

Ectoparasitic sea lice (*Lepeophtheirus salmonis* and *Caligus elongatus*) infestations of wild, adult, one sea-winter Atlantic salmon *Salmo salar* returning to Scotland

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ABSTRACT: Caligid ectoparasitic copepods are major pathological pests on cultured Atlantic salmon *Salmo salar* L., and their population biology has been well studied in the farm environment. The ecology of caligid infestations of wild salmon is, by contrast, rather poorly understood. We monitored return migrant one sea-winter wild Atlantic salmon in Scotland annually for infestations of 2 caligids, *Lepeophtheirus salmonis* (Krøyer) (between 1998 and 2005) and *Caligus elongatus* Nordmann (between 1999 and 2005). Prevalence of *L. salmonis* was 100% in all years, whereas *C. elongatus* prevalence ranged from 90 to 100%. Abundances fluctuated markedly between years and *L. salmonis* mean abundance (min. to max.: 17.4 to 31.0) was significantly greater than for *C. elongatus* (min. to max.: 2.9 to 23.8) in all except one year. A positive association in abundance of the 2 species, for individual fish within any one year, indicates weak or absent competitive effects on abundances for individual hosts. Individual fish within any one year appeared similarly vulnerable to infestation by either species, although Taylor's power regression showed clear differences in density-related patterns of overdispersion amongst hosts for the 2 species. Host condition factor (expressed either as Fulton's index, K , or the relative mass index, W_R) showed significant variation among years. Parasite species abundances were not, however, determined by host condition factor, and poor condition fish were no more likely to carry high infestations than were high condition fish.

KEY WORDS: Copepoda · Caligidae · Ectoparasite · *Lepeophtheirus salmonis* · *Caligus elongatus* · *Salmo salar*

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INTRODUCTION

Throughout the North Atlantic and North Pacific, the specialist copepod *Lepeophtheirus salmonis* (Krøyer) is a natural ectoparasite of salmonid fishes in their marine phase (Pike & Wadsworth 1999). *L. salmonis*, and the more host-generalist, *Caligus elongatus* Nordmann (which is recorded from >80 species of marine fish) are the most economically important pathogens to the Atlantic salmon *Salmo salar* L. aquaculture industry (Johnson et al. 2004). Expansion of Atlantic salmon

farming has been rapid since its inception ~35 yr ago, and global annual production in both hemispheres presently exceeds 1.1 million t (ICES 2004). As a consequence, much research effort has focused on the life cycle of *L. salmonis* on salmon farms and on methods of therapeutic control (Pike & Wadsworth 1999, Tully & Nolan 2002). Although considerable progress has been made in modeling the dynamics of *L. salmonis* populations on farms (e.g. Revie et al. 2002), comparatively little is known of the ecological interactions with its wild host associations (e.g. Jacobsen & Gaard 1997,

Todd et al. 2000, 2004, Bjørn & Finstad 2002). Even less is known of *C. elongatus*, which in the NE Atlantic has been variously recorded as scarce to abundant on wild sea trout *Salmo trutta* L. (e.g. Berland 1993, MacKenzie et al. 1998, Schram et al. 1998), Atlantic salmon (Jacobsen & Gaard 1997) and Arctic char (*Salvelinus alpinus* (L.), Bjørn et al. 2001).

Despite their differences in adult size, both species have similarly short generation times of 50 to 90 d (Pike & Wadsworth 1999) and can cause pathological damage and host death, with the small post-smolt stage being the most vulnerable (Finstad et al. 2000). The quantitative extent to which salmon farms contribute to wild fish infestations is a matter of some debate, but the evidence now is considerable that farm-origin caligids are at least a contributory factor to recent stock declines of wild salmonids proximate to salmon farms in areas of Norway, the British Isles and W Canada (Bjørn & Finstad 2002, Butler 2002, McKibben & Hay 2004, Penston et al. 2004, Todd et al. 2004, Krkošek et al. 2005).

We monitored *Lepeophtheirus salmonis* (1998–2005) and *Caligus elongatus* (1999–2005) infestations of return migrant one sea-winter (1SW) Atlantic salmon in Scotland against the backdrop of declining abundances and marine survival of wild salmon over at least 3 decades (Anonymous 2004). Our primary objectives were to quantify variations in the annual abundance and the age-structure of the 2 parasite species on returning 1SW adults, and to ascertain whether year-to-year variations in infestation might correlate with host fish parameters, including individual condition factor (CF). Returning 1SW salmon re-enter freshwater in Scotland between May and November following their one winter at sea, and they tend to increase in length and weight as the summer netting/sampling season progresses (own unpubl. data). Host CF can be calculated for individual fish using a range of standard protocols based on mass–length relationships (Neff & Cargnelli 2004). Analysis of within- and between-year variation in CF for 13 year classes of mixed-stock 1SW salmon, netted on multiple dates during June to August each year at the same location as the present study (1993–2005, n = 4916; our unpubl. data), showed the unexpected result that in 12 yr CF did not vary significantly within a season. CF was calculated as the predicted weight of a fish of standard length on each sampling date, and for only 1 year (1994) did weighted regression show a significant decrease ($p = 0.017$) in CF during the season. CF therefore essentially is 'set' for entire year classes of 1SW return migrants and among-year variation in CF exceeded within-year variation. Given that low intensity caligid ectoparasite infestations can result in physiological stress, or even death, of the host fish, the clear possibility was that

between-year variations in CF of wild hosts might be determined by, or correlated with, ectoparasite abundances.

MATERIALS AND METHODS

Field site and sample data. All data were for wild salmon trapped (but still free-swimming) in bag nets set within ~100 m of the shoreline at Strathy Point, N Scotland (58° 06' N, 04° 00' W). Salmon caught at Strathy Point possibly are at their first migratory land-fall and are destined not only for the rivers of both W and E Scotland, but also for Ireland (Shearer 1986). For management purposes, the International Council for the Exploration of the Sea (ICES) distinguishes European stocks of Atlantic salmon in 4 entities: viz. 1SW and multi sea-winter (MSW) 'northern' (Russia to Scandinavia) European, and 1SW and MSW 'southern' (British Isles to Spain) European components (see: www.ices.dk/reports/ACFM/2005/WGNAS/wgnas05.pdf). Salmon taken at the interceptory fishery at Strathy Point undoubtedly are of mixed stocks and are representative of a significant element of the ICES southern European component (ICES 2004). Both *Lepeophtheirus salmonis* and (especially) *Caligus elongatus* have a propensity to detach from the host fish on encountering hyposaline water (see e.g. Todd et al. 2000 for data from the river Tay estuary, E Scotland). Because of (1) the coastal distance of Strathy Point from large river estuaries, (2) the method of trapping, and (3) the minimal post-capture handling of the fish, salmon taken there offer the most realistic abundance data for these 2 parasites on adult wild salmon in the British Isles. Additional unique features are that, prior to their interception, these salmon have not been subject to recent fishery pressure (which may, for example, be size selective), and will not recently have encountered salmon farms.

The traps were inspected twice daily, the fish removed individually by hand, and killed with a single blow to the head. St Andrews and Fisheries Research Services (FRS) personnel collected independent sets of fish data over the period 1998 to 2005. St Andrews personnel were permitted to sample salmon (n = 403) for parasites on a single occasion in each season between 1998 and 2005. Fork length (to 0.1 cm) and weight (to 0.05 kg) were recorded and scale samples removed from the standard area (Anonymous 1985) for subsequent ageing of all fish. MSW fish, farm escapees, and any wild fish that had previously spawned would be subject to different infestation histories from the 1SW fish which comprised the bulk of the sample in each year; these fish (n = 38) were identified by scale reading and excluded from the data.

The annual parasite data generally were obtained on 2 consecutive days, during Weeks 25 to 30. In 1998, however, separate day visits were made in June (Week 26) and July (Week 30).

The FRS has routinely monitored length, weight and sea age of salmon captured at Strathy Point since 1993. The multiple repeat FRS samplings throughout each summer netting season thus provide a comprehensive time series of fish data (but no parasite information). FRS sample days within years ranged from 8 (1998) to 20 (2003), with the earliest and latest dates of their monitoring being (days of the year) Days 168 (Week 24, 2003) and 232 (Week 33, 2002 and 2003), respectively. In total 4584 fish were sampled by FRS between 1993 and 2004: the length/weight data for these fish provided the specific length–mass equation used for calculating condition factor (CF, as the relative mass index, W_R , below) of the fish sampled independently (1998–2005) by St Andrews for parasites. The FRS 1998–2004 data set ($n = 2145$ fish), which was contemporaneous with the St Andrews salmon/parasite data, was reduced to 2110 by the exclusion of 11 d on which <5 fish were sampled.

Over the course of the 9 wk June to August netting season, returning salmon tend to increase in length and weight (own unpubl. data), and both host fish size and CF were considered likely to be important independent variables for the analysis of within- and between-year variation in parasite abundances. That the parasite data could be obtained only for single annual visits therefore necessitated an assessment of how representative are single samples of, for example, host CF for each year. The FRS data allowed within- and between-year analysis of fish parameters, including CF.

During sampling for parasites, fish were inspected by eye and all postlarval caligids removed and preserved for later confirmation of developmental stage and sex. For *Lepeophtheirus salmonis*, the pre-adult I, pre-adult II and adult stages of both sexes were categorized; there is no pre-adult stage in *Caligus elongatus*, which moults directly from the sessile chalimus IV larva to the mobile adult. Although stages C III and C IV chalimi can be visually assessed, reliable counts of all the attached postlarval chalimus stages can be obtained only by microscopic examination of fish. Time did not permit such a detailed examination because this is a commercial operation, with the fish being destined for human consumption and requiring icing, processing and onward transport. Typically, and in common with previous reports (e.g. Jacobsen & Gaard 1997), visible (mostly C III and C IV) chalimi were very rare and usually attached to the dorsal, caudal or paired fins. Data for chalimi were not included in the present analyses, which are confined to 'mobile' (pre-adult I, pre-adult II, adult) *L. salmonis* and (adult) *C. elongatus*.

Fish and parasite data analyses. Data for both parasite species were obtained for 1999 to 2005 inclusive: *Caligus elongatus* was present in 1998, but time constraints precluded their enumeration. Separate analyses were undertaken of the variation in the proportion of female parasites (each species), and of pre-adults (stages I and II pooled, *Lepeophtheirus salmonis*) over the period 1999 to 2005. Host CF was calculated for all fish sampled for parasite analysis (except 1998, since weights were lacking for the 18 fish sampled in June 1998), using 2 of the standard measures. Fulton's index, i.e. $K = 100$ [weight in g/(length in cm)³], is a widely used measure; it assumes growth to be isometric and scaled to the cube of the length. Any departure from an exponent of 3 will, therefore, result in a length-dependence of individual fish CF. A measure more independent of length is the relative mass index, W_R ($W_R = W/W_S$), whereby W is the observed mass and W_S the standard mass of individual fish calculated from a specific length–weight equation (Neff & Cargnelli 2004).

The specific length–weight relationship for *Salmo salar* was determined from the FRS 1993–2004 data ($n = 4584$ fish). Regression of y (log weight, g) on x (log length, cm) was highly significant ($y = -2.17 + 3.14x$; $r = 0.934$, $p < 0.001$), and from this the geometric mean regression ($y = -2.57 + 3.36x$; see Ricker 1973) was derived for calculating the standard mass (W_S) of individual fish, and thence W_R . Body surface area of all individual fish (except 18 from June 1998) was estimated by applying the *S. salar* regression model of Jaworski & Holm (1992), whereby, for a given weight in g, surface area = $9.5864 \times 10^{\log(\text{weight}) \times 0.629}$. This model is the most appropriate available for present purposes, but will not be precise for wild salmon because it was derived for cultured salmon (length range 25 to 62 cm).

All parasite count data for replicate fish were $\log(x+1)$ -transformed, and all proportion data for females and pre-adults, within years and for the separate species, were arcsine-transformed prior to analysis. Prior to ANOVA, homogeneity of variances was assessed by Levene's test and inspection of standardized residuals. In some instances variances remained heterogeneous following transformation, but ANOVA is robust to departures from the assumption of equality of variances in cases where samples are large and the number of treatments >6 (Underwood 1997). Where they occurred, significant outcomes for Levene's test are reported. Variation in parasite species abundances among years was analyzed by 1-way ANOVA, followed by Tukey post hoc tests. For more detailed analyses of variation in the 2 species' abundances, of the proportions of pre-adult *Lepeophtheirus salmonis*, and of the proportionality of females among individual fish and within each species, stepwise multiple regression analysis was applied to the 1999–2005 data (i.e.

excluding 1998 when *Caligus elongatus* were not enumerated). Separate stepwise analyses were undertaken by including either K or W_R as the measure of fish CF. Ten stepwise analyses concerned the separate parasite species, with a further 2 for both species pooled (total lice). Both forward and backward stepwise regression was undertaken for each analysis, and in all cases both procedures gave an identical outcome.

In addition to assessing the possibility of interspecific competition between *Lepeophtheirus salmonis* and *Caligus elongatus*, we investigated whether or not fish size might influence parasite abundances, parasite loadings might drive host CF, or whether fish in poor condition are perhaps disproportionately vulnerable to parasite infestation by showing, for example, high proportions of pre-adult *L. salmonis*. Furthermore, the degree of aggregation, or overdispersion, that parasite species display amongst individual hosts can have important consequences for inter- and intraspecific interactions on individual hosts, and is conveniently expressed by least-squares linear regression of log variance on log mean abundance (Taylor 1961). Taylor's 'power law' typically results in species-specific slopes to such regressions.

RESULTS

Choice of measure of CF

The 2 CF measures, K and W_R , were highly correlated (FRS data, 1993–2004; $r = 0.954$, $n = 4584$, $p < 0.001$) and K showed the expected positive dependence on fish length ($r = 0.110$, $n = 4584$, $p < 0.001$). In contrast, W_R showed a significant negative correlation with length for 1993–2004 overall ($r = -0.192$, $n = 4584$, $p < 0.001$). Thus, despite calculation of W_R with an exponent of 3.36 to preclude the mathematical problem of length-dependence, W_R does reveal a tendency for longer salmon to have weighed less than predicted by the overall geometric mean mass–length relationship, and thereby to show poorer condition.

Variation in host fish size and CF

As expected, host length and weight of the FRS fish increased during each 9 wk season. For example, correlation analyses for mean fish length and day (day of the year) of sampling showed significant outcomes for every year over the period 1998 to 2004 (FRS data, p ranging from 0.033 [1999] to < 0.001 [1998, 2000]). In contrast, mean CF (as measured by K) showed no significant correlation with day of the year for any of the 7 years. W_R showed consistently negative correlation coefficients for mean CF against day of sampling for all 7 years, but none was significant. Thus, the single

annual St Andrews samples can be considered representative of CF (here preferably expressed as the length-corrected index, W_R) for the 1SW cohort of salmon for each of the years sampled.

For those fish sampled by St Andrews personnel, log length varied significantly among years (ANOVA 1998–2005, $F_{7,402} = 4.54$, $p < 0.001$), as did log weight (ANOVA 1999–2005, $F_{6,360} = 3.09$, $p = 0.006$), K (ANOVA 1999–2005, $F_{6,360} = 47.34$, $p < 0.001$; Levene's test = 2.532, $p = 0.021$) and W_R (ANOVA 1999–2005, $F_{6,360} = 49.50$, $p < 0.001$; Levene's test = 2.951, $p = 0.008$). There was an overall decline in host weight and W_R throughout the study period (Fig. 1), excluding 1998 (for which weights were missing for 18 fish), but no obvious trend in host length (Table 1).

Lepeophtheirus salmonis and *Caligus elongatus* annual abundances

Lepeophtheirus salmonis occurred at 100% prevalence throughout all 8 years. *Caligus elongatus* prevalence in 4 of the 7 years also was 100%, but otherwise varied between 90.2 and 97.4%. *L. salmonis* mean abundance ranged between 17.4 and 31.0 and there were significant between-year variations (ANOVA $F_{7,402} = 7.95$, $p < 0.001$; Levene's test = 2.256, $p = 0.029$), with 2 statistically homogeneous groupings (Fig. 2). For *C. elongatus*, abundances typically were low but 2002 was exceptionally high, resulting in annual means ranging from 2.9 (2000) to 23.8 (2002). The 1-way ANOVA for *C. elongatus* log abundance also was highly significant for year ($F_{6,360} = 37.04$, $p < 0.001$), and there were 5 homogeneous abundance groupings (Fig. 2).

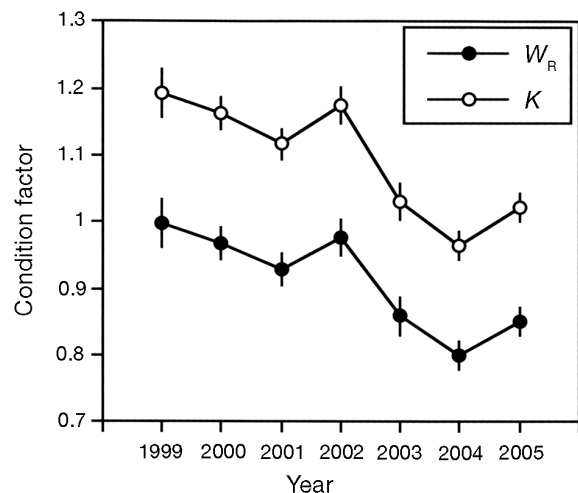


Fig. 1. *Salmo salar*. Annual variation (mean \pm 95% CI) in host salmon condition factor (Fulton's index, K), and the relative mass index, W_R), 1999 to 2005, for fish sampled by St Andrews personnel ($n = 361$)

Table 1. *Salmo salar*. Minimum to maximum and means of sampled fish lengths (log cm), weights (log kg) and condition factors (K [exponent 3], W_R [exponent 3.36]) for fish sampled for *Lepeophtheirus salmonis* and *Caligus elongatus*. n: no. of fish

Year	n	Fork length		Weight		K		W_R	
		Min.–Max.	Mean	Min.–Max.	Mean	Min.–Max.	Mean	Min.–Max.	Mean
1998	42	48.5–69.8	61.6	1.20–3.80 ^a	2.38 ^a	0.84–1.24 ^a	1.01 ^a	0.71–1.02 ^a	0.85 ^a
1999	39	52.3–66.4	58.9	1.40–3.60	2.43	0.91–1.40	1.19	0.75–1.17	1.00
2000	41	52.0–70.5	60.2	1.60–4.40	2.54	1.02–1.35	1.16	0.85–1.11	0.97
2001	43	51.4–71.2	61.0	1.60–4.00	2.53	0.98–1.30	1.12	0.82–1.08	0.93
2002	53	49.4–71.0	60.3	1.60–4.15	2.57	0.99–1.47	1.17	0.83–1.23	0.98
2003	64	54.0–66.0	60.5	1.40–3.40	2.27	0.68–1.36	1.03	0.57–1.13	0.86
2004	62	54.0–74.0	63.4	1.40–4.60	2.46	0.82–1.18	0.97	0.68–0.97	0.80
2005	59	52.3–74.4	60.3	1.27–4.10	2.23	0.88–1.4	1.02	0.74–1.18	0.85

^aWeights were lacking for 18 fish in June 1998; n = 24 for weights and condition factors

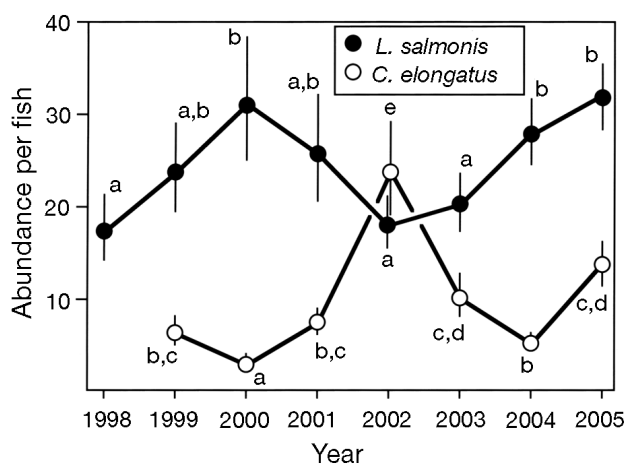


Fig. 2. *Lepeophtheirus salmonis* and *Caligus elongatus*. Annual variations in mean [$\log(x+1)$ -transformed] abundance \pm 95% CI. Prevalence was 100% for both species, except for *C. elongatus* in 1999 (97.4%), 2000 (90.2%) and 2004 (96.8%). a–d: post-hoc Tukey groupings, following ANOVA (*L. salmonis*: $F_{6,343} = 6.10$, $p < 0.001$; *C. elongatus*: $F_{5,301} = 38.76$, $p < 0.001$)

An inverse relationship between the mean annual abundances *Lepeophtheirus salmonis* (*L. s.*) and *Caligus elongatus* (*C. e.*) at the population level (Fig. 2) superficially might be indicative of interspecific competition. The loadings of the 2 species on individual fish did, however, reveal an overall significant positive correlation ($r = 0.169$, $n = 361$, $p < 0.001$; Fig. 3), which was consistent across 5 of the 7 years (analyses not shown). The exceptions were 2000, when abundances of *C. elongatus* were extremely low and thus the correlation test weak, and 2005 when abundances of both species were moderate to high. In general, within any one year, individual fish that are vulnerable to infestation by one species tend also to be at risk from the other, but it is likely that the 2 species' annual abundance patterns vary independently. The 1-way ANOVA for total sea lice abundances [$\log(L.s. + C.e.)+1$] on individual fish (1999–2005), showed a significant year effect ($F_{6,360} = 2.37$, $p = 0.029$; Levene's test = 3.650, $p = 0.002$). It was expedient, therefore, to ascertain whether or not variation in putatively impor-

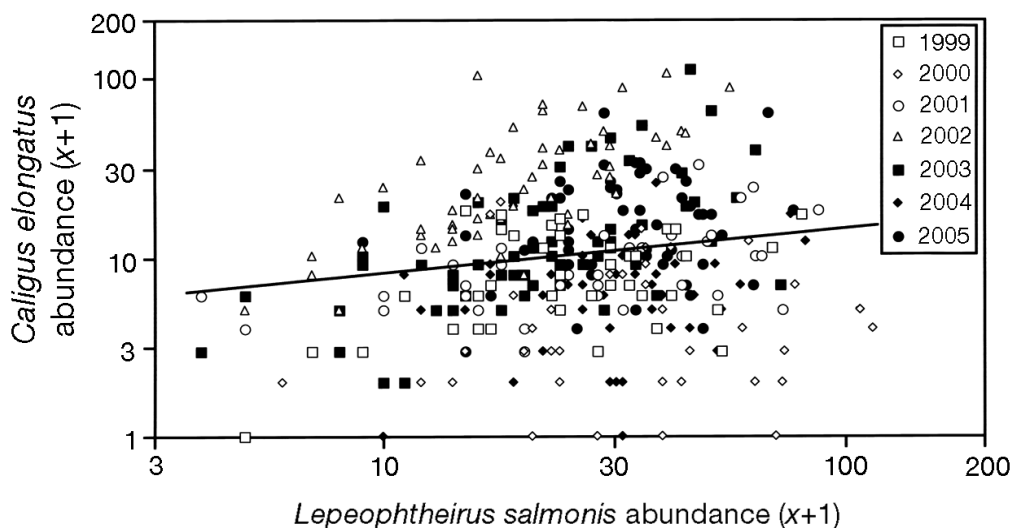


Fig. 3. *Lepeophtheirus salmonis* and *Caligus elongatus*. Co-occurrence on individual host fish, 1999–2005. For 5 of the 7 years there was a significant power regression. The fitted regression ($\log y = 0.628 + 0.254 \times \log x$, $r = 0.169$, $p = 0.001$) is for the pooled data

tant host fish parameters might explain either this variation, or the abundances of the 2 species at the population level.

***Lepeophtheirus salmonis* and host/ *Caligus elongatus* parameters**

Least-squares linear regression showed a significant positive correlation between log abundance of *Lepeophtheirus salmonis* and log host fish length ($n = 403$, $r = 0.245$, $p < 0.001$), but the bulk of this variation amongst hosts could be explained by the greater body surface area of the longer fish ($\log L. salmonis = -1.292 + 0.867 \times \log \text{surface area}$; $n = 385$, $r = 0.216$, $p < 0.001$). It is important to note, however, that *L. salmonis* tends to aggregate in restricted, preferred areas on the host fish body surface (Todd et al. 2000). *L. salmonis* abundance showed very significant (and positive) partial correlations only with the abundance of *Caligus elongatus* and with host fish length (Table 2). Within any one year, longer fish tended to bear greater infestations of either species, and fish with high *L. salmonis* infestations tended also to carry higher intensity infestations of *C. elongatus*. The proportion of female *L. salmonis* on individual fish showed strong positive partial correlations with the abundance both of *L. salmonis* and of *C. elongatus* (Table 2). A similar outcome was shown for the proportion of pre-adult *L. salmonis*, except that the partial correlation with *C. elongatus* was negative. For both of these *L. salmo-*

nis dependents, therefore, parasite abundance alone appears to be the primary determining factor. Higher proportions of females arise as a result of accumulation of the longer-lived gender, and greater proportions of pre-adult *L. salmonis* are characteristic of recent infestation.

***Caligus elongatus* and host/ *Lepeophtheirus salmonis* parameters**

As for *Lepeophtheirus salmonis*, *Caligus elongatus* abundance showed an overall significant positive correlation with host fish length ($\log C. elongatus = -2.264 + 1.824 \times \log \text{fish length}$; $n = 360$, $r = 0.151$, $p = 0.004$), but this was significant for only 3 (2001, 2003, 2005) of the 7 years. The 2 stepwise analyses for *C. elongatus* abundance (including either K or W_R as the measure of CF) showed closely similar outcomes, and a clear difference from the analytical outcomes for *L. salmonis* abundance. For *C. elongatus* abundance, year, CF and *L. salmonis* abundance all proved to be (positive) significant independents (Table 2). The proportion of female *C. elongatus* on individual fish was consistently high (mean annual min. to max. = 0.835 [2002] to 0.926 [1999]), and significantly higher than for *L. salmonis* (mean annual min. to max. = 0.598 [2001] to 0.724 [1998]). The consistency of this *C. elongatus* parameter amongst individual fish resulted in no significant correlation with any of the independents investigated (Table 2).

Table 2. *Lepeophtheirus salmonis* (*L.s.*) and *Caligus elongatus* (*C.e.*). Summary of stepwise multiple regression for infestation parameters of individual host salmon ($n = 361$; 1999–2005), for each species and the 2 summed ('Total lice'). Parasite abundances, host fish length and host surface area were log-transformed. The respective regression coefficients, partial correlation coefficients (in parentheses) and associated multiple regression correlation coefficients (r), and probabilities (p) are shown. –: independents excluded by stepwise analysis; ns: not significant

Independent variables	Dependent variables					
	Total <i>L.s.</i>	Proportion		Total		Total lice
		Female <i>L.s.</i>	Pre-adult <i>L.s.</i>	<i>C.e.</i> (K)	<i>C.e.</i> (W_R)	
Total <i>L.s.</i> (log)		6.998 (<0.001)	13.657 (<0.001)	0.238 (0.002)	0.242 (0.002)	–
Total <i>C.e.</i> (log)	0.087 (0.010)	4.753 (<0.001)	–4.867 (0.001)			–
Host length (log)	2.185 (<0.001)	–	–	–	–	2.200 (<0.001)
Condition factor (K)	–	–	–	0.382 (0.030)		–
Condition factor (W_R)	–	–	–		0.528 (0.022)	–
Host surface area (log)	–	–	–	–	–	–
Year	–	–	–	0.055 (<0.001)	0.057 (<0.001)	–
r	0.319	0.303	0.321	0.300	0.293	0.288
p	<0.001	<0.001	<0.001	<0.001	<0.001	ns <0.001

Total lice and host parameters

Within any one year, the wide range of abundances on individual fish (*Lepeophtheirus salmonis*, 1–114; *Caligus elongatus*, 0–107; both species pooled, 4–152) shows that salmon generally do not bear a maximal loading of either species, or the 2 combined. Stepwise regression confirmed that host length was the only significant independent for total parasite burden ('Total lice': Table 2). The finding for individual fish that is, perhaps, of especial importance is that reduced CF (either as K or W_R) was not associated with, or driven by, total parasite loading although this independent was (positively) significant for *C. elongatus* (see above). Years of poorer condition fish (i.e. 2003–2005) were not characterized by exceptionally high total parasite loadings and, overall, poorer condition fish in any one year showed no greater tendency to carry greater (or lesser) burdens of sea lice than did higher condition fish.

The patterns of overdispersion for the 2 species (excluding chalimi) are summarized by the power regressions in Fig. 4. Although the regression coefficients indicate a convergence of the species' patterns of spatial dispersion amongst host fish at extremely high mean population densities (~68 mobile stages of each species), over the observed density ranges *Caligus elongatus* showed consistently greater aggregation, and especially so at low densities. The infection dynamics, demographics and overdispersion of these parasite species among individual hosts are, therefore, fundamentally distinct.

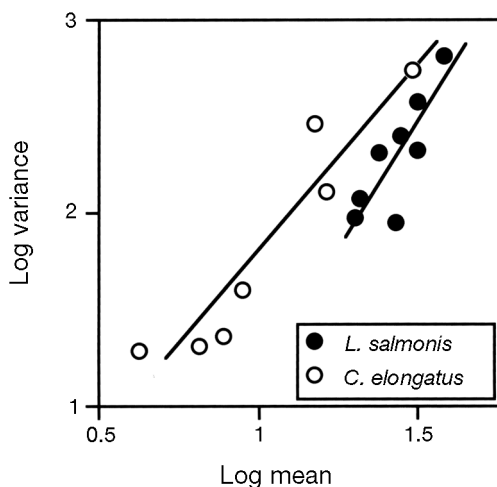


Fig. 4. *Lepeophtheirus salmonis* and *Caligus elongatus*. Taylor's power law (regression, log variance on log mean abundance) fits for all 8 years (*L. salmonis*; $\log y = -1.47 + 2.64 \times \log x$, $r = 0.833$, $p = 0.010$) and 7 years (*C. elongatus*; $\log y = 0.42 + 1.53 \times \log x$, $r = 0.774$, $p = 0.041$), respectively. Data for *C. elongatus* include zero abundances

DISCUSSION

Initially, *Caligus elongatus* was the only major pest caligid to the Atlantic salmon farming industry in E Canada (Piasecki & MacKinnon 1995), and Hogans & Trudeau (1989) reported *C. elongatus* at prevalences up to 100%, compared to *Lepeophtheirus salmonis* at a maximum of only 8%. In recent years, however, *L. salmonis* has become the primary pest species, just as it is in the Atlantic salmon farming industry in both Europe (e.g. Pike & Wadsworth 1999) and on the Pacific coast of Canada (e.g. Morton et al. 2004). Nonetheless, analyses of potential interspecific interactions for ectoparasites on individual host fish are presently lacking. Detailed analyses have been undertaken of the spatial disposition of *L. salmonis* within host fish, and of the spatial segregation of the genders (Todd et al. 2000), but the lack of comparable data for *C. elongatus* within individual hosts presently precludes detailed analysis of interspecific interactions. Irrespective of this, Bakke & Harris (1998) concluded that these 2 species were amongst the pathogens most likely to detrimentally impact both wild and farmed Canadian salmonid stocks in the future. Certainly, the importance of *C. elongatus* to the Scottish industry has long been recognized, but only recently have population modeling studies, founded on extensive commercial databases, begun to lead to a better understanding of the strong seasonal dynamics of *C. elongatus* in the farm environment (e.g. McKenzie et al. 2004).

Our annual time-series of mean abundances for the 2 species on wild salmon did show a generally inverse relationship (Fig. 2), but this pattern cannot be attributed to interspecific competition: in 5 of 7 years, individual fish that bore higher intensity infestations of *Lepeophtheirus salmonis* tended also to carry a higher intensity of *Caligus elongatus*. Assessments of competitive interactions between these 2 species are, however, additionally problematic, because caligid ectoparasites typically aggregate in restricted areas of the host body surface and yet the mobile pre-adult and adult stages can readily move over the host body surface. *C. elongatus* is more vagile than *L. salmonis*, and the males and females of *L. salmonis* are spatially segregated on individual host fish. Females predominate along the posterior dorsal and ventral midlines, and males on the anterior dorsal midline as well as the head (Todd et al. 2000). Rohde (1993) suggested that microhabitat restrictions or specialization could enhance ectoparasite mating encounters, especially for species which typically are sessile and of low population density. The combination of their high to absolute prevalence, and the motility of the pre-adult/adult stages of *L. salmonis* and adults of *C. elongatus*, ought to confer high frequencies of male–female encounters.

In contrast to Rohde's (1993) suggestion, sexual segregation of *L. salmonis* may actually be determined by intraspecific agonistic interactions, with the (large) females aggressively maintaining themselves in the most preferred body regions. Both genders of *C. elongatus* are small and may similarly be displaced from these areas by female *L. salmonis*, but there is no evidence from the present data of *L. salmonis* abundance on individual fish exerting a negative effect on *C. elongatus* abundance.

Open ocean infestation, and interactions with host CF

Larval chalimus stages are rare on Atlantic salmon captured on their oceanic feeding grounds (e.g. Jacobsen & Gaard 1997). Returning two sea-winter (2SW) salmon do, however, typically bear significantly greater mean abundances of mobile *Lepeophtheirus salmonis* than do 1SW fish (Todd et al. 2000) and, as a generalization, overdispersion amongst individual hosts (Fig. 4) is characteristic of host–parasite associations (e.g. Shaw & Dobson 1995). Wild post-smolt *Salmo salar* can acquire chalimi within days of first entering seawater (Finstad et al. 2000), but the adult lice burdens of return migrant 1SW and 2SW salmon, captured some 12+ or 24+ mo later, are most unlikely to be survivors of initial infestation (Todd et al. 2000). Post-settlement development from the infective, planktonic copepodid larva to the final sessile (chalimus C IV) larval stage can take up to 270 degree-days post infection (ddpi) for *Caligus elongatus* (Piasecki & MacKinnon 1995) or 350 ddpi for *L. salmonis* (Johnson & Albright 1991). At oceanic spring/early summer temperatures, our fish carrying pre-adult *L. salmonis* will have been most recently infected 4 to 6 wk before capture. Continued re-infestation in the open ocean therefore is a persistent feature of *L. salmonis* on wild salmon (Jacobsen & Gaard 1997, Todd et al. 2000) but, because *C. elongatus* lacks a pre-adult stage, it is not possible to extend this conclusion to that species with certainty.

Host CF is not a significant determinant of abundance of mobile *Lepeophtheirus salmonis* or total sea lice for wild salmon (Table 2). For *Caligus elongatus* abundance, CF was shown by stepwise regression to have a positive partial correlation; that is, fish of higher CF tended to carry higher intensities of *C. elongatus*. The positive association between the 2 species on individual fish for 5 of the 7 years (Fig. 3), and the outcomes of stepwise multiple regression (Table 2), all show that individual fish are similarly vulnerable to infestation by the 2 species. Within any one year, fish with a large burden of *L. salmonis* tended also to carry

a relatively high infestation of *C. elongatus*, but among years the population abundances of the 2 species probably fluctuate independently.

Irrespective of the evidently highly adapted reproductive strategy of *Lepeophtheirus salmonis* in colonizing wild *Salmo salar* with 100% success every year, there clearly must be a sharp dichotomy between the processes and risks of initial infestation of post-smolt *S. salar* (and both juvenile and adult *S. trutta*) in coastal waters as opposed to the open ocean. Available in-shore data indicate that the planktonic larval copepod stages undergo vertical migrations, but typically they are close to the surface and tend to be caught in any numbers only adjacent to salmon farms or at river mouths (e.g. Tully & Nolan 2002, McKibben & Hay 2004, Penston et al. 2004). The apparent importance of hyposaline fronts to the local concentration of infective copepodids in coastal waters (McKibben & Hay 2004) can have no relevance to infestation dynamics in the open ocean. It is quite likely that oceanic infestation arises simply as a result of the larvae maintaining the appropriate depth near the surface or at thermal fronts and the salmon encountering the parasite by chance whilst foraging.

A fundamental constraint of any study of parasite abundance and demography on free-ranging wild hosts is that, almost by definition, the observer can sample only surviving hosts and this constraint is especially acute for migratory salmonids. Despite their large sample sizes, Tully et al. (1993) failed to capture sea trout *Salmo trutta* juveniles bearing adult *Lepeophtheirus salmonis* and they concluded that any such host fish probably had died as a consequence of the infestation. MacKenzie et al. (1998) reported a negative relationship between C I–II intensity and host sea trout CF (W_R), but also a positive relationship between CF and C III–IV intensity. This they deduced to arise from the differential periods of fish in seawater, but equally these contrasts could be attributable to early mortality of heavily-infested individual fish which were no longer available for capture. The interpretation of those results is further exacerbated because MacKenzie et al. (1998) calculated host W_R for their various sample sites, not from a single standard length–weight relationship, but by using the length–weight relationship for each site. Their estimates of CF will therefore be conservative and converge on unity for each site, hence precluding comparability between sites.

There is no clear evidence to suggest that poor condition *Salmo trutta* are especially susceptible to infestation by sea lice copepodids, or that poor individual host CF is caused by caligid infestation (Schram et al. 1998, Murray 2002); the latter would, however, seem intuitive at least for heavy (but sublethal) parasite

loadings. Although no inferences can be drawn for post-smolt early mortalities, for *S. salar* 1SW adults the present data give no indication that ectoparasitic infestation has any detrimental effect on condition of fish that have survived to return to home waters. Notwithstanding the positive partial correlation for CF with *Caligus elongatus* (Table 2), the indications are that the significant among-year variation in CF reported here (Fig. 1) for 8 cohorts of 1SW Atlantic salmon is not driven by parasite abundance, but most probably by fluctuations in host feeding and growth opportunities, as has been reported for Pacific salmon species (e.g. Hinch et al. 1995).

Demography of *Lepeophtheirus salmonis* and *Caligus elongatus*, and risks of infestation

Female and adult predominance is characteristic of *Lepeophtheirus salmonis* infestations of wild salmon (e.g. Johnson et al. 1996, Jacobsen & Gaard 1997). For individual fish, higher abundance *L. salmonis* infestations correlated positively with a greater proportion of females ($r = 0.166$, $n = 403$, $p = 0.001$; annual mean min. to max. = 0.598 [2001] to 0.724 [1998]), and a greater proportion of pre-adult stages ($r = 0.305$, $n = 403$, $p < 0.001$; annual mean min. to max. = 0.033 [1999] to 0.191 [2000]). Higher intensity infestations could be attributable either to elevated rates of recent infestation (high proportion of pre-adults), and/or elevated rates of past infestation (accumulation of the larger and longer-lived gender). Infestation risk almost certainly is not continuous, and high(er) overall past rates of infestation may be temporally and/or spatially heterogeneous as individual fish transit through relatively high(er) and low(er) risk areas (e.g. Shaw & Dobson 1995). A convergence in this regard is apparent from the 2 species' patterns of overdispersion amongst host fish (Fig. 4): certain individual fish clearly are at either higher risk of infestation or, by chance, encounter high risk areas of infestation more frequently than most other fish.

Demographic comparisons between *Lepeophtheirus salmonis* and *Caligus elongatus* infestations of wild adult salmon are problematic, if only because of the lack of field data on the oceanic distribution of the infective larval stage, there being no *C. elongatus* pre-adult stage (precluding the ageing of infestations for individual fish), and the far broader host species range of *C. elongatus*. Multiple host species might be expected to result in *C. elongatus* larval production being more widespread and continuous throughout the North Atlantic, and for its infestation probability to be spatially and temporally more homogeneous. Although Taylor's power regression (Fig. 4) showed the expected overdispersion and significant difference

in regression coefficient for the 2 species, this analysis actually affirms the opposite—a tendency for greater heterogeneity of infestation risk and aggregation at low abundance for *C. elongatus*. Quantitatively, the infestation risk that *C. elongatus* presents to wild salmon is distinct from that presented by *L. salmonis*, and the difference may well be explained by interspecific contrasts in fecundity and successful production (and host encounter) of infective copepodids. A conservative estimate of typical lifetime fecundity for *L. salmonis* females on wild salmon is several thousand eggs (e.g. Heuch et al. 2000), but for *C. elongatus* this will be markedly lower, at perhaps only a few hundred, even if several pairs of eggstrings are produced in a female's lifetime (Pike & Wadsworth 1999).

Female *Lepeophtheirus salmonis* are much larger, slower-developing and longer-lived than males, and the levels of female predominance reported here (annual min. to max. = 0.598 to 0.724) appear typical of *L. salmonis* infestations of wild *Salmo salar* (Jacobsen & Gaard 1997, see also Johnson et al. 1996 for *Oncorhynchus nerka*). For *Caligus elongatus*, however, despite the genders being the same size, female predominance is even greater (annual min. to max. = 0.835 to 0.948), indicating a marked differential longevity of males and females on wild fish. Piasecki & MacKinnon (1995) found that male *C. elongatus* (infesting experimental char *Salvelinus alpinus*) die soon after copulation. None of the independents here analyzed by stepwise regression (Table 2) correlated significantly with variation in the proportion of female *C. elongatus* amongst individual fish; but if male post-copulatory death is typical of *C. elongatus* on wild salmon, then this alone could explain the extreme female bias. *C. elongatus* adults are, however, very much more active across the host fish surface than *L. salmonis*, and their vagility apparently leads to their commonly detaching from the host fish (e.g. review by Pike & Wadsworth 1999). The possibility therefore remains that males might be more likely to detach from host fish and at least temporarily become planktonic. Certainly, adult *C. elongatus* commonly can be caught in surface plankton net tows in coastal waters (own unpubl. obs.).

The focus of research into the impacts of sea lice on salmon aquaculture has necessarily remained primarily on *Lepeophtheirus salmonis* (e.g. Pike & Wadsworth 1999), although *Caligus elongatus* can—especially in the summer months—be problematic to cultured fish (e.g. Revie et al. 2002). Our data show that *C. elongatus* infestation of wild salmon can in some years (2002; Fig. 2) equal that of *L. salmonis* and that in the past *C. elongatus* has been underestimated in its importance on wild fish, either because of the method of fish capture or the interception of host fish in

brackish waters. We found consistently high infestations of *L. salmonis* and that intensities show no statistical association with host CF. Furthermore, the apparent pattern of a decline in CF of returning adult 1SW salmon in recent years appears not to be related to *L. salmonis* or *C. elongatus* infestation.

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