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Adjustment of anisakid nematode life cycles to the high Antarctic food web as shown by *Contracaecum radiatum* and *C. osculatum* in the Weddell Sea

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Abstract: The infestation of Weddell seals and several fish species by the anisakid nematodes *Contracaecum osculatum* and *C. radiatum* was compared. Nematode numbers in Weddell seal stomachs ranged from 30 560 to 122 640. Third stage larvae from seals and fish were separated into a short and a long type. The short type was related to *C. radiatum* and the long type to *C. osculatum*. The short type was more abundant in pelagic fish species, whereas the long type prevailed in benthic fish species. Fish-feeding channichthyids *Cryodraco antarcticus* and *Chionodraco myersi* seemed to play an important role as paratenic hosts for the third stage larvae of both *Contracaecum* species. Different advantageous and detrimental features of a benthic versus a pelagic life cycle under high Antarctic ecological conditions are discussed. Varying abundance of the two nematode species in hosts may be controlled by differences in their life cycles, which follow either a pelagic or a benthic food web. Crucial importance is thus given to the local availability of pelagic versus benthic food resources for Weddell seals.

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Introduction

Antarctic pinnipeds have been reported to be highly infested by stomach-inhabiting anisakid nematodes (Railliet & Henry 1907, Johnston 1938, Bertram 1941, Prévost 1964, Beverley-Burton 1971), which were assumed to be an important mortality factor for the seals (Bertram 1941, Kooyman 1981, Siniff, 1981). Although usually only crude estimates are given, these suggest that the abundance of anisakids in Antarctic seals exceeds that in Northern Hemisphere seals, for which maximal infestations of several hundreds (Keyes 1965, Bishop 1979, Claussen 1990) to a few thousands per seal (Scott & Fisher 1958, Machida 1971, Popov, 1975) of the genera *Anisakis*, *Contracaecum*, *Pseudoterranova* and *Phocascaris* have been reported. To explain this difference, information is required on the adjustment of anisakid life cycles to the peculiarities of the marine Antarctic ecosystem. Early anisakid larval stages are generally assumed to develop in a variety of invertebrate hosts. Fish serve as paratenic hosts for the infective third stage larva, which matures after being ingested by the final hosts, i.e. seals or seabirds. In the present study, we compared the infestation of Weddell seals with infestations of several fish species. Potential transmission pathways of larvae in the pelagic and benthic food web are discussed.

Material and methods

During the Antarctic expedition ANT I of the RV *Polarstern*, eight Weddell seals (*Leptonychotes weddelli*) were collected at the Weddell Sea coast between early January and late February (Fig. 1). The seals were eviscerated within an hour of killing and stomach contents were flushed into tubs using sea water. Contents were repeatedly washed to ensure good separation and then decanted through graded sieves. Emptied stomachs were examined for retained nematodes. The nematodes were stored in 70% cold ethanol.

For light microscopic examination (Nomarksy interference contrast) nematodes were cleared using lactophenol. The large number of nematodes in the stomachs necessitated partitioning of the material into subsamples. Developmental stages of nematodes were recorded. All nematodes were measured to 1 mm. Generic identification relied on characters given by Baylis (1920). To avoid misidentifications in *Contracaecum*, only adult males were assigned to species by using spicules, tail and labial structures (Klöser & Plötz in press).

On the same expedition and on the expedition ANT V/3 fish were caught with midwater trawl and bottom trawl (Fig. 1) and then frozen for later analysis. Pelagic *Pleuragramma antarcticum* and bottom-dwelling *Trematomus scotti* were selected from the ANT I material and examined for parasites. The results supplied the basis for the investigation of 10 fish species of the ANT V material (Table IV).

Length, weight and sex of fish was determined and the body cavity, internal organs and musculature examined for nematodes in the laboratory. All nematodes were removed, preserved in 70% ethanol, cleared in 100% glycerol and counted.

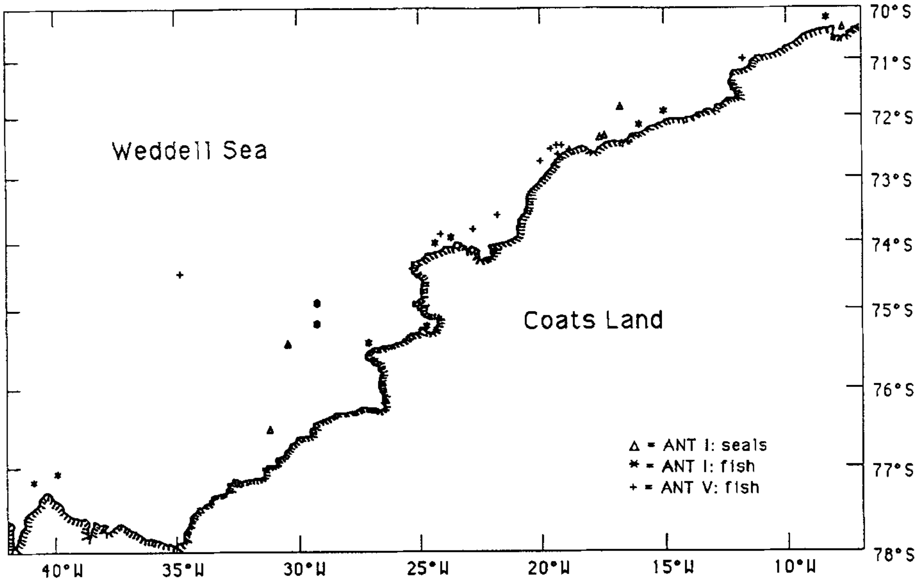

Fig. 1. Map of where samples were taken for this study.

Results

The Weddell seal stomachs contained extremely high numbers of *Contracaecum* (Table I). On average, 13.2% of the nematodes were third stage larvae, 48.5% fourth stage larvae, 15.8% subadults with immature reproductive organs, and 22.5% adults. However, variation in total numbers as well as in different life stages was considerable between individual seals (Table I). The mean sex ratio was 2.6 females : 1 male. *Contracaecum* sex ratio also varied considerably between individual seals, but always showed a strong preponderance of females. Adult males of *C. radiatum* were more abundant than those of *C. osculatum*, especially in southernmost localities (Fig. 2). The seals appeared to be healthy, not showing any detrimental effects caused by the high infestation.

All nematodes found in *Trematomus scotti* and *Pleuragramma antarcticum* (ANT I material) were third stage larvae and were mostly encapsulated. Larval length spectrum was bimodal (Fig. 3). A comparison of length spectra of nematode stocks in the two fish species (Fig. 3a) showed a distinct preponderance of short type in pelagic *Pleuragramma antarcticum* and of long type in benthic *Trematomus scotti*. Two larval types (Table II) could be separated by relating absolute total length to a ratio of lengths of caecum and oesophagus (Table III), although no specific morphological differences were detectable (Fig. 3).

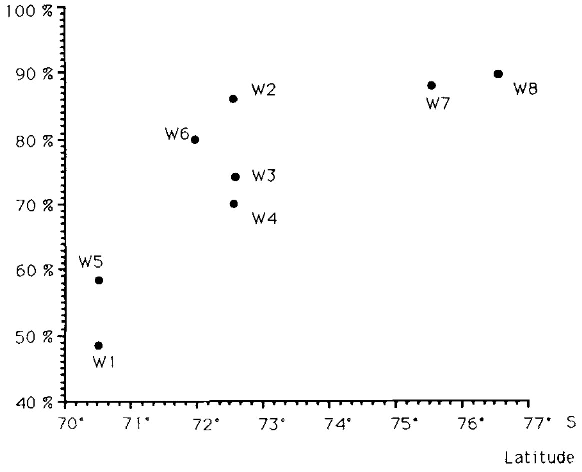

Fig. 2. Percentage contribution of *Contracaecum radiatum* to adult *Contracaecum* males in individual Weddell seals from different latitudes.

Table I. Ontogenic stages of *Contracaecum* in Weddell seal stomachs.

Seal	third stage	fourth stage	subadults	adults	total
W1	12 240	36 320	9 040	15 760	76 400
W2	9 920	43 520	22 400	26 160	112 400
W3	10 960	24 800	8 720	20 080	68 700
W4	10 880	52 960	16 000	25 040	122 640
W5	9 920	40 320	10 080	12 880	87 280
W6	3 920	14 880	2 960	3 360	30 560
W7	8 000	24 800	8 800	18 320	68 320
W8	5 440	28 800	13 040	9 120	59 760

Table II. Absolute length measurements of several characters of third stage larvae. Absolute values are given as mean values with standard deviations.

character	short type	long type
total length	5.8 mm ± 1.02	15.7 mm ± 2.37
length of caecum	246 μm ± 39.4	768 μm ± 148.8
length of appendix	308 μm ± 42.2	997 μm ± 117.8
length of oesophagus	503 μm ± 70.6	1315 μm ± 152.5

In fish from ANT V material, again only third stage larvae were found. The short type prevailed in the channichthyids *Cryodraco antarcticus* and *Chionodraco myersi*, and in the bathydraconid *Gerlachea australis* (Table IV). The long

Table III. Mean ratio oesophagus : caecum (O : C) of length classes in long and short type of third stage larvae. Length classes 8–11 mm were too rare to be treated statistically.

Short type			
Total length	investigated number	O : C ± sd	95%-confidence interval
4 mm	8	2.05 ± 0.40	1.72 < u < 2.38
5 mm	10	2.13 ± 0.29	1.80 < u < 2.24
6 mm	27	2.02 ± 0.26	1.92 < u < 2.12
7 mm	7	2.02 ± 0.24	1.92 < u < 2.34
Long type			
total length	investigated number	O : C ± sd	95%-confidence interval
12 mm	4	1.57 ± 0.22	1.22 < u < 1.92
13 mm	7	1.66 ± 0.24	1.44 < u < 1.88
14 mm	14	1.68 ± 0.20	1.56 < u < 1.80
15 mm	16	1.57 ± 0.21	1.46 < u < 1.68
16 mm	12	1.60 ± 0.18	1.49 < u < 1.71

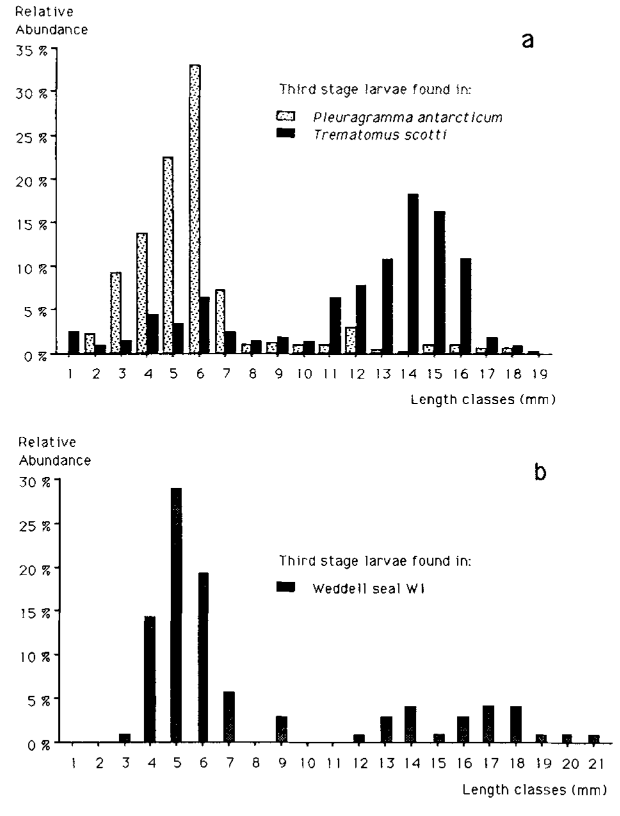

Fig. 3. a. Length spectrum of third stage *Contracaecum* larvae in *Pleuragramma antarcticum* and *Trematomus scotti* **b.** Length spectrum in Weddell seal Wl (Wl has been chosen because of the almost equal abundance of adult *Contracaecum radiatum* and *C. osculatum*).

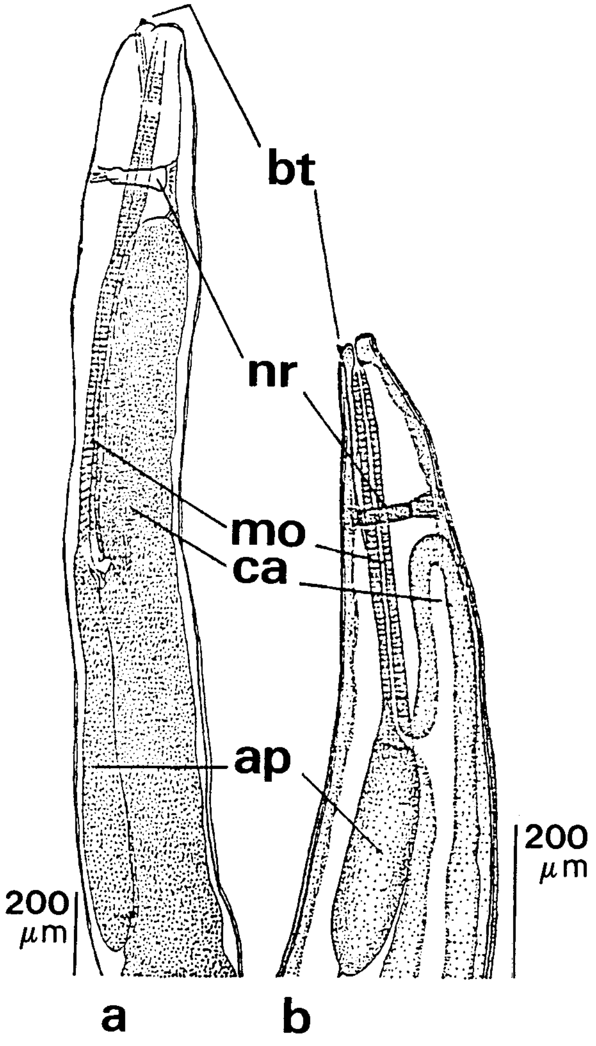

Fig. 4. Long **a.** and short type **b.** of third stage larvae, drawn by camera lucida from Nomarsky contrast light microscope at 400 fold magnification (bt = boring tooth, nr = nerve ring, mo = muscular oesophagus, ca caecum, ap appendix). Morphological similarity is obvious, but different ratios of structures of the alimentary tract can be recognized.

type was more abundant in the other fish species except the artedidraconid *Dolloidraco longedorsalis*, which was free of *Contracaecum*. Compared to the other fish species the high infestations in *Cryodraco antarcticus* and *Chionodraco myersi* were conspicuous (Fig. 5). In no case could a correlation be found between nematode abundance and condition of the fish.

Besides *Contracaecum*, three adult specimens of *Pseudoterranova decipiens* were found in two seals and small numbers of its third stage larva in two benthic fish species (*Trematomus scotti* and *Cygnodraco mawsonii*). This species is, however, omitted from further consideration here because of its scarcity.

Discussion

Nematode numbers in the Weddell seal stomachs were unexpectedly high. The range of 30 560–122 640 *Contracaecum* in this study compares with 7537–26 444 *Contracaecum* found in seven stomachs from McMurdo Sound (Beverley-Burton 1971), which are the only published

Table IV. Numbers of third stage *Contracaecum* larvae extracted from fish.

Fish species	Numbers investigated	Mean fish wt. (g)	Numbers larvae (short type)	Numbers larvae (long type)
ANT I material:				
Nototheniidae				
Pleuragramma antarcticum	112	31.1	386	37
Trematomus scotti	55	20.7	49	216
ANT V material:				
Nototheniidae				
Trematomus eulepidotus	21	121.0	8	27
Trematomus lepidorhinus	20	27.9	0	2
Trematomus scotti	17	12.0	5	21
Channichthyidae				
Chionodraco myersi	35	148.3	1231	581
Cryodraco antarcticus	14	90.0	1436	370
Pagetopsis maculatus	10	35.3	50	45
Bathydraconidae				
Cygnodraco mawsoni	20	205.5	43	142
Gerlachea australis	10	35.2	18	7
Racovitzia glacialus	12	48.8	0	2
Artedidraconidae				
Dolloidraco longedorsalis	13	6.3	0	0

quantitative data of Weddell seal infestations, and with 16 718 *Contracaecum* in a grey seal (*Halichoerus grypus*) from Nova Scotia (McClelland 1980c), which to our knowledge is the highest record from the northern hemisphere.

At present, the daily influx of larvae into the seals is not known. In this investigation, 3920–12 240 third stage larvae were found in the seals (Table I). To explain these numbers, the period between the arrival of the third stage in the seal stomach and its moult to the fourth stage must be considered. Third stage larvae of the anisakid *Pseudoterranova decipiens* had moulted within two to five days in feeding experiments (McClelland 1980a), and Fagerholm (1988b) reported moulting of *C. osculatum* larvae "within a few days" in a similar experiment. Assuming a mean period of 3.5 days until moulting takes place, about 1000–3500 larvae would have been ingested by the seals each day. These numbers readily pinpoint the key position of highly infested channichthyids in the life cycle of Antarctic *Contracaecum* (Fig. 6).

In high Antarctic waters, two species parasitic on pinnipeds evidently exist : *C. osculatum* and the endemic *C. radiatum* (see Fagerholm 1988a, Klöser & Plötz in press). The presence of two *Contracaecum* species is assumed to be reflected in the bimodal length spectrum of third stage larvae in combination with different ratios of caecum to oesophagus length in long and short larvae. To distinguish larval *Contracaecum*, morphometric measurements have already been used by Johnston & Mawson (1945). The authors assigned their short type (type IV) to *C. radiatum* and their long type (type V) to *C. osculatum*. This was questioned by Berland (1964), who took allometric growth into account. Allometric growth, however, would only allow gradual shifts of the ratio considered here. As ratios of caecum to oesophagus length in long and short larvae were clearly different with no tendency to intermediate values (Table III), it is justifiable to relate the two larval types to the corresponding two types of adults in the seals.

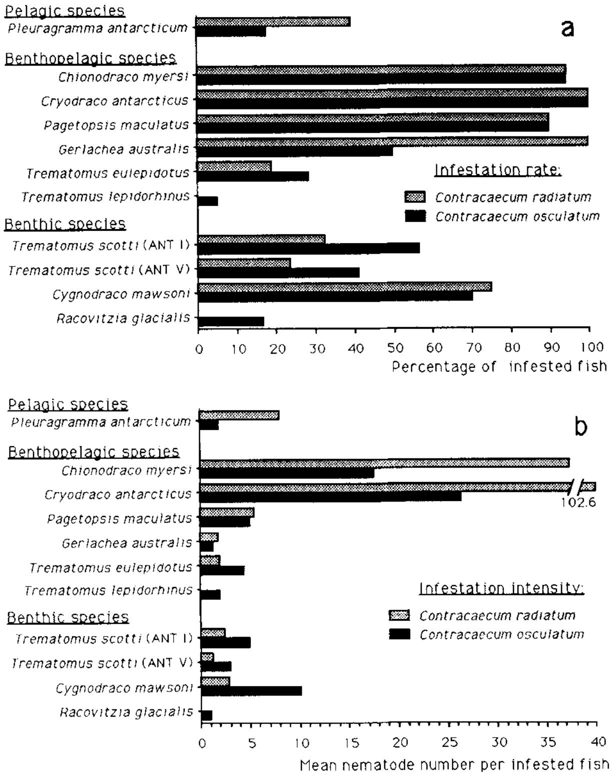

Fig. 5. Infestation rates (number of infested fish/total number of fish) and infestation intensities (mean number of nematodes/ number of infested fish) of investigated fish species. Ecological grouping of fish species according to Eastman 1985a, Hubold & Ekau 1987, Schwarzbach 1988, and Ekau 1988, 1990.

Both species undergo development from third stage larvae to adults in the seal stomach, where they have to share resources. Whereas niche separation between *Contracaecum* and *Pseudoterranova* has been found insofar as *Pseudoterranova* invades the intestine if the stomach is occupied by high numbers of *Contracaecum* (Berland 1964, McClelland 1980c); no similar differentiation has been observed between the two *Contracaecum* species. If this indeed reflects largely identical niches in the stomach, co-occurrence of the two species might be contrary to Gause's principle of exclusion. An escape from this dilemma would only be possible if populations of both species were not

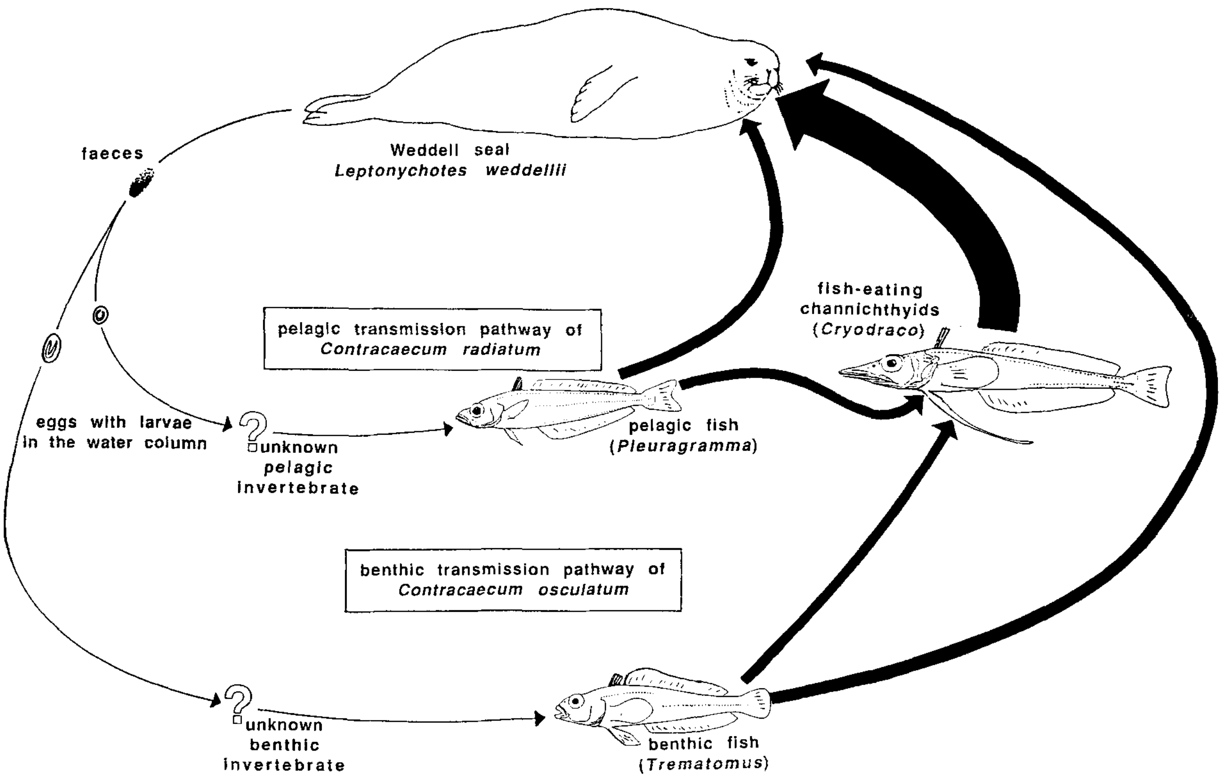

Fig. 6. Tentative scheme of potential transmission pathways of *Contracaecum radiatum* and *C. osculatum* in the Weddell Sea. Thickness of arrows indicates accumulation steps in the food web.

regulated in the seal. If populations were strictly controlled in an intermediate host, the remaining numbers of the parasites might be too low to exhaust the carrying capacity of the final host (Anderson 1976). Competition would then be avoided as both nematode species had not been subject to any limitation in the seal. The absence of pathological consequences in the seals would agree with this hypothesis.

In the intermediate hosts, competition between the two species might be avoided by spatial separation. The dissimilar distribution of short (aff. *C. radiatum*) and long type (aff. *C. osculatum*) larvae in *Pleuragramma antarcticum* and *Trematomus scotti* (Fig. 3) suggests a life cycle of *C. radiatum* and of *C. osculatum*, which follows a pelagic and benthic food chain, respectively. This interpretation also agrees with the observations from ANT V fish material. In particular, different prevalence of long type larvae (aff. *C. osculatum*) or short type larvae (aff. *C. radiatum*) in benthopelagic fish species (Fig. 5) coincided with differences in preference for benthic or pelagic food (Table V). For example, channichthyids feeding on pelagic *Pleuragramma antarcticum* were heavily infested with short type larvae, whereas they were lacking in *Trematomus lephdorhinus*, which feeds mainly on benthic invertebrates. However, co-occurrence of both larval types in most fish species combined with no evidence for pathological problems would support the same hypothesis as for the seals. Regulation of the nematode populations must then be expected to take place in the first intermediate host. Unfortunately, while in other seas a variety of invertebrate taxa have been found to harbour *Contracaecum* larvae (Popova & Val'ter 1971, Shimazu & Oshima 1972, Smith 1984, Mazzoni 1986), nothing is known about anisakid infestations of invertebrates in Antarctic waters, except a single record in a benthic amphipod (Feiler 1984) and the exclusion of krill as an intermediate host (Kagei *et al.* 1978, Siegel 1980).

The use of pelagic hosts by *C. radiatum* may perhaps be considered as an adaptation to conditions of perennially ice-covered seas. Johnston & Mawson (1945) noted that, in the Pacific Sector, *C. radiatum* was restricted to high Antarctic conditions. Our own data from only eight Weddell seals will not allow statistical statements, but at least they do not contradict the observation of Johnston & Mawson (1945). Additionally, an analogy is known from the Arctic: *C. osculatum* in the Greenland Sea has been split up into two sibling species, of which one predominantly infests the coastal bearded seal (*Erignathus barbatus*) and the other one the harp seal (*Pagophilus groenlandicus*) in off-shore pack ice areas (Nascetti *et al.* 1986). As long as seals are only abundant in coastal waters, pelagic intermediate hosts would be detrimental for the parasite due to constant exports into off-shore areas, where the life cycle is interrupted. Floating sea ice, however, would

Table V. Food items of investigated fish species. Compiled from various authors. Only reports on high Antarctic regions have been considered. Main food items are underlined.

Species	benthic prey items	pelagic prey items	source
Pelagic species:			
Pleuragramma antarcticum	-	euphausiids, copepods amphipods, gastropods, polychaetes, chaetognaths	1
Benthopelagic species:			
Chionodraco myersi	-	euphausiids, *Pleuragramma*	2
Cryodraco antarcticus	-	euphausiids, *Pleuragramma*	3
Pagetopsis maculatus	-	euphausiids, Pleuragramma	4
Gerlachea australis	amphipods, mysids	euphausiids hyperiids, copepods	5
Trematomus eulepidotus	amphipods, polychaetes copepods, chaetognaths	euphausiids, pteropods,	6
Trematomus Lepidorhinus	polychaetes, amphipods	mysids, copepods, amphipods	7
Benthic species			
Trematomus scotti	polychaetes, amphipods, isopods, echinoderms	-	8
Racovitzia glacialis	mysids, fish	-	6
Cygnodraco mawsonii	fish, mysids, amphipods, polychaetes	-	5
Dolloidraco longedorsalis	polychaetes, crustaceans	-	6

1 DeWitt & Hopkins 1977, Takahashi & Nemoto 1984, Eastman 1985b, Hubold 1985a, b, Williams 1985, Hubold & Ekau 1990.
2 Williams 1985, Schwarzbach 1988, Hubold & Ekau 1990.
3 Takahashi & Nemoto 1984, Schwarzbach 1988, Hubold & Ekau 1990.
4 Schwarzbach 1988, Hubold & Ekau 1990.
5 Kock *et al.* 1984, Schwarzbach 1988, Hubold & Ekau 1990.
6 Schwarzbach 1988.
7 Takahashi & Nemoto 1984, Schwarzbach 1988.
8 Naito & Iwami 1982, Schwarzbach 1988.

allow seals to disperse over wide areas, as they can use ice floes to haul out (Gilbert & Erickson 1977). Pelagic intermediate hosts would then be advantageous as they guarantee that the parasite is present wherever the seals feed in the pelagic zone.

Among the ice-inhabiting seal species, however, the Weddell seal is an exception as it shows strong affinities to the fast ice along the ice shelf border for most of the year. Whereas pelagic *Pleuragramma antarcticum* is preferentially taken by Weddell seals (Testa *et al.* 1985, Plötz 1986, Green & Burton 1987), this species seems not to be equally abundant at the ice shelf border throughout the year. Thus at times piscivorous, bentho-pelagic channichtyids are preferred prey (Plötz *et al.* 1991) and thereby may occupy an important integrative role as an additional accumulation step for *C. radiatum* larvae in the food web. As they collect similar amounts of larvae from *Pleuragramma* as the seals, channichthyids may transmit large numbers of larvae to the seals, when *Pleuragramma* may already have left the eastern Weddell Sea shelf.

While these considerations cast some light on the accumulation process, the question remains about how the seals tolerate such extreme concentrations of anisakids. Severe stomach lesions caused by anisakids are well documented (Lauckner 1985), but possibly restricted to cases of previous breakdown of the mutual tolerance of host and parasite (Young & Lowe 1969, Wilson & Stockdale 1970, McClelland 1980c). Moreover, seals seem to be able to reduce their anisakid load effectively in periods of limited food supply (Berland 1964, Feltz 1969, Johnstone, 1975, McClelland, 1980b). As availability of breathing holes and suitable breeding sites will most probably limit increase of Weddell seal populations (Stirling 1969, 1971, 1972, Siniff *et al.* 1977), seals may only exceptionally be so numerous that they suffer from food shortages. Very favourable feeding conditions, which have been documented repeatedly (SapinJaloustre 1952, Calhaem & Christoffel 1969, Stirling 1972, Davis *et al.* 1982), may then allow for a commensalic rather than a strictly parasitic habit for the stomach nematodes (McClelland 1980c). In this case, nematodes would hardly cause any harm and hence rarely induce control mechanisms in the seal.

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