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Anisakid (Nematoda) Infestations in Icelandic Grey Seals (*Halichoerus grypus* Fabr.)

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Abstract

Anisakid nematode infestations in stomachs of 196 grey seals from Icleandic waters were examined during the period 1989–93, and *Pseudoterranova decipiens s.l.*, *Contracaecum osculatum s.l.*, *Phocascaris cystophorae* and *Anisakis simplex* s.l. were found in seals from all areas and seasons. No difference in nematode abundance was observed between the sexes of grey seal but the number of worms increased with the weight of the seals. Abundance of *P. decipiens* and *C. osculatum* showed geographical and seasonal differences. Seals from the Breidafjord and Faxafloi areas had greatest abundance of *P. decipiens* with an increasing trend from spring to autumn, reaching the highest levels during period of reduced feeding in the breeding season in October to December. Abundance of *C. osculatum* was greatest in seals from the Breidafjord area and decreased from spring to autumn. The abundance was low in seals from the Faxafloi area and remained unchanged from spring to autumn. Most samples from the south coast were collected from August to December and showed low and declining abundance of all anisakid species during the breeding season. No indications of changes in *P. decipiens* abundance were observed in grey seals from West Iceland between 1979–82 and 1989–93. Proportions of adult *P. decipiens* and *C. osculatum* showed a decreasing trend when abundance of each species in the seal stomachs was increasing.

Key words: anisakid, *Anisakis simplex*, *Contracaecum osculatum*, *Halichoerus grypus*, Iceland, parasites, *Phocascaris cystophorae*, *Pseudoterranova decipiens*.

Introduction

Four genera of Anisakidae nematodes are observed in seal stomachs in the North Atlantic, i.e. *Pseudoterranova*, *Contracaecum*, *Phocascaris* and *Anisakis* (Young, 1972; Bjorge, MS 1984; Brattey and Stobo, 1990; Brattey and Ni, 1992; Brattey and Stenson, 1993). Genetic studies have shown that anisakid species from phocids in the North Atlantic consist of complexes of genetically isolated but morphologically similar sibling species (Nascetti *et al.*, 1986; Paggi *et al.*, 1991; Brattey and Stenson, 1993; Nascetti *et al.*, 1993). The life cycles of these species are similar, involving crustacean invertebrates and fish as intermediate or paratenic hosts and a marine mammal as a final host (McClelland *et al.*, 1990).

Grey seal (*Halichoerus grypus*) is the most important final host for *Pseudoterranova decipiens s.l.* and *Contracaecum osculatum s.l.* in the North Atlantic, but abundance and species composition of the worms vary between areas (Young, 1972; Brattey and Stobo, 1990; Brattey and Stenson, 1993). Seasonal changes in infestations are also observed within the same area following seasonal changes in the seal feeding habits (Brattey and Ni, 1992; Stobo *et al.*, 1990; Brattey and Stenson, 1993). Reduced diet of grey seals during breeding (October–December) and moulting (March) consists mainly of groundfish and fishes living close to shore, but pelagic and offshore teleosts become more prominent in the diet during the actual feeding seasons (January–February and April–September) (Benoit and Bowen, 1990a; 1990b; Hauksson and Ólafsdóttir, 1995; Hauksson, 1997).

The grey seal population around Iceland was estimated about 12 000 animals in the years of collecting samples for the present study (1989–93)

but seems to have declined in recent years (Hauksson and Bogason, 1997). Grey seals are mainly distributed along the west and the northwest coasts of Iceland and large breeding sites are located on the southeast coast (Hauksson and Bogason, 1997).

Investigations on nematodes in Icelandic seals have previously been carried out (Pálsson, MS 1977; Ólafsdóttir, 1993; Ólafsdóttir and Hauksson, 1997), working with samples from common and grey seals collected in 1979–82. The present paper adds further information about seasonal and regional variations in nematode infestations in grey seals. This paper further reports on findings regarding possible changes in nematode *P. decipiens* burden in the main final host in Icelandic waters, in the recent decade.

Methods

Samples from 196 grey seals were collected by local seal hunters in the years 1989–93. Most samples were collected from the Breidafjord area (West Iceland), the Faxafloi area (Southwest Iceland) and the south coast (Fig. 1). Fewer samples were collected from areas of low grey seal abundance, particularly the north and the east coasts of Iceland. Samples from the Breidafjord and Faxafloi areas were obtained from May to the end of November but samples from the south coast were mostly collected from September to November. Samples from December to April were few in all areas.

During the seal sampling, the nematodes in the oesophagus of the seals were pushed into the stomach before the stomach was cut from the rest of the digestive tract. The lower jaw and sex organs were removed for determination of age and sexual status. Age of seals was determined by counting growth layers in their teeth (Hauksson, 1992a). Weights of males and females (Table 1) were then estimated from the age-weight relationships reported in earlier studies (Hauksson, 1992a).

The nematode worms were separated from the stomach contents and picked from the stomach wall.

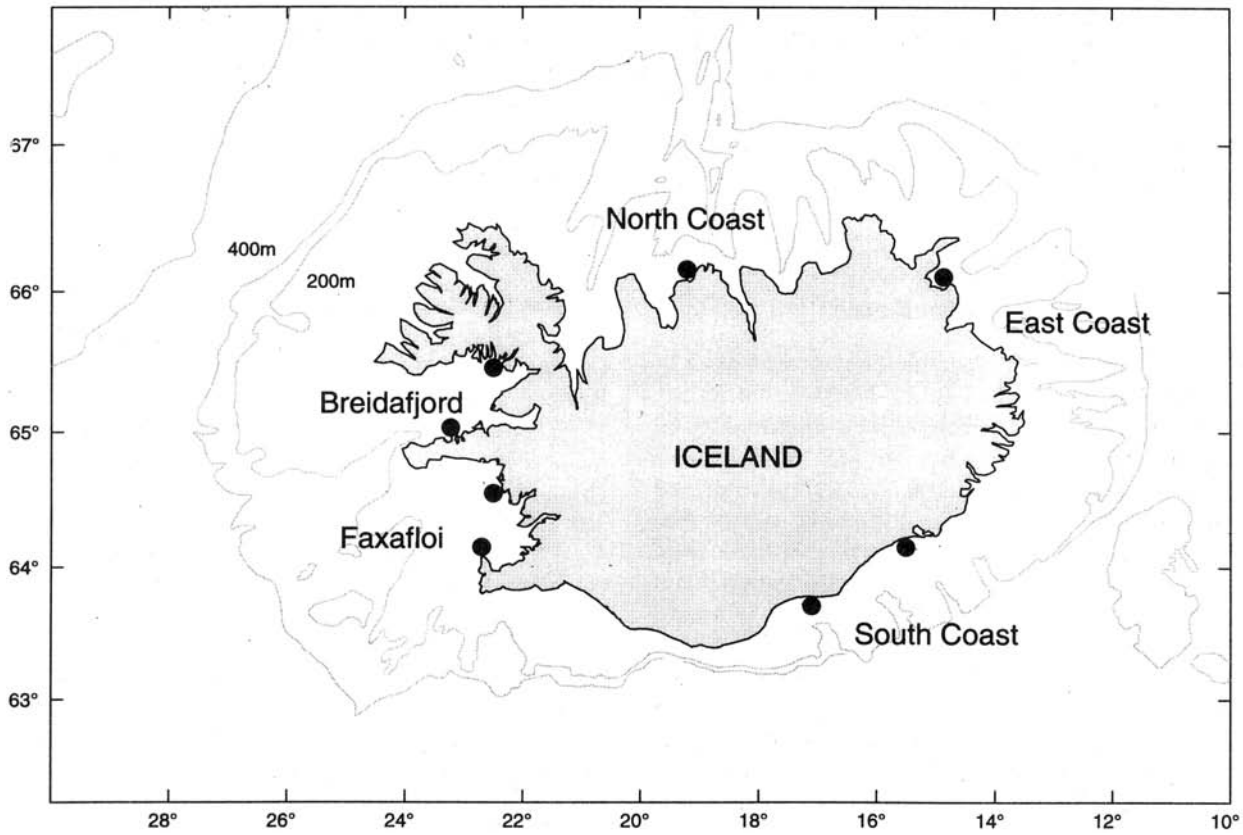

Fig. 1. Sites of grey seal sampling around Iceland 1989–93.

TABLE 1. Age (years) and weight (kg) of grey seals used in the present study (weight from Hauksson, 1992a).

Seal sex	Variables	Areas		
		Breidafjord	Faxafloi	south coast
Females	No. of samples	63	27	20
	Average age	9.7	16.0	19.1
	(range)	(0–32)	(2–34)	(3–32)
	Average weight	124.0	137.0	147.4
	(range)	(81–148)	(81–148)	(106–256)
Males	No. of samples	33	6	26
	Average age	4.6	3.7	12.5
	(range)	(0–21)	(0–9)	(0–25)
	Average weight	132.0	128.7	218.6
	(range)	(82–258)	(82–209)	(82–263)

They were stored in 70% isopropanol and cleared in 90% lactic acid before microscopic identification. Counts of worms were estimated from subsamples of known fraction in samples containing more than 200 worms.

Species identification of *P. decipiens s.l.* and *A. simplex s.l.*, fifth stage *C. osculatum s.l.* and fifth stage *P. cystophorae* was based on descriptions given by Myers (1960), Grabda (1976), Fagerholm (1989) and Berland (1963), respectively.

Pseudoterranova decipiens, *C. osculatum* and *P. cystophorae* were classified into the three categories: immature worms (third and fourth stage larvae and immature fifth stage), adult females and adult males. Adult categories were considered only when females were with developed eggs and males were with developed spicules and sperm. Since the interlabia of *C. osculatum* appear after the last moult (McClelland and Ronald, 1974; Likely and Burt, 1992), no attempt was made to distinguish between *Contracaecum* sp. and *Phocascaris* sp. before they reached the fifth stage and these larvae were excluded from statistical calculations. *Anisakis simplex* was classified into third stage larvae, preadults (fourth stage larvae and immature fifth stage worms), and in adult females and males when they were with developed eggs, and spicules and sperm, respectively.

The terms prevalence (percentage of infested individuals), abundance (mean number of parasites per host, including uninfected individuals) and intensity (number of parasites in each infested host) are used according to standard usage (Margolis *et al.*, 1982).

Seasonal, geographical, sexual and weight related differences in abundance of all anisakid species pooled together, *P. decipiens* and *C. osculatum* were analysed by comparing worm counts per seal (including zeros) from Breidafjord, Faxafloi and the south coast, respectively, using analyses of covariance (ANCOVA) with seal weights and months of the year as covariates. Same method and covariates were used when analysing changes in *P. decipiens* and *C. osculatum* abundance in seals from Breidafjord between surveys from 1979–82 and the present, and when analysing seasonal and geographical differences in proportions of adult *P. decipiens* and *C. osculatum* . All worm counts (x) were transformed with $Ln(x+1)$ and the proportions of adult worms were transformed with $arcsin\,(x)^{0.5}$ before statistical calculations. The level of significance was in all cases set at 5% and tested by paired comparisons by using the Tukey Kramer method (Sokal and Rohlf, 1981).

Results

Anisakids in grey seal stomachs

The four anisakid species complexes known from phocids were found in grey seal stomachs from all areas and seasons studied (Tables 2–5). The most common species were *P. decipiens s.l.* and *C. osculatum s.l.*, while *Phocascaris cystophorae*

TABLE 2. Statistics of anisakid infestation in stomachs of grey seals in the Breidafjord area, West Iceland in 1989–93[1].

		3 months to 4 year old seals		5 year and older seals	
Nematode	Variable[2]	January–August n = 37	September–December n = 2	January–August n = 27	September–December n = 30
Pseudoterranova decipiens s.l.	Prevalence	100	100	100	100
	Abundance (S.E.)	499.54 (471.11)	807.50 (296.50)	416.52 (301.26)	2672.43 (3574.31)
	variance: mean ratio	456.64	217.74	226.28	4945.40
	maximum infestation	2256	1104	1648	18048
	% immature worms	61.8	85.3	54.6	80.0
	% adult males	21.2	9.2	23.5	12.6
	% adult females	17.0	5.6	21.8	7.4
Contracaecum osclulatum s.l.	Prevalence	100	100	100	100
	Abundance (S.E.)	845.46 (662.74)	53.00 (17.00)	910.26 (667.22)	308.90 (451.52)
	variance: mean ratio	533.94	10.91	507.88	682.76
	maximum infestation	2856	70	2768	2312
	% immature worms	63.5	50.9	70.9	71.2
	% adult males	19.1	20.8	14.4	13.9
	% adult females	17.4	28.3	14.7	14.9
Phocascaris cystophorae	Prevalence	29.73	100	44.44	23.33
	Abundance (S.E.)	17.46 (61.77)	19.00 (7.00)	8.56 (21.65)	5.43 (14.23)
	variance: mean ratio	224.60	5.16	56.88	38.56
	maximum infestation	368	26	11264	
	% immature worms	60.1	68.4	59.37.4	
	% adult males	15.8	10.5	20.36.1	
	% adult females	24.1	21.1	20.386.5	
Contracaecum sp./ *Phocascaris* sp. third and fourth stage	Prevalence	21.62	0	22.220	
	Abundance (S.E.)	80.59 (199.51)	– (–)	73.81 (264.18)	– (–)
	variance:mean ratio	507.62	–	981.83	–
	maximum infestation	968	–	1252	–
Anisakis simplex s.l.	Prevalence	70.27	100	70.37	36.67
	Abundance (S.E.)	38.19 (61.77)	3.00 (1.00)	218.07 (502.52)	6.13 (11.57)
	variance:mean ratio	146.77	0.67	1202.51	22.56
	maximum infestation	322	4	2328	43
	% Third stage larvae	69.4	100	62.2	97.8
	% preadult	30.6	0	37.3	0
	% adult males	0	0	0.1	0
	% adult females	0	0	0.3	2.2

[1] Values are based on real counts in samples with <200 worms and estimated counts from subsamples of a known fraction in samples with >200 worms.

[2] n = sample size; Prevalence = % of infested seals; Abundance = mean number of nematodes per seal including uninfested seals; SE = standard error; preadult = fourth and immature fifth stage worms; adult males and females = fifth stage worms with spicules and developed eggs, respectively.

occurred sporadically and in small numbers in the stomachs. *Anisakis simplex s.l.* worms were also rare and consisted mainly of third stage larvae. Preadult fourth and fifth stage *Anisakis simplex* worms were occasionally found but fully mature worms were rare. Finally, in addition to the four main species, *Hysterothylacium aduncum* was found in few seal stomachs.

TABLE 3. Statistics of anisakid infestations in stomachs of grey seals in the Faxafloi area, West Iceland in 1989–93[1].

		3 months to 4 year old seals		5 year and older seals	
		January–August	September–December	January–August	September–December
Nematode	Variable[2]	*n* = 6	–	*n* = 17	*n* = 10
Pseudoterranova decipiens s.l.	Prevalence	100	–	100	100
	Abundance (S.E.)	419.17 (599.35)	– (–)	753.65 (965.50)	5455.60 (6136.74)
	variance: mean ratio	1028.39	–	1314.20	7669.92
	maximum infestation	1744	–	3184	21471
	% immature worms	76.18	–	56.068	9.31
	% adult males	15.35	–	24.65	6.31
	% adult females	8.47	–	19.29	4.37
Contracaecum osclulatum s.l.	Prevalence	100	–	94.12	80.00
	Abundance (S.E.)	77.50 (66.84)	– (–)	225.53 (206.60)	277.10 (323.51)
	variance: mean ratio	69.18	–	201.09	419.66
	maximum infestation	176	–	880	1056
	% immature worms	52.69	–	50.18	48.79
	% adult males	21.51	–	22.25	22.88
	% adult females	25.81	–	27.57	28.33
Phocascaris cystophorae	Prevalence	83.33	–	88.24	0
	Abundance (S.E.)	27.67 (31.97)	– (–)	101.24 (285.57)	– (–)
	variance: mean ratio	44.32	–	855.93	–
	maximum infestation	96	–	1237	–
	% immature worms	12.05	–	75.36	–
	% adult males	51.81	–	10.58	–
	% adult females	36.14	–	14.06	–
Contracaecum sp./ *Phocascaris* sp. third and fourth stage	Prevalence	33.33	–	47.0620.00	
	Abundance (S.E.)	29.83 (50.64)	– (–)	161.76 (396.72)	71.80 (150.81)
	variance: mean ratio	103.14	–	1033.77	351.95
	maximum infestation	138	–	1685462	
Anisakis simplex s.l.	Prevalence	83.33	–	88.24	10.00
	Abundance (S.E.)	37.33 (31.97)	– (–)	63.82 (80.46)	11.50 (34.50)
	variance: mean ratio	127.45	–	107.78	115.00
	maximum infestation	176	–	260	115
	% Third stage larvae	100	–	67.6	100
	% preadult	0	–	32.3	0
	% adult males	0	–	0.2	0
	% adult females	0	–	0	0

[1] Values are based on real counts in samples with <200 worms and estimated counts from subsamples of a known fraction in samples with >200 worms.

[2] *n* = sample size; Prevalence = % of infested seals; Abundance = mean number of nematodes per seal including uninfested seals; SE = standard error; preadult = fourth and immature fifth stage worms; adult males and females = fifth stage worms with spicules and developed eggs, respectively.

In all seal stomachs investigated some anisakid worms were found. The youngest pups in the catch were about 3 months old caught off the north coast and the intensity of anisakids ranged from 139 to 382 worms. Anisakid infestations in pups seem to increase rapidly during the first months of a seal's life and soon reach levels seen in older seals. The species composition of worms in pups was also similar to the species composition in older seals (Tables 2–5).

TABLE 4. Statistics of anisakid infestations in stomachs of grey seals from the south coast of Iceland in 1989–93[1].

		3 months to 4 year old seals		5 year and older seals	
Nematode	Variable[2]	January–August n = 1	September–December n = 1	January–August n = 8	September–December n = 40
Pseudoterranova decipiens s.l.	Prevalence	–	–	100	100
	Abundance (S.E.)	6.00 (–)	472.00 (–)	413.25 (482.08)	534.43 (831.10)
	variance: mean ratio	–	–	642.70	1325.62
	maximum infestation	6	472	1648	4320
	% immature worms	66.67	24.58	62.25	33.28
	% adult males	0.00	36.44	22.38	35.98
	% adult females	33.33	38.98	15.37	30.73
Contracaecum osclulatum s.l.	Prevalence	–	–	100.00	100.00
	Abundance (S.E.)	0.00 (–)	112.00 (–)	511.25 (639.90)	441.10 (674.95)
	variance: mean ratio	–	–	915.35	1059.26
	maximum infestation	0	112	1920	2752
	% immature worms	–	17.86	65.97	46.46
	% adult males	–	28.57	19.02	28.10
	% adult females	–	53.57	15.01	25.44
Phocascaris cystophorae	Prevalence	–	–	75.00	60
	Abundance (S.E.)	470.00 (–)	4.00 (–)	455.00 (628.51)	8.55 (21.12)
	variance: mean ratio	–	–	992.2	353.49
	maximum infestation	470	4	1776	128.00
	% immature worms	96.17	0.00	89.51	43.27
	% adult males	1.28	0.00	6.04	26.02
	% adult females	2.55	100.00	4.45	26.02
Contracaecum sp./ *Phocascaris* sp. third and fourth stage	Prevalence	–	–	37.50	2.50
	Abundance (S.E.)	0.00 (–)	0.00 (–)	1034.00 (2058.02)	1.08 (6.71)
	variance: mean ratio	–	–	4681.33	43.00
	maximum infestation	0	0	6176	43
Anisakis simplex s.l.	Prevalence	–	–	87.50	52.50
	Abundance (S.E.)	4.00 –	40.00 –	289.00 (318.33)	84.68 (151.10)
	variance: mean ratio	–	–	400.74	276.56
	maximum infestation	4	40	896	584
	% Third stage larvae	100	20.00	29.1	30
	% preadult	0	50.00	63.9	67
	% adult males	0	0.00	3.8	1
	% adult females	0	30.00	3	2

[1] Values are based on real counts in samples with <200 worms and estimated counts from subsamples of a known fraction in samples with >200 worms.

[2] n = sample size; Prevalence = % of infested seals; Abundance = mean number of nematodes per seal including uninfested seals; SE = standard error; preadult = fourth and immature fifth stage worms; adult males and females = fifth stage worms with spicules and developed eggs, respectively.

Abundance

Differences in abundance of all anisakid species pooled together, between male and female seals, was not statistically significant. However, the worm counts per seal covaried significantly with the weight of the seals ($F_{1, 171} = 8.37$; $p = 0.004$; slope = 0.01). Comparisons of *P. decipiens* and *C. osculatum* gave the same results. No significant difference was observed between the sexes of seals but the worm counts per seal of each

TABLE 5. Statistics of anisakid infestations in stomachs of grey seals from the north– and east coasts of Iceland in 1989–93[1].

		3 months to 4 year old seals		5 year and older seals	
Nematode	Variable[2]	January–August *n = 7*	September–December –	January–August *n = 10*	September–December –
Pseudoterranova decipiens s.l.	Prevalence	100	–	100	–
	Abundance (S.E.)	112.29 (94.91)	– (–)	841.40 (953.79)	– (–)
	variance: mean ratio	93.60	–	1201.33	–
	maximum infestation	292	–	2776	–
	% immature worms	76.97	–	68.30	–
	% adult males	14.25	–	16.76	–
	% adult females	8.78	–	14.94	–
Contracaecum osclulatum s.l.	Prevalence	100	–	80.00	–
	Abundance (S.E.)	54.86 (39.71)	– (–)	45.80 (46.68)	– (–)
	variance: mean ratio	33.53	–	52.86	–
	maximum infestation	130	–	122	–
	% immature worms	70.57	–	35.37	–
	% adult males	14.32	–	31.22	–
	% adult females	15.10	–	33.41	–
Phocascaris cystophorae	Prevalence	42.86	–	60.00	–
	Abundance (S.E.)	2.00 (2.56)	– (–)	16.30 (28.66)	– (–)
	variance: mean ratio	3.83	–	56.01	–
	maximum infestation	7	–	92	–
	% immature worms	50.00	–	14.11	–
	% adult males	21.43	–	38.65	–
	% adult females	28.57	–	47.24	–
Contracaecum sp./ *Phocascaris* sp. third and fourth stage	Prevalence	14.29	–	10.00	–
	Abundance (S.E.)	2.29 (5.60)	– (–)	0.40 (1.2)	– (–)
	variance: mean ratio	16.00	–	4.00	–
	maximum infestation	16	–	4	–
Anisakis simplex s.l.	Prevalence	85.71	–	90.00	–
	Abundance (S.E.)	38.29 (2.56)	– (–)	24.60 (23.27)	– (–)
	variance: mean ratio	43.63	–	24.46	–
	maximum infestation	118	–	72	–
	% Third stage larvae	96	–	40.2	–
	% preadult	4	–	59.8	–
	% adult males	0	–	0.0	–
	% adult females	0	–	0	–

[1] Values are based on real counts in samples with <200 worms and estimated counts from subsamples of a known fraction in samples with >200 worms.

[2] *n* = sample size; Prevalence = % of infested seals; Abundance = mean number of nematodes per seal including uninfested seals; SE = standard error; preadult = fourth and immature fifth stage worms; adult males and females = fifth stage worms with spicules and developed eggs, respectively.

species covaried with the seal weight (*P. decipiens*: $F_{1, 171} = 9.53$; $p < 0.001$; slope = 0.01; *C. osculatum*: $F_{1, 171} = 10.60$; $p = 0.001$; slope = 0.01).

Seasonal changes in abundance of all anisakids pooled together in grey seals from Breidafjord, Faxafloi and the south coast of Iceland were not found to be significant. The abundance of

P. decipiens, on the other hand, increased ($F_{1, 171} = 21.13$; $p < 0.001$, slope = 0.21) and the abundance of *C. osculatum* decreased ($F_{1, 171} = 12.82$; $p < 0.001$; slope = -0.174) significantly from spring to autumn.

Geographical differences were observed in abundance of all anisakid species pooled together ($F_{2, 171} = 13.51$; $p < 0.001$). It was highest in seals from the Breidafjord area and lowest in seals from the south coast of Iceland. The observed significance was only due to the difference between these two areas ($|Y_1 - Y_2| = 0.71$; $MSD_{0.01[3, 176]} = 0.49$).

The abundance of *P. decipiens* also differed significantly between areas ($F_{2, 171} = 22.86$; $p < 0.001$). It was highest in seals from the Faxafloi area but lowest in seals from the south coast. No significant difference was observed between seals from the Faxafloi and Breidafjord areas but there was a significant difference in *P. decipiens* infestations in seals from the south coast and the Faxafloi area ($|Y_1 - Y_2| = 1.09$; $MSD_{0.01[3, 176]} = 0.82$) and also in seals from the south coast and the Breidafjord area ($|Y_1 - Y_2| = 0.96$; $MSD_{0.01[3, 176]} = 0.71$).

Similarly, the abundance of *C. osculatum* differed significantly between areas ($F_{2,171} = 19.17$; $p < 0.001$). Infestations were greatest in seals from the Breidafjord area but least in seals from Faxafloi. Paired comparisons indicated a significant difference between all three areas; Breidafjord and Faxafloi: ($|Y_1 - Y_2| = 1.49$; $MSD_{0.01[3, 176]} = 0.80$), Faxafloi and the south coast: ($|Y_1 - Y_2| = 0.79$; $MSD_{0.05[3, 176]} = 0.71$) and between Breidafjord and the south coast: ($|Y_1 - Y_2| = 0.07$; $MSD_{0.01[3, 176]} = 0.690$).

No statistical comparisons were made on data from seals from the north and the east coasts due to small sample sizes and a total lack of samples from September through December. However, our data indicated low abundance of anisakids in the area, especially of *C. osculatum* (Table 5).

No change in abundance of *P. decipiens* was observed in grey seals from the Breidafjord area between a survey made in 1979–82 and the present study but the abundance of *C. osculatum* showed a significant increased in the period ($F_{1, 129} = 10.02$; $p < 0.01$).

Proportions of adult *P. decipiens* and *C. osculatum*

Proportion of adult *P. decipiens* in grey seals decreased slightly from spring to autumn, although not statistically significant ($F_{1, 171} = 3.64$, $p = 0.06$; slope = -0.20), while it differed significantly between areas ($F_{2, 171} = 1\,308$; $p < 0.001$). It was highest in seals from the south coast but lowest in seals from the Faxafloi and Breidafjord areas (Tables 2–4). The overall difference was due to the marked difference between the south coast and Faxafloi ($|Y_1 - Y_2| = 0.27$; $MSD_{0.01[3, 176]} = 0.15$), on the one hand and between the south coast and Breidafjord ($|Y_1 - Y_2| = 0.27$; $MSD_{0.01[3, 176]} = 0.19$) on the other. No such difference was found between the Faxafloi and Breidafjord areas.

Proportions of adult *C. osculatum* increased significantly from spring to autumn ($F_{1, 171} = 5.24$; $p = 0.02$; slope = 0.25). It was highest in seals from the south coast but lowest in seals from the Breidafjord area (Table 2–4). The overall difference was caused by the marked difference between the south coast and Breidafjord area ($|Y_1 - Y_2| = 0.26$; $MSD_{0.01[3, 176]} = 0.15$) and between the Faxafloi and Breidafjord areas ($|Y_1 - Y_2| = 0.22$; $MSD_{0.01[3, 176]} = 0.17$).

Discussion

The same anisakid species were found in grey seal stomachs in the present study as in earlier investigations around Iceland (Pálsson, MS 1977; Ólafsdóttir, 1993; Ólafsdóttir and Hauksson, 1997) and elsewhere in the North Atlantic Ocean (Young, 1972; Bjorge, MS 1984; Brattey and Stobo, 1990; Brattey and Stenson, 1993). *Pseudoterranova decipiens s.l.* and *C. osculatum s.l.* were the most common species. The abundance of *Phocascaris cystophorae* in seal stomachs was not high as worms of this genus are usually found in greater abundance in the seal intestine (Berland, 1963). *Anisakis simplex s.l.* can survive in seals for some time and their abundance can apparently reach high levels. Their growth and development in seals are, however, poor and maturity is seldom reached. *H. aduncum* was observed in few seals; this species matures in a fish host and probably does not survive for long in a digestive tract of a seal.

Worm burden of the anisakids was related to the weight of the host but no significant difference was found between the sexes. Stobo *et al.* (1990) reported similar results, where the length of seals best explained differences in worm abundance, but as males and females differ in size, sex was only indirectly related. Brattey and Stenson (1993) found no significant difference in prevalence nor abundance between the sexes or with age in five phocid

species from Newfoundland and Labrador. A difference in infestations between the sexes may, however, be expected as females and males differ in behaviour, especially during the breeding season.

The abundance of *C. osculatum* decreased while the abundance of *P. decipiens* increased in grey seals from the west coast from spring to autumn. Abundance of the latter species was highest when feeding was largely reduced during the breeding season in October to December. This does not occur in grey seals from the south coast and is contradictory to results from the east coast of Canada where abundance of anisakids declined during breeding (Stobo *et al*. 1990). The reason behind this lies most probably in seasonal variations in prey selection. The grey seal diet in the Breidafjord area during the feeding period (January to February and April to September) consists mainly of lumpsucker (*Cyclopterus lumpus*), sand eels (*Ammodytes* spp.) and cod (*Gadus morhua*). The importance of these species in the diet decreases, on the other hand, during breeding (October to December) when sculpin (*Myoxocephalus scorpius*) becomes the predominant prey (Hauksson and Ólafsdóttir, 1995; Hauksson, 1997). Sculpins probably also play an important role in the Faxafloi area, especially close to the large breeding sites on the northern side of the bay (Hauksson, unpubl. data). Sand eels are the most common prey off the south coast in the autumn (Hauksson, 1997). Investigations on nematodes in fishes inhabiting the coastal areas around Iceland show high *P. decipiens* infestations in sculpins from the Breidafjord and Faxafloi areas (Hauksson, 1992b; Hauksson and Ólafsdóttir, 1995). *Contracaecum sp*. larvae are found in number of fish species but the greatest infestations are observed in sand eels (Hauksson, 1992b).

The abundance of *P. decipiens* was found significantly higher in seals from the Breidafjord and Faxafloi areas compared to the south coast even though the data from the south coast originated from the largest seals (Table 1). This may be attributed to the large number of *P. decipiens* in grey seals from the west coast in the autumn.

The present results are compatible with earlier investigations on anisakid infestations in Icelandic grey seals, carried out in the period 1979–82 (Ólafsdóttir, 1993). Although the two surveys are not completely comparable due to differences in sampling and analyses of results, both investigations give information of the largest infestations in seals from the west coast. These results are consistent with previous findings of the heaviest *P. decipiens* burdens in seals from areas close to the largest grey seal colonies (Young, 1972; Mansfield and Beck, 1977; McClelland, 1980; Ólafsdóttir, 1993; Ólafsdóttir and Hauksson, 1997).

Differences in sea temperature around the Icelandic coast (Kristmannsson, 1989; 1991) are also likely to account for the great *P. decipiens* abundance off the west coast. Prolonged exposure to temperature below 0°C is lethal for the unhatched *P. decipiens* larvae (Measures, 1996). Hatching time of the egg is stimulated, but post hatch longevity of the free-living larva is decreased with increased temperature (McClelland, 1982; 1990; Burt *et al*., 1990; Brattey, 1990; Measures, 1996). Sea temperature in Icelandic coastal areas does not fall below 0°C but relatively warm water south and west off Iceland compared to colder areas north and east of the country is, however, likely to be more suitable for development and successful transmission of the larvae (Measures, 1996).

Large grey seal population and relatively warm sea in combination with shallow water and large kelp forests inhabited by rich fauna in Breidafjord and northern Faxafloi (Gunnarsson, 1991), thus seem to sustain great abundance of *P. decipiens* off the Icelandic west coast. Finally, heavily infected sculpins in the kelp beds probably play a major role in transmission of *P. decipiens* in the area.

Distribution of *C. osculatum* seemed to be more restricted to areas off the south and the west coasts than distribution of *P. decipiens*. Sand eels are probably the main fish host for *C. osculatum* in Icelandic waters.

During experimental infestations, *P. decipiens* larvae reach maturity in 15–25 days in seals and the worms may survive up to 80 days after infestation (McClelland, 1980). Observed proportions of adult worms in different seasons agree with expected lower proportions when infestations of that particular species are increasing.

A change in the proportions of developmental stages of *P. decipiens* from spring to autumn was not significant when infestations from all three areas were analysed. Here the decrease in proportions

of adult *P. decipiens* observed in the Faxafloi and Breidafjord areas from spring to autumn were counterbalanced with the increase of proportion of adult *P. decipiens* in seals from the south coast. On the other hand, proportions of adult *C. osculatum* increased significantly from spring to autumn. A significant difference in proportions of adult *C. osculatum* between areas was probably due to the fact that more samples from Breidafjord were collected in the spring and that the samples from the south coast mainly represented infestations in the autumn.

Stobo *et al*. (1990) found increased proportions of adult worms during periods of reduced worm burdens. This was linked to changes in the seal diet. Declining proportion of adult *P. decipiens* in adult grey seals during the breeding period was, on the other hand, explained by shedding of retarded adult worms and sustained development of the larvae during low food intake. The high proportion of *P. decipiens* larvae in seals from the west coast in the autumn in the present study was probably caused both by increase in new infestation and also by sustained development of larvae until after the breeding season.

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