

Prevalence and intensity of the ectoparasite *Echinophthirius horridus* on harbour seals (*Phoca vitulina*): effects of host age and inter-annual variability in host food availability

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SUMMARY

The epidemiology of the sucking lice *Echinophthirius horridus* was studied over a 4 year period in which their harbour seal hosts experienced marked inter-annual changes in food availability. Prevalence and intensity of infection varied in relation to host age but not sex. Burdens were highest on immature seals, but both prevalence and intensity of infection were significantly higher in years when food availability was low. Observed intra-population variations in ectoparasite dynamics suggested that reported geographical differences in the prevalence of *E. horridus* may have resulted from methodological differences. In contrast to previous studies of other pinnipeds, lice were also absent on weaned pups, suggesting that *E. horridus* is transferred horizontally. No significant differences were found in the haematological parameters of infected and uninfected hosts. Nevertheless, there was a significant negative correlation between intensity of infection and several erythrocyte parameters, suggesting that high burdens of lice may compromise diving ability.

Key words: *Echinophthirius horridus*, epidemiology, harbour seals, inter-annual variation, pinniped.

INTRODUCTION

Variations in environmental conditions may influence ectoparasite population dynamics either through their influence on host behaviour or nutritional condition (Crompton, 1991). In turn, this may result in geographical or inter-annual variation in the dynamics both of the host–parasite associations and of any diseases for which ectoparasites are a vector. Amongst the pinnipedia, there is considerable inter- and intra-specific variation in the extent to which individuals return ashore (haul out) to breed, moult or rest (Reidman, 1990). Such behavioural variability may be a particularly strong influence on the dynamics of pinniped ectoparasites, as they will experience abrupt changes in temperature, pressure, desiccation and abrasion when their hosts move between aquatic foraging areas and terrestrial haul-out sites.

Suckling lice (Anoplura) have been recorded on a wide range of pinniped hosts (Hopkins, 1949; Ferris, 1951; Kim, Repenning & Morejohn, 1975), and have also been identified as intermediate hosts for other internal parasites (Geraci *et al.* 1981). Currently, however, our understanding of these host–parasite associations is based largely on studies of Antarctic species; (Murray, 1958; Murray & Nicholls, 1965; Murray Smith & Soucek, 1965). In these cases, lice

reproduced only when seals were on land and variations in the abundance of lice appeared to be determined by species and age-specific variations in the hosts' terrestrial haul-out patterns (Murray *et al.* 1965). Studies of ectoparasites on temperate pinnipeds are less detailed, but data on host behaviour suggest that their dynamics may exhibit greater intra-specific variation than those studied in Antarctic waters. The temperate harbour seal (*Phoca vitulina* L.), for example, is the most widely distributed of pinnipeds, occurs in many different habitats, and exhibits variations in haul-out behaviour which reflect local environmental conditions (Pauli & Terhune, 1987; Thompson *et al.* 1989; Watts, 1992). Their tendency to form groups at traditional haul-out sites can result in the rapid spread of infectious diseases (Grenfell, Lonergan & Harwood, 1992; Heide-Jorgensen *et al.* 1992) and it has been suggested that this may also facilitate the spread of ectoparasites (Geraci *et al.* 1981). In contrast, studies of Antarctic species indicated that ectoparasites were transmitted vertically from mother to pup.

The sucking louse *Echinophthirius horridus* Olfers has now been recorded in several harbour seal populations (Bonner, 1972; Reijnders *et al.* 1981; Skírnisson & Ólafsson, 1990), but the only 2 quantitative studies have produced quite different results. Dailey & Fallace (1989) found *E. horridus* on 45% of 77 Pacific harbour seals (*P. v. richardsii*) collected from an estuary in Washington state. Whereas Lunneryd (1992) reported a complete

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absence of *E. horridus* on 158 *P. v. vitulina* recovered from the Kateggat-Skaggerak. Whilst these findings may reflect real geographical differences in the population dynamics of *E. horridus*, both studies were carried out within a single season. Pinniped behaviour or condition can vary markedly in relation to inter-annual changes in food availability (Trillmich & Ono, 1991; Boyd *et al.* 1994), and resulting variations in either contact rates or susceptibility could lead to temporal variations in ectoparasite dynamics. Consequently, longer-term studies of within-population variability in the prevalence and intensity of infection are required before one can draw more detailed conclusions about the extent of spatial variations in dynamics.

In N.E. Scotland, our long-term studies of harbour seal ecology have identified marked inter-annual variations in winter food availability, primarily due to changes in the local abundance of the clupeids herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) (Tollit, Greenstreet & Thompson, 1997). In turn, this has led to inter-annual variations in the seals' diet composition, behaviour, body condition and haematological parameters (Thompson *et al.* 1996a, 1997a; Tollit & Thompson, 1996). In this study our primary aim was to determine whether previously observed between-year changes in host food availability influenced the dynamics of *E. horridus* in this host population. In addition, we aimed to assess whether host age influenced ectoparasite burdens, and to determine whether the presence of ectoparasites could be related to host haematological parameters.

MATERIALS AND METHODS

Study area and population

The study was carried out between 1991 and 1995 in the Moray Firth, N.E. Scotland (57° 40' N, 04° 00' W). An estimated 1651 harbour seals were recorded on inter-tidal sandbanks in the study area in 1993 (Thompson *et al.* 1997b). The nearest alternative breeding sites are found in Orkney and in the Tay estuary, located 130 km to the north and 325 km to the south respectively (Hiby, Duck & Thompson, 1993). Based on radio-tracking and marking studies (Thompson *et al.* 1996b) and molecular genetic data (Stanley *et al.* 1995; Goodman, 1995) we assume that individual seals studied in different years were from the same resident population (Thompson *et al.* 1997a).

Capture and sampling techniques

Data on the abundance of *E. horridus* on free-living seals were collected during a regular capture-release programme. Most seals were captured at haul-out sites in spring (March–May) and autumn (August–

October) of 1992, 1993, 1994 and 1995. Additional captures were made over the winters of 1993–1995 to permit the study of changes in prevalence and intensity of infection during the seals' first year of life. In all cases, capture and handling protocols were those of Thompson *et al.* (1992).

To provide an estimate of intensity of *E. horridus* infection on captured harbour seals, we counted the total number of lice (adults and nymphs) present on the dorsal surface of their left hind flipper. This procedure was carried out while the seal was restrained, allowing us to count lice by spreading the digits of the flipper and combing the hairs backwards using the side of a pair of forceps. In exceptional cases where more than 500 lice were present on a flipper, numbers were recorded as > 500.

Comparisons of prevalence and intensity in relation to host age were based upon measurements of the seals' dorsal standard length (see McLaren, 1993). Seals were judged to be immature or adult according to the most detailed life-history data available for this sub-species of harbour seal (*P. v. vitulina*). Males > 130 cm were considered adult on the basis of a marked increase in testes weight. Females > 125 cm were considered adult based on an average length at first ovulation of 126.8 cm (Härkönen & Heide-Jørgensen, 1990). Following the method outlined by Corpe, Thompson & Porter (1998), a sample of hair was taken from the mid-dorsal region and hair-width measured under a binocular microscope to determine whether or not immature seals were in their first year.

Independent assessments of host condition were made using ultrasound (Gales & Burton, 1987; Rosen & Renouf, 1997). A 2–3 cm area of skin was shaved at a point 60% down the dorsal surface of the seal (see Ryg *et al.* 1990), and covered with lubricating jelly. Blubber thickness was then estimated using a commercial machine designed for measuring fat depth in pigs (Meritronics Ltd, Kent, UK). Blood samples were taken from the epidural vein of restrained seals using vacutainers containing anti-coagulant (EDTA). Samples were stored at 4 °C and haematological analyses were made within 24 h at the Scottish Agricultural College, Inverness as described by Thompson *et al.* (1997a).

Statistical analyses

To compare ectoparasite burdens during periods in which their hosts experienced contrasting levels of food availability, years were divided into 2 year classes (Thompson *et al.* 1996a; 1997a); 'good' clupeid years (1993/94, 1994/95) where > 50% of the winter diet (by weight) consisted of clupeids, and 'bad' clupeid years (1991/92, 1992/93) where < 11% of the diet was clupeids. Between-group comparisons of lice prevalence were made using 2 × 2 contingency tables with Yates correction. Com-

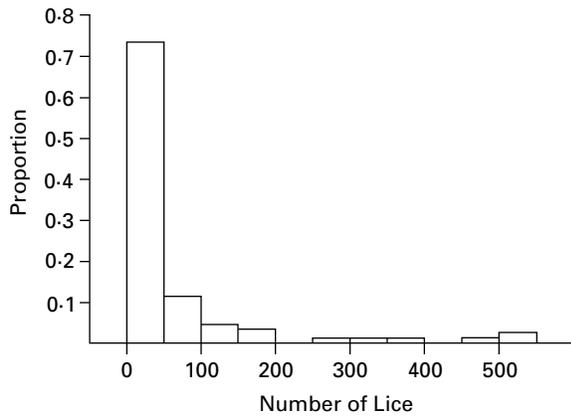


Fig. 1. Frequency histogram of the number of *Echinophthirius horridus* counted on one hind-flipper of Moray Firth harbour seals. Data are only presented for those 87 individuals which were found to be infested with at least 1 individual louse. The total sample size including the zero class was 223 harbour seals.

parisons of intensity were made using ANOVA after logarithmically transforming counts of lice. A moment estimate of the negative binomial parameter, k ,

of the frequency distributions of lice on different age classes of seals was made using the equation

$$k = (x^2)/(s^2 - x),$$

where s^2 is the variance, x the mean (Smith, 1995).

The relative contribution of the different factors affecting parasite burdens were determined using multiple ANOVA. Sample sizes were insufficiently large or balanced to use a 4-way ANOVA to explore the effect of the seal sex and age, and of the season and year-class in which seals were captured. We therefore used a 2-stage approach, using a 3-way ANOVA to first compare sex, age and season. Insignificant factor(s) were then dropped (after checking that they were not involved in any 2-way or 3-way interactions) from a second 3-way ANOVA which also included year class.

Erythrocyte parameters were normally distributed and separate variance t tests were used to compare total erythrocyte counts, haemoglobin concentration (Hb), mean cell volume (MCV) and mean cell haemoglobin concentration (MCHC) on infested and non-infested individuals. Some leukocyte para-

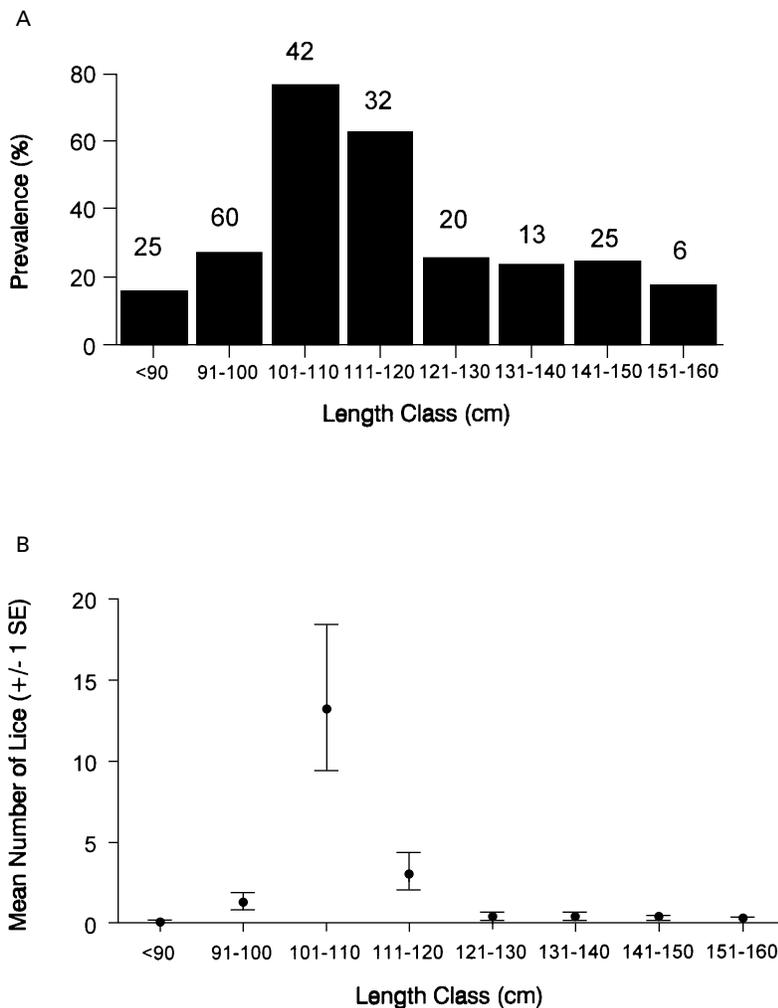


Fig. 2. Size-related differences in (A) prevalence (B) intensity of *Echinophthirius horridus* infestation on Moray Firth harbour seals captured between 1992 and 1995. Intensity data are presented as back-transformed means (± 1 standard error). Sample sizes are presented above each size category in (A).

Table 1. ANOVA of intensity of *Echinophthirius horridus* infection on harbour seals in relation to (A) seal age (mature or immature), sex and season of capture (spring or autumn), (B) seal age (mature or immature), season of capture (spring or autumn) and inter-annual variability in host food availability (good years versus bad years)

(Intensity was compared using logarithmically transformed data. $n = 208$ harbour seals. In (B) data from different years were pooled to provide sufficient sample sizes to compare the effects of food availability.)

Source of variation	Sum of squares	D.F.	F	Significance of F (P)
(A)				
Age	12.11	1	34.63	< 0.001
Season	7.69	1	21.99	< 0.001
Sex	0.05	1	0.13	0.72
Two-way interactions				
Age \times Season	5.31	1	15.17	< 0.001
Age \times Sex	0.10	1	0.28	0.60
Season \times Sex	0.08	1	0.22	0.64
Three-way interaction				
Age \times Season \times Sex	0.01	1	0.03	0.86
(B)				
Age	8.44	1	27.60	< 0.001
Season	4.94	1	16.17	< 0.001
Year class	1.24	1	4.07	< 0.05
Two-way interactions				
Age \times Season	3.93	1	12.86	< 0.001
Age \times Year Class	1.28	1	1.19	< 0.05
Season \times Year Class	2.05	1	6.70	< 0.05
Three-way interaction				
Age \times Season \times Year Class	0.97	1	3.16	0.08

meters were not normally distributed and could not be transformed. These comparisons were made using a Mann-Whitney U test. All analyses were carried out using SYSTAT (Wilkinson *et al.* 1992). Because blood samples, estimates of age (from hair widths) and blubber thickness were not available from all seals, sample sizes varied for different comparisons.

RESULTS

A total of 223 individual harbour seals were captured during the study. *E. horridus* were found on the hind flipper of 87 seals (39%). The distribution of parasites was highly aggregated, and showed a negative binomial distribution ($x = 20.74$, variance = 5120.4, $k = 0.084$, $n = 233$) (Fig. 1). Extremely high burdens of several hundred lice were found on a few individuals, and these severely infested seals commonly carried large numbers of lice over large portions of their dorsal and ventral surface.

Both prevalence and intensity of infection varied with length class, with the highest burden on immature seals of between 100 and 120 cm (Fig. 2). Because sample sizes for several length classes were small, data were pooled into immature and adult groups for further comparison. No sex differences

were found in the prevalence (immatures: $\chi^2 = 0.76$, $P = 0.38$, $n = 74$ male, 100 female; adults: $\chi^2 = 0.15$, $P = 0.70$, $n = 31$ male, 18 female) of infection. Furthermore, the first 3-way ANOVA showed that there were no sex differences in intensity of infection (Table 1A) and sex was dropped from the model. The second 3-way ANOVA stage indicated that age, season and year class all influenced the intensity of lice, but that age and then season had the strongest effects (Table 1B). There were also significant 2-way interactions involving all 3 factors. Adults showed no seasonal variation in burdens, but lice were significantly more prevalent and in higher numbers on immature seals in the spring (Table 2). Immatures had significantly higher prevalence of infection than adults in the spring but differences between age classes were not significant in autumn (Table 2).

As a result of the age-related and seasonal differences in lice prevalence and intensity, more detailed comparisons of the effects of between-year differences in host food availability were stratified for age and confined to samples of seals captured in spring. Furthermore, because sample sizes were insufficient for adults, these analyses were restricted to immature animals. Comparisons of blubber thickness of these animals confirmed that there were

Table 2. Comparison of prevalence and intensity of *Echinophthirius horridus* infection on immature and adult harbour seals captured in different seasons

(Intensity was compared using logarithmically transformed data.)

Season	Age class	Prevalence (%)	<i>n</i>	χ^2	<i>P</i>	Mean intensity	<i>k</i>	F	<i>P</i>
Spring	Immature	83.7	49	12.15	< 0.001	52.18	0.31	28.33	< 0.001
	Adult	35.3	17			0.47	1.31		
Autumn	Immature	24.5	110	0.68	0.411	16.71	0.05	3.39	0.068
	Adult	15.6	32			0.22	0.56		
Spring	Immature	83.7	49	46.03	< 0.001	52.18	0.31	62.36	< 0.001
	Adult	35.3	17			0.47	1.31		
Autumn	Immature	24.5	110	1.47	0.226	16.71	0.05	1.93	0.17
Spring	Adult	35.3	17			0.47	1.31		
Autumn	Adult	15.6	32			0.22	0.56		

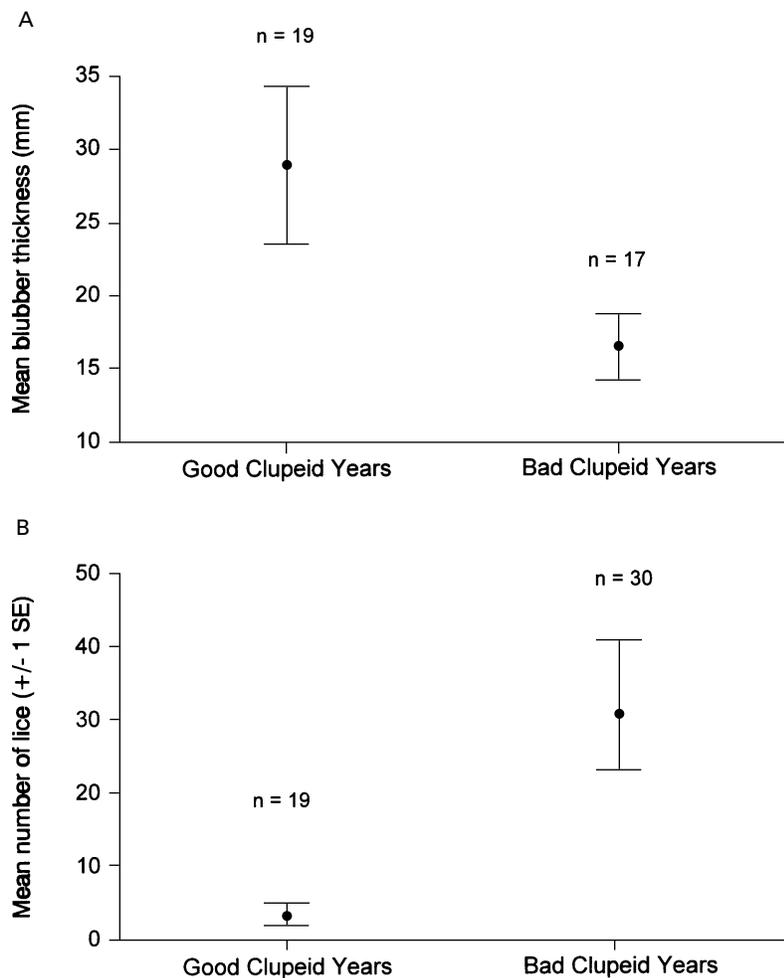


Fig. 3. Differences in (A) estimates of mean blubber thickness in mm (± 1 standard error) and (B) intensity of *Echinophthirius horridus* infestation of immature Moray Firth harbour seals in relation to inter-annual differences in the availability of their clupeid prey over the previous winter. Intensity data are presented as back-transformed means (± 1 standard error).

marked between-year differences in body condition (Fig. 3). Both prevalence and intensity of infestations were greater after 'bad' clupeid years when seals were in poor condition (Table 3; Fig. 3).

Ninety-five seals were confirmed to be below 15 months old on the basis of their hair width measurements. Overall, prevalence was low in the first few months following weaning, but this in-

Table 3. Variation in the prevalence and intensity of *Echinophthirius horridus* on immature seals in periods when hosts experienced contrasting levels of food availability

(Data are from seals captured in the spring following winters which differed in the availability of the seals clupeid prey, and are pooled from different good and bad years to provide sufficient sample sizes. Comparisons of intensity were made using logarithmically transformed data, and presented values are back-transformed means.)

	Prevalence (%)	<i>n</i>	χ^2	<i>P</i>	Mean intensity	F	<i>P</i>
Good clupeid years	63.0	19	7.27	< 0.01	3.12	20.54	< 0.001
Bad clupeid years	96.7	30			30.47		

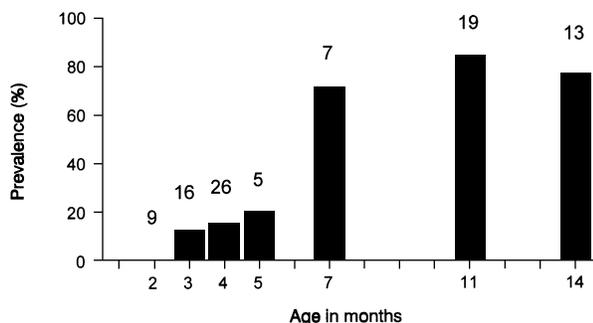


Fig. 4. Changes in the prevalence of *Echinophthirius horridus* infestation on young harbour seals in their first 14 months. Sample sizes are presented above each frequency bar, and include only those individual seals whose year of birth could be confirmed from measurements of their hair width.

creased markedly by January, when seals were approximately 7 months old (Fig. 4). Intensity of infection also increased in the second 6 months of life, but this increase was greater for those seals encountering bad clupeid years in their first winter (Fig. 5).

There were no significant differences in haematological parameters of infested and non-infested seals (Tables 4 and 5). However, there were significant negative correlations between the number of lice found on an individual seal and its total erythrocyte count (Pearson Correlation = -0.28 , $P < 0.001$),

haematocrit (Pearson Correlation = -0.37 , $P < 0.001$) and haemoglobin concentrations (Pearson Correlation = -0.40 , $P < 0.001$) (Fig. 6). All other haematological parameters showed non-significant relationships with lice burdens ($P > 0.14$ in all cases).

DISCUSSION

Previous studies of *E. horridus* on harbour seals were based on analyses of dead seals. The opportunity to make counts of lice on live seals had several advantages, particularly the absence of uncertainty over the time since death and any influence which this had on counts (see Lunneryd, 1992). However, the integration of this study into a broader capture-release programme prevented us from making counts of lice over the whole of a seal's body; total body counts would simply be too dangerous to carry out on wild harbour seals under acceptable levels of anaesthesia. Instead, we used counts of lice on the dorsal surface of 1 hind flipper to provide an index of intensity. Previous studies of other phocid seals have shown that the hind flipper is the principal site of lice infestation (Murray & Nicholls, 1965; Murray *et al.* 1965). Our general observations prior to and during the present study suggest that this pattern held for *E. horridus* on harbour seals, and lice were only obvious on other parts of the body when there were extreme burdens on the flippers. Our choice of a preferred

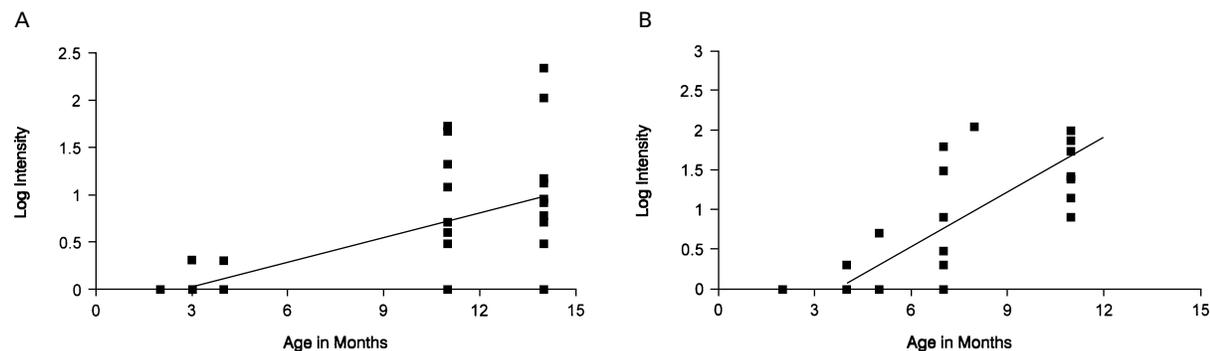


Fig. 5. Relationships between \log_{10} intensity and age for harbour seal pups of less than 14 months old on the basis of their hair-width measurements. (A) Data for seals whose first winter was a good clupeid year ($y = 0.086x - 0.228$; $F_{1,57} = 48.59$, $r^2 = 0.46$, $p < 0.001$). (B) Data for seals whose first winter was a bad clupeid year ($y = 0.23x - 0.854$; $F_{1,34} = 76.53$; $r^2 = 0.69$; $P < 0.001$).

Table 4. Comparison of erythrocyte parameters in relation to the presence or absence of *Echinophthirius horridus*

(Data are provided for all seals pooled, and also for immatures only. Comparisons between groups were made using a separate variance *t*-test.)

Parameter	Lice absent			Lice present			<i>t</i>	<i>P</i>
	<i>x</i>	S.D.	<i>n</i>	<i>x</i>	S.D.	<i>n</i>		
All seals								
Total count (10 ⁹ /l)	4.46	0.62	123	4.34	0.79	81	-1.196	0.23
HCT (%)	51.7	4.5	123	51.3	7.6	81	-0.445	0.66
Hb (g/dl)	19.57	2.08	123	19.32	3.2	81	-0.616	0.54
MCHC (g/dl)	37.95	4.03	123	37.66	3.53	81	-0.55	0.59
MCV (fl)	117.78	24.8	123	119.5	15.42	81	0.609	0.54
Immature seals								
Total count (10 ⁹ /l)	4.59	0.63	86	4.36	0.82	72	-1.943	0.06
HCT (%)	51.8	4.6	86	51.3	8.0	72	-0.429	0.67
Hb (g/dl)	19.71	2.03	86	19.23	3.37	72	-1.063	0.29
MCHC (g/dl)	38.14	3.51	86	37.45	3.57	72	-1.212	0.23
MCV (fl)	114.88	27.4	86	119.29	16.02	72	1.256	0.21

Table 5. Comparison of leukocyte parameters in relation to the presence or absence of *Echinophthirius horridus*

(Data are provided for all seals pooled, and also for immatures only. Comparisons between groups were made using a Mann-Whitney U test.)

Parameter (10 ⁹ /l)	Lice absent		Lice present		U	<i>P</i>
	Median	<i>n</i>	Median	<i>n</i>		
All seals						
Total count	10.9	123	10.6	81	5406.0	0.30
Neutrophils	6.96	123	6.67	81	5513.0	0.20
Eosinophils	0.76	123	0.74	81	4934.0	0.91
Basophils	0.47	123	0.58	81	4166.0	< 0.05
Lymphocytes	1.8	123	1.79	81	4166.0	0.79
Monocytes	0.74	123	0.74	81	5513.0	0.68
Immature seals						
Total count	10.75	86	10.55	72	3365.0	0.35
Neutrophils	6.86	86	6.49	72	3390.0	0.31
Eosinophils	0.70	86	0.72	72	3124.0	0.92
Basophils	0.51	86	0.58	72	2739.5	0.21
Lymphocytes	1.83	86	1.79	72	2954.0	0.62
Monocytes	0.69	86	0.76	72	3075.5	0.94

site therefore means that our index of intensity is unlikely to correlate directly with total body burdens but will reflect it. It therefore provides a reasonably robust estimate of prevalence and, on balance, we suggest it is the most appropriate approach given the constraints of working with live seals.

Overall, the prevalence of *E. horridus* in Moray Firth harbour seals was similar to that found in samples of seals shot at a similar estuarine site in Washington State (Dailey & Fallace, 1989). In contrast, Lunneryd (1991), found no *E. horridus* on seals which were recovered dead in the Kattegat-Skaggerak after the 1988 phocine distemper virus. Whilst one cannot rule out geographical differences in population dynamics, it seems more likely that the

complete absence of lice in the Kattegat-Skaggerak sample was due to lice leaving their hosts before the bodies were recovered. Dailey & Fallace (1989) reported a significant correlation between the presence of *E. horridus* and the heartworm *Dipetalonema spirocauda* Leidy, providing support for earlier evidence that *E. horridus* is an intermediate host for this species (Geraci *et al.* 1981). The presence of *D. spirocauda* in 18% of Lunneryd's sample of harbour seals further suggests that the absence of lice was due to dispersal after the death of hosts.

Our study also found marked differences in prevalence and intensity of infection in relation to host age. In contrast, Dailey & Fallace (1989) found no significant differences between age classes. How-

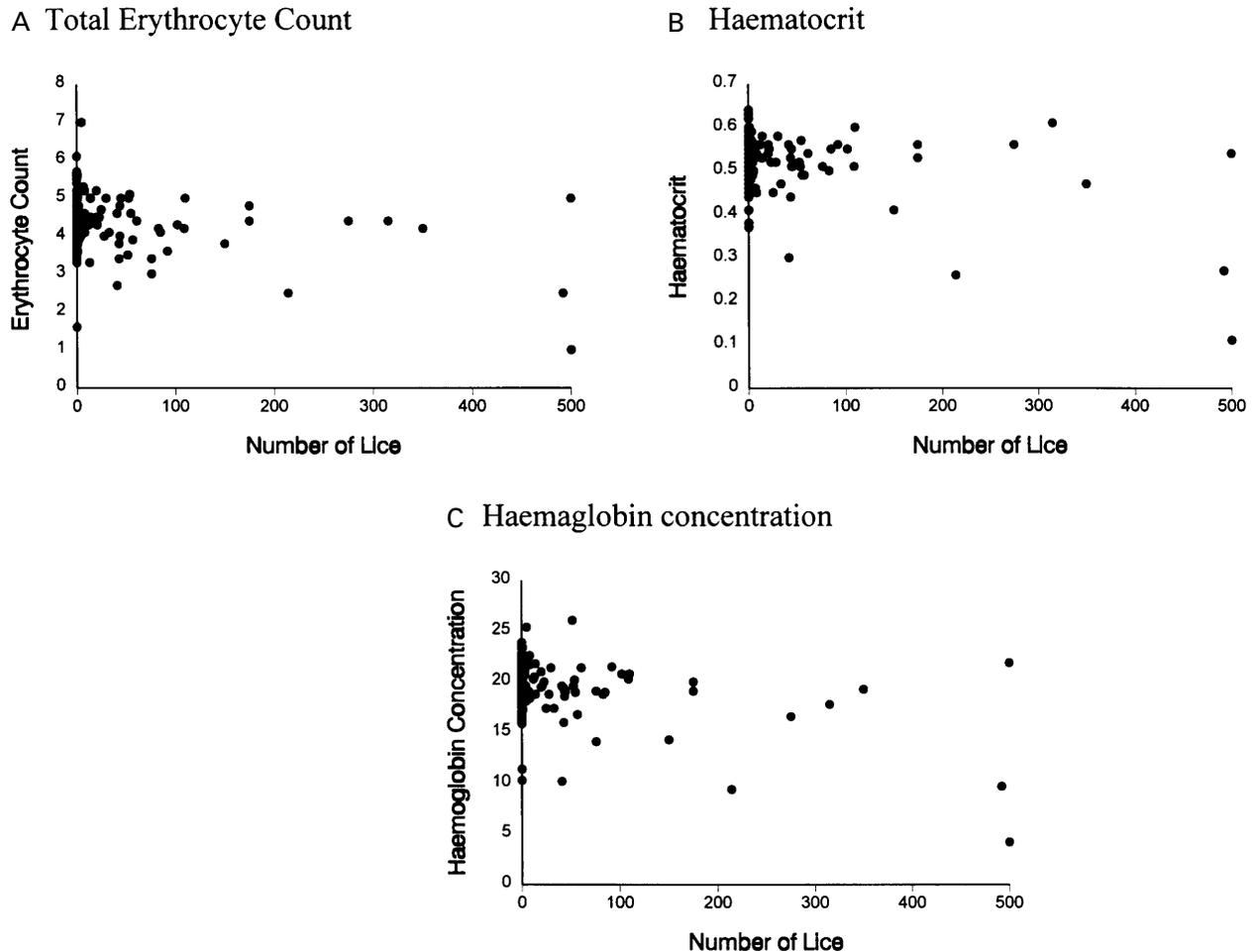


Fig. 6. Relationships between erythrocyte parameters and intensity of infestation by *Echinophthirius horridus* on Moray Firth harbour seals. Data are presented for those parameters which were significantly correlated with lice burden.

ever, sample sizes in their study were small for many age groups and, as in the Moray Firth, prevalence was highest in seals of around 1 year old. Amongst Weddell seals, older individuals also had lower prevalence of lice (Murray *et al.* 1965), whereas prevalence remained high on elephant seals of all age classes (Murray & Nicholls, 1965). Observed age differences in prevalence and intensity have also been reported in other parasites of harbour seals (Lunneryd, 1992) and could be due either to acquired immunity (Randolph, 1979) or to age-related differences in behaviours which affect host contact rate or ectoparasite survival. Harbour seals of different age-classes and sex segregate both within (Allen, 1988) and between (Kovacs, Jonas & Welke, 1990; Thompson, 1989) haul-out sites, potentially influencing contact rates. Alternatively, larger harbour seals spend less time hauled out and make longer foraging trips (Thompson *et al.* 1998). Murray & Nicholls (1965) showed that *Lepidophthirus macrorhini* Enderlein could survive on elephant seals (*Mirounga leonina* L.) during long foraging trips, but that the abundance of lice was

reduced when seals returned ashore. Consequently, survival rates of *E. horridus* may be lower on larger harbour seals which spend more time at sea.

Previous studies of both phocid and otariid seals have found a high prevalence (75–100%) of ectoparasites on weaned pups, and concluded that vertical transmission from mother to pup was the most important form of dispersal (Murray *et al.* 1965; Murray & Nicholls, 1965; Kim, 1975). In contrast, we found low prevalence and intensity of infections until seals were older than 6 months. Harbour seal pups are weaned at 3–4 weeks old (Muelbert & Bowen, 1993). Unlike many other pinnipeds, they spend a high proportion of their time at sea both during lactation and post-weaning periods, potentially reducing opportunities for lice populations to develop on very young seals. The presence of these recently weaned animals in the autumn sample probably explains the seasonal difference in both prevalence and intensity of infection in immatures. The life-cycles of other lice species on Antarctic and subarctic pinnipeds range from 17 to 28 days, with a tendency for development

to occur faster in warmer air temperatures (Murray *et al.* 1965; Murray & Nicholls, 1965; Kim, 1975). Low numbers of lice on both adult females and weaned pups suggest either that *E. horridus* life-cycles are considerably longer, or that horizontal transmission occurs at haul-out sites. Individual harbour seals tend to remain widely spaced at haul-out sites. Consequently, if horizontal transmission does occur, lice must either travel distances of several metres between individual seals, or survive within the haul-out substrate until it is used by another host. Harbour seals may use sand-banks, muddy shores, ice and a variety of rock types as a haul-out substrate (Bigg, 1981), and all are likely to differ in their suitability for dispersing lice. Geographical variations in host-ectoparasite dynamics could therefore also result from differences in site characteristics. Further work is now required to determine whether free-living lice are present at haul-out sites, and whether their presence or activity varies in relation to habitat or other local environmental conditions.

Inter-annual variation in prevalence and intensity

Previous work has shown that inter-annual variations in winter food availability affect the haul-out distribution, condition and early growth of harbour seals from this population (Thompson *et al.* 1996a, 1997a; Corpe, 1996). Data from the present study show that ectoparasite burdens on immature seals also differed markedly in relation to the host's winter food availability, both in terms of prevalence and intensity. As seen in other vertebrate species these variations may be a direct response to the poor condition of hosts during a period of stress (Crompton, 1991; Murray, Cary & Keith, 1997). Alternatively, there may be indirect effects resulting from changes in host behaviour. However, behavioural changes are most likely to involve increases in foraging effort (and thus time spent at sea) during periods of lower food availability; a change which would be expected to reduce rather than increase the abundance of lice on their hosts.

Comparison of haematological values for parasitized and unparasitized seals suggests that there were no marked effects of the lice on these measures of host health. On the other hand, correlations do indicate that higher burdens of lice tended to result in lower erythrocyte counts, HCT and haemoglobin concentrations. In a few cases where extreme burdens were recorded, very low HCT values of < 20% were found. Similar relationships have been found between ectoparasite burdens and HCT in seabirds (Wanless, Barton & Harris, 1997). The long-term impact of these burdens on host reproduction and survival remain unknown, but severely depressed HCT values may compromise diving ability, particularly in small seals (Corpe,

1996). In years where food availability is low, high burdens of ectoparasites may therefore interact with these other factors to reduce survival in young seals.

Although there were significant relationships between lice intensity and total erythrocyte counts, HCT and haemoglobin concentrations, there was no clear effect on other haematological parameters. Previous studies showed a marked change in a wider range of erythrocyte and leukocyte parameters in relation to the seal's winter diet, indicative of a fish-induced anaemia (Thompson *et al.* 1997a). On the other hand, could some of these changes instead be related to inter-annual differences in ectoparasite burden? We think not, first, because the relationships between lice burdens and most haematological parameters were non-significant. Second, the most dramatic haematological changes in relation to bad clupeid years were an increase in the MCV of both immature and adult seals (Thompson *et al.* 1997a). The present study has shown that, whilst ectoparasite burdens of immature seals differed in relation to host food availability, prevalence and intensity on adult seals was low in all years. Thus, variations in ectoparasite burdens cannot explain the previously reported inter-annual differences in haematological parameters of adult seals.

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