ANISAKID NEMATODES IN THE COMMON SEAL (*PHOCA VITULINA* L.) IN ICELANDIC WATERS

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The occurrence of anisakid nematodes in the common seal in Icelandic waters was studied by investigating digestive tracts of 95 seals during 1979-82. The most abundant adult species was *Pseudoterranova decipiens*. *Contracaecum osculatum*, and *Phocascaris cystophorae* were less frequent. In addition larvae of *Anisakis simplex* were common. The prevalence and abundance of these nematode species did not differ significantly between seasons. The prevalence and abundance of *P. decipiens* showed marked geographic variations, with higher frequency and higher numbers in common seals from the west and northwestern coast, than from other coastal areas of Iceland. Male common seals had higher abundance of *P. decipiens* than females, and the number of *P. decipiens* worms was positively correlated with age in male seals. The sex ratios of *P. decipiens* and *C. osculatum* worms were close to 1:1, but the sex ratio of *P. cystophorae* was close to 1:1.7, in favour of females. A significant positive correlation was observed between numbers of *P. decipiens* and *C. osculatum*.

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INTRODUCTION

Anisakid nematodes occurring in seals are of economic and medical significance because of the infective third stage larvae, which are common in the muscle and other organs of infected fish (HAUKSSON 1991). Four species are regularly found in the digestive tract of common seals (*Phoca vitulina* L.) in Icelandic waters; *Pseudoterranova decipiens* (KRABBE, 1878) – sealworm, *Contracaecum osculatum* (RUDOLFI, 1802), *Phocascaris cystophorae* (BERLAND, 1963) and *Anisakis simplex* (RUDOLFI, 1845) – herring worm (ÓLAFSDÓTTIR 1993). Genetic studies have shown that some ascaridoids in the Northern Atlantic consist of morphologically similar but reproductively isolated siblings (PAGGI & al. 1991; NASCETTI & al. 1986, 1993). *Pseudoterranova decipiens* consists of three sibling species in the northern Atlantic of which common seal mainly hosts *P. decipiens* B, but also *P. decipiens* A (PAGGI & al. 1991; BRATTEY & STENSON 1993). Three sibling species of *Contracaecum osculatum* are found in the northern Atlantic but only *C. osculatum* C seems to mature in common seals (NASCETTI & al. 1993; BRATTEY & STENSON 1993). *Anisakis simplex* consists of two sibling species in the northern Atlantic. Electrophoretic analyses of *A. simplex* in seals have not been performed but *A. simplex* B is more abundant than *A. simplex* A in fish hosts in the northern North Atlantic (NASCETTI & al. 1986). Similar fractions of the two species are thus likely to occur in phocids if their probability of surviving in phocids is equal.

The early phases of the life cycles of these nematode species are similar. First intermediate hosts are various crustacean species and second intermediate or paratenic hosts are various bony fishes. The first three mentioned nematode species mature in phocids. *A. simplex* may survive and occasionally develop to maturity in phocids but cetaceans seem to be the main final hosts (YOUNG 1972; BRATTEY & STENSON 1993).

Investigations on anisakids in seals from the North Atlantic have shown lower abundance of *P. decipiens* and *C. osculatum* in common seals than in grey seals (*Halichoerus grypus*), and higher abundance in grey seals in areas inhabited by large grey seal populations (YOUNG 1972; BRATTEY & STOBO 1990). Furthermore, abundance of *P. decipiens* in cod (*Gadus morhua* L., 1758) has been recorded higher close to seal haul-out sites (BJØRGE 1985; BRATTEY & al. 1990; JENSEN & IDÅS 1992; MCCLELLAND & MARCOGLIESE 1994; JENSEN & al. 1994).

Common seals are distributed along the whole Icelandic coastline but grey seals are only abundant along the northwest, the west and the south coasts (PLATT 1975;

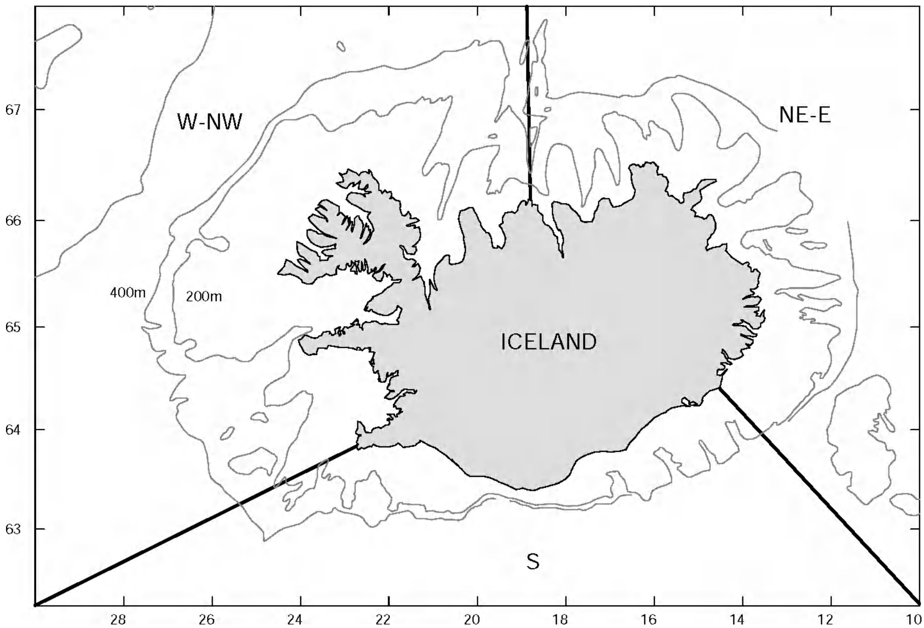

Fig. 1. Areas of the coast of Iceland investigated in this study. W-NW: West to north-western coastal waters, NE-E: Northeast to eastern coastal waters and S: South coast.

HAUKSSON 1992a; HAUKSSON & ÓLAFSDÓTTIR 1995). Investigations on anisakids in various fish and seal hosts in Icelandic waters have shown the highest worm burdens of *P. decipiens* off the west coast (PLATT 1975; HAUKSSON & ÓLAFSDÓTTIR 1995; ÓLAFSDÓTTIR & HAUKSSON 1997).

The aim of the present study was to investigate seasonal and spatial variation in occurrence of anisakids in Icelandic common seals. Various factors likely to affect the nematode burden and the variability recorded, in common seals from different coastal regions of Iceland, are discussed.

MATERIAL AND METHODS

Collection and treatment of samples

Nematodes were collected from the entire digestive tract of 95 common seals in Icelandic waters in the period of 1979-82 (see HAUKSSON 1984). The nematodes were preserved in 70 % isopropanol with 5 % glycerol, and cleared in lactic acid or glycerine. Worms were examined in a binocular light microscope. Adult worms (fifth stage) and third and fourth stage larvae were identified to species, according to DELYAMURE'S (1955), FAGERHOLM'S (1989), BERLAND'S (1963) and GRABDA'S (1976) descriptions of *P. decipiens*, *C. osculatum*, *P. cystophorae* and *A. simplex* respectively. No attempt was made to differentiate between *Contracaecum* sp. and *Phocascaris* sp. third stage larvae and these larvae were combined into one group. They were included in statistical comparisons and statistical analyses when total numbers of worms were used, but excluded from all statistical work on species level. Number of each species in samples with more than 200 worms was estimated on the basis of subsampling of samples divided to a known fraction.

The samples were divided into several groups, based on origin (three coastal areas) and seasons of the year. The Icelandic coastline was thus divided into, a west to northwestern (W-NW), a northeast to eastern (NE-E) and a southern (S) area (Fig. 1). The W-NW area is shallow with wide continental shelf, numerous fjords, bays and islands and large seal populations compared to the NE-E and the S-areas (HAUKSSON 1992a). Relatively shallow and wide fjords dominate the north coast of Iceland, while the east coast of Iceland consists of narrow deep fjords. The south coast of Iceland has a narrow continental shelf and open sandy shores with vast estuaries of glacier rivers dominating. The sea temperature off the south and west coasts is relatively temperate compared to colder areas off the northeast and east coasts of Iceland (KRISTMANSSON 1989).

The year was divided into two periods, the breeding season (June to August) and feeding season (September to May) of common seals.

The terms prevalence (percentage of seals infected), abundance (mean number of parasites of hosts studied, including uninfected hosts) and intensity (number of individuals of parasites in an infected host) are used following standard usage (MARGOLIS & al. 1982). In statistical analyses where zero values from uninfected seals were included, the term number of worms (number of individuals of parasites in a host, including uninfected hosts) was used.

Statistics

The distribution of worm counts for each nematode species was non-normal and the data showed sever heteroscedasticity. Transformations of data did not correct for this, so we had to resort to use less efficient non-parametric statistical tests for analysing the data.

Using Pearson's Chi-square test, observed differences in prevalences of nematodes in the digestive tract of common seals, from the three areas and two seasons, were examined for statistical significance. Differences in nematode abundance in relation to coastal areas and seasons were tested separately with the non-parametric Kruskal-Wallis one-way analysis of variance for ranks (H). Comparisons of prevalence of nematode species between sexes and age of seals, was tested with Pearson's Chi-square, and differences in number of worms of male and female seals were tested with Mann-Whitney U-test. Proportions of mature worms of each nematode species in the seals between the two seasons were compared with Pearson's Chi-square. Correlation between numbers of worms and age of seals was investigated using the Spearman's rank correlation coefficient (r_s). The sex ratios of mature nematodes in seals were compared, using the G-test for replicated goodness of fit (Sokal & Rohlf 1981). Correlation between sex ratios of each worm species and intensity of infection, and correlation of proportions of mature worms and intensity of infection, were investigated with Spearman's rank correlation coefficient (r_s). Spearman's rank correlation coefficient was used to test the null hypothesis that correlation between intensity of different nematode species pairs did not vary significantly from zero.

Statistical analysis was carried out by using the SPSS® statistical package, for OS/2, release 4.1, 1990.

RESULTS

Prevalence and abundance of nematode species

Animals of different age and sex were distributed differently between coastal areas and seasons, as measured with Pearson's Chi-square (Chi-square = 10.27; df = 4; p = 0.04). The main difference was that pups were lacking in the samples from the south coast of Iceland. This was not, however, regarded as serious drawback to further analysis, and age and sex of common seals were excluded as factors when prevalence and abundance of nematodes were compared between areas and seasons. Investigation of the worm data also point out that pups quite early pick up similar number of worms as the older seals, i.e. as soon as they start feeding on marine fauna about one month of age. Pups, seals of age 0, in this study were all older than 2 months.

Almost every examined common seal was infected with some worms. The abundance of nematodes was 180 and intensity of infection ranged from 12 to 22120 worms. Prevalence of *P. decipiens* in common seals was, 75-100 %, but prevalences of *C. osculatum* and *P. cystophorae* were lower; less than 80 % (Table 1). Larvae of *A. simplex* were often quite abundant (median 14; range 0-623), but mature *A. simplex* worms were absent and premature females and males occurred only occasionally. This species was therefore omitted from further analysis.

Geographic and seasonal differences in nematode infections

Prevalence of *P. decipiens*, *C. osculatum* and *P. cystophorae* were not significantly different between areas or seasons (Chi-squares for each nematode species were lower than 5.76; df = 2; p > 0.06). Abundance of *P. decipiens* was significantly higher in the W-NW area than in the other areas (H = 13.29; p = 0.001), but there was no significant difference between seasons (H = 1.01; p = 0.32). Furthermore, no significant difference was found in abundance of the other nematode species in common seals, between areas or seasons (Table 1).

Host sex and age related differences in nematode infections

Prevalence of nematode species was not significantly different between ages or sexes of common seals, except in case of female pups, which had significantly higher prevalence of *C. osculatum* than male pups, 84.6 % and 37.5 % respectively (Chi-square = 6.45; p = 0.04).

Abundance of *P. decipiens* nematodes was significantly higher in male than female seals (Mann-Whitney U-test, U = 661.0; approximate normal deviate Z = –2.35; p = 0.02). Other nematode species did not show significant difference in abundance between sexes (Table 2), but number of *P. decipiens* and *C. osculatum* worms correlated significantly with age of male common seals (Table 3).

Table 1. Prevalence (% of seals infected) and abundance (mean number of nematodes of seals studied, including uninfected seals) of Anisakid nematodes in common seals from different coastal areas of Icelandic waters and seasons (N = number of seals; SE = standard error).

Coastal areas	W-NW			NE-E	S
Seasons	June-Aug.	Sept.-May	Yearly basis	Yearly basis	Yearly basis
N	24	44	68	14	13
Pseudoterranova decipiens (larvae and adult)					
Prevalence (%)	100.0	97.7	98.5	85.7	92.3
Abundance	186.5	673.8	501.7	84.1	27.9
SE	43.7	461.4	299.1	57.8	10.8
Contracaecum osculatum (fourth stage larvae and adult)					
Prevalence (%)	66.7	52.3	57.4	57.1	53.8
Abundance	31.0	30.9	31.0	19.1	21.7
SE	9.20	18.9	12.6	9.4	18.9
Phocascaris cystophorae (fourth stage larvae and adult)					
Prevalence (%)	79.2	72.7	75.0	78.6	92.3
Abundance	46.7	36.6	40.2	16.6	12.3
SE	24.2	10.8	11.0	6.3	3.6

Nematode sex-ratios and maturity

P. cystophorae females (F) were more numerous than males (M), in 43 out of 95 common seals, but in only 15 seals did males outnumber females, and the M:F ratio varied significantly from unity; being 1:1.72 (G-test, G_T = 88.33; $p < 0.001$). *P. decipiens* males, on the other hand, outnumbered females in 46 seals and vice versa in 26 out of the 95 common seals; M:F is 1:1.02. However, this little difference from unity did show a slight significance in favour of the females (G-test, G_T = 303.87; $p < 0.001$). The M:F ratio of *C. osculatum* is 1:0.93, but on the whole, males outnumbered females in 17 seals, and vice versa in 16 seals of the 95 common seals studied, and a significant difference in the sex-ratio was not observed (G-test, G_T = 28.52; $p > 0.1$).

Correlation analysis of sex ratios (M:F) of nematode species with intensity of infection in the digestive tract of seals showed a highly significant positive r_s in *P. cystophorae* and in *P. decipiens*. That is, female worms were proportionally less numerous in seals as intensity of the same species increased. On the other hand, a significant negative r_s occurred between sex-ratio (M:F) of *C. osculatum* and intensity of *P. cystophorae*; so in this case *C. osculatum* male worms got proportionally less numerous as intensity of *P. cystophorae* increased (Table 4).

The Spearman's rank correlation coefficient, of the ratio of mature worms to intensities of each worm species, and intensities of all species in the digestive tract in common seals is given in (Table 4). Two significant correlations were found; proportion of mature *P. cystophorae* was negatively correlated with intensity of *P. cystophorae*, and proportion of mature *P. decipiens* was negatively correlated with intensity of all worm species in the digestive tract.

No seasonality could be found in proportions of mature worms of each nematode species. The mean percentage for mature *P. decipiens, C. osculatum* and *P. cystophorae,* was 26.1 %, 38.6 % and 57.9 %.

Co-occurrence of nematode species

One significant positive correlation between nematode species was found, between *P. decipiens* and *C. osculatum* (r_s = 0.28; p = 0.006). Correlations between *P. decipiens* and *P. cystophorae*, and between *C. osculatum* and *P. cystophorae* were not significant; r_s –0.03 and –0.07 respectively.

DISCUSSION

Common seals in Icelandic waters largely host the same nematode species as common seals in other parts of the North Atlantic (see Bjørge 1984; Weber 1988; Lick 1989; Brattey & Stobo 1990; Lunneryd 1991; Brattey & Stenson 1993). *P. decipiens* seems to be the most abundant worm. Its abundance in common seals, from the W-NW area, in the present study was similar to recorded values from common seals off Newfoundland and Labrador (Bratttey & Stenson 1993). The abundance observed in the seals from the N-NE and S areas were, however, similar to observed values from the British Isles (Young 1972), Norway (Bjørge 1984; Aspholm & al. 1995), the German and Danish Wadden Seas (Lick 1989), Kattegat-Skagerrak and the SW-Baltic (Lunneryd 1991).

Abundance of *C. osculatum* was similar to values from common seals off Newfoundland and Labrador (Brattey & Stenson 1993) but higher than findings in common seals from Northern Europe (Young 1972; Bjørge 1985; Lick 1989; Lunneryd 1991).

Abundance of *P. cystophorae* in the present study was considerably higher than reported from common seals from the British Isles (Young 1972) and East Canadian waters (Brattey & Stenson 1993). Large *P. cystophorae* worms are often abundant in the duodenum with the head region attached to the intestine wall. These worms were included in the samples, in the present study, because the whole digestive tract was investigated, whereas the other studies focused only on infections of the stomach.

The geographic analysis of the worm burden in common seals in this study showed higher abundance of *P. decipiens* in seals from the W-NW part of the coast than elsewhere. In that region, there is in addition, a great individual variation in the intensity of *P. decipiens*, hence resulting in very great standard deviations around the means. It is not obvious what causes the variations in worm intensities. It may be caused by differences in prey selection, where individual common seals prefer fish

Table 2. Prevalence (% of seals infected) and abundance (mean number of nematodes of seals studied, including uninfected seals) of Anisakid nematodes in male and female common seals in Icelandic waters (N = number of seals, SD = standard deviation).

	Male seals (N= 39)			Female seals (N= 48)		
Nematode species	Prevalence	Abundance	SD	Prevalence	Abundance	SD
Pseudoterranova decipiens	44.0	758.4	3246.0	56.0	96.1	163.4
Contracaecum osculatum	43.8	45.5	137.7	56.3	15.3	31.8
Phocascaris cystophorae	47.1	34.5	66.5	52.9	36.1	91.6

species with high abundance of nematodes, more than the average common seal. It may also be influenced by individual variation in resistance to natural reinfections by nematodes as found experimentally by McClelland (1980).

The geographic difference in abundance of nematodes in Icelandic common seals, observed in this study, is probably influenced by geographic difference in the diet of the seals. But difference in environmental factors is also likely to be of great importance. Common seals from the W-NW area forage more on gadoids like cod and saithe (*Pollachius virens* L., 1758) and flatfishes like plaice (*Pleuronectes platessa* L., 1758) but capelin (*Mallotus villosus* Müller, 1776) is more frequently consumed off the east coast of Iceland (Hauksson 1984). Codfishes and flatfishes are more frequently infected with *P. decipiens* larvae than capelin (Hauksson & Ólafsdóttir 1995).

No difference in abundance of *C. osculatum* in spite of its higher abundance in capelin than in gadoids or flatfishes (Hauksson & Ólafsdóttir 1995), may be due to a high infection of *Contracaecum* in sand eels (*Ammodytes* spp.), which is frequently eaten by the seals together with cod (Hauksson 1984).

Higher abundance of *P. decipiens* in grey seals and various fish hosts off the west coast, than off other coasts of Iceland (Platt 1975; Hauksson & Ólafsdóttir 1995; Ólafsdóttir & Hauksson 1997), indicates that there are some other important factors than food selection causing larger abundance of *P. decipiens* there. The large grey seal populations off the west coast and the rare occurrence of this species off the northeast and east coasts may cause the geographical difference in the abundance of *P. decipiens*. Similar positive correlations of *P. decipiens* abundance and grey seal distributions are known from British (Young 1972) and Norwegian waters (Bjørge 1984; 1985). The biotas off the west coast, which are characterised by numerous small islands and large *Laminaria* forests, inhabited by number of invertebrates, small fish and seals (Gunnarsson 1991), facilitate efficient transmission of *P. decipiens* through the necessary steps in the life cycle of the parasite.

The development of ascaridoid larvae are highly influenced by sea temperature (Brattey 1990) and the generation time is likely to be longer in areas off the north and east coasts than in the warmer waters off the west and south coasts of Iceland (Kristmannsson 1989). It is however, not clear how temperature may affect population sizes of *P. decipiens,* except that temperature below 0 °C seems to be lethal to the unhatched larva (Measures 1996). This should not affect abundance of *P. decipiens* in Icelandic waters as bottom temperature in coastal waters around the Icelandic coast does not fall below 0 °C (Kristmannsson 1989).

A lack of seasonal differences in nematode infections in the present study may partly be due to the small number of samples analysed. Pálsson (1977) found trends of increasing abundance of *P. decipiens* and reduction in *P. cystophorae* abundance in common seals from spring to autumn and connected it to a consequent reduction of

Table 3. Correlation (r_s) of number of Anisakid nematodes, in male and female common seals, from Icelandic waters, with age of seals (N = number of seals).

Number of worms	Male seals (N = 39)	Female seals (N = 48)
Pseudoterranova decipiens	0.59***	0.13NS
*Contracaecum osculatum*1)	0.44**	–0.20NS
*Phocascaris cystophorae*1)	0.12NS	0.16NS

1) fourth stage larvae and adult worms
*** p < 0.001; ** 0.01 > p > 0.001; NS not significant

Table 4. Results of correlation analysis with Spearman's rank correlation coefficient, of sex ratio (M:F) of adult anisakids and intensity and percentage of mature anisakids and intensity in the digestive tract of common seals from Icelandic waters (N = number of infected seals).

		Intensity			
Nematode species	Sex ratio (M:F) of adult worms Percentage mature worms	*P. decipiens* larvae and adult	*C. osculatum* fourth stage and adult	*P. cystophorae* fourth stage and adult	All worm species larvae and adult
P. decipiens	M:F (N = 71)	0.39**	0.4NS	–0.09NS	0.20NS
	%-mature (N = 91)	–0.19NS	–0.18NS	0.03NS	–0.21*
C. osculatum	M:F (N = 32)	0.01NS	0.02NS	–0.38*	–0.13NS
	%-mature(N = 54)	0.11NS	0.02NS	–0.03NS	–0.01NS
P. cystophorae	M:F (N = 59)	–0.15NS	–0.12NS	0.45***	–0.09NS
	%-mature (N = 74)	0.00NS	0.17NS	–0.36**	–0.20NS

*** p < 0.001; ** 0.01 > p > 0.001; * 0.05 > p > 0.01; NS not significant capelin in the diet. Observation on nematode infection in Canadian common seals indicates higher abundance of *P. decipiens* in the winter months (Brattey & Stobo 1990). Brattey & Stenson (1993) observed highest abundance of *C. osculatum* in common seals off Newfoundland and Labrador in April to June but the abundance of *Phocascaris* spp. and *P. decipiens* reached their peak in July to September. Weber (1988) and Lick (1989) observed a decline in nematode abundance in common seals from the German and Danish Wadden Seas in July and Lick (1989) found also a higher abundance of *C. osculatum* in the summer months.

A higher abundance of *P. decipiens* in male, than female common seal, was observed. Males being, on average, larger than the females (Hauksson 1992b) could explain this. Increased size, with age, could also account for the positive correlation between number of *P. decipiens* and *C. osculatum*, with age of seals. However, this was only found in males but not in females. Lick (1989) observed an increase in mean intensity of nematodes with the hosts' age in common seals from the German and Danish Wadden Seas. Weber (1988) found a decline in relative intensity of *A. simplex* but increase in relative intensity of *P. decipiens* and *C. osculatum* with age of the host. And in his study, Lunneryd (1991) found significant positive correlation of number of *P. decipiens* and negative correlation of number of *A. simplex* with age of common seals.

Sex ratios of the nematodes, in the digestive tract, differed from equality only in *P. cystophorae*, with an excess of females. Only worms with developed sex organs were sexed, which may result in 1:1 sex ratio of *P. decipiens* and *C. osculatum* in the present study, as in McClelland's (1980) Stobo's et al. (1990) and Lunneryd's (1991) studies. Brattey & Stenson (1993), on the other hand, sexed all L_4 worms and observed biased sex ratio towards females in common and other seal species. Sex ratios of Anisakid worms seem to be influenced by worms' intensities in the digestive tract. In *P. decipiens* and *P. cystophorae* the mean sex ratio was 49.8 % and 38.1 % males, respectively, but the sex ratio increased with increasing intensity of their own worm species. The negative correlation between male:female ratio of *C. osculatum* intensity of *P. cystophorae* worms is interesting. The proportion of *C. osculatum* females gets higher, with increasing intensity of *P. cystophorae* (Table 4). This is, however, unexpected, as the two species prefer different sites in the digestive tract of the host.

Percentage of mature *P. cystophorae* worms was lower when intensity of that worm in the seals was high. Percentage of mature *P. decipiens* worms was lower, when intensity of all species and development stages in the digestive tract was high (Table 4). This may be related to higher proportions of young larvae in periods of increased feeding or change in the diet, and vice versa, however no significant seasonal change in nematode infections were observed. This could also be caused by reduced development at high levels of worm intensities, as has been seen in other host-parasite systems (Roepstorff & al. 1996).

Nematode species seem not to be strongly associated; negatively or positively. The positive correlation observed between the abundance of *P. decipiens* and *C. osculatum*, could be explained with aggregation of larvae of these two species in intermediate hosts. Both nematode species are, for example, common in cod (Hauksson 1992c). They may also occur in different hosts, both of which are frequently consumed by the seals, e.g. cods and sand eels.

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