

# Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer (*Rangifer tarandus platyrhynchus*)

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## SUMMARY

The observation that the total abundance of adult nematodes in the abomasum of Svalbard reindeer increases between October and April suggests adaptation to cope with the Arctic winter. Here we investigate the extent to which selection has led to similar life-history strategies in the 3 most numerous trichostrongyle species. The life-histories are found to differ markedly. We use flexible statistical models for the abundance and dispersion of parasites in the host population. One of the taxa, *Marshallagia marshalli*, was most abundant and had its highest egg output in the winter. In contrast, the abundance of the most common taxa, *Ostertagia gruehneri*, m. *gruehneri* was stable or declined from autumn to late winter, and the closely related taxa, *O. gruehneri*, m. *arcticus*, showed a similar over winter drop. The faecal egg output of these 2 taxa was highest in summer, as found in temperate trichostrongyle species. Despite the apparent contamination of summer pastures with *O. gruehneri*, calves showed negligible burdens until their second summer and the abundance of infection reached an asymptote within their third year. In contrast, the abundance of *M. marshalli* in calves showed a rapid increase over the first summer and by late winter was similar to peak levels found in adults (8000 worms). This increase could not be accounted for by the developing abomasum larvae population and is therefore evidence for transmission over the winter for this taxa. While *M. marshalli* showed little between-year variation, *O. gruehneri* showed 2-fold fluctuation in the abundance of infection. *O. gruehneri* may therefore play a role in the fluctuating population dynamics of the host. Since there was no apparent decline in abundance with host age in any of the 3 taxa there was no evidence of reindeer mounting an immune response.

Key words: abomasum nematodes, seasonality, age intensity, reindeer, aggregation.

## INTRODUCTION

Trichostrongyle nematodes show strongly seasonal dynamics in ruminants in temperate environments with transmission and peak burdens occurring in the main summer grazing period (Smith & Grenfell, 1985; Armour, 1980). Both primary production and development of the free-living stages of the nematode life-cycle are strongly correlated with temperature and humidity. Transmission may occur over 6 months or more and provides the opportunity for nematode species with different life-history strategies to occur with successional changes in abundance of species with different developmental rates (Crofton, 1957, 1963; Boag & Thomas, 1977). In contrast, during the winter period low tem-

perature limits egg and larval development and as a result reduces transmission (Smeal, Fraser & Robinson, 1981; Familton & McAnulty, 1995). In order to survive this unfavourable period trichostrongyle infections have developed 2 main strategies: some species survive in the host (e.g. *Teladorsagia circumcincta*), while others survive on the pasture (e.g. *Nematodirus battus*) (Soulsby, 1982). Over-wintering in the host provides the opportunity to resume development and start reproduction as soon as the ambient conditions are favourable for the development of free-living stages and may be less risky than being on pasture.

The extreme environmental conditions prevailing in the arctic would be expected to focus nematode transmission and reproduction in the short arctic summer. In the Svalbard archipelago the snow-free period lasts for only 3 months and mean summer temperature (June–August) is 3.6 °C and rainfall averages 53 mm (Førland, Hanssen-Bauer & Nordli, 1997). Compared to mainland Norwegian reindeer

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herds, Svalbard reindeer (*Rangifer tarandus platyrhynchus*) are non-migratory (Tyler & Øritsland, 1989), occur at locally high population densities (Alendal & Byrkjedal, 1976; Reimers, 1977) and experience high levels of parasitic infection (Bye & Halvorsen, 1983), sufficient to depress fecundity (unpublished data). Previous studies of the abomasal nematodes of Svalbard reindeer (Bye & Halvorsen, 1983; Halvorsen & Bye, 1999; Halvorseen *et al.* 1999) have revealed dynamics in the infections indicative of life-history traits at variance with those found in related species studied in sheep and cattle. These include continued transmission of nematodes in the arctic winter, reduced role of arrested development and extended life-expectancy of the parasitic phase. Earlier work has dealt mainly with the infection as infra-communities without separating the different taxa. Seven nominal taxa of abomasal nematodes representing 2 dimorphic and 1 trimorphic species have been found in the Svalbard reindeer (Halvorsen & Bye, 1999). Here we report the abundance of these taxa in 2 reindeer populations in Svalbard. Two taxa dominate: the major morph of *Ostertagia gruehneri* and the major morph *Marshallagia marshalli*, which together account for more than 95% of the adult worm burden. The minor morph of *O. gruehneri*, i.e. morph *articus*, accounts for about 4% of the total worm population. We compare and contrast the life-cycle strategies and population dynamics of these taxa.

The variation in adult abundance of the nematode taxa are analysed in relation to host age, season, year and reindeer population and variation in egg output in relation to season, to investigate whether taxa have evolved different life-histories. The relationship between the abundance and distribution of infection and host age can also provide evidence for density-dependent processes in the parasite population dynamics such as parasite-induced host mortality or immunity (Anderson & Gordon, 1982; Pacala & Dobson, 1988; Grenfell, Dietz & Roberts, 1995*a*; Rousset, 1996, but see Fulford *et al.* 1992) and heterogeneities in host responses to infection (e.g. host survival and immunity, Grenfell *et al.* 1995*b*). With no density dependence or heterogeneities in host response to infection the aggregation of parasites in the host population, measured by the variance parameter ( $k$ ) of the negative binomial distribution, is expected to track the abundance of infection (Grenfell *et al.* 1995*b*). However, density-dependent processes combined with heterogeneities in host exposure may cause  $k$  to increase and the abundance of infection to decrease at increasing host age (Pacala & Dobson, 1988; Grenfell *et al.* 1995*a*), but heterogeneities in host immune responses may cause  $k$  to decrease at increasing host age (Grenfell *et al.* 1995*b*). To evaluate this aspect we incorporate an analysis of how  $k$  varies with both abundance of infection and host age.

## MATERIALS AND METHODS

### Reindeer hosts

Animals were culled every year in the autumn, October (1994–1997) and again in late winter, either February (1997–1998), March (1996–1998) or April (1995–1998). An additional 25 in late August 1994 and 23 in early September 1996 provided material in late summer. The focus of the culling was on female reindeer, because the relationship between fecundity and worm burden was of primary interest for the overall research project, but also males and calves were culled, especially in 1994–1995. Accurate ages of culled animals were derived from annuli in the cementum of extracted ( $I_1$ ) incisors (Reimers & Nordby, 1968).

Culling took place in 2 different valley systems in Nordenskiöldland, Spitsbergen (77° 50′–78° 20′ N and 15° 00′–17° 30′ E). Approximately two-thirds of the animals (120 adult females, 17 adult males and 33 calves) were culled in Sassendalen about 40 km East of Longyearbyen and the rest (64 adult females, 9 adult males and 18 calves) in Colesdalen 20 km South West of Longyearbyen. Movement of reindeer between these valleys is thought to be unlikely (Øritsland & Arendal, 1985; Tyler & Øritsland, 1989) and we refer to these 2 locations as separate populations. On Svalbard, reindeer grazing density is estimated at 3.2/km<sup>2</sup> (Tyler, 1987) and is higher than that commonly found at the Norwegian mainland (range 0.6–2.5 reindeer/km<sup>2</sup>, Skogland, 1984).

### Parasitology – abomasum worm burdens

The species composition and abundance of trichostrongyle nematodes in the abomasa of 261 culled reindeer were analysed (Table 1). The abomasum was ligated and extracted from the shot animal and frozen within 3 h of death. After thawing the abomasum was opened along the greater curvature and the contents washed out into 4 litres of water. Six 5% subsamples were extracted using a vacuum pump during thorough agitation of the suspension. Each 5% was washed through a 150-µm sieve and the retained proportion examined for adult nematodes and larvae. Nematodes were counted until at least 100 of both male and female worms were extracted or until 20% of the content had been examined. Any worm with clearly defined genital structures was regarded as an adult. Species profiles of the individual host worm burdens were based on the taxonomy of the extracted adult male worms (Drózd, 1965) and the proportions were assumed to be the same in the adult female fraction. References to *Marshallagia marshalli* in the text will refer to the major morph *marshalli* unless otherwise stated and *Ostertagia gruehneri* will refer to major morph *gruehneri* unless morph *articus* is appended. *Grossipicularis occidentalis* was reclassified as

*Marshallagia marshalli*, morph *occidentalis* (Drózd, 1965).

### Parasitology – faecal egg counts

Faecal egg count data were obtained from individually marked reindeer from April to October in 1994–1998 in the Colesdalen reindeer population. Faeces from individually marked animals were collected immediately after excretion, stored at around 4 °C and processed within 48 h to avoid complications of larval development. Three grammes of faeces were suspended in 42 ml of saturated salt solution and one third of this was put in a glass centrifuge tube with a ground rim. The tube was filled until there was a positive meniscus and a cover-slip was placed on the top. Tubes were centrifuged at 95 g for 2 min. The cover-slip was removed and placed on a microscope slide. The whole area was counted at ×100 magnification and the number of eggs was recorded as eggs per gramme of faeces. Eggs of the *M. marshalli* taxa are larger (100 × 70 μm) than other strongyle eggs and have more developed morulla than nematodirus eggs, and can therefore be readily distinguished from other trichostrongyle eggs (MAFF/ADAS, 1986). Given that the nematode fauna is dominated by *O. gruehneri*, m. *gruehneri* and *M. marshalli*, it seems reasonable to assume that the other trichostrongylid fraction is largely from the *O. gruehneri*, m. *gruehneri* and *O. gruehneri*, m. *arcticus* taxa and we will call this *Ostertagia* eggs.

### Anthelmintic treatment

The hypothesis that these abomasal parasites influence the hosts' fecundity is the subject of ongoing work. However, treated animals were utilized here to determine if animals became re-infected. Reindeer caught in April/May 1998 were randomly allocated to anthelmintic treatment groups. The treated group was injected subcutaneously with 0.2 mg Moxidectin per kg live weight. The control group received nothing. Faecal egg output was estimated as above.

### Statistical analysis

Because of the few males available in the data set we have focused our analysis of worm burdens on female reindeer, but included male calves. Adult worm burdens were analysed assuming the nematode counts came from a negative binomial distribution (Wilson, Grenfell & Shaw, 1996; Wilson & Grenfell, 1997) and the models were fitted by maximum likelihood method. Neglecting constant terms in the log likelihood function for the negative binomial

distribution this is equivalent to minimizing log  $l$  given by

$$\log l = \ln(\Gamma(y+k)) - \ln(\Gamma(y+1)) - \ln(\Gamma(k)) + y \ln(\hat{y}/(\hat{y}+k)) - k \ln(1+\hat{y}/k), \quad (1)$$

where  $y$  is the observed nematode intensity,  $\hat{y}$  is the predicted abundance of nematodes,  $k$  is the negative binomial variance parameter and  $\Gamma$  the gamma function. Recent studies (Grenfell *et al.* 1995a; Shaw, Grenfell & Dobson, 1998) have suggested that the variance parameter  $k$  is likely to be positively related to the abundance of infection. Figure 4 in Shaw *et al.* (1998) suggests that linear or log-linear models are candidates for this relationship. To investigate this we tried 3 simple models for  $k$ : (1)  $k$  constant ( $k = \text{constant}$ ), (2)  $k$  a linear function of  $\hat{y}$  ( $k = k_1 + k_2 \hat{y} 10^{-3}$  with constraints  $k_1 > 0$  and  $k_2 > 0$  to ensure  $k$  to be positive for all  $\hat{y}$ ), and (3)  $k$  an exponential function of  $\hat{y}$  ( $k = \exp(k_1 + k_2 \hat{y} 10^{-3})$ ). When fitting these models for  $k$  we used an over-parameterized model for  $\hat{y}$ , with the parameter  $a$  in the Gompertz function described below varying with reindeer population and  $\gamma$  varying with population, month and year of sampling and the interactions between these predictor variables. Additional patterns of variation in  $k$  at increasing host age were investigated by (1) estimating  $k$  for each age class of reindeer and (2) using an extended version of the above models for  $k$ , while modelling the abundance of infection using the best-fit model from the analysis with no age effect on  $k$ . In the second approach, we constrained our model of the effect of age on  $k$  to the data for animals older than the age at which the abundance of infection had reached its early maximum ( $c$ ) using the models:

$$k = \begin{cases} \exp(k_1 + k_2 \hat{y} 10^{-3}) & \text{for age} \leq c \\ \exp(k_1 + k_2 \hat{y} 10^{-3} + k_3 \text{ age}) & \text{for age} > c \end{cases}$$

for the species with a log linear relationship between  $k$  and the abundance of infection, and

$$k = \begin{cases} k_1 + k_2 \hat{y} 10^{-3} & \text{for age} \leq c \\ k_1 + k_2 \hat{y} 10^{-3} + k_3 \text{ age} & \text{for age} > c \end{cases}$$

for species with a linear relationship between  $k$  and the abundance of infection. This was to investigate the possibility of a change in  $k$  with increasing host age after the initial age related increase in  $\hat{y}$ , but independent of the effects on  $k$  of seasonal and between year variation in  $\hat{y}$ .

For the systematic component of the models (i.e. modelling  $\hat{y}$ ), we used both linear and non-linear models. The age-intensity relationship was assumed to follow a Gompertz function given by

$$\hat{y} = \alpha + (\gamma - \alpha) \exp(-\exp(-\kappa(\text{Age} - \phi))), \quad (2)$$

where  $\hat{y}$  is as above,  $\alpha$  is the lower asymptotic abundance of infection for  $\text{Age} \rightarrow \infty$ ,  $\gamma$  is the upper asymptotic abundance of infection for  $\text{Age} \rightarrow \infty$ ,

Table 1. Prevalence (%), abundance of infection and species profiles for nematode taxa in the abomasum of Svalbard reindeer

(Estimates are given separately for adult females, males and calves and for samples collected in the late summer period (August–October) (upper table) and late winter period (February–May) (lower table). Data are combined for both reindeer populations.)

Species	Females			Males			Calves		
	Prevalence	Abundance (s.d.)	Species profile (%)	Prevalence	Abundance (s.d.)	Species profile (%)	Prevalence	Abundance (s.d.)	Species profile (%)
Late summer	(n = 112)			(n = 20)			(n = 39)		
<i>O. morph gruehneri</i>	100	7124 (3999)	72	100	7039 (5391)	68.6	44	15 (26)	1.3
<i>M. morph marshalli</i>	100	2290 (1761)	23	100	2621 (1622)	25.5	97	1192 (1140)	98.6
<i>O. morph arcticus</i>	93	385 (319)	3.9	100	438 (307)	4.3	5.2	0.7 (3.0)	0.06
<i>T. circumcincta</i>	26	49 (154)	0.5	60	142 (192)	1.4	0	0	0
<i>T. trifurcata</i>	1.8	1.4 (11)	0.01	10	18 (54)	0.17	0	0	0
<i>M. morph occidentalis</i>	0.9	2.0 (21)	0.02	5	4.0 (18)	0.04	2.6	0.3 (2.1)	0.03
Total		9852 (4562)			10262 (5940)			1209 (1133)	
Late winter	(n = 72)			(n = 6)			(n = 12)		
<i>O. morph gruehneri</i>	100	6712 (3774)	52	100	2788 (1480)	25	58	201 (531)	3.1
<i>M. morph marshalli</i>	100	5951 (3587)	46	100	8275 (3772)	74	100	6422 (3000)	96.1
<i>O. morph arcticus</i>	79	221 (286)	1.7	50	126 (178)	0.9	17	42 (128)	0.6
<i>T. circumcincta</i>	25	46 (108)	0.36	33	20 (31)	0.1	8	3.8 (13)	0.06
<i>T. trifurcata</i>	2.8	2.3 (14)	0.02	0	0	0	0	0	0
<i>M. morph occidentalis</i>	11	11 (32)	0.08	17	19 (46)	0.2	17	5.2 (13)	0.09
Total		12943 (5016)			11227 (4012)			6675 (3210)	

Age =  $\phi$  is the inflection point and  $\kappa$  determines the rate at which the curve approaches the asymptote. Seasonal variation, locality and year effects on worm burden were modelled as additive effects on  $\alpha$ ,  $\gamma$ ,  $\kappa$  and  $\phi$  through a log-link function, giving for example  $\alpha = \exp(\mathbf{X}\beta)$ , where  $\beta$  is a vector of regression coefficients and  $\mathbf{X}$  a matrix of predictor variables. To investigate the structure of seasonal effects we also fitted a sine function for  $\gamma$

$$\gamma(\text{season}) = a + A (\sin (2\pi (\text{season} - \delta))), \quad (3)$$

where season is a continuous measure of time of year between 0 and 1,  $a$  is the abundance of infection at the inflection point,  $A$  the amplitude of the wave, and  $\delta$  determines the time of year the curve passes the seasonal inflection point. Also in this model the parameters  $a$  and  $A$  were allowed to vary with predictor variables through a log-link function. Models were compared using likelihood ratio tests (McCullagh & Nelder, 1989) where the difference in  $-2 \log$  likelihood of 2 nested models were assumed to be distributed as  $\chi^2$  with degrees of freedom equal to the difference in residual degrees of freedom between the 2 models. Likelihood ratio-based confidence intervals (C.I.) were used as measure of the precision of parameter estimates (McCullagh & Nelder, 1989). Nematode egg count data from faeces were  $\log_e(X+1)$  transformed and the seasonal pattern in mean egg counts was described using a smoothing spline (Hastie & Tibshirani, 1990).

## RESULTS

### Species composition, prevalence and profiles

Taxonomic analysis of Svalbard reindeer abomasum helminths confirmed the existence of 6 taxa found in an earlier study (Bye & Halvorsen, 1983). *O. gruehneri* and *M. marshalli* accounted for more than 95% of the abomasum parasite population found in adult reindeer of both sexes and all adult reindeer were infected with both (Table 1). However, the relative proportions of these 2 species appeared to differ between late summer/autumn (August/September/October) and late winter (February/March/April). The proportion of *M. marshalli* was higher, relative to *O. gruehneri* in the late winter because of an apparent increase in the abundance of *M. marshalli* (Table 1). Male and female reindeer had similar species profiles and abundances in late summer/autumn but in late winter the small sample of males appeared to have a disproportionately high proportion of *M. marshalli* relative to *O. gruehneri*.

*O. gruehneri*, m. arcticus, the third most abundant abomasum nematode, accounted for no more than 5% of the total worm burden but infected more than 90% of the adult reindeer (females = 93%, males 100%). In late summer the abundance in adult female and male reindeer were similar at 385 (s.d. = 319) and 438 (s.d. = 307) worms per host. In

calves prevalence was around 5% in late summer but abundance was on average less than 1 worm per abomasum. In late winter abundance tended to be higher (41 nematodes per host) but prevalence was still low (9%). The other 3 species occurred erratically at low prevalence and abundance (Table 1).

### Modelling $k$

For both *M. marshalli* and *O. gruehneri* models with  $k$  varying with  $\hat{y}$  were found to fit the data significantly better than models with a constant  $k$  (Table 2). For *M. marshalli* the log-linear model gave a marginally lower  $-2 \log$  likelihood value than the linear model for  $k$ . The linear model for  $k$  had a much lower  $-2 \log$  likelihood value for *O. gruehneri* than the log-linear model, while the opposite was true for *O. gruehneri*, m. arcticus. We used the best-fit dispersion models in the subsequent formal analyses of worm burdens of *M. marshalli*, *O. gruehneri* and *O. gruehneri*, m. arcticus, respectively. Analyses of residuals showed that these gave a good description of the variance structure in the data.

### Age-intensity relationships

At the end of their first summer (October), calves were infected with, on average, 2100 adult *M. marshalli* and 22 *O. gruehneri* in Sassendalen (Fig. 1). By April of their first winter the abundance of *M. marshalli* had increased to around 9000 (Fig. 1), similar to that found in yearlings of 22 months (Fig. 1) and not significantly different from adults in late winter ( $\chi^2 = 0.22$ , D.F. = 1,  $P = 0.63$ , see Fig. 2A). Thus, after the first winter, there was no evidence of the abundance of *M. marshalli* infection changing with age (Fig. 2A and B). The abundance of *M. marshalli* in Sassendalen was about twice as high as in Colesdalen and this was significant for both calves and yearlings ( $\chi^2 = 58.76$ , D.F. = 1,  $P < 0.001$ ) and adult reindeer ( $\chi^2 = 25.77$ , D.F. = 1,  $P < 0.001$ , see Fig. 2A and B).

In contrast to *M. marshalli*, the abundance of *O. gruehneri* did not increase significantly from October to late winter in the reindeer's first year (Fig. 1,  $\chi^2 = 1.81$ , D.F. = 1,  $P = 0.18$ ). However, during the second summer of life the abundance increased by a factor of 40 (from less than 50 to more than 2000, Fig. 1). The pattern of the age-intensity relationship differed between the 2 populations ( $\chi^2 = 12.72$ , D.F. = 1,  $P = 0.0001$ , Table 3: Model 9 versus 7). In Colesdalen the increase in abundance was relatively fast, reaching an asymptote of about 11000 in their second year, whereas in Sassendalen, the rate of increase was slower reaching the asymptote in their third year (Fig. 2C and D). The asymptotic levels of infection differed significantly between our 2 study populations ( $\chi^2 = 4.49$ , D.F. = 1,  $P < 0.05$ ).

Table 2. Analysis of likelihood ratio table for the fit of different functions for the negative binomial dispersion parameter  $k$  to the data on the intensity of *M. marshalli*, *O. gruehneri* and *O. gruehneri*, m. arcticus in calves and adult female Svalbard reindeer

( $-2 \log l$  gives the  $-2 \log$  likelihood of the model, np the number of parameters fitted, and  $P$ , the  $P$ -value, for the test for a significantly better fit using the linear and log-linear functions when compared to the model with a constant  $k$ . The predicted abundance of infection ( $\hat{y}$ ) was estimated using an over-parameterized model including a non-linear age-intensity relationship, and asymptotic values with age depending on year, month and reindeer population sampled (see main text).)

Function	<i>M. marshalli</i> , m. marshalli			<i>O. gruehneri</i> , m. gruehneri			<i>O. gruehneri</i> , m. arcticus		
	$-2 \log l$	np	$P$	$-2 \log l$	np	$P$	$-2 \log l$	np	$P$
$k = \text{constant}$	3938.08	30		3884.81	30		2459.35	30	
$k = k_1 + k_2 \hat{y} 10^{-3}$	3932.00	31	0.01	3684.27	31	< 0.0001	2398.84	31	< 0.0001
$k = \exp(k_1 + k_2 \hat{y} 10^{-3})$	3930.77	31	0.007	3703.24	31	< 0.0001	2387.98	31	< 0.0001

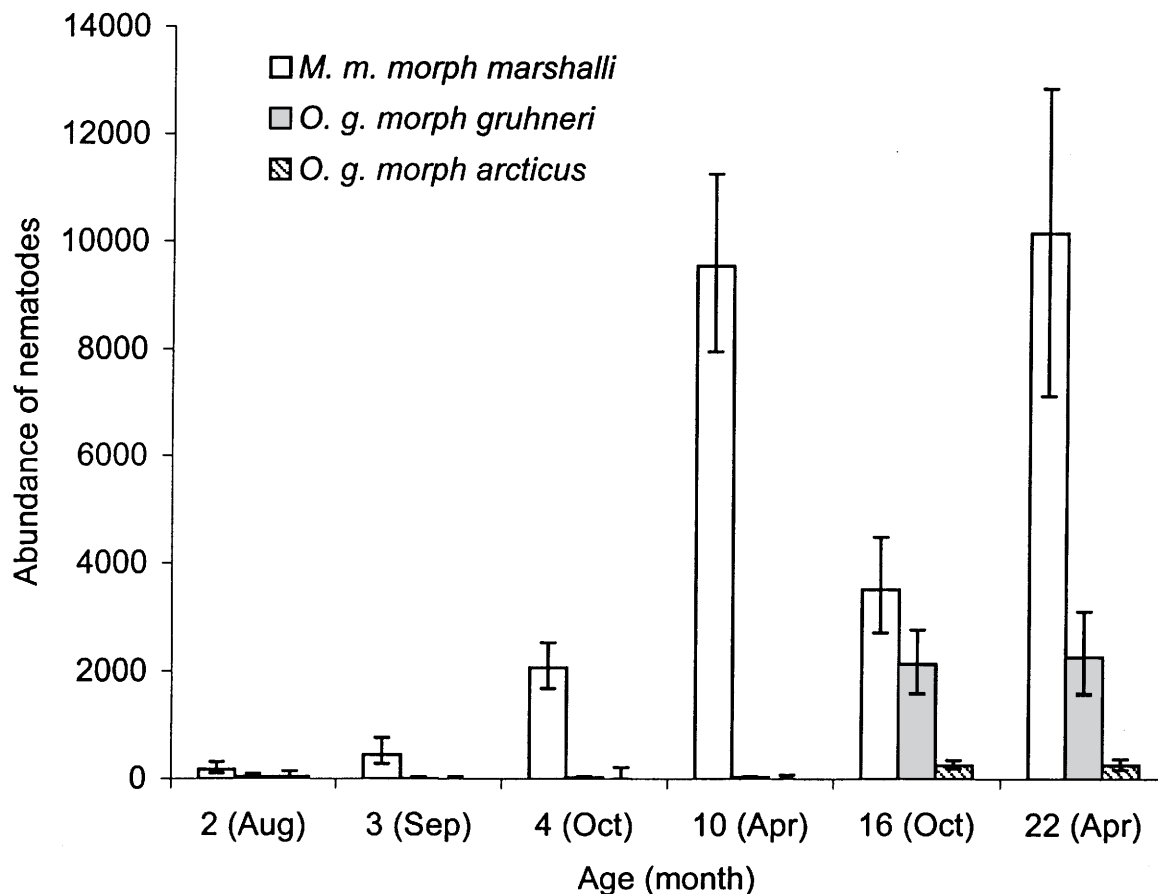


Fig. 1. The estimated abundance (with 95% confidence intervals) of adult *Marshallagia marshalli*, *Ostertagia gruehneri* and *O. gruehneri*, m. arcticus in reindeer from Sassendalen in calves and yearling females. The abundances were estimated using a linear model with log-link function and assuming a negative binomial error distribution with  $k$  fitted as a linear function of the estimated abundance of infection for *O. gruehneri* and a log linear function for *M. marshalli* and *O. gruehneri*, m. arcticus. For Colesdalen the estimates are a multiplicative factor  $\alpha$  of the plotted ones, with estimates:  $\alpha_{M.marshalli} = 0.30$ ,  $\alpha_{O.gruehneri} = 3$ ,  $\alpha_{O.gruehneri,m.arcticus} = 0.77$ . Estimates of parameters in the model for the negative binomial parameter  $k$ :  $k_{1M.marshalli} = 0.91$ ,  $k_{2M.marshalli} = 0.25$ ,  $k_{1O.gruehneri} = 0.016$ ,  $k_{2O.gruehneri} = 2.59$ ,  $k_{1O.gruehneri,m.arcticus} = -4.66$ ,  $k_{2O.gruehneri,m.arcticus} = 23.97$ .

Interestingly, the population differences in *O. gruehneri*, m. gruehneri abundance were reversed compared to *M. marshalli* with *O. gruehneri* abundance in adult reindeer lower in Sassendalen and on average 0.73 of that in Colesdalen (Fig. 2C and D).

Age-intensity patterns in *O. gruehneri*, m. arcticus

were similar to those observed for *O. gruehneri*. The abundance of *O. gruehneri*, m. arcticus was very low through the reindeers' first year but by the end of their second summer burdens had increased to the asymptotic value at around 400 (Fig. 2E and F). Although relatively low, significantly higher

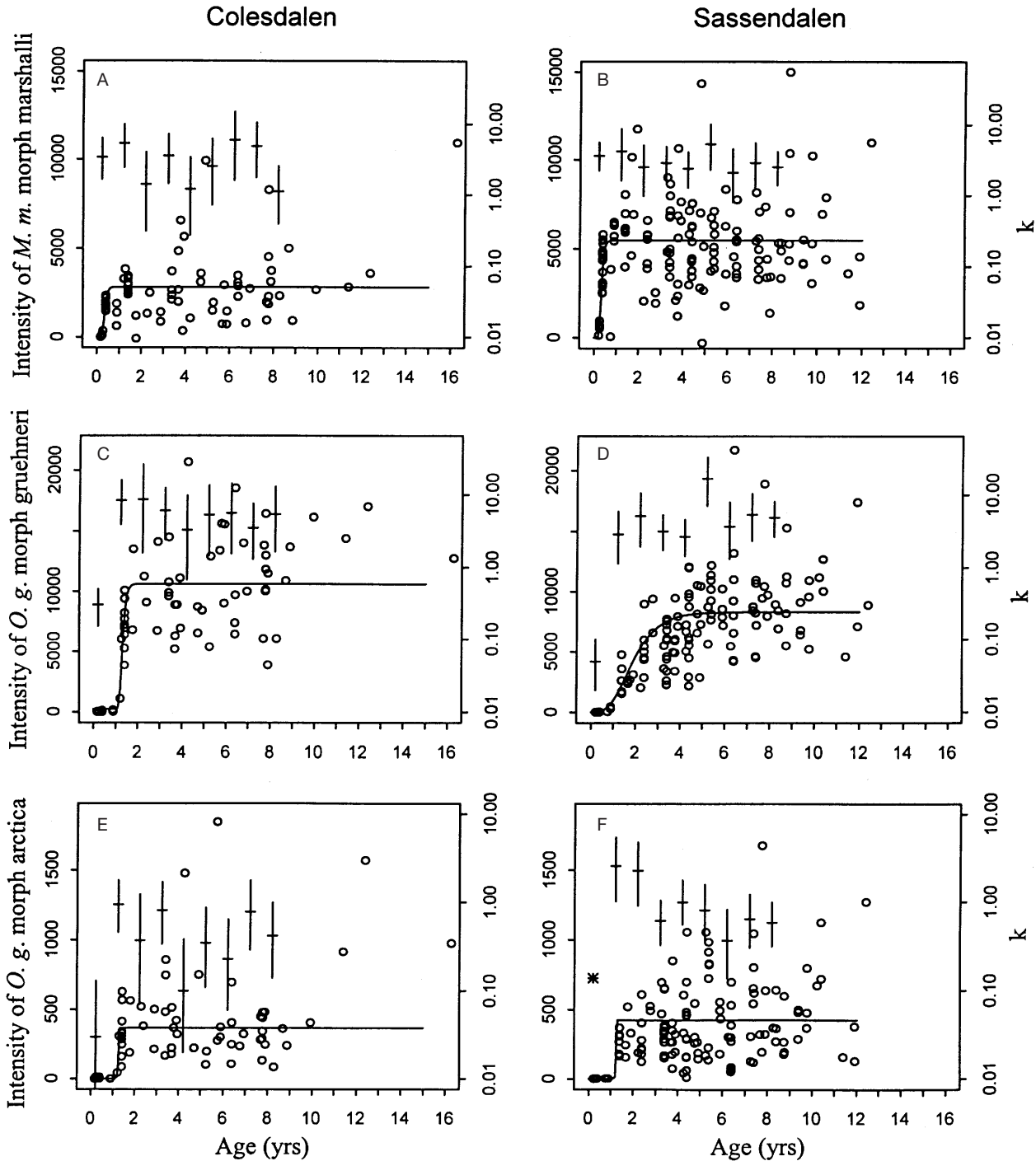


Fig. 2. Gompertz age-intensity curves and estimates of *k* (crosses) with 95% confidence intervals for adult *Marshallagia marshalli* (A, B), *Ostertagia gruehneri* (C, D) and *O. gruehneri*, m. arcticus (E, F) sampled from the calves and adult female reindeer in Colesdalen (A, C, E) and the Sassendalen (B, D, F). Observed values for the nematode taxa corrected for seasonal and between year variation in nematode abundances are plotted around the curves. The seasonal components of the model are shown in Fig. 3. For *M. marshalli* there were no significant between year variation in the asymptotic abundance of infection (Table 3). The fitted curves and adjusted residuals for *O. gruehneri* and *O. gruehneri*, m. arcticus are standardized for the 1997–98 winter. Estimates of *k* are given for each age class of reindeer with animals older than 8 years combined. The 95% confidence interval for *O. gruehneri*, m. arcticus in calves in Sassendalen was [0, ∞) and only the parameter estimate is plotted (\*). (Estimates of the negative binomial parameter *k* in the overall model:  $k_{1M.marshalli}=0.67$ ,  $k_{2M.marshalli}=0.12$ ,  $k_{1O.gruehneri}=0.043$ ,  $k_{2O.gruehneri}=0.69$ ,  $k_{1O.gruehneri,m.arcticus}=3.18$ ,  $k_{2O.gruehneri,m.arcticus}=8.55$ .)

abundances were found in Sassendalen ( $\chi^2=3.89$ , D.F.=1,  $P<0.05$ ).

There was no evidence for acquired immunity

since there was no decrease in the abundance of infection in any of the species with increasing age (Fig. 2). The dispersion parameter *k* also increased

Table 3. Comparison of models for the abundance of adult *M. marshalli*, *O. gruehneri* and *O. gruehneri*, m. arcticus in calves and adult female Svalbard reindeer

(ai denotes the Gompertz age-intensity model given by  $\hat{y} = \alpha + (\gamma - \alpha) \exp(-\exp(-\kappa(\text{Age} - \phi)))$  where  $\alpha$ ,  $\gamma$ ,  $\kappa$  and  $\phi$  are parameters estimated from the data.  $\gamma(S)$  denotes fitting  $\gamma$  in the Gompertz function as a sine function  $\gamma = a + A(\sin(2\pi(\text{season} - \delta)))$  where  $a$ ,  $A$  and  $\delta$  are parameters estimated from data. Parameters were allowed to vary with the predictor variables reindeer population (P) and year (Y) of sampling through a log-link function. For example, model 5 is a model with a sine function for  $\gamma$ , and with  $\alpha$  and  $a$  varying with reindeer population.  $P \times Y$  denote an interaction between the predictor variables, reindeer population (P) and year (Y). Adding a term letting  $\kappa$  and  $\phi$  vary between the reindeer populations in the most complex model above with significant terms for  $\alpha$  and  $\gamma$  is denoted  $+\kappa(P) + \phi(P)$ , and dropping a term giving a constant amplitude in the seasonal fluctuations in both populations is denoted  $-A(P)$ . np gives the number of parameters fitted in the model,  $-2 \log l$  the  $-2 \log$  likelihood value of the model and  $P$  the significance level when comparing the model with the last significant model above. The best fitting models are highlighted with bold numbers. For all models the error distributions were assumed to be negative binomial with variance parameter  $k = \exp(k_1 + k_2 \hat{y} 10^{-3})$  for *M. marshalli* and *O. gruehneri*, m. arcticus, and  $k = k_1 + k_2 \hat{y} 10^{-3}$  for *O. gruehneri*.)

Model	Terms	Np	<i>M. marshalli</i> , m. marshalli		<i>O. gruehneri</i> , m. gruehneri		<i>O. gruehneri</i> , m. arcticus	
			$-2 \log l$	$P$	$-2 \log l$	$P$	$-2 \log l$	$P$
1	Intercept	2	4204.74		4231.58		2680.12	
2	AI	6	4109.98	< 0.0001	3764.20	< 0.0001	2461.64	< 0.0001
3	ai( $\alpha(P)$ )	7	4096.13	0.0002	3753.73	0.001	2457.70	0.05
4	ai( $\alpha(P)$ , $\gamma(P)$ )	8	4081.83	0.0001	3738.58	0.0001	2451.03	0.01
5	ai( $\alpha(P)$ , $\gamma(S(a(P), A(P)))$ )	11	<b>3950.96</b>	<b>&lt; 0.0001</b>	3726.66	0.008	2424.97	< 0.0001
6	ai( $\alpha(P)$ , $\gamma(S(a(P+Y), A(P)))$ )	14	3950.43	0.91	3721.09	0.13	2410.88	0.003
7	ai( $\alpha(P)$ , $\gamma(S(a(P+Y), A(P+Y)))$ )	17	3945.15	0.44	3699.25	0.0001	2404.53	0.10
8	ai( $\alpha(P)$ , $\gamma(S(a(P \times Y), A(P \times Y)))$ )	23	3943.60	0.83	3694.96	0.64	2397.86	0.16
9	$+\kappa(P) + \phi(P)$	+1	3947.89	0.21	3686.53	0.002	2410.88	0.99
10	$-A(P)$	-1	4006.43	< 0.0001	<b>3687.53</b>	<b>0.21</b>	<b>2413.26</b>	<b>0.12</b>



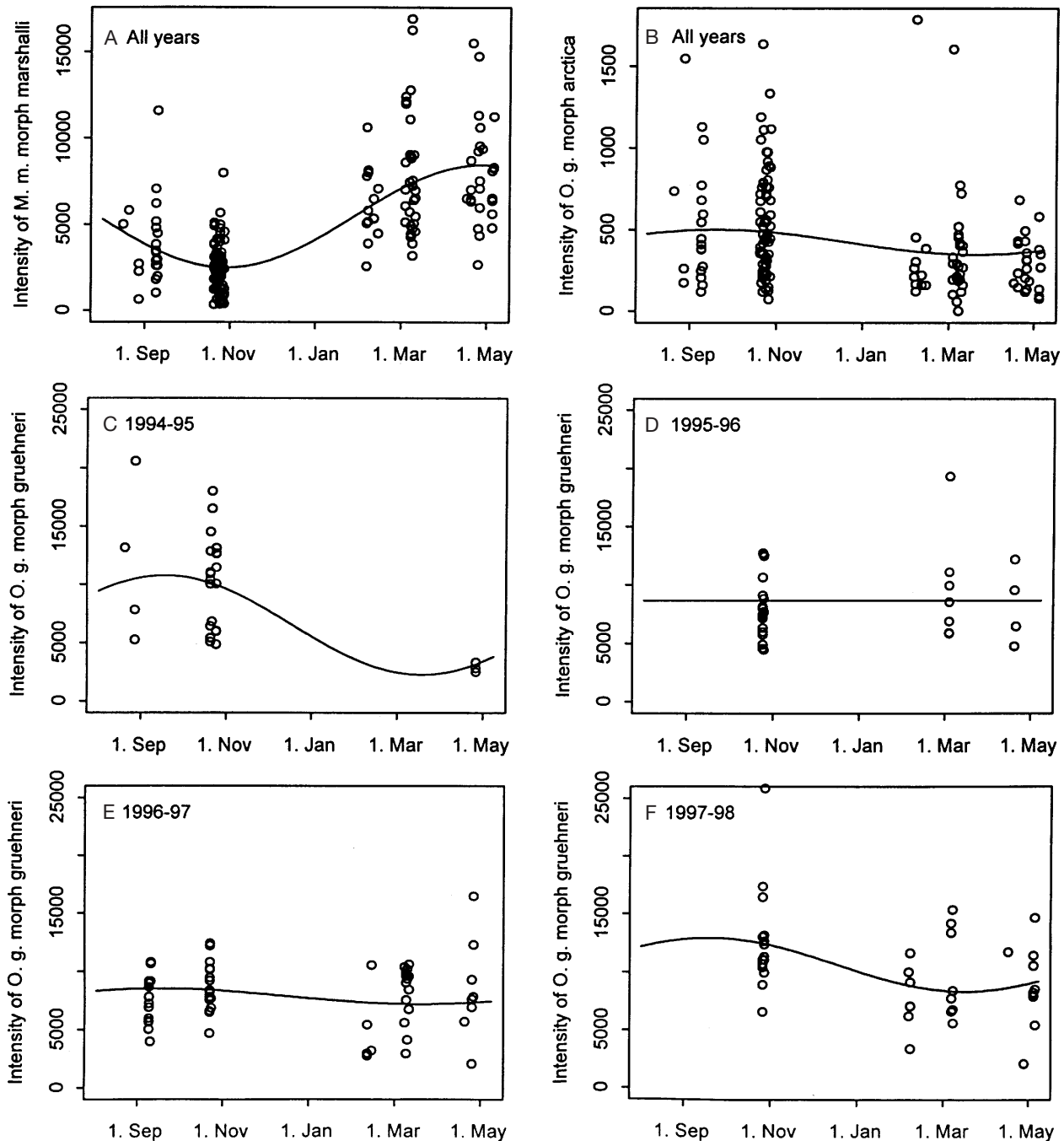


Fig. 3. Sine curves describing the seasonal component of the variation in the abundance of adult abomasal nematodes from calves and adult female Svalbard reindeer. (A) *Marshallagia marshalli* (all years), (B) *Ostertagia gruehneri*, m. arcticus (all years) and (C–F) *O. gruehneri*. Observed values in nematode abundances are plotted around the curves for the nematode taxa correcting for reindeer age and between-year variation from the best-fit models. In Fig. 3(A) and (B) the curve for *M. marshalli* and *O. gruehneri*, m. arcticus is standardized to the Sassendalen reindeer population and for *O. gruehneri*, m. arcticus the asymptotic abundance with reindeer age is for the 1997–98 winter. The curves for *O. gruehneri* are given for samples from the Colesdalen reindeer population and the winters (C) 1994–95, (D) 1995–96, (E) 1996–97 and (F) 1997–98.

from calves to older animals, but showed no evidence for a continuing increase at higher ages (Fig. 2). The estimates for  $k$  in adult reindeer were in the range of 1.1–5.9 for *M. marshalli*, 2.7–16.9 for *O. gruehneri*, m. gruehneri and 0.1–2.6 for *O. gruehneri*, m. arcticus and showed little evidence for a change with age except for a decrease for *O. gruehneri*, m. arcticus in

the samples from Sassendalen (Fig. 2F). When modelling the change in  $k$  as a continuous function of increasing age while controlling for the effect of the abundance of infection on  $k$ , the cut off points ( $c$ ) were chosen as  $c=1$  year for *M. marshalli*,  $c=2$  years for *O. gruehneri*, m. arcticus and  $c=3$  years for *O. gruehneri* on the basis of the age–intensity profiles

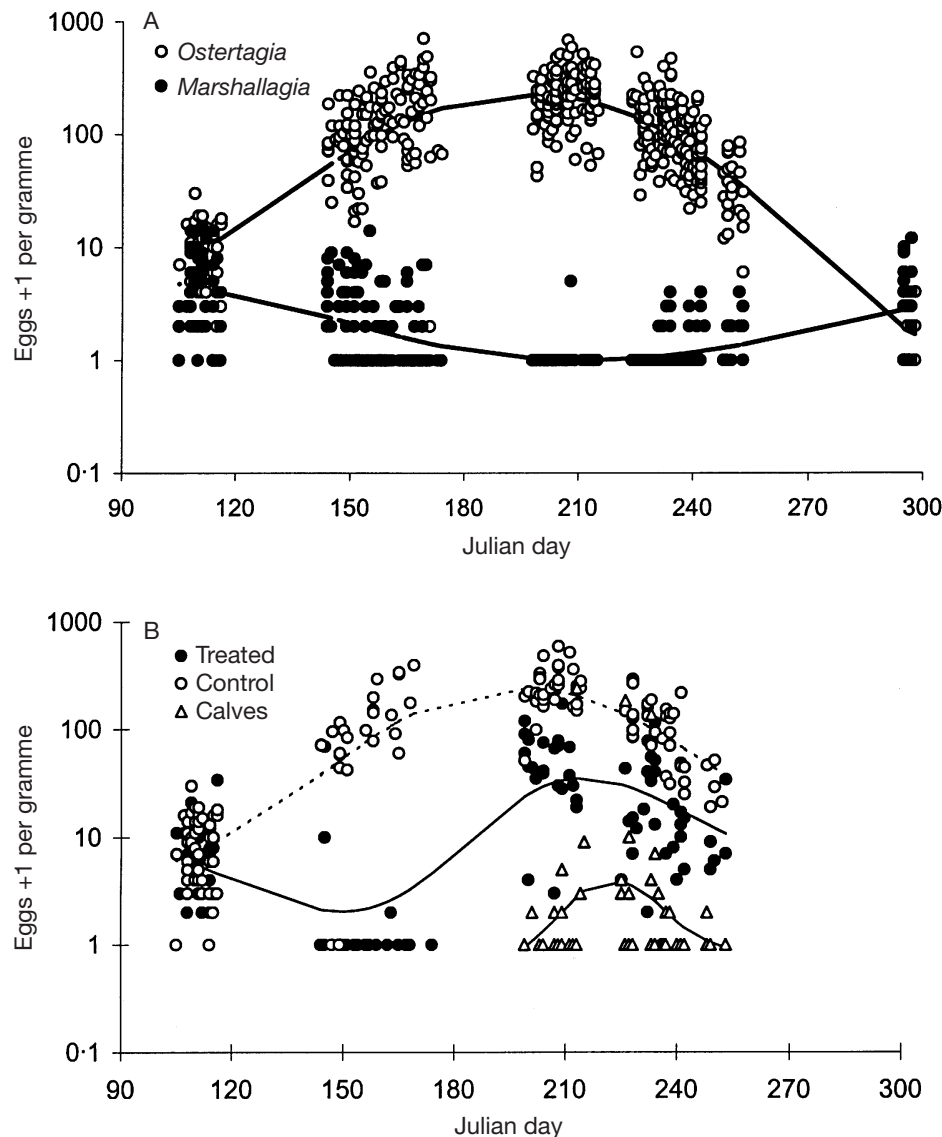


Fig. 4. (A) Faecal egg count data collected from adult females between April and September 1997 plotted against Julian day (days after 1 January) for trichostrongyle eggs. (●) *Marshallagia marshalli* taxa; (○) *Ostertagia* eggs (largely *O. gruehneri*, *m. gruehneri* and *O. gruehneri*, *m. arcticus*). A smoothing spline was fitted to both data sets to guide the eye. (B) Seasonal pattern in *Ostertagia* egg output for adult reindeer either treated with an anthelmintic (●) or untreated (○) and untreated calves (△) with fitted smoothing splines. This figure demonstrates that treated adult animals produce patent infections after the treatment wears off and that the autumn decline is similar in all cases.

(Fig. 2). The analysis suggested that  $k$  decreased with increasing age for *M. marshalli* ( $\chi^2=8.40$ , D.F. = 1,  $P=0.004$ ,  $k_{3M.marshalli} = -0.075$ ) even though there was no such pattern in  $k$  when estimated for each age class separately (Fig. 2 A and B). The difference in outcome of these 2 analyses is likely to be due to the confounding effect on  $k$  of the strong seasonal variation in abundance of *M. marshalli* which was not controlled for when the age-specific estimates of  $k$  were calculated. The slopes for  $k$  against age were also negative for *O. gruehneri*, *m. gruehneri* and *O. gruehneri*, *m. arcticus* but not significantly different from zero (respectively:  $\chi^2=0.63$ , D.F. = 1,  $P=0.43$ ,  $k_{3O.gruehneri,m.gruehneri} = -0.14$ , and  $\chi^2=2.87$ , D.F. = 1,  $P=0.09$ ,  $k_{3O.gruehneri,m.arcticus} = -0.072$ ).

#### Seasonality of infection

**Worm burdens.** The abundance of adult *M. marshalli* showed a significant seasonal cycle captured by fitting the annual sine curve (Table 3 and Fig. 3A). In all 4 years there were consistently higher abundances at the end of winter than in late summer. The 2 populations differed significantly in the mean and amplitude of the cycle in abundance of adult *M. marshalli* (Table 3, model 5 versus 4 and 4 versus 3). However, there was no significant variation in this pattern between years (Table 3, models 6–8 versus 5,  $P>0.4$ ). Female reindeer in Sassendalen had a seasonal mean abundance of 5473 and amplitude of 2983, compared to a mean abundance of 2826 and amplitude of 1725 in Colesdalen. Although the

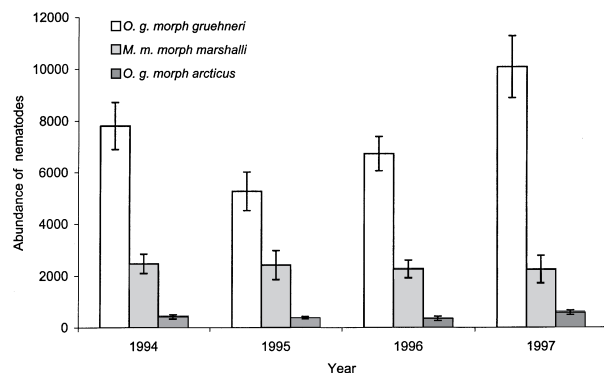


Fig. 5. The abundance with 95% confidence intervals of *Marshallagia marshalli*, *Ostertagia gruehneri* and *O. gruehneri*, m. arcticus in October in adult female Svalbard reindeer from Sassendalen (1994–98).

amplitude of the fluctuation was higher in Sassendalen than in Colesdalen it was a similar proportion of the mean in each population (0.55 and 0.61 respectively). The seasonal fluctuations were significant in both populations ( $P < 0.0001$ ) and did not differ significantly in phase (governed by  $\delta$ ,  $\chi^2 = 0.45$ , D.F. = 1,  $P = 0.50$ ).

There was also a significant seasonal component in the abundance of *O. gruehneri* (Table 3), but in contrast to *M. marshalli* infections, this seasonality was not consistent between years and giving a significant interaction with year ( $\chi^2 = 27.41$ , 6 D.F.,  $P < 0.0001$ , Table 3, Model 7 versus 5). In 2 out of 4 years, 1995–96 and 1996–97, the abundance of *O. gruehneri* did not change significantly from the late summer to the late winter period ( $P > 0.1$ , Fig. 3B and C). However, in 1994–95 and 1997–98, there was a drop in abundance from late summer to late winter ( $P < 0.005$ , Fig. 3C and F). Also, for *O. gruehneri*, m. arcticus there was a seasonal drop in abundance over the winter period as indicated in some years for *O. gruehneri* ( $\chi^2 = 49.14$ , 1 D.F.,  $P < 0.0001$ , Fig. 3B).

**Faecal egg output.** Unfortunately to date we have no abomasum nematode abundance data from animals between May and mid-August because no reindeer were culled in this period. However, we do have substantial faecal egg count data collected from live animals in 1 of the study populations (Colesdalen/Reindalen) between April and September. In April output of both the *M. marshalli* taxa eggs and *Ostertagia* eggs was low and very similar at about 5 (s.d. = 3.9) and 8 (s.d. = 6.2) eggs per gramme (Fig. 4A), but prevalence was high at 91% and 98%, respectively. As expected, as snow melt accelerated in June, the output of the *Ostertagia* eggs increased dramatically and continued to rise to a peak in July with a mean of 235 (s.d. = 124) eggs per g faeces. This peak level did not differ significantly between summers ( $F_{4,675} = 0.688$ ,  $P = 0.601$ ). From August onwards, *Ostertagia* egg output declined, although

*Ostertagia* eggs were still 100% prevalent in September. By October the *Ostertagia* egg prevalence had fallen to 65% and mean egg output had dropped to 2.5 (s.d. = 2.8) eggs per gramme of faeces. In contrast, in June the *M. marshalli* taxa egg output declined so that by July eggs were found in very few (1.3%) of the faecal samples (Fig. 4A). In the autumn *M. marshalli* taxa prevalence increased to 41% but the mean eggs per gramme in the faeces was still less than 1 (0.82, s.d. = 1.01).

Adult reindeer treated with anthelmintics in late April/early May were infected with *Ostertagia* eggs by mid-July (Fig. 5B), and although egg output was lower in treated than in untreated animals, the decline from July to September paralleled that found in the untreated adults. Despite low abundance of adult *O. gruehneri* in naïve calves the prevalence of *Ostertagia* eggs in July was 25% ( $n = 20$ ). By August this had increased to 55% ( $n = 51$ , mean = 14) and by September prevalence had declined again to 17% ( $n = 24$ , s.d. = 46.3). The decline in calves of *Ostertagia* egg output was parallel but lower than that of the treated adult reindeer group (Fig. 4B). By this time prevalence of the *M. marshalli* taxa eggs in calves was 46% although mean egg output was less than 1 in both groups.

#### Annual variation in abundance

The abundance of adult *M. marshalli* did not differ significantly between the 4 years from 1994 to 1997 (Table 3, models 6–8 versus 5). In contrast, the abundance of both *O. gruehneri* and *O. gruehneri*, m. arcticus varied significantly between years (Table 3, Model 7 versus 5). In October, the abundance of *O. gruehneri* varied significantly between years from around 5000 in 1995 to 11000 worms per host in 1997 (Fig. 5). The between-year pattern in *O. gruehneri*, m. arcticus was similar to that found for *O. gruehneri* in October, with highest abundance in 1997.

#### Correlations in the intensity of nematode species

In adult reindeer, there was no correlation between *O. gruehneri* and *M. marshalli* in either late winter ( $r = -0.045$ ,  $P = 0.71$ ,  $n = 96$ ) or in late summer ( $r = -0.042$ ,  $P = 0.69$ ,  $n = 93$ ) and within each season there was no relationship within each reindeer population ( $P > 0.2$ ). As could be expected, there was a strong positive relationship between the closely related taxa *O. gruehneri* and *O. gruehneri*, m. arcticus ( $r = 0.588$ ,  $P = 0.001$ ,  $n = 261$ ). This was true for adult reindeer from both reindeer populations ( $r = 0.496$ ,  $P < 0.001$ ,  $n = 129$  and  $r = 0.528$ ,  $P < 0.001$ ,  $n = 55$  for Sassendalen and Colesdalen respectively). There was no relationship between *O. gruehneri*, m. arcticus taxa and *M. marshalli* ( $r = -0.058$ ,  $P = 0.407$ ,  $n = 207$ ).

## DISCUSSION

Our study of gastrointestinal nematodes in Svalbard reindeer hosts provides compelling evidence of differences in the life-histories and population dynamics of the 2 most abundant nematode species.

*Aetiology of infection*

Although worm burdens remain elevated throughout the adult age range, there are species differences in the rate of infection of hosts. Infection with *M. marshalli* increased rapidly in the host's first year of life, whereas very low levels of infection with *O. gruehneri* and *O. gruehneri*, m. arcticus were found in animals during their first summer and winter and increased mainly over their second summer. This is late compared with sheep and cattle where peak infection is reached during the first summer grazing (Anderson *et al.* 1979; Armour, 1989). From the anthelmintic experiment we know that treated adult reindeer become re-infected within the same summer as treatment, therefore it is possible for transmission and development of a patent infection to occur within the host within one summer. We therefore suspect the low intensities of *O. gruehneri* in calves to be due to (1) transfer of protective antibodies from the mother to the calf, (2) the gut morphology of immature ruminants differs from adults (McDonald Edwards & Greenhalgh, 1984), therefore it may be unsuitable for *O. gruehneri* in calves, (3) a difference between nematode taxa in their distribution across vegetation communities, the calf grazing strategy and feeding preferences may cause low contact rates with the infective larvae of *O. gruehneri* while they still pick up *M. marshalli*.

*Contrasting seasonal patterns in the dominant taxa*

*M. marshalli* had significantly higher adult worm abundance in late winter than in late autumn. Our previous observation of an increase in total abundance of nematodes over winter (Halvorsen *et al.* 1999) was mainly due to the change in the abundance of adult *M. marshalli*. In calves, *M. marshalli* increased from around 2000 in October to around 9500 in April in Sassendalen. This increase could not be accounted for solely by the development of larvae present in the animals at the end of summer because the abundance of larvae was only 895 (range = 186–4800, Halvorsen *et al.* 1999). Therefore a large proportion of the increase in calves must be due to transmission from the pasture during the winter, and is also likely to cause the increase in *M. marshalli* in adult reindeer. Faecal egg output in this species also occurred mainly in the winter months.

The evidence for over-winter transmission and egg production by *M. marshalli* suggests that this species has adapted to long winters. Still, preliminary work

indicates that eggs deposited in the winter have high survival but no development at subzero temperatures (A. Stien, unpublished observations). Our working hypothesis is that the transmission strategy adopted by *M. marshalli* is one of remaining as eggs in the faeces through the winter and developing to the infective stage in the summer. If infective larvae stay in faeces, there is the possibility that coprophagy is of major importance for transmission in the winter when the availability of grazing for the reindeer is very sparse. *M. marshalli* has a wide geographical distribution and host range (Urquhart *et al.* 1996), but comparable data are lacking from other climatic zones. Whether the observed life-history pattern is an adaptation to High Arctic conditions or a general trait of *M. marshalli* is therefore unclear.

In contrast to *M. marshalli*, the output of *Ostertagia* eggs showed a seasonal pattern similar to that found in temperate trichostrongylosis with very low levels in the winter but a peak in mid-summer (Anderson *et al.* 1979). In addition the abundance of *O. gruehneri* in adult reindeer did not increase from late autumn to late winter. In fact, in 2 years, *O. gruehneri* declined over the winter months suggesting a rate of transmission and larval development that do not compensate for adult worm mortality. *O. gruehneri*, m. arcticus behaved in a similar way to *O. gruehneri*.

In models of the population dynamics of trichostrongyle nematodes, the seasonality in egg output is generally assumed to be due to changes in adult nematode population size sometimes modified by density-dependent effects on nematode fecundity (e.g. Smith & Grenfell, 1985; Leathwick, Barlow & Vlassoff, 1992). We found that in the late summer, *Ostertagia* egg output showed a similar decline between groups of animals with different worm burdens (calves, treated and untreated adults), suggesting that the drop in egg output in late summer is not purely due to density-dependent effects on nematode fecundity. Also, egg output approaches zero in animals that have on average 10000 adult abomasal nematodes. This suggests that external environmental factors may have a strong influence on the seasonality in *Ostertagia* egg production in this system. Data on worm burdens from animals culled during the summer period will allow a more detailed analysis of this phenomenon.

*Contrasting annual patterns between the dominant taxa*

The pattern of increase in *M. marshalli* over the winter did not vary between years. This suggests that *M. marshalli* population dynamics is not strongly influenced by external environmental factors such as climate or host density. For example, *M. marshalli* burdens in Sassendalen did not vary with a 2-fold change in reindeer population size

(range=400–1000 in the period 1994–98; Sysselmannen, unpublished helicopter counts). This pattern suggests that the nematode population dynamics may be governed by intrinsic density-dependent mechanisms within the host. Compared to *M. marshalli*, the between-year variation in abundance of *O. gruehneri* suggests that its population dynamics are sensitive to external factors and that it may play a role in the fluctuating population dynamics of its host.

#### Population differences in species profile

At the reindeer population level the abundance of *M. marshalli* and *O. gruehneri* were inversely related. *M. marshalli* burdens were higher in Sassendalen, the population with the lower *O. gruehneri* levels. This could suggest the existence of competitive interactions between species as has been found for other trichostrongyle systems (Diez-Baños, Cabaret & Diez-Baños, 1992). However, this interpretation was not supported at the level of individual reindeer since we found no evidence for a negative correlation between the intensity of *O. gruehneri* and *M. marshalli*. The lack of any significant correlation between these 2 species is consistent with the idea that they have different dynamics in time and space. This is likely since grazing in winter, when *M. marshalli* appears to concentrate its transmission effort, is confined to relatively small wind-blown ridges and areas where snow cover is thin. In contrast, in the summer, when *O. gruehneri* appears to have its transmission window, reindeer forage over wide areas in the valley floors.

#### Immunity

The age–intensity profiles of *M. marshalli*, *O. gruehneri* and *O. gruehneri*, m. arcticus do not provide evidence for any strongly acquired immune response affecting the abundance of these nematode taxa. While in domestic livestock the abundance of abomasal nematodes is high in calves and lambs and lower in adults due to acquired immunity, in Svalbard reindeer, once the asymptote of infection is reached it remains high with increasing age.

It has been suggested that the dispersion parameter,  $k$ , may increase with age in the host population due to the density-dependent effect of acquired immunity (Paccala & Dobson, 1988; Grenfell *et al.* 1995*a, b*). In this study we find no evidence for an increase in  $k$  with host age. After correcting for the effect of the abundance of infection  $k$  was found to decrease with increasing age for *M. marshalli*. The crude age-specific estimates of  $k$  also indicated a drop in  $k$  with age for *O. gruehneri*, m. arcticus in Sassendalen. This pattern has previously been found for trichostrongyle nematodes in sheep (Barnes & Dobson, 1990). A drop in  $k$  with age

may be the outcome of acquired immunity in combination with heterogeneities in the hosts' immune response with some hosts responding more efficiently than others (Grenfell *et al.* 1995*b*). However, the effect of different possible population processes on the distribution of parasites has not been fully investigated (Fulford *et al.* 1992; Smith *et al.* 1995). Evidence for acquired immunity based on patterns in  $k$  will therefore be weak. We therefore find it unreasonable to interpret the inconsistent patterns in the  $k$  estimates as evidence for acquired immunity when this conflicts with the evidence from the age–intensity relationship.

The probability of reindeer being pregnant in late winter is negatively related to the abundance of *O. gruehneri* (S. D. Albon, unpublished observations). One would expect this pathogenic effect to cause selection for immunity. Since the nutritional status or general condition of hosts may influence their ability to mount an immune response (Lloyd, 1995), the absence of evidence for acquired immunity in Svalbard reindeer may indicate that the cost associated with an immune response is relatively high for these animals. Alternatively, direct measures of immune competence may be necessary to uncover its importance in this host–parasite interaction.

#### Statistical modelling of variation in $k$

Our analysis supported the suggestion that the variance parameter  $k$  of the negative binomial distribution varies with abundance (Grenfell *et al.* 1995*a, b*). The best fit functional relationship between  $k$  and mean worm burden varied between the nematode taxa. We therefore suspect that if a common functional form for the relationship between  $k$  and the abundance of infection exists, it will be a more complex function than those we adopted. Still, analyses of residuals suggested that our models for  $k$  gave a good description of the variance structure in the data. It was also our experience that modelling these data using a constant  $k$  affected our conclusions significantly. The assumption of a constant  $k$  should therefore be checked when analysing complex data sets. Shaw *et al.* (1998) have recently suggested methods for analyses of grouped data on macro-parasites with separate estimation of  $k$ s within groups. Our suggestion of modelling  $k$  as a simple continuous function of the mean may be an alternative to their approach when analysing data with respect to continuous predictor variables or when sample sizes in different groups are small. Even though our simple models for  $k$  may not capture the true relationship between  $k$  and the mean, the method is likely to be robust to relatively substantial errors in the functional form of this relationship as found for models for overdispersion in log-linear models (McCullagh & Nelder, 1989). Simulation studies are needed to evaluate this claim.

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