Distribution and abundance of sealworm (*Pseudoterranova decipiens*) and other anisakid nematodes in fish and seals in the Gulf of St. Lawrence: potential importance of climatic conditions

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ABSTRACT

Prevalence and abundance of sealworm (*Pseudoterranova decipiens*) and other anisakid nematodes were determined in a variety of fishes from the Gulf of St. Lawrence in 1990 and 1992. Sealworm abundance and prevalence were also determined in three species of seals in the Gulf between 1988 and 1992. Atlantic cod (*Gadus morhua*) and shorthorn (*Myoxocephalus scorpius*) and longhorn sculpin (*M. octodecemspinosus*) were the fishes most heavily infected with sealworm. Grey seals (*Halichoerus grypus*) proved to be the most important definitive hosts for sealworm in the Gulf. Abundance of sealworm increased, whereas that of *Anisakis simplex* and contracaecine nematodes decreased, from north to south in the Gulf. Abundance of sealworm increased compared to earlier surveys in most areas of the Gulf, but decreased in both cod and grey seals during the course of this study. In contrast, abundance of *Contracaecum osculatum* and *Phocascaris* spp. in grey seals and cod continued to increase during the study period. Observed increases of nematodes are attributed to growing populations of grey seals (for sealworm) and harp seals (for Contracaecinea). Levels of *A. simplex* remained relatively constant between 1988 and 1992 in both grey seals and cod. There is no evidence suggesting that observed patterns in nematode abundance were due to changes in grey seal diet. Nor was there any evidence of competition between *P. decipiens* and *C. osculatum* in grey seals affecting either sealworm abundance or fecundity. The trends detected herein are attributed to climatic events in the Gulf of St. Lawrence, where water temperatures in the cold intermediate layer consistently decreased between 1986 and 1994. It is suggested that low temperatures inhibited development and hatching of sealworm eggs, but not those of *C. osculatum*.

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INTRODUCTION

Sealworm (*Pseudoterranova decipiens*) is an anisakid nematode found in the flesh of commercially important groundfish such as Atlantic cod (*Gadus morhua*). This parasite poses a cosmetic problem for the fishing industry in North Atlantic waters, as its large larvae are easily visible and distasteful to consumers. Losses to the fishing industry resulting from costs associated with manual removal of larvae, degradation of fish product and discarding of heavily infected fillets were estimated to be approximately $30 million (Canadian) for cod alone in eastern Canada in 1982 (Malouf 1986).

Definitive hosts for sealworm are phocids, the most important being the grey seal (*Halichoerus grypus*) (Mansfield and Beck 1977, McClelland 1980). Among fishes, sealworm are found primarily in demersal and not pelagic fishes (McClelland *et al*. 1990). Over 60 species are infected in the North Atlantic alone (McClelland *et al*. 1990). While three sibling species of *P. decipiens* exist in the North Atlantic, designated A, B, and C (Paggi *et al*. 1991), it is presumed that sealworm from the Gulf of St. Lawrence belong to *P. decipiens* B (see Boily and Marcogliese 1995, Marcogliese *et al*. 1996, Marcogliese, 2001), now formally referred to as *P. decipiens* (sensu stricto) (Paggi *et al*. 2000).

In addition to sealworm, phocids and fishes in eastern Canada are infected with other anisakid nematodes, including *Anisakis simplex*, *Contracaecum osculatum* and *Phocascaris* spp. (McClelland *et al*. 1983). These anisakids are found in seal stomachs, with *Phocascaris* sp. also found in the anterior portion of the intestine (Brattey and Stenson 1993). However, cetaceans are the normal definitive host for *A. simplex* (van Thiel 1966). In fishes, *C. oscula-*

Fig. 1
Map of the Gulf of St. Lawrence, eastern Canada, showing locations mentioned in the text.

tum, *A. simplex* and *Phocascaris* spp. typically occur in the viscera, with some *A. simplex* also inhabiting the flesh, especially the flaps (McClelland *et al*. 1983).

In this paper long-term trends in abundance of sealworm in fish and seals in the Gulf of St. Lawrence (Fig. 1) are summarised and examined in the context of various hypotheses proposed by Marcogliese *et al*. (1996). In addition, temporal changes in distribution and abundance of other anisakid species including the Contracaecinea (*C. osculatum* and *Phocascaris*) and *A. simplex* in fish and seals are examined over the same time period to help evaluate the long-term patterns observed for sealworm.

MATERIALS AND METHODS

Atlantic cod were collected from various areas in the Gulf of St. Lawrence in 1990 and 1992 as indicated in Boily and Marcogliese (1995). Sampling, technical, and analytical procedures are described therein. Data from McClelland *et al*. (1983, 1985) are used graphically for long-term comparisons with 1990 and 1992. Given that there is little information indicating that susceptibility to sealworm varies among groundfish, observations in cod are considered representative of trends in most groundfish species. Similarly, McClelland *et al*. (1985) demonstrated that geographic variations in sealworm abundance in American plaice (*Hippoglossoides platessoides*) were similar to those in cod.

Grey seals, harp seals (*Phoca groenlandica*), and harbour seals (*Phoca vitulina*) were collected in 1988 and 1992 from various sites in the Gulf of St. Lawrence. The harbour seal data has not been presented previously. Harbour seals were collected from Les Escoumins (n = 7) in 1988 and Anticosti Island (n = 4) in 1992. Descriptions of seal sampling and processing, and analytical procedures, are presented in Marcogliese *et al*. (1996).

Abundance is defined as the mean number of parasites of a given species in a host sample, including both infected and uninfected animals. Variations in anisakid nematode abundance between 1988 and 1992 were analyzed using one-way and two-way ANOVAs (Boily and Marcogliese 1995, Marcogliese 1995, Marcogliese *et al*. 1996). Comparisons with earlier surveys of nematode abundance in fish and seals are qualitative and descriptive.

RESULTS

Trends in sealworm abundance

Typically, with the exception of a sample of Atlantic cod from Anticosti Island in 1990, sealworm abundance is much higher in fish (Templeman *et al*. 1957, McClelland *et al*. 1985, 1987, Boily and Marcogliese 1995, Marcogliese 1995) and seals (Marcogliese *et al*. 1996) from the southern Gulf than from the northern Gulf.

Sealworm has been common in groundfish in the southern Gulf of St. Lawrence since studies were first undertaken in the 1940s and 1950s, and presumably before that. Sealworm abundance was high in southern Gulf cod and flatfish in the early surveys of Scott and Martin (1957) and Templeman *et al*. (1957), and in 1980-81 (McClelland *et al*. 1983). Infections tended to increase in American plaice in the southern Gulf between 1983 and 1985 (McClelland *et al*. 1987), through to 1992 (Boily and Marcogliese 1995). Sealworm abundance in southeastern Gulf inshore cod and in cod from Bradelle Bank was greater in 1990 than in 1981 (McClelland *et al*. 1983, Boily and Marcogliese 1995).

In the northern Gulf, sealworm abundance increased between the 1950s and the 1980s (Templeman *et al*. 1957, McClelland *et al*. 1985) in both Atlantic cod and American plaice, and continued to increase in plaice through the 1980s (McClelland *et al*. 1987).

A drastic and significant decrease in abundance of sealworm was observed in cod from St. Georges Bay and Bradelle Bank in the southern Gulf and near Anticosti Island in the northern Gulf between 1990 and 1992 (Fig. 2) (Boily and Marcogliese 1995). A corresponding significant decline was also observed in longhorn

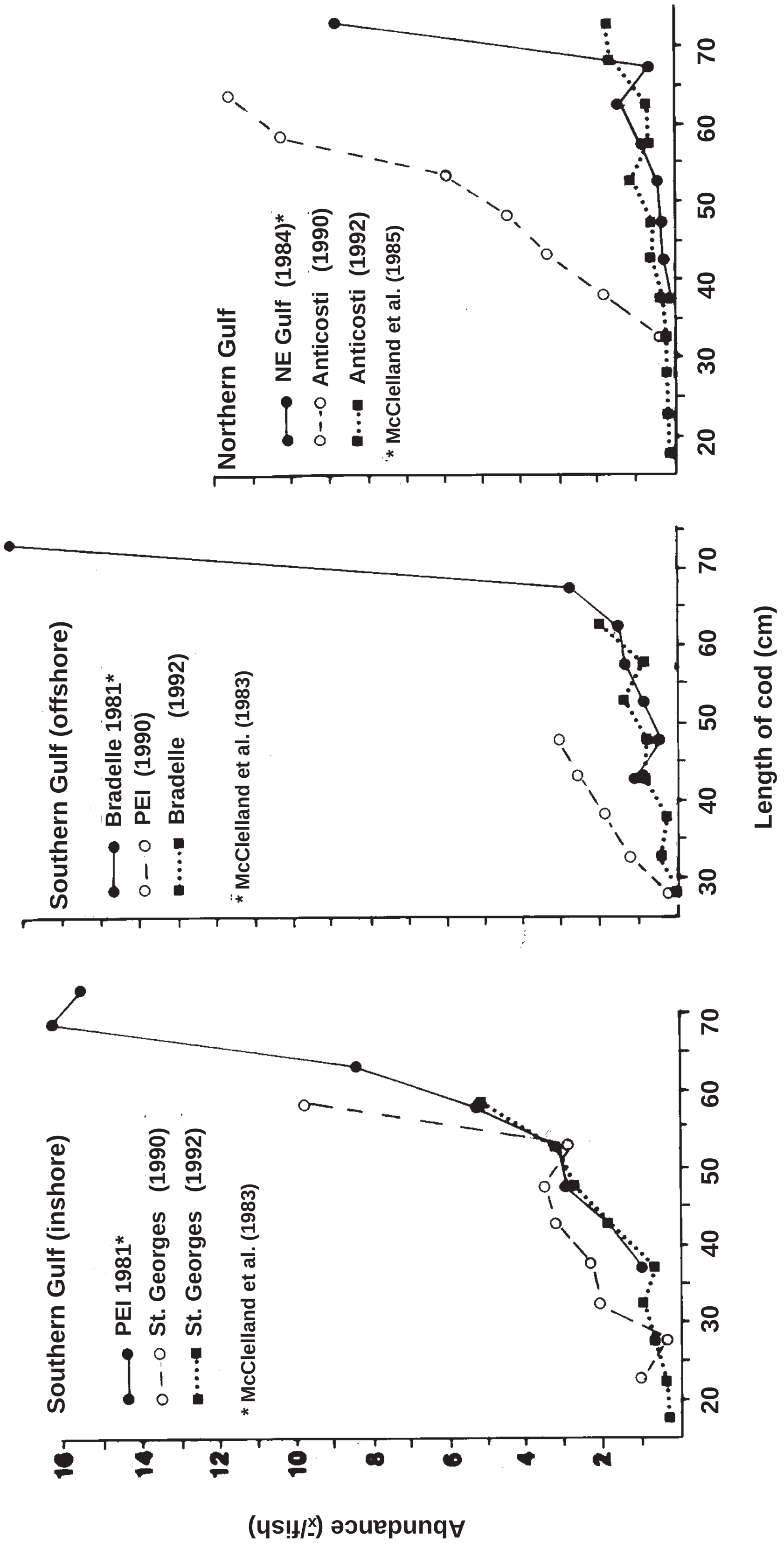


Fig. 2
Abundance (mean number per fish) of sealworm (<u>Pseudoterranova decipiens</u>) in relation to length of Atlantic cod (<u>Gadus morhua</u>) from three regions of the Gulf of St. Lawrence between 1981 and 1992. Southern gulf inshore and offshore data in 1981 are from McClelland et al. (1983). Data for the northern Gulf in 1984 are from McClelland et al. (1985).

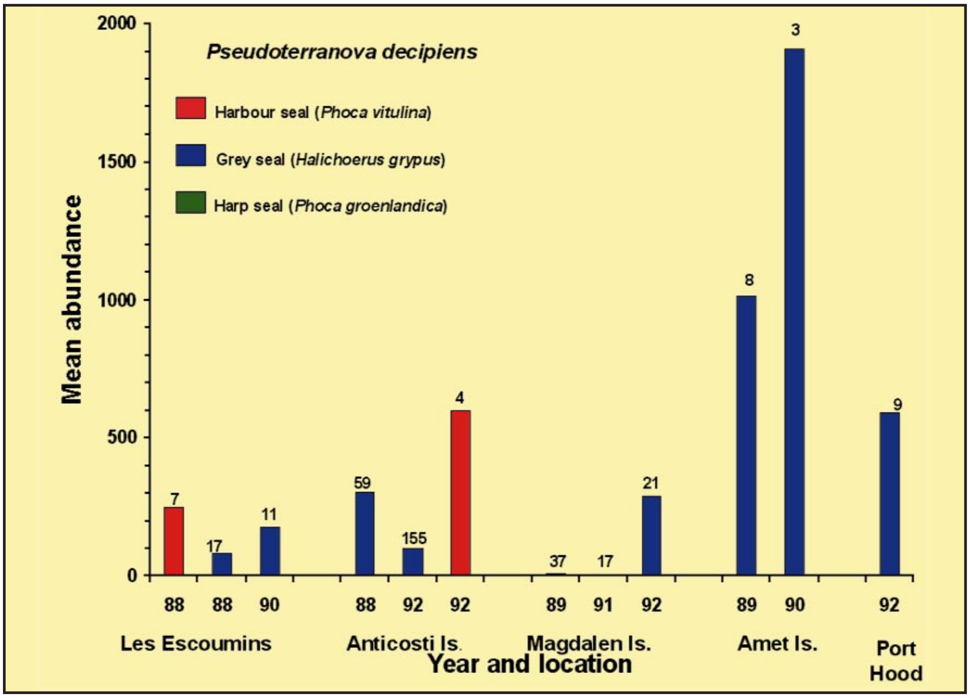


Fig. 3
Abundance (mean number per seal) of sealworm (Pseudoterranova decipiens) in grey seals (Halichoerus grypus), harp seals (Phoca groenlandica), and harbour seals (Phoca vitulina) from various areas in the Gulf of St. Lawrence between 1988 and 1992. Numbers above each histogram refer to the sample size.

sculpin (*Myoxocephalus octodecemspinosus*) and white hake (*Urophycis tenuis*) (Marcogliese 1995). The most heavily infected fish in the Gulf in 1990-92 were Atlantic cod, American plaice, longhorn sculpin, shorthorn sculpin (*Myoxocephalus scorpius*) and ocean pout (*Macrozoarces americanus*) (Boily and Marcogliese 1995, Marcogliese 1995).

Similarly, sealworm levels increased in grey seals in 1988 from the earlier surveys of Scott and Fisher (1958) in 1948 and 1956 and McClelland (1980) in 1975-78 (Marcogliese *et al*. 1996). However, as in Atlantic cod and other fishes, *P. decipiens* abundance decreased in all age groups of Anticosti seals, and significantly so in adults, between 1988 and 1992 (Fig. 3) (Marcogliese *et al*. 1996). Harp seals were only lightly infected, with few adult sealworm found (Marcogliese *et al*. 1996). Harbour seals from Anticosti Island and Les Escoumins were more heavily infected than grey seals from the same areas (Fig. 3).

Trends in abundance of Contracaecinea

Third stage larvae of *Contracaecum osculatum* and *Phocascaris* spp. from fish are extremely difficult to differentiate (McClelland *et al*. 1985, Brattey 1995). In fish surveys the two are often combined and referred to as Contracaecinea (Arthur and Albert 1993, Arthur *et al*. 1995, Boily and Marcogliese 1995). Levels are normally higher in Atlantic cod (McClelland *et al*. 1983, McClelland *et al*. 1985, Boily and Marcogliese 1995) and grey seals (Marcogliese *et al*. 1996) from the northern Gulf compared to those from the southern Gulf. The most important definitive host of *Contracaecum osculatum* is considered to be the harp seal (McClelland *et al*. 1985, Brattey and Ni 1992, Marcogliese *et al*. 1996), and that of *Phocascaris* spp., the hooded seal (*Cystophora cristata*) (Berland 1963, McClelland *et al*. 1983, Brattey and Stenson 1993). Contracaecinea found in southern Gulf fishes are considered to be primarily *Contracaecum osculatum* on the basis of morphological criteria (McClelland *et al*. 1983, McClelland *et al*. 1985) combined with the distribution of hooded seals and the limited presence of *Phocascaris* spp. in seals from the southern Gulf (Marcogliese *et al*. 1996). Two sibling species of *C. osculatum* occur in Canadian waters south of Labrador (Brattey and Stenson 1993, Nascetti *et al*. 1993). One (Type A) occurs mainly in bearded seals (*Erignathus barbatus*), which are rare in the Gulf of St. Lawrence. The second type, *C. osculatum* B, is primarily a parasite of harp seals but also occurs in grey seals. Thus, it is presumed that parasites in the Gulf are *C. osculatum* B.

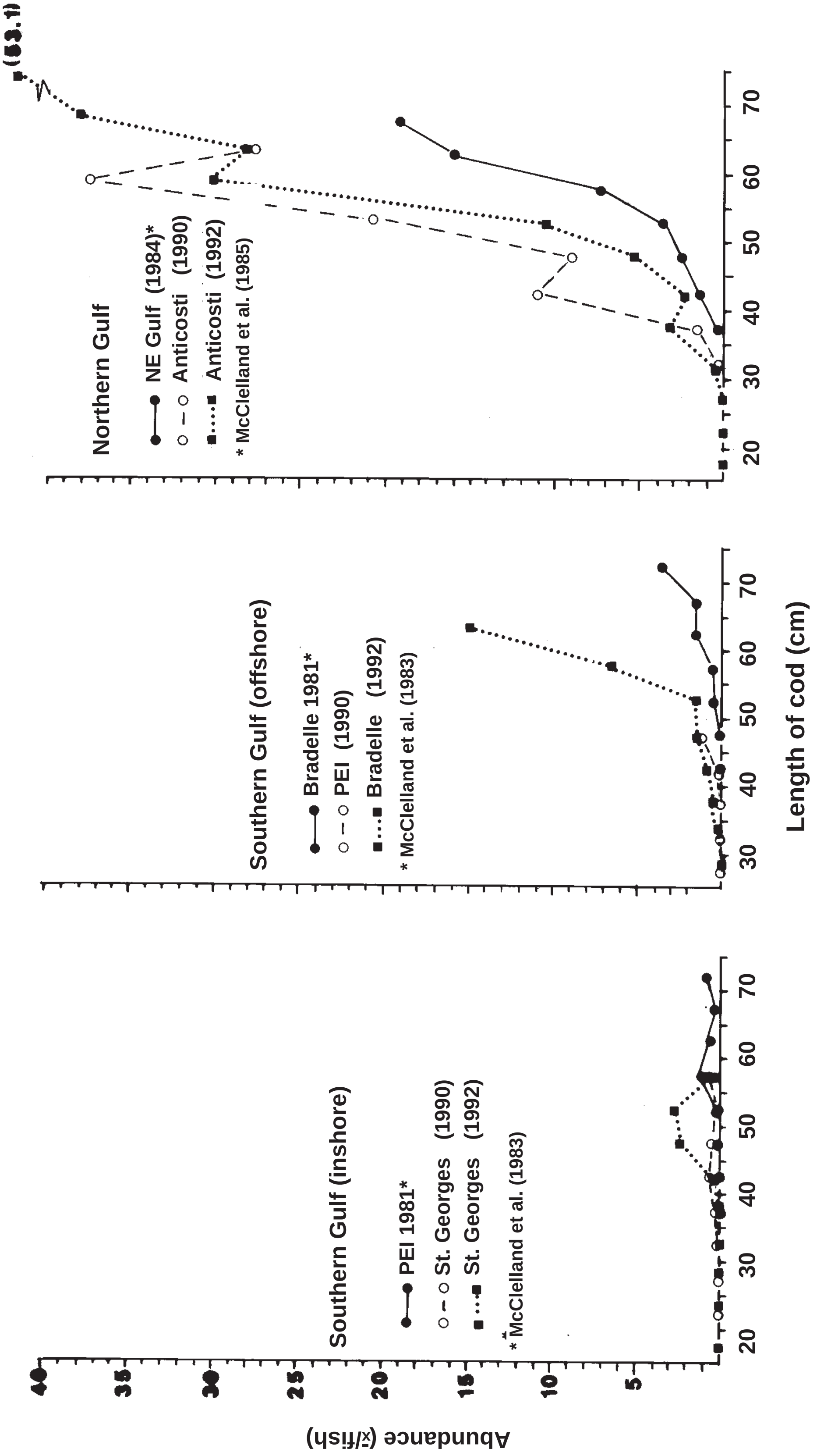


Fig. 4
Abundance (mean number per fish) of Contracaecinea (Contracaecum osculatum and Phocascaris spp.*) in relation to length of Atlantic cod (Gadus morhua) from three regions of the Gulf of St. Lawrence between 1981 and 1992. Southern Gulf inshore and offshore data in 1981 are from McClelland et al. (1983). Data for the northern Gulf in 1984 are from McClelland et al. (1985).*

Among *Phocascaris* spp., *P. cystophorae* is more common in grey seals from the Northwest Atlantic than is *P. phocae*, but recombinants do occur (Paggi and Bullini 1994). Therefore specimens are referred to collectively as *Phocascaris* spp. Among fishes, contracaecines are found in both demersal and pelagic fishes (McClelland *et al*. 1985, Boily and Marcogliese 1995, Marcogliese 1995).

Contracaecines increased in abundance in Atlantic cod in the northern Gulf from 1984 to 1992 (McClelland *et al*. 1985, Boily and Marcogliese 1995). In the southeastern Gulf inshore, abundances were low in 1981 and 1990, with a slight increase in 1992 (McClelland *et al*. 1983, Boily and Marcogliese 1995). On Bradelle Bank in the southern Gulf offshore, abundances increased tremendously between 1981 and 1992 (Fig. 4) (McClelland *et al*. 1983, Boily and Marcogliese 1995). The most heavily infected fish in the Gulf in 1990-94 included Atlantic cod, longhorn and shorthorn sculpin, Greenland halibut (*Reinhardtius hippoglossoides*) and capelin (*Mallotus villosus*) (Arthur and Albert 1993, Arthur *et al*. 1995, Boily and Marcogliese 1995, Marcogliese 1995).

Abundance of *C. osculatum* increased in harp seals between the 1950s and 1989-92 in harp seals from the Magdalen Islands (Myers 1957, Scott and Fisher 1958, Marcogliese *et al*. 1996), and all age groups of grey seals (significantly in pups and old adults > 10 years of age) from Anticosti Island between 1988 and 1992 (Fig. 5) (Marcogliese *et al*. 1996). Grey and harp seals were the most heavily infected with *C. osculatum*, with few worms found in harbour seals in the Gulf (Fig. 5). Abundance of *Phocascaris* spp. generally was low in Gulf seal stomachs, but higher in the northern Gulf compared to the southern Gulf. Among Anticosti grey seals, abundance increased significantly between 1988 and 1992 (Fig. 6) (Marcogliese *et al*.

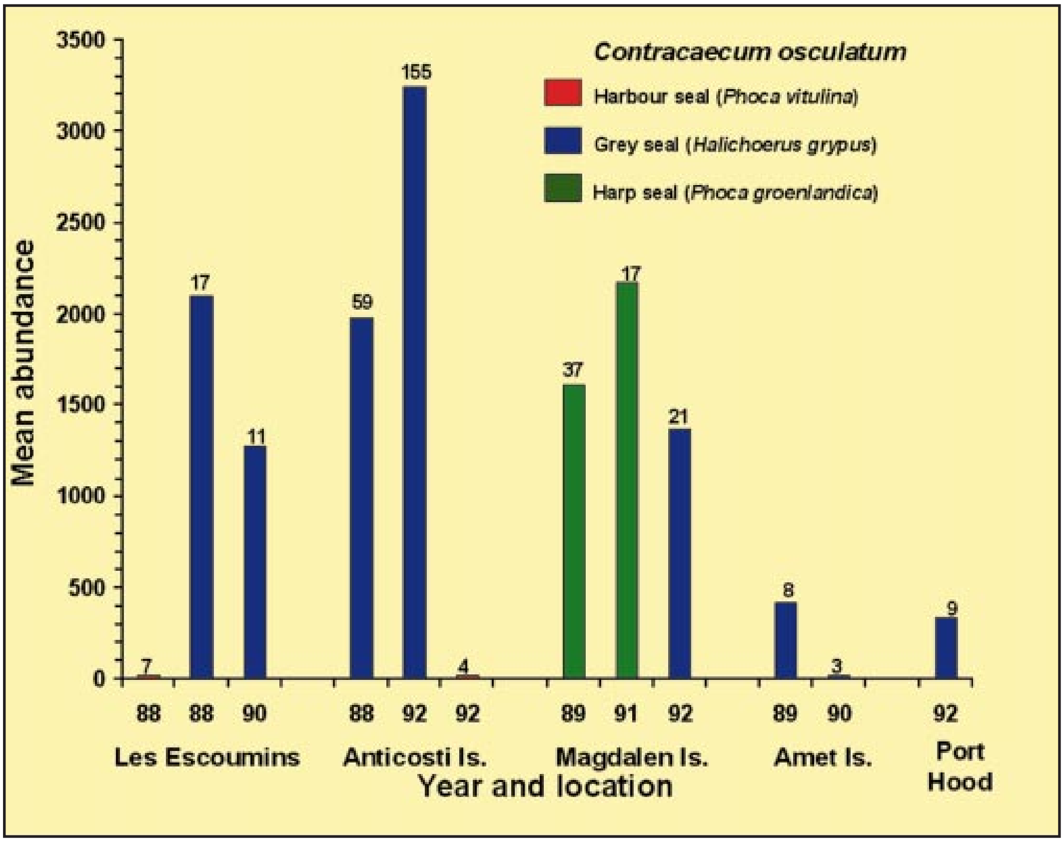


Fig. 5
Abundance (mean number per seal) of Contracaecum osculatum in grey seals (Halichoerus grypus), harp seals (Phoca groenlandica), and harbour seals (Phoca vitulina) from various areas in the Gulf of St. Lawrence between 1988 and 1992. Numbers above each histogram refer to the sample size.

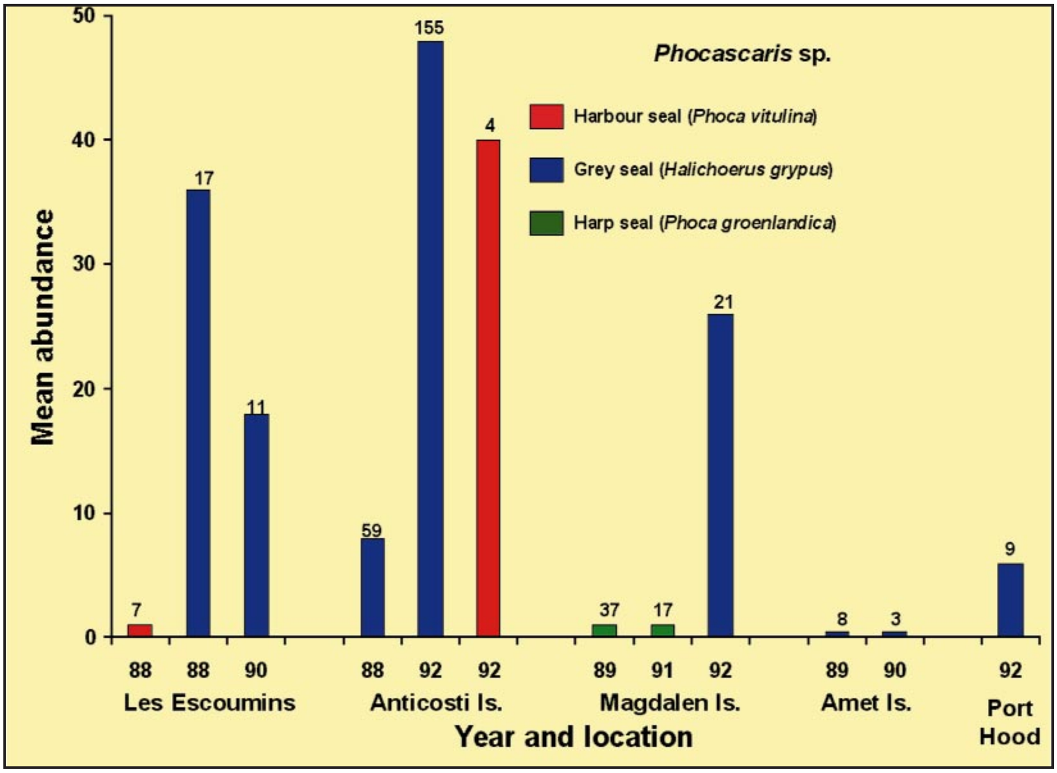


Fig. 6. *Abundance (mean number per seal) of Phocascaris spp. in grey seals (Halichoerus grypus), harp seals (Phoca groenlandica), and harbour seals (Phoca vitulina) from various areas in the Gulf of St. Lawrence between 1988 and 1992. Numbers above each histogram refer to the sample size.*

1996). Grey and harbour seals were the most heavily infected, with few *Phocascaris* spp. found in harp seal stomachs (Fig. 6).

Trends in whaleworm abundance

The whaleworm (*Anisakis simplex*) uses cetaceans as a definitive host, but can be found in phocid stomachs, where it rarely matures (Brattey and Stenson 1993, Marcogliese *et al*. 1996). Pelagic fishes tend to be heavily infected, though demersal piscivores may carry large infections (McClelland *et al*. 1990). Whaleworm infect more than 75 species of fish in the North Atlantic (McClelland *et al*. 1990). Of the two sibling species which occur (Orrechia *et al*. 1986), *A. simplex* B is the most common off northeastern North America (Brattey and Clark 1992).

Abundance levels of *A. simplex* typically are lower in the southern Gulf than in the northern Gulf in both Atlantic cod (McClelland *et al*. 1983, Boily and Marcogliese 1995) and grey seals (Marcogliese *et al*. 1996). Since the early 1980s, the abundance of *A. simplex* in cod from the different areas of the Gulf has remained relatively constant (Fig. 7) (McClelland *et al*. 1983, 1985, Boily and Marcogliese 1995). No significant differences in abundance were detected between 1990 and 1992 in Gulf cod (Boily and Marcogliese 1995) nor between 1988 and 1992 in Gulf seals (Fig. 8) (Marcogliese *et al*. 1996). Among fishes in the Gulf, Atlantic cod, shorthorn sculpin, Greenland halibut and Atlantic herring (*Clupea harengus*) were the most heavily infected in 1990-92 (Arthur and Albert 1993, Boily and Marcogliese 1995, Marcogliese 1995). Among Gulf seals, both harp and harbour seals were very lightly infected compared to grey seals in 1988-92 (Fig. 8).

DISCUSSION

Unexpected patterns and potential explanations

Increases in abundance of *P. decipiens* and *C. osculatum* in fish and seals in the Gulf of St. Lawrence until 1988-90 are attributed to large increases in the populations of grey and harp seals in the Gulf (Zwanenburg and Bowen 1990, Stenson *et al*. 1993, Hammill *et al*. 1998). However, the decline in abundance of sealworm in both fish and seals between 1988/1990 and 1992 is puzzling. Three hypotheses have been

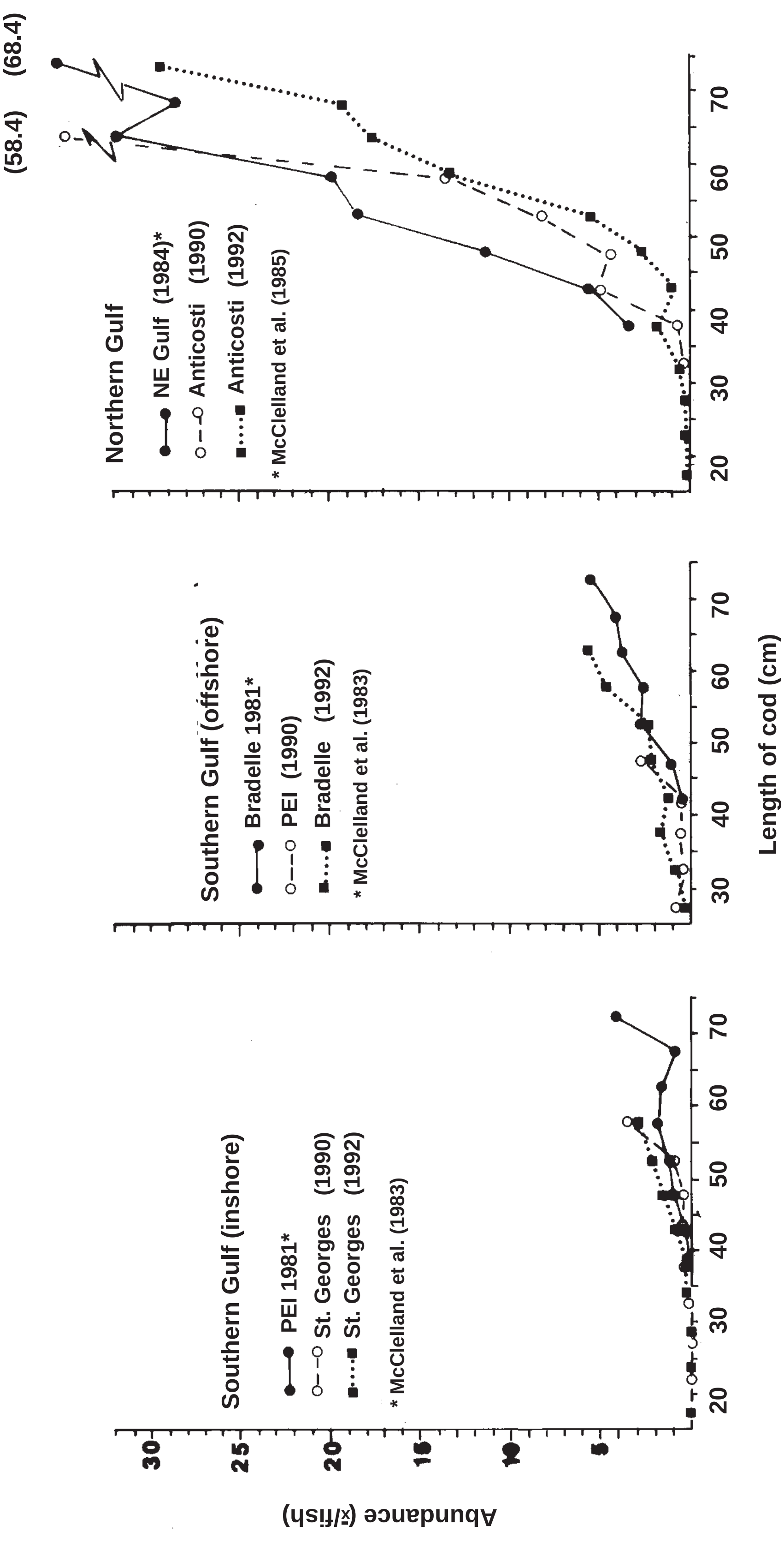
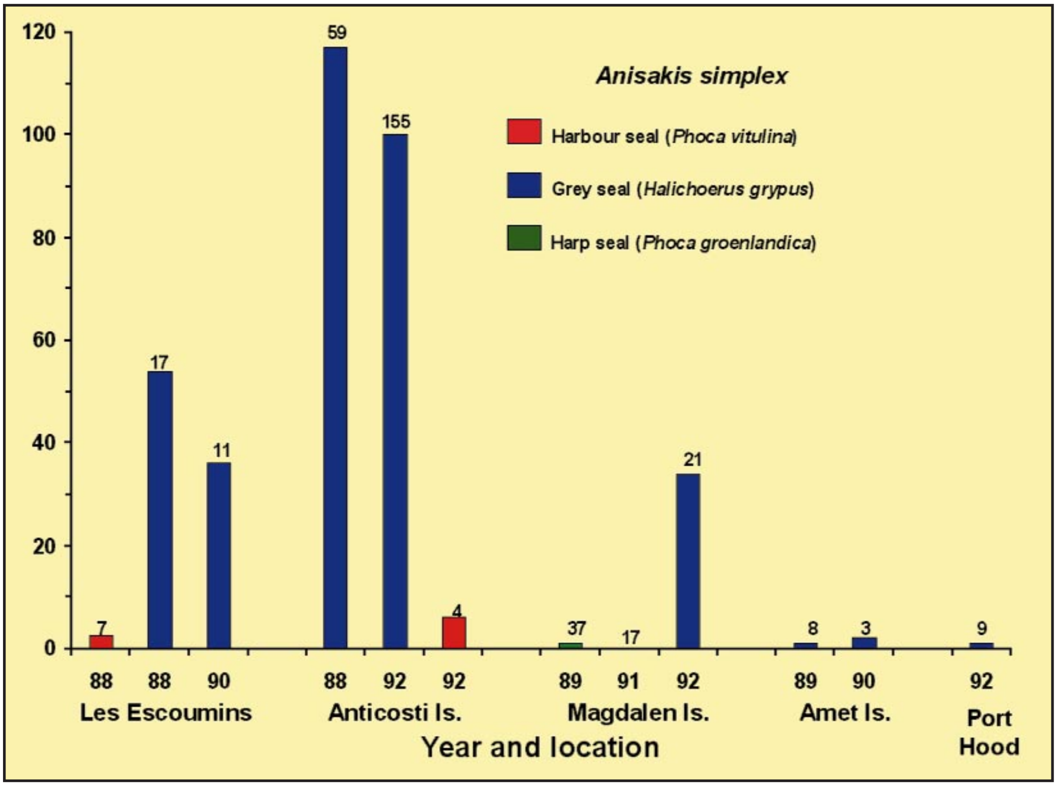


Fig. 7 *Abundance (mean number per fish) of whaleworm (<u>Anisakis simplex</u>) in relation to length of Atlantic cod (<u>Gadus morhua</u>) from three regions of the Gulf of St. Lawrence between 1981 and 1992. Southern gulf in-shore and offshore data in 1981 are from McClelland et al. (1983). Data for the northern Gulf in 1984 are from McClelland et al. (1985).*

Fig. 8
Abundance (mean number per seal) of whaleworm (Anisakis simplex) in grey seals (Halichoerus grypus), harp seals (Phoca groenlandica), and harbour seals (Phoca vitulina) from various areas in the Gulf of St. Lawrence between 1988 and 1992. Numbers above each histogram refer to the sample size.



proposed to explain these recent trends (Marcogliese *et al*. 1996). First, changes in diet of seals, such that in 1988 seals fed more on demersal fish and in 1992 more on pelagic fish, could account for a decrease in sealworm and a concomitant increase in *C. osculatum* in the Gulf. This change in diet may have been precipitated by the collapse of groundfish stocks in the Northwest Atlantic (Sinclair 1993). Second, there may be competitive interactions between the two nematode species in the seal stomach, with *C. osculatum* being dominant and displacing sealworm (McClelland *et al*. 1985, Burt 1994). McClelland *et al*. (1985) observed that sealworm abundance in the Gulf of St. Lawrence was relatively stable, despite large increases in the size of the grey seal populations, whereas sealworm levels had increased on the Scotian Shelf. Coincidentally, levels of *C. osculatum* were high in the Gulf of St. Lawrence, but low on the Scotian Shelf. Using an *in vitro* culture system to grow *P. decipiens* and *C. osculatum* (Likely and Burt 1989, 1992), Burt (1994) found that sealworm fecundity was reduced when reared in the presence of *C. osculatum*. Third, free-living stages of the two parasite species may respond differently to abiotic conditions, thus leading to opposite trends in population abundance (Marcogliese *et al*. 1996).

Hypothesis 1: seal diets

Samples from the same seals from Anticosti Island were used in both the diet and the parasite studies in 1988 and 1992. In contrast to expectations, grey seals from Anticosti Island fed more on pelagic prey, especially capelin, and less on Atlantic cod, in 1988 than did those sampled in 1992 (Proust 1996). Thus, sealworm should not have decreased in abundance. Moreover, an increase in pelagic consumption should have led to an increase in the abundance of whaleworm, but its abundance remained stable (Boily and Marcogliese 1995, Marcogliese *et al*. 1996). Alterations in diet cannot account for the observed changes in nematode abundance, where *P. decipiens* decreased, contracaecines increased, and *A. simplex* remained unchanged between 1988 and 1992 (Marcogliese *et al*. 1996). The grey seals apparently could find sufficient Atlantic cod to eat in 1992, despite the collapse of the groundfish stocks.

Hypothesis 2: competition

No effect of *C. osculatum* abundance on sealworm abundance in seal stomachs was observ-

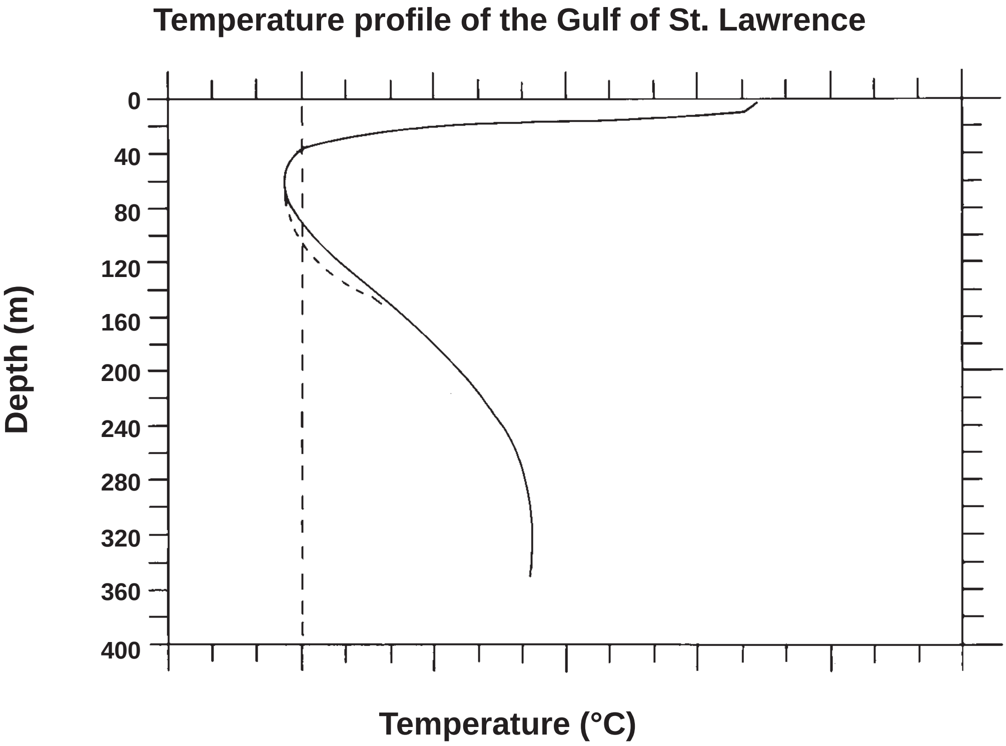


Fig. 9
Temperature profile in the Gulf of St. Lawrence, showing warm surface layer, cold intermediate layer, and warm deep waters. Dotted line represents expansion of the cold intermediate layer with decreasing temperatures.

ed in seals from Newfoundland (Brattey and Stenson 1993) or the Gulf of St. Lawrence (Marcogliese *et al*. 1996). In addition, Marcogliese *et al*. (1996) could not detect any effect of *C. osculatum* abundance on the proportion of adult sealworm occurring in grey seals in the Gulf. Thus, development and maturation of sealworm does not seem to be affected by *C. osculatum*. Lastly, the fecundity of individual sealworms is density-independent at intensities observed in grey seals from Anticosti Island; it is not affected by the density of sealworms or of *C. osculatum* (Marcogliese 1997), despite results obtained by Burt (1994) in *in vitro* experiments. Thus, no density-dependent effects of *C. osculatum* on sealworm abundance, development or fecundity would be expected given the densities of sealworm observed over the time period. Marcogliese (1997) acknowledged the possibility that the mere presence of *C. osculatum* in seal stomachs could have an inhibitory effect on sealworm growth and/or fecundity. All seals used in that study were infected with *C. osculatum*, and adult sealworm, generally, were smaller and less fecund in that study than those from grey seals in other regions of eastern Canada (McClelland 1980). Interestingly, although Berland (1963) is usually cited as the first to mention that *C. osculatum* may competitively displace other anisakids in seal stomachs, he actually makes no mention of this phenomenon at all.

Hypothesis 3: abiotic effects

The Gulf of St. Lawrence is stratified into three layers most of the year, with a warm surface layer (30-50 m), a cold intermediate layer (30-100 m) typically defined by water temperatures less than 2 ˚C, and deep waters at about 4-5 ˚C (Fig. 9). Water temperatures became progressively colder in the Gulf of St. Lawrence after 1986, with the cold intermediate layer becoming progressively colder and thicker, increasing the bottom surface area covered with waters less than 0 ˚C in the process (Fig. 10; Gilbert *et al*. 1996). Grey seals typically forage and presumably defecate at depths within the cold intermediate layer (Thompson *et al*. 1991). Anisakid nematode eggs are passed into the water with the feces of the definitive host. Sealworm eggs sink in sea water at a velocity of 1.01×10^{-4} m/sec (McConnell *et al*. 1997). Eggs of both sealworm and *C. osculatum* hatch at 1.7˚C (Brattey 1990). However, only eggs of *C. osculatum* (L. Measures, Dept. of Fisheries & Oceans, Maurice Lamontagne Institute, Mont-

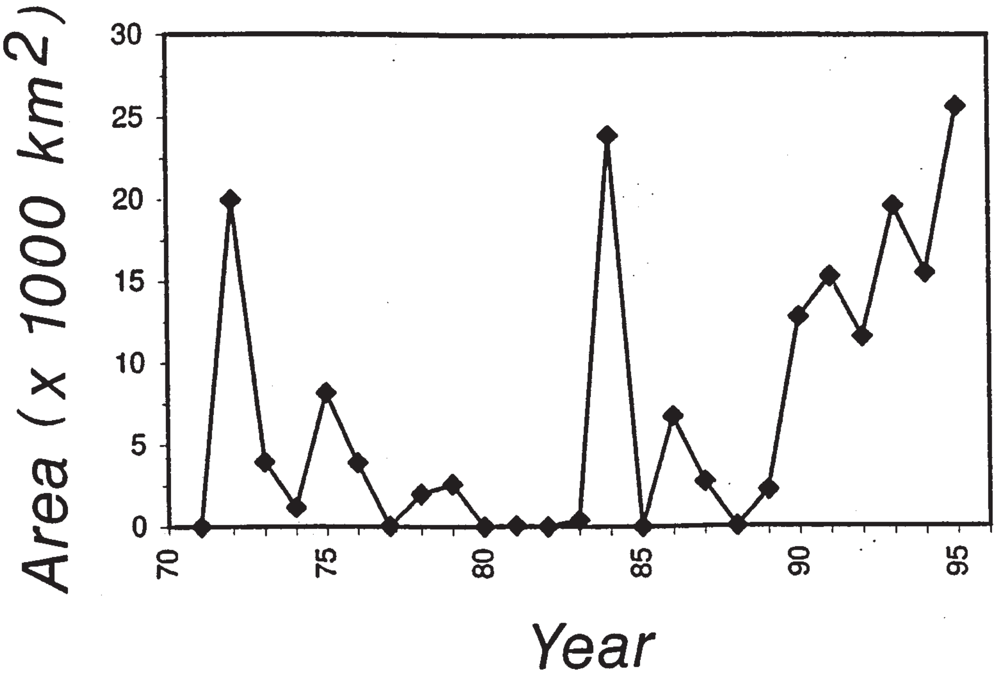


Fig. 10 *Graph showing bottom surface layer in the southern Gulf of St. Lawrence where temperatures are less than 0 ˚C (redrawn from Gilbert et al. 1996). Note the progressive increase in bottom surface area since 1988.*

Joli, Quebec, personal communication), and not those of sealworm (Measures 1996), hatch at 0 ˚C. Eggs of *C. osculatum* falling onto bottom sediments covered by the cold waters of the cold intermediate layer will hatch, but those of sealworm will not (Marcogliese *et al*. 1996). Presumably eggs of *Phocascaris* spp. are cold tolerant like *C. osculatum*, as this parasite has a northern distribution in fish, not being observed in the southern Gulf nor on the Scotian Shelf, and in the hooded seal, which summers off northern Canada and Greenland (Stenson *et al*. 1997). This parasite also increased in grey seals between 1988 and 1992 at Anticosti Island. Thus, changes in climate causing colder bottom temperatures may have led to the recent opposite trends in the abundance of sealworm and contracaecine nematodes in the Gulf of St. Lawrence.

We can also ask why the abundance of sealworm increased so much between 1981 and 1990. Perhaps the increase in seal numbers is only part of the answer. Inspection of Fig. 10 indicates that with the exception of 1984, only a small portion of the bottom surface area of the southern Gulf was at temperatures of 0 ˚C or less between 1977 and 1989. Relatively warm bottom temperatures may have contributed to the increased abundance of sealworm through enhanced rate of development in poilkilothermic hosts. A parallel increase in abundance was observed in nine species of fish including cod between 1985-86 and 1989-90 on Sable Island Bank off Nova Scotia (McClelland and Martell 2001), suggesting that factors on a geographically large scale, such as climate, may be at work. It is predicted that the groundfish industry in Atlantic Canada will encounter problems with sealworm if and when the fish stocks are rebuilt, especially if water temperatures increase, as is predicted in association with increasing atmospheric CO_2 content and other greenhouse gases (Wright *et al*. 1986).

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