Patterns of abundance and maturity among three species of parasitic nematodes (*Pseudoterranova decipiens, Contracaecum osculatum, Anisakis simplex*) co-existing in Sable Island grey seals (*Halichoerus grypus*).

G. Mark Fowler and Wayne T. Stobo

Marine Fish Division
Bedford Institute of Oceanography
P. 0. Box 1006
Dartmouth, Nova Scotia
B2Y 4A2

ABSTRACT

The abundance and maturity of three species of anisakine nematode (*Pseudoterranova decipiens*, *Contracaecum osculatum*, *Anisakis simplex*) that co-occurred in the stomachs of Sable Island grey seals were examined in relation to seal growth and seasonal considerations. Sealworm (*P. decipiens*), the predominant nematode in these seals, typically reached numbers of 400 to 2000 worms per stomach. *C. osculatum* and *A. simplex* were usually found in much smaller numbers of 40 to 100 and 20 to 60 worms, respectively, per stomach. All three species initially increased in abundance as the seals grew, but after most of a seals' growth had been attained *P. decipiens* abundance continued to increase with age, *A. simplex* numbers either continued to increase or were simply maintained, while *C. osculatum* abundance declined. Numbers of both *P. decipiens* and *A. simplex* declined during winter breeding/pupping and summer moulting fasts or partial fasts, and rose during the regular feeding periods between the fasts. Conversely, numbers of *C. osculatum* rose during the breeding period, and also during the moulting period in younger seals. We believe this could be attributed to some degree of feeding on prey species in the immediate vicinity of Sable Island that were not preferred during focused feeding periods, and that the inclination to feed during fasting periods decreased as seals grew. An inverse relationship between worm abundance and worm maturity, attributable to the seasonal changes in rates of ingestion of immature worms, was more pronounced for *C. osculatum* than *P. decipiens*. *C. osculatum* was usually represented by much higher proportions of mature worms than *P. decipiens*. This could be entirely related to the longer periods of time dedicated to feeding than spent breeding or moulting, but higher mortality rates of immature *C. osculatum* or greater longevity of mature *C. osculatum* could also have occurred. *A. simplex*, generally associated with cetacean species as final hosts, rarely matured in grey seals. We have doubts that the grey seal could be considered a final host for *A. simplex*.

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INTRODUCTION

During investigations into the relationship between the sealworm *Pseudoterranova decipiens*, and the grey seal *Halichoerus grypus*, the stomachs of 553 grey seals were sampled over the course of two years (1983 and 1989) to elucidate seasonal and long-term changes in sealworm abundance (Stobo *et al*. 1990, Stobo and Fowler 2001). All animals were taken at Sable Island, a major North Atlantic haulout and pupping site approximately 160 km off the east coast of Nova Scotia, Canada. The primary focus of this field work was the sealworm, but specimens of two other prevalent species of anisakine nematodes, *Contracaecum osculatum* and *Anisakis simplex*, were also counted and staged for maturity in the same fashion as *P. decipiens*. Subsequent analysis of the data showed a relationship between *P. decipiens* and *C. osculatum* abundances (Stobo and Fowler 2001). In this paper, the abundance and maturity of the 3 most common species of stomach nematodes found in grey seals (*P. decipiens*, *C. osculatum*, and *A. simplex*) are examined in relation to the age, length and sex of the seal host, as well as season and year of sampling.

All three anisakine nematode species in this study are characterized by life cycles that 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, Marcogliese 1995), and include most of the groundfish species of interest to fisheries in the northwest Atlantic. Capelin (*Mallotus villosus*) and cod (*Gadus morhua*) are known to be major intermediate hosts in the Gulf of St Lawrence (McClelland *et al*. 1985, Boily and Marcogliese 1995, Marcogliese 1995). In the vicinity of Sable Island, only large cod and white hake (*Urophycis tenuis*) have been found to host *C. osculatum*, and only in small numbers (McClelland *et al*. 1990). However, capelin in this area have not been examined for nematode infestations.

The grey seal (*Halichoerus grypus*) appears to be the main final host of *P. decipiens* in the North Atlantic (Scott and Fisher 1958, Young 1972, Mansfield and Beck 1977, McClelland 1980, Bjørge MS 1984), and a major final host of *C. osculatum* in the Gulf of St Lawrence (Marcogliese *et al*. 1996). Grey seals have not been regarded as an important final host of *A. simplex*, rather cetaceans are considered the usual final hosts of this nematode (van Thiel 1966). Experimental work with captive seals (McClelland 1980) indicated that *P. decipiens* often survived 6 weeks in grey seals, during which time they completed their life cycle (produced eggs). We lack similar data related to longevities of sexually viable *C. osculatum* and *A. simplex* in the grey seal.

Grey seal pups begin to acquire stomach nematodes shortly after they commence independent feeding (Stobo *et al.* 1990, Stobo and Fowler 2001). Grey seals of all subsequent ages are infected, worm abundance increasing as the seals grow larger (Bjørge MS 1984, Stobo and Beck 1985, Wiig 1988, Stobo *et al*. 1990, Stobo and Fowler 2001). Due to sexual dimorphism in grey seals (males grow faster and larger than females), males carry more worms than females of the same age (Stobo and Fowler 2001). Grey seals do not appear to completely eliminate their stomach nematodes at any time during the year but seasonal fluctuations in abundance have been observed, possibly due to the breeding fast (late December to early February) or changes in diet composition (Wiig 1988, Stobo *et al*. 1990, Haug *et al*. MS 1991, Stobo and Fowler 2001). In previous analyses, Stobo *et al*. (1990) and Stobo and Fowler (2001) described a seasonal cycle of abundance of *P. decipiens* in grey seals, suggesting declines in abundance coincident with increases in proportions of mature worms during the breeding season when the adult seals are fasting. Declines were also observed following the moulting season (roughly middle of May to middle of June) when partial fasting may occur.

MATERIALS AND METHODS

Details of the field sampling and processing of the 553 grey seals in this study, and the general analytical approach are provided in Stobo and Fowler (2001). The specific methods of analysis used here represent a subset of the methods presented in Stobo and Fowler (2001), which applied some older analytical techniques to facilitate direct comparisons with results of an earlier study (Stobo *et al*. 1990). In this paper we have applied generalized linear analysis of deviance (McCullagh and Nelder 1983) to log-transformed nematode abundances, using the statistical utilities in S_Plus (Chambers and Hastie 1992). For statistical hypothesis testing, probability levels $\leq .05$ were considered significant. Estimation of the number of polynomial parameters to reflect curvature of the relationships between worm abundance and explanatory variates, and the order of entry of effects into models, were determined using the S-Plus step function, which iteratively applies a χ^2 test of significance for entry or removal of a term in successive models.

Seven sampling trips were made in each of 1983 and 1989, with the later 1989 study scheduled to correspond temporally with 1983 sampling. As in Stobo and Fowler (2001), we designated the January-February trip as month 2, and the March trip (very end of month) as month 4, to more reasonably scale the magnitudes of time passed between trips for the modelling process. The seal samples were partitioned into 3 life history groups (corresponding approximately to pups, juveniles, and adults) for descriptive and analytical purposes, and each life history stage was modelled separately. The pups were treated as a separate group since they do not develop nematode infections until they begin independent feeding; for this reason, no pups were taken during the January trips. However yearlings taken in January 1983 and 1989 (12 to 14 months old) were included in the pup life stage group to represent the infections carried by the pups at the end of the first year of life. The 2 older life stages were determined from preliminary analyses of deviance as ages 1 to 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 in modelling *P. decipiens* abundance (Stobo and Fowler 2001). As such these stages reflected phases of infestation that were generally, but loosely, associated with the stages of maturity of the seals. With respect to *C. osculatum* and *A. simplex* abundance in the current analysis, these stages presented one instance of a significant interaction, pertaining to the model of *C. osculatum* infections in pups (Stobo and Fowler 2001). But since this interaction occurred between age in months of pups and study year (1983 versus 1989 sampling), we saw no reason to change our maturity classification.

The analysis of *P. decipiens* infections was reproduced from the earlier paper (Stobo and Fowler 2001), and the same approach was applied to *C. osculatum* and *A. simplex* in this paper. The original inclusion of *C. osculatum* as a covariate in the *P. decipiens* model is our only instance of treating the abundance of a co-occurring nematode species as a variate. We knew from exploratory analyses that *A. simplex* abundance exhibited serial correlation with *P. decipiens* abundance, and the *C. osculatum* and *A. simplex* data were too dispersed to resolve covariance with other species in their own models.

RESULTS AND DISCUSSION

P. decipiens was the most abundant nematode species in the stomachs of grey seals, although *C. osculatum* attained appreciable numbers in the fall and winter, especially in pups (Table 1). *A. simplex* usually occurred only in small numbers. The results of modelling (Table 2) indicated that growth (age or length) and season (trip) were the major significant effects determining the abundance of the three species of nematode in grey seals, with sex and study year attaining significance as lesser effects in some models. Age or length of seals were relevant to the abundances of all three nematodes in every life history stage with the possible exception of *A. simplex* in adults (but see below). Seasonal effects on nematode abundances were evident in juvenile and adult life history stages, but could not be investigated with pups. During the first year of life the pups acquire worms for the first time as they learn to feed, no minima or maxima in worm abundances yet established to correlate with seasons. The assumption of normality of the distributions of log-transformed nematode counts appears reasonable for all models (Fig. 1).

The abundances of all three parasite species increase as seals grow older or larger (Fig. 2).

Table 1. Mean abundances of nematodes, by life history stage, in the stomachs of grey seals during each trip period on Sable Island.

Pups
0 - 14 months

Trip	No. of seals	Pseudoterranova decipiens		Contracaecum osculatum		Anisakis simplex	
		Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Jan. 10 - Feb. 9	15*	669	496	32	65	17	23
Mar. 2 - Mar. 21	24	226	236	2	7	4	7
May 7 - May 11	22	328	422	5	13	11	36
May 31 - June 7	19	233	208	7	17	6	8
Aug. 2 - Aug. 7	20	407	263	19	36	29	31
Sep. 29 - Oct. 5	20	570	575	271	602	12	24
Nov. 23 - Dec. 1	21	470	348	505	1062	57	88

*These are 14 month old animals, not newborns.

Juveniles
16 months - 6 yrs

Trip	No. of seals	Pseudoterranova decipiens		Contracaecum osculatum		Anisakis simplex	
		Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Jan. 10 - Feb. 9	11	458	251	58	144	3	5
Mar. 2 - Mar. 21	35	754	503	11	20	47	75
May 7 - May 11	38	995	702	34	75	21	36
May 31 - June 7	10	694	649	93	180	18	23
Aug. 2 - Aug. 7	12	588	445	7	8	12	13
Sep. 29 - Oct. 5	19	1136	780	3	4	25	28
Nov. 23 - Dec. 1	29	387	360	100	198	28	26

Adults
7+ yrs

Trip	No. of seals	Pseudoterranova decipiens		Contracaecum osculatum		Anisakis simplex	
		Mean	St. Dev.	Mean	St. Dev.	Mean	St. Dev.
Jan. 10 - Feb. 9	47	734	555	259	538	3	8
Mar. 2 - Mar. 21	29	2343	2473	170	553	96	176
May 7 - May 11	32	2306	1416	27	45	43	65
May 31 - June 7	44	2067	1618	50	92	21	29
Aug. 2 - Aug. 7	39	1396	1227	11	14	48	108
Sep. 29 - Oct. 5	38	1472	1659	55	301	36	85
Nov. 23 - Dec. 1	29	2263	1967	236	651	192	265

This trend is maintained for *P. decipiens* throughout the life of a seal. The trend for *C. osculatum* is maintained until seals are nearly fully grown, after which the numbers begin to decline. The reason for the eventual decline in *C. osculatum* abundance remains a matter of conjecture. It may result from competitive displacement by *P. decipiens* or simply change in prey preference with age or size of seals, as originally speculated (Stobo and Fowler 2001).

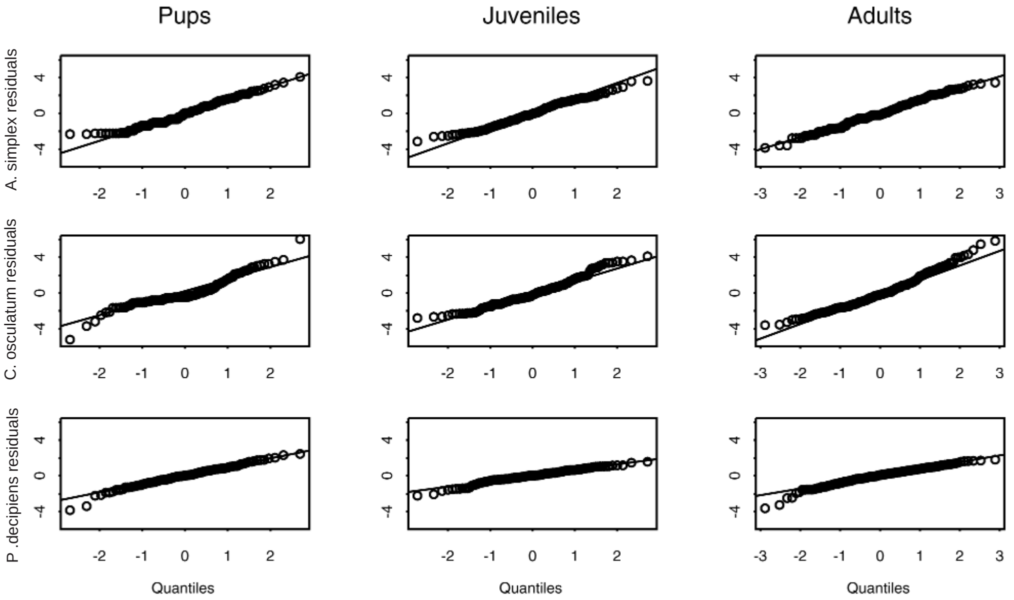


Fig. 1
Quantile plots of the residuals from the final models of worm abundance in grey seals. A perfect Gaussian fit line for each model is included.

The increasing trend is only evident for *A. simplex* among younger animals, although the difference between sexes of adults (Table 2) may represent a growth component (male grey seals are larger than females). Similarly, the significance of sex in the pup model of *P. decipiens* abundance may be capturing the onset of sexual dimorphism in grey seals, a feature that the length variable is inadequate to characterise (Stobo and Fowler 2001). The animals can increase their mass, in terms of weight, at a greater rate than their length alone represents.

Two seasonal patterns in nematode abundances predominate for adult and juvenile seals (Fig. 3). The abundances of *P. decipiens* and *A. simplex* decrease during winter breeding/pupping and summer moulting periods, and increase during the normal feeding periods between these events. *C. osculatum* abundance, however, only parallels the other nematodes during the moulting decline and post-moult increase in adult seals. The pattern is reversed with respect to the winter and spring. *C. osculatum* abundances rise during breeding and drop off during the post-breeding feeding period. In juveniles the entire pattern of *C. osculatum* abundance is inverted relative to that of *P. decipiens* and *A. simplex*. The association between increasing *C. osculatum* abundance and breeding or moulting periods suggests some degree of feeding in the local area at these times, but likely on prey species not usually preferred. Mothers with pups are known to fast during the breeding period, but could become infested with *C. osculatum* upon arrival at the island, prior to giving birth. Male and juvenile seals may do the same, but may also be feeding to some extent during the pupping and mating period. Younger animals may be more inclined towards feeding during breeding or moulting periods than older animals. This would account for the full inversion of the *C. osculatum* pattern in juveniles, assuming that older seals feed less during the moult.

A portion of the *C. osculatum* infections apparent during the breeding period may be associated with animals that feed in the Gulf of St Lawrence, where this nematode typically predominates over *P. decipiens* in grey seals (Marcogliese *et al*. 1996). We were unable to distinguish relative likelihoods of the origin of the *C. osculatum* infections. But the highest *C. osculatum* abundances found in pups were in animals born on Sable Island (all animals born on Sable Island during the study years were tagged shortly after birth). This confirms the availability of *C. osculatum* in the immediate vicinity of Sable Island. A study of anisakine nematodes in fish around Sable Island (McClelland *et al*. 1990) indicated that *C. osculatum* was not likely transmitted by local fish species. Capelin, infrequently resident on the Scotian Shelf, have been present in waters just north of Sable Island (the edge of Sable Island

Table 2. Analyses of deviance of log worm abundance in grey seals. 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. Insignificant interactions are not shown. The age variable denotes months in pups, and years in juveniles and adults.

Pseudoterranova decipiens

PUPS (141 animals) Null deviance = 202.76

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
AGE	1	34.177	28.264	0.00000
poly(C.o.,2)	2	16.434	7.523	0.00080
SEX	1	5.481	5.018	0.02673
STUDY	1	0.262	0.240	0.62517
LENGTH	1	0.058	0.054	0.81733

JUVENILES (154 animals) Null deviance = 114.50

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
poly(TRIP,5)	5	21.450	8.074	0.00000
poly(AGE,3)	3	15.487	9.716	0.00001
poly(C.o.,2)	2	3.699	3.600	0.02993
SEX	1	1.011	1.968	0.16296
STUDY	1	1.004	1.953	0.16447
poly(LENGTH,3)	3	0.947	0.614	0.60694

ADULTS (258 animals) Null deviance = 274.71

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
poly(LENGTH, 3)	3	50.400	22.766	0.00000
poly(TRIP, 5)	5	33.474	9.072	0.00000
poly(AGE, 3)	3	10.328	4.665	0.00344
STUDY	1	0.350	0.474	0.49171
SEX	1	0.099	0.134	0.71449
poly(C.o.,2)	2	0.089	0.060	0.94184

Contracaecum osculatum

PUPS (142 animals) Null deviance = 588.68

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
poly(AGE,3)	3	154.970	17.082	0.00000
STUDY	1	14.420	4.767	0.03074
SEX	1	4.110	1.336	0.24980
LENGTH	1	0.090	0.028	0.86691
poly(AGE,3):STUDY	3	98.000	13.623	0.00000

JUVENILES (154 animals) Null deviance = 431.51

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
poly(TRIP,5)	5	62777	5.269	0.00018
AGE	1	10.470	4.394	0.03783
SEX	1	6.063	2.544	0.11290
poly(LENGTH,2)	2	8.812	1.849	0.16112
STUDY	1	2.658	1.116	0.29267

ADULTS (258 animals) Null deviance = 1033.40

Gaussian Model	Df	Deviance Explained	F value	Pr(F)
NULL	NA	NA	NA	NA
poly(TRIP,2)	2	109.520	17.761	0.00000
poly(LENGTH,3)	3	83.400	9.017	0.00001
STUDY	1	55.410	17.972	0.00003
poly(AGE,2)	2	20.420	3.312	0.03807
SEX	1	0.000	0.000	0.99137

Table 2. (cont.)

Anisakis simplex				
PUPS (142 animals)		**Null deviance = 360.51**		
Gaussian Model	**Df**	**Deviance Explained**	**F value**	**Pr(F)**
NULL	NA	NA	NA	NA
poly(AGE,2)	2	58.493	13.446	0.00000
poly(LENGTH,2)	2	7.749	1.781	0.17235
SEX	1	0.082	0.038	0.84631
STUDY	1	0.555	0.255	0.61435
JUVENILES (154 animals)		**Null deviance = 388.15**		
Gaussian Model	**Df**	**Deviance Explained**	**F value**	**Pr(F)**
NULL	NA	NA	NA	NA
LENGTH	1	28.872	13.524	0.00033
poly(TRIP,4)	4	41.129	4.816	0.00112
STUDY	1	6.230	2.918	0.08972
AGE	1	1.753	0.821	0.36629
SEX	1	0.620	0.290	0.59077
ADULTS (258 animals)		**Null deviance = 973.99**		
Gaussian Model	**Df**	**Deviance Explained**	**F value**	**Pr(F)**
NULL	NA	NA	NA	NA
poly(TRIP,5)	5	340.470	30.259	0.00000
SEX	1	65.240	28.990	0.00000
LENGTH	1	3.920	1.743	0.18796
AGE	1	5.140	2.283	0.13206
STUDY	1	1.120	0.498	0.48093
poly(TRIP,5):SEX	5	43.310	4.059	0.00147

Bank that grades into the Gully) since the mid-1980's, cooler water temperatures having made the eastern part of the Shelf suitable for this species (Frank *et al*. 1996). Capelin are the only known major fish host of *C. osculatum* (Marcogliese 1995) that might qualify as a transient candidate, and are common closer to Sable Island than the fish sampled by McClelland *et al*. (1990), but to the east of the waters McClelland *et al*. (1990) sampled. Estimates of capelin abundance were also greater in 1989 than 1983 (Frank *et al*. 1996). This is consistent with the higher abundances of *C. osculatum* carried by adult grey seals in 1989 relative to 1983. However, the prey contents of 57 grey seal stomachs, taken from Sable Island during the breeding season (Benoit and Bowen 1990), included invertebrates but no capelin. This suggests that invertebrate hosts might seem a likelier source of *C. osculatum* than fish around Sable Island, and could explain the large *C. osculatum* infections attained by pups and young seals that are probably less skilled at catching mobile fish prey than older seals. But only 6 of the 57 stomachs in the Benoit and Bowen (1990) study contained any food at all (and we do not know the ages of these 6 animals). Furthermore, the differences between study years in the pup and adult *C. osculatum* models do not parallel each other. The 1983 abundances in pups were usually greater than 1989 abundances (see Fig. 2), whereas for adults 1989 abundances were greater than 1983 abundances (see Fig. 3). This reversal in relative abundances of *C. osculatum* between years for pups and adults may denote differences in mechanisms of transmission with age. These confounding differences between sample years and age groups prevent us from determining the extent to which prior residency in the Gulf of St Lawrence might be relevant to the magnitudes of *C. osculatum* infections in juvenile and adult seals around Sable Island.

Maturity of *P. decipiens* and *C. osculatum* appears to be inversely related to abundance, with an offset of about a month (Fig. 4). The general pattern was discussed for *P. decipiens* by Stobo

Fig. 2
Predicted relationships between worm abundance and growth, in terms of age or length of grey seals. Only data for significant effects in the models are plotted. Each species of nematode may be represented by one or two prediction lines. In models where neither sex nor study were significant effects, one line denoted "all or ____ seals" is used. Where sex or study were relevant, the "all" line represents male seals or the 1983 study, while the other line represents female seals or the 1989 study.

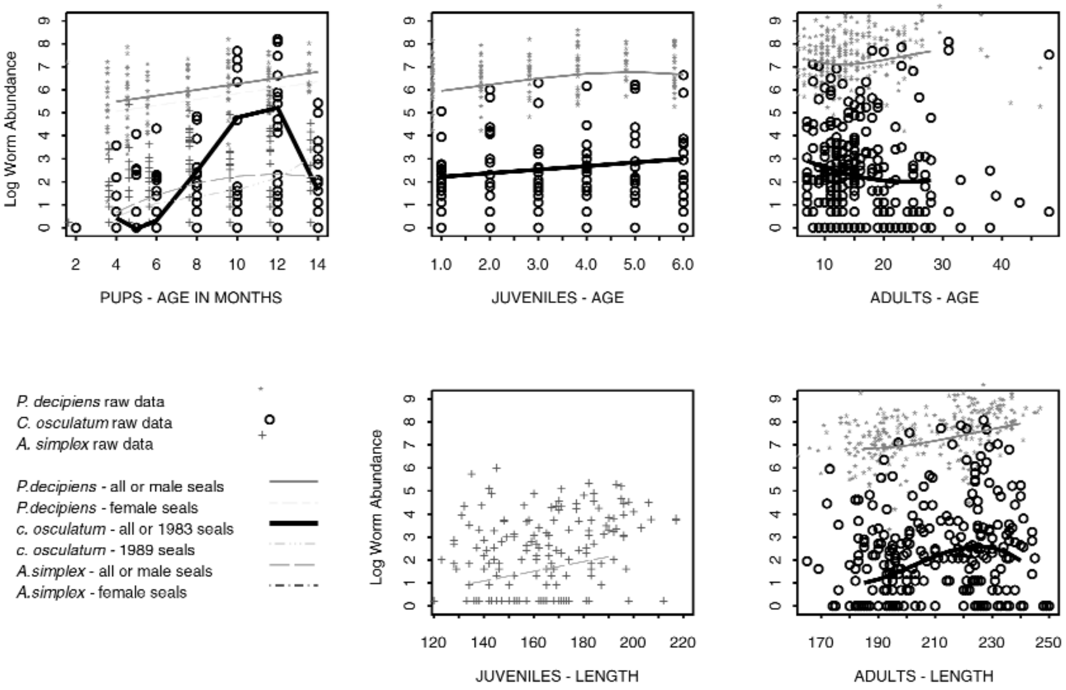
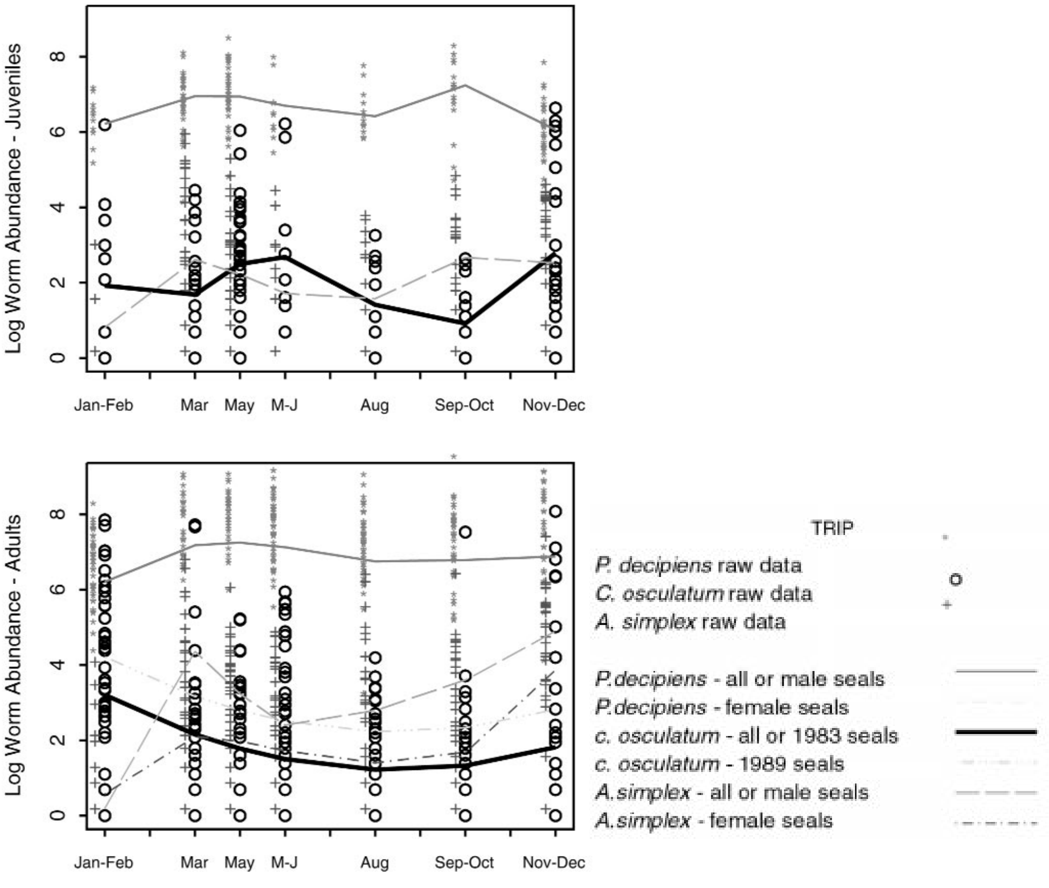


Fig. 3
Predicted relationships between worm abundance of grey seals and seasons of year. Only data for significant effects in the models are plotted. Each species of nematode may be represented by one or two prediction lines. In models where neither sex nor study were significant effects, one line denoted "all or ___ seals" is used. Where sex or study were relevant, the all line represents male seals or the 1983 study, while the other line represents female seals or the 1989 study.



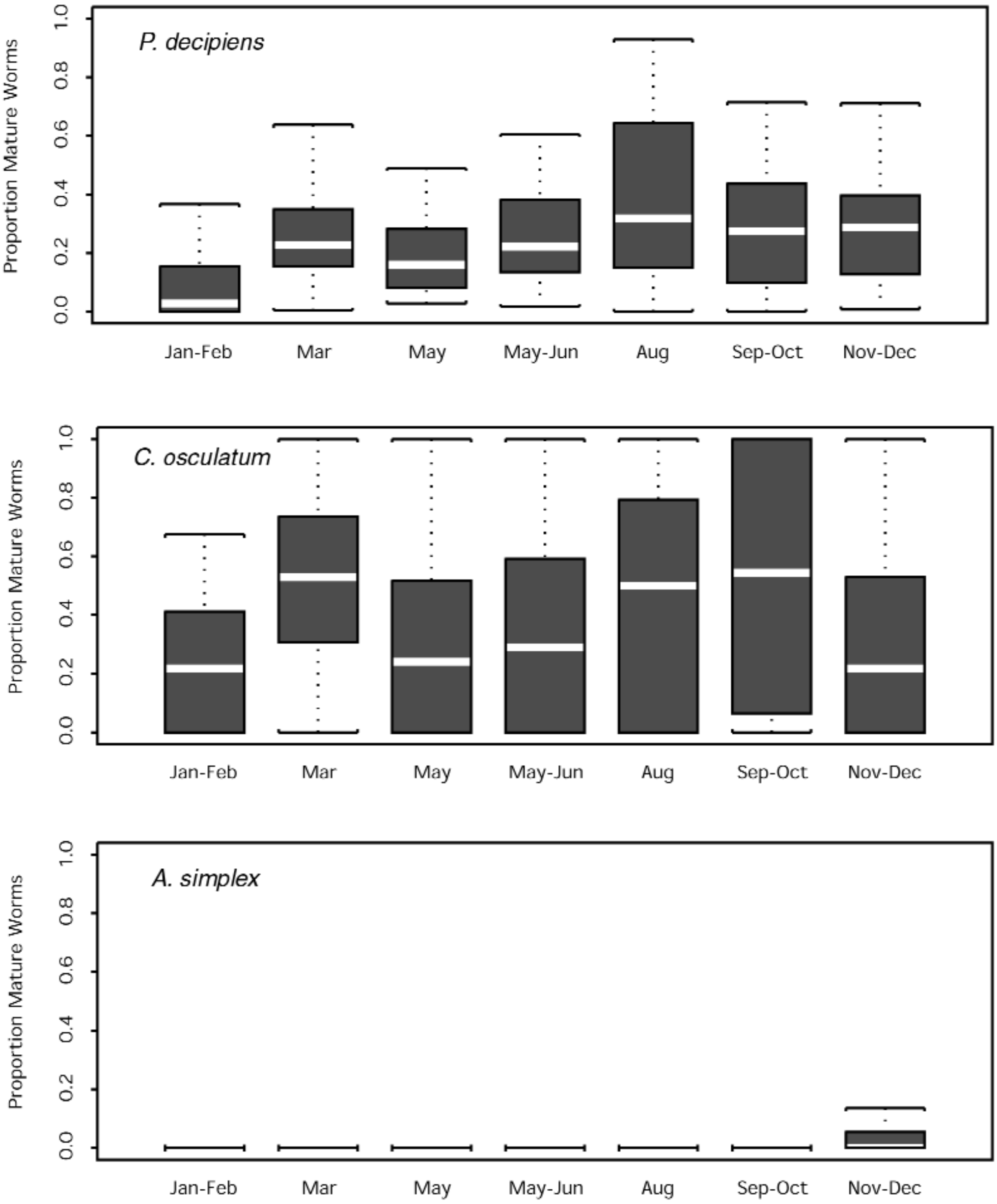


Fig 4. Seasonal proportions of sexually mature worms in adult grey seals (sexes combined) collected during 1983 and 1989 on Sable Island.

and Fowler (2001), who attributed fluctuations in the proportions of mature worms to lack of recruitment during full or partial fasts (existing worms maturing) and recruitment of immature worms during more dedicated feeding periods. It was also noted that the proportions of mature *P. decipiens* were higher in 1983 than 1989 during four of the seven trip pairs (no difference between years for the other three trip pairs). We speculated that this could be due to colder water temperatures in the late 1980's slowing development in intermediate hosts, or that gradual reduction in size of intermediate fish hosts over time (due to commercial fishing) resulted in progressively smaller worms being ingested by grey seals. In either case the worms would require more time to mature in the final host. There was no suggestion of any significant differences in *C. osculatum* maturity between 1983 and 1989 studies in this analysis (Table 3). This might lend greater weight to the smaller-prey-size/smaller-worm-size hypothesis over the colder water hypothesis as the explanation for the lesser proportion of mature *P. decipiens* in 1989. Both parasites were subjected to the change in temperature while *C. osculatum* is

Table 3. Comparison of the mean proportion of mature *Pseudoterranova decipiens* and *Contracaecum osculatum* in the stomachs of adult grey seals by trip between 1983 and 1989.

	Pseudoterranova decipiens				**Contracaecum osculatum**			
	Mean Proportion Mature				**Mean Proportion Mature**			
Trip	**1983**	**1989**	**t value**	**Pr(t)**	**1983**	**1989**	**t value**	**Pr(t)**
Jan. 10 - Feb. 9	0.103	0.062	0.24	0.809	0.233	0.231	-0.08	0.940
Mar. 2 - Mar. 21	0.351	0.176	2.77*	0.009	0.397	0.593	-0.24	0.815
May 4 - May 11	0.297	0.171	3.57	0.001	0.351	0.276	0.20*	0.842
May 31 - June 7	0.272	0.275	-0.21	0.836	0.404	0.325	0.57*	0.574
Aug. 1 - Aug. 8	0.607	0.263	7.33	0.000	0.428	0.462	1.23	0.221
Sep. 29 - Oct. 5	0.462	0.151	4.97	0.000	0.719	0.411	1.80*	0.077
Nov. 23 - Dec. 6	0.255	0.328	-1.26*	0.212	0.270	0.360	1.33*	0.191

* t-test for samples with unequal variances used

less common in the commercial fish species of the Scotian Shelf. But *C. osculatum* are more prevalent in grey seals in colder northern waters than *P. decipiens*, and their eggs can hatch at lower temperatures than *P. decipiens* (Marcogliese *et al*. 1996). Thus we might not expect the drop in temperature on the Scotian Shelf to have as much (if any) effect on *C. osculatum* abundance relative to *P. decipiens*. Hence both hypotheses remain equally likely mechanisms to influence *P. decipiens* maturity.

Although the relationship between abundance and maturity for *C. osculatum* is similar to that observed for *P. decipiens*, the magnitude of the seasonal change in *C. osculatum* abundance is more pronounced in adult seals, probably due to the prolonged period of low recruitment of *C. osculatum* between breeding periods. *C. osculatum* infections in adult seals are generally characterised by higher proportions of mature worms than those of *P. decipiens* at all times of the year (Table 3). Much or all of this difference could be attributable to the single dominant recruitment pulse, but does not rule out the possibilities that *C. osculatum* experiences higher juvenile mortality rates, or simply lives longer than *P. decipiens*.

A. simplex rarely matures in adult grey seals, and then only during the breeding period when mature *A. simplex* typically represented 4-8% of total numbers of infected animals. This suggests that the grey seal is not truly a final host of *A. simplex*, but that the worm can persist for some time post-ingestion. While a few mature individuals were found, we question whether they were reproductively viable.

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