae in the Northwest
Atlantic. J Northwest Atl Fish Sci. 1981,267–72.
25. Klimpel S, Palm HW, Busch MW, Kellermanns E, Rückert S. Fish parasites in the
Arctic deep-sea: Poor diversity in pelagic fish species vs. heavy parasite load in
a demersal fish. Deep Sea Res Part Oceanogr Res Pap. 2006;53:1167–81.
26. Zdzitowicki AV. On the fauna of Macrouridae parasites in North Atlantic. Tr Poljarn Choz Okeanogri PINRO. 1975;35:234–8.
27. Bray RA. Digenea in marine fishes from the eastern seaboard of Canada. J Nat Hist. 1979;13:399–431.
65. Solovyeva G. Metacobronema insulatum sp. n. (Nematoda, Spirurina) a parasite of deep-water fishes from the Pacific. Moscow: Mekhunarochnaya Kniga; 1991.
66. Campbell RA, Haedrich RL, Munroe TA. Parasitism and ecological relationships among deep-sea benthic fishes. Mar Biol. 1980;57:301–13.
67. Campbell RA, Munroe TA. New hemiurid trematodes from deep-sea benthic fishes in the western North Atlantic. J Parasitol. 1977;63:285–94.
68. Campbell RA, Bray RA. Lepidopedon spp. (Digenea: Lepocreadiidae) from deep-sea gadiform fishes of the NW Atlantic Ocean, including four new species. Syst Parasitol. 1993;24:99–110.
69. Bray RA, Gibson DI. The Lepocreadiidae (Digenea) of fishes from the north-east Atlantic: a review of the genus Lepidopedon Stafford, 1904. Syst Parasitol. 1999;31:81–132.
70. Bray RA, des Cleris SA. Multivariate analyses of metrical features in the Lepidopedon elongatum (Lobour, 1908) species-complex (Digenea, Lepocreadiidae) in deep and shallow water gadiform fishes of the NE Atlantic. Syst Parasitol. 1992;21:223–32.
71. Bray RA, Gibson DI. The Acanthocotilidae (Digenea) of fishes from the north-east Atlantic: the status of Neophysis Stafford, 1904 (Digenea) and a study of North Atlantic forms. Syst Parasitol. 1991;19:15–17.
72. Palm H. Untersuchungen zur Systematik von Rüsselbandwürmern (Cestoda: Trypanorhyncha) aus atlantischen Fischen. Institut für Meereskunde; 1995.
73. Ho J-S. Chondracanthid copepods (Poecilostomatoida) parasitic on Japanese deep-sea fishes, with a key to the genera of the Chondracanthidae. J Nat Hist. 1994;28:305–17.
74. Bray RA, Stergiouphon Ohnther, 1905 (Digenea: Fellodistomidae) in deep-sea fishes from the northeastern Atlantic, with the description of Soringophorus margolini n. sp. Can J Fish Aquat Sci. 1995;52:71–7.
75. Kitsky DC, Klimpel S. Cyclocoelotyloides bergstadi n. sp. (Monogenea: Diclidophoridae: Diclidophorosporinae) from the Gills of Grenadiers, Coryphaenoides rex, Brevibarbis (Teleostei: Macrouridae), in the Northeast Atlantic Ocean. Comp Parasitol. 2007;74:23–30.
76. Roehde K, Williams A. Taxonomy of monogeneans of deep sea fishes in southeastern Australia. Syst Parasitol. 1987;10:45–71.
77. Ho J-S. New species of Allopodocotyle (Trypanorhynchida, Trypanorhyncha) aus atlantischen Fischen. Institut für Meereskunde; 1995.
78. Solovjeva G. Metacobronema insulatum sp. n. (Nematoda, Spirurina) a parasite of deep-water fishes from the Pacific. Moscow: Mekhunarochnaya Kniga; 1991.
79. Nepal ER, Orias JD, Rodella TA. Parasitic fauna of the deep-sea fish, Macrourus rupestris (Gunnerus) from Kordfjorden, Norway. Saras. 1972;50:47–50.
80. Mauchline J, Gordon JDM. Feeding and bathymetric distribution of the deep-sea fish, Macrourus rupestris (Gunnerus), off Hvaler, Oslofjord, Norway. Pap. Norwegian Polar Res. 2009;30:49–58.
108. Klöser H, Plötz J, Palm H, Bartsch A, Hubold G. Adjustment of anisakid nematode life cycles to the high Antarctic food web as shown by Contracaecum radiatum and C. osculatum in the Weddell Sea. Antarct Sci. 1992;4:171–8.

109. Zdzitowiecki K, Presler P. Occurrence of Acanthocephala in intermediate hosts, Amphipoda, in Admiralty Bay, South Shetland Islands, Antarctica. Pol Polar Res. 2001;22:205–12.

110. Zdzitowiecki K. Acanthocephala occurring in intermediate hosts, amphipods, in Admiralty Bay (South Shetland Islands, Antarctica). Acta Parasitol. 2001;46:202–7.

111. Brickle P, Mackenzie K, Pike A. Parasites of the Patagonian toothfish, Dissostichus eleginoides Smitt 1898, in different parts of the Subantarctic. Polar Biol. 2005;28:663–71.

112. Palm HW, Klimpel S, Walter T. Demersal fish parasite fauna around the South Shetland Islands: high species richness and low host specificity in deep Antarctic waters. Polar Biol. 2007;30:1513–22.

113. Silveira T, Bianchini A, Robaldo R, Colares EP, Mueller M, Martínez PE, et al. Corynosoma spp. (Acanthocephala, Polymorphidae) in Mirounga leonina (Pinnipedia, Phocidae) of South Shetlands Islands: a new host for Corynosoma cetaceum. Pan-Am J Aquat Sci. 2014;9:66–9.

114. Pinkerton MH, Forman J, Stevens DW, Bury SJ, Brown J. Diet and trophic niche of Macrourus spp. (Gadiformes, Macrouridae) in the Ross Sea region of the Southern Ocean. J Ichthyol. 2012;52:787–99.

115. Würzberg L, Peters J, Flores H, Brandt A. Demersal fishes from the Antarctic shelf and deep sea: A diet study based on fatty acid patterns and gut content analyses. Deep Sea Res Part II Top Stud Oceanogr. 2011;58:2036–42.

116. Laskowski Z, Jezewski W, Zdzitowiecki K. New data on the occurrence of Acanthocephala in Antarctic Amphipoda. Acta Parasitol. 2010;55:161–6.

117. Busch MW, Kuhn T, Münster J, Klimpel S. Marine crustaceans as potential hosts and vectors for metazoan parasites. Arthropods Vectors Emerg Dis Springer; 2012. p. 329–360.

118. Fenaughty JM, Stevens DW, Hanchet SM. Diet of the Antarctic toothfish (Dissostichus mawsoni) from the Ross Sea, Antarctica (subarea 88.1). CCAMLR Sci. 2003;10:113–23.

119. Laptikhovsky W. A trophic ecology of two grenadier species (Macrouridae, Pisces) in deep waters of the Southwest Atlantic. Deep Sea Res Part Oceanogr Res Pap. 2005;52:1502–14.

120. Mackintosh NA. The pattern of distribution of the Antarctic fauna. Proc R Soc Lond B Biol Sci. 1960;152:264–31.

121. Eastman JT, McCune AR. Fishes on the Antarctic continental shelf: evolution of amarine species flock? J Fish Biol. 2000;57:84–102.