Spatial and temporal distributions of larval sealworm, *Pseudoterranova decipiens* (Nematoda: Anisakinae), in *Hippoglossoides platessoides* (Pleuronectidae) in the Canadian Maritime Region from 1993 to 1999

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ABSTRACT

Spatial and temporal trends of larval sealworm (*Pseudoterranova decipiens*) infection in eastern Canadian groundfish were monitored in an indicator host, Canadian plaice (*Hippoglossoides platessoides*), in the 31 to 40 cm length range. Between February 1993 and September 1999, a total of 8,482 plaice were collected from 33 locations in Canadian Maritime waters (NAFO Subdivisions 4TVWX-5ZE), and their fillets and napes were examined for sealworm. Prevalence (P) and abundance (A) of the parasite were greatest (P ranging from 95 to 100%, A from 7.48 to 15.60) in fish collected from the central Scotian shelf (4VSW) near Sable Island, site of the largest grey seal (*Halichoerus grypus*) colony in the northwest Atlantic, and from Jordan Basin in the northeastern Gulf of Maine (4X). The infection of greatest intensity (I=158) occurred in a fish from "The Gully" slopewaters of Banquereau (4VS), a few kilometres northeast of Sable Island. By 1995-99, sealworm prevalence and/or abundance had increased significantly in plaice from most locations where stable or declining infection parameters were observed from 1989 to 1993, but abundance of the parasite continued to decline in the Sable Island area. While spatial and temporal distributions of larval sealworm in plaice seemed largely related to the distribution and growth of grey seal populations, the influence of definitive hosts was probably mitigated by other factors such as changes in environmental temperature and parasite density limiting effects in the indicator host.

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INTRODUCTION

The "sealworm index" time series was established to monitor spatial and temporal trends of larval sealworm (*Pseudoterranova decipiens*) infection in eastern Canadian groundfish, through surveys of a single "indicator" host (McClelland *et al.* 2000). Although Atlantic cod (*Gadus morhua*) has been frequently surveyed for larval sealworm in the North Atlantic (Scott and Martin 1957, Templeman *et al.* 1957, Young 1972, McClelland *et al.* 1983a, 1983b, 1985, Platt 1975, Hauksson 1984, Brattey *et al.* 1990, McClelland and Marcogliese 1994, des Clers and Andersen 1995, Boily and Marcogliese 1995), *Hippoglossoides platessoides*, commonly known as Canadian (McAllister 1990) or American plaice (retained by Robins *et al.* 1991) was chosen as the indicator host following the rationale of McClelland *et al.* (1983b, 1985, 2000).

Between June 1983 and October 1990, index surveys were conducted biennially throughout eastern Canada, from Labrador (NAFO subdivision 2J) to the Gulf of Maine (4X-5ZE) (McClelland *et al.* 1985, 1987, 2000). Samples were taken from 38 to 55 locations in the 1983-84, 1985-86, 1987-88 and 1989-90 surveys. Also included in the time series were earlier (1980-82) samples from 11 locations in the southern Gulf of St. Lawrence (4T), and on the Breton (4VN), and central and eastern Scotian shelves (4VSW) (McClelland *et al.* 1983a, 1983b). Prevalence (P) and abundance (A) of *P. decipiens* were greatest (P ranging from 96 to 100%, A from 12.47 to 22.32) in 1989-90 samples from the central Scotian Shelf near Sable Island (4W), while plaice from northeastern Newfoundland and the Grand Banks (3KLNO) were seldom infected (P<1%) (McClelland *et al*. 2000). Temporal trend analyses revealed that, between 1980 and 1990, sealworm infection levels increased significantly in plaice from 33 of 41 locations in the Gulf of St. Lawrence, on the Breton and Scotian shelves, and in the Gulf of Maine. Spatial and temporal distributions of larval *P. decipiens* in plaice seemed to reflect the distribution and growing abundance of grey seals (*Halichoerus grypus*), important definitive hosts of the parasite, but may also have been influenced by relatively warm near-bottom temperatures prevalent in eastern Canada during the late seventies and early eighties (McClelland *et al*. 2000).

As a consequence of declining plaice stocks and changing research priorities, it became increasingly difficult to obtain samples from Labrador, northeastern and southern Newfoundland, and the northern Gulf of St. Lawrence, and, since 1990, surveys were confined to the Canadian Maritime region (4TVWX-5ZE). The present study documents infection parameters of larval sealworm in Canadian plaice sampled in the Maritimes between February 1993 and September 1999 along with, for the sake of continuity, 1987–90 data from McClelland *et al.* (2000). Changes in sealworm prevalence and abundance since the late 1980s are analysed, and biotic and abiotic factors that may have influenced infection parameters in our indicator host are also discussed.

MATERIALS AND METHODS

Canadian plaice were sampled from the 'Alfred E. Needler' during Department of Fisheries and Oceans (DFO) groundfish surveys conducted in the southern Gulf of St. Lawrence (NAFO subdivision 4T) in September 1995, 1998 and 1999. Samples were also collected on the Breton (4VN) and Scotian (4VS-W-X) shelves, and in the Gulf of Maine (4X-5ZE) from groundfish cruises in February, March and July of 1993 and 1996, and September 1995, and during dedicated surveys of 4VWX plaice in August 1993 and October 1996 (Fig.1). Samples consisted primarily of fish in the 31-40 cm length range (n = 7,158), but "extended" samples, including fish ≤30, and ≥41 cm total length (TL) (n = 1,324), were taken at six 4VS-W locations in 1996, and from Georges Bank (5ZE) in 1993 and 1996. Plaice were bagged, labelled, frozen at sea, and stored in a -17°C walk-in freezer on return to the Halifax Fisheries Research Laboratory, Halifax, Nova Scotia. Prior to inspection, the fish were allowed to thaw for 24 h at room temperature (18 to 22° C). After TL, weight, and sex were recorded, each fish was boned, and fillets, napes (hypaxial musculature enclosing the body cavity) and flesh which remained on the frame were examined for nematodes by slicing, candling

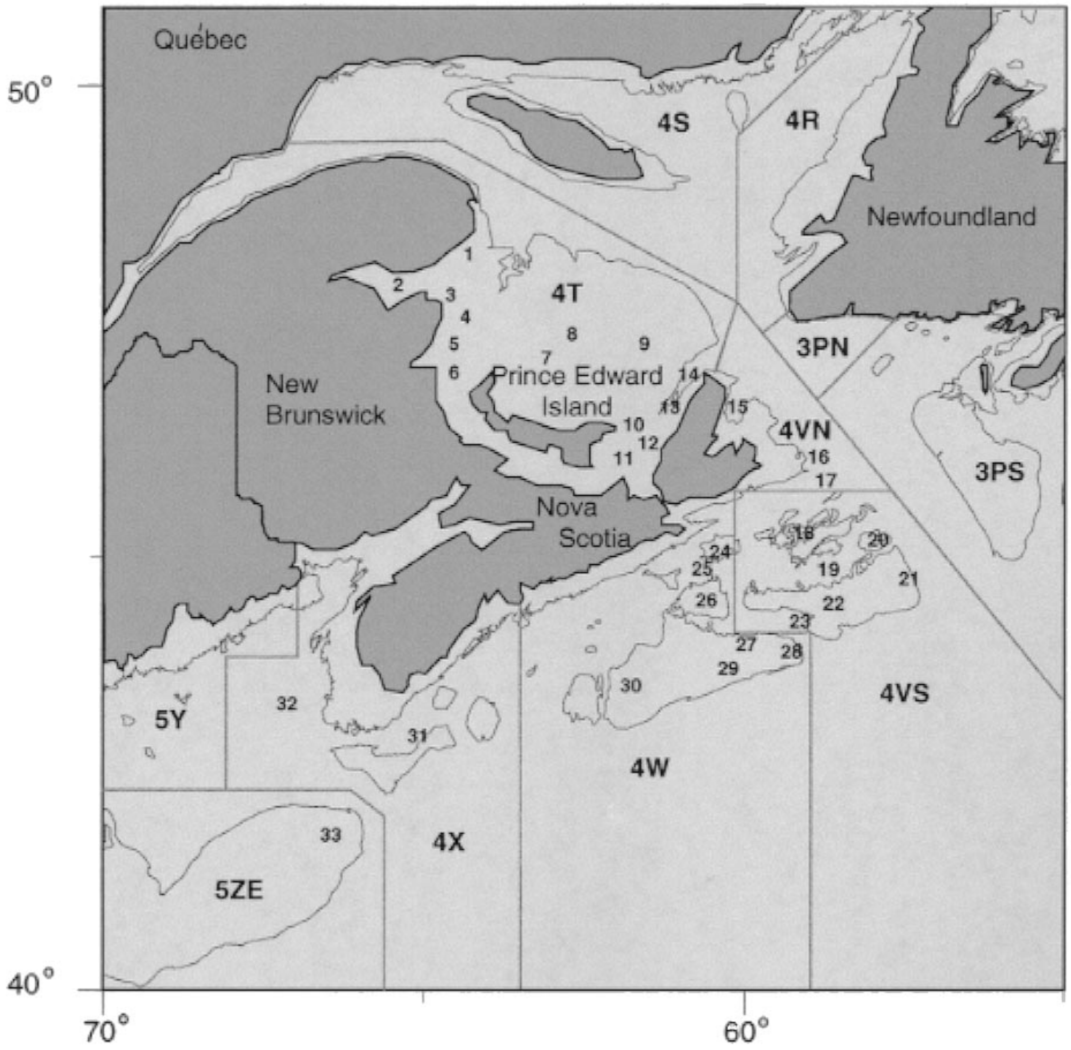


Fig. 1
Sampling locations for surveys of spatial and temporal distributions of larval sealworm, <u>Pseudoterranova decipiens</u>, in 31-40 cm (TL) Canadian plaice (<u>Hippoglossoides platessoides</u>) in the Canadian Maritime region (4TVWX, 5ZE) from 1993 to 1999; refer to Tables 1-3 for names of locations.

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 during boning and slicing of flesh. Because larval sealworm is seldom found in the body cavity of plaice (McClelland *et al.* 1983a), the viscera were not inspected. It was assumed that all sealworm larvae encountered in this survey were *P. decipiens* sibling species B, or, as recently proposed by Paggi *et al.* (2000), *P. decipiens* (*sensu stricto*). While both *P. decipiens* species B and C occur in pinnipeds and fish in eastern Canada (Paggi *et al.* 1991), species C, or *P. bulbosa* (Mattiucci *et al.* 1998), has been reported only from the more northerly waters of Labrador and northeastern Newfoundland (Brattey and Davidson 1996). Moreover, the larvae of species C (*P. bulbosa*) are found primarily in the body cavity of fish hosts (Bristow and Berland 1992).

Quantitative parameters of infection such as prevalence (P), abundance (A), intensity (I), and density (D) are defined according to Margolis *et al.* (1982). Data from the 1989-90, and, for some locations, from the 1987-88 survey were included in analyses of temporal variations of infection parameters. Variations in prevalence and abundance were analysed by one-way ANOVA (SYSTAT) of time series samples nested within location (McClelland *et al*. 1987, 2000). In 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 (Sokal and Rohlf 1969, Platt 1975). Significance of *F* values for contrasts were tested at 1% Bonferroni probability (Morrison 1976).

RESULTS

Between February 1993 and October 1996, filets and napes of 8,482 Canadian plaice, predominantly in the 31 to 40 cm length range (n = 6,892), were examined for larval sealworm. Plaice examined included 2,549 sampled from the Breton (4VN) and Scotian shelves (4VS-WX), and Gulf of Maine (4X-5ZE) in 1993; 4,427 collected from southern Gulf of St. Lawrence (4T) and 4VWX-5ZE in 1995-96, and 1506 taken from 4T groundfish cruises in September of 1998 and 1999.

Southern Gulf of St. Lawrence (4T)
In 1995, 1,411 plaice in the 31 to 40 cm length range were collected from 12 locations in the southern Gulf of St. Lawrence. Southeastern Gulf fish were generally more heavily infected than those from southwestern 4T, and the most heavily infected fish overall (P ranging from 87 to 97%, A, from 2.73 to 6.94) were found off southeastern Prince Edward Island (PEI), southwestern Cape Breton, and the St. Georges Bay area of mainland Nova Scotia (Table 1). Contrasts of infection parameters in 1995 and 1989 (or 1987-88) samples from 10 southern Gulf locations reveal that sealworm prevalence and abundance were significantly greater in the more recent samples of plaice from Baie des Chaleurs, the Magdelen Shoals, St. Georges Bay and Chéticamp, and that there was also a significant increase in abundance of the parasite in Bradelle Bank fish. Temporal disparities in infection levels in plaice from Banc Miscou, the north Shediac Valley, Port Hood and the Cape Breton Channel were not significant, while declines in prevalence and abundance were confined to fish from the Gaspé Peninsula.

A total of 1,506 plaice were sampled from 13 4T locations in 1998-99. While the heaviest infections occurred in samples from St. Georges Bay, southeastern PEI and southwestern Cape Breton, infection levels in southwestern Gulf plaice (P = 82 to 92%; A = 2.10 to 3.15) now rivalled those found in fish from the southeastern Gulf (P = 87 to 97%; A = 2.27 to 6.94). Contrasts of 1995 and 1998-99 samples at 11 locations reveal that infection levels had increased significantly at five southwestern Gulf locations, including Gaspé, Baie des Chaleurs, North Shediac Valley, northwestern PEI. and Bradelle Bank, while the only significant change observed at southeastern Gulf sites between 1995 and 1998-99 was an increase in sealworm abundance in plaice from St. Georges Bay. Contrasts of 1998-99 and 1989 (or 1987-88) samples, however, indicate that infection parameters were significantly greater in the more recent samples at four of five southeastern, and five of six southwestern Gulf locations.

Breton and eastern Scotian shelves (4V)
In 1993, 1,173 plaice, 31 to 40 cm (TL) in length were collected from 9 sampling sites in 4V. Among Breton Shelf (4VN) plaice, sealworm was most prevalent (P = 85%) and abundant (A = 3.52) in fish from Smoky Channel, while on the eastern Scotian Shelf (4VS), infection parameters were greatest (P = 85 to 94%; A = 3.62 to 8.12) in samples from Banquereau (Table 2). The lightest infections (P = 58 to 65%; A = 1.41 to 1.87) occurred in fish from adjacent locations in southeastern 4VN and Misaine Bank (4VS). The infection of greatest intensity (I = 63) was found in a specimen from “The Gully” slopewaters of Banquereau.

A total of 1,053 plaice (31 to 40 cm TL) were taken from the same 9 sites in 1995-96. Again, infection parameters were greatest (P = 85 to 100%; A = 4.49 to 12.43) in Smoky Channel and Banquereau fish, and the most intense infection (I = 158) was found in a plaice taken from “The Gully” slopewaters of Banquereau. Plaice from Misaine Bank had the lightest infections (P = 57%; A = 1.35).

ANOVA of sealworm infection parameters in 1989, 1993 and 1995-96 samples reveals significant variation in prevalence and/or abundance at six of 9 locations in 4V (Table 2). Abundance of larval *P. decipiens* in plaice from the Smoky Channel (4VN), east Misaine Channel, and central and western Banquereau (4VS) increased

Table 1. Prevalence (P), abundance (A) and maximum intensity (I_{max}) of larval *Pseudoterranova decipiens* infection in *Hippoglossoides platessoides*, 31-40 cm in length, from the southern Gulf of St. Lawrence, with temporal contrasts of prevalence and abundance.

Host Location (map reference)[1]	Sample No.	Sample year(s)	N	*P. decipiens* infection P	A	I_{max}	Infection parameter	Significance of variation[2] Temporal	Contrasts of samples 1&2	1&3	2&3
Gaspé (1)	1	1989	149	50	0.91	16	P	**	*	**	**
	2	1995	144	36	0.58	11	A	**	*	**	**
	3	1998	48	85	2.10	12					
Baie des Chaleurs (2)	1	1987-88	247	67	1.58	8	P	**	**	**	**
	2	1995	79	82	2.17	10	A	**	*	**	**
	3	1998	26	92	2.85	9					
Banc Miscou (3)	1	1987-88	187	57	1.39	21	P	—			
	2	1995	44	75	1.71	5	A	—			
N Shediac Valley (research) (4)	1	1989-90	181	60	1.13	9	P	**	—	**	**
	2	1995	120	60	1.19	8	A	**	—	**	**
	3	1998	105	82	2.32	11					
Shediac Valley (Tracadie) (5)	1	1989	196	83	2.11	9	P	—			
	2	1998	39	92	3.15	13	A	*			
Shediac Valley (Miramichi) (6)	1	1989	58	83	2.86	13	P	—			
	2	1998	49	92	2.89	8	A	—			
North P.E.I. (7)	1	1995	107	79	2.42	19	P	*			
	2	1998	326	90	2.92	38	A	*			
Bradelle Bank (8)	1	1989-90	185	56	1.26	11	P	**	—	**	*
	2	1995	86	63	1.84	9	A	**	*	**	-
	3	1998	101	82	2.37	24					
Magdalen Shoals (9)	1	1987-88	535	66	1.83	37	P	**	**	**	—
	2	1995	294	81	2.47	33	A	**	**	**	—
	3	1998	124	88	2.51	14					
Souris (10)	1	1995	98	97	5.12	23	P	—			
	2	1998	149	97	5.64	21	A	—			
St. Georges Bay (11)	1	1989-90	184	85	3.26	38	P	**	***	***	—
	2	1995	155	96	4.79	32	A	***	**	***	***
	3	1999	266	97	6.94	41					
Cape Breton Shoals (12) (Port Hood)	1	1989-90	175	79	2.51	29	P	—	—	*	—
	2	1995	97	87	2.73	8	A	*	—	**	—
	3	1998	96		91	3.46	32				
Cape Breton Shoals (13) (Chéticamp)	1	1989-90	202	65	2.07	21	P	**	**	**	—
	2	1995	106	92	2.93	22	A	**	**	*	—
	3	1998	135	87	2.27	16					
Cape Breton Channel (14)	1	1987-88	233	65	1.58	23	P	—	—	—	—
	2	1995	81	68	1.48	11	A	—	—	—	—
	3	1998	42	69	1.64	10					

1 See Fig. 1.
2 Significance when probability (Pr) ≤0.01 (*), ≤0.001 (**), and ≤0.0001 (***).

between 1989 and 1995-96. Infection parameters in southwestern Breton Shelf plaice fell significantly in 1993, but recovered in 1995. A net decline in sealworm parameters between 1989 and 1996 was evident only in samples from Louisbourg Hole.

Table 2. Prevalence (P), abundance (A) and maximum intensity (I_{max}) of larval *Pseudoterranova decipiens* infection in *Hippoglossoides platessoides*, 31-40 cm in length, from the Breton and eastern Scotian shelves, with temporal contrasts of prevalence and abundance.

Host Location (map reference)[1]	Sample No.	Sample year(s)	N	*P. decipiens* infection P	A	I_{max}	Infection parameter	Significance of variation[2] Temporal	Contrasts of samples 1&2	1&3	2&3
Smoky Channel (15)	1	1989	140	89	2.83	13	P	—	—	—	—
	2	1993	33	85	3.52	12	A	*	—	**	—
	3	1995	83	94	4.61	19					
SE Breton Shelf (16)	1	1989	143	86	2.95	28	P	***	***	—	***
	2	1993	165	58	1.41	13	A	***	***	—	***
	3	1996	122	84	2.30	11					
Louisbourg Hole (17)	1	1989	161	80	2.58	16	P	*	*	*	—
	2	1993	161	65	1.61	14	A	*	*	*	—
	3	1996	147	63	2.26	55					
Misaine Bank (19)	1	1989	110	68	1.89	21	P	—	—	—	—
	2	1993	105	65	1.87	34	A	—	—	—	—
	3	1996	113	57	1.35	17					
East Misaine Channel (20)	1	1989	119	80	2.11	15	P	—	—	—	—
	2	1993	176	80	2.92	34	A	—	—	**	—
	3	1996	99	84	3.50	51					
Artimon Bank (21)	1	1989	130	88	2.72	20	P	—	—	—	—
	2	1993	128	78	2.81	24	A	—	—	—	—
	3	1996	162	83	2.94	27					
East Banquereau (22)	1	1989	133	87	3.62	21	P	—	—	—	—
	2	1993	152	85	3.92	26	A	—	—	—	—
	3	1996	127	85	4.49	48					
Central Banquereau (23)	1	1989	121	89	3.84	21	P	—	—	—	—
	2	1993	122	88	5.05	38	A	*	—	**	*
	3	1996	142	96	6.37	38					
Edge of Gully (24)	1	1989	148	89	5.79	61	P	—	—	*	—
	2	1993	131	94	8.12	63	A	***	*	***	—
	3	1996	58	100	12.43	158					

1 See Fig. 1.

2 Significance when probability (Pr) ≤ 0.01 (*), ≤0.001 (**), and ≤0.0001 (***).

Central and western Scotian Shelf and Gulf of Maine (4WX-5ZE)

Samples from 4WX-5ZE included 1,222 plaice (31 to 40 TL) collected from 9 locations in 1993, and 793 taken from eight sites in 1996. In 1993, the heaviest infections (P = 94 to 97%; A = 7.48 to 13.37) occurred in fish from the vicinity of Sable Island (4W), and the lightest (P = 32 to 40%; A = 0.59 to 0.64), in Roseway Basin (4X) and Georges Bank (5ZE) fish (Table 3). In 1996, heavily infected fish (P = 89 to 100%; A = 7.28 to 15.60) were found, not only in plaice from the Sable Island area, but also in those from Jordan Basin in the northeastern Gulf of Maine (4X). The most intense infection (I = 92) occurred in a Jordan Basin fish.

ANOVA of infection parameters in 1989-90, 1993 and 1996 samples from 4WX-5ZE indicates significant change in sealworm prevalence and/or abundance at 7 of 10 locations (Table 3). While infection parameters in plaice from banks on the central Scotian Shelf (4W) declined, significant increases in sealworm abundance were observed in fish from deeper waters in Canso Hole (4W), and Roseway and Jordan Basins (4X) between 1993 and 1996. Infection parameters in Georges Bank (5ZE) plaice collapsed in 1993, but rebounded in 1996.

Extended samples

Samples taken from six 4VWX locations in 1996 were "run of the catch", including additional plaice (n = 1,037), in the 5 to 30 cm length range. Plaice in the 8 to 30 and 41 to 61 cm length ranges were also taken with "index" samples from Georges Bank (5ZE) in 1993 (n = 154) and 1996 (n = 133). Sealworm prevalence and

Table 3. Prevalence (P), abundance (A) and maximum intensity (I_{max}) of larval *Pseudoterranova decipiens* infection in *Hippoglossoides platessoides*, 31-40 cm in length, from the central and southwestern Scotian Shelf, and the Gulf of Maine, with temporal contrasts of prevalence and abundance.

Host Location (map reference)[1]	Sample No.	Sample year(s)	N	P. decipiens infection P	P. decipiens infection A	P. decipiens infection I_{max}	Infection parameter	Significance of variation[2] Temporal	Contrasts of samples 1&2	Contrasts of samples 1&3	Contrasts of samples 2&3
Canso Bank (25)	1	1989	123	81	2.83	28	P	—	*	—	—
	2	1993	120	65	2.06	32	A	*	**	*	—
	3	1996	93	68	1.77	8					
Canso Hole (26)	1	1989	130	73	2.22	30	P	—	—	*	—
	2	1993	119	76	2.13	17	A	***	—	***	***
	3	1996	111	87	5.34	43					
Middle Bank (27)	1	1989	59	100	17.98	128	P	—	—	—	—
	2	1993	142	94	13.37	82	A	***	*	***	**
	3	1996	47	89	7.28	53					
North Sable Is. Bank (28)	1	1989-90	178	96	12.47	114	P	—	—	—	—
	2	1993	96	94	9.01	53	A	—	—	—	—
	3	1996	90	92	8.83	77					
East Sable Is. Bank (29)	1	1989-90	192	98	22.32	122	P	—	—	—	—
	2	1996	30	100	15.60	42	A	—			
SW Sable Is. Bank (30)	1	1989-90	252	100	17.53	82	P	**	—	—	—
	2	1993	155	95	7.48	49	A	***			
Western Bank (31)	1	1989	104	98	12.64	59	P	—	—	—	—
	2	1993	108	97	10.65	68	A	—			
Roseway Basin (32)	1	1989	118	48	0.95	8	P	*	—	—	*
	2	1993	137	40	0.64	5	A	***	—	*	***
	3	1996	110	60	1.86	34					
Jordan Basin (33)	1	1989-90	91	93	4.77	24	P	—	—	—	—
	2	1993	108	88	4.35	23	A	***	—	*	***
	3	1996	108	95	9.06	94					
Georges Bank (34)	1	1989-90	100	51	1.46	11	P	***	*	—	***
	2	1993	237	32	0.59	11	A	***	**	—	***
	3	1996	204	63	1.61	23					

1 See Fig. 1.
2 Significance when probability (Pr) $\leq$ 0.01 (*), $\leq$ 0.001 (**), and $\leq$ 0.0001 (***).

abundance increased with host length in fish from each of three 4V locations, Louisbourg Hole, Misaine Bank, and east Banquereau, as well as in Roseway Basin (4X) fish (Fig. 2). Notably, sealworm were not found in fish ranging from 6 to 30 cm in length (n = 127), from a single set (no. 97, July 1996 Groundfish Cruise) on the western half of Misaine Bank. In fish of "index" size (31 to 40 cm in length) from the same set, sealworm prevalence of was 47%, and abundance, 1.00, (n = 30), and 8 of 10 fish (A = 2.30) in the 36 to 40 cm length range were infected. In contrast, sealworm prevalence and abundance in Middle Bank plaice peaked in 16 to 25 cm fish, and there were no consistent relationships between infection parameters and host length in Georges Bank samples.

DISCUSSION

The spatial and temporal distributions of larval *Pseudoterranova decipiens* in eastern Canadian groundfish seem to be related, primarily, to the geographical distribution and growth of Northwest Atlantic grey seal populations. Sealworm infection parameters recorded in Canadian plaice and other groundfish species over the past two decades (McClelland *et al.* 1983a, 1983b, 1985, 1987, 2000, Boily and Marcogliese 1995, Marcogliese 1996, Marcogliese 2001, McClelland and Martell 2001) were greatest in fish from southern Newfoundland (3P), the Gulf of St. Lawrence (4RST), the Breton and Scotian Shelves (4VWX), and the northeastern Gulf of Maine

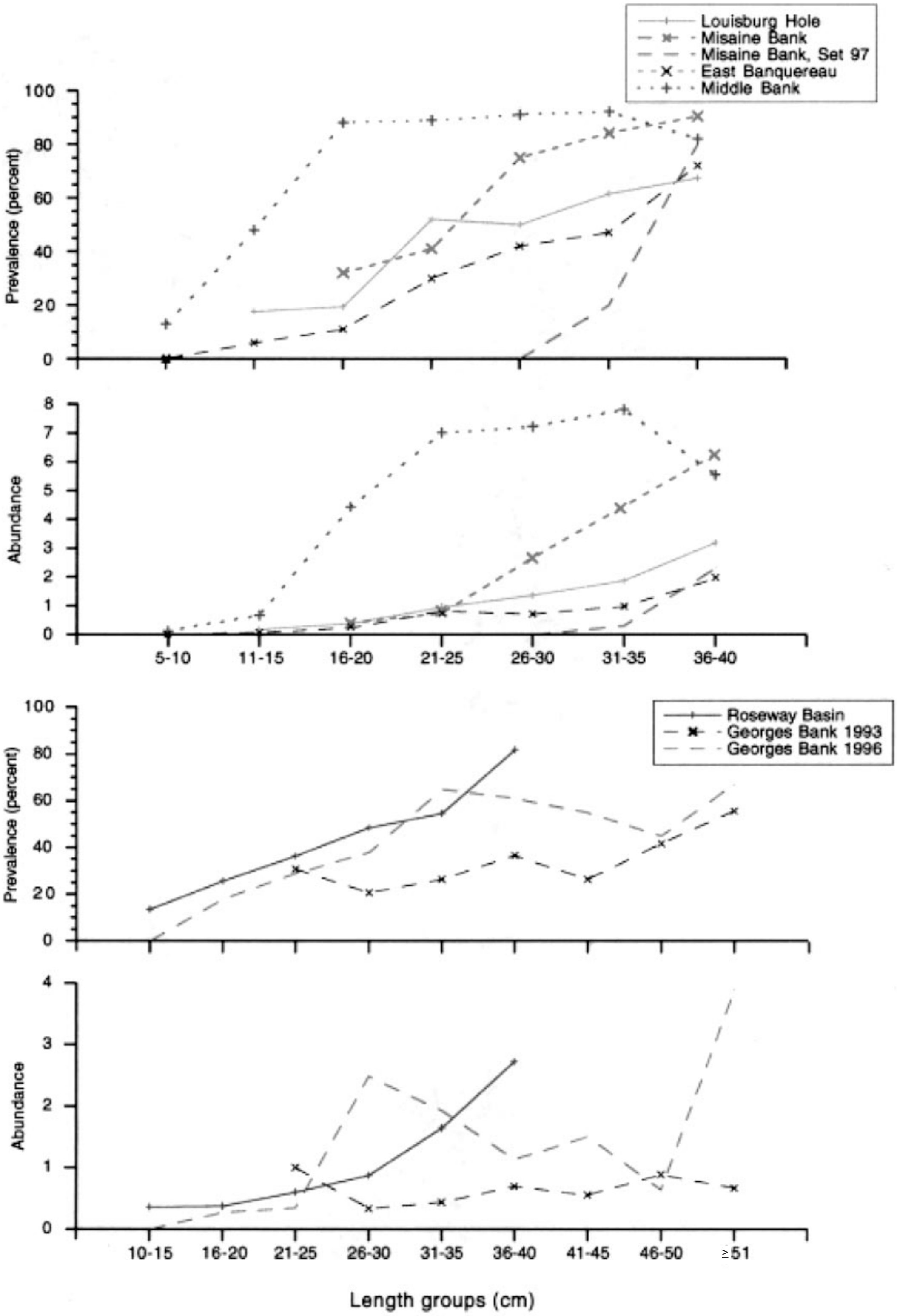


Fig. 2
Variations in prevalence and abundance of larval sealworm (<u>Pseudoterranova decipiens</u>) infection with length of host Canadian plaice (<u>Hippoglossoides platessoides</u>) from the Breton and Scotian shelves, and the northeastern Gulf of Maine.

(4X-5ZE) (Fig. 1). These areas encompass the majority of grey seal breeding and haulout sites in eastern Canada (Stobo *et al.* 1990). By 1980-84, sealworm infection parameters in 4RS (Northern Gulf of St. Lawrence), 4VW and 4X-5ZE cod and flatfishes (McClelland *et al.* 1983a, 1983b, 1985) were higher than those documented three decades earlier (Scott and Martin

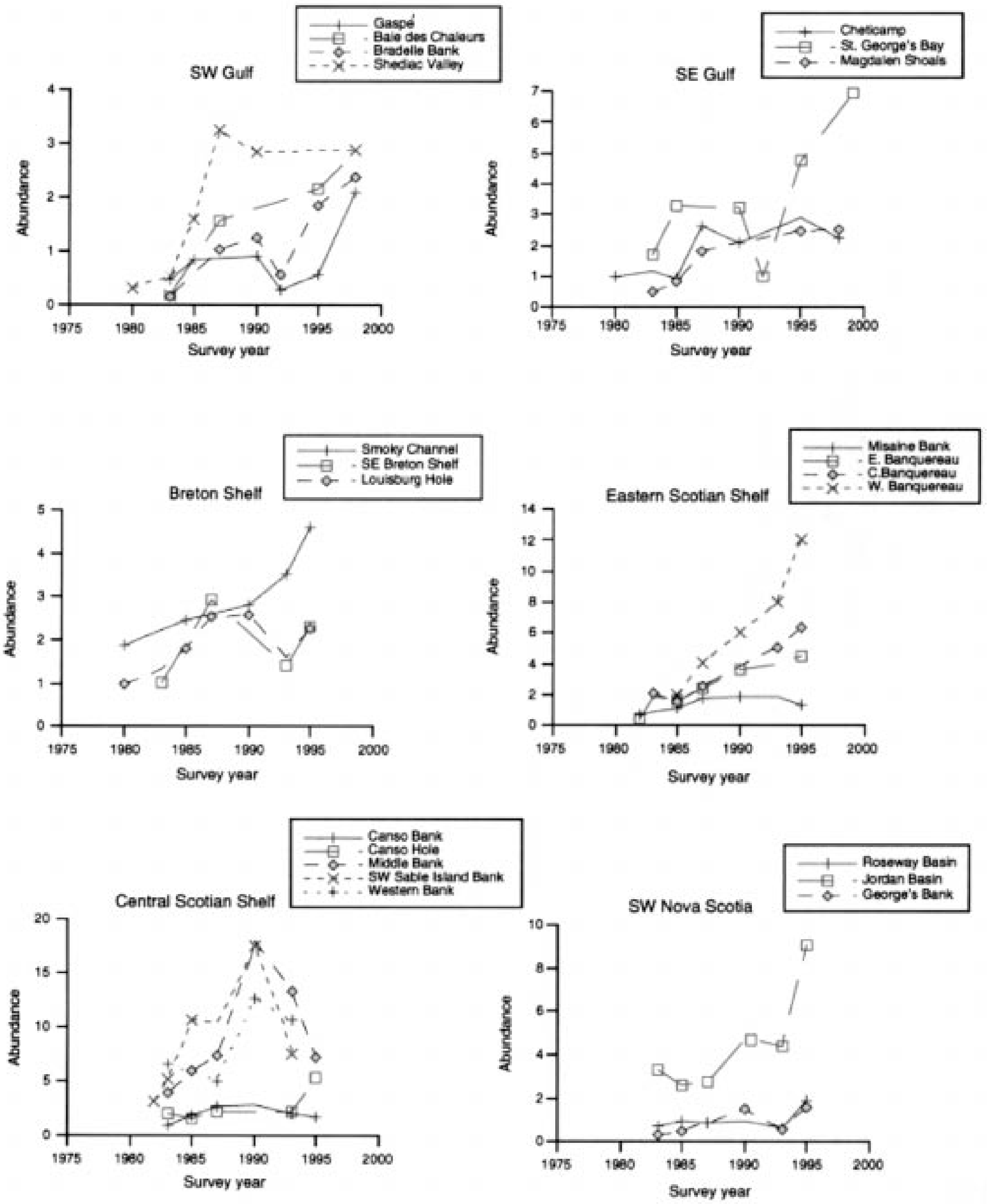
1957, Templeman *et al*. 1957), but there appeared to have been little or no change in infection parameters in groundfish from the southern Gulf of St. Lawrence (4T). Temporal trend analyses of infections in Canadian plaice collected from 1980 to 1990 revealed continued increases of sealworm prevalence at 19 of 33, and abundance, at 22 of 33 locations in 3P, 4RS and 4VWX-5ZE. Between 1983 and 1990, however, prevalence also increased significantly at 10, and abundance, at 11 of 12 4T locations (McClelland *et al.* 2000).

Prior to 1990, the most dramatic increases in larval sealworm parameters occurred in groundfish from the central and eastern Scotian Shelf (4VW) near Sable Island (McClelland *et al*. 1983b, 1990, 2000) (Fig. 3). This may be attributable to the fact that the Sable Island component of the eastern Canadian grey seal population grew by more than 20 fold between the early 1960s and 1988, whereas the remainder of the population, partly as a consequence of a DFO bounty program and a cull/controlled commercial hunt, is estimated to have increased by only two- to five- fold (Zwanenburg and Bowen 1990). Zwanenburg and Bowen (1990) speculate that, following the cessation of the annual cull of ice-breeding seals in the southeastern Gulf of St. Lawrence in 1983, the growth of the Gulf grey seal population may have accelerated to an exponential rate. It is, perhaps, no coincidence that sealworm infection parameters in 4T plaice appeared to remain stable from the 1950s to the early 1980s (McClelland *et al*. 1985), but increased significantly in the mid- to late 1980s (McClelland *et al.* 2000) after the suspension of the cull. As evident in the present study (Fig. 3), sealworm infections appeared to collapse or plateau in plaice from many sites in eastern Canada during the late 1980s to early 1990s. A resumption of positive trends in sealworm prevalence and/or abundance has since been observed in plaice from most the latter locations with the exception of those sampled from the central Scotian Shelf near Sable Island.

While grey seals are the most important definitive hosts of *P. decipiens* in Atlantic Canada (Marcogliese *et al.* 1996, Marcogliese 2001), other seal species may also have a significant impact on larval sealworm levels in groundfish. *Pseudoterranova decipiens* B (*sensu stricto*) commonly occurs in harbour seals (Brattey and Stenson 1993), and, as there is no evidence of reproductive isolation, cross infection between harbour and grey seals and interbreeding between progeny of nematodes from the two host species may occur. The parasite is usually far less abundant in harbour seals than in grey seals (McClelland 1980a, Brattey, Stobo *et al*. 1990, Brattey and Stenson 1993, Hauksson and Ólafsdóttir 1995; Marcogliese *et al*. 1996), and the former seem less suitable hosts than the latter in terms of nematode survival, growth, gravidity, and the magnitude of the host tissue response (McClelland 1980b, Aspholm *et al.* 1995). Nevertheless, in areas where they outnumber grey seals, e.g. inshore waters of the southern Gulf of St. Lawrence and southwestern Nova Scotia (Scott and Martin 1959), the lower Bay of Fundy (McClelland 1985), and southern Norway (Aspholm *et al*. 1995, des Clers and Anderson 1995), harbour seals may have considerable influence on larval sealworm abundance in groundfish. Although few *P. decipiens* reach maturity in harp seals (*Phoca groen- landicus*) (Brattey and Ni 1992, Marcogliese *et al*. 1996), the cumulative progeny of adult nematodes hosted by large harp seal breeding colonies, especially during the pre- and postwhelping periods (Scott and Fisher 1958), may account for a significant proportion of the larval sealworm in Newfoundland and Gulf of St. Lawrence groundfish (McClelland *et al*. 1983a).

The distribution and growth of seal populations are clearly not the only factors influencing the dynamics of larval sealworm in groundfish. Despite the continued growth of local seal populations (Mohn and Bowen 1996), infection parameters in plaice stabilised or declined at many sites off southern Newfoundland and in the northern Gulf of St. Lawrence, between 1985 and 1990 (McClelland *et al.* 2000). By the early 1990s (this study), sealworm infections collapsed in southern Gulf of St. Lawrence, Breton Shelf, Scotian Shelf and Gulf of Maine plaice (Fig. 3). Between 1990 and 1992, sharp declines in sealworm infection parameters were also recorded in cod, longhorn (*Myoxocephalus octodecemspinosus*) and shorthorn (*M. scorpius*) sculpin, Canadian plaice, yellowtail floun-

Fig. 3
Temporal variations in abundance of larval sealworm, Pseudoterranova decipiens, in Canadian plaice, Hippoglossoides platessoides, at selected sampling locations in the southern Gulf of St. Lawrence, on the Breton and Scotian shelves and in the northeastern Gulf of Maine, from 1980 to 1999.



der (*Pleuronectes ferruginneus)* and turbot (*Reinhardtius hippoglossoides*) (Boily and Marcogliese 1995, Marcogliese 1995) sampled throughout the Gulf of St. Lawrence.

Spatial and temporal distributions of *P. decipiens* in our indicator host may be influenced by various biotic phenomena including changes in distribution and abundance of intermediate hosts, and mechanisms that limit parasite density in intermediate and final hosts (des Clers *et al.* 1990, Marcogliese and McClelland 1994, McClelland 1995, McClelland *et al.*2000). The parasite's distribution may also be influenced by abiotic factors such as ocean currents (dispersal of ova passed in seal feces) (McConnell *et al.* 1997) and environmental temperatures (des Clers *et al.* 1990, Marcogliese *et al.* 1996, Marcogliese 2001, Measures 1996). Near-bottom temperature would be particularly important in that it directly regulates the parasite's prehatch developmental rate, post-hatch survival of the free-living ensheathed larvae, efficiency of transmission of larvae to and between poikilothermic intermediate hosts, and developmental rates of larvae in the these hosts (McClelland 1982, 1990). Temperature may also affect sealworm transmission and survival indirectly by influencing growth rates, abundance and distribution (hence, availability) of important intermediate hosts (Swain and Kramer 1993, Campana *et al*. 1995, Swain 1996, 1997).

Marcogliese (2001) speculates that declines in levels of *P. decipiens* infection, apparent in 1992 samples of grey seals and groundfish from the Gulf of St. Lawrence, were largely attributable to the relatively low near bottom temperatures in the central Gulf during the late 1980s and early 1990s. Near bottom temperatures in the southern Gulf of St. Lawrence remained ≥ 0° C over an area of 20,000 km^2 during a cold water anomaly in 1984 (Swain 1993), and an area varying from 12,000 to 25,000 km^2 between 1990 and 1996 (Gilbert *et al.* 1996; D.P. Swain, Department of Fisheries and Oceans, Gulf Fisheries Centre, Moncton, N.B., personal communication). Evidently, embryonation and larvation of sealworm eggs cease when temperatures fall to the 0 to 1° C range, and prehatch mortalities may result from prolonged incubation at these temperatures (McClelland 1982, Measures 1996). Low near-bottom temperatures prevalent in Atlantic Canadian waters since the mid 1980s (Campana *et al*. 1995) may have resulted, not only in declining sealworm abundance in plaice from the Gulf of St. Lawrence in the late 1980s (McClelland *et al.* 2000), but also in the collapse of infection parameters in plaice from the Breton and Scotian shelves, and Gulf of Maine in the early 1990s (present study).

In the present study, larval sealworm were not found in plaice 6 to 30 cm in length (n = 127), from a single set (no. 97, July 1996 Groundfish Cruise) on the western half of Misaine Bank. On the other hand, plaice of similar size from adjacent areas of Misaine Bank and nearby Middle Bank, and larger fish (≥31 cm in length) from set 97 were heavily infected (Fig. 2). Much of Misaine Bank lies in a pocket of colder water on the eastern Scotian Shelf (Campana *et al* 1995), and bottom temperatures recorded in the vicinity of set 97 in recent years have been in the 0 to 2° C range (Anonymous MS 1993a, 1993b, 1994). Bearing in mind a time lag factor, on which we speculate below, the presence of sealworm in "index" plaice from set 97 may indicate that bottom temperatures found in the area several years ago were warm enough to support the development and hatching of sealworm eggs. The lack of parasites in the smaller (younger) fish might be indicative of the inhibition of development and mortality of ova related to more recent declines in bottom temperatures. It is also possible that "index" plaice, being larger and more mobile than the smaller fish, may have incurred infections through seasonal excursions to deeper, warmer waters, or may simply be immigrants from other areas. A dip in near bottom temperatures in the northeastern Gulf of Maine during the early nineties (Campana *et al.* 1995), similarly, may have resulted in the decline of sealworm infection levels in Georges Bank plaice in 1993, and contributed to the erratic relationships of infection parameters and host length in both the 1993 and 1996 samples from this location (Fig. 2).

Results presented here, and in other reports (Marcogliese *et al.* 1996, Marcogliese 2001, McClelland *et al.* 2000) suggest that low near bottom temperatures experienced in eastern Canadian waters in recent years may have had a mitigating effect on abundance of *P. decipiens* in both groundfish and seals. Some of the data from plaice in the Canadian Maritime region (herein), however, seem difficult to interpret in terms of distribution and abundance of definitive hosts, or environmental temperature. By 1995-99, infection parameters in Canadian plaice had reached unprecedented highs at most (4TVWX-5ZE) locations where they had stabilised or fallen between 1989 and 1993. For example, infection parameters in Bradelle Bank and Magdalen Shoal plaice in 1998 were the highest yet recorded at these locations, despite the fact that bottom temperatures (≤0 °C) prevailing in central 4T since 1990 (Swain 1993, Gilbert *et al.* 1996) may have been lethal to sealworm eggs (Measures 1996). Moreover, uninterrupted increases in prevalence and abundance of larval sealworm were documented in plaice from many locations (e.g. Banquereau sites on the eastern Scotian Shelf) from 1980 to 1996, regardless of temperature trends. Finally, since 1993, declines in infection parameters were observed in plaice from only a few locations on the central and eastern Scotian Shelf. These fish were collected, not only from isolated cold water areas (Misaine Bank), but also from warmer sites (Middle, Sable Island and Western Banks) frequented by grey seals from the large and rapidly growing Sable Island colony.

Recent declines of sealworm infections in plaice from the Sable Island Bank complex might be attributable to parasite density limiting factors in our indicator host. Sealworm infection may prove lethal to fish, through damage to vital tissues and organs by feeding and migrating nematodes, or, perhaps, through chemical impairment of the host's ability to forage and avoid predators (McClelland 1995). Plaice appear to accumulate sealworm most frequently as 0-group or yearling fish, ≤ 15 cm in length (Martell and McClelland 1995; McClelland 2000, McClelland and Martell 2001), and the likelihood of survival to "index" size (31 to 40 cm TL) may decline as intensity of infection increases. Mortalities among the most heavily infected hosts would result in the attenuation of the tails of worm count distributions. Data from Sable Island and Middle Bank fish seem to support this scenario. While prevalence of the parasite in plaice remained at or near 100%, abundance and maximum intensity of infection fell dramatically between 1989 and '96 (Table 3). Evidence of mortality of heavily infected juvenile hosts from the Sable Island area may also be found in the 1996 "extended" sample from Middle Bank. Whereas data from "extended" samples collected in 1996, and during earlier surveys (McClelland *et al.* 1983a, 1983b, 1985, 1990) show that sealworm infection levels generally increase as plaice mature, sealworm abundance in the 1996 Middle Bank sample peaks in 16 to 25 cm juveniles and declines in larger (older) fish (Fig. 2).

One final factor, which must be taken into consideration when interpreting spatial and temporal variations in infection levels in plaice, is the likelihood that events or processes which result in changes in sealworm levels may predate our surveys by months to years (McClelland *et al.* 1990). During this time, hosts may migrate some distance from locations where many of their worms were acquired. Embryonation, larvation and hatching of *P. decipiens* ova occur on the seabed, where the parasites developmental rates are regulated by environmental temperature. In cold waters favoured by plaice in eastern Canada (Scott 1982, Swain 1997), development time to hatch for *P. decipiens* eggs may range from several weeks to the better part of a year (McClelland 1982, Brattey 1990, Measures 1996). Subsequent growth and development to the infective stage (advanced L3) in poikilothermic intermediate hosts may also require additional months or years (McClelland 1990, 1995). Moreover, upon reaching the infective stage, sealworm may survive indefinitely in a fish host (Hemmingsen *et al.* 1993), although, the longevity of the *P. decipiens* L3 in fish seems largely dependent on the host response and varies with host species and age, and density of infection (McClelland 1995).

Evidence of larval sealworm mortality and the host encapsulation response were lacking in naturally infected Canadian plaice held at the Halifax Fisheries Research Laboratory from June 1992 to January 1998 (McClelland 2000). This indicates that infections in plaice are cumulative, with nematodes from the earliest transmissions persisting as the host matures. Plaice diet studies (Martell and McClelland 1994, 1995), and analyses of the lengths of *P. decipiens* recovered from by digestion of juvenile plaice (McClelland 2000, McClelland and Martell 2001) further reveal that larval sealworm accumulate most rapidly in 0-group and yearling fish <15 cm in length. In contrast, the 31-40 cm length range used in our "index" surveys encompasses the mean lengths-at-age for six- to eleven-year-old females, and six- to fifteen-year-old males (Beacham 1982). Hence, a significant proportion of the sealworm found in our indicator hosts may have been acquired years earlier.

Given a lag time of several years between cause and effect, it is possible that relatively high near-bottom temperatures prevalent in eastern Canadian waters during the late seventies and early eighties (Swain 1993, Campana *et al.*

1995) may have played a significant role in promoting marked increases in levels of *P. decipiens* observed in Canadian plaice during the eighties (McClelland *et al.* 2000). This is particularly true in the Gulf of St. Lawrence, where increases in infection levels of the magnitude detected in plaice between 1983 and 1989 (Fig. 3) could not be attributed solely to the growth of definitive host populations. As noted above, growth of the Gulf grey seal population had stalled as a consequence of a bounty program and an annual cull/controlled hunt conducted from 1967 to 1983 (Zwanenburg and Bowen 1990).

It follows that the impact of the cold water anomaly of 1984 (Swain 1993) may not have been felt until 1992, when sealworm infection parameters in plaice from Bradelle Bank, and elsewhere in the Gulf of St. Lawrence fell precipitously (Boily and Marcogliese 1995). Near-bottom temperatures, which were ≤ 0 °C throughout central 4T in 1984 would probably have proven lethal to sealworm eggs (Measures 1996). Yet, levels of larval sealworm infection in plaice sampled from Bradelle Bank and the Magdalen shoals, locations which lay within the 0 °C contour in 1984, increased significantly between 1983 and 1989 (Fig. 3). In Bradelle Bank fish, sealworm prevalence increased more than three-fold, and abundance more than seven-fold. In any event, low near bottom temperatures prevalent in the Canadian Maritimes during the late eighties and early nineties (Campana *et al.* 1995, Swain 1997) seemed to have resulted in only a brief interruption in the positive trends of sealworm infection parameters observed in plaice over the last two decades. In the present study, sealworm infections in many Maritime plaice populations appeared to reach a plateau or collapse briefly in the late eighties to early nineties, but significant increases in infection parameters were subsequently detected in most of these populations during the mid to late nineties.

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