Review of the ecology of sealworm, *Pseudoterranova* sp (p) (Nematoda: Ascaridoidea) in Icelandic waters.

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ABSTRACT

The early life cycle of sealworm in Icelandic waters is not known. Various fish serve as transport hosts but benthic coastal fish, especially bull rout (*Myoxocephalus scorpius*), probably have a major role in transmission of larvae to the final hosts, seals. Grey seals (*Halichoerus grypus*) are more heavily infected with sealworm than common seals (*Phoca vitulina*) and the grey seal population, estimated at 6,000, probably plays a larger role in the dynamics of the worm than the estimated 15,000 common seals. Other seals seem to play a small or insignificant role in sealworm dynamics in the area. Sealworm abundances in fish and final hosts are higher off the west coast than in other areas in Iceland. A combination of shallow, temperate waters, large numbers of small islands inhabited by numerous seals and grey seals' consumption of heavily infected bull rout during the breeding season in autumn are important factors responsible for maintaining an abundance of sealworm in this area. Future research on sealworm in Iceland should focus on long term monitoring of worm abundance in all potential hosts in order to observe, interpret and predict possible changes, the dynamics of infections in fish frequently consumed by seals and on seasonal and spatial variations in worm fecundity.

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INTRODUCTION

Sealworm (*Pseudoterranova decipiens*) is abundant in commercial fish species in Icelandic waters and the fishing industry spends considerable time and effort searching for and removing larvae from the fillets. The life cycle of sealworm includes crustaceans and fish as intermediate and paratenic hosts respectively and seals as final hosts. Sealworm abundance seems higher in Icelandic Atlantic cod (*Gadus morhua*) than in cod from adjacent waters, and occasional migrations of "larvae-free" cod from Greenland into Icelandic waters have been welcomed by the fishing industry (Platt 1976). The abundance of sealworm is similar to that on the Scotian Shelf off Eastern Canada (McClelland *et al.* 1990) where grey seal populations are large (Templeman 1990). On the other hand, worm abundance is considerably higher in Iceland than in the British Isles (Wootten and Waddell 1977) where the grey seal population was estimated at about 97,000 animals in 1994 (Hiby *et al*. 1996). The two main seal species in Iceland, grey (*Halichoerus grypus*) and common (*Phoca vitulina*) seals, are estimated at present to number about 6,000 and 15,000 seals respectively (Hauksson 1999). It is therefore evident that seal abundance alone cannot account for the relatively high worm burden in Iceland and that other ecological and environmental factors must be taken into consideration.

Studies on sealworm in Icelandic waters date back to the late 1930's. Most of these studies have focused on infections in commercial fish, cod in particular. Emphasis on investigating other hosts and interpreting regional and temporal differences from an ecological perspective has increased in recent years. The bulk of these studies have been published in various reports and articles (Kahl 1939, Cutting and Burgess 1960, Platt 1976, Pálsson MS 1977, Pálsson MS 1979, Hauksson 1984, 1992a, 1992b, Hauksson and Ólafsdóttir 1995, Hauksson MS 1996, Ólafsdóttir and Hauksson 1997, 1998, Eydal *et al.* 1999). The aim of this review is to compile and synthesise this information to give a picture of the present status of knowledge on sealworm in Icelandic waters and to propose future research.

Genetic studies on sealworms from the north Atlantic have shown that sealworms in Icelandic common and grey seals consist of two morphologically similar but reproductively isolated species, *P. decipiens krabbei* and *P. decipiens* (sensu stricto) (Paggi *et al.* 2000). This has, however, not been taken into consideration in other studies on sealworm in Icelandic waters.

The first studies on sealworm in Icelandic waters were conducted on cod and redfish (*Sebastes marinus*) (Kahl 1939). Cutting and Burgess (1960) reported some results from investigations of cod in the north Atlantic including Icelandic waters. Platt (1975) compared sealworm infections in various cod populations in the north Atlantic and recommended the use of sealworm abundances to estimate the extent of mixing of stocks between Greenland and Iceland (Platt 1976). Studies of ascaridoid infections in young cod (Pálsson MS 1979, Eydal *et al.* 1999) and in commercial sizes of cod (Pálsson MS 1975, Hauksson 1984, 1992a, 1996) have been conducted repeatedly. A recent investigation on long rough dab (*Hippoglossoides platessoides*) has added information on regional variation in sealworm abundance in Icelandic waters (present paper). Knowledge of infections in other fishes is still limited, however some effort has been made to collect data from the most frequent prey species consumed by seals from coastal waters (Hauksson, Erlingur, The Icelandic Fisheries Laboratories, Skúlagata 4, 101-Reykjaík, Iceland, pers. comm., Hauksson 1992b). A preliminary study on worm infection in Icelandic seals was performed in 1975 (Pálsson MS 1977), followed by surveys in 1979-1982 on common seals (Ólafsdóttir and Hauksson 1998) and on grey seals in 1979-1982 and 1989-1993 (Ólafsdóttir and Hauksson 1997). There have also been preliminary surveys of hooded (*Cystophora cristata*), harp (*Phoca groenlandica*), ringed (*P. hispida*) and bearded seals (*Erignathus barbatus*) (Hauksson MS 1996).

ENVIRONMENTAL CONDITIONS

Temperature and salinity

Iceland is situated at the boundary between warm and cold waters in the north Atlantic and sea temperature in Icelandic waters varies greatly. The south and west coasts are bathed by relatively warm and saline Atlantic water carried by a branch of the Gulf Stream. Northern currents of cold and low salinity water, on the other hand, influence the water conditions north and east off Iceland (Stefánsson and Jakobsson 1989). For example, the bottom temperatures in the coldest and warmest months in 1998 were 5°C and 9°C off the south coast but 2°C and 4°C in the same months off the Northeast coast (Fig 1) (Anonymous 1999).

Coast types

The Icelandic coast is variable with large glacial river estuaries characterising the south coast. The coastal shelf there, however, is narrow with strong currents along the coast carrying the sediment away. Bays on the west coast are shallow with numerous small islands and large sublittoral zones occupied by *Laminaria* beds and rich fauna while deep fjords with narrow coasts and sublittoral zones dominate the northwest and east coasts of Iceland. Relatively shallow bays and fjords are found on the north and

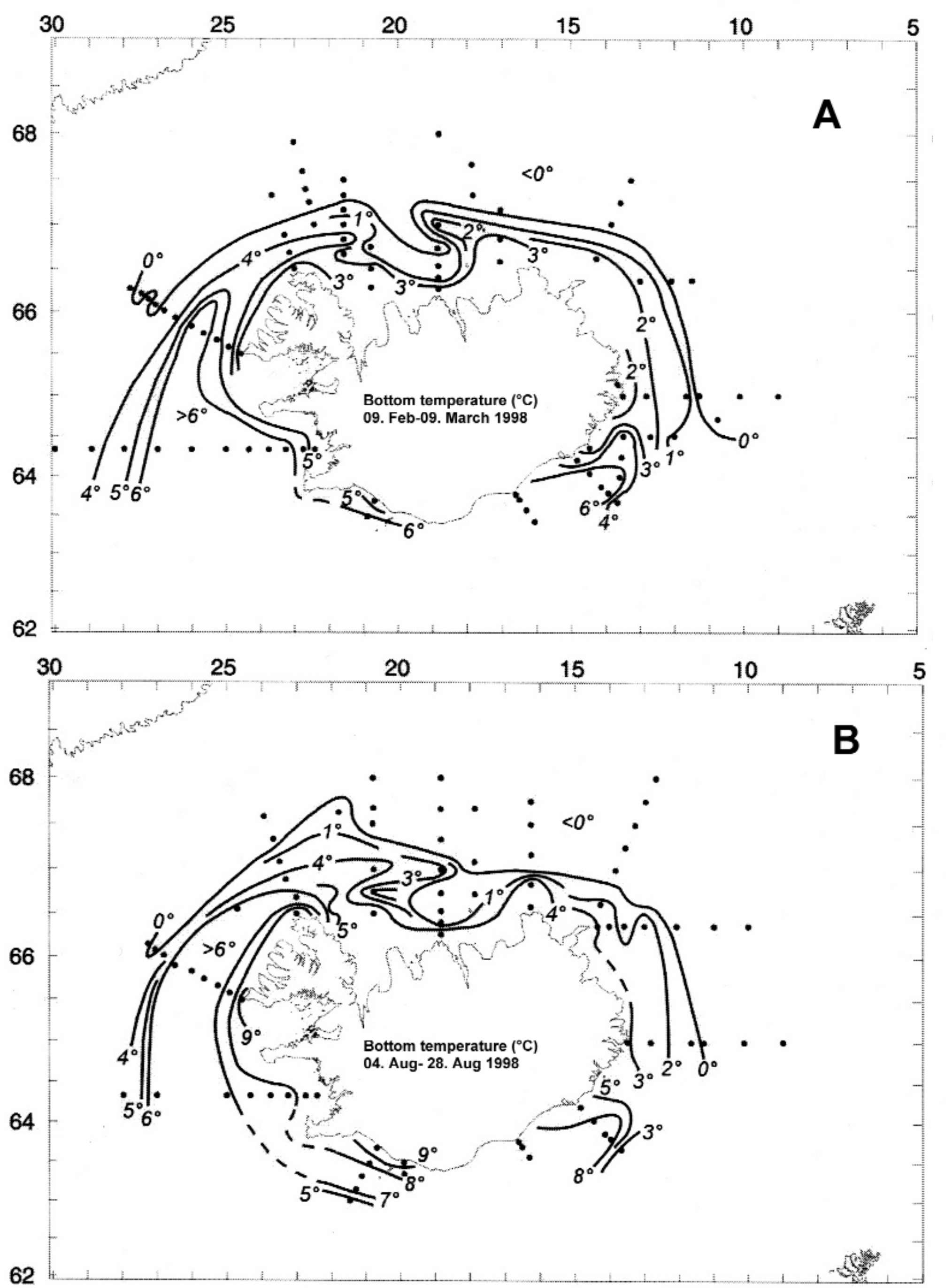

Fig. 1
Near bottom temperature (°C) in Icelandic waters. A) in February/March 1998, B) in August 1998 (Anonymous 1999).

northeast parts of Iceland but areas with steep cliffs are also found there.

HOSTS

Invertebrate hosts

In a survey of crustaceans collected near seal haul outs on the west coast in 1992, no ascaridoids were found in 170 mysids (*Macromysis flexuosa*), 50 amphipods (*Calliopius laevsculum, Gammarus finmarchicus, G, oceanicus, G. obtusatus*), 40 idoteas (*Idotea baltica, I. emarginata, I. granulosa*), 30 common spider crabs (*Hyas araneus*) 10 common hermit crabs (*Eupagurus bernhardus*) and 6 common shore crabs (*Carcinus maenas*) (Hauksson and Ólafsdóttir, unpublished data).

Fish hosts

Cod

An investigation of cod of 0 to III year age classes off northwest Iceland in 1977 showed that juvenile cod may become infected with sealworm in the early months of their lives (Pálsson MS 1979). Cod larvae hatch in April to May in Iceland (Marteinsdóttir *et al.* 2000) but one worm was found in the abdominal cavity in 2 of 208 juvenile cod in August (Table 1). Sealworm prevalence (percentage of hosts infected) and abundance (mean number of parasites per host, including uninfected hosts) increased with host age in year classes I, II and III. Larvae lengths did not differ with host age but larvae in the peritoneal cavity were smaller than those in the musculature. The highest prevalence and abundance were found in an area where common seals were most numerous. Few grey seals, however, occurred in the areas surveyed. In contrast to Pálsson's (MS 1979) results, a parasite study on cod larvae in May, August and October in 1998 showed no sealworm infections (Eydal *et al.* 1999).

Comparisons of cod from Icelandic waters and those from Greenland (Platt, 1975, 1976), northern Norway (Kahl 1939, Platt 1976), the Norwegian coast, North Sea and the Baltic (Kahl 1939) have shown that sealworm was most abundant in Icelandic fish. Platt (1976), on the other hand, observed that abundances of sealworm in cod from the Faroe Plateau and in those from north and east Iceland were similar. Worm abundance in cod varies within Icelandic waters being highest off the west coast (Pálsson MS 1975, Platt 1975, Hauksson 1984, 1992a). Platt (1975) found the lowest abundance off southwest Iceland and assumed it to be attributable to the presence of lightly infected migrant cod from Greenland. Mixing of migrant Greenland and local stocks may also account for the lower abundance sometimes observed in the largest fish from this coast (Table 1) (Kahl 1939, Hauksson 1992a).

Sealworm abundances reported in cod since the 1930s have varied but this is not conclusive evidence of changes in infection parameters. Kahl (1939) and Cutting and Burgess (1960), for example, observed much lower abundance than subsequent observers, but it is not clear how thoroughly they inspected the fish. In more recent studies on sealworm in cod, fillets have been inspected by slicing the flesh on a candling table (Pálsson MS 1975, Platt 1975, Hauksson 1984, 1992a). Platt (1975) and Pálsson (MS 1975) report somewhat lower abundances than Hauksson (1984, 1992a) (Table 1) but methods of grouping the data geographically and by length differ in these studies. Hauksson has detected a declining trend in sealworm abundance in cod from 1980 to 1999 (Hauksson pers. comm.) but the trend lacks significance despite the reduction in the seal populations by 50% over the same period (Hauksson and Bogason 1997a, Hauksson 1999). Possibly the minimum threshold size of the seal population needed to sustain the present worm abundance in cod has not yet been reached. Alternatively, declines in infection parameters may not be detected in long lived, migrant species such as cod over the short term.

Long rough dab

Sealworm infections in long rough dab were investigated in fish from five locations around Iceland in 1989-1991 (Table 2). The flesh was examined by slicing on a candling table and organs and digestive tracts were inspected under a stereoscope. Sealworm abundance was lowest in fish from northeastern Iceland (Fig 2). Long rough dab is considered a sedentary species and sealworm larvae in the fish are therefore likely to have been acquired in the sampling area.

Bull routs

Bull routs (*Myoxocephalus scorpius*) in Iceland are often heavily infected with sealworm (Fig 3, Table 3) (Hauksson, pers. comm., Hauksson 1992b, Hauksson and Ólafsdótttir 1995). Fish from the west coast carry much greater numbers of worms than fish from the east coast. Worm abundance declined in bull routs from an enclosed area at Hvalseyjar off the west coast between surveys in 1992 and 1996 (Table 3). The decline was coincident with local reductions in seal populations. Between 1992 and 1996 numbers of common seals fell from 1200 to 600, and grey seals, from 140 to 10 (Hauksson, pers. comm.).

Other fishes

Kahl (1939) studied sealworm infections in red-

Table 1 Historical information of prevalence and abundance of sealworm (*Pseudoterranova decipiens*) in cod (*Gadus morhua*) fillets in Icelandic waters.

Area[1]	Year	Fish length (cm)	N	Prevalence (%)	Abundance	S.E.	Range	Reference
Iceland	<1939[2]	<60	172	2.3				Kahl 1939
		60-80	150	31.3				
		>80	2357	8.5				
Off shore NW	1973[2]		21	61.9	2.2			Pálsson MS 1975
Vestfirdir/								
Breidafj (W)			40	95.0	11.3			
Faxafloi (W)			53	67.9	3.4			
Southwest			28	53.6	9.6			
South coast			26	80.8	7.7			
East coast			25	76.0	3.0			
Eyjafj. (N)			8	37.5	1.0			
NW Iceland	1971-73[2]	65.4	831	56	2.4		0-110	Platt 1995
W Iceland		66.0	297	72	8.4		0-340	
N Iceland		59.2	188	55	1.4		0-13	
NE Iceland		65.2	175	50	1.3		0-12	
E Iceland		60.9	465	50	1.2		0-44	
SW Iceland		76.5	155	29	0.8		0-11	
SE Iceland		66.6	482	59	1.9		0-32	
Breidafj. (W)	1982	19-56	31	51.6	1.7		0-9	Hauksson 1992b
Hvalseyjar (N)	1992[2]	40-59	68	70.6	3.0		0-4	Hauksson unpubl.
data								
Lodmundarfj. (E)	1994	12-42	16	25.0	1.4		0-8	Hauksson MS
1996								
Area 1	1977	3.7-8.1 (0)[3]						Pálsson MS 1979
(NW)		12-29 (I)						
		23-38 (II)	39	62	1.0		0-6	
		29-48 (III)	40	63	1.6		0-10	
Area 2		3.7-8.1 (0)	208	1	2.1		0-1	
(NW)		12-29 (I)	129	53	68.4		0-9	
		23-38 (II)	24	88	21.1		0-16	
		29-48 (III)	21	95	19.9		0-19	
Area 3		3.7-8.1 (0)						
(NW)		12-29 (I)	112	13	14.6		0-5	
		23-38 (II)	29	66	19.1		0-20	
		29-48 (III)	3	67	2.0		0-5	
Faxaflói (W)	1985-88[2]	30-39	40	40	0.7	0.20	0-5	Hauksson 1992a
		40-49	128	38	0.7	0.10	0-6	
		50-59	39	62	2.8	0.95	0-35	
		60-69	4	100	49.2	37.36	1-159	
		70-79	30	80	11.4	3.35	0-76	
		80-89	13	69	3.5	1.91	0-26	
Breidafj. (W)	1985-88[2]	30-39	4	25	0.2	0.25	0-1	Hauksson 1992a
		40-49	53	57	1.7	0.48	0-23	
		50-59	52	73	3.4	0.76	0-37	
		60-69	29	83	12.0	4.68	0-101	
		70-79	7	100	12.6	6.98	1-54	
		80-89	9	100	21.7	14.97	1-141	
		>90	4	100	29.5	10.93	1-54	
Vestfirdir	1985-88[2]	20-29	27	37	0.7	0.22	0-4	Hauksson 1992a
(NW)		30-39	13	46	0.6	0.21	0-2	
		40-49	15	80	3.8	0.97	0-10	

Table 1 (cont.)								
Area[1)]	Year	Fish length (cm)	N	Preva-lence (%)	Abun-dance	S.E.	Range	Reference
		50-59	25	88	4.6	0.98	0-22	
		60-69	19	89	7.4	1.64	0-22	
		70-79	21	95	15.7	5.98	0-124	
NW-Iceland	1985-88[2]	40-49	17	65	2.8	0.93	0-13	Hauksson 1992a
		50-59	23	91	3.6	0.88	0-17	
		60-69	18	94	17.9	3.79	0-68	
		70-79	20	100	30.4	8.73	1-163	
		80-89	20	100	10.9	3.05	1-56	
		>90	20	100	24.5	5.81	5-117	
NE-Iceland	1985-88[2]	40-49	23	74	3.1	0.70	0-11	Hauksson 1992a
		50-59	19	68	2.9	1.04	0-20	
		60-69	23	83	5.3	1.01	0-15	
		70-79	20	80	8.3	1.96	0-29	
		80-89	26	92	11.3	2.60	0-46	
		>90	8	88	9.0	2.67	0-23	
East coast	1985-88[2]	30-39	3	67	3.0	1.53	0-5	Hauksson 1992a
		40-49	19	53	2.5	0.80	0-12	
		50-59	26	77	3.1	0.83	0-16	
		60-69	23	83	6.7	1.66	0-27	
		70-79	13	92	14.4	4.88	0-63	
		80-89	8	100	11.0	3.18	1-25	
		>90	2	100	105.5	84.50	21-190	
South coast	1985-88[2]	40-49	20	40	1.0	0.59	0-12	Hauksson 1992a
		50-59	25	48	1.6	0.45	0-9	
		60-69	18	56	1.7	0.52	0-7	
		70-79	21	43	0.9	0.34	0-6	
		80-89	20	70	5.0	2.14	0-35	
		>90	19	95	19.6	6.19	0-91	

[1] See Figure 2
[2] Fillets
[3] Age class in brackets

fish (*Sebastes marinus*) from Iceland (Table 4), the Barents Sea, the Norwegian coast and the North Sea and observed the highest abundance in the Icelandic redfish. An attempt has been made in recent years to collect information on sealworm infections in near shore fishes, which are common seal prey in Icelandic waters (Hauksson 1992b, Hauksson and Ólafsdóttir 1995). In general, abundances tend to be lower in fish from the east than the west coast (Table 4).

Final hosts

Grey seals

Population biology

The grey seal population in Icelandic waters was estimated at approximately 6,000 animals in 1998 and has been declining gradually from about 14,000 seals in 1986 (Hauksson 1999, Hauksson and Bogason 1997a). Grey seals are mainly distributed off the west and northwest coasts, but a small haul out site is also located on the southeast coast. Grey seals also breed on the sandy south coast in the autumn, but are not observed there in other seasons (Fig 2).

Diet

Off the south coast, grey seals feed mostly on sand-eels (*Ammodytes* spp.) (15 to 35 cm) throughout the year but in other areas cod (30 to 50 cm), lumpsucker (*Cyclopterus lumpus*) and wolffish (*Anarhichas lupus*) (20 to 60 cm) are most prominent in the diet in January through September (Hauksson and Bogason 1997b). Food consumption is reduced and prey living

Table 2. Prevalence and abundance of sealworm (*Pseudoterranova decipiens*) in long rough dab (*Hippoglossoides platessoides*) of different length classes at various locations in shallow waters around Iceland in 1980-91 .

Area[1]	Fish length (cm)	N	Prevalence (%)	Abundance	S.E.	Range
Langanes (NE)	10-19	4	50	1.0	0.667	0-2
	20-29	57	59.6	1.3	0.188	0-5
	30-42	58	68.9	1.9	0.243	0-8
Hornafjordur (SE)	20-29	42	88.1	2.5	0.287	0-8
	30-42	56	91.1	5.2	1.318	0-72
Selvogsgrunn (S)	10-19	5	40	2.0	1.414	0-6
	20-29	51	82.3	4.6	0.816	0-38
	30-42	42	61.9	2.4	0.455	0-13
Látrabjarg (W)	20-29	40	35	0.7	0.226	0-6
	30-42	61	54.1	5.0	1.541	0-53
Húnaflói (N)	10-19	46	50	0.9	0.157	0-4
	20-29	75	70	2.0	0.282	0-13
	30-42	20	90	5.3	0.884	0-17

[1] See Figure 2

closer to shore is consumed during the breeding period from October to December. The most striking seasonal change in the diet is the increased consumption of bull routs (15 to 35cm) and common spider crabs (*Hyas araneus*) during the breeding period off the west and northwest coasts (Hauksson and Bogason 1997b).

Sealworm infections

A preliminary study on nematode infections in seals in Iceland in 1975 showed 100% prevalence in 6 adult grey seals (Pálsson MS 1977). Two follow-up surveys were conducted on 69 grey seals in 1979-1982 (Ólafsdóttir 1993) and on 196 grey seals in 1989-1993 (Ólafsdóttir and

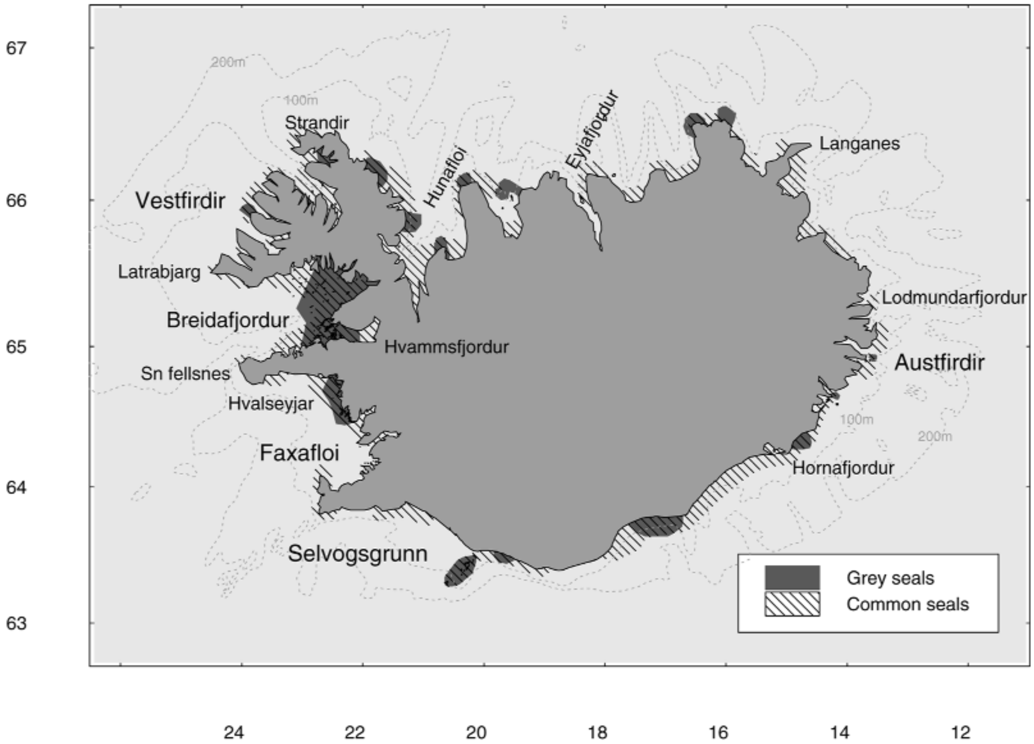

Fig. 2 *Distribution of common seals and grey seals in October in Icelandic waters (from Hauksson and Bogason 1997a).*

__Fig. 3.__
The trouble with sealworms... Heavily infected bull rout from Hvalseyjar, west Iceland. Photo: D. Ólafsdóttir

Hauksson 1997). Seasonal and regional variations in sealworm abundance observed in the latter surveys, were similar and discussion below will refer to the 1989-1993 survey. Sealworms were found in grey seals from all seasons and study areas and young seals seemed to become infected once they begin to feed independently (Table 5). The lowest abundance was found in seals from the south coast from January to August. The largest regional difference was, however, observed during the breeding season in autumn. On the south coast, the abundance increased from summer to September but declined rapidly, as expected, after the breeding began in October (Table 5). On the west coast, on the other hand, the sealworm abundance increased greatly during the breeding season in autumn and no decline was observed when the sampling halted in late October.

Proportions of developmental stages varied with worm abundance (Table 5) (Ólafsdóttir and Hauksson 1997). In thewest coast seals, the proportion of adult worms declined with increased worm abundance in autumn. The high proportion of adult worms in seals from the south coast in September, on the other hand, is indicative of a decline in the rate of reinfection, as can be seen one month later when a pronounced fall in worm abundance was observed. Sealworm abundance in female and male grey seals did not differ significantly, but there was a significant correlation between sealworm abundance and host weight.

Common seals

Population biology

Common seals are distributed in all regions around Iceland but are more frequent off the west and south coasts than in the north- and east regions (Fig 2). The population size was estimated at about 15,000 animals in 1998. It has remained stable since 1989 but declined from about 34,000 animals in the eighties (Hauksson 1999, Hauksson and Bogason 1997a). Common seals in Iceland breed in June and July and moult in August.

Diet

Cod (10 to 40 cm) is the most frequent food for common seals year round and in all areas except off the south coast. Capelin (*Mallotus villosus*) (10 to 20 cm) and sand eels (10 to 20 cm) are the main food species off the south coast and occur also in the diet in other areas. Redfish (10 to 30 cm), saithe (*Pollachius virens*) (10 to

Table 3. Prevalence and abundance of sealworm (*Pseudoterranova decipiens*) in bull rout (*Myoxocephalus scorpius*) at various locations in shallow waters around Iceland in 1982-96 (Hauksson unpubl. data).

Area[1]	Year	Fish length (cm)	N	Preva -lence (%)	Abun-dance	S.E.	Range	Reference
Hvalseyjar (W)	1992	15-19	15	100	27.9	5.674	9-83	Hauksson 1992b,
		20-24.5	23	100	59.6	9.159	13-188	Hauksson
		25-29.5	32	100	142.8	20.119	19-448	unpubl. data
		30+	1	-	401.0	-	-	
Hvalseyjar (W)	1996	15-19	1	100	4	-	-	Hauksson
		20-24.5	13	100	34.1	12.999	6-170	unpubl. data
		25-29.5	64	100	60.9	7.950	2-411	
		30+	26	100	103.2	13.474	7-333	
Hvammsfj. (W)	1995	18-26	3	66.7	5.7		0-15	Hauksson unpubl. data
Snæfellsnes, Vestfirdir, Strandir (W)	1982	17-31	60	91.7	30.5		0-193	Hauksson 1992b
Mjóifjordur (NW)	1995	20-24.5	8	87.5	8.8	4.108	0-33	Hauksson
		25-29.5	6	100	36.2	6.672	23-55	unpubl. data
Lodmundar-fjordur (E)	1994	20-24.5	2	100	3.0	2.830	1-5	Hauksson
		25-29.5	15	93.3	3.9	1.053	0-13	unpubl. data
		30+	3	100	7.3	3.189	3-12	

[1] See Figure 2

40 cm), catfish (*Anarhichas lupus*) (10 to 50 cm) and various flatfish species (10 to 30 cm) are all common food items. Seasonal variations in food consumption are not as prominent in common seals as in grey seals. Capelin and herring are exploited during autumn and winter but consumption of sand eels is greater in the summer. The importance of cod in the diet as proportion of weight, on the other hand, seems not to change between seasons (Hauksson and Bogason 1997b).

Sealworm infections

Preliminary studies on nematode infections in 36 Icelandic common seals were performed in 1975 (Pálsson MS 1977) and followed by more thorough investigation in 95 common seals from all areas and seasons around Iceland in 1979-82 (Table 6) (Ólafsdóttir and Hauksson 1998). Sealworm abundance was highest in seals from the west coast. Seasonal variation was not great in the west coast seals: the high worm abundance observed from September to May was attributable to a few heavily infected individuals. When median values were compared the difference was much smaller. The fact that seasonal variations in proportions of developmental stages were not apparent is evidence that the rate of re-infection varied little between seasons. The negative correlation of the proportion of mature sealworm with the total number of worms in the stomach may be indicative of slower development and delayed maturation of the parasite in heavily infected seals. Worm abundance was significantly higher in male than female common seals and increased significantly with age in the former.

Other seals

Hooded, harp, ringed and bearded seals migrate into Icelandic waters from the breeding grounds in the arctic pack ice. They are mainly found off the north coast (Hauksson and Bogason 1997c) and abundances vary from year to year. Years with large numbers of harp and hooded seals were reported in the past (Gudmundsson 1944) but large migrations of these seals into Icelandic waters have been rare in recent decades (Hauksson 1993). Small numbers of hooded seals reach the northeast coast in spring after

Table 4. Historical information on prevalence and abundance of sealworm (*Pseudoterranova decipiens*) in various fish species from Icelandic waters.

Fish species	Area[1]	Year	Fish Length (cm)	N	Prevalence (%)	Abundance	Range	Reference
Redfish Sebastes marinus	Iceland	1939	<36	1480	8.7			Kahl 1939
			>36	551	10.2			
Wolffish (Aniarichas lupus)	Vestfirdir (NW)	1997	44-77	118	46	1.4	0-15	Hauksson unpubl. data
Tusk (Brosme brosme)	Grindavik (SW)	1997	34-49	24	16.7	0.2	0-1	Hauksson unpubl. data
			50-59	19	57.9	0.9	0-4	
			60-69	4	75.0	2.3	0-4	
			70-79	2	50.0	4.5	0-9	
	Horna-fjodur (SE)	1997	34-49	12	83.3	13.2	0-61	Hauksson unpubl. data
			50-59	22	90.9	10.2	0-50	
			60-69	12	100	12.2	1-78	
			70-79	3	100	6.0	3-9	
Saithe (Pollachius virens)	Breida-fjordur (W)	1982	26-39	36	0.0	0.0		Hauksson 1992b
	N-Faxafloi (W)	1992	17-42	73	42.5	2.1	0-22	Hauksson and Ólafsdóttir '95
	Lodmun darfj. (E)	1994	21-29	2	0.0	0.0		Hauksson MS 1996
Whiting (Merlangius merlangus)	Hornaf jordur (SE)	1989	32-54	17	52.9	1.2	0-6	Hauksson 1992b
Dab (Limanda limanda)	Breida-fjordur (W)	1982	13-29	16	0	0.0		Hauksson 1992b
Halibut (Hippoglossus hippoglossus)	Breida-fjordur (W)	1982	19-50	4	25.0	0.2	0-1	Hauksson 1992b
Plaice (Pleuronectes platessa)	Breida fjordur (W)	1982	14-34	7	0.0	0.0		Hauksson 1992b
	N-Faxafloi (W)	1992	14-32	18	11.1	0.1	0-1	Hauksson and Ólafsdóttir '95
Witch (Glyptocephalus cynoglossus)	Selvogs-grunn (S)	1990	25-49	56	17.9	0.2	0-2	Hauksson '92b
Lumpsucker (Cyclopterus lumpus)	N-Faxafloi (W)	1992	19-23	8	37.5	0.5	0-2	Hauksson and Ólafsdóttir '95
Sand-eel (Ammodytes sp.)	Breida-fjordur (W)	1990	8-18	137	0.0	0.0		Hauksson 1992b
Herring (Clupea harengus)	Breida-fjordur(W)	1982	21-35	10	0.0	0.0		Hauksson 1992b

[1] See Figure 2

Table 5. Characteristics of sealworm (*Pseudoterranova decipiens*) infections in stomachs of grey seals (*Halichoerus grypus*) in Icelandic waters in 1989-93.[1] (Ólafsdóttir and Hauksson 1997).

		3 months-4 year old seals		5 year and older seals		
		January-August	September-November	March-August	September	October-November
Region[2]	**Variable**[3]			**(Feeding time)**		**(Breeding time)**
West coast	Number of seals	43	2	44	0	40
	Prevalence	100	100	100	-	100
	Abundance	488.3	807.5	546.8	-	3368.2
	S.E.	76.786	419.314	102.651	-	733.334
	median	408.0	807.5	372.0	-	1483.0
	maximum infection	2256	1104	3184	-	21471
	% larvae and preadult	63.5	85.3	55.4	-	83.7
	% adult males	20.5	9.2	24.1	-	10.1
	% adult females	16.0	5.6	20.5	-	6.2
North and East coasts	Number of seals	7	0	10	0	0
	Prevalence	100	-	100	-	-
	Abundance	112.3	-	841.4	-	-
	S.E.	41.746	-	335.128	-	-
	median	80.0	-	234.0	-	-
	maximum infection	292	-	2776	-	-
	% larvae and preadult	77.0	-	68.3	-	-
	% adult males	14.2	-	16.8	-	-
	% adult females	8.8	-	14.9	-	-
South coast	Number of seals	1	1	8	24	16
	Prevalence	-	-	100	100	100
	Abundance	6.0	472.0	413.2	743.8	220.3
	S.E.	-	-	194.788	210.4584	83.465
	median	-	-	242.0	594.0	90.5
	maximum infection	6	472	1648	4320	1128
	% larvae and preadult	66.7	24.6	62.3	29.87	50.55
	% adult males	0.0	36.4	22.4	36.95	31.06
	% adult females	33.3	39.0	15.4	33.17	18.38

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

[2] See Figure 2

[3] Prevalence = % of infected seals; Abundance = mean number of nematodes per seal including uninfected seals; SE = standard error; preadult = fourth and fifth stage worms with undeveloped sex organs; adult males and females = fifth stage worms with spicules and developed eggs, respectively

breeding and again in autumn after moulting on the pack ice north of Iceland (Sæmundsson 1939).

Studies of sealworm in ringed, harp and hooded seals are at a preliminary stage. Examinations of 9 ringed seals yielded only 2 individuals infected with one sealworm larva each (Pálsson MS 1977). Sealworm were also found in 3 of 16 harp and 2 of 7 hooded seals examined (Hauksson MS 1996).

DISCUSSION

It is not known which invertebrates serve as intermediate hosts for sealworm in Icelandic waters. The fact that juvenile cod may become infected in August before or about the time they metamorphose and seek bottom indicates that small crustacea may serve as hosts (Thorisson 1989). Canadian investigations have shown that mysids may be important invertebrate hosts (Martell and McClelland 1995, Jackson *et al.* 1997).

Table 6. Characteristics of sealworm (*Pseudoterranova decipiens*) infections in stomachs of common seals (*Phoca vitulina*) older than four months in Icelandic waters in 1979-82.[1] (Ólafsdóttir and Hauksson 1998).

Region[2]	Variable[3]	June-August (Breeding time)	September-May (Feeding time)
West coast	Number of seals	22	42
	Prevalence	100	97.6
	Abundance	196.6	699.8
	S.E.	47.061	488.608
	median	92.0	52.0
	maximum infection	747	20340
	% larvae and preadult	68.3	89.4
	% adult males	16.9	5.0
	% adult females	14.8	5.5
North and East coasts	Number of seals	6	14
	Prevalence	83.3	92.9
	Abundance	48.8	162.6
	S.E.	29.695	74.768
	median	29.5	34.5
	maximum infection	178	818
	% larvae and preadult	90.4	82.2
	% adult males	4.8	10.4
	% adult females	4.8	7.5
South coast	Number of seals	7	6
	Prevalence	85.7	100
	Abundance	36.1	18.5
	S.E.	21.376	5.940
	median	9.0	19.5
	maximum infection	126	34
	% larvae and preadult	64.8	73.0
	% adult males	23.3	18.9
	% adult females	11.9	8.1

[1] See Table 5.
[2] See Figure 2.
[3] See Table 5.

Large piscivorous fish are often heavily infected with sealworm, but fish of this size are seldom consumed by seals and are not likely to play an essential role in the life cycle of the worm. Small benthic fish from shallow waters may also become highly infected with sealworm (NAMMCO 1998). These fish are usually of little importance to the fishing industry, but their importance in transmission of the larvae may be underestimated. In Iceland, bull routs seem to play an important role in transmission of sealworm. The fish is heavily infected off the west coast and although it is not a prominent food item for grey seals on an annual basis, it becomes almost the only food item during the breeding season (Hauksson and Bogason 1997b). Jensen *et al.* (1994) and Andersen *et al.* (1995) also concluded that small long-lived benthic species were important in the life cycle of sealworm in Norway. Aspholm *et al.* (1995) felt that the role of bull rout in the Kloster area of south Norway was to transmit sealworm larvae to cod which were in turn consumed by common seals.

Grey seals seem to be far more important hosts for sealworm than common seals in the north Atlantic (Brattey and Stobo 1990). This is partly because grey seals are larger and consume greater quantities of food, but comparisons of worm survival and fecundity in common and grey seals indicate also that the latter are better hosts for the parasites than common seals (McClelland 1980). In Iceland, the consumption of heavily infected bull routs by grey seals may also contribute to disparities in sealworm abundance in sympatric grey and common seals.

The common seal population is estimated to be twice the size of the grey seal population in Iceland. The worm abundance in common seals, on the other hand, is one tenth of that observed in grey seals. Common seals are therefore likely to play a much smaller role than grey seals in the population dynamics of sealworm in Icelandic waters. Hooded, harp, ringed and bearded seals probably are of less significance yet in the transmission of the parasite in these waters. These seals migrate from cold areas north of Iceland where worm abundance in fish is low. Numbers of migrant seals may vary from year to year but these seals rarely become abundant in Icelandic waters and they do not spend sufficient time in the area to accumulate large numbers of worms. Grey and common seals also seem to be the most important final hosts in eastern Canada, although large populations of harp seal may play a significant role in the population dynamics of the worm (Brattey and Stobo 1990, Brattey and I-Hsun 1992, Brattey and Stenson 1993)

Regional differences

In all studies where regional differences have been observed, the highest worm abundance was observed in hosts from the west coast, and the lowest off the northeast coast. These differences may be related to the greater abundance of seals, especially grey seals, off the west coast. Other factors must, however, play an important role since worm abundances in fish in western Iceland are similar to those found in fish on the Scotian Shelf, off eastern Canada, another area with large seal populations, while in the British Isles, where grey seals are even more abundant, sealworm abundances in fish are low.

Coastal areas in Faxafloi and Breidafjordur at the west coast are likely to favour successful transmission of sealworm larvae. These areas are shallow, with dense beds of seaweed, inhabited by numerous invertebrates and fish. Finally, these areas host the largest Icelandic seal populations. The relatively temperate waters of the west coast possibly also favour successful transmission of the early stages in the life cycle of sealworm. It is, however, not clear how temperature may affect transmission of the early developmental stages except hatching does not occur at temperatures < 0°C (Measures 1996). While development of the egg is temperature dependent, temperatures above 0°C do not seem to affect survival of the larvae (Measures 1996). The bottom temperature at the north and east coasts of Iceland rarely falls below 0°C but at temperatures slightly above 0°C in these areas, the likelihood of eggs being eaten before hatching may increase.

Temporal differences

No studies have been conducted to detect seasonality of sealworm recruitment in Icelandic fish. Investigations of common seals did not reveal seasonal variations in worm recruitment. Pálsson (MS 1977) reported a declining trend in sealworm abundance in common seals in April when consumption of capelin was highest. These findings, however, were not confirmed in a more thorough survey of common seals in 1979-82 (Ólafsdóttir and Hauksson 1998). The dramatic increase in worm abundance during the breeding season in grey seals on the west coast seems to be attributable to increased consumption of bull routs. As a result, peak sealworm egg production may be expected on the west coast in December. The larvae hatch in about 8 weeks at 5°C (Measures 1996), the mean near-bottom temperature in November-December (Kristmannson 1991). The post-hatch survival time of larvae in 5°C seawater has been reported as 91 days (Measures 1996) and 140 days (McClelland 1982). Larvae produced during the infection peak in autumn in west coast grey seals are thus likely to be infective to invertebrates in the following spring and ultimately result in an elevation of the rate of re-infection in fish in late summer and autumn.

Further research

Future research on sealworm in Iceland should focus on long term monitoring of sealworm abundance and the population dynamics of the parasite. Long term monitoring of sealworm abundance in various hosts is essential in order to interpret possible changes in worm abundance in the future. Introduction of this kind of monitoring is especially urgent following the greatly reduced seal populations in Icelandic waters in recent years. It may give answers to vital questions regarding the relationships between sealworm population dynamics and seal abundance. It is important that such studies report worm abundance in both large commercial and small sedentary fish. Abundances in the latter may be more indicative of sealworm abundance in the sampling area.

Unfortunately, a variety of methods have been used for collecting and analyzing data in Icelandic studies of sealworm. This makes comparisons of results from these studies difficult and weakens interpretations of trends in sealworm abundance over prolonged periods. It is therefore important that procedures of future research on sealworm be standardized.

In future research in Iceland, emphasis must be placed on increasing knowledge of the population dynamics of sealworm. The identities of invertebrates which serve as intermediate hosts are still lacking. Studies on invertebrates, crustaceans in particular, in areas with high worm abundance in fish and seals, may provide information on the early part of the life cycle.

Earlier studies on sealworm in Icelandic waters have mainly focused on worm abundance in large commercial fish such as cod, and the most abundant definitive hosts, common and grey seals. The results show regional and spatial variations in sealworm infections in fish and seal hosts in Icelandic waters but give limited information on the population dynamics of the worm. Further studies where emphasis is placed on fish frequently consumed by seals, and where worm fecundity in addition to worm abundance in the final hosts are analysed, however, are needed in order to elucidate the population dynamics of sealworm. Fecundity of the worms in heavily infected grey seals from the west coast in autumn may be reduced due to density dependent effects on worm growth. Future research on population dynamics of sealworm must therefore take into consideration possible seasonal and geographical variation in worm fecundity when interpreting the influence of worm intensity in seals on worm dynamics.

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