Context-dependent reduction in somatic condition of wild Atlantic salmon infested with sea lice

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ABSTRACT: Wild Atlantic salmon *Salmo salar* stocks have globally declined over recent decades. On their migratory return to coastal waters, individuals typically are infested by ectoparasitic caligid sea lice (*Lepeophtheirus salmonis* Krøyer, *Caligus elongatus* Nordmann). Infestation in laboratory trials can exert non-lethal impacts on the host fish, including increased stress levels and reduced growth, physical condition and swimming performance. However, to date no evidence exists for non-lethal effects of sea lice on wild adult Atlantic salmon. Using observations for >6000 return-migrant adult salmon captured from the coastline at Strathy Point (SP), North Scotland, in the estuary of the River North Esk (NE), East Scotland, and the lower reach of the River Tamar (TA), Southwest England, we show that the somatic condition (weight at length) of wild salmon is associated with mobile sea lice density. This putative sea lice-mediated reduction of condition varied with year and seasonal date of freshwater return, and increased with the proportion of adult female parasites on a given fish. Influence of host sex, sea-age and smolt age was negligible. The estimated impact differed between the 3 sampling sites likely due to underestimation of infestation levels at NE and TA — largely attributable to negative influences of reduced salinity on parasite retention prior to sampling. Caligid infestation in the present samples explained a small, but discernible, proportion of the variation in host condition. Reductions in somatic condition of Atlantic salmon are associated with disproportionate declines in accreted lipid reserves, which are critical to up-river migration and ultimately the provisioning of eggs.

KEY WORDS: Atlantic salmon · *Salmo salar* · Condition effect · Parasite–host interaction · Sea lice · *Lepeophtheirus salmonis* · *Caligus elongatus*

INTRODUCTION

Parasitism is the most common consumer strategy (Lafferty et al. 2006), and the effect on a host ranges from commensalism, causing negligible, if any, damage, to inevitable host death (parasitoids) (Anderson & May 1978). The indirect effects of parasites are varied, from augmenting the flow of energy in ecosystems, altering the strength of species interactions, changing productivity and causing trophic cascades (Lafferty et al. 2008). In a natural setting, the influence of parasitism on the host is typically confounded with other factors, and may be difficult to identify when populations are at equilibrium (Tompkins et al. 2002). Accordingly, parasite-mediated effects have commonly been revealed through anthropogenic perturbations such as introduction of non-native species (Britton 2013) and spill-over from livestock (Smith et al. 2009).

Ectoparasitic sea lice (Copepoda; Caligidae) are associated with a wide range of marine fish species. Their occurrence on wild salmon has long been

known (Pontoppidan 1755, Calderwood 1905); our understanding of the effect of sea lice infestations on wild salmonid stocks remains debated.

The salmon louse *Lepeophtheirus salmonis* (Krøyer) is a specialist caligid ectoparasite of salmonids in seawater, and infestations of wild Atlantic salmon *Salmo salar* returning to Scotland's north coast show a prevalence of 100%; similarly, the prevalence of the host generalist caligid *Caligus elongatus* (Nordmann) also typically approaches 100% (Todd et al. 2006). Notwithstanding the fact that all return adult wild salmon in Scotland are infested with caligids, it remains likely that recent changes in the dynamics of caligid–wild salmonid interactions have occurred as a consequence of climate change, pollution (MacKinnon 1998, Lafferty & Kuris 1999) and perhaps especially the development since the 1970s of intensive cultivation of Atlantic salmon in coastal open net cages (e.g. Fjørtoft et al. 2017, Ugelvik et al. 2017, Halttunen et al. 2018, Thorstad & Finstad 2018). In contrast to the strong seasonality of return migration of wild adult Atlantic salmon from the open ocean to fresh water, industrial production of salmon now results in high densities of potential host fish resident in coastal waters throughout the year (Torrissen et al. 2013). Caligid infestations continue to present a major husbandry and fish health challenge to the salmon aquaculture industry (Hall & Murray 2018), and fjords and sea lochs in the vicinity of salmon farms tend to be subject to increased densities of the planktonic and infective sea lice life stages (e.g. McKibben & Hay 2004, Penston et al. 2011, Harte et al. 2017); this can increase infestation pressure both for local farmed (Jansen et al. 2012) and wild salmonid stocks (e.g. Tully & Nolan 2002). Springtime (April–June) is a season of particular concern to managers of wild stocks of Atlantic salmon and sea trout because this is the out-migration period for the juvenile smolts (Thorstad et al. 2015). The small size of Atlantic salmon and sea trout smolts (9–19 cm) renders these fish vulnerable to physiological stress from sea lice infestation whilst also undergoing osmotic adaptation to seawater (Wells et al. 2006). The sea lice infestation pressure in coastal areas is likely elevated in spring, as a result of the build-up of the run of wild adult salmon returning from the open ocean (Jackson et al. 1997). In addition, the metabolic rate and fecundity of gravid female sea lice both are elevated in springtime due to increasing water temperatures (Johnson & Albright 1991). Wild smolts may therefore encounter relatively high sea lice infestation pressures whilst migrating outward into offshore waters (e.g. Revie et al. 2009, Halttunen et al. 2018).

The pathophysiological effects of parasites on the host fish largely depend on host size and immunological status, but also will vary according to the infestation intensity, and size and metabolic demand of the parasite (determined by ambient conditions, parasite species, developmental stage, sex and origin [i.e. farm or wild]; Ugelvik et al. 2017). In the specific case of caligid copepods infesting salmonids, the pre-adult and adult stages (which are mobile across the body surface of the host fish) are more virulent than are the sessile larval (chalimus) stages (Finstad et al. 2000). Laboratory infestation with *L. salmonis* can elicit non-lethal physiological effects in salmonids which — at high intensities — can be lethal. Reported responses range from increased physiological stress (Atlantic salmon: Finstad et al. 2000) to reductions in growth rate, survival and body condition (Arctic charr *Salvelinus alpinus*: Tveiten et al. 2010). Salmon lice infestation can also decrease host swimming performance (Atlantic salmon: Wagner et al. 2008, Bui et al. 2016) and compromise their foraging ability (sockeye salmon *Oncorhynchus nerka*: Godwin et al. 2015). Unsurprisingly, somatic growth in wild sockeye salmon smolts is associated with sea louse infestation (Godwin et al. 2017). Other proximate effects include possible compromise of disease resistance (sea trout *Salmo trutta*: Bjørn & Finstad 1997, Wells et al. 2007) and elevated vulnerability to predation (pink salmon *O. gorbuscha*: Peacock et al. 2015).

Population abundance indices of Scottish and Norwegian salmon stocks have declined particularly in areas with high salmon farm densities (and thus potentially high caligid infestation rates), but such correlative observations do not necessarily prove a cause–effect relationship (Vøllestad et al. 2009). A correlation between stress levels and caligid infestation has been reported for wild sea trout in Norway (Bjørn et al. 2001), and smolt survival rate of sea trout increased 2-fold for fish medicinally treated against sea lice before release to the natural environment (Skaala et al. 2014). In field trials using cultured Atlantic salmon smolts, survival to return as adults was also overall higher for anti-parasite treated fish (Krkošek et al. 2012, Vollset et al. 2016). In this natural setting (as opposed to laboratory), sea lice also had non-lethal effects on the host fish: for example, medicinal treatment of released salmon smolts increased the weight of adults returning to fresh water after 1 winter at sea (so-called 1 sea-winter [1SW] adults) by 123 g (95% CI: 45–200 g; Vollset et al. 2016). However, neither mean length nor weight of fish returning after multiple sea-winters (MSW) was affected by treatment. Furthermore, untreated con-

trol smolts tended to stay at sea longer and to return as MSW adults, indicating the possibility of a sea lice-mediated delay in maturation (Vollset et al. 2014). In this context, it should not be overlooked that hatchery-reared smolts, like those used in these experiments, typically perform poorly in the natural environment in comparison to wild smolts, because of differences in their feeding behaviour, predator avoidance, migratory behaviour (Jonsson et al. 2003, Skilbrei & Wennevik 2006) and possibly also their tolerance of sea lice. Furthermore, these treatment–release–recapture studies are restricted to an assessment of sea lice impacts on smolts during their outward migration, because prophylactic treatment against infestation is effective only for 1 to 2 mo following application.

While mortality has classically been regarded as the primary mechanism behind parasite effects, there is growing consensus that trait-mediated effects on the host (direct) (as well as non-host species [indirect]) are similarly or more important for community structure and function (Ohgushi et al. 2012). Non-lethal consequences of sea lice infestation including physiological stress, and reduced growth rate and somatic condition (Finstad et al. 2000, Tveiten et al. 2010, Øverli et al. 2014) all can lead to shifts in age at maturation (Vollset et al. 2014), reduced adult fecundity (Burton et al. 2013b) and a potential impairment both of progeny size and early freshwater survival (Todd et al. 2012, Burton et al. 2013a). Here, we aimed to assess possible non-lethal effects that might influence individual host growth, somatic condition and hence ultimately individual quality and reproductive potential of Atlantic salmon. Morphometric body condition (weight at length) of return adult Atlantic salmon is strongly associated with lipid stores accreted during the marine phase (Todd et al. 2008) and presumably individual survival during river ascent and fecundity. The primary aim of the present study was to assess whether sea lice infestation intensity and parasite life stage composition is associated with somatic condition of adult wild Atlantic salmon that had survived to return to coastal waters.

MATERIALS AND METHODS

Data collection

Infestation and host trait data were collated for Atlantic salmon caught in commercial net fisheries at Strathy Point (SP; North Scotland, 58° 36′ N, 04° 00′ W) and River North Esk (NE; East Scotland,

56° 45′ N, 02° 26′ W), and from monitoring of a trap weir in the River Tamar (TA; South England, 50° 31′ N, 04° 12′ W) (Environment Agency 2004, Murray & Simpson 2006, Todd et al. 2006). The salinity levels in the 3 catchments ranged from fully saline (ca. 35 ppt, SP) through brackish (ca. 5–25 ppt, NE) to fresh water (ca. 0–5 ppt, TA). All catchments were remote from aquaculture facilities, with SP being almost 40 km in a straight line over land from the nearest farm.

Salmon sampled from the coastal fishery at SP were destined for several rivers across Britain (Shearer 1986), and possibly at their first migratory landfall. Wild maiden 1SW (n = 491, no MSW sampled) trapped in bag nets set at SP within approximately 100 m of the shoreline were examined between June and July of each year (1999–2007) (Todd et al. 2006). Sex was ascribed from external observation for 251 individuals (2003–2007). No information on smolt age was available for SP. At NE, sea lice data were available for 1176 1SW and 922 MSW fish caught using a sweep net and coble between May and August (2001–2003) (Murray & Simpson 2006). Similar data were collated for 2583 1SW and 1150 MSW salmon trapped at the Gunnislake weir (TA) between March and November in 2004–2005, 2008–2013 and 2015–2016 (for details, see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m606p091_supp.pdf; all Supplement files for this article are located at this URL). The sampling gear at all 3 field locations was non-selective; all adult salmon that were intercepted would have been captured.

For the NE and TA data, no distinction was made between the 2 endemic parasite species (*Lepeophtheirus salmonis* and *Caligus elongatus*) during sampling. Thus, to maintain analytical consistency between all 3 sites, both species were combined for analysis. During sampling, living (TA) or dead (SP and NE) fish were inspected by eye, and only mobile lice (pre-adult and adult stages) were enumerated. Because the impact on host physiology from the smaller (and very rarely observed) chalimus stages is low (Finstad et al. 2000), these developmental stages were ignored. At SP, mobile lice were further classified (to species, sex and developmental stage) using a microscope. This enabled us to determine how the effect of infestation on host condition varied according to the proportion of adult female *L. salmonis*, which — due to their size and metabolic demand for egg production — is potentially the most virulent stage. The number of sea lice a host can accommodate will depend on its surface area, hence its weight. Thus, assuming that the effect from *n* mobile sea lice on a host is best described as a function of

host weight, we used sea lice density D (mobile lice kg^{-1}) as a comparative measure of infestation.

Body condition index K

Atlantic salmon routinely sampled by fisheries research staff were used to determine the length (l) to weight (w) relationship (LWR, regression of log$_{10}$-transformed w and l). Prior to any analysis, fish missing relevant information (i.e. w or l), farm escapees or repeat spawners (both identified by scale reading) were discarded. One individual with a Fulton's condition factor of 0.1 (indicating measurement error) was also removed. This left 491 1SW from SP (1999–2007), 3680 1SW and 2024 MSW from NE (2001–2003) and 3750 1SW and 1707 MSW from TA (2003–2013, 2015, 2016) (Table S2 in Supplement 1). LWR coefficients (intercept β_0, slope β_1) were estimated for each sea age class separately.

Each LWR was used to derive the expected standard weight w_s (regression line) at any given l for each sample:

$$\log(w_s) \ = \ \beta_0 + \beta_1 \log(l) \tag{1}$$

The deviation of log-transformed w_i in any individual i from the regression line (w_s for i; $w_{s,i}$) — i.e. the residual of the LWR — was used as body condition index K in the present work (see Fig. S1 in Supplement 2):

$$K_i \ = \ \log(w_i) - \log(w_{s,i}) \tag{2}$$

K was the dependent variable in all analyses. It was strongly correlated with other morphometric condition indices including Fulton's index ($R^2 > 0.95$) and relative mass index ($R^2 > 0.98$). K was not correlated with l, and was assumed to provide a reliable proxy for individual condition (Supplement 2).

Sea-age determination (NE and TA)

Sea age (a) may well influence possible effects of sea lice infestation on host K (Vollset et al. 2014). For fish of unknown a, sea age was estimated using a 2-component (1SW and MSW) Gaussian mixture model (R-package 'flexmix' v.2.3-13, Grün & Leisch 2008); 2SW and 3SW fish from each site were compiled into a single category (MSW). A comparison between modelled and known (scale reading) a values validated the models to a precision of >98% (NE) and >95% (TA) (see Table S3 & Figs. S2–S4 in Supplement 3).

Model specification

The sampling location (marine coastal [SP] versus estuary [NE] versus freshwater [TA]), capture methods (static bag nets [SP] versus sweep nets [NE] versus the fixed trap [TA]) differed between catchments. This could introduce a catchment-specific bias in the data. In particular, it should be noted that sea lice density (D) estimates were not comparable between sites (Fig. S9 in Supplement 5), likely because the capture method and location (salinity) affected how many lice were lost in the process. Thus comparisons between catchments were inappropriate, and each catchment was analysed separately.

Throughout the analysis, only predictors with strong biological reasoning (based on *a priori* investigations or literature) were included from the outset to prevent overparameterisation (Burnham & Anderson 2002).

Strathy Point

Data for the parasite life stage and species were available for all 491 1SW fish at SP. This enabled assessment for this site of a potential effect of predictors D, parasite life stage composition (proportion of female adult *Lepeophtheirus salmonis*) θ, y and s (for 251/491 fish). To assess the influence of θ, we used values representative of our sample: 0.115, 0.4 and 0.745 corresponding to the 2.5th, 50th and 97.5th percentiles of θ observed at SP. Both continuous variables D and θ were scaled (SD = 1, mean = 0) prior to analysis. We used a linear mixed effects model with y as a random variable (random intercepts and slopes of θ [slopes of D resulted in model singularity]) to determine the effect on K (see Table S4 in Supplement 4).

North Esk

No 1SW fish were captured in April, and for the MSW stock component none were captured in April 2001. We therefore combined the months April and May in order to use the whole sample. We used a linear model to determine the effects of D and factors y, m and s on K (Table S5 in Supplement 4).

Tamar

To avoid erroneous pooling of sampling years, the data were restricted to the main run of each sea age

group. These comprised the months March to November (MSW) and June to November (1SW) each year. Fish trapped outside this period (151/2734 1SW and 42/1192 MSW) were discarded. Due to unbalanced data, we first introduced a new time parameter, 'season' (t), to reduce the temporal resolution for each y: these were, respectively, March to end of May ($t = 1$, MSW only), June and July ($t = 2$), August and September ($t = 3$) and October and November ($t = 4$). These non-overlapping seasonal components were chosen because they incorporate the returning cohort within a particular spawning season, and each component comprised sufficient numbers (at least 30) of 1SW or MSW of each sex (Table S2 in Supplement 1). Overall, 2583 1SW and 1150 MSW salmon from TA with known D and factors y, t, s were analysed separately. Here we treated y as a random variable (random intercepts only, as random slopes caused model singularity), with t being nested within y (Tables S6 & S7 in Supplement 4).

Model selection and inference

For each catchment, a full model containing all reasonable predictors (SP: D, y and θ; NE: D, m, y and s; TA: D, t, y, s and a) and reasonable 2-way interaction terms permitted by sample size, was fitted (Tables S4–S7 in Supplement 4). An information theoretic (IT)

approach was used to identify the best set of competing models via Akaike's information criterion corrected for small sample sizes (AICc; 'dredge' in the R package MuMIn; Barton 2018). We considered models with an AICc deviating <4 from the lowest AICc as our 'top model set' for each catchment. Inferences were made based on weighted support from all top set models by model averaging (Grueber et al. 2011).

Mixed effects linear models (SP and TA) were fitted in the R-package lme4 (Bates et al. 2015). The merTools package in R (Knowles & Frederick 2016) was used to calculate 95% prediction intervals (function 'predictInterval'). Median K values and 95% confidence intervals were obtained by means of a parametric bootstrap (function 'bootMer'; 10 000 iterations), which is the gold-standard approach in mixed models (Knowles & Frederick 2016). Conditional R^2 (interpreted as variance explained by both fixed and random effects) was determined using the function 'rsquaredGLMM' from the R-package MuMIn (Barton 2018). An overview of parameters is given in Table 1.

Sampling bias and stochasticity

Measurements of l and w in TA were recorded to a precision of 1 mm and 10 g respectively, so that measurement error here was considered negligible.

Table 1. Abbreviations and explanations of parameters used in the present work. 1SW: 1 sea-winter; MSW: multiple sea-winters; TA: River Tamar; NE: River North Esk; SP: Strathy Point

Abbreviation	Parameter
w	Whole fish mass in kg
l	Fork length in cm
s	Sex of fish
w_s	Standard or expected fish mass in kg at any l given $l \sim w$ relationship (LWR)
K	Body condition index applied in analysis (residuals from LWR)
a	Sea age (1SW or MSW): number of years spent at sea
r	Smolt age: number of years spent as juvenile in fresh water
d	Day of the year (0–365)
t	Season parameter (TA only) covering the salmon run (March–November): March–May ($t = 1$, MSW only); June–July ($t = 2$); August–September ($t = 3$); October–November ($t = 4$)
m	Month (NE only): April–May (4/5); June (6); July (7) and August (8)
y	Year
D	Individual infestation density, i.e. mobile sea lice kg^{-1} host
θ	Proportion of female adult *Lepeophtheirus salmonis* in relation to total abundance of mobile sea lice on a host (SP only)
β_0	Intercept of log-log transformed LWR: −5.02 (SP 1SW); −5.36 & −5.48 (NE 1SW & MSW, respectively); −4.47 & −4.69 (TA 1SW & MSW, respectively)
β_1	Slope of log-log transformed LWR: 3.02 (SP 1SW); 3.23 & 3.28 (NE 1SW & MSW, respectively); 2.72 & 2.85 (TA 1SW & MSW, respectively)
M	Effect of sea lice on individual w in percent

In contrast, the SP and NE measurements of l were rounded down at 4 mm precision, and w was recorded to a precision of 50 g. Here we bootstrapped our data to appraise how this precision error propagates to influence our results. The following procedure was iterated 1000 times for SP and NE each. For each of n individual fish i, we randomly drew 1 l and w pair from uniform distributions $U(l_i, l_i + 0.4\ \mathrm{cm})$ and $U(w_i - 0.025, w_i + 0.025\ \mathrm{kg})$, respectively. This resulted in a new LWR for each catchment:

$$\log(w_{s1:n}) = \beta_0 + \beta_1 \log(l_{1:n}) \qquad (3)$$

and accordingly new K values:

$$K_{1:n} = \log(w_{1:n}) - \log(w_{s1:n}) \qquad (4)$$

The full model for SP and NE (Tables S4 & S5, respectively, in Supplement 4) was updated using the new set of K values as the response variable and the top set of models was determined (AICc difference <4). Weighted model average (see above) was used to assess the parasite-mediated effect on condition by simulating host condition using 2 infestation scenarios: (1) actual infestation levels $D_{1:n}$ resulting in condition parameter $K_{p1:n}$ and (2) zero infestation ($D_{1:n} = 0$) resulting in $K_{01:n}$. Given the 1000 iterations, this resulted in 1000 K_p and K_0 values for each individual fish. For TA (negligible measurement error), 1000 K_p and K_0 values per fish were simply simulated using the same LWR (and thus same top model set).

For each catchment and individual i, the sea lice-mediated condition effect, $E_{i1:1000}$, was expressed as the difference between $K_{0i1:1000}$ and $K_{pi1:1000}$. Thus, a positive E_i corresponded to an increase in K_i if infestation was 0. However, because K (and accordingly E) is merely a dimensionless measure of weight at given length, the effect of the observed infestation levels was demonstrable as the percentage gain (termed G_i) in individual w_i if infestation was 0. Expected weight at 0 infestation (w_{0i}) was obtained by 'adding' each predicted change in condition $E_{i1:1000}$ (log$_{10}$-scale) to the observed $w_{i1:1000}$ (linear scale):

$$w_{0i1:1000} = w_{i1:1000}\, 10^{E_{i1:1000}} \qquad (5)$$

$G_{i1:1000}$ was then given as:

$$G_{i1:1000} = 100\ \frac{w_{0i1:1000}}{w_{i1:1000}} - 100 \qquad (6)$$

For each individual fish, the median of $G_{i1:1000}$ (termed M_i) was used as a point estimate to quantify the lice-mediated effect (percentage mass gain) on K in each catchment.

RESULTS

Strathy Point

The influence of host sex s (allocated for a subset of n = 251/491 fish) on the parasite-mediated condition-effect (i.e. on the slope) was relatively unimportant: the interaction terms $s{:}D$ and $s{:}\theta$ were retained only in 5/13 and 4/13 models from the top model set (not shown). Thus the main analysis was undertaken without s in order to use the entire sample of 491 fish. No information on smolt age of SP fish was available for inclusion in the models.

The model set used to predict the condition-effect of infestation D in salmon from SP contained 3 models, all of which retained covariate D (Table 2). These models explained about 45% of the variance in the data (conditional R^2). No data points were eminently influential (all Cook's distances below 0.05; see Fig. S5 in Supplement 4).

Sea lice density D was associated with host condition K, and its effect increased with the proportion of adult female *Lepeophtheirus salmonis* (Fig. 1, and see Table S4 in Supplement 4). Simulating infestation removal ($D = 0$) for the SP 1SW sample resulted in a predicted mass increase M of median 3.7% (95% CI: 3.5–3.9%; Fig. 2), corresponding to 85 g (95% CI: 80–90 g). The SP top model set explained a large proportion of the variation (45%) in host condition (Table 2).

North Esk

The estimated effect of infestation on host condition was not influenced by smolt age r (allocated for a

Table 2. Top model set (ΔAICc < 4, n = 3) with potential fixed (D, θ and $D{:}\theta$) and random (y) effects used to predict the influence of sea lice density D on condition in 1 sea-winter Atlantic salmon from Strathy Point

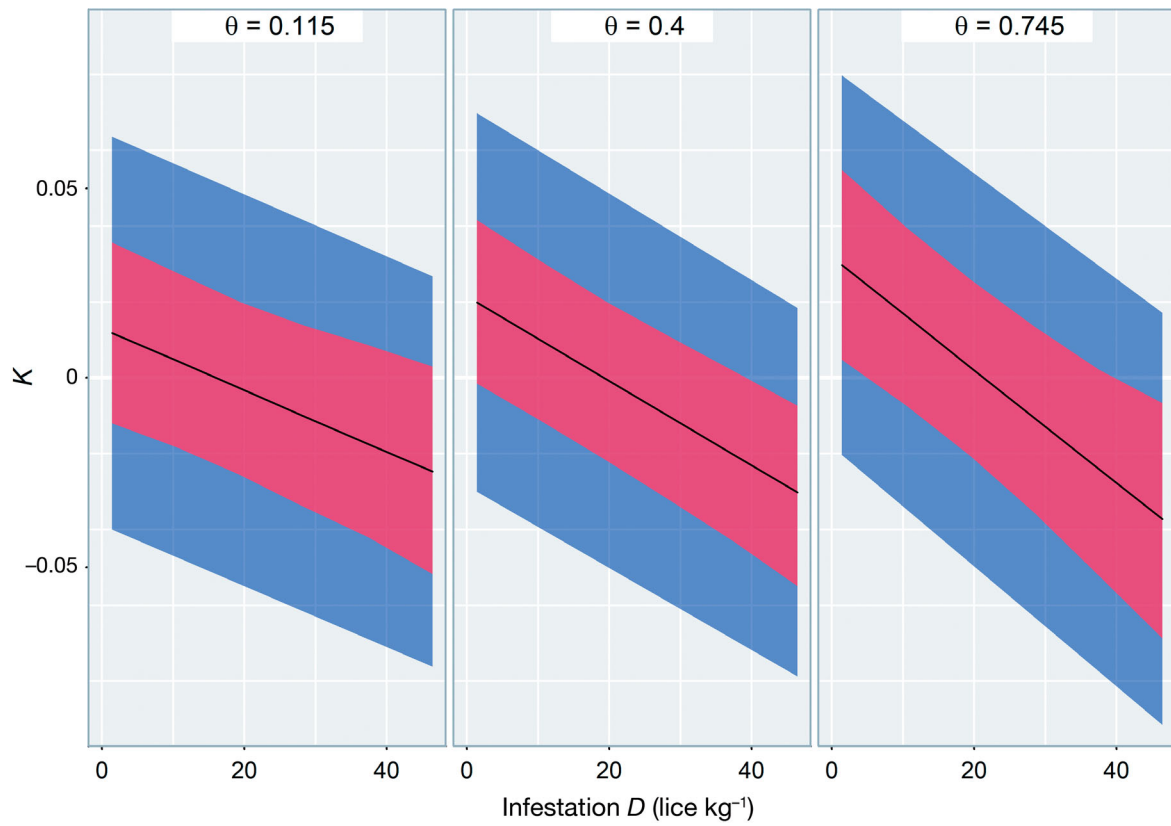| Intercept	D	θ	$D{:}\theta$	df	LogLik	AICc	Delta	Weight	R^2
0.003776	−0.011160	0.002961	−0.003436	8	912.96	−1809.6	0	0.5	0.459
0.003942	−0.009786			6	910.41	−1808.7	0.98	0.31	0.446
0.003890	−0.009745	0.003236		7	910.98	−1807.7	1.90	0.19	0.455

Fig. 1. Relationship between individual condition index K and sea lice infestation density D for Strathy Point 1 sea-winter Atlantic salmon given 3 representative values (0.115, 0.4 and 0.745) of female adult *Lepeophtheirus salmonis* proportion θ. Predicted K is depicted as solid black regression lines with 95% CI (purple area) and 95% prediction intervals (blue area)

subset of 2054/2098 fish). Thus the analysis was carried out without r using all 2098 fish. Furthermore, the effect of sea age a was relatively unimportant (retained only in 1/5 top set models) and was thus ignored during analysis to prevent 0 or low sample size in certain month–year combinations. The models explained 9.7% of the variance in the data (Table 3). No data points were eminently influential (all Cook's distances below 0.05; see Fig. S6 in Supplement 4)

The determined sea louse effect on condition increased from April/May to August, and over the period 2001 to 2003, and was essentially equal for both sexes (Fig. 3; and see Table S5 in Supplement 4). In the NE sample, simulating sea lice removal resulted in a median mass gain M of 0.46% (95% CI: 0.37–0.56%) for male and 0.33% (95% CI: 0.25–0.42%) for female fish (Fig. 4). This corresponded to an increase in weight of 14 g (95% CI: 12–17 g) for males and 9 g (95% CI: 7–12 g) for females.
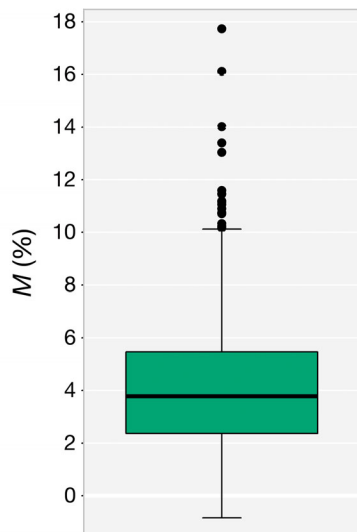

Fig. 2. Predicted increase in whole mass in percent M for sampled 1 sea-winter Atlantic salmon at Strathy Point if sea lice infestation is analytically removed (i.e. $D = 0$). The box covers the inter-quartile range (IQR) (25th to 75th percentile) with the median shown as black bar within the box, and the whiskers extend to 1.5× IQR below or above the 25th or 75th percentile, respectively (default in R). Black dots are outliers

Table 3. Top model set (ΔAICc < 4, n = 2) with potential covariates (*D*, *m*, *s*, *y*, *D:m*, *D:s*, *D:y* and *m:y*) used to predict the influence of sea lice density *D* on condition in Atlantic salmon from River North Esk

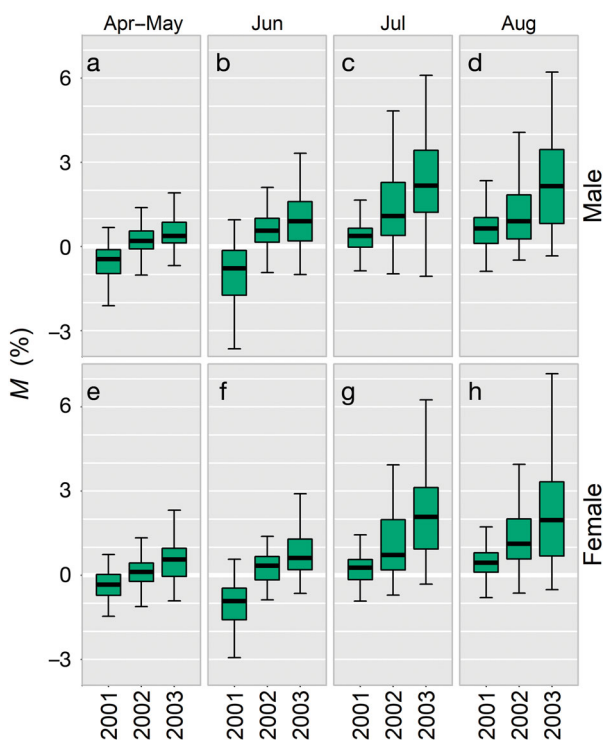| Intercept	*D*	*m*	*s*	*y*	*D:m*	*D:s*	*D:y*	*m:y*	df	LogLik	AICc	Delta	Weight	R²
−0.00834	0.00166	+	+	+	+		+	±	20	4066.4	−8092.5	0	0.714	0.097
−0.00794	0.00148	+	+	+	+	+	+	±	21	4066.5	−8090.7	1.83	0.286	0.097
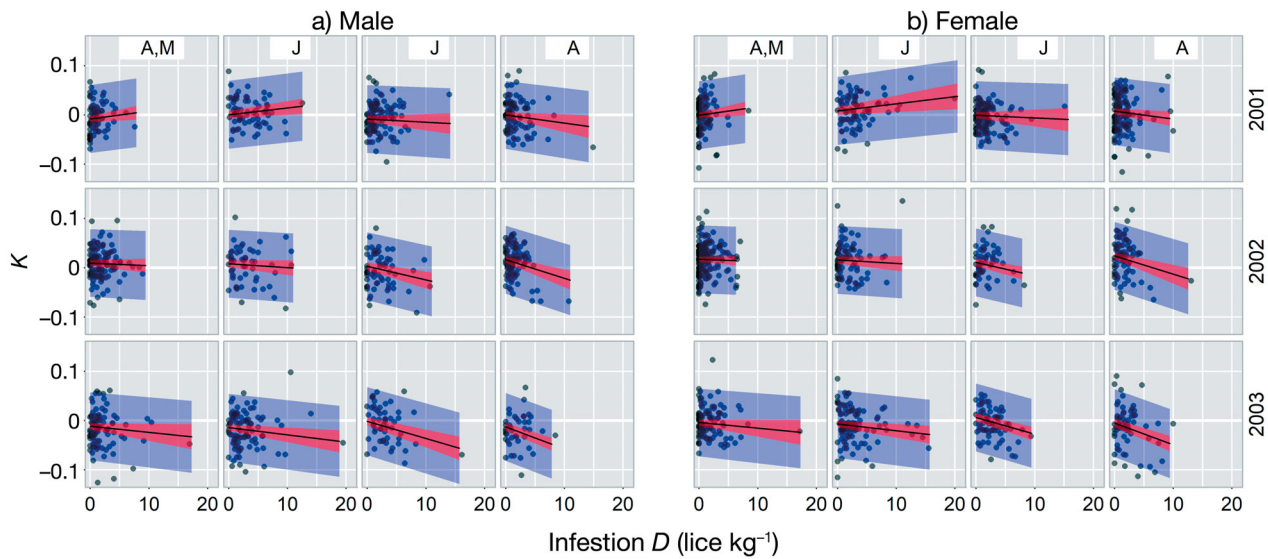
Fig. 3. Relationship between condition *K* and lice density *D* for each sex, month and year-class for North Esk (a) male and (b) female Atlantic salmon, with predicted *K* (black lines), 95% CI (purple area) and 95% prediction intervals (blue area). Details as in Fig. 1. Left to right: A, M: April, May; J: June; J: July; A: August

Fig. 4. Predicted mass gain percentage (*M*) for (a–d) male and (e–h) female Atlantic salmon sampled at North Esk in April/May–August 2001–2003 if sea lice infestation is analytically removed (i.e. *D* = 0). Boxes and whisker range as in Fig. 2

Tamar

The model set used to predict the effect on somatic condition of infestation *D* in salmon from TA comprised 5 and 3 models for 1SW and MSW, respectively, all of which retained *D*, *s* and *t* as covariates (Tables 4 & 5). These models explained over 20% of the variance in the data (conditional R²). No data points were markedly influential (all Cook's distances below 0.15; and see Figs. S7 & S8 in Supplement 4).

The estimated influence of sea louse infestation on condition was largely unaffected by season *t* or host sex, but tended to be higher for MSW adults (Fig. 5; see Tables S6 & S7 in Supplement 4). For the sampled TA salmon, our model predicted a mass gain *M* of median 0.19% (95% CI: 0.16–0.21%) for 1SW and 0.23% (95% CI: 0.16–0.30%) for MSW salmon (Fig. 6)

Table 4. Top model set (ΔAICc < 4, n = 5) with potential fixed (*D*, *s*, *t*, *D:s*, *D:t* and *s:t*) and random (*y*) effects used to predict the influence of sea lice density *D* on condition in 1 sea-winter Atlantic salmon from River Tamar

Intercept	D	s	t	$D{:}s$	$D{:}t$	$s{:}t$	df	LogLik	AICc	Delta	Weight	R^2
−0.00407	−0.00128	+	+				8	4735.103	−9454.1	0	0.451	0.227
−0.00102	−0.00127	+	+			+	10	4736.43	−9452.8	1.37	0.227	0.228
−0.00413	−0.00124	+	+	+			9	4735.107	−9452.1	2	0.166	0.227
−0.00103	−0.00127	+	+	+		+	11	4736.431	−9450.8	3.39	0.083	0.228
−0.0035	−0.00165	+	+		+		10	4735.298	−9450.5	3.64	0.073	0.227

Table 5. Top model set (ΔAICc < 4, n = 3) with potential fixed (*D*, *s*, *t*, *D:s*, *D:t* and *s:t*) and random (*y*) effects used to predict the influence of sea lice density *D* on condition in multiple sea-winter Atlantic salmon from River Tamar

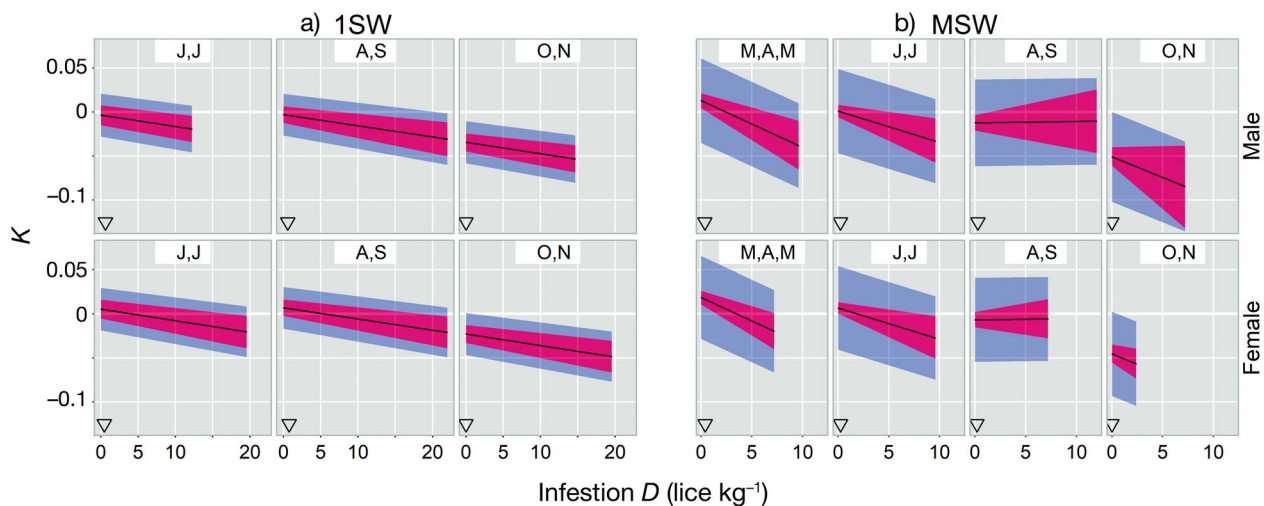| Intercept	D	s	t	$D{:}s$	$D{:}t$	$s{:}t$	df	LogLik	AICc	Delta	Weight	R^2
0.01361	−0.00579	+	+		+		12	2194.057	−4363.8	0	0.607	0.209
0.01362	−0.00581	+	+	+	+		13	2194.057	−4361.8	2.05	0.218	0.208
0.01119	−0.00316	+	+				9	2189.753	−4361.3	2.49	0.175	0.211

Fig. 5. Relationship between condition factor *K* and lice density *D* for male (top row) and female (bottom row) (a) 1 sea-winter (1SW) and (b) multiple sea-winter (MSW) Tamar Atlantic salmon in relation to season *t* (J,J: June, July; A,S: August, September; O,N: October, November; M,A,M: March, April, May). Details as in Fig. 1

if infestation was removed. This corresponded to an increase in predicted weight of 4.6 g (95% CI: 4.0–5.3 g) for 1SW fish and 10.7 g (95% CI: 7.8–13.7 g) for MSW salmon.

DISCUSSION

All returning adult 1SW salmon sampled at SP carry mobile sea lice (Todd et al. 2006). This demonstrates the exceptional capacity of these parasites to locate and infest their host. Nonetheless, the proximate impact of caligid ectoparasitic load on individ-

ual salmon remains the subject of debate. Previous work at SP did not find salmon condition (Fulton's *K* or relative mass index W_R) to be associated with abundance (sea lice fish^{-1}) of the 2 parasite species pooled, or of *Lepeophtheirus salmonis* alone (Todd et al. 2006). Murray & Simpson (2006) previously analysed the River North Esk sea lice infestation patterns for the same data set (NE) as in the present work. They compared the weight–length relationships for fish carrying either 0 or >10 sea lice and found no evidence for a significant relationship between sea lice abundance and host condition. However, given a wide host size range (as is the case in our samples),
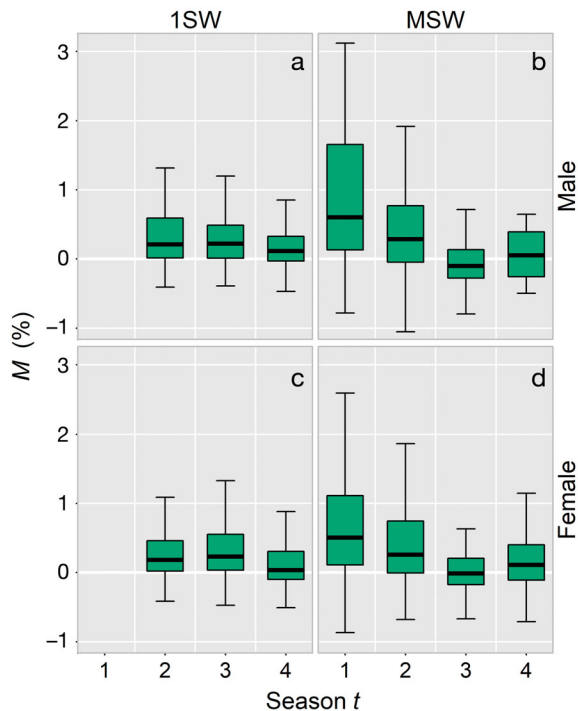
Fig. 6. Predicted mass gain percentage (*M*) for (a,c) 1 sea-winter (1SW) and (b,d) multiple sea-winter (MSW) (a,b) male and (c,d) female Atlantic salmon from River Tamar if sea lice infestation is analytically removed (i.e. *D* = 0). Each column represents a sampling season *t*. Boxes and whisker range as in Fig. 2

parasite abundance is an inaccurate measure for assessing the potential influence of sea lice on a given individual host.

Here we show that sea lice density, rather than abundance, is associated with the somatic condition of wild Atlantic salmon. However, this effect was context-dependent. The observed relationship could indicate either a sea lice preference for low-condition hosts, an effect on host condition of parasitic sea lice load, a negative relationship between infestation pressure and food abundance at sea, or perhaps a combination of these. There is, however, no evidence to suggest that wild Atlantic salmon of relatively poor somatic condition (i.e. weight at length) are more susceptible to further sea lice infestation, or that infestation pressure decreases with food abundance. Numerous laboratory investigations and field trials using cultured smolts, on the other hand, have shown that sea lice do cause lethal and non-lethal effects on host salmonids (Finstad et al. 2000, Tveiten et al. 2010, Vollset et al. 2016, Godwin et al. 2017). Thus the likelihood is that the relationships observed here describe a complex sea lice-mediated condition ef-

fect, which is dependent largely upon seasonal date and year of freshwater entry, as well as parasite life stage composition. Taking host mass into consideration, we parameterised host infestation in terms of the mobile sea lice density (lice kg^{-1}) rather than numbers of lice per individual fish. This approach provided a means of assessing whether or not the cost of parasite load is host context-dependent. As a result, and from independent data for 3 sites in the UK, we likely could show an overall detrimental effect of mobile sea lice (*L. salmonis* and *Caligus elongatus* pooled) on host condition in wild Atlantic salmon returning to Scotland and England.

The determined effect of infestation *D* on *K* was clearer at SP, whereby there was lower variation in *K* and relatively evenly dispersed values observed for *D* (Figs. 1, 3 & 5). The SP final model explained 45% of the variation in the data (Table 2) and predicted a median mass increase of 3.7% (95% CI: 3.5–3.9%) for 1SW fish (Fig. 2) if sea lice were removed. This corresponded to a mass gain of 85 g (95% CI: 80–90 g), which concurs well with the reported 123 g (45–200 g) mass loss in 1SW salmon attributable to sea lice infection during outward migration in Norway (Vollset et al. 2016). As expected, an increasing proportion of the relatively large, and more virulent, adult female *L. salmonis* life stage elevated the impact on condition (Fig. 1). One constraint for the SP data is that sex of host fish was available only for a sub-sample of the 1SW adults, and no data were available on smolt age of the sampled fish. Thus, despite the SP observations being more limited, they are important in the present context because they are likely to best represent the true infestation levels of caligid ectoparasites on return-migrant adult Atlantic salmon: the fish were captured in fully marine conditions and remained free-swimming in the capture bag nets. Thus, the inevitable loss of parasites (to an unknown extent) as a result of abrasion during capture (e.g. by sweep-netting at NE), or exposure to reduced salinity in the estuary or subsequently in fresh water (i.e. the in-river weir trap at TA) do not extend to the sample data for SP.

For NE, only 9.7% of the variation in host condition was explained by the final model. The predicted median mass increase was only 0.46% (95% CI: 0.37–0.56%) for male and 0.33% (95% CI: 0.25–0.42%) for female fish (Fig. 4), corresponding to increases of 14 g (95% CI: 12–17 g) and 9 g (95% CI: 7–12 g), respectively. This impact increased from 2001 to 2003, and from May to August of each year (Fig. 3). Accordingly, only fish returning in July and August tended to be impacted by infestation. Diffe-

rences in infestation or susceptibility among the differing sea age stock components at NE could explain this variation, or this could reflect the higher summer seawater temperatures and their influences on caligid metabolism (Tully 1992, Heuch et al. 2000). Thus, individuals returning late in the summer season (August) may have been exposed for longer to conditions of increased parasite mobility and virulence, and this may be manifest as an increased impact on host somatic condition.

The final models for TA explained 23 and 21% of data variation (conditional R^2 considering both fixed and random effects; Nakagawa & Schielzeth 2013) for 1SW and MSW adults, respectively (Tables 4 & 5). The predicted median mass gain was 0.19% (95% CI: 0.16–0.21%) for 1SW and 0.23% (95% CI: 0.16–0.30%) for MSW salmon (Fig. 6), corresponding to increases of 4.6 g (95% CI: 4.0–5.3 g) and 10.7 g (95% CI: 7.8–13.7 g) respectively. By contrast to NE, the parasite-mediated effect on somatic condition (i.e. slope) tended to be higher in MSW and unaffected by season t (Fig. 5).

In the present context, direct comparisons between the 3 sampling sites are difficult to draw because of the different capture methods (bag net, SP; beach seine net, NE; fixed weir trap, TA) and sampling environments (marine, SP; brackish, NE; freshwater, TA). Indeed, overall observed sea lice density differed between the 3 sites accordingly (Fig. S9). Furthermore, the influence of sea lice impacts on the host fish will quite probably depend upon other interdependent factors prevailing at sea (e.g. marine prey and predator abundance, which will vary spatially and temporally; Vollset et al. 2016) which may therefore differentially impact upon populations and sea-age groups. However, our multi-site analysis does provide an insight into the relative dynamics of sea louse effects on somatic condition of individual salmon. Whilst the results obtained for NE and TA salmon should be interpreted tentatively, they can be viewed as complementing the analysis of SP 1SW salmon by providing insight in the potential influence of additional host parameters including the seasonal timing of migratory return, sea age, smolt age and sex.

The overall impact of sea lice on host condition varied with time (month, season or year) and parasite life stage composition (θ), but was independent of host sea age or sex. Smolt age at river emigration was not associated with condition. Nonetheless, the described impact engendered by mobile sea lice stages on wild salmonid condition is in accord with previous laboratory findings (e.g. Arctic charr: Tveiten et al.

2010). Even though the modelled lice density effect showed similarity across all 3 catchments, there were important discrepancies in the variance explained by each effect model (SP: 45%, NE: 9.7% and TA: >20%) in addition to differences in the predicted mass gain for the sampled fish in the absence of caligids (median of 3.7% [SP] vs. <1% [NE or TA]). Such discrepancies are likely attributable to the differing infestation levels recorded between sites (median D of 13.9 [SP], 1.4 [NE] and 0.4 [TA]) (Fig. S9), which themselves are most likely accountable by the sampling locale (marine, estuarine, in-river) and differences in capture method (bag net, seine net, weir) for the 3 sites. The severity of the introduced bias in observed parasite levels and its effect on the analysis are unknown.

We emphasize that the putative somatic condition effect on returning adults is likely an underestimate for the population throughout the marine phase, and perhaps especially so for the early post-smolt stage, which is a critical period of high marine mortality in the salmon life cycle (Thorstad et al. 2012). It must be stressed that, by definition, sampling of only the successfully returning adults precludes investigation of the large majority of each emigrant smolt cohort. The condition of returning adults is not necessarily representative of the entire population, because no comparative information is available for non-survivors earlier in the post-smolt phase. A further concern is posed by a possible bias caused by condition-dependent survival of salmon during the marine phase: highly infested hosts in relatively low or poor somatic condition may be more likely to die at sea and therefore effectively become unavailable for sampling. Thus, over successive years, one might record an apparent increase in condition of returning adults within a given population, simply reflecting an increasing proportion of (poor condition) individuals within the population dying unobserved at an earlier stage in the marine phase. In addition, it will be important for future studies to determine whether the reported contrasting sea lice density effect on condition as salmon travel north to south (e.g. SP to NE and TA) is in fact masking a survival effect, with salmon with lowered condition being more likely to die along the coastline journey.

Irrespective of sea lice-induced mortality of post-smolt Atlantic salmon prior to their migratory return to coastal waters (and therefore their availability to be sampled), the magnitude of the observed parasite effect on host condition that we report for SP does present some cause for concern in the management of wild salmon populations (Susdorf et al. 2018). The

3.7% reduction in adult body mass attributable to sea lice that we found for SP might appear superficially to be rather trivial, but this should be more fully considered in relation to the corresponding and disproportionate reduction in the accreted lipid reserves of individual adults. Previously, Todd et al. (2008) showed marked declines in somatic condition factor for salmon captured at SP and NE between 1997 and 2006. Their conclusion was that the primary driver of the observed time-series decline in somatic condition (weight at length) of 1SW salmon was climate-associated changes in oceanic prey availability. In the present context, however, it is notable that they also found a markedly sigmoid relationship between individual condition factor and lipid reserves. The poorest condition adults they observed were ~30% under-weight for their length and yet their lipid reserves were reduced by as much as ~80%. The implications for salmon population regulation and the management of wild stocks are clear, in that such compromise of individuals' lipid reserves will have marked consequences for egg number and quality (lipoprotein provisioning) of females at spawning (Todd et al. 2008, Burton et al. 2013b). Furthermore, it is important to emphasize that the present study areas are relatively remote from salmon aquaculture sites in Scotland: the nearest salmon farm to a sampling site (SP) has a Euclidean distance overland of almost 40 km, not accounting for hydrodynamics or seaways distance, which is greater than the distance reported for sea lice transport from salmon farms in a Scottish system (Adams et al. 2012, Salama et al. 2016). Thus, the sea lice-condition effect that we report here might be predicted to be yet higher for wild stocks of out-migrating smolts passing through areas with dense salmon farming activity (McKibben & Hay 2004, Penston et al. 2011, Harte et al. 2017).

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