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

4

5 **Running page head:** Sea louse effect on salmon condition

6

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

39

40

INTRODUCTION

41

42 Parasitism is the most common consumer strategy (Lafferty, Dobson & Kuris 2006), and the effect on
43 a host ranges from commensalism – causing negligible, if any, damage – to inevitable host death
44 (parasitoids) (Anderson & May 1978). The indirect effects of parasites are varied from augmenting the
45 flow of energy in ecosystems, altering the strength of species interactions, changing productivity and
46 causing trophic cascades (Lafferty et al. 2008). In a natural setting, the influence of parasitism on the
47 host is typically confounded with other factors, and may be difficult to identify when populations are
48 at equilibrium (Tompkins et al. 2002). Accordingly, parasite-mediated effects have commonly been
49 revealed through anthropogenic perturbations such as introduction of non-native species (Britton
50 2013) and spill-over from livestock (Smith et al. 2009).

51 Ectoparasitic sea lice (Copepoda; Caligidae) are associated with a wide range of marine fish species.
52 Their occurrence on wild salmon has long been known (Pontoppidan 1755, Calderwood 1905); our
53 understanding of the effect of sea lice infestations on wild salmonid stocks remains debated.

54 The salmon louse (*Lepeophtheirus salmonis* (Krøyer)) is a specialist caligid ectoparasite of salmonids
55 in seawater, and infestations of wild Atlantic salmon *Salmo salar* returning to Scotland's north coast
56 show a prevalence of 100%; similarly, the prevalence of the host generalist caligid *Caligus elongatus*
57 (Nordmann) also typically approaches 100% (Todd et al. 2006). Notwithstanding the fact that all return
58 adult wild salmon in Scotland carry caligid infestations, it remains likely that recent changes in the
59 dynamics of caligid-wild salmonid interactions have occurred as a consequence of climate change,
60 pollution (MacKinnon 1998, Lafferty & Kuris 1999), and perhaps especially the development since the
61 1970s of intensive cultivation of Atlantic salmon in coastal open net cages (e.g. Ugelvik et al. 2017,
62 Fjørtoft et al. 2017, Thorstad & Finstad 2018, Halttunen et al. 2018). In contrast to the strong
63 seasonality of return migration of wild adult Atlantic salmon from the open ocean to freshwater,
64 industrial production of salmon now results in high densities of potential host fish resident in coastal
65 waters throughout the year (Torrissen et al. 2013). Caligid infestations continue to present a major

66 husbandry and fish health challenge to the salmon aquaculture industry (Hall & Murray 2018), and
67 fjords and sea lochs in the vicinity of salmon farms tend to be subject to increased densities of the
68 planktonic and infective sea lice life stages (e.g. McKibben & Hay 2004, Penston et al. 2011, Harte et
69 al. 2017)., This can increase infestation pressure both for local farmed (Jansen et al. 2012) and wild
70 salmonid stocks (e.g. Tully & Nolan 2002). Springtime (April-June) is a season of particular concern to
71 managers of wild stocks of Atlantic salmon and sea trout because this is the out-migration period for
72 the juvenile smolts (Thorstad et al. 2015, 2018). The small size of Atlantic salmon and sea trout smolts
73 (9-19cm) renders these fish vulnerable to physiological stress from sea lice infestation whilst also
74 undergoing osmotic adaptation to seawater (Wells et al. 2006). The sea lice infestation pressure in
75 coastal areas is likely elevated in spring, as a result of the build-up of the run of wild adult salmon
76 returning from the open ocean (Jackson et al. 1997). In addition, the metabolic rate and fecundity of
77 gravid female sea lice both are elevated in springtime due to increasing water temperatures (Johnson
78 & Albright 1991). Wild smolts may therefore encounter relatively high sea lice infestation pressures
79 whilst migrating outward into offshore waters (e.g. Revie et al. 2009, Halttunen et al. 2018).

80 The pathophysiological effects of parasites on the host fish largely depend on host size and
81 immunological status, but also will vary according to the infestation intensity, and size and metabolic
82 demand of the parasite (determined by ambient conditions, parasite species, developmental stage,
83 sex and origin (i.e. farm or wild) (Ugelvik et al. 2017)). In the specific case of caligid copepods infesting
84 salmonids, the pre-adult and adult stages (which are mobile across the body surface of the host fish)
85 are more virulent than are the sessile larval (chalimus) stages (Finstad et al. 2000). Laboratory
86 infestation with *L. salmonis* can elicit non-lethal physiological effects in salmonids which – at high
87 intensities – can be lethal. Reported responses range from increased physiological stress (Atlantic
88 salmon: Finstad et al. 2000) to reductions in growth rate, survival and body condition (Arctic charr
89 *Salvelinus alpinus*: Tveiten et al. 2010). Salmon lice infestation also can decrease host swimming
90 performance (Atlantic salmon: Wagner et al. 2008, Bui et al. 2016) and compromise their foraging
91 ability (sockeye salmon *Oncorhynchus nerka*: Godwin et al. 2015). Unsurprisingly, somatic growth in

92 wild sockeye salmon smolts is associated with sea louse infestation (Godwin et al. 2017). Other
93 proximate effects include possible compromise of disease resistance (sea trout *Salmo trutta*: Bjørn &
94 Finstad 1997, Wells et al. 2007) and elevated vulnerability to predation (pink salmon *Oncorhynchus*
95 *gorbuscha*: Peacock et al. 2015).

96 Population abundance indices of Scottish and Norwegian salmon stocks have declined particularly in
97 areas with high salmon farm densities (and thus potentially high caligid infestation rates); but such
98 correlative observations do not necessarily prove a cause-effect relationship (Vøllestad et al. 2009). A
99 correlation between stress levels and caligid infestation has been reported for wild sea trout in
100 Norway (Bjørn et al. 2001), and smolt survival rate of sea trout increased twofold for fish medicinally
101 treated against sea lice before release to the natural environment (Skaala et al. 2014). In field trials
102 using cultured Atlantic salmon smolts, survival to return as adult was also overall higher for anti-
103 parasite treated fish (Krkošek et al. 2012, Vollset et al. 2015). In this natural setting (as opposed to
104 laboratory), sea lice also had non-lethal effects on the host fish: for example, medicinal treatment of
105 released salmon smolts increased the weight of adults returning to freshwater after one winter at sea
106 (so-called one sea-winter (1SW) adults) by 123 g (95%CI: 45-200 g; Vollset et al. 2015). However,
107 neither mean length nor weight of fish returning after multiple sea-winters (MSW) was affected by
108 treatment. Furthermore, untreated control smolts tended to stay longer at sea and to return as MSW
109 adults, indicating the possibility of a sea lice-mediated delay in maturation (Vollset et al. 2014). In this
110 context, it should not be overlooked that hatchery-reared smolts, like those used in these
111 experiments, typically perform poorly in the natural environment in comparison to wild smolts,
112 because of differences in their feeding behaviour, predator avoidance, migratory behaviour (Jonsson
113 et al. 2003, Skilbrei & Wennevik 2006), and possibly also their tolerance of sea lice. Furthermore, these
114 treatment-release-recapture studies are restricted to an assessment of sea lice impacts on smolts
115 during their outward migration, because prophylactic treatment against infestation is effective only
116 for one to two months following application.

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

131 **MATERIALS AND METHODS**

132 Infestation and host trait data were collated for Atlantic salmon caught in commercial net fisheries at
133 Strathy Point (SP; North Scotland, 58°60' N, 04°00' W) and River North Esk (NE; East Scotland, 56°75'
134 N, 02°44' W), and from monitoring of a trap weir in the River Tamar (TA; S England, 50°52' N, -04°21')
135 (Anon 2004, Murray & Simpson 2006, Todd et al. 2006). The salinity levels in the three catchments
136 ranged from fully saline (ca. 35 ppt, SP) through brackish (ca. 5 – 25 ppt, NE) to fresh water (ca. 0 – 5
137 ppt, TA). All catchments were remote from aquaculture facilities, with SP being almost 40 km in a
138 straight line over land from the nearest farm.

139 Salmon sampled from the coastal fishery at SP were destined for several rivers across Britain (Shearer
140 1986), and possibly at their first migratory landfall. 491 wild maiden 1SW (no MSW sampled) trapped
141 in bag nets set at SP within approximately 100 m of the shoreline were examined between June and
142 July of each year (1999-2007) (Todd et al. 2006). Sex was ascribed from external observation for 251
143 individuals (2003-2007). No information on smolt age was available for SP. At NE, sea lice data were
144 available for 1176 1SW and 922 MSW fish caught using a sweep net and coble between May and
145 August (2001-2003) (Murray & Simpson 2006). Similar data were collated for 2583 1SW and 1150
146 MSW salmon trapped at the Gunnislake weir (TA) between March and November in 2004-2005, 2008-
147 2013 and 2015-2016 (see Table S1 (Supplement) for details). The sampling gear at all three field
148 locations is non-selective; all adult salmon that were intercepted would have been captured.

149 For the NE and TA data no distinction was made between the two endemic parasite species
150 (*Lepeophtheirus salmonis* and *Caligus elongatus*) during sampling. Thus, to maintain analytical
151 consistency between all three sites, both species were combined for analysis. During sampling, living
152 (TA) or dead (SP and NE) fish were inspected by eye, and only mobile lice (pre-adult and adult stages)
153 enumerated. Because the impact on host physiology from the smaller (and very rarely observed)
154 chalimus stages is low (Finstad et al. 2000), these developmental stages were ignored. At SP, mobile
155 lice were further classified (to species, sex and developmental stage) using a microscope. This enabled
156 us to determine how the effect of infestation on host condition varied according to the proportion of
157 adult female *L. salmonis*, which – due to their size and metabolic demand for egg production – is
158 potentially the most virulent stage. The number of sea lice a host can accommodate will depend on
159 its surface area, hence its weight. Thus, assuming that the effect from n mobile sea lice on a host is
160 best described as a function of host weight, we used sea lice density D (mobile lice kg^{-1}) as a
161 comparative measure of infestation.

162

163

Body condition index K

164 Atlantic salmon routinely sampled by fisheries research staff were used to determine the length (l) –
165 weight (w) relationship (LWR, regression of \log_{10} -transformed w and l). Prior to any analysis, fish
166 missing relevant information (i.e. w or l), farm escapees or repeat spawners (both identified by scale
167 reading) were discarded. One individual with a Fulton's condition factor of 0.1 (indicating
168 measurement error) was also removed. This left 491 1SW from SP (1999-2007), 3680 1SW and 2024
169 MSW from NE (2001-2003) and 3750 1SW and 1707 MSW from TA (2003-2013, 2015, 2016) (Table
170 S2). LWR coefficients (intercept β_0 , slope β_1) were estimated for each sea age class separately.
171 Each LWR was used to derive the expected standard weight w_s (regression line) at any given l for each
172 sample:

$$173 \quad \log(w_s) = \beta_0 + \beta_1 \log(l) \quad (1)$$

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

$$176 \quad K_i = \log(w_i) - \log(w_{s,i}) \quad (2)$$

177 K was the dependent variable in all analyses. It was strongly correlated with other morphometric
178 condition indices including Fulton's index ($R^2 > 0.95$) and relative mass index ($R^2 > 0.98$). K was not
179 correlated with l , and was assumed to provide a reliable proxy for individual condition (Supplement
180 2).

181

Sea-age determination (NE and TA)

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

187

Model specification

188 The sampling location (marine coastal (SP) *versus* estuary (NE) *versus* freshwater (TA)), capture
189 methods (static bag nets (SP) *versus* sweep nets (NE) *versus* the fixed trap (TA)) differed between
190 catchments. This could introduce a catchment-specific bias in the data. In particular, it should be noted
191 that sea lice density (D) estimates were not comparable between sites (Figure S9) likely because the
192 capture method and location (salinity) affected how many lice were lost in the process. Thus
193 comparisons between catchments were inappropriate, and each catchment was analysed separately.
194 Throughout the analysis, only predictors with strong biological reasoning (based on *a priori*
195 investigations or literature) were included from the outset to prevent overparameterisation
196 (Burnham & Anderson 2002).

197

Strathy Point

198 Data for the parasite life stage and species were available for all 491 1SW fish at SP. This enabled
199 assessment for this site of a potential effect of predictors D , parasite life stage composition
200 (proportion of female adult *L. salmonis*) θ , y and s (for 251/491 fish). To assess the influence of θ , we
201 used values representative of our sample: 0.115, 0.4 and 0.745 corresponding to the 2.5th, 50th and
202 97.5th percentiles of θ observed at SP. Both continuous variables D and θ were scaled ($sd=1$, $mean=0$)
203 prior analysis. We used a linear mixed effects model with y as random variable (random intercepts
204 and slopes of θ (slopes of D resulted in model singularity)) to determine the effect on K (Table S4).

205

North Esk

206 No 1SW fish were captured in April and for the MSW stock component none were captured in April
207 2001. We therefore combined the months April and May in order to utilize the whole sample. We
208 used a linear model to determine the effects of D and factors y , m and s on K (Table S5).

209

Tamar

210 To avoid erroneous pooling of sampling years, the data were restricted to the main run of each sea
211 age group. These comprised the months March to November (MSW) and June to November (1SW)

212 each year. Fish trapped outside this period (151/2734 1SW and 42/1192 MSW) were discarded. Due
213 to unbalanced data we first introduced a new time parameter, “season” (t), to reduce the temporal
214 resolution for each y : these were, respectively, March to end of May ($t = 1$, MSW only), June and July
215 ($t = 2$), August and September ($t = 3$) and October and November ($t = 4$). These non-overlapping
216 seasonal components were chosen because they incorporate the returning cohort within a particular
217 spawning season, and each component comprised sufficient numbers (at least 30) of 1SW or MSW of
218 each sex (Table S2). Overall, 2583 1SW and 1150 MSW salmon from TA with known D and factors y ,
219 t , s were analysed separately. Here we treated y as a random variable (random intercepts only, as
220 random slopes caused model singularity) with t being nested within y (Table S6 & S7).

221

222

Model selection and inference

223 For each catchment, a full model containing all reasonable predictors (SP: D , y and θ ; NE: D , m , y and
224 s ; TA: D , t , y , s and a) and reasonable two-way interaction terms permitted by sample size, was fitted
225 (Table S4-S7). An information theoretic (IT) approach was used to identify the best set of competing
226 models via AICc (dredge in R package MuMIn (Barton 2018)). We considered models with an AICc
227 deviating less than 4 from the lowest AICc as our “top model set” for each catchment. Inferences were
228 made based on weighted support from all top set models by model averaging (Grueber et al. 2011).

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

236 An overview of parameters is given in Table 1.

237

238 **Sampling bias and stochasticity**

239 Measurements of l and w in TA were recorded to a precision of 1 mm and 10 g respectively, so that
240 measurement error here was considered negligible. In contrast, the SP and NE measurements of l
241 were rounded down at 4 mm precision, and w was recorded to a precision of 50 g. Here we
242 bootstrapped our data to appraise how this precision error propagates to influence our results. The
243 following procedure was iterated 1000 times for SP and NE each:

244 for each of n individual fish i we randomly drew one l and w pair from uniform distributions $U(l_i, l_i +$
245 $0.4 \text{ cm})$ and $U(w_i - 0.025, w_i + 0.025 \text{ kg})$ respectively. This resulted in a new LWR for each
246 catchment:

$$247 \log(w_{s_{1:n}}) = \beta_0 + \beta_1 \log(l_{1:n}) \quad (3)$$

248 and accordingly new K values:

$$249 K_{1:n} = \log(w_{1:n}) - \log(w_{s_{1:n}}) \quad (4)$$

250 The full model for SP (Table S4) and NE (Table S5) was updated using the new set of K values as the
251 response variable and the top set of models was determined (AICc difference <4). Weighted model
252 average (see above) was used to assess the parasite-mediated effect on condition by simulating host
253 condition using two infestation scenarios: (i) actual infestation levels $D_{1:n}$ resulting in condition
254 parameter $K_{p_{1:n}}$, and (ii) zero infestation ($D_{1:n} = 0$) resulting in $K_{0_{1:n}}$.

255 Given the 1000 iterations this resulted in 1000 K_p and K_0 values for each individual fish.

256 For TA (negligible measurement error), 1000 K_p and K_0 values per fish were simply simulated using
257 the same LWR (and thus same top model set).

258

259 For each catchment and individual i the sea lice-mediated condition effect, $E_{i:1:1000}$, was expressed as
 260 the difference between $K_{0i:1:1000}$ and $K_{pi:1:1000}$. Thus, a positive E_i corresponded to an increase in K_i
 261 if infestation was zero. However, because K (and accordingly E) is merely a dimensionless measure of
 262 weight at given length, the effect of the observed infestation levels was demonstrable as the
 263 percentage gain (termed G_i) in individual w_i if infestation was zero. Expected weight at zero
 264 infestation (w_{0i}) was obtained by ‘adding’ each predicted change in condition $E_{i:1:1000}$ (log₁₀-scale) to
 265 the observed $w_{i:1:1000}$ (linear scale):

$$266 \quad w_{0i:1:1000} = w_{i:1:1000} 10^{E_{i:1:1000}} \quad (5)$$

267 $G_{i:1:1000}$ was then given as:

$$268 \quad G_{i:1:1000} = 100 \frac{w_{0i:1:1000}}{w_{i:1:1000}} - 100 \quad (6)$$

269 For each individual fish the median of $G_{i:1:1000}$ (termed M_i) was used as point estimate to quantify the
 270 lice-mediated effect (percentage mass gain) on K in each catchment.

271

272 RESULTS

273 Strathy Point

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

279 The model set used to predict the condition-effect of infestation D in salmon from SP contained three
 280 models, all of which retained covariate D (Table 2). These models explained about 45 % variance in
 281 the data (conditional R^2). No data points were eminently influential (all Cook’s distances below 0.05).

282 Sea lice density, D , was associated with host condition K , and its effect increased with the proportion
283 of adult female *Lepeophtheirus salmonis*, θ (Figure 1, Supplement 4). Simulating infestation removal
284 ($D = 0$) for the SP 1SW sample resulted in a predicted mass increase M of median 3.7 % (95%CI: 3.5
285 – 3.9 %) (Figure 2), corresponding to 85 g (95%CI: 80 – 90 g). The SP top model set explained a large
286 proportion of the variation (45 %) in host condition (Table 2).

287 **North Esk**

288 The estimated effect of infestation on host condition was not influenced by smolt age r (allocated for
289 a subset of 2054/2098 fish). Thus the analysis was carried out without r using all 2098 fish.
290 Furthermore, the effect of sea age a was relatively unimportant (retained only in 1/5 top set models)
291 and thus ignored during analysis to prevent zero or low sample size in certain month-year
292 combinations. The models explained 9.7 % variance in the data (Table 3). No data points were
293 eminently influential (all Cook's distances below 0.05)

294

295 The determined sea louse effect on condition increased from April/May to August, and over the period
296 2001 to 2003, and was essentially equal for both sexes (Figure 3). In the NE sample, simulating sea lice
297 removal resulted in a median mass gain M of 0.46 % (95%CI: 0.37 – 0.56 %) for male and 0.33 % (95%CI:
298 0.25 – 0.42 %) for female fish (Figure 4). This corresponded to an increase in weight of 14 g (95%CI: 12
299 – 17 g) for male and 9 g (95%CI: 7 – 12 g) for female salmon.

300 **Tamar**

301 The model set used to predict the effect on somatic condition of infestation D in salmon from TA
302 comprised five and three models for 1SW and MSW respectively, all of which retained D , s and t as
303 covariates (Table 4 & 5). These models explained over 20 % variance in the data (conditional R^2). No
304 data points were markedly influential (all Cook's distances below 0.15).

305 The estimated influence of sea louse infestation on condition was largely unaffected by season t or
306 host sex, but tended to be higher for MSW adults (Figure 5). For the sampled TA salmon, our model
307 predicted a mass gain M of median 0.19 % (95%CI: 0.16 – 0.21 %) for 1SW and 0.23 % (95%CI: 0.16 –
308 0.30 %) for MSW salmon (Figure 6) if infestation was removed. This corresponded to an increase in
309 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
310 salmon.

311

312

313 DISCUSSION

314 All returning adult 1SW salmon sampled at SP carry mobile sea lice (Todd et al. 2006). This
315 demonstrates the exceptional capacity of these parasites to locate and infest their host. Nonetheless,
316 the proximate impact of caligid ectoparasitic load on individual salmon remains the subject of debate.
317 Previous work at SP did not find salmon condition (Fulton's K or relative mass index Wr) to be
318 associated with abundance (sea lice fish⁻¹) of the two parasite species pooled, or of *Lepeophtheirus*
319 *salmonis* alone (Todd et al. 2006). Murray & Simpson (2006) previously analysed the River North Esk
320 sea lice infestation patterns for the same data set (NE) as in the present work. They compared the
321 weight-length relationships for fish carrying either zero or >10 sea lice and found no evidence for a
322 significant relationship between sea lice abundance and host condition. However, given a wide host
323 size range (as is the case in our samples), parasite abundance is an inaccurate measure for assessing
324 the potential influence of sea lice on a given individual host.

325 Here we show that sea lice density, rather than abundance, is associated with the somatic condition
326 of wild Atlantic salmon. However, this effect was context-dependent. The observed relationship could
327 indicate either a sea lice preference for low-condition hosts, an effect on host condition of parasitic

328 sea lice load, a negative relationship between infestation pressure and food abundance at sea, or
329 perhaps a combination of these. There is, however, no evidence to suggest that wild Atlantic salmon
330 of relatively poor somatic condition (i.e. weight at length) are more susceptible to further sea lice
331 infestation, or that infestation pressure decreases with food abundance. Numerous laboratory
332 investigations and field trials using cultured smolts, on the other hand, have shown that sea lice do
333 cause lethal and non-lethal effects on host salmonids (Finstad et al. 2000, Tveiten et al. 2010, Vollset
334 et al. 2015, Godwin et al. 2017). Thus the likelihood is that the presently observed relationships
335 describe a complex sea lice-mediated condition effect, which is dependent largely upon seasonal date
336 and year of freshwater entry, as well as parasite life stage composition. Taking host mass into
337 consideration, we parameterised host infestation in terms of the mobile sea lice density (lice kg⁻¹)
338 rather than numbers of lice per individual fish. This approach provided a means of assessing whether
339 or not the cost of parasite load is host context-dependent. As a result, and from independent data for
340 three sites in the UK, we likely could show an overall detrimental effect of mobile sea lice
341 (*Lepeophtheirus salmonis* and *Caligus elongatus* pooled) on host condition in wild Atlantic salmon
342 returning to Scotland and England.

343 The determined effect of infestation D on K was clearer at SP, whereby there was lower variation in
344 K and relatively evenly dispersed values observed for D (Figures 1, 3 and 5). The SP final model
345 explained 45 % variation in the data (Table 2) and predicted a median mass increase of 3.7 % (95%CI:
346 3.5 – 3.9 %) for 1SW fish (Figure 2) if sea lice were removed. This corresponded to a mass gain of 85 g
347 (95%CI: 80 – 90 g), which concurs well with the reported 123 g (45 – 200 g) mass loss in 1SW salmon
348 attributable to sea lice infection during outward migration in Norway (Vollset et al. 2015). As expected,
349 an increasing proportion of the relatively large, and more virulent, adult female *L. salmonis* life stage
350 elevated the impact on condition (Figure 1). One constraint for the SP data is that sex of host fish was
351 available only for a sub-sample of the 1SW adults, and no data were available on smolt age of the
352 sampled fish. Thus, despite the SP observations being more limited, they are important in the present
353 context because they are likely to best represent the true infestation levels of caligid ectoparasites on

354 return-migrant adult Atlantic salmon: the fish were captured in fully marine conditions and remained
355 free-swimming in the capture bag nets. Thus, the inevitable loss of parasites (to unknown extent) as
356 a result of abrasion during capture (e.g. by sweep-netting at NE), or exposure to reduced salinity in
357 the estuary or subsequently in freshwater (i.e. the in-river weir trap at TA) do not extend to the sample
358 data for SP.

359 For NE, only 9.7 % of the variation in host condition was explained by the final model. The predicted
360 median mass increase was only 0.46 % (95%CI: 0.37 – 0.56 %) for male and 0.33 % (95%CI: 0.25 – 0.42
361 %) for female fish (Figure 4), corresponding to increases of 14 g (95%CI: 12 – 17 g) and 9 g (95%CI: 7 –
362 12 g) respectively. This impact increased from 2001 to 2003, and from May to August of each year
363 (Figure 3). Accordingly, only fish returning in July and August tended to be impacted by infestation.
364 Differences in infestation or susceptibility among the differing sea age stock components at NE could
365 explain this variation, or this could reflect the higher summer seawater temperatures and their
366 influences on caligid metabolism (Tully 1992, Heuch et al. 2000). Thus, individuals returning late in the
367 summer season (August) may have been exposed for longer to conditions of increased parasite
368 mobility and virulence, and this may be manifest as an increased impact on host somatic condition.

369
370 The final models for TA explained 23 and 21 % of data variation (conditional R^2 considering both fixed
371 and random effects (Nakagawa & Schielzeth 2013)) for 1SW and MSW adults respectively (Table 4 &
372 5). The predicted median mass gain was 0.19 % (95%CI: 0.16 – 0.21 %) for 1SW and 0.23 % (95%CI:
373 0.16 – 0.30 %) for MSW salmon (Figure 6), corresponding to increases of 4.6 g (95%CI: 4.0 – 5.3 g) and
374 10.7 g (95%CI: 7.8 – 13.7 g) respectively. By contrast to NE, the parasite-mediated effect on somatic
375 condition (i.e. slope) tended to be higher in MSW and unaffected by season t (Figure 5).

376

377 In the present context, direct comparisons between the three sampling sites are difficult to draw
378 because of the different capture methods (bag net, SP; beach seine net, NE; fixed weir trap, TA) and

379 sampling environments (marine, SP; brackish, NE; freshwater, TA). Indeed overall observed sea lice
380 density differed between the three sites accordingly (Figure S9). Furthermore, the influence of sea lice
381 impacts on the host fish will quite probably depend upon other interdependent factors prevailing at
382 sea (e.g. marine prey and predator abundance, which will vary spatially and temporally) (Vollset et al.
383 2015) which may therefore differentially impact upon populations and sea-age groups. However, our
384 multi-site analysis does provide an insight into the relative dynamics of sea louse effects on somatic
385 condition of individual salmon. Whilst the results obtained for NE and TA salmon should be interpreted
386 tentatively, they can be viewed as complementing the analysis of SP 1SW salmon by providing insight
387 in the potential influence of additional host parameters including the seasonal timing of migratory
388 return, sea age, smolt age and sex.

389

390 The overall impact of sea lice on host condition varied with time (month, season or year) and parasite
391 life stage composition (θ), but was independent of host sea age or sex. Smolt age at river emigration
392 was not associated with condition. None the less, the described impact engendered by mobile sea lice
393 stages on wild salmonid condition is in accord with previous laboratory findings (e.g. Arctic charr:
394 Tveiten et al. 2010). Even though the modelled lice density effect showed similarity across all three
395 catchments, there were important discrepancies in the variance explained by each effect model (45%
396 (SP), 9.7% (NE) and >20% (TA)) in addition to differences in the predicted mass gain for the sampled
397 fish in the absence of caligids (median of 3.7% (SP) vs <1% (NE or TA)). Such discrepancies are likely
398 attributable to the differing infestation levels recorded between sites (median D of 13.9 (SP), 1.4 (NE)
399 and 0.4 (TA)) (Figure S9), which themselves are most likely accountable by the sampling locale (marine,
400 estuarine, in-river) and differences in capture method (bag net, seine net, weir) for the three sites.
401 The severity of the introduced bias in observed parasite levels and its effect on the analysis are
402 unknown.

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

419 Irrespective of sea lice-induced mortality of post-smolt Atlantic salmon prior to their migratory return
420 to coastal waters (and therefore their availability to be sampled), the magnitude of the observed
421 parasite effect on host condition that we report for SP does present some cause for concern in the
422 management of wild salmon populations (Susdorf et al. 2018). The 3.7% reduction in adult body mass
423 attributable to sea lice that we found for SP might appear superficially to be rather trivial, but this
424 should be more fully considered in relation to the corresponding and disproportionate reduction in
425 the accreted lipid reserves of individual adults. Previously, Todd et al. (2008) showed marked declines
426 in somatic condition factor for salmon captured at SP and NE between 1997 and 2006. Their
427 conclusion was that the primary driver of the observed time-series decline in somatic condition
428 (weight at length) of 1SW salmon was climate-associated changes in oceanic prey availability. In the

429 present context, however, it is notable that they also found a markedly sigmoid relationship between
430 individual condition factor and lipid reserves. The poorest condition adults they observed were ~30%
431 under-weight for their length and yet their lipid reserves were reduced by as much as ~80%. The
432 implications for salmon population regulation and the management of wild stocks are clear, in that
433 such compromise of individuals' lipid reserves will have marked consequences for egg number and
434 quality (lipoprotein provisioning) of females at spawning (Todd et al. 2008; Burton et al. 2013b).
435 Furthermore, it is important to emphasize that the present study areas are relatively remote from
436 salmon aquaculture sites in Scotland: the nearest salmon farm to a sampling site (SP) has a Euclidean
437 distance overland of almost 40 km not accounting for hydrodynamics or seaways distance, which is
438 greater than the distance reported for sea lice transport from salmon farms in a Scottish system
439 (Adams 2012; Salama et al. 2016). Thus, the sea lice-condition effect that we report here might be
440 predicted to be yet higher for wild stocks of out-migrating smolts passing through areas with dense
441 salmon farming activity (McKibben & Hay 2004, Penston et al. 2011, Harte et al. 2017).

442

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450 LITERATURE CITED

451 Adams T, Black K, MacIntyre C, MacIntyre I, Dean R (2012) Connectivity modelling and network
452 analysis of sea lice infection in Loch Fyne. *Aquaculture Environment Interactions* 3:51–63

- 453 Anderson RM, May RM (1978) Regulation and stability of host-parasite population interactions: I.
454 Regulatory processes. *The Journal of Animal Ecology*:219–247
- 455 Anon (2004) River Tamar marine index river: summary report of trapping of adult migratory salmonids
456 at Gunnislake during 2003 season. Environment Agency South West Region Cornwall Area,
457 Bodmin
- 458 Barton K (2018) MuMIn: multi-model inference.
- 459 Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal*
460 *of Statistical Software* 67
- 461 Birkeland K (1996) Consequences of premature return by sea trout (*Salmo trutta*) infested with the
462 salmon louse (*Lepeophtheirus salmonis* Krøyer): migration, growth, and mortality. *Canadian*
463 *Journal of Fisheries and Aquatic Sciences* 53:2808–2813
- 464 Bjørn PA, Finstad B (1997) The physiological effects of salmon lice infection on sea trout post smolts.
465 *Nordic Journal of Freshwater Research* 73:60–72
- 466 Bjørn PA, Finstad B, Kristoffersen R (2001) Salmon lice infection of wild sea trout and Arctic char in
467 marine and freshwaters: the effects of salmon farms. *Aquaculture Research* 32:947–962
- 468 Borgsteede FHM (1996) The effect of parasites on wildlife. *Veterinary Quarterly* 18:138–140
- 469 Britton JR (2013) Introduced parasites in food webs: new species, shifting structures? *Trends in*
470 *Ecology & Evolution* 28:93–99
- 471 Bui S, Dempster T, Remen M, Oppedal F (2016) Effect of ectoparasite infestation density and
472 life-history stages on the swimming performance of Atlantic salmon *Salmo salar*. *Aquaculture*
473 *Environment Interactions* 8:387–395
- 474 Burnham KP, Anderson DR (Eds) (2002) *Model Selection and Multimodel Inference*, 2nd edn. Springer
475 New York, New York, NY
- 476 Burton T, McKelvey S, Stewart DC, Armstrong JD, Metcalfe NB (2013a) Early maternal experience
477 shapes offspring performance in the wild. *Ecology* 94:618–626
- 478 Burton T, McKelvey S, Stewart DC, Armstrong JD, Metcalfe NB (2013b) Offspring investment in wild
479 Atlantic salmon (*Salmo salar*): relationships with smolt age and spawning condition. *Ecology*
480 *of Freshwater Fish* 22:317–321
- 481 Calderwood WL (1905) “The white spot” affecting salmon in the Island of Lewis. *Annu. Rep. Fish. Board*
482 *Scotl.* 24, 77-79.
- 483 Finstad B, Bjørn PA, Grimnes A, Hvidsten NA (2000) Laboratory and field investigations of salmon lice
484 [*Lepeophtheirus salmonis* (Krøyer)] infestation on Atlantic salmon (*Salmo salar* L.) post-smolts.
485 *Aquaculture Research* 31:795–803

486 Fjørtoft HB, Besnier F, Stene A, Nilsen F, Bjørn PA, Tveten A-K, Finstad B, Aspehaug V, Glover KA (2017)
487 The Phe362Tyr mutation conveying resistance to organophosphates occurs in high
488 frequencies in salmon lice collected from wild salmon and trout. *Scientific Reports* 7

489 Godwin SC, Dill LM, Krkošek M, Price MHH, Reynolds JD (2017) Reduced growth in wild juvenile
490 sockeye salmon *Oncorhynchus nerka* infected with sea lice: reduced growth in sea-louse
491 infected *o. nerka*. *Journal of Fish Biology* 91:41–57

492 Godwin SC, Dill LM, Reynolds JD, Krkošek M (2015) Sea lice, sockeye salmon, and foraging competition:
493 lousy fish are lousy competitors. *Canadian Journal of Fisheries and Aquatic Sciences* 72:1113–
494 1120

495 Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution:
496 challenges and solutions: Multimodel inference. *Journal of Evolutionary Biology* 24:699–711

497 Grün B, Leisch F (2008) FlexMix Version 2: finite mixtures with concomitant variables and varying and
498 constant parameters. *Journal of Statistical Software* 28

499 Hall LM, Murray AG (2018) Describing temporal change in adult female *Lepeophtheirus salmonis*
500 abundance on Scottish farmed Atlantic salmon at the national and regional levels.
501 *Aquaculture* 489:148-153

502 Halttunen E, Gjelland K, Glover K, Askeland Johnsen I, Serra-Llinares R, Skaala Ø, Nilsen R, Bjørn P,
503 Karlsen Ø, Finstad B, Skilbrei O (2018) Migration of Atlantic salmon post-smolts in a fjord with
504 high infestation pressure of salmon lice. *Marine Ecology Progress Series* 592:243–256

505 Harte A, Bowman A, Salama N, Pert C (2017) Factors influencing the long-term dynamics of larval sea
506 lice density at east and west coast locations in Scotland. *Diseases of Aquatic Organisms*
507 123:181–192

508 Heuch PA, Nordhagen JR, Schram TA (2000) Egg production in the salmon louse [*Lepeophtheirus*
509 *salmonis* (Krøyer)] in relation to origin and water temperature. *Aquaculture Research* 31:805–
510 814

511 Jackson D, Deady S, Leahy Y, Hassett D (1997) Variations in parasitic caligid infestations on farmed
512 salmonids and implications for their management. *ICES Journal of Marine Science: Journal du*
513 *Conseil* 54:1104–1112

514 Jansen PA, Kristoffersen AB, Viljugrein H, Jimenez D, Aldrin M, Stien A (2012) Sea lice as a density-
515 dependent constraint to salmonid farming. *Proceedings of the Royal Society B: Biological*
516 *Sciences* 279:2330–2338

517 Johnson SC, Albright LJ (1991) Development, growth, and survival of *Lepeophtheirus salmonis*
518 (Copepoda: Caligidae) under laboratory conditions. *Journal of the Marine Biological*
519 *Association of the United Kingdom* 71:425–436

520 Jonsson N, Jonsson B, Hansen LP (2003) The marine survival and growth of wild and hatchery-reared
521 Atlantic salmon. *Journal of Applied Ecology* 40:900–911

- 522 Knowles JE, Frederick C (2016) Package 'merTools.'
- 523 Krkošek M, Revie CW, Gargan PG, Skilbrei OT, Finstad B, Todd CD (2012) Impact of parasites on salmon
524 recruitment in the Northeast Atlantic Ocean. *Proceedings of the Royal Society B: Biological*
525 *Sciences* 280:2012.2359
- 526 Lafferty KD, Allesina S, Arim M, Briggs CJ, De Leo G, Dobson AP, Dunne JA, Johnson PTJ, Kuris AM,
527 Marcogliese DJ, Martinez ND, Memmott J, Marquet PA, McLaughlin JP, Mordecai EA, Pascual
528 M, Poulin R, Thielges DW (2008) Parasites in food webs: the ultimate missing links: Parasites
529 in food webs. *Ecology Letters* 11:533–546
- 530 Lafferty KD, Dobson AP, Kuris AM (2006) Parasites dominate food web links. *Proceedings of the*
531 *National Academy of Sciences* 103:11211–11216
- 532 Lafferty KD, Kuris AM (1999) How environmental stress affects the impacts of parasites. *Limnology*
533 *and Oceanography* 44:925–931
- 534 MacKinnon B (1998) Host factors important in sea lice infections. *ICES Journal of Marine Science*
535 55:188–192
- 536 McKibben MA, Hay DW (2004) Distributions of planktonic sea lice larvae, *Lepeophtheirus salmonis*, in
537 the inter-tidal zone in Loch Torridon, Western Scotland in relation to salmon farm production
538 cycles. *Aquaculture Research*, 35: 742-750.
- 539 Murray AG, Simpson I (2006) Patterns in sea lice infestation on wild Atlantic salmon returning to the
540 North Esk river in eastern Scotland 2001-2003. Fisheries Research Services Internal Report No
541 20/06
- 542 Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear
543 mixed-effects models (RB O'Hara, Ed.). *Methods in Ecology and Evolution* 4:133–142
- 544 Ohgushi T, Schmitz O, Holt RD (2012) Trait-mediated indirect interactions: ecological and evolutionary
545 perspectives. Cambridge University Press
- 546 Øverli Ø, Nordgreen J, Mejdell CM, Janczak AM, Kittilsen S, Johansen IB, Horsberg TE (2014)
547 Ectoparasitic sea lice (*Lepeophtheirus salmonis*) affect behavior and brain serotonergic activity
548 in Atlantic salmon (*Salmo salar* L.): Perspectives on animal welfare. *Physiology & Behavior*
549 132:44–50
- 550 Peacock SJ, Krkošek M, Bateman AW, Lewis MA (2015) Parasitism and food web dynamics of juvenile
551 Pacific salmon. *Ecosphere* 6:art264
- 552 Penston M, McBeath A, Millar C (2011) Densities of planktonic *Lepeophtheirus salmonis* before and
553 after an Atlantic salmon farm relocation. *Aquaculture Environment Interactions* 1:225–232
- 554 Pontoppidan E (1755) *The natural history of Norway: Containing, a particular and accurate account of*
555 *the temperature of the air, the different soils, waters, vegetables, metals, minerals, stones,*
556 *beasts, birds, and fishes; together with the dispositions, customs, and manner of living of the*

557 inhabitants; interspersed with physiological notes from eminent writers, and transactions of
558 academies. London: Printed for A. Linde.

559 Revie C, Dill L, Finstad B, Todd CD (2009) “Salmon Aquaculture Dialogue Working Group Report on Sea
560 Lice” commissioned by the Salmon Aquaculture Dialogue.

561 Salama NKG, Murray AG, Rabe B (2016) Simulated environmental transport distances of
562 *Lepeophtheirus salmonis* in Loch Linnhe, Scotland, for informing aquaculture area
563 management structures. *Journal of Fish Diseases* 39:419–428

564 Shearer WM (1986) The exploitation of Atlantic salmon in Scottish home water fisheries in 1952-
565 83. In: Jenkins D, Shearer WM (eds) *The status of the Atlantic salmon in Scotland*. Institute of
566 Terrestrial Ecology, Abbots Ripton, p 37–49

567 Skaala Ø, Kålås S, Borgstrøm R (2014) Evidence of salmon lice-induced mortality of anadromous brown
568 trout (*Salmo trutta*) in the Hardangerfjord, Norway. *Marine Biology Research* 10:279–288

569 Skilbrei O, Wennevik V (2006) Survival and growth of sea-ranched Atlantic salmon, *Salmo salar* L.,
570 treated against sea lice before release. *ICES Journal of Marine Science* 63:1317–1325

571 Smith KF, Acevedo-Whitehouse K, Pedersen AB (2009) The role of infectious diseases in biological
572 conservation. *Animal Conservation* 12:1–12

573 Susdorf R, Salama NKG, Lusseau D (2018) Influence of body condition on the population dynamics of
574 Atlantic salmon with consideration of the potential impact of sea lice. *Journal of Fish Diseases*
575 41:941–951

576 Thorstad EB, Finstad B (2018) Impacts of salmon lice emanating from salmon farms on wild Atlantic
577 salmon and sea trout. NINA, Trondheim, Norway

578 Thorstad EB, Todd CD, Uglem I, Bjørn PA, Gargan PG, Vollset KW, Halttunen E, Kålås S, Berg M, Finstad
579 B (2015) Effects of salmon lice *Lepeophtheirus salmonis* on wild sea trout *Salmo trutta* – a
580 literature review. *Aquaculture Environment Interactions* 7:91-113

581 Thorstad EB, Whoriskey F, Uglem I, Moore A, Rikardsen AH, Finstad B (2012) A critical life stage of the
582 Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt
583 migration. *Journal of Fish Biology* 81:500–542

584 Todd CD, Friedland KD, MacLean JC, Whyte BD, Russell IC, Lonergan ME, Morrissey MB (2012)
585 Phenological and phenotypic changes in Atlantic salmon populations in response to a changing
586 climate. *ICES Journal of Marine Science* 69:1686–1698

587 Todd CD, Hughes SL, Marshall CT, MacLean JC, Lonergan ME, Biuw EM (2008) Detrimental effects of
588 recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology*
589 14:958–970

- 590 Todd CD, Whyte B, MacLean J, Walker A (2006) Ectoparasitic sea lice (*Lepeophtheirus salmonis* and
591 *Caligus elongatus*) infestations of wild, adult, one sea-winter Atlantic salmon *Salmo salar*
592 returning to Scotland. Marine Ecology Progress Series 328:183–193
- 593 Tompkins DM, Dobson AP, Arneberg P, Begon ME, Cattadori IM, Greenman JV, Heesterbeek JAP,
594 Hudson PJ, Newborn D, Pugliese A (2002) Parasites and host population dynamics. The ecology
595 of wildlife diseases:45–62
- 596 Torrissen O, Jones S, Asche F, Guttormsen A, Skilbrei OT, Nilsen F, Horsberg TE, Jackson D (2013)
597 Salmon lice - impact on wild salmonids and salmon aquaculture. Journal of Fish Diseases
598 36:171–194
- 599 Tully O (1992) Predicting infestation parameters and impacts of caligid copepods in wild and cultured
600 fish populations. Invertebrate Reproduction & Development 22:91–102
- 601 Tully O, Nolan DT (2002) A review of the population biology and host–parasite interactions of the sea
602 louse *Lepeophtheirus salmonis* (Copepoda: Caligidae). Parasitology 124:165–182
- 603 Tveiten H, Bjørn PA, Johnsen HK, Finstad B, McKinley RS (2010) Effects of the sea louse *Lepeophtheirus*
604 *salmonis* on temporal changes in cortisol, sex steroids, growth and reproductive investment
605 in Arctic charr *Salvelinus alpinus*. Journal of Fish Biology 76:2318–2341
- 606 Ugelvik MS, Skorping A, Moberg O, Mennerat A (2017) Evolution of virulence under intensive farming:
607 salmon lice increase skin lesions and reduce host growth in salmon farms. Journal of
608 Evolutionary Biology 30:1136–1142
- 609 Vøllestad LA, Hirst D, L’Abee-Lund JH, Armstrong JD, MacLean JC, Youngson AF, Stenseth NC (2009)
610 Divergent trends in anadromous salmonid populations in Norwegian and Scottish rivers.
611 Proceedings of the Royal Society B: Biological Sciences 276:1021–1027
- 612 Vollset KW, Barlaup BT, Skoglund H, Normann ES, Skilbrei OT (2014) Salmon lice increase the age of
613 returning Atlantic salmon. Biology Letters 10:20130896–20130896
- 614 Vollset KW, Krontveit RI, Jansen PA, Finstad B, Barlaup BT, Skilbrei OT, Krkošek M, Romunstad P,
615 Aunsmo A, Jensen AJ, Dohoo I (2015) Impacts of parasites on marine survival of Atlantic
616 salmon: a meta-analysis. Fish and Fisheries:714–730
- 617 Wagner GN, Fast MD, Johnson SC (2008) Physiology and immunology of *Lepeophtheirus salmonis*
618 infections of salmonids. Trends in Parasitology 24:176–183
- 619 Wells A, Grierson CE, Marshall L, MacKenzie M, Russon IJ, Reinardy H, Sivertsgård R, Bjørn PA, Finstad
620 B, Wendelaar Bonga SE, Todd CD, Hazon N (2007) Physiological consequences of “premature
621 freshwater return” for wild sea-run brown trout (*Salmo trutta*) postsmolts infested with sea
622 lice (*Lepeophtheirus salmonis*). Canadian Journal of Fisheries and Aquatic Sciences 64:1360–
623 1369
- 624

625 Table 1: Abbreviation and explanation of parameters used in the present work

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 freshwater
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 <i>L. salmonis</i> 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 resp); -4.47 & -4.69 (TA 1SW & MSW resp)
β_1	Slope of log-log transformed LWR: 3.02 (SP 1SW); 3.23 & 3.28 (NE 1SW & MSW resp); 2.72 & 2.85 (TA 1SW & MSW resp).
M	Effect of sea lice on individual w in percent

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

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

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636 Table 3: Top model set ($\Delta\text{AICc} < 4$, $n=2$) with potential covariates (D , m , s , y , $D:m$, $D:s$, $D:y$ and $m:y$) used
 637 to predict the influence of sea lice density D on condition in Atlantic salmon from River North Esk (NE).

Intercept	D	m	s	y	$D:m$	$D:s$	$D:y$	$m:y$	df	logLik	AICc	delta	weight	R^2
-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

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642 Table 4: Top model set ($\Delta AICc < 4$, $n=5$) with potential fixed (D , s , t , $D:s$, $D:t$ and $s:t$) and random (y)
643 effects used to predict the influence of sea lice density D on condition in 1SW Atlantic salmon from
644 River Tamar (TA).

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

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648 Table 5: Top model set ($\Delta AICc < 4$, $n=3$) with potential fixed (D , s , t , $D:s$, $D:t$ and $s:t$) and random (y)
649 effects used to predict the influence of sea lice density D on condition in MSW Atlantic salmon from
650 River Tamar (TA).

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

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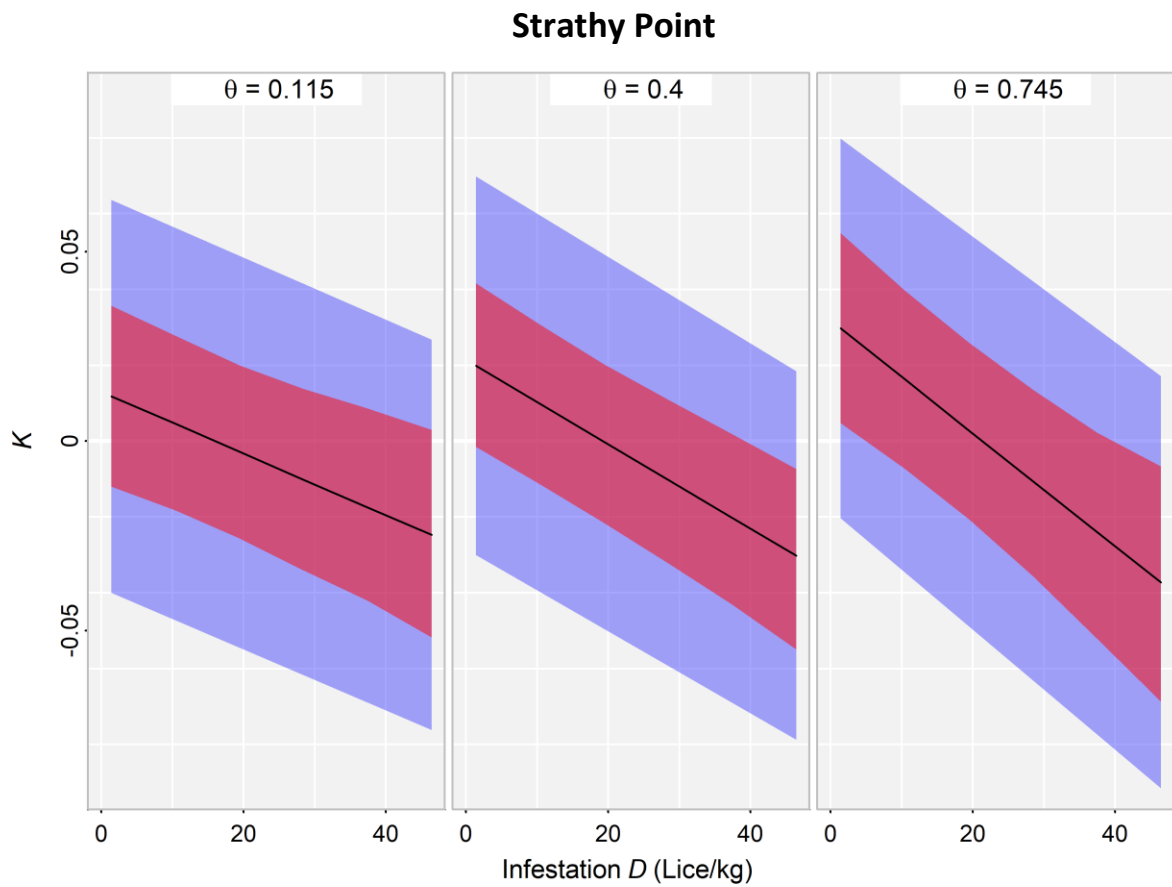


Figure 1: Relationship between individual condition index K (y-axis) and infestation density D (x-axis) for Strathy Point 1SW salmon given three representative values (0.115, 0.4 and 0.745) of female adult *L. salmonis* proportion θ . Predicted K is depicted as solid black regression lines with 95%CI (purple area), and 95 % prediction intervals (blue area).

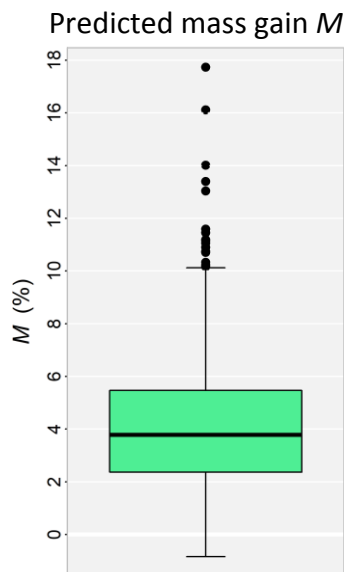


Figure 2: Predicted increase in whole mass in percent M for sampled 1SW at Strathy Point if sea lice infestation is analytically removed (i.e. $D = 0$). The boxes cover the inter-quartile range (IQR) (25th to 75th percentile), and the whiskers extend to $1.5 \cdot \text{IQR}$ below or above the 25th or 75th percentile respectively (default in R).

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North Esk

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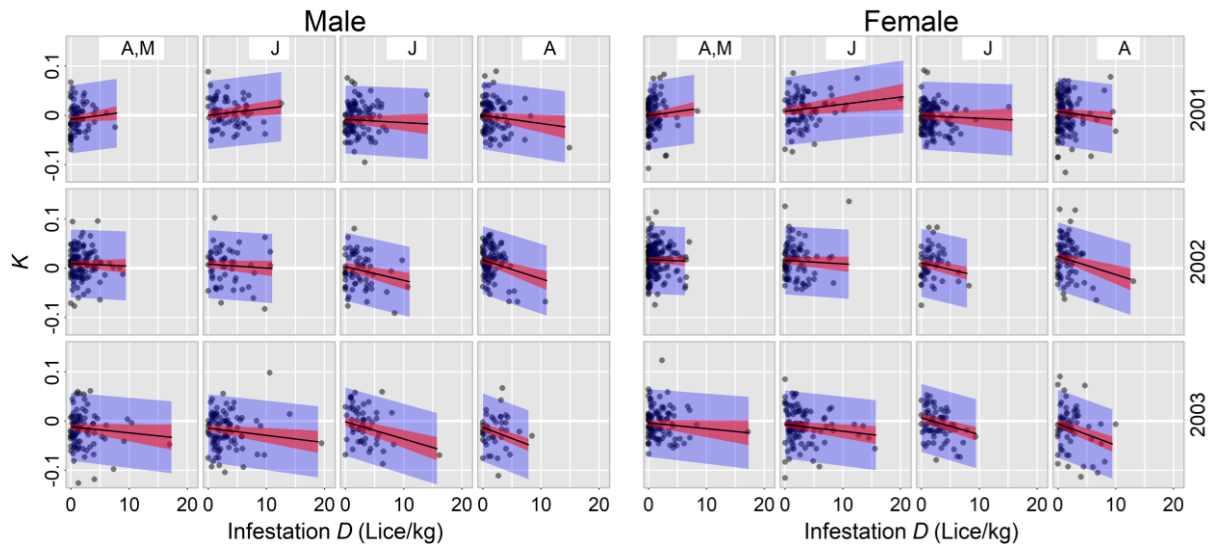
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Figure 3: Relationship between condition K (y-axis) and lice density D (x-axis) for each sex, month, and year-class for North Esk male (left) and female (right) salmon, with predicted K (black lines), 95%CI (purple area), and 95 % prediction intervals (blue area). Details as for Figure 1.

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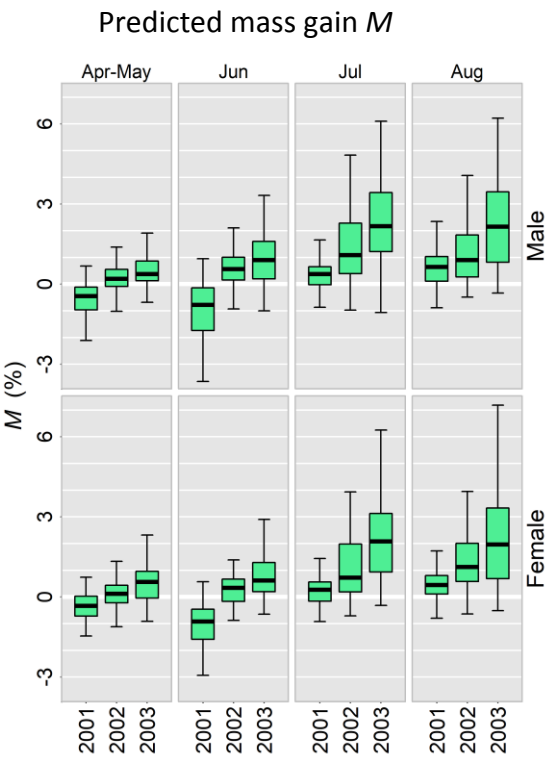
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Figure 4: Predicted mass gain percentage (M) for male (top) and female (bottom) salmon sampled at North Esk in April/May-August 2001-2003 if sea lice infestation is analytically removed (i.e. $D = 0$). Box and whisker range as for Figure 2.

Tamar

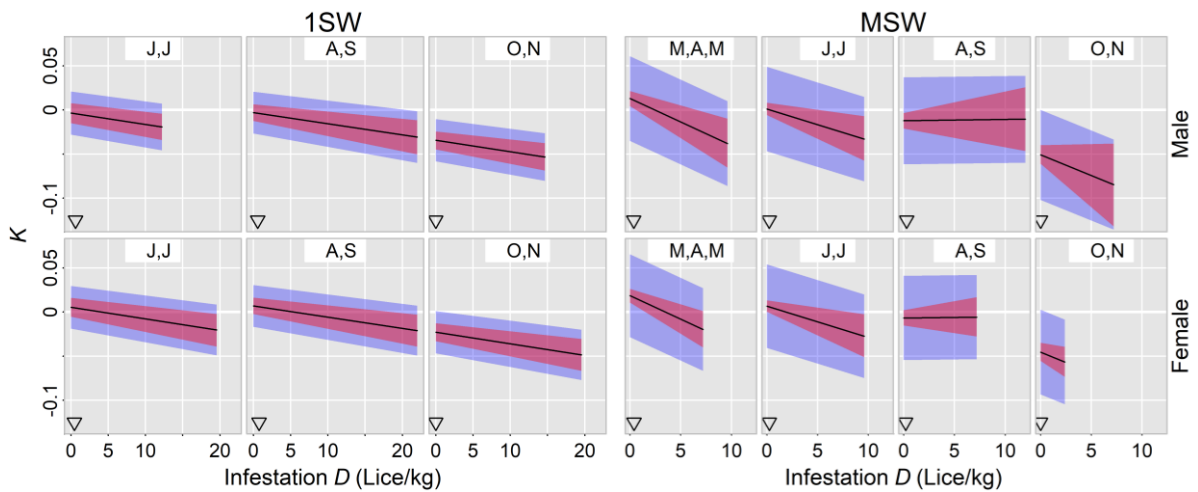


Figure 5: Relationship between condition factor K (y-axis) and lice density D (x-axis) for male (top) and female (bottom) 1SW (left) and MSW (right) Tamar salmon in relation to season t (months abbreviated to letter). Details as for Figure 1.

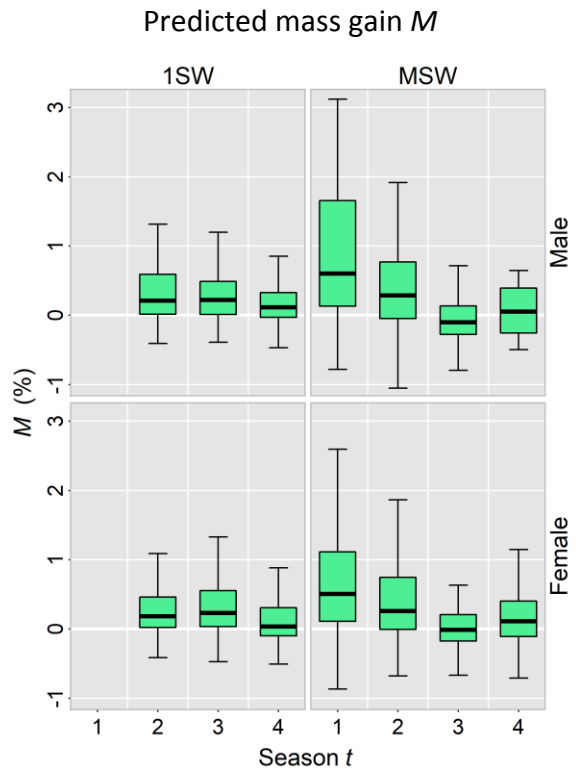


Figure 6: Predicted mass gain percentage (M) for 1SW (left) and MSW (right) male (top) or female (bottom) salmon from River Tamar if sea lice infestation is analytically removed (i.e. $D = 0$). Each column represents a sampling season t (x-axis). Box and whisker range as for Figure 2.