Surveys of larval sealworm (*Pseudoterranova decipiens*) infection in various fish species sampled from Nova Scotian waters between 1988 and 1996, with an assessment of examination procedures

G. McClelland[1] and D.J. Martell[2]

[1]*Department of Fisheries and Oceans, Gulf Fisheries Centre, P.O. Box 5030, Moncton, New Brunswick, Canada E1C 9B6.*
[2]*Department of Fisheries and Oceans, St. Andrews Biological Station, St. Andrews, New Brunswick, Canada E0G 2XO.*

ABSTRACT

Between November 1988 and October 1996, >10,000 fish from the Breton Shelf, Sable Island Bank and the northeastern Gulf of Maine were examined for larval anisakines. Larval sealworm, *Pseudoterranova decipiens*, occurred in 30 of 39 species surveyed, including 8 new host records, *Enchelyopus cimbrius*, *Lycodes reticulatus*, *Eumesogrammus praecisus*, *Lumpenus lumpretaeformis*, *Lumpenus maculatus*, *Cryptacanthodes maculatus*, *Artediellus atlanticus* and *Triglops murrayi*. The parasite was most prevalent and abundant in mature demersal piscivores and benthic consumers. Sealworm densities (nr kg^{-1} host wt.), however, were greatest in small benthophagous fish including mature *E. cimbrius*, *A. atlanticus*, *T. murrayi* and *Aspidophoroides monopterygius*, and juvenile *Hippoglossoides platessoides*. ANOVA revealed that geographical disparities in sealworm prevalence and abundance were highly significant in 14 of 20 species tested, although significant disparities between samples from each of the three areas were evident only in *H. platessoides*. Almost invariably, infection parameters were greatest in fish from Sable Island Bank. ANOVA also indicated that sealworm prevalence and/or abundance increased significantly in Sable Island Bank populations of *Gadus morhua*, *H. platessoides*, and seven other species between 1985-1986 and 1989-1990. Routine examinations, in which host flesh was sliced and candled, proved as efficacious as digestion in warm (35° C) pepsin-HCl for detection of larval sealworm in the flesh of large frozen fish. Procedures employing fresh (iced) samples, digestion at ambient temperature and microscopy are recommended, however, for surveys of small benthic consumers. Many of the sealworm infecting the latter hosts are tiny (2 to 10 mm in length) nematodes, which escape detection by routine inspection, and may not survive in warm pepsin-HCl solution.

McClelland, G. and Martell, D.J. 2001. Surveys of larval sealworm (*Pseudoterranova decipiens*) infection in various fish species sampled from Nova Scotian waters between 1988 and 1996, with an assessment of examination procedures. *NAMMCO Sci. Publ.* 3: 57-76.

INTRODUCTION

As they lack direct economic significance, small benthophagous fish, which include the juveniles of commercially important demersal species as well as underutilised species, are often overlooked as potential reservoirs of *Pseudoterranova decipiens* larvae. Recent field and laboratory studies have shown, however, that they may be essential in the transmission of sealworm to larger, commercially exploited fish, if not directly to definitive (seal) hosts (McClelland 1995). In an earlier survey of Sable Island Bank on the central Scotian Shelf (McClelland *et al. 1990*), larval sealworm were found in 26 of 32 marine fish species. While it was most prevalent and abundant in large demersal piscivores, *P. decipiens* often occurred in greatest density (nr/unit host weight) in small (juvenile and mature) benthic consumers (Fig. 1).

Laboratory experiments (McClelland 1995), in which *P. decipiens* larvae were transmitted to fish via benthic copepod and amphipod intermediaries, revealed that sealworm grew to a length of 8 mm in crustacean hosts, but larvae as small as 2 mm in length were infective to small fish. One of the conclusions drawn from this study was that the primary fish hosts of sealworm are probably small benthic consumers. It was also apparent that sealworm larvae recently transmitted to these hosts would be considerably smaller than those detected by candling procedures typically employed in sealworm surveys. Hence, in order to obtain accurate worm counts when surveying infections in smaller demersal fish, more refined examination procedures involving microscopic inspection of host tissue squashes or digested host tissues might be required.

Given that fishes of diverse phylogeny are equally susceptible to sealworm infection in the laboratory, light infection or absence of infection in natural populations of certain host species is probably attributable to ecological, behavioural and physiological (e.g. host response) barriers to the transmission of the parasite (McClelland 1995). Surveys of the diets and ascaridoid infections of flatfishes inhabiting Sable Island Bank (Martell and McClelland 1994, 1995), for example, indicated that disparities in parameters of sealworm infection among sympatric flatfish species was largely related to the exploitation of different prey. Juvenile Canadian plaice (*Hippoglossoides platessoides*), which were heavily infected with sealworm, fed on benthic suprafauna, i.e. free swimming organisms (amphipods, mysids etc.) closely associated with bottom. Winter flounder (*Pleuronectes americanus*), which was rarely infected with larval sealworm, consumed more sedentary infauna and attached epifauna.

As suggested by analyses of their diets, seals may incur *P. decipiens* infections primarily through consumption of smaller fish. Larger demersal fish, while often heavily infected, are seldom exploited by grey (*Halichoerus grypus*) (Benoit and Bowen 1990a, 1990b, Bowen *et al*. 1993) or harbour seals (*Phoca vitulina*) (Bowen and Harrison 1996) seals in Atlantic Canadian waters. Nevertheless, seals may accumulate the majority of their sealworm by consumption of relatively few, large, heavily infected fish (McClelland *et al*. 1990). Moreover, in light of anecdotal reports that heads of

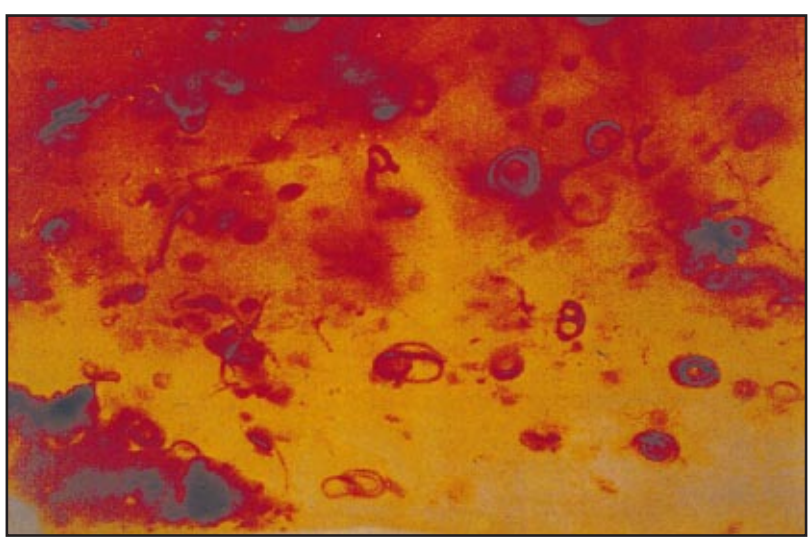

Fig. 1. *Microscopic view of larval sealworm in fish muscle tissue. The worms in the photo are about 3-5 cm in length. Photo: T. Jensen*

larger prey are often discarded by seals, it is possible that exploitation of heavily infected mature piscivores is underestimated in surveys which rely on otoliths for identifying and ageing seal prey.

The "seal prey" time series was designed to provide data for a predictive sealworm model proposed at a two-part sealworm workshop held in Halifax Nova Scotia in April 1987 and June 1988 (Bowen 1990). Rather than monitoring larval sealworm infections in a single indicator host, as is the case in the "sealworm index" time series (McClelland and Martell 2001, McClelland *et al.* 2000), the parasite was monitored in numerous fish species, at a few specified locations. As a consequence of dwindling groundfish resources and changing research priorities, the project was abandoned before completion. Some of the data collected in the Gulf of St. Lawrence have been reported (Boily and Marcogliese 1995, Marcogliese 1995), but much of it remains unpublished.

"Seal prey" surveys of fish from the Scotia-Fundy region proved useful in revealing small benthic consumers of potential importance in sealworm transmission. The results of surveys of the Breton Shelf, Sable Island Bank, and the northeastern Gulf of Maine are documented here, with analyses of spatial variations in sealworm prevalence and abundance in 1989-1990, and changes in infection parameters in fish from Sable Island Bank since 1986-1987 (McClelland *et al.* 1990). The efficiencies of procedures used for detecting sealworm larvae, namely candling, dissection and digestion, are also assessed.

MATERIALS AND METHODS

Marine fish samples were collected primarily from Department of Fisheries and Oceans (DFO) research vessels, Alfred E. Needler and Lady Hammond during cruises dedicated to surveys of larval *P. decipiens*, and other parasites of marine fish and benthic macrofauna. Samples for an inventory of larval anisakines in seal prey (the "seal prey" survey) were taken from the southeastern Breton Shelf, Sable Island Bank and the northeastern Gulf of Maine between November 1988 and August 1993, but primarily from February 1989 to October 1990 (Fig. 2). Fish were caught in sets of 30 to60 min. duration, with a Western IIA otter trawl towed at 6.5 km h^{-1}, and stored in the freezer. On return to the DFO Halifax Fisheries Research Laboratory, samples were allowed to thaw for 24 h at room temperature (15 to 20° C) prior to inspection. After total length, weight and sex were recorded, visceral organs and mesenteries were inspected for larval anisakines. Each fish was then boned, and fillets, napes (hypaxial musculature enclosing the body cavity) and flesh which remained on the frame were examined for nematodes by slicing and mechanical destruction of tissues (Power 1961). As a rule, nematodes were identified by eye and counted, but inspection with a dissecting microscope was sometimes necessary in order to identify smaller worms and specimens damaged (e.g. cut into fragments) during boning and slicing of flesh. *P. decipiens* sibling species B, recently designated as *P. decipiens* (*sensu stricto*) (Paggi *et al.* 2000) is the only species of sealworm known to occur in the waters surveyed here (Brattey and Davidson 1996).

Efficiencies of routine examinations of the musculature of groundfish were tested using procedures described by McClelland *et al.* (2000). Atlantic cod (*Gadus morhua*) (n = 90), sea raven (*Hemitripterus americanus*) (n = 23), long horned sculpin (*Myoxocephalus octodecemspinosus*) (n = 30) and Canadian plaice (n = 163) were collected from the Scotian Shelf and southwestern Nova Scotia during groundfish sampling cruises in June and July 1991. The flesh of individual fish, together with nematodes identified and counted following routine inspection, were placed in a 4 L beaker containing 2 L of 1% HCl with 5 g of 1:10,000 pepsin L^{-1}. After incubation for 2 to 3 h at 35 to 40° C with continuous stirring, the contents of each beaker were strained through a series of sieves ranging from 5.0 to 0.3 mm in mesh size. All nematodes recovered, including those severed during boning and slicing of the flesh, were identified and counted as above.

To determine the frequencies of occurrence of smaller sealworm larvae (2 to10 mm in length) in demersal fish, samples of various benthic

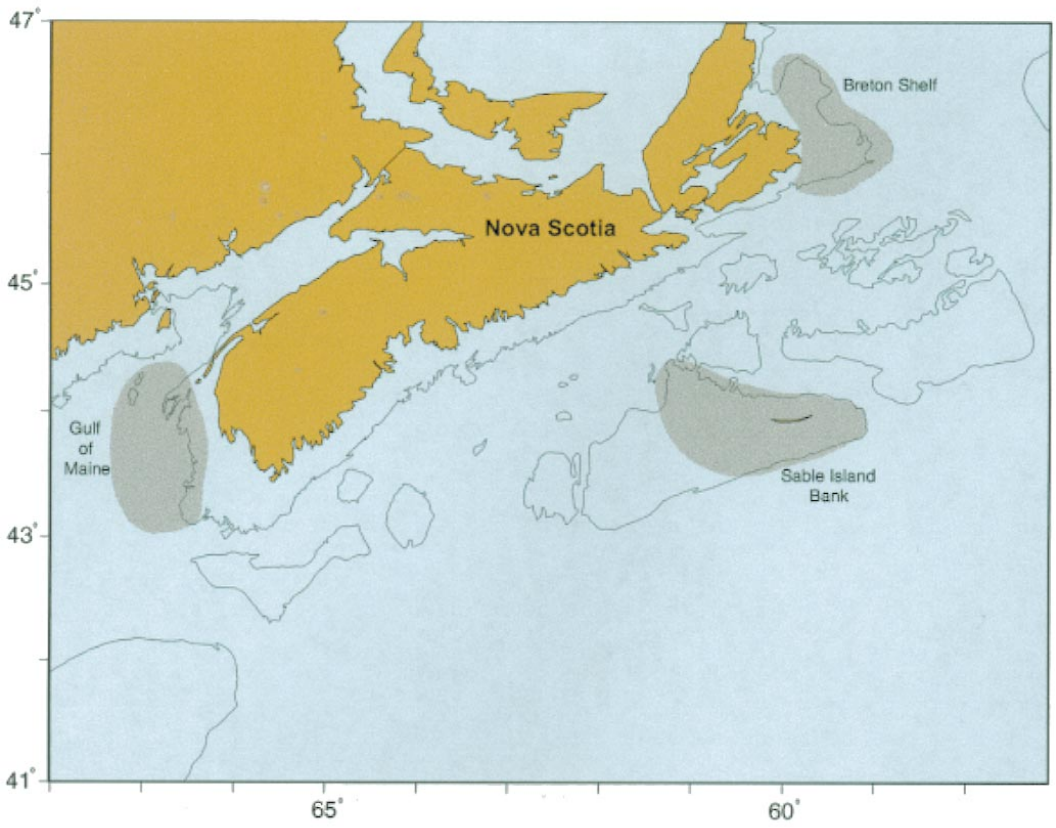

Fig. 2 *Sampling areas (shaded) for surveys of larval sealworm (Pseudoterranova decipiens) infection in various fish species from the Breton Shelf, Sable Island Bank and the northeastern Gulf of Maine.*

consumers were collected from the northern and southern slopewaters of Sable Island Bank. They were stored on ice in portable coolers while at sea, and refrigerated at 0 to 2° C on return to the Halifax Lab. Within 2 to 5 days of capture, the fish were measured, weighed and gutted. The viscera were inspected for nematodes under low magnification with a 'Luxor' lamp. Bodies of fourbeard rockling (*Enchelyopus cimbrius*), Vahl's eelpout (*Lycodes vahlii*), hookear (*Artediellus atlanticus*) and mailed sculpin (*Triglops murrayi*), alligatorfish (*Aspidophoroides monopterygius*), spiny lumpsucker (*Eumicrotremus spinosus*), and juvenile plaice, collected from October 1991 to August 1993, were examined by mechanical destruction of the flesh under a "Luxor" lamp. Bodies of alligatorfish, sampled in August '93, and those of rockling, juvenile cod and haddock (*Melanogrammus aeglefinus*), mailed sculpin, lumpsucker, and juvenile plaice and halibut (*Hippoglossus hippoglossus*), sampled from May 1994 to October 1996, were placed, individually, according to size, in 0.4 to 4.0 L beakers containing 200 to 2000 ml of pepsin - HCl solution. After incubation at room temperature (18 to 22° C) for 2 to 3 h with continuous stirring, the digests were inspected for nematodes by decanting into finger bowls in 50 to 100 ml aliquots, and examining with a dissecting microscope at medium to high power. All nematodes recovered, viable or necrotic, were identified (with the aid of a compound microscope for smaller worms), counted, rinsed in 0.9% saline, fixed in hot 5% glycerin in 70% ETOH, and cleared in glycerin. Lengths of sealworm were ascertained by placing cleared nematodes on a dissecting scope equipped with a drawing tube, and tracing their outlines onto a computer graphic tablet with an electronic pen. The images were fed directly to a Mackintosh Quadra 700 where they were converted to actual nematode length on a precalibrated template from NIH Image (version 1.61).

Quantitative parameters of infection such as prevalence (P), abundance (A), intensity (I), and density (D) are defined according to Margolis *et al.* (1982). Samples were partitioned into 10 cm host length strata with num-

bers and length ranges of strata varying with host species according to length structures of samples. Spatial and temporal variations in prevalence and abundance were analysed by two-way (location • length, or survey • length) ANOVA (SYSTAT) for each host species (McClelland *et al.* 1983a). For ANOVA of prevalence, individual infected fish were assigned the value "1", and each uninfected fish, the value "0" (Li 1964; Neter *et al.* 1985). To permit ANOVA of abundance, frequency distributions of sealworm counts, which were positively skewed to varying degrees, were brought closer to normality by a log (n + 1) transformation (Platt 1975).

RESULTS

Seal prey survey

From November 1988 to August 1993, a total of 9,523 fish belonging to 39 species were collected from the Breton Shelf, Sable Island Bank and the northeastern Gulf of Maine. Sable Island Bank samples included 4,847 fish from 32 species, while those from the Breton Shelf and Gulf of Maine were comprised of 2,122 fish from 24 species, and 2,554 fish from 22 species respectively. All fish from the Breton Shelf and Gulf of Maine, and the majority of those from Sable Island Bank were sampled between February 1989 and October 1990. Additional specimens of benthic consumers such as fourbeard rockling, Vahl's eelpout, snakeblenny (*Lumpenus lumpretaeformis*), wrymouth (*Cryptacanthodes maculatus*), hookear and mailed sculpin, alligatorfish and spiny lumpsucker were collected from Sable Island Bank between October 1991 and August 1993. Data from Canadian plaice collected during the latter period are not included in Table 1 or in analyses of spatial and temporal variation below.

When examined by routine procedures in which the musculature was sliced and candled, and the viscera inspected by eye, larval sealworm and whaleworm (*Anisakis simplex*) were found in the majority of fish species (30 and 26 of 39 host species respectively) inventoried. Larvae of a third anisakine species, *Contracaecum osculatum*, were found only in Atlantic cod and white hake (*Urophycis tenuis*) from the Breton Shelf and on Sable Island Bank. In this document, we report on but one of the three species, *P. decipiens.*

On Sable Island Bank, prevalence and abundance of larval sealworm were greatest (P=100%, A, ranging from 31.08 to 151.31) in large sea raven, cod and monkfish (*Lophius americanus*), but heavy infections (P ranging from 92 to 100%, A=12.54 to 17.56) were also recorded in mature ocean pout (*Macrozoarces americanus*) , longhorn sculpin, and Canadian plaice (Table 1). Mature sea raven, cusk (*Brosme brosme*), cod, monkfish and ocean pout were the most heavily infected hosts (P=96% to 100%, A=13.44 to 108.20) in the northeastern Gulf of Maine. On the Breton Shelf, where no monkfish, and only two sea raven and two ocean pout were collected, the parasite was most prevalent (P=100%) and abundant (A=20.00) in cod >70 cm in length. The infection of greatest intensity (I=721) occurred in a 112 cm cod from the continental slope waters southeast of Sable Island.

Densities of larval sealworm infection were greatest (D >100 worms kg^{-1} host round weight) in mature hookear sculpin, mailed sculpin and alligatorfish, as well as juvenile (<20 cm in length) sea raven, longhorn sculpin and Canadian plaice from Sable Island Bank (Table 1). High sealworm densities (D ranging from 30 to 100 kg^{-1}) also occurred in Sable Island Bank samples of juvenile windowpane (*Scophthalmus aquosus*), and mature fourbeard rockling, ocean pout, wrymouth, sea raven, longhorn sculpin, spiny lumpsucker and plaice. When compared with their counterparts on the central Scotian Shelf, small benthic consumers from the Breton Shelf and Gulf of Maine were (relatively) lightly infected (D=2 to 42 kg^{-1}). Remarkably, the parasite was not found in hookear sculpin and alligatorfish from the Gulf of Maine.

Although sealworm larvae were confined primarily (>90%) to the fillets in the majority of fish surveyed, large numbers occupied body cavities and napes of large piscivores such as mature monkfish and various mature gadids and cottids. In large (> 50 cm in length) monkfish from Sable Island Bank (n=12), 132 (35%)

Table 1. Prevalence (P), abundance (A), maximum intensity (I_{max}) and density (D) (no. kg $^{-1}$ host round weight) of *Pseudoterranova decipiens* larvae in various fish species from the Breton Shelf, Sable Island Bank and the northeastern Gulf of Maine,1988-1993.

Host		Parameters of P. decipiens infection														
Species	Length range (cm)	Breton Shelf					Sable Island Bank					Gulf of Maine				
		n	P	A	I_{max}	D	n	P	A	I_{max}	D	n	P	A	I_{max}	D
Squalus acanthias	58-77	—	—	—	—	—	20	0	—	—	—	—	—	—	—	—
Raja radiata	6-42	—	—	—	—	—	81	0	—	—	—	39	0	—	—	—
Alosa sapidissima	15-49	—	—	—	—	—	—	—	—	—	—	25	0	—	—	—
Alosa pseudoharengus	16-30	—	—	—	—	—	—	—	—	—	—	47	0	—	—	—
Mallotus villosus	11-17	30	0	—	—	—	92	0	—	—	—	—	—	—	—	—
Lophius americanus	30	—	—	—	—	—	15	60	5.07	29	21.49	27	7	0.07	2	1.22
	31-50	—	—	—	—	—	37	100	27.03	109	20.20	5	100	11.60	27	10.95
	51	—	—	—	—	—	12	100	31.08	96	11.14	4	100	23.00	47	6.77
Brosme brosme	51-85	—	—	—	—	—	—	—	—	—	—	12	100	29.17	66	10.92
Enchelyopus cimbrius	25	12	9	0.09	1	2.22	141	74	2.64	21	77.23	9	33	0.67	4	13.73
	26	11	100	2.82	10	29.47	—	—	—	—	—	—	—	—	—	—
Gadus morhua	20	35	11	0.14	2	3.68	2	20	0.20	1	8.10	9	44	0.89	2	14.73
	21-30	50	52	1.18	6	8.13	42	67	1.81	8	10.65	36	50	1.36	15	9.31
	31-40	45	96	4.44	25	11.55	81	90	4.74	21	11.02	37	70	3.08	23	7.30
	41-50	68	88	4.35	22	5.36	64	92	6.94	52	9.47	46	74	2.28	11	2.55
	51-60	56	97	6.31	37	4.24	39	97	10.67	45	7.23	49	84	4.43	46	2.88
	61-70	44	95	9.55	56	3.96	37	97	14.78	74	5.86	44	95	7.86	39	3.00
	71	25	100	30.80	142	6.47	24	100	59.79	721	10.27	22	100	20.00	81	5.15
Melanogrammus aeglefinus	20	—	—	—	—	—	25	28	0.28	1	5.38	13	8	0.08	1	1.50
	21-30	—	—	—	—	—	81	36	0.72	7	4.42	38	3	0.03	1	0.18
	31-40	—	—	—	—	—	51	41	0.53	3	1.25	49	22	0.31	3	0.67
	41-50	22	36	0.36	1	0.39	43	26	0.40	3	0.42	47	13	0.13	1	0.12
	51-60	31	39	0.42	2	0.24	39	51	0.82	4	0.53	52	25	0.31	2	0.16
	61	—	—	—	—	—	—	—	—	—	—	26	46	0.62	3	0.18
Merluccius bilinearis	20	—	—	—	—	—	9	0	—	—	—	24	0	—	—	—
	21-30	—	—	—	—	—	129	4	0.05	3	0.48	59	0	—	—	—
	31-40	—	—	—	—	—	73	7	0.07	1	0.20	79	1	0.01	1	0.04
	41	—	—	—	—	—	22	9	0.36	7	0.63	—	—	—	—	—

Table 1. (cont'd)

Host		Parameters of P. decipiens infection														
		Breton Shelf					Sable Island Bank					Gulf of Maine				
Species	Length range (cm)	n	P	A	I_{max}	D	n	P	A	I_{max}	D	n	P	A	I_{max}	D
Pollachius virens	30	—	—	—	—	—	—	—	—	—	—	21	0	—	—	—
	31-40	—	—	—	—	—	—	—	—	—	—	49	4	0.04	1	0.08
	41-50	—	—	—	—	—	—	—	—	—	—	51	8	0.08	1	0.07
	51	—	—	—	—	—	—	—	—	—	—	76	14	0.20	2	0.08
Urophycis tenuis	20	—	—	—	—	—	17	0	0	0	0	12	0	0	0	0
	21-30	16	6	0.06	1	0.39	129	13	0.39	18	3.47	57	2	0.02	1	0.14
	31-40	41	12	0.20	2	0.60	47	32	0.53	4	1.68	62	13	0.15	2	0.48
	41-50	56	45	0.73	6	1.05	35	77	2.71	20	4.28	57	26	0.49	5	0.72
	51-60	45	53	1.33	6	1.00	10	90	5.20	16	3.59	49	39	0.86	10	0.65
	61	—	—	—	—	—	—	—	—	—	—	24	71	3.21	30	1.13
Macrourus berglax	14-30	22	0	0	0	0	—	—	—	—	—	—	—	—	—	—
Tautogolabrus adsperus	12-33	—	—	—	—	—	15	0	0	0	0	—	—	—	—	—
Lycodes reticulatus	30	16	38	0.56	3	7.28	—	—	—	—	—	—	—	—	—	—
	31	14	88	2.86	21	7.56	—	—	—	—	—	—	—	—	—	—
Lycodes vahlii	25	37	0	0	0	0	16	13	0.50	7	18.14	—	—	—	—	—
	26	100	32	0.49	5	3.44	38	37	1.18	24	11.93	—	—	—	—	—
Macrozoarces americanus	30	2	100	—	9	—	8	63	2.00	8	19.63	58	47	1.28	9	22.00
	31-50	—	—	—	—	—	48	92	12.54	57	56.11	77	86	3.62	26	12.48
	51	—	—	—	—	—	8	100	13.00	72	13.12	25	96	13.44	84	13.69
Eumesogrammus praecisus	9-20	46	20	0.20	1	6.75	—	—	—	—	—	—	—	—	—	—
Lumpenus lumpretaeformis	13-42	11	9	0.09	1	3.11	26	15	0.19	2	6.81	—	—	—	—	—
Lumpenus maculatus	13-42	—	—	—	—	—	8	13	0.13	1	14.92	—	—	—	—	—
Anarhichas lupus	30	34	3	0.06	2	0.43	6	17	0.17	1	1.65	17	0	0	0	0
	31	34	38	0.71	4	0.78	5	60	1.20	3	2.07	12	33	1.08	9	0.56
Cryptacanthodes maculatus	35	—	—	—	—	—	14	29	0.36	2	7.50	—	—	—	—	—
	36	—	—	—	—	—	10	70	10.50	58	33.54	—	—	—	—	—
Ammodytes dubius	14-24	—	—	—	—	—	56	0	0	0	0	—	—	—	—	—

Table1. (cont'd)

Host		Parameters of P. decipiens infection													
Species	Length range (cm)	Breton Shelf					Sable Island Bank					Gulf of Maine			
		n	P	A	I_{max}	D	n	P	A	I_{max}	D	n	P	A	Imax	D
Peprilus triacanthus	13-23	—	—	—	—	—	133	12	0.15	2	1.13	—	—	—	—	—
Sebastes fasciatus	20	26	0	0	0	0	37	3	0.03	1	0.56	25	0	0	0	0
	21-30	50	16	0.16	1	0.40	51	12	0.03	1	0.56	55	7	0.13	4	0.46
	31-40	51	25	0.45	3	0.63	19	37	0.58	3	1.22	28	21	0.32	5	0.50
	41	25	12	0.20	2	0.20	—	—	—	—	—	—	—	—	—	—
Artediellus atlanticus	4-9	59	5	0.05	1	10.62	129	36	0.922	17	222.18	30	0	0	0	0
Hemitripterus americanus	20	—	—	—	—	—	22	41	13.41	40	157.33	19	42	0.95	7	11.06
	21-30	1	—	—	51	—	56	100	42.84	277	136.86	39	95	17.15	72	51.56
	31-40	2	100	—	57	—	48	100	84.88	289	104.99	52	100	64.00	235	76.74
	41	—	—	—	—	—	13	100	151.31	338	97.74	20	100	108.20	283	65.77
Myoxocephalus octodecemspinosus	20	—	—	—	—	—	44	84	5.57	26	186.60	20	10	0.20	3	5.14
	21-25	2	50	—	2	—	46	93	8.70	38	66.29	35	20	0.43	4	3.43
	26-30	—	—	—	—	—	50	98	12.22	59	58.64	27	59	1.37	7	7.08
	31	—	—	—	—	—	15	93	13.73	62	44.15	20	75	2.90	15	8.80
Triglops murrayi	4-16	63	33	0.52	4	40.77	259	63	2.71	37	317.97	156	8	0.12	3	17.18
Aspidophoroides monopterygius	8-18	17	6	0.06	1	14.51	129	37	0.64	6	198.93	38	0	0	0	0
Cyclopterus lumpus	31-40	—	—	—	—	—	17	6	0.06	1	0.03	—	—	—	—	—
Eumicrotremus spinosus	3-9	5	20	0.20	1	20.24	220	34	0.57	7	31.458	—	—	—	—	—
Scophthalmus aquosus	20	—	—	—	—	—	55	85	3.22	25	61.65	—	—	—	—	—
	21-30	—	—	—	—	—	70	76	2.56	22	12.45	—	—	—	—	—
Glyptocephalus cynoglossus	20	—	—	—	—	—	17	0	0	0	0	—	—	—	—	—
	21-30	22	18	0.27	3	2.63	60	15	0.32	2	3.69	17	24	0.41	3	3.85
	31-40	48	19	0.21	2	0.84	37	62	2.46	18	10.61	35	40	0.69	5	2.70
	41	42	22	0.86	7	0.86	28	71	1.86	9	3.99	41	80	2.46	11	3.42

Table1. (cont'd)

Host		Parameters of P. decipiens infection														
Species	Length range (cm)	Breton Shelf					Sable Island Bank					Gulf of Maine				
		n	P	A	I_{max}	D	n	P	A	I_{max}	D	n	P	A	Imax	D
Hippoglossoides platessoides	10	—	—	—	—	—	36	22	0.44	5	112.05	—	—	—	—	—
	11-20	83	33	0.46	3	14.43	165	72	5.44	42	185.58	67	55	1.60	12	41.76
	21-30	152	67	2.14	33	17.86	186	95	11.88	61	103.15	96	74	3.90	51	38.36
	31-40	379	87	2.83	28	8.86	622	98	17.56	122	64.87	132	95	5.20	35	15.43
	41	39	77	2.46	12	2.80	15	100	12.33	48	15.05	15	100	4.53	11	4.79
Pleuronectes ferrugineus	20	20	0	0	0	0	121	22	0.32	4	10.20	—	—	—	—	—
	21-30	47	38	0.57	4	4.27	164	46	0.91	7	7.77	—	—	—	—	—
	31	—	—	—	—	—	123	71	1.80	12	6.63	—	—	—	—	—
Pleuronectes americanus	13-47	65	6	0.06	1	0.14	157	1	0.01	1	0.04	142	4	0.04	1	0.10
Reinhardtius hippoglossoides	14-30	11	0	0	0	0	18	11	0.22	2	1.68	—	—	—	—	—
	31-51	10	40	0.60	3	1.71	30	53	1.70	16	4.50	—	—	—	—	—

of 373 sealworm were found in the body cavity, and 114 (31%), in the napes. Of 1,435 larvae in Sable Island Bank cod >70 cm in length (n=24), 318 (22%) occurred in the body cavity, and 668 (47%), in the napes; 385 (20%) and 532 (27%) of 1,967 larvae respectively occupied the body cavities and napes of 13 Sable Island Bank sea raven > 41 cm in length. In the Gulf of Maine, 246 (70%) of 350 *P. decipiens* from 12 cusk >50 cm in length, and 54 (70%) of 77 from 24 white hake >60 cm in length were recovered from the napes. High frequencies of sealworm in body cavities and napes were not unique to larger fish. In a 1990 sample of mailed sculpin from Sable Island Bank, 17 (11%) of 161 larvae infecting 12 to 15 cm fish (n=20) occurred in the body cavity, and the same number in the napes. Sixteen (31%) of 52 nematodes were found on the ovary, or free in the body cavity of 5.6 to 9.5 cm spiny lumpsucker (n=84) sampled from Sable Island Bank in October '91.

ANOVA revealed that geographical disparities in prevalence and/or abundance of sealworm were significant ($P \leq 0.01$) in 14 of 20 host species sampled in at least two of the three survey areas (Table 2). Levels of infection in samples from Sable Island Bank were significantly greater than those found in Breton Shelf samples in 10 of 14 species contrasted, and also exceeded those recorded in samples of 11 of 17 corresponding host species from the Gulf of Maine. Contrasts of Breton Shelf and Gulf of Maine samples, however, indicated that among 11 species common to both areas, only grey sole (*Glyptocephalus cynoglossus*) and plaice differed significantly in regard to parameters of sealworm infection. Invariably, spatial disparities in infection levels in four lightly infected hosts, silver hake (*Merluccius bilinearis*), wolffish (*Anarhichas lupus*), redfish (*Sebastes fasciatus*) and winter flounder, were not significant. Plaice was the only host species in which sealworm prevalence and abundance differed significantly in each of the three survey areas.

Contrasts of 1986-87 (McClelland *et al.* 1990) and 1989-90 samples (herein) indicate that apparent increases in sealworm infection parameters in 8 of 10 host species from Sable Island Bank were statistically significant (Table 3).

Table 2. Larval sealworm (*Pseudoterranova decipiens*) infections in various groundfish species from the Breton Shelf (1), Sable Island Bank (2) and the northeastern Gulf of Maine (3); results of 2-way-ANOVAs of sealworm prevalence (P) and abundance (A) with host length and geographic origin.

Host Species	Infection level	Variation in *P. decipiens* infection parameters[1] By area	With host length	Area/length interaction	Contrasts of areas 1 & 2	1 & 3	2 & 3
Lophius americanus	P	***	***	***	—	—	—
(areas 2 & 3)	A	***	***	***	—	—	—
Enchelyopus cimbrius	P	***	—	—	***	ns	**
	A	***	—	—	***	ns	**
Gadus morhua	P	ns	***	**	***	ns	*
	A	**	***	*	***	ns	***
Melanogrammus aeglefinus	P	***	ns	ns	—	—	—
(areas 2 & 3)	A	***	ns	ns	—	—	—
Merluccius bilinearis	P	ns	ns	ns	—	—	—
(areas 2 & 3)	A	ns	ns	ns	—	—	—
Urophysis tenuis	P	***	***	***	ns	**	*
	A	***	***	***	ns	*	***
Lycodes vahlii	P	*	—	—	—	—	—
(areas 1 & 2)	A	**	—	—	—	—	—
Macrozoarces americanus	P	ns	***	ns	—	—	—
(areas 2 & 3)	A	ns	***	ns	—	—	—
Anarhichas lupus	P	ns	***	ns	ns	ns	ns
	A	ns	***	ns	ns	ns	ns
Sebastes fasciatus	P	ns	*	ns	ns	ns	ns
	A	ns	**	ns	ns	ns	ns
Artediellus atlanticus	P	***	—	—	***	ns	***
	A	***	—	—	***	ns	***
Hemitripterus americanus	P	***	***	***	—	—	—
(areas 2 & 3)	A	***	***	*	—	—	—
Myoxocephalus	P	***	***	**	—	—	—
octodecemspinosis (areas 2 & 3)	A	***	***	ns	—	—	—
Triglops murrayi	P	***	—	—	***	ns	***
	A	***	—	—	***	ns	***
Aspidophoroides monopterygius	P	***	—	—	***	ns	***
	A	**	—	—	***	ns	***
Glyptocephalus cynoglossus	P	**	***	ns	*	**	ns
	A	***	***	**	**	***	ns
Hippoglossoides platessoides	P	***	***	***	***	***	***
	A	***	***	***	***	***	***
Pleuronectes ferrugineus	P	***	—	—	—	—	—
(areas 1 & 2)	A	***	—	—	—	—	—
Pleuronectes americanus	P	ns	—	—	ns	ns	ns
	A	ns	—	—	ns	ns	ns
Reinhardtius hippoglossoides	P	ns	—	—	—	—	—
(areas 1 & 2)	A	ns	—	—	—	—	—

[1]significance when probability (*Pr*) ≤ 0.01 (*), ≤ 0.001 (**), ≤ 0.0001 (***);
not significant (ns)
or not tested (—)

Table 3. Two-way ANOVA's of prevalence and abundance of larval *P. decipiens* in 1986-87 (McClelland *et al*. 1990) and 1989-90 samples of groundfish from Sable Island Bank.

Host Species	Total No. 1986-87	Total No. 1989-90	Contrasts of Parameters of P. decipiens infection: Source of variation	Prevalence P[1]	Prevalence Trend[2]	Abundance P	Abundance Trend
Lophius americanus	65	64	Sample	.0001*	+	.0000*	+
			Length	.0000*		.0000*	
			Sample x Length	.0000*		.0000*	
Gadus morhua	318	289	Sample	.0293		.0000*	+
			Length	.0000*		.0000*	
			Sample x Length	.0128		.0000*	
Melanogrammus aeglefinus	356	239	Sample	.0000*	+	.0000*	+
			Length	.0000*		.0000*	
			Sample x Length	.0000*		.0000*	
Urophycis tenuis	230	238	Sample	.0988		.0000*	+
			Length	.0000*		.0000*	
			Sample x Length	.2235		.0001*	
Sebastes fasciatus	264	107	Sample	.0131		.0172	
			Length	.0000*		.0000*	
			Sample x Length	.5222		.6570	
Hemitripterus americanus	103	139	Sample	.3183		.0137	
			Length	.0000*		.0000*	
			Sample x Length	.3972		.4878	
Myoxocephalus octodecemspinosus	174	155	Sample	.0048	+	.0001*	+
			Length	.0000*		.0000*	
			Sample x Length	.0000*		.0000*	
Glyptocephalus cynoglossus	156	142	Sample	.0000*	+	.0000*	+
			Length	.1083		.0572	
			Sample x Length	.5598		.3261	
Hippoglossoides platessoides	278	1024	Sample	.1472		.0003*	+
			Length	.0000*		.0000*	
			Sample x Length	.0000*		.0000*	
Pleuronectes ferrugineus	216	408	Sample	.0000*	+	.0000*	+
			Length	.0000*		.0000*	
			Sample x Length	.0000*		.0000*	

[1]contrast significant (*) when probability $P \leq 0.01$.
[2]infection parameter greater in more recent sample (+).

Both prevalence and abundance of the parasite had increased in monkfish, haddock, longhorn sculpin, grey sole and yellowtail flounder (*Pleuronectes ferrugineus*), while abundance alone had increased in cod, white hake and plaice.

Efficacy of examination procedures

Routine examinations (slicing and candling) for *P. decipiens* in the flesh of groundfish proved very efficient when tested against digestion procedures (Table 4). A total of 24 worms were recovered from cod ≤ 30 cm in length by routine

Table 4. Prevalence (P), abundance (A), maximum intensity (I_{max}) and density (D) (no. kg-1 host round weight) of *Pseudoterranova decipiens* larvae found in frozen samples of Scotian Shelf and Gulf of Maine groundfish by routine examination employing slicing and candling of host flesh, and following digestion of flesh in pepsin-HCl solution at 35º C; groundfish samples were collected in June and July 1991.

Host			Examination	Parameters of *P. decipiens* infection			
Species	Length range (cm)	n	Procedure	P	A	I_{max}	D
Gadus morhua	20-30	29	Routine	31	0.83	5	6.17
			Digestion	34	0.83	5	6.17
	31-50	27	Routine	78	6.63	23	13.32
			Digestion	81	6.96	23	13.99
	51-68	34	Routine	53	1.97	21	1.40
			Digestion	56	2.24	24	1.58
Hemitripterus americanus	22-40	23	Routine	100	26.13	97	43.93
			Digestion	100	21.07	78	34.54
Myoxocephalus octodecemspinosus	24-28	30	Routine	30	0.53	3	3.22
			Digestion	30	0.30	1	1.81
Hippoglossoides platessoides	13-20	30	Routine	37	0.40	2	11.19
			Digestion	37	0.40	2	11.19
	21-30	30	Routine	70	2.03	12	19.97
			Digestion	70	2.00	12	19.66
	31-40	83	Routine	84	5.57	45	16.46
			Digestion	90	5.35	40	15.82
	41-53	20	Routine	85	3.15	11	4.14
			Digestion	85	3.02	6	4.01

inspection and by subsequent Pepsin-HCl digestion. Prevalence increased when digestion yielded a additional single worm infection not detected mechanically. Nine (4%) of a total of 188 larvae in 31 to 50 cm cod, and 9 (10%) of 89 larvae in 51 to 68 cm cod, escaped detection by slicing and candling, and there were marginal increases in sealworm prevalence in both length categories following digestion.

In plaice ≤ 30 cm in length, a total of 73 worms were found by routine inspection, and there was a net loss of a one nematode following digestion. While digestion procedures revealed infection in one additional fish in the 31-40 cm length range, the total number of nematodes found (and hence, abundance) declined from 458 following routine inspection to 440 after the flesh was digested and sieved. Some nematodes severed during boning and slicing of the flesh did not survive digestion, and the extremities of many intact nematodes had also deteriorated. In plaice ≥41 cm in length, sealworm prevalence remained the same following digestion of the flesh, but there was a net loss of two worms; 62 larvae were found by mechanical inspection, and although digestion revealed a total of four previously undetected worms from three fish, six nematodes from two other fish were lost.

Evidently, many encapsulated, necrotic sealworm in the flesh of sculpins were lost when incubated in pepsin-HCl at 35°C. Only 9 (56%) of 15, and 439 (72%) of 611 *P. decipiens*, detected by mechanical inspection of the flesh of longhorn sculpin and sea raven, respectively, were recovered after digestion.

Digestion of small benthophagous hosts

Digestion of host bodies at ambient temperature, followed by decanting and microscopic examination of the sediment proved far more efficacious for detecting sealworm in the flesh of small benthic consumers than routine dissections conducted with the naked eye or under low magnification with a "Luxor" lamp. Infection parameters revealed by dissection of fresh iced specimens (Table 5) were not dissimilar to those obtained through routine examination of frozen samples (Table 1). Aside from three (14%) of 21 larvae from alligatorfish, and one (0.5%) of 196 larvae from mailed sculpin, all sealworm detected by dissection of small demersal fish exceeded 10 mm in length, the smallest larvae being an 8.96 mm specimen from alligatorfish.

When digestion procedures were employed, on the other hand, 36 (24%) of 159 sealworm found in rockling, 34 (46%) of 73 in mailed sculpin, 72 (84%) of 86 in alligatorfish were ≤10.00 mm in length. In yearling plaice (≤15.0 cm in length) and 0-group halibut, 31% (86 of 277) and 55% (6 of 11) of the larvae, respectively, were ≤10.00 mm long. Rockling yielded the smallest larva, a 2.14 mm specimen, but sealworm as small as 3.01-3.27 mm in length were also detected in mailed sculpin, alligatorfish and juvenile plaice. As apparent from summaries of sealworm infection parameters (Table 5), digestion of rockling, mailed sculpin, alligatorfish, and plaice (≥15.0 cm long) yielded far greater numbers of nematodes than dissection. Abundances of the parasite in digested samples were greater than those found in dissected samples by a factor of 16 in rockling, three in mailed sculpin, 19 in alligatorfish, and five in plaice; densities in digested samples exceeded those found in dissected samples by 4- to 17-fold.

Only three (5% of 62) sealworm from juvenile cod, and 8 (4% of 196) from plaice >15 cm in length were <10 mm in length. Infection parameters in digested plaice 18-26 cm in length did not differ significantly from those found in dissected plaice or previously frozen plaice (Table 1) of similar size. Digestion of 32 lumpsuckers yielded only 11 worms, all of which exceeded 25 mm in length, while three sealworm, 9, 16 and 26 mm in length, were recovered from digests of four juvenile haddock, 14-16 cm in length.

DISCUSSION

The present survey confirms earlier observations (McClelland *et al* 1990) that, in Atlantic Canadian waters, larval sealworm is most prevalent and abundant in mature demersal piscivores (monkfish, Atlantic cod, cusk, and sea raven), and, to a lesser extent, in mature benthic consumers (ocean pout, longhorn sculpin and Canadian plaice). The survey further reveals, however, that sealworm densities are greatest, not only in the juveniles of sea raven, longhorn sculpin and plaice, but also in small, non-commercial benthophagous species, such as fourbeard rockling, Atlantic hookear and mailed sculpin, alligatorfish and spiny lumpsucker. Rockling, hookear sculpin and mailed sculpin are new host records for sealworm, and the parasite is also reported, for the first time, from arctic eelpout (*Lycodes reticulatus*), fourline snakeblenny (*Eumesogrammus praecisus*), snakeblenny, daubed shanny (*Lumpenus maculatus*) and wrymouth (see McDonald and Margolis 1995 for most recent list).

Analyses of spatial disparities in sealworm prevalence and abundance in the present study revealed that infection parameters in samples from Sable Island Bank were significantly greater than those found in Breton Shelf samples for 10 of 14 species contrasted, and also exceeded those recorded in samples of 11 of 17 corresponding host species from the Gulf of Maine. These results are consistent with the findings of earlier multispecies, and "sealworm index" surveys (McClelland and Martell 2001, McClelland *et al.* 1990, 2000), and clearly reflect the impact of the large Sable Island grey seal colony on *P. decipiens* infections in local groundfish populations. Grey seals probably have a marked influence on infections in groundfish from the Breton Shelf and northeastern Gulf of Maine groundfish as well, although harbour seals may play a significant role as definitive hosts in the latter region (McClelland *et al*. 2000). Along the southern Norwegian inshore, where grey seals are outnumbered or absent, heavy sealworm infections

Table 5. Prevalence (P), abundance (A), maximum intensity (I_{max}), densities (no. kg^{-1} host round weight) (D) and lengths of *Pseudoterranova decipiens* larvae recovered from fresh iced samples of small benthic consumers by dissection, and by digestion of host bodies in pepsin-HCl at ambient temperature; samples were collected from Sable Island Bank between October 1991 and October 1996.

Host			Procedure	Parameters of P. decipiens infection				P. decipiens length (mm)		
Species	Length range (cm)	n		P	A	I_{max}	D	n	mean	≈(range)
Enchelyopus cimbrius	15-35	85	Dissection	66	1.84	12	53	125	26.42	(15.16-36.21)
	19-27	6	Digestion	100	28.83	63	665	159	18.72	(2.14-36.40)
Gadus morhua	20-29	30	Digestion	63	2.43	9	22	62	29.20	(5.93-43.59)
Lycodes vahlii	21-38	41	Dissection	20	0.46	7	6	11	26.15	(20.08-31.53)
Artediellus atlanticus	5-9	88	Dissection	28	0.55	5	141	41	28.24	(13.71-41.87)
Triglops murrayi	7-15	136	Dissection	56	1.76	20	181	196	24.90	(9.68-36.33)
	8-13	19	Digestion	100	5.74	15	806	73	15.15	(3.01-35.11)
Aspidophoroides monopterygius	12-15	78	Dissection	29	0.37	3	142	21	14.04	(8.96-32.00)
	11-15	27	Digestion	85	7.19	50	2465	86	7.17	(3.08-17.01)
Eumicrotremus spinosus	5-10	140	Dissection	31	0.49	7	24	62	26.98	(13.71-37.11)
	4-10	32	Digestion	28	0.38	2	21		--	--
Hippoglossoides platessoides	10-15	43	Dissection	37	1.58	17	179	66	22.56	(10.86-35.32)
	9-15	39	Digestion	82	8.21	50	684	277	19.59	(3.27-41.70)
	15-43	178	Dissection	96	10.73	87	97	1269	36.06	(11.70-53.20)
	15-26	29	Digestion	90	7.17	25	147	196	31.10	(4.10-59.30)
Hippoglossus hippoglossus	25-29	6	Digestion	83	1.83	3	6	11	10.56	(6.38-15.42)

in groundfish are attributed to harbour seals (Aspholm *et al.* 1995, des Clers and Anderson 1995). In the past, this was also true for inshore areas of the southern Gulf of St. Lawrence, and the south shore of Nova Scotia (Scott and Martin 1959).

There were great disparities in larval sealworm infection parameters in small benthic consumers from our three survey areas (Table 1). Hence, it would seem that these species might prove useful, like Canadian plaice (McClelland and Martell 2001, McClelland *et al*. 2000), as indicator hosts for monitoring geographical and temporal distributions of the parasite. However, while surveys of these smaller fish may provide a more accurate picture of local distributions of larval sealworm at specific sites, e.g. Sable Island Bank, they would be difficult to conduct on a larger scale. As evident from research cruises employing trawls equipped with liners, these hosts are neither as widely distributed nor as abundant as plaice, and, because of their small size, they are not caught with commercial gear. Further, a significant proportion of larval sealworm found in these smaller hosts are < 10 mm in length (below), and can be detected only through time consuming digestion or tissue squash procedures and microscopy. Plaice of the size (31 to 40 cm TL) monitored in our "index" surveys (McClelland and Martell 2001, McClelland *et al.* 2000) are seldom infected with smaller larvae, and can be examined efficiently by slicing and candling of the flesh. Notably, of 11 host species which were common to the three areas surveyed here, plaice was the only the only species having significant disparities in sealworm prevalence and abundance in each area.

Given the growth of the Sable Island grey seal population over the course of the decade (Zwanenberg and Bowen 1990), it was not surprising that parameters of sealworm infection in our 1989-1990 samples of groundfish from Sable Island Bank were significantly greater than those recorded during an earlier survey (McClelland *et al*. 1990). As shown in our more recent "sealworm index" surveys (McClelland and Martell 2001), however, sealworm abundance in 31-40 cm plaice from Sable Island Bank has been declining since 1990, despite the continued growth of the grey seal population. Although this fact was not brought out in the present document, falling infection levels were detected in small benthic consumers collected from 1991 to 1993 even though they were subjected to more rigorous examinations. Heavy sealworm infections could prove lethal to fish of this size, either directly, through damage to vital organs and tissues, or indirectly, by impairing the host's ability to forage and avoid predators (McClelland 1995). Possibly, the most heavily infected benthic consumers have become increasingly vulnerable to predation pressure as predator (seal) populations continue to grow, and groundfish stocks decline (Mohn and Bowen 1996). In support of this hypothesis, the tails of worm count distributions in plaice from Sable Island bank have become increasingly truncated in more recent "index" surveys (McClelland and Martell 2001).

As evident from the results of earlier surveys (Young 1972, Platt 1975, Wootten and Waddell 1977, McClelland *et al.* 1990), accurate estimates of sealworm levels in large piscivores, including mature monkfish, gadids and sculpins, can only be obtained by examining napes and body cavities, as well as fillets. The present study shows that nematodes occupying the body cavity and napes may represent a significant proportion, if not the majority of sealworm in large demersal piscivores, and also in tiny (<10 cm in length) benthic consumers such as mailed sculpin and lumpsucker. Power (1961) demonstrated that candling procedures, routinely conducted at fish plants for detection and removal of larval sealworm from cod fillets, were not very effective. Using "destructive" examinations in which fillets were cut into thin slices prior to candling, he found that the majority of sealworm in the fillets of larger cod escaped detection on the production line. An assessment of Power's slicing and candling technique (herein) reveals that this approach, used in our present and earlier surveys (McClelland *et al.* 1990, 2000, McClelland and Martell 2001), may be as efficacious as more laborious and time consuming digestion procedures. Indeed, some moribund nematodes from frozen samples, especially those damaged during boning or filleting, may be destroyed when incubated in warm pepsin-HCl solution. Unfortunately, since de-

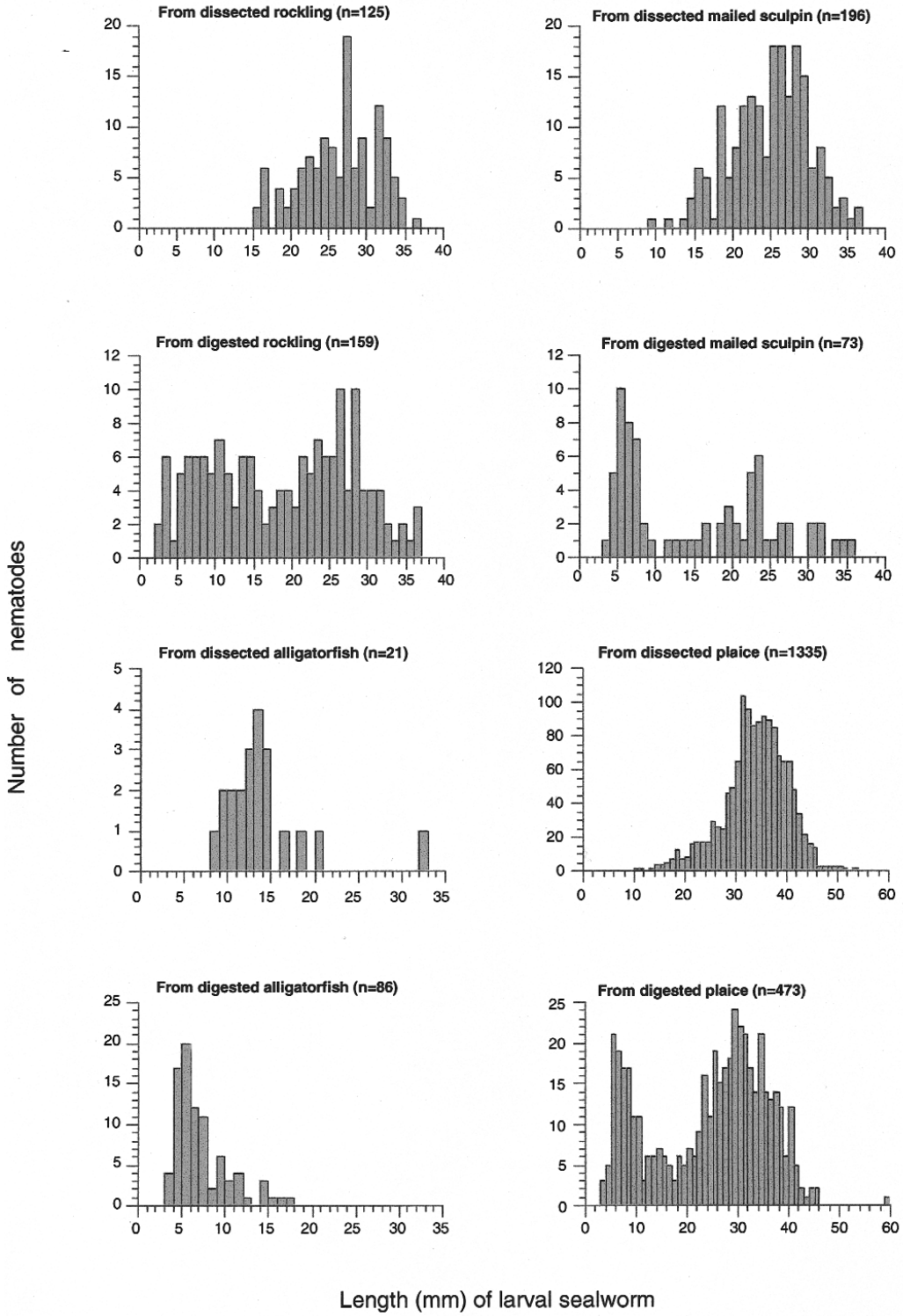

Fig. 3 *Length frequency distributions of larval sealworm,* Pseudoterranova decipiens, *recovered from fourbeard rockling (Enchelyopus cimbrius), mailed sculpin (Triglops murrayi), alligatorfish (Aspidophoroides monopterygius) and juvenile Canadian plaice (Hippoglossoides platessoides) by dissection and digestion procedures; all fish were collected from north Sable Island Bank.*

structive examination of both fillets and napes, along with inspection the visceral organs and body have not been universally employed in sealworm surveys, it is often difficult to make temporal and spatial comparisons with the results of other investigators (McClelland *et al.* 1990).

One final factor that must be considered when assessing the accuracy of survey results is the possibility that some sealworm larvae may simply be too small to detect in the white flesh of groundfish with the unaided eye. Larval sealworm as small as 2 mm in length are infective to fish hosts in laboratory transmissions (McClelland 1995), and 4 to 5 mm sealworm have been found in juvenile Icelandic cod through microscopic examinations of tissue squashes (Pálsson MS 1979). However, the smallest larvae typically reported from surveys employing candling of sliced or whole fillets have been 14 to 15 mm in length (Scott and Martin 1957, Templeman *et al.* 1957). Present results reveal that failure to detect smaller nematodes is cause for concern, but perhaps, only when it pertains to data from small benthophagous hosts. Whereas the smallest nematodes detected by slicing the flesh of small benthic consumers were about 9 mm long, larvae as small as 2 mm in length were recovered by digestion of host bodies at ambient temperature and microscopic examination of the sediment. Twenty-four to 84 % of the larvae yielded by digestion of fourbeard rockling, mailed sculpin, alligatorfish, and 9 to 15 cm juvenile plaice were <10 mm in length. Sealworm of this size also occurred in juveniles of cod and other commercially exploited species including haddock (*Melanogrammus aeglefinus*), plaice >15 cm in length, and halibut (*Hippoglossus hippoglossus*), but were not nearly as numerous in these latter hosts. Only 4% to 5% of the larvae from 20 to 29 cm cod and 15 to 26 cm plaice were <10 mm in length. The especially low worm yields from dissections of alligatorfish (Table 5) are attributable mainly to the anatomy of the species. Alligatorfish are thin elongate fish with thick skin and relatively little flesh, and often weigh only a gram or two. Sealworm larvae, which average ca. 7 mm in length in alligatorfish, were probably destroyed by the knife during dissection.

Larval sealworm recovered by digestion of tiny benthophagous fish (mature fourbeard rockling, hookear and mailed sculpin, alligatorfish and 9 to 15 cm juvenile plaice) had bi- to polymodal length distributions (Fig. 3). The first mode consisted primarily of larvae in the 2 to 10 mm length range, i.e. similar in size to *P. decipiens* larvae, naturally found in benthic crustaceans, and to those successfully transmitted to fish in the laboratory (McClelland 1995). This would seem to indicate that these hosts acquire *P. decipiens* larvae by feeding on invertebrate hosts during a particular season or seasons, rather than continuously throughout the year. Notably, *Mysis mixta*, which are naturally infected with larval sealworm on Sable Island Bank (Martell and McClelland 1995), are consumed by juvenile plaice most frequently during winter (Martell and McClelland 1994). As a probable consequence of exploitation of *M. mixta* in winter, there is a strong pulse of 2-10 mm sealworm larvae in spring samples of juvenile plaice from Sable Island Bank (McClelland 2000).

While not prominent in seal diets (Benoit and Bowen 1990*a*, 1990*b*, Bowen and Harrison 1996, Bowen *et al* 1993) small, seemingly inconsequential benthic consumers such as rockling, hookear and mailed sculpin, alligatorfish and juvenile plaice are frequently consumed by larger, economically important species such as cod (Scott and Scott 1988). Hence, they may be the source of heavy sealworm infections in commercially exploited fish, and play a significant, albeit indirect role in the transmission of *P. decipiens* to seals. Aspholm *et al.* (1995) speculate that bullrout (*M. scorpius*) (shorthorn sculpin in the northwest Atlantic) performs a similar function in Norwegian inshore waters. In some instances, sealworm may be transmitted directly to seals by invertebrate hosts. Larvae >5 mm in length appeared to be capable of maturing in an *in vitro* system (McClelland and Ronald 1974). *P. decipiens* L4s as small as 8 mm in length have been found in stomachs of newly weaned harbour (Boulva and McLaren 1979) and grey seal pups (unpublished data) feeding on invertebrates.

ACKNOWLEDGMENTS

The authors thank Dave Marcogliese (Environment Canada, Montreal) and Johanne Guerin (Department of Fisheries and Oceans Maurice-Lamontagne Institute, Mont-Joli, Quebec) for assisting in the collection of samples during research cruises in February 1990 and January 1995. Gratitude is also extended to Ione von Herbing (University of Maine) and Mark

Tupper who assisted in sampling from cruises in October of 1990 and 1991, and June 1992, and to Treena Skory, who participated in the June 1992 and August 1993 cruises, conducted pepsin-HCl digestions, and measured nematodes. We would finally like to thank Andrew Bauder (National Research Council, Halifax, NS), who helped with collections from an October 1996 cruise, and Jason Melendy (Gulf Fisheries Centre, Moncton, N.B.) who assisted in revisions to tables and graphics.

REFERENCES

Aspholm, P.E., Ugland, K.E., Jødestøl, K.A., and Berland, B. 1995. Sealworm (*Pseudoterranova decipiens*) infection in common seals (*Phoca vitulina*) and potential intermediate hosts from the outer Oslofjord. *Int. J. Parasitol*. 25: 367-373.

Benoit, D. and Bowen, W.B. 1990a. Seasonal and geographical variation in the diet of grey seals (*Halichoerus grypus)*. In Bowen, W.D. (ed). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 215-226.

Benoit, D. and Bowen, W.B. 1990b. Summer diet of grey seals (*Halichoerus grypus*) at Anticosti Island, Gulf of St. Lawrence, Canada. In Bowen, W.D. (ed). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 227-242.

Bliss, C.I. 1967. *Statistics in Biology*. Vol. I. McGraw-Hill Book Co., Toronto. xiii + 558pp.

Boily, F., and Marcogliese, D.J. 1995. Geographical variations in abundance of larval anisakine nematodes in Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) from the Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci*. 52 (Suppl. 1): 105-115.

Boulva, J., and McLaren, I.A. 1979. Biology of the harbour seal, *Phoca vitulina*, in eastern Canada. *Bull. Fish. Res. Board of Can*. 200: 1-24.

Bowen, W.D. (ed). 1990. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 306pp.

Bowen, W.D. and Harrison, G.D. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Can. J. Zool*. 74: 125-135.

Bowen, W.D., Lawson, J.W. and Beck, B., 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci*. 50: 168-178.

Brattey, J., and Davidson, W.S. 1996. Genetic variation within *Pseudoterranova decipiens* (Nematoda: Ascaridoidea) from Canadian Atlantic marine fishes and seals: characterization by RFLP analysis of genomic DNA. *Can. J. Fish. Aquat. Sci*. 53: 33-341.

des Clers, S., and Anderson, K. 1995. Sealworm (*Pseudoterranova decipiens*) transmission to fish trawled from Hvaler, Oslofjord, Norway. *J. Fish Biol*. 46: 8-17.

Li, J.C.R. 1964. *Statistical Inference*. Vol. I. Edwards Bros. Inc., Ann Arbor, MI. 658 pp.

Marcogliese, D.J. 1995. Geographic and temporal variations in levels of anisakid nematode larvae among fishes in the Gulf of St. Lawrence, eastern Canada. *Can. Tech. Rep. Fish. Aquat. Sci.* 2029: viii + 16 pp.

Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M., and Schad, G.A. 1982. The use of ecological terms in parasitology (report of an *ad hoc* committee of the American Society of Parasitology). *J. Parasitol*. 68: 131-133.

Martell, D.J. and McClelland, G. 1994. Diets of sympatric flatfishes, *Hippoglossoides platessoides* (Fabricius), *Pleuronectes ferrugineus* (Storer), *Pleuronectes americanus* (Walbaum), from Sable Island Bank, Canada. *J. Fish Biol*. 44: 821-848.

Martell, D.J. and McClelland, G.. 1995. Transmission of *Pseudoterranova decipiens*(Nematoda: Ascaridoidea) via benthic macrofauna to sympatric flatfishes (*Hippoglossoides platessoides, Pleuronectes ferrugineus, Pleuronectes americanus*) on Sable Island Bank, Canada. *Mar. Biol*. 122: 129-135.

McClelland, G. 1990. Larval sealworm (*Pseudoterranova decipiens*) infections in benthic macrofauna. In Bowen, W.D. (ed). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 47-65.

McClelland, G. 1995. Experimental Infection of fish with larval sealworm, *Pseudoterranova decipiens* (Nematoda, Anisakinae), transmitted by amphipods. *Can. J. Fish. Aquat. Sci*. 52 (Suppl. 1): 140-155.

McClelland, G. 2000. Natural transmission of larval sealworm *Pseudoterranova decipiens* to juvenile Canadian plaice *Hippoglossoides platessoides* and other small benthic consumers. *Bull. Can. Soc. Zool*. 31: 83.

McClelland, G. and Martell, D.J. 2001. Spatial and temporal distributions of larval sealworm, *Pseudoterranova decipiens* (Nematoda; Anisakinae), in *Hippoglossoides platessoides*, in the Canadian Maritime Region from 1993 to 1999. *NAMMCO Sci. Publ*. 3 : 57 - 76.

McClelland, G. and Ronald, K. 1974. The *in vitro* development of *Terranova decipiens* (Nematoda) (Krabbe, 1878). *Can. J. Zool.* 52: 471-479.

McClelland, G., Misra. R.K., and Martell, D.J. 1990. Larval anisakine nematodes in various fish species from Sable Island Bank and vicinity. In Bowen, W.D. (ed.). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 83-118.

McClelland, G., Misra. R.K., and Martell, D.J. 2000. Spatial and temporal distributions of larval sealworm (*Pseudoterranova decipiens*, Nematoda: Anisakinae), in *Hippoglossoides platessoides* (Pleuronectidae) in eastern Canada from 1980 to 1990. *ICES J. Mar. Sci*. 57: 69-88.

Mohn, R., and Bowen, W.D. 1996. Grey seal predation on the eastern Scotian Shelf: modeling the impact on Atlantic cod. *Can. J. Fish. Aquat. Sci*. 53: 2722-2738.

Neter, J., Wassermann, W., and Kutner, M.H. 1985. *Applied Linear Statistical Models: Regression, Analysis of Variance, and Experimental Design.* Homewood: Richard D. Irwin Inc.. Homewood, IL. 1127 pp.

Paggi, L., Matiucci, S., Gibson, D.I., Berland, B., Nascetti, G., Cianchi, R., and Bullini, L. 2000. *Pseudoterranova decipiens* species A and B (Nematoda: Ascaridoidea): nomenclatural designation, morphological diagnostic characters and genetic markers. *Syst. Parasitol*. 45: 185-197.

Pálsson, J. (MS) 1979. Larval ascaridoid nematodes in young cod (age classes 0-III) from Icelandic waters. M.Sc. thesis, Univ. of Southern Mississippi.

Platt, N.E. 1975. Infestation of cod (*Gadus morhua* L.) with the larvae of codworm (*Terranova decipiens*) and herringworm, *Anisakis* sp. (Nematoda: Ascaridata) in North Atlantic and Arctic waters. *J. Appl. Ecol*. 12: 437 450.

Power, H.E. 1961. Slicing of fillets as an aid in detection and removal of codworms from Atlantic cod fillets. *J. Fish. Res. Bd. Can*. 18: 137-140.

Scott, D.M., and Martin, W.R. 1957. Variation in the incidence of larval nematodes in Atlantic cod fillets along the southern Canadian mainland. *J. Fish. Res. Bd. Can*. 14: 975-996.

Scott, D.M., and Martin, W.R. 1959. The incidence of nematodes in the fillets of small cod from Lockeport, N.S. and the southwestern Gulf of St. Lawrence. *J. Fish. Res. Bd. Can*. 16: 213-221.

Scott, W.B. and Scott, M.G. 1988. Atlantic Fishes of Canada. *Can. Bull. Fish. Aquat. Sci*. 219: 1-731.

Templeman, W., Squires, H.J., and Fleming, A.M. 1957. Nematodes in the fillets of cod and other fishes in Newfoundland and neighboring areas. *J. Fish. Res. Bd. Can*. 14: 831-897.

Wootten, R. and Waddell, J.F. 1977. Studies on the biology of larval nematodes from the musculature of cod and whiting in Scottish waters. *J. Cons. Int. Explor. Mer.* 37: 266-273.

Young, P.C. 1972. The relationship between the presence of larval Anisakine nematodes in cod and marine mammals in British home waters. *J. Appl. Ecol*. 9: 459-485.

Zwanenburg, K.T.C., and Bowen, W.D. 1990. Population trends of the grey seal (*Halichoerus grypus*) in eastern Canada. In Bowen, W.D. (ed). Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. *Can. Bull. Fish. Aquat. Sci*. 222: 185-197.