Sealworm (*Pseudoterranova decipiens*) dynamics in Sable Island grey seals (*Halichoerus grypus*): seasonal fluctuations and other changes in worm infections during the 1980s.

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ABSTRACT

The abundance of *P. decipiens* sampled from the stomachs of 553 grey seals (aged 0-48 years) collected during 14 field trips to Sable Island in 1983 and 1989 did not change significantly between years, even though the seal population has been increasing at over 12% annually and there has been a substantial decline in the fish biomass upon which they depend. The proportion of mature worms in the seals' stomachs has decreased, however. Seal growth, expressed in terms of either age or length, showed the strongest correlation with total worm abundance. These infections were not completely eliminated at any time during the year, but a seasonal pattern in worm abundance was apparent. Among the youngest seals an inverse relationship was demonstrated between the abundance of *P. decipiens* and another parasitic nematode, *Contracaecum osculatum*. Sexually mature *P. decipiens* were found in pups within 3 to 4 months of the commencement of independent feeding, and the abundance of *P. decipiens* progressively increased throughout the first year of life. Male pups contracted more worms than female pups of the same age. *P. decipiens* abundances in juvenile seals were primarily associated with seasonal pattern and age, with *C. osculatum* abundance still influencing the abundance of *P. decipiens*, but to a much lesser extent than seen with pups. Length of seals was the main predictor of total worm abundance in adult seals, with a seasonal pattern being next in order of importance. Age was also significant, possibly representing a component of growth not accounted for by length alone. No relationship between the abundances of *P. decipiens* and *C. osculatum* was apparent for adult seals. The seasonal pattern in total worm abundance of juvenile and adult seals was characterized by declines during the winter and mid-summer. We suggest these declines are due, respectively, to the breeding season fast and one or both of 1) a change in seal diet from primarily highly infected fish species to less infected ones, and 2) a partial fast during the annual moult. The proportion of mature worms increased during reductions in worm abundance throughout most of the year, but during the breeding fast both total abundance and the proportion mature declined.

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INTRODUCTION

Sealworm, *Pseudoterranova decipiens*, is one of a number of anisakine nematodes whose life cycles include fish species as intermediate hosts (Scott and Martin 1957, Young 1972, Platt 1975, Margolis and Arthur 1979). The majority of these hosts are demersal (McClelland *et al*. 1990), and include most of the groundfish species of commercial interest to fisheries in the Northwest Atlantic. Studies in the Northwest Atlantic have shown that levels of infection in cod (*Gadus morhua*) and other commercially important demersal fish species, increased during the 1980's (McClelland *et al*. 1983a, b, 1985, Brattey and Stenson 1993, Boily and Marcogliese 1995, Marcogliese 1995). The increased occurrence of sealworm in the flesh has significantly raised the cost of processing these fish for the consumer market (Malouf 1986). Although the lifecycle of this parasite and its interactions with its intermediate and final hosts are not completely understood (Bowen 1990), recent studies indicate that of the three sibling species (*P. decipiens* A, *P. decipiens* B, *P. decipiens* C) known to occur in the North Atlantic (Paggi *et al*. 1991), only *P. decipiens* B has been found in seals and fish off Nova Scotia, Newfoundland, and in the Gulf of St. Lawrence (Brattey and Davidson 1996, Brattey and Stenson 1993).

The grey seal (*Halichoerus grypus*) (Fig. 1) appears to be the predominant final host to *P. decipiens* in the North Atlantic (Scott and Fisher 1958, Young 1972, Mansfield and Beck 1977, McClelland 1980, Bjørge MS 1984), and pups begin to develop worm infections in their stomachs shortly after they commence independent feeding (Stobo *et al*. 1990). Grey seals of all subsequent life stages are infected, worm abundance increasing as the seals grow larger (Bjørge MS 1984, Stobo and Beck 1985, Wiig 1988, Stobo *et al*. 1990). They do not appear to lose these infections completely at any time during the year but seasonal fluctuations in abundance have been observed, possibly due to the breeding fast or changes in diet composition (Wiig 1988, Stobo *et al*. 1990, Haug *et al*. MS 1991). Stobo *et al*. (1990) described a seasonal cycle of abundance based on a study conducted from 1983 to 1984 on Sable Island. Although based on a large sample size (234 animals), it was partitioned into 8 trips spread over a 13 month period (one trip in 1984), and represented only a single observation of a seasonal pattern. The need for multiple or time series observations of *P. decipiens* and grey seals has been emphasised (Brattey and Stobo 1990, des Clers and Mohn 1990). The present paper examines the consistency of that seasonal pattern based on the results of a 1989 study designed as a

Fig. 1
The grey seal is the major reservoir for sealworm in Northwest Atlantic waters.
Photo: D. Marcogliese

replicate of the 1983 work (the first 7 trips). It also examines changes in abundance between the two periods, during which the Sable Island grey seal population increased at a rate of over 12% annually (Stobo and Zwanenburg 1990).

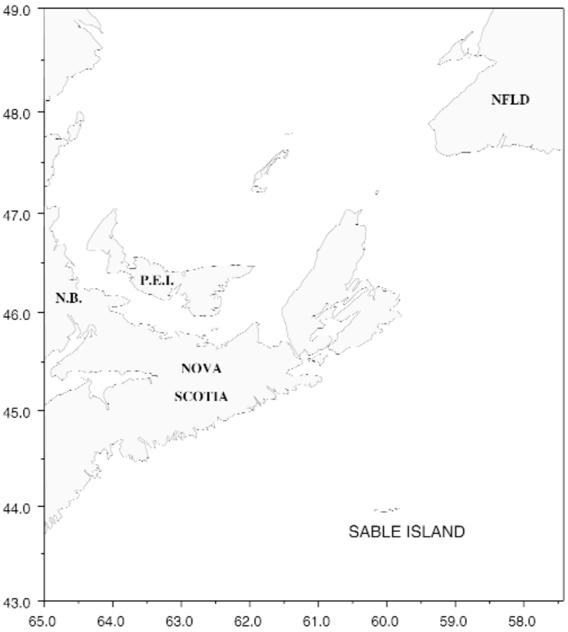


Fig. 2 *Location of Sable Island on the Scotian Shelf of the north Atlantic Ocean.*

MATERIALS AND METHODS

Collection and Analysis Methods

Two hundred and fourteen adult and juvenile grey seals collected during 7 trips to Sable Island, Nova Scotia (Fig. 2) in 1983, and 339 collected during 7 trips in 1989 were used in the present analysis (Table 1). The samples were partitioned into 3 maturity stages (approximately pups, juveniles, adults) for descriptive and analytical purposes. The pups were treated as a separate group since they do not develop nematode infections until they begin independent feeding, starting from late February (Brattey and Stobo 1990); for this reason, no pups were taken during the January trips. However yearlings taken in January 1983 and 1989 (12-14 months old) were included in the pup age group to represent the infections carried by the pups at the end of the first year of life. The two older maturity stages were determined from preliminary analyses of deviance as ages 1-6 (designated as juveniles) and ages 7 and older (designated as adults). This partitioning of the ages was considered optimal due to the absence of significant interactions between age and other explanatory variables during the modelling process (treating older animals as members of the 'juvenile' group or younger animals as 'adults' complicated the models with interaction terms). As such they reflect phases of infestation that are generally, but loosely, associated with the purported ages of the life history stages used.

The lower jaw was removed for subsequent age determination. The stomach was ligated at the oesophagus and near the pyloric sphincter before removal to prevent loss of parasites, and the 1983 samples were processed as described in Stobo *et al*. (1990). In 1989, the worms were left in the stomachs and frozen within 5 hours of removal from the seal. The stomachs were later thawed in the lab and the worms removed. The worms were then fixed and cleared following the same procedure used with the formalin preserved specimens in the 1983 study.

The nematodes in each stomach were sorted by species and enumerated. Only adults were enumerated by sex because the sex of immature worms is not discernible by simple microscopy. Worms were considered mature if they had a distinct vulva (females) or a dorso-ventrally flattened, ventrally recurved tail and spicules (males). We understand that these criteria may be subjective to some extent (Dr G. McClelland, personal communication), such that comparisons between 1983 and 1989 could be confounded by differences in interpretation of worm maturity between sorters.

Although 3 species of nematodes (*Pseudoterranova decipiens*, *Contracaecum osculatum*, *Anisakis simplex*) were found in the stomach, only the data on the sealworm, *P. decipiens*, will be presented here. Abundances of *C. osculatum* were included in the modelling process to account for variations in *P. decipiens* abundance that would otherwise appear anomalous. Box and whisker plots (Tukey 1977) were used to summarise the data.

Three characteristics of *P. decipiens* infections (sex ratio, total worm abundance, and proportion mature worms) were examined in relation

Table 1. Numbers of grey seals by age group and sex sampled during each trip to Sable Island.

Year: 1983		1	2	3	Trip 4	5	6	7	
Age Group	**Sex**	**Jan. 10 - Feb. 9**	**Mar. 2 - Mar. 21**	**May 7 - May 11**	**May 31 - June 7**	**Aug. 2 - Aug. 7**	**Sep. 29 - Oct. 5**	**Nov. 23 - Dec. 1**	**Totals**
0	M	4	3	4	4	2	5	5	27
	F	5	5	2	1	5	1	3	22
1-6	M	0	5	4	3	3	4	0	19
	F	8	3	3	0	2	5	4	25
7+	M	14	7	9	14	6	3	12	65
	F	13	4	3	8	9	13	6	56
Totals	M	18	15	17	21	11	12	17	111
	F	26	12	8	9	16	19	13	103
Year: 1989		**1**	**2**	**3**	**Trip 4**	**5**	**6**	**7**	
Age Group	**Sex**	**Jan. 14 - Feb. 3**	**Mar. 14 - Mar. 18**	**May 4 - May 6**	**May 31 - June 4**	**Aug. 1 - Aug. 8**	**Sep. 29 - Oct. 4**	**Dec. 1 - Dec. 6**	**Totals**
0	M	3	4	11	6	9	9	6	48
	F	3	12	5	8	4	5	7	44
1-6	M	0	18	21	2	2	5	18	66
	F	3	9	10	5	5	5	7	44
7+	M	11	7	12	10	13	6	4	63
	F	9	11	8	12	11	16	7	74
Totals	M	14	29	44	18	24	20	28	177
	F	15	32	23	25	20	26	21	162

to the grey seal host. Direct comparisons of proportions (male versus female worms, 1983 versus 1989 within-season worm maturities) were made using t-tests. Direct comparisons of proportions (males compared with females, 1983 compared with 1989 by season and seal maturity) were made using t-tests. For each test, variances were first compared between samples to determine whether the t-test should be computed assuming equal variance or not, and then the appropriate test chosen. In the earlier analysis of the 1983 data (Stobo *et al*. 1990) generalised linear models (McCullagh and Nelder 1983) were used to investigate the relationship between worm abundance and the length, age and sex of the seal host using the GLIM program (Payne 1986). Explanatory variables were fitted to the data and tested for inclusion in a linear model according to the amount of deviance explained. The theory of generalised linear models refers to deviance as the measure of discrepancy between the observed and fitted values (McCullagh and Nelder 1983) and the form of this measure is specific to the error distribution being used. We initially assumed a Poisson distribution since it is generally considered to be the appropriate error distribution for count data (McCullagh and Nelder 1983). The significance of the amount of deviance accounted for by the inclusion of each variable is tested with a χ^2 statistic. The resulting GLIM models all had very large deviances, indicating that the model was inadequate; in particular, the data were overdispersed with respect to the Poisson distribution. A log transformation made the data more symmetrical, so the data were log-transformed and modelled using a normal distribution and identity link with *F* tests of the significance of the amount of deviance explained by each variable. We repeated this procedure on the 1989 samples to determine if the same conclusions would be obtained, as a check on the validity of the 1989 data as a second sampling according to 1983 protocols. We then used S-Plus (Chambers and Hastie 1992) to analyse the combined 1983 and 1989 data set.

For this analysis, we have made four major adjustments relative to the earlier examination (Stobo *et al*. 1990) of worm infections: 1) each seal maturity stage was modelled separately; 2) we dropped the constraint that the relationship between log-transformed worm counts and explanatory variates (age, length) be linear, by estimating any curvature of the relationships and applying suitable polynomial transformations to the explanatory variates; 3) sampling trip was included as a seasonal polynomial explanatory variates; 4) the logged abundance of *C. osculatum* was included as a polynomial explanatory variate. We also included the year (1983 and 1989) as a study factor. Order of entry of effects was determined using the S-Plus step function (χ^2 test of significance for entry or removal of a term). Initial parameterisations of polynomial terms were derived using non-parametric smoothing and loess transformations in generalised additive models (Chambers and Hastie 1992) to estimate suitable degrees of freedom as starting points for subsequent generalised linear models.

Variability in the timing of sampling within months distorted the representation of a temporal trend during January-March sampling relative to subsequent months, the apparent timing being earlier in the year than was actually the case. For the modeling process, we numerated the January-February trip as month 2, and the March trip as month 4, to better reflect the magnitudes of time passed between trips. Most of the March samples were taken near the end of the month. In the text, we have labelled the sampling periods as the January(1), March(2), May(3), June(4), August(5), October(6) and December(7) trips.

In all statistical tests, probability levels of $\leq$ .05 were considered significant while levels > 0.05 but $\leq$ 0.1 were considered marginally significant.

Description of seal specimens

While the majority of animals in the samples were less than 30 years old, eleven were older, the oldest being 48. Testing for growth differences between 1983 and 1989 (Fig. 3) for either males (F=1.75, df=283, p=0.89) or females (F=0.79, df=260, p=0.37) showed no significant differences between years. We modeled male and female growth using the von Bertalanffy growth equation (Fig. 4), using age in months as the time axis. Sexual dimorphism was strongly evident in both years, even in pups. The estimated maximum size of males (L_∞) was 227.4 cm, substantially larger than that of females (199.4 cm).

RESULTS

Sex Ratio

The proportion of adult male *P. decipiens*, based on mean worm counts, was 0.49 and 0.50

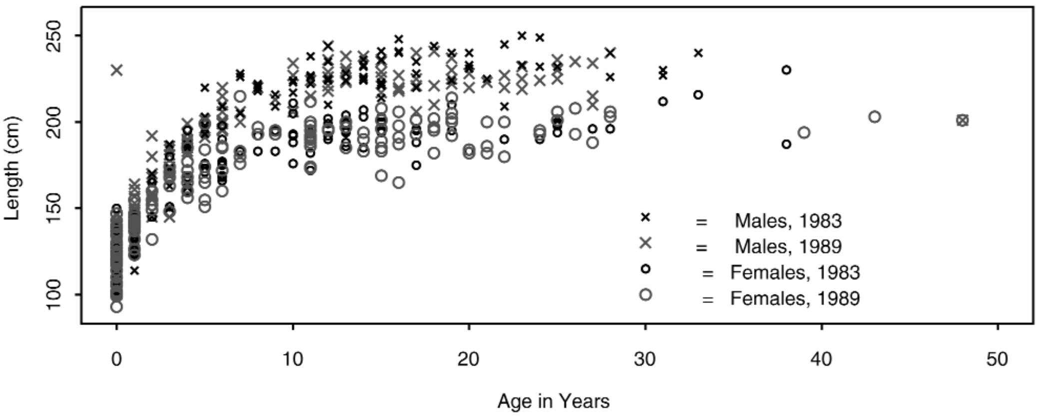


Fig. 3
Length at age of male and female grey seals collected during 1983 and 1989 on Sable Island.

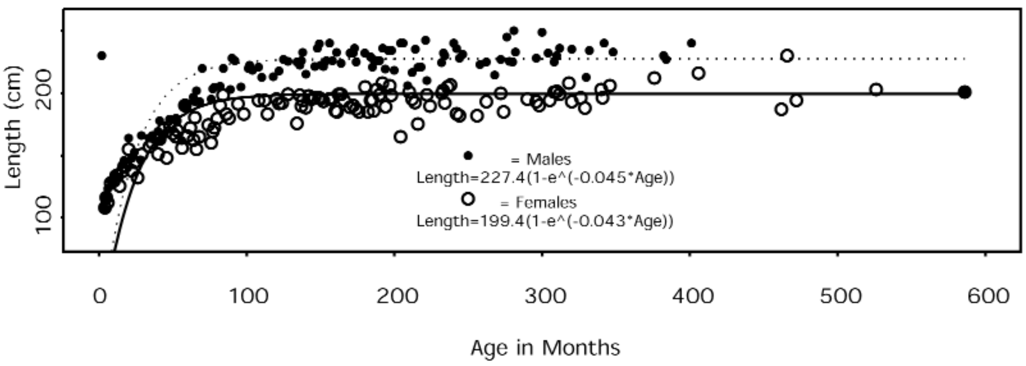


Fig. 4 *Length at age (in months) of male and female grey seals combining 1983 and 1989 data. The fitted lines reflect the von Bertalanffy growth equations given.*

in 1983 and 1989 respectively. With the male and female adult worms in each stomach treated as a paired sample, the difference in this proportion from 0.5 was significant (*P*=0.026) in 1983, insignificant in 1989 (*P*=0.571), and marginally significant when the two years were combined (*P*=0.092). For the present analysis, the ratios were sufficiently close to a 1:1 sex ratio among adult worms to warrant combining the two sexes in further analyses.

Maturity in Worms

Due to the different behavioural cycles of mature and immature seals, worm maturity, defined as the proportion of mature worms in each seal, was examined separately for each seal maturity stage (Fig. 5). Median worm maturity in pups was lowest in March, increased to a peak in June, declined through late summer and fall, then increased again during early winter. The January data consisted of animals approximately 14 months old and represents the seals’ worm infections at the end of the first year of life. Juveniles exhibited an increase in the proportion of mature worms from a low during January to February to a peak in May to June, a slight decline in summer and fall, followed by an increase in November to December. Adults exhibited 2 annual peaks in the median worm maturity, with a weak peak in March and a much stronger peak in August. The patterns of worm maturity for all three seal maturity stages indicated the highest proportion of mature worms occurred in midsummer, and the lowest proportion during late winter.

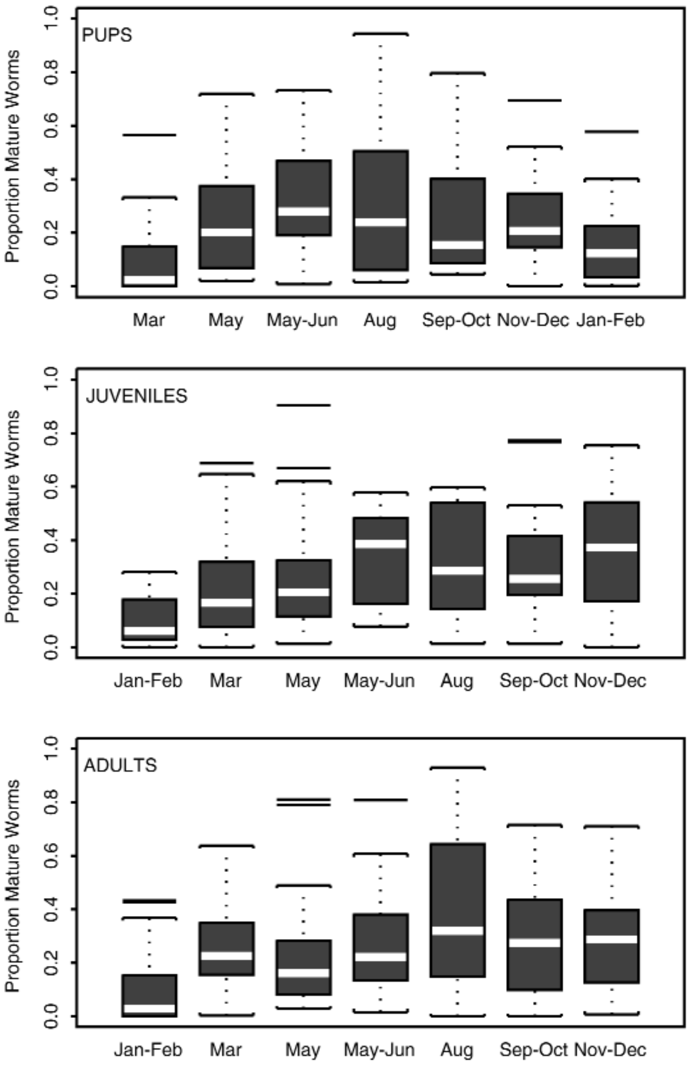


Fig. 5 *Box-and-whisker plots showing seasonal proportions of sexually mature* P. decipiens *in grey seals (sexes combined) collected during 1983 and 1989 on Sable Island. The light bar inside each box corresponds to the median proportion, the box encompasses 50% of the observations, and the lines (whiskers) bracket the 95% confidence interval for the observations.*

Table 2. Comparison of the mean proportion of mature worms in the stomachs of grey seals by trip between 1983 and 1989.

	1983		1989			
Trip	**Mean**	**St. Dev.**	**Mean**	**St. Dev.**	**t value**	**Pr(t)**
Jan. 10 - Feb. 9	0.108	0.115	0.101	0.145	0.24	0.809
Mar. 2 - Mar. 21	0.281	0.208	0.156	0.156	2.80	0.008
May 4 - May 11	0.349	0.217	0.196	0.166	3.63	0.000
May 31 - June 7	0.290	0.186	0.300	0.207	-0.21	0.836
Aug. 1 - Aug. 8	0.580	0.230	0.225	0.175	7.33	0.000
Sep. 29 - Oct. 5	0.401	0.167	0.197	0.190	4.97	0.000
Nov. 23 - Dec. 6	0.275	0.159	0.329	0.223	-1.26	0.212

* t-test for samples with unequal variances used

The proportion of mature worms in the stomachs of the 1983 samples were generally higher than that observed in 1989. In 4 of the 7 trips (March, May, August, October), the 1983 samples had a significantly higher mean proportion of mature worms than the comparable 1989 trips (Table 2).

Abundance

Individual worm abundances ranged from 4 to 12,680 in 1983 and 2 to 6,119 in 1989; the lowest numbers were carried by pups while the highest numbers were carried by a 31 year old female and a 16 year old male in 1983 and 1989 respectively. Mean log-transformed abundances and standard deviations summarised by trip, maturity stage, and sex are presented in Table 3. The GLIM analysis procedure used by Stobo *et al*. (1990), when applied to the 1989 data, indicated that the dominant influences on worm abundance in 1989 were the same as found with the 1983 data. Length was the most important single effect, and neither age nor sex were significant factors when entered subsequent to length (Table 4). The results of modelling using S-Plus (Tables 5 to 8) indicated that the differences in worm abundance in any of the seal maturity stages between 1983 and 1989 studies was insignificant, and that there were no significant interactions between any of the terms in any of the models. The assumption of normality appears reasonable for all three models (Fig. 6).

The age of the seals was a major effect on worm abundance in every model (Fig. 7), with *P. decipiens* abundance increasing as the seals grew older. The model for pups (Table 5) indicated that age (in months) during the first year of life had the greatest effect on total worm abundance; the relationship was positive and linear when worm counts were log-transformed. Having commenced independent feeding in February, pups already exhibited relatively high worm counts by March. Subsequently the abundance of worms increased throughout the re-

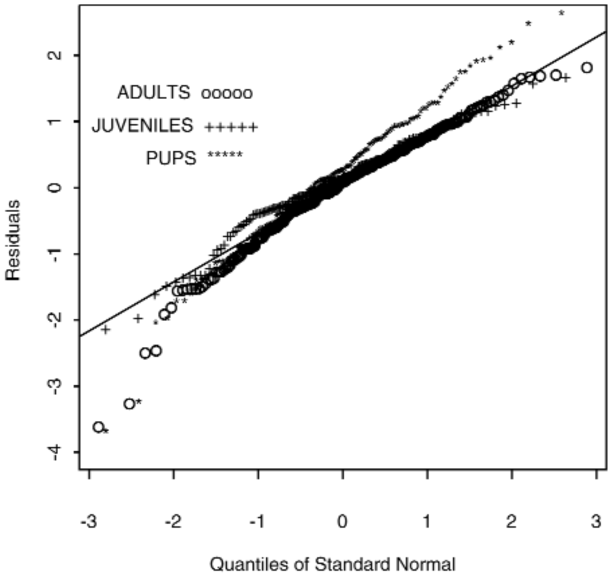


Fig. 6
Quantile plots of the residuals from the final models of P. decipiens abundance in grey seals. A perfect Gaussian fit line for the adult model is included.

mainder of their first year of life. In both juvenile and adult models (Tables 6 and 7), optimal results were obtained by curve fitting a third degree polynomial for age.

A seasonal pattern in *P. decipiens* abundance (Fig. 8) was pronounced for both juveniles and adults, and subsumed for pups by age in months. High worm abundances were maintained throughout the year by juveniles and adults, but both groups demonstrated a consistent sequence of peaks and troughs in abundance throughout the year. This pattern fit best as a fifth degree polynomial in the juvenile and adult models (Fig. 9). An increase in worm abundance following the breeding season (late December to early February) continued until May. Subsequently both groups exhibited a decline in worm abundance through the summer, followed by another increase in the fall prior to the breeding period (more gradual for adults, but maintained a little longer).

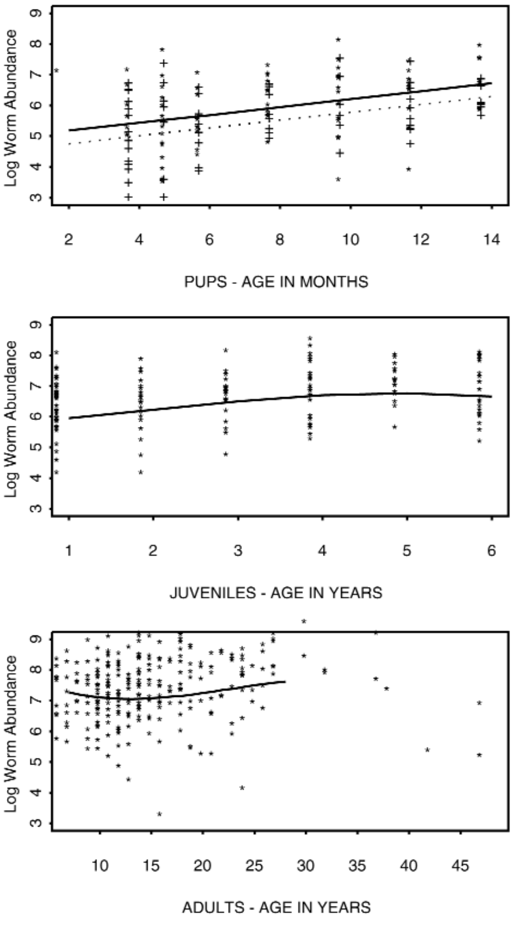


Fig. 7
*Total <u>P. decipiens</u> abundance in pups (males +, solid line; females *, dashed line), juveniles and adult grey seals sampled during 1983 and 1989. The fitted lines were predicted from analysis of deviance models. Pup and juvenile trend lines were calculated for average <u>C. osculatum</u> abundance, juvenile and adult trend lines were calculated for October, and the adult trend line was calculated for an animal of average length.*

Table 3. Mean worm counts and their standard deviations by trip.

		TRIP													
		1 Jan. 10 - Feb. 9		**2 Mar. 2 - Mar. 21 - May 11**		**3 May 4 - June 7**		**4 May 31 - Aug. 8**		**5 Aug. 1 - Oct. 5**		**6 Sep. 29 - Dec. 6**		**7 Nov. 23**	
AGE	**SEX**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**	**Mean**	**Std Dev**
2 to 14 months	Males	877	590	315	285	292	425	252	232	454	291	591	607	531	319
	Females	460	215	188	211	404	438	211	188	350	228	520	545	403	383
16 months to 6 years	Males	-	-	788	505	1,042	780	995	835	800	630	1,362	681	349	211
	Females	458	251	690	514	903	537	393	152	437	187	933	840	450	530
7+ years	Males	733	431	2,696	1,868	2,844	1,380	2,610	1,511	1,880	1,585	2,693	2,843	3,378	1,952
	Females	734	680	2,014	3,030	1,279	914	1,414	1,529	935	413	1,093	837	890	751

Table 4. Analysis of deviance to model effects of age, sex and length to explain variability of log worm counts from grey seals taken in 1989. All models use an identity link and normal error distribution. The amount of deviance explained by factor B is given that factor A is already in the model as indicated by R(B|A).

Model Factors	Degrees of Freedom	Deviance	Reduction in d.f.	Deviance Explained [a]		R(.|.)
MEAN	341	486.3				M
LENGTH	340	310.0	1	176.3		L|M
+SEX	339	308.6	1	1.4	n.s.	S|M,L
+AGE	339	309.9	1	0.1	n.s.	A|M,L
SEX	340	472.5	1	13.8		S|M
AGE	340	386.5	1	99.8		A|M

[a] all values are significant (p<=0.05) except those followed by n.s.

Table 5. Analysis of deviance of log *Pseudoterranova decipiens* abundance in pups. Terms in italics not retained in final model. The preceder "poly" defines the term as a polynomial (term,degrees of freedom). The C.o. term denotes log *Contracaecum osculatum* abundance.

Gaussian Model	Df	Deviance Explained	Residual Df	Residual Deviance	F value	Pr(F)	Dispersion
NULL	NA	NA	140	203	NA	NA	1.450
+AGE IN MONTHS	1	34.177	139	169	28.264	0.00000	
+poly (C.o.,2)	2	16.434	137	152	7.523	0.00080	
+SEX	1	5.481	136	147	5.018	0.02673	1.078
+STUDY	1	0.262	135	146	0.240	0.62517	
+LENGTH	1	0.058	134	146	0.054	0.81733	
- STUDY - LENGTH							
+AGE IN MONTHS : SEX	1	0.001	135	147	0.001	0.98095	
+poly(C.o.,2) : SEX	2	1.635	133	145	0.750	0.47460	
+AGE IN MONTHS :poly(C.o.,2)	2	2.163	131	143	0.992	0.37370	
- AGE IN MONTHS:SEX - poly(C.o.,2):SEX - AGE IN MONTHS:poly(C.o.,2)							

The role of coincident abundances of *C. osculatum* graded in importance across maturity stages. They were a major negative influence on *P. decipiens* abundance in pups, a minor but significant effect in juveniles, and no effect in adults. The best fits were obtained by treating logged *C. osculatum* counts as a second degree polynomial (Fig. 10).

Sex was a significant, but minor, effect only in the pup model, with males carrying slightly larger numbers than females (see Fig. 7 for sexually differentiated predictions for age in months). The size (length) of a seal was the biggest influence on the worm abundance of adult seals (Fig. 11), yet proved insignificant for pups and juveniles. The shape of the relationship between length and worm abundance is the same as that between age and worm abundance for adult seals, both fitting best as third degree polynomials during modelling. To examine if the relative significances of age and length exhibit a time-dependent relationship, successive models were iterated with cumulative exclusion of ages younger than 8 through 17 years, beyond which model integrity was eroded for lack of data. The ratio of deviance explained by age to that of length fluctuated

Table 6. Analysis of deviance of log Pseudoterranova decipiens abundance in juveniles. Terms in italics not retained in final model. The preceder "poly" defines the term as a polynomial (term,degrees of freedom). The C.o. term denotes log *Contracaecum osculatum* abundance.

Gaussian Model	Df	Deviance Explained	Residual Df	Residual Deviance	F value	Pr(F)	Dis-persion
NULL	NA	NA	153	114.5	NA	NA	0.748
+poly(TRIP,5)	5	21.450	148	93.05	8.074	0.00000	
+poly(AGE,3)	3	15.487	145	77.56	9.716	0.00001	
+poly(C.o.,2)	2	3.699	143	73.86	3.600	0.02993	0.517
+SEX	1	1.011	142	72.85	1.968	0.16296	
+STUDY	1	1.004	141	71.85	1.953	0.16447	
+poly(LENGTH,3)	3	0.947	138	70.90	0.614	0.60694	
- SEX - STUDY - poly(LENGTH,3)							
+poly(C.o.,2):poly(AGE,3)	6	1.838	137	72.02	0.575	0.74985	
+poly(TRIP,5):poly(C.o..2)	10	3.971	127	68.05	0.745	0.68109	
+poly(TRIP,5):poly(AGE,3)	15	8.330	112	59.72	1.042	0.41926	
- poly(C.o.,2):poly(AGE,3) - poly(TRIP,5):poly(C.o.,2) - poly(TRIP,5):poly(AGE,3)							

Table 7. Analysis of deviance of log *Pseudoterranova decipiens* abundance in adults. Terms in italics not retained in final model. The preceder "poly" defines the term as a polynomial (term,degrees of freedom). The C.o. term denotes log *Contracaecum osculatum* abundance.

Gaussian Model	Df	Deviance Explained	Residual Df	Residual Deviance	F value	Pr(F)	Dispersion
NULL	NA	NA	257	275	NA	NA	1.069
+poly(LENGTH, 3)	3	50.400	254	224	22.766	0.00000	
+poly(TRIP, 5)	5	33.474	249	191	9.072	0.00000	
+poly(AGE, 3)	3	10.328	246	181	4.665	0.00344	0.734
+STUDY	1	0.350	245	180	0.474	0.49171	
+SEX	1	0.099	244	180	0.134	0.71449	
+poly(C.o.,2)	2	0.089	242	180	0.060	0.94184	
- STUDY - SEX - poly(C.o.,2)							
+poly(LENGTH, 3):poly(AGE, 3)	9	9.971	237	171	1.522	0.14189	
+poly(LENGTH, 3):poly(TRIP, 5)	15	11.811	222	159	1.082	0.37521	
+poly(TRIP, 5):poly(AGE, 3)	15	8.026	207	151	0.735	0.74730	
- poly(LENGTH,3):poly(AGE,3) - poly(LENGTH,3):poly(TRIP,5) - poly(TRIP,5):poly(AGE,3)							

trendlessly between 0.19 and 0.27, providing no evidence of a systematic change in the relative influence of either effect over time.

DISCUSSION

Our analysis indicated that there has been no change in *P. decipiens* abundance in grey seals between 1983 and 1989 in any of the seal maturity stages (Tables 5 to 7). During that 7-year period, we estimated that the Sable Island grey seal population increased from approximately 31,000 to 55,000 animals, using the pup production numbers from Stobo and Zwanenburg (1990) and the assumption that pups represented 17.5% of the total population, as predicted by a stable age distribution (Zwanenburg and Bowen 1990). During the same period, the *P. decipiens* infections carried by many of the prime finfish prey of seals had increased (McClelland *et al*. 1985, Brattey *et al*. 1990, Marcogliese 1995). This suggests that the intensity of infestation of fish is positively influenced by seal population size, but that the intensity of infestation of seals is unaffected by increases in worm abundance in fish. It could be hypothesised that an upper limit has been reached in the carrying capacity of the seal population for sealworm, but the high variation in individual worm counts of seals in both 1983

Table 8. Parameter estimates from analysis of deviance of grey seal log worm counts by life history stage. The preceder "poly" defines the term as a polynomial(term, degrees of freedom).

a) PUPS

Coefficients	Value	Standard Error	t value
Intercept	5.019	0.380	13.203
AGE IN MONTHS	0.136	0.030	4.508
poly(C.o.,2)1	-1.378	2.355	-0.585
poly(C.o.,2)2	-7.897	2.075	-3.805
SEX	-0.399	0.177	-2.254

b) JUVENILES

Coefficients	Value	Standard Error	t value
Intercept	-19.074	39.340	-0.485
poly(TRIP, 5)1	-0.627	1.604	-0.391
poly(TRIP, 5)2	-6.131	1739	-3.525
poly(TRIP, 5)3	-0.407	1.606	-0.253
poly(TRIP, 5)4	-6.784	1.585	-4.281
poly(TRIP, 5)5	-2.681	1.471	-1.823
poly(AGE, 3)1	-1380.640	2231.791	-0.619
poly(AGE, 3)2	-1372.612	2295.022	-0.598
poly(AGE, 3)3	-366.372	673.276	-0.544
poly(C.o.,2)1	0.226	1.868	0.121
poly(C.o.,2)2	-4.646	1.851	-2.510

c) ADULTS

Coefficients	Value	Standard Error	t value
Intercept	8.528	1.251	6.816
poly(LEN, 3)1	-36.005	39.521	-0.911
poly(LEN, 3)2	31.026	24.023	1.292
poly(LEN, 3)3	-8.213	8.811	-0.932
poly(TRIP, 5)1	1.492	1.346	1.108
poly(TRIP, 5)2	-5.391	1.290	-4.180
poly(TRIP, 5)3	5.776	1.359	4.251
poly(TRIP, 5)4	-1.763	1.315	-1.340
poly(TRIP, 5)5	-0.681	1.264	-0.538
poly(AGE, 3)1	-8.034	5.360	-1.499
poly(AGE, 3)2	5.486	3.178	1.727
poly(AGE, 3)3	-6.027	1.968	-3.063

and 1989 does not support that conclusion. Although the magnitudes of individual *P. decipiens* counts appear to reflect a stasis over the years, a decline in the proportion of mature worms in the seals' stomachs in most of the months in which samples were taken between 1983 and 1989 was evident (Table 2). Two possible explanations for this change are water temperature and fish size. During the 1980's, bottom water temperatures on the Scotian Shelf cooled significantly (Anonymous 1995a, Drinkwater and Pettipas 1994, Simon and Comeau 1994). Associated with the cooling trend, the growth rates of several commercial fish species declined (Anonymous 2000, Fowler and Stobo 2000). If the same relationship between temperature and growth rate observed for fish applies to other cold-blooded species, the cooling phenomenon may have slowed development of the worms as well, re-

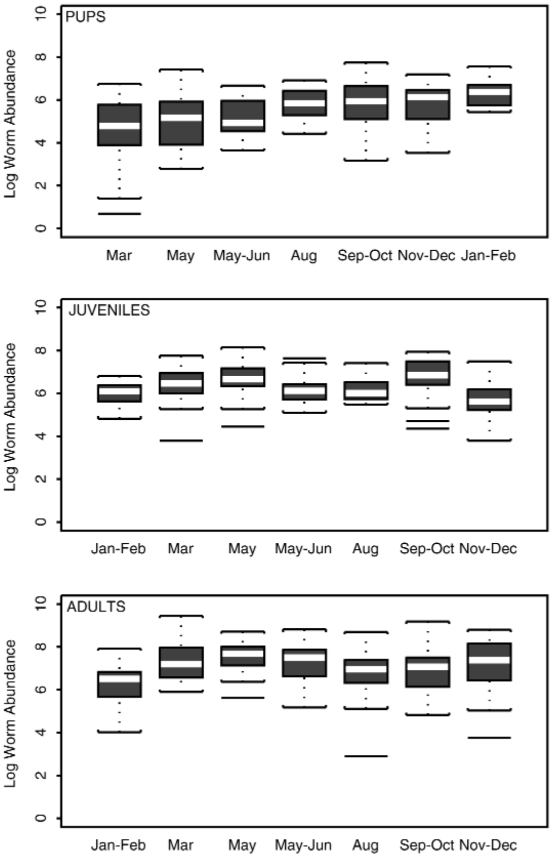


Fig. 8 *Seasonal P. decipiens abundance in grey seals (sexes combined) collected during 1983 and 1989 on Sable Island. The light bar inside each box corresponds to the median proportion, the box encompasses 50% of the observations, and the lines (whiskers) bracket the 95% confidence interval for the observations.*

sulting in smaller, more immature worms being ingested by seals. Secondly, concurrent with dramatic declines in the biomass of commercial fish species over the last couple of decades (Anonymous 1995b, 1996, Simon and Comeau 1994), the size compositions of major fish stocks (including gadoid and flatfish species) have generally shifted toward smaller fish (Anonymous 2000, Fowler and Stobo 2000, Stobo et al 1997). Hence the majority of commercial fish prey available to the seals were smaller in 1989 than 1983. McClelland *et al*. (1983b, 1990) noted that sealworm abundance in fish increases with fish size, and Moller and Klatt (1990) noted that in smelt, sealworm length increased with size of the fish host. Because small fish tend to consume smaller prey than large fish, fish in 1989 might have been exposed to a higher proportion of smaller, immature sealworm larvae than fish in 1983. Thus while the seals may have consumed more of these smaller fish in 1989 to satisfy their energy requirements and thereby maintain the same overall abundance levels, they could also have ingested more immature worms. If this is correct, the production of sealworm eggs in the Northwest Atlantic may have been reduced due to a longer period of time required for the worms to reach sexual maturation in the stomachs of the seals.

Seasonal fluctuation in the proportion of mature worms in seals may be a consequence of seasonal changes in worm ingestion rate. Increases in the proportion of mature worms in adult seals usually corresponded with decreases in worm abundance throughout most of the year, with the highest proportion of mature worms coinciding with low worm abundance in August, our first sampling after the moult (mid-May to mid-June). This might indicate lack of recruitment of immature worms (fewer being ingested due to partial fasting) and the development of pre-existing immature worms into sexually mature adults. This inverse relationship between maturity and abundance of *P. decipiens* was not observed, however, during the January –February trip, at the end of the breeding fast (late December to early February). These seals are characterised by both the lowest number of worms and the lowest proportion of mature worms. This difference may be explained by the complete and prolonged fast undertaken by the adult seals during the breeding season. During that period mature worms were being shed (personal observation). That, in combination with the acquisition of immature worms when feeding resumed, could explain our observations.

The observed seasonal patterns of nematode abundance in grey seals, and trends associated with host maturity, may be influenced by the composition of grey seal prey and nematode infestations of intermediate hosts in the vicinity of Sable Island. However, diet studies of Sable Island grey seals and studies examining nematode infestation rates in potential prey species of grey seals do not provide the necessary temporal resolution to compare with seasonal patterns in nematode infestations of grey seals. Only 47 of the 247 grey seal stomachs from Sable Island examined by Benoit and Bowen (1990) and 39 stomachs examined by Bowen *et al*. (1993) contained any food at all, most seals having completed digestion before hauling out and being sampled. As well, the majority of these animals were sampled during breeding and moulting periods, when they were more inclined to haul out and less inclined to feed. Both studies combined provide only 30 stomachs to represent 9 months of normal feeding periods across 3 stages of seal maturity, producing insufficient information to correlate with nematode abundance patterns in grey seals. Scat data from 393 collections on Sable Island (Bowen and Harrison 1994) provides better seasonal coverage, though without any corresponding seal maturity data. But scat samples provide only identifiable hard parts, are often incapable of separating out species of potential interest from broader taxonomic groups, and preclude consideration of softer prey items. Finally, we are dealing with nematode species that exhibit residency periods in seal stomachs of up to 2 months, versus food retention times of a few hours. Intermediate host sampling in the vicinity of Sable Island (McClelland *et al*. 1990) did not provide seasonal information, and targeted groundfish species, whereas we are interested in the seasonal infestation patterns of any number of commercial and non-commercial fish, invertebrate, and pelagic fish species. To properly identify the source(s) of nematode infestations would require synch- ronous sampling of seal stomachs for newly ingested worms and prey species for nematode contributions, or results will be confounded by any short-term or seasonal variations in diet.

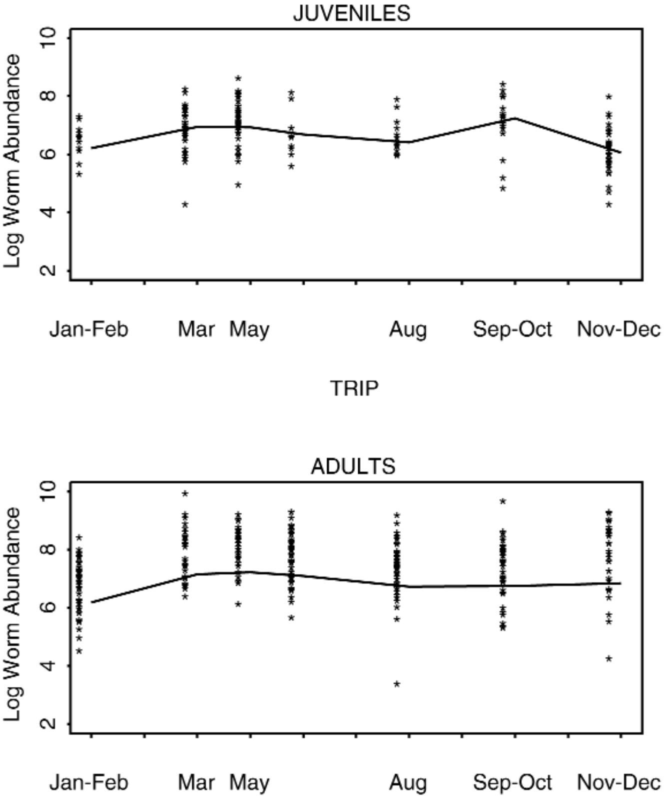


Fig. 9
Predicted seasonal changes in P. decipiens abundance in juvenile (age 4) and adult (210 cm, age 16) grey seals. The observed values for individual seals are also shown.

Stobo *et al*. (1990) found that seal length, as a proxy for size, was the main influence on *P. decipiens* abundance, when the total length range of the seals in the 1983 samples was modelled. We obtained the same result with the 1989 data using the 1990 analysis procedure (Table 4), but when we established three seal maturity stages and modelled them separately, it became apparent that the relative importance of length with respect to worm abundance varied between maturity stages.

Log worm counts in grey seals during the first year of life were related to age (Table 5), and log counts increased linearly with age in months (Fig. 7). Although length was not a sig-

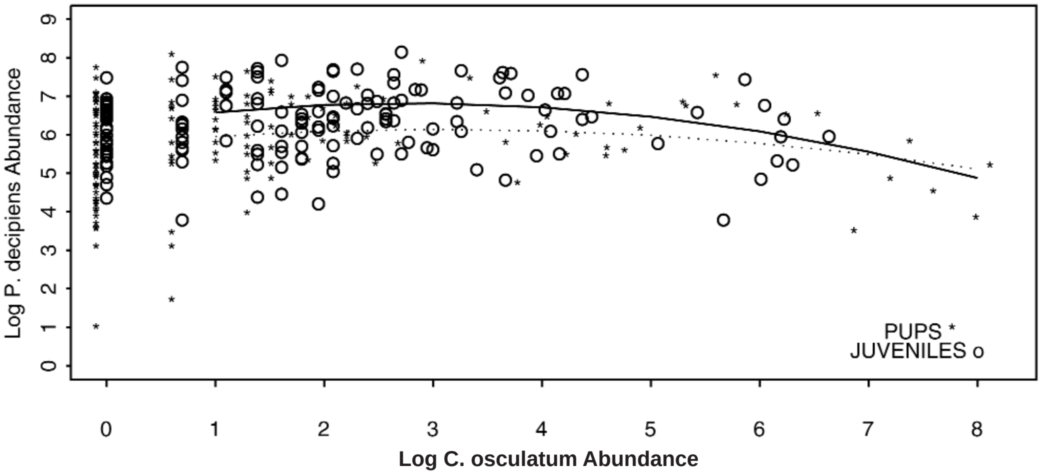
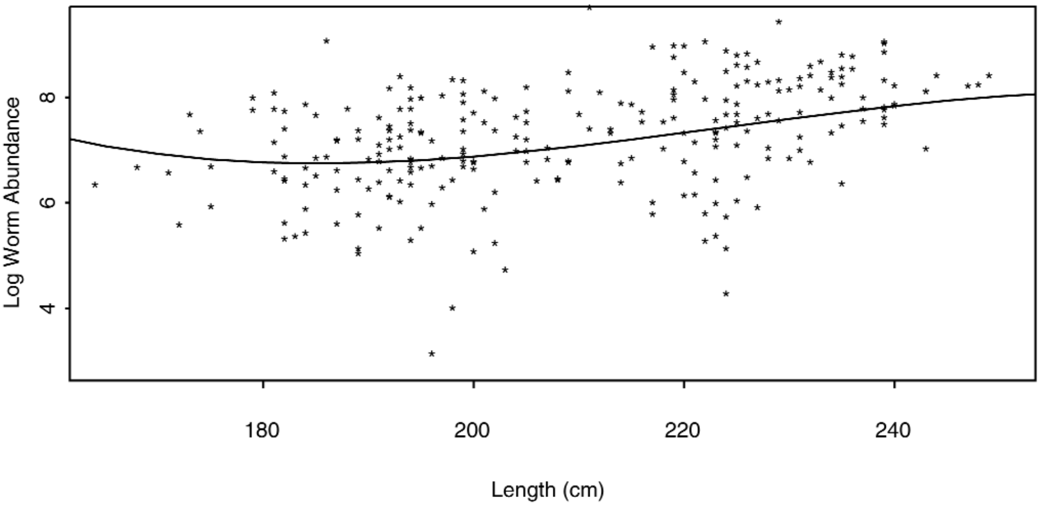


Fig. 10
The relationship between P. decipiens and C. osculatum worm abundance in younger seals. Model predictions are included for a 14-month old male pup (solid line) and a 3-year old male juvenile (dotted line). The juvenile prediction was derived for a Jan.-Feb. trip corresponding with the trips for which pups are 14 months old.

Fig. 11
P. decipiens abundance with length of grey seals. A prediction for 11-yr old grey seals in Sep-Oct is included.



nificant effect, age (in months) represented both change in size and duration of exposure in the model. Because the pups were developing their initial infections of sealworm, it is not surprising that no seasonal pattern was evident. Sex was a minor effect probably because even in the first year of life, the sexual dimorphism in seal size becomes apparent.

It is interesting that *C. osculatum*, commonly associated with Gulf of St Lawrence (Marcogliese *et al* 1996) and Newfoundland seals (Brattey and Stenson 1993), is most abundant in pups on Sable Island. We speculate that this nematode might be abundant in some of the smaller prey species around Sable Island, and that these species become progressively less desirable as the seals become more adept at catching larger prey. As a means of distinguishing the recent origins of Sable Island breeding seals in terms of Gulf or Shelf feeding grounds, predominance of *C. osculatum* in adult seals seems likely to denote a Gulf feeder, but the potential to distinguish seals is probably restricted to mature animals.

The importance of *C. osculatum* abundance as a negative influence on *P. decipiens* abundance appears consistent with the principle of competitive exclusion. The two species share the same resource, density dependence becoming apparent at higher combined worm abundance. Potential for competitive interaction between these two nematodes was hypothesised by McClelland *et al.* (1985), but subsequent investigations (Brattey and Stenson 1993, Marcogliese *et al*. 1996) provided no proof of competitive exclusion, inverse relationships in abundances being attributable to geographic, prey or temperature effects. We believe that for Sable Island seals we can reduce the possibilities to either competition or diet. That the effect diminishes with age in this study, to the point of insignificance for adults, suggests that either *P. decipiens* is better adapted to the host species and competitively displaces *C. osculatum*, or that *C. osculatum* recruitment is reduced as the seals age due to change in host diet. All our specimens were collected on Sable Island, and no significant interactions between *C. osculatum* abundance and trip are evident. This effectively rules out geographic differences and temperature effects as causative factors governing relative abundances of the two nematodes. If changes in temperature affected the balance, or our data were seriously confounded by migrant seals from the Gulf of St Lawrence, we would expect significant interaction between *C. osculatum* abundance and trip (or age in months).

Worm abundance in juveniles was affected primarily by season (trip) and age, with *C. osculatum* abundance a minor effect (Table 6). The predicted abundance trend shown in Fig. 7 for juveniles illustrates the increase with age. Since this continues to be a rapid growth period for grey seals (Fig. 3), age may represent an increase in mass not fully reflected by length alone. The seasonal effect on worm abundance in juvenile grey seals (Fig. 8) describes a pattern similar to that observed for adults. Given the preponderance of immature seals in this group, it is interesting that a late winter drop in worm abundance can be discerned. It may be that even juveniles have a physiological response to the breeding season and undergo some degree of fasting, resulting in a winter decline in worm abundance similar to that observed in adults.

Worm abundance in adults (aged 7 and older) was affected by length, season (trip), and age, in order of importance (Table 7). Sex was not significant. These results confirm those of Stobo *et al*. (1990), that sex is not important once we account for the effect of length. This means that males and females of the same size will carry similar infections, and since males grow larger than females, they will generally carry larger numbers at age. But even with length in the model, age was still a significant effect. We suggest that, although length becomes asymptotic in older grey seals (Fig. 4), the animals continue to increase their mass, their food intake, and consequently their worm counts; thus age may be accounting for a portion of growth and potential worm abundance not explained by length alone. The seasonal effect (Figures 8 and 9) indicated a polynomial relationship which described the declines in total worm abundance during the breeding season and during midsummer. These results support the hypothesis of Stobo *et al*. (1990) that, during the breeding season, fasting grey seal adults lose some of their worms, but they are regained soon after resumption of feeding. During midsummer, worm abundance again declines, but our modelling supports the conclusion (Stobo *et al*. 1990) that the timing of the decline in worm abundance in mid-summer cannot be entirely accounted for by a partial fast during the moult. We suggest a seasonal change in availability of, or preference for, prey species may also be involved. Worm abundance then slowly builds back up through the fall.

Generally, this analysis comes to many of the same conclusions as that of Stobo *et al*. (1990). The 1983 study however, was a single observation of a complex of interactions between a parasite and host over the space of a year. As such the conclusions might describe only the situation in that year with potential built-in biases due to sampling or environmental conditions. By replicating the 1983 study and analysis in 1989 we have established that the relationships are accurate descriptions of the biological interactions between parasite and host. We have confirmed that grey seals acquire sealworm infections shortly after they commence independent feeding, that numbers of worms continue to increase as they grow and that they do not lose any major portion of their infection throughout the year. We also have determined that worm abundances were not different between 1983 and 1989, spanning a period of many changes in grey seal population status, prey availability and environmental conditions. Lastly we have refined our understanding of some of the interactions between the *P. decipiens* nematode and its primary host, including the relationship with *C. osculatum* in younger seals.

The results of this study may have significant implications relevant to the management of the sealworm problem. Because grey seals retain a large proportion of their worm infection during the breeding season, control of the infections in actively breeding seals could have a significant impact on the annual production of sealworm in the Northwest Atlantic Ocean. As grey seals are accessible to non-lethal control measures during the breeding season, and relatively inaccessible at other times of the year, the potential vulnerability of sealworm at this time is of practical significance. If lethal control measures are considered, then culling the larger seals might be expected to have the greatest impact on worm egg production in the subsequent years. However a relationship between *P. decipiens* fecundity and subsequent numbers of larvae in fish has not been established (Brattey and Stobo 1990, des Clers and Mohn 1990). Thus any efficacy of reducing sealworm infections in grey seals during the breeding season, in terms of subsequent infestation of fish, should not be assumed. Similarly, the magnitude of a cull necessary to effectively reduce the abundance of sealworm in fish cannot be determined until this relationship is quantified.

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