

1 Heavy sea louse infection is associated with decreased stomach fullness in wild juvenile sockeye  
2 salmon

3 Sean C. Godwin<sup>1,\*</sup>, Martin Krkošek<sup>2,3</sup>, John D. Reynolds<sup>1</sup>, Luke A. Rogers<sup>2</sup>, Lawrence M. Dill<sup>1</sup>

4  
5 <sup>1</sup> *Earth to Ocean Research Group, Department of Biological Sciences, Simon Fraser University,*  
6 *Burnaby, British Columbia, Canada, V5A 1S6*

7 <sup>2</sup> *Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario,*  
8 *Canada, M5S 3B2*

9 <sup>3</sup> *Salmon Coast Field Station, Simoom Sound, British Columbia, Canada, V0P 1S0*

10 *\* Corresponding author: E-mail: sgodwin@sfu.ca, Tel: 778-782-3989*

11  
12 *Co-author e-mail addresses:*

13 *Martin Krkošek: martin.krkošek@utoronto.ca*

14 *John Reynolds: reynolds@sfu.ca*

15 *Luke Rogers: luke.rogers@mail.utoronto.ca*

16 *Lawrence Dill: ldill@sfu.ca*

## Abstract

Foraging success can be mediated by parasites, but this is poorly understood for marine fish whose aggregations and patchy prey fields create conditions for intense intraspecific competition. We evaluated whether sea louse infection is associated with decreased stomach fullness of wild juvenile sockeye salmon (*Oncorhynchus nerka*) in Johnstone Strait, BC during their marine migration from the Fraser River. *Caligus clemensi* comprised 98.6% of the pre-adult and adult lice and 86.5% of the copepodites (freshly attached juvenile lice); the rest were *Lepeophtheirus salmonis*. We found that infection status was an important predictor of relative stomach fullness for juvenile sockeye (wet stomach content weight divided by body weight), as indicated by mixed-effects model selection, and that highly infected fish had 17%  $\pm$  8% lower relative stomach fullness than did lightly infected fish. This louse-associated reduction in relative stomach fullness occurs as the juvenile sockeye migrate through a food-limited environment, and presumably elevated competition. Given that early marine growth for juvenile salmon is often a predictor of survival, our results highlight the importance of understanding sub-lethal effects of parasites on salmonids and possibly other fish species.

## 32 **Introduction**

33 Foraging success is tightly linked to growth and survival of individuals, both of which are  
34 predictors of fitness and population dynamics (Crombie 1947; Sutherland 1996). Fish frequently  
35 experience patchy foraging opportunities and aggregate in large groups that intensify  
36 competition (see review by Ward et al. (2006)), and consequently survival often depends on  
37 these competitive outcomes (e.g., Resetarits 1995; Welker et al. 1994). This is especially the case  
38 for juvenile fishes, whose early growth depends on food supply and often determines survival  
39 and recruitment (Anderson 1988; Bergenius et al. 2002; Houde and Hoyt 1987). Evidence  
40 suggests that parasites affect competitive foraging outcomes of hosts, thereby influencing host  
41 population dynamics, community structure, and biodiversity (see Hatcher et al. 2006). However,  
42 this evidence is primarily from terrestrial species (e.g., Grosholz 1992; Maksimowich and Mathis  
43 2000; Schall 1992). Despite what is likely a more competitive environment with food patchiness  
44 and consumer aggregation for fishes, there is little work in the fisheries literature on how  
45 parasites mediate competition in wild fish and whether this translates to decreased survival  
46 through reduced foraging success and growth (but see Finley and Forrester 2003).

47 Pacific salmon (*Oncorhynchus* spp.), like many fishes, experience high juvenile mortality  
48 from predation and starvation (Groot and Margolis 1991; Parker 1968). Consequently, the  
49 impacts of parasitism may be primarily expressed through the mechanisms by which parasitism  
50 affects inter- and intra- specific interactions. Juvenile Pacific salmon migrate in large groups to  
51 swamp and evade predators (Eggers 1978; Furey et al. 2016), so competition for food is probable  
52 in regions with low prey availability (McKinnell et al. 2014). Foraging success during the marine  
53 migration of juvenile salmon likely affects growth, which is often a predictor of survival (Duffy  
54 and Beauchamp 2011; Farley et al. 2007; Moss et al. 2005), so competition in environments of

55 low foraging opportunity is one plausible mechanism through which parasites may affect  
56 survival of juvenile salmon (Godwin et al. 2015). Although parasitism can raise energetic  
57 requirements and thereby increase foraging rate (e.g., Giles 1987; Shi et al. 2002), parasitism  
58 may also interfere with the behavioural process of obtaining food in a food-limited environment  
59 and thereby reduce foraging success (e.g., Barber and Ruxton 1998).

60         During the ocean phase of their juvenile migration, Pacific salmon are susceptible to  
61 infection by sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*), which are native  
62 ectoparasites that feed on the surface tissue of their host (Wootten et al. 1982). Juvenile Pacific  
63 salmon normally have low infection levels of sea lice, especially the salmonid specialist *L.*  
64 *salmonis*, because these salmon are temporally and spatially separated from adult Pacific salmon  
65 (Krkošek et al. 2007). However, in recent decades domesticated Atlantic salmon (*Salmo salar*)  
66 farmed in open-net pens in coastal British Columbia (BC) have provided year-round reservoirs  
67 for sea lice that allow substantial transmission of *L. salmonis* to juvenile Pacific salmon (Costello  
68 2009b; Groner et al. 2016). For the generalist *C. clemensi*, there also exist other natural host  
69 infection reservoirs, such as Pacific herring (*Clupea pallasii*) (Beamish et al. 2009; Morton et al.  
70 2008), which share nearshore coastal waters with juvenile salmon as spawners and larvae  
71 (Beamish et al. 2012).

72         In recent years, the generalist *C. clemensi* has infected over 98% of out-migrating  
73 juvenile sockeye salmon (*O. nerka*) from the Fraser River (Godwin et al. 2015; Godwin et al.  
74 2017), an iconic set of Pacific salmon populations that forms Canada's largest sockeye run.  
75 Juvenile sockeye salmon that experience high infection intensity by *C. clemensi* exhibit reduced  
76 foraging success in a competitive and food-limited experimental setting (Godwin et al. 2015).  
77 Whether this translates to reduced foraging success in the wild is still unknown, but is the focus

78 of this work. Here, we tested whether the relative stomach fullness (wet stomach content weight  
79 divided by body weight) of wild juvenile sockeye is lower when sea louse infection intensity is  
80 higher, which has implications for our understanding of how parasites mediate competition in  
81 fishes and potentially for the management of *C. clemensi* in BC.

## 83 **Methods**

### 84 *Fish collection*

85 We collected juvenile sockeye salmon in the wild as they migrated through western  
86 Johnstone Strait, BC, between May 26 and June 7, 2014 (Fig. 1). At this point in their migration,  
87 the sockeye post-smolts have well-developed scales and average 114 mm in fork length. We  
88 used a hand-operated purse seine net (bunt: 27 x 9 m with 13 mm mesh, tow: 46 x 9 m with 76  
89 mm mesh) that we set from a small (6 m) open boat. After surrounding the fish, we brought the  
90 net next to the boat to form a pocket of sufficient width and depth to allow the fish to swim  
91 freely and minimize their contact with the mesh.

92 We transferred captured fish from the net into an insulated fish tote (0.58 m deep and  
93 0.97 x 0.55 m across) filled with fresh seawater. We moved fish from the net into the tote by  
94 dipping them and their surrounding seawater into a 3.79 L container (an inverted milk jug with  
95 the top capped and bottom cut off). This transfer method minimized or prevented sea louse  
96 detachment as fish were never exposed to air and there was minimal contact between the fish and  
97 sampling equipment (Godwin et al. 2015). All subsequent transfers were also performed using  
98 the same method. We used ice packs to regulate water temperature in the tote and aquarium  
99 bubblers to maintain adequate aeration. We transferred 50–100 sockeye into the tote during each  
100 capture event. See Supplementary Table S1 for collection locations, catch sizes, and

101 oceanographic data.

102  
103 *Infection status assessment*

104 We transferred sockeye individually from the tote into 13.2 L clear plastic aquaria and  
105 assessed them for sea louse infection by eye. If a fish appeared to be in one of our two infection  
106 categories (see below), we recorded that category and transferred the fish to an individual sterile  
107 532 mL sample bag (Whirl-Pak® Write-On Bags; Nasco, Fort Atkinson, Wisconsin, USA) and  
108 euthanized it with an overdose of MS-222 (240 mg L<sup>-1</sup>). After euthanizing a fish, we performed a  
109 full assessment of its infection status using a hand lens (Krkošek et al. 2005a) to confirm its  
110 infection category. Fish that were euthanized but found not to meet our infection category  
111 criteria were not used; such fish accounted for approximately 10% of euthanized fish and were  
112 usually identified initially to be in the lightly infected category by eye but then found to have too  
113 many small juvenile lice upon inspection by hand lens. We alternated between processing highly  
114 infected and lightly infected fish so as to not confound digestion time with infection status.

115 Larger, more developed sea lice have greater effects on their hosts (Jakob et al. 2013;  
116 Nendick et al. 2011; Wootten et al. 1982). We created infection categories that reflected this  
117 differential level of pathogenicity, so that small juvenile lice were not weighted equally to large  
118 adult lice (similar to Peacock et al. 2015). Sea lice initially attach to their host as copepodites,  
119 then develop through two (*L. salmonis*; Hamre et al. 2013) or four (*C. clemensi*; Kabata 1972)  
120 attached chalimus stages of increasing size before molting into their motile pre-adult and adult  
121 stages. Here, we consider individuals in their second *L. salmonis* chalimus stage or their third or  
122 fourth *C. clemensi* chalimus stages as ‘large chalimus’ sea lice; we also consider pre-adult and  
123 adult individuals as ‘motile’ sea lice. To weight the infection statuses of fish according to the

124 development of lice infecting them, we defined a louse infection scale in which one large  
125 chalimus louse was equal to one infection unit, one motile louse was equal to two infection units,  
126 and copepodite and small chalimus lice were equal to zero. Because of the high infection  
127 prevalence observed (> 98%), we were unable to create a category for uninfected fish. Instead,  
128 we created a 'lightly infected' category in which all the fish had zero infection units and no more  
129 than three copepodite or small chalimus lice (Table 1). In all collections, the 'lightly infected'  
130 and 'highly infected' categories differed by a minimum of three infection units. See  
131 Supplementary Table S2 for the detailed sea louse infection data.

132           Approximately one hour after capture, we released the remaining fish at the collection  
133 site. In each collection, we retained five to seven pairs of fish, each consisting of a lightly and  
134 highly infected sockeye. In total, we retained 130 juvenile sockeye salmon from across 11  
135 collections to analyze stomach fullness in relation to infection status.

### 136 137 *Zooplankton sampling and analysis*

138           Immediately following the infection status assessments and subsequent release of fish, we  
139 collected zooplankton samples with a horizontal plankton tow at the fish capture site. Plankton  
140 tows were performed with a 0.5 m diameter plankton net with 250 µm mesh. The top of the net  
141 was kept 5-10 cm below the ocean surface, on average, and the tow lasted for 30 s. We attached  
142 a calibrated flow meter (General Oceanics, Miami, Florida, USA) at the mouth of the net to  
143 measure the volume of water sampled. We used horizontal tows instead of vertical ones because  
144 plankton samples near the surface are more similar to sockeye diets than those from deeper in the  
145 water column (Landingham et al. 1998) and our field observations indicate that juvenile sockeye  
146 frequently occupy the surface waters at the collection sites.

147 Each plankton sample was placed in a glass jar containing 250 mL of 10% formalin-  
148 seawater solution. Within three days of the collection, the samples were poured into a 63  $\mu\text{m}$   
149 sieve and rinsed with distilled water. The samples were then halved repeatedly using a Folsom  
150 plankton splitter (Aquatic Research Instruments, Hope, Idaho, USA) until approximately 200-  
151 250 individuals remained, after which they were transferred to a Bogorov counting tray (Wildlife  
152 Supply Company, Yulee, Florida, USA). From these samples, we identified and enumerated  
153 individuals from the high-level taxa previously found in juvenile Fraser River sockeye salmon  
154 stomachs (Price et al. 2013); these were termed ‘sockeye prey’. These high-level taxa from Price  
155 et al. (2013) were: Copepoda, Brachyura, Oikopleura, Euphausiacea, Cladocera, Pteropoda,  
156 Decapoda, Amphipoda, Insecta, Cumacea, fish, and eggs. We calculated sockeye prey density by  
157 multiplying the number of sockeye prey in the Bogorov tray by the reciprocal of the splitting  
158 fraction, then dividing by the volume of water that passed through the plankton net.

#### 159 *Determination of relative stomach fullness*

161 We used wet stomach content weight as our measure of stomach fullness, and divided  
162 this by the fish’s body weight to calculate relative stomach fullness. Following the field  
163 collections, we transported the euthanized fish on ice to a laboratory facility 45 min away by  
164 boat. Upon arrival at the laboratory, fish were analyzed in the original order of collection by  
165 dissecting them immediately to weigh the wet stomach contents. Stomachs were excised between  
166 the lower oesophagus and the pyloric sphincter, and their contents extruded with forceps and  
167 weighed, as in Godwin et al. (2015).

#### 168 *Statistical analysis*



170 To determine which biological variables best explained juvenile sockeye salmon relative  
171 stomach fullness, we fit a suite of 13 mixed-effects models to our data (see Supplementary Table  
172 S3 for the full model set). Our models included the biologically relevant combinations of five  
173 fixed effects: infection status, body size, prey density, the two-way interaction between infection  
174 status and body size, and the two-way interaction between infection status and prey density. We  
175 included infection status as a fixed effect to test our main hypothesis that relative stomach  
176 fullness decreases with high intensities of sea louse infection. We included body size and its  
177 interaction with infection status to account for any additional benefit of a larger body size to  
178 relative stomach fullness, and the potential decreasing effect of infection with body size (Godwin  
179 et al. 2015). Finally, we included prey density and its interaction with infection status to account  
180 for the probable association between relative stomach fullness and prey density, and the possible  
181 decreasing effect of infection with increasing density of prey. Prey density and relative stomach  
182 fullness were centered and scaled by one standard deviation to allow the model-fitting optimizer  
183 to function correctly, since their variances were different by 10 orders of magnitude. Each model  
184 included a random effect of collection number on the intercept, which was determined *a priori* to  
185 account for the hierarchical structure of the sampling design, and a variance structure allowing  
186 for different variances in each collection to account for heteroscedasticity in the residuals. We  
187 performed model selection using Akaike Information Criterion corrected for small sample sizes  
188 (Hurvich and Tsai 1989) as our measure of model parsimony. We calculated relative variable  
189 importance (RVI) values based on the AICc weights.

190 We derived our measure of body size from a principal component analysis using three  
191 highly correlated body metrics: fork length, body depth, and weight. The first principal  
192 component explained 98% of the original variation in these metrics and so we used that as the

193 variable representing body size in the statistical analyses.

194 We tested for differences in body size between infection categories using a two-sample  $t$ -  
195 test, and used linear regression to assess whether motile or overall louse abundance increased  
196 with body size for the highly infected fish. We completed all our analysis in R 3.2.1 (R  
197 Foundation for Statistical Computing, 2015) using the nlme and MuMIn packages.

## 198 **Results**

200 The juvenile sockeye salmon in our highly infected category were primarily infected by  
201 *C. clemensi* rather than *L. salmonis*, with 98.6% of the motile sea lice and 86.5% of the  
202 copepodid lice infecting these fish belonging to the former species. Neither motile abundance ( $R^2$   
203 = 0.009, d.f. = 63,  $p = 0.455$ ) nor overall louse abundance ( $R^2 = 0.025$ , d.f. = 63,  $p = 0.207$ )  
204 increased with body size for fish in the highly infected category. Body size also did not differ  
205 between infection categories ( $t = 0.282$ , d.f. = 128,  $p = 0.779$ ). The mean ( $\pm$  SE) zooplankton  
206 density across all collections was 941 individuals  $L^{-1} \pm 141$  individuals  $L^{-1}$ , and the mean  
207 sockeye prey density was 772 individuals  $L^{-1} \pm 134$  individuals  $L^{-1}$ , indicating that potential  
208 sockeye prey constituted 82% of the zooplankton community in the surface waters during our  
209 collections.

210 Lightly infected fish had higher relative stomach fullness than highly infected fish (Fig.  
211 2), and this trend held in each of the 11 collections (Fig. 3). Infection status was the most  
212 important predictor of relative stomach fullness; of the 13 mixed-effects models, the top nine all  
213 included an infection status term, while none of the bottom four did (Supplementary Table S3).  
214 The importance of infection status to relative stomach fullness was corroborated by this predictor  
215 having the highest RVI (0.97), compared with body size (0.66), prey density (0.60), the

216 interaction between infection status and prey density (0.16), and the interaction between  
217 infection status and body size (0.14). Regardless of their rank, all models with the relevant terms  
218 revealed that relative stomach fullness was higher for lightly infected fish, that it increased with  
219 body size, and that it increased with prey density. The top-ranked model included only an  
220 infection status term, but two other models were within 2 AICc units of the top model and  
221 therefore also had substantial support (Burnham and Anderson 2002; Table 2). One of these  
222 highly-supported models included a body size term, while the other included a predictor for prey  
223 density (Table 2).

224 The highest-ranked model without an infection status predictor was 7.8 AICc units higher  
225 than the top model and accounted for only 0.7% of model support, as judged by AICc weights  
226 (Supplementary Table S2). The top-ranked model was 51 times more likely than the highest-  
227 ranked model without an infection status predictor, and its coefficients indicated that highly  
228 infected fish had  $17\% \pm 8\%$  lower relative stomach fullness than lightly infected fish, on  
229 average.

## 231 Discussion

232 Theory and empirical evidence suggest that pathogens and parasites can influence host  
233 survival and population dynamics by modulating competitive foraging interactions (Hatcher et  
234 al. 2006). However, there is little evidence of parasite-mediated intraspecific competition in wild  
235 fishes, for whom intraspecific competition may be particularly intense due to fish aggregation  
236 and food patchiness. Our results indicate that, for wild juvenile sockeye salmon, high levels of  
237 sea louse infection are associated with reduced relative stomach fullness. The juvenile sockeye  
238 used in this study were captured during their early marine migration from their natal freshwater

239 systems, which based on the timing of capture and genetic analyses from previous studies  
240 (Godwin et al. 2017; Groot and Cooke 1987; Price et al. 2011) were mostly in the Fraser River  
241 watershed of BC.

242 While our stomach fullness data describe the quantity of prey consumed by sockeye, it  
243 should be noted that stomach fullness is not a true measure of foraging success or efficiency.  
244 Stomach fullness does not account for the energy densities or digestibility of prey, which vary  
245 among the zooplankton prey items that dominate the diet of juvenile sockeye (Foy and Norcross  
246 1999; Lee 1974) as well as spatially and temporally with the availability of those items  
247 (Landingham et al. 1998; Mackas et al. 2013; Tanasichuk and Routledge 2011). Parasitized  
248 individuals can shift their diet to prey items of lower energy density or digestibility when they  
249 struggle to compete with unparasitized conspecifics for higher-quality prey (Milinski 1984).  
250 Since juvenile sockeye with heavy sea louse infection have lower competitive foraging abilities  
251 (Godwin et al. 2015), it is possible that they too shift toward capturing more prey items of lower  
252 quality. If that were the case, then by using stomach fullness data we produced conservative  
253 estimates of the differences in foraging success between infection categories.

254 Animal migration is generally demanding metabolically, so managing energy gain and  
255 depletion is vital for most migrating animals to avoid starvation or the sub-lethal effects of  
256 depleted energy reserves (Sapir et al. 2011). Unlike some migratory species, juvenile sockeye  
257 salmon forage during their migration, but this foraging is temporally variable because feeding  
258 opportunities are patchy (McKinnell et al. 2014; Parsons et al. 1970). In regions with relatively  
259 high productivity, such as the northern Strait of Georgia, BC (Masson and Peña 2009; Parsons et  
260 al. 1970), no evidence of food limitation has been observed (Price et al. 2013). By contrast, the  
261 region in which we captured fish for this study, Johnstone Strait, has a sparse prey field due to

262 strong tidal mixing (B. Hunt et al., Hakai Institute, unpublished data), which may cause high  
263 mortality for juvenile sockeye that enter the Strait with insufficient energy reserves (McKinnell  
264 et al. 2014). Sea lice levels on juvenile sockeye are also considerably higher in Johnstone Strait  
265 than in the more productive southern regions (Godwin et al. 2015; Price et al. 2011). Hence, the  
266 potential effects of sea lice on sockeye salmon growth and survival in Johnstone Strait are likely  
267 to involve the elevated abundances of the parasite itself, its effects on intraspecific competition,  
268 and the intensification of competition due to food limitation and the energy expenditure of  
269 migration.

270 Our results provide equivocal evidence for an association between prey density and the  
271 relative stomach fullness of juvenile sockeye. If food competition is indeed higher in Johnstone  
272 Strait for sockeye than in nearby regions and that contributed to our finding that relative stomach  
273 fullness is associated with heavy sea louse infection, then we might have expected to find a  
274 stronger relationship between prey density and relative stomach fullness. Only one our three  
275 models with considerable support (as judged by AICc values; Burnham and Anderson 2002)  
276 contained a prey density predictor, which across our model set was our third most important  
277 predictor variable (RVI = 0.60). It is possible that prey density did not severely limit relative  
278 stomach fullness of sockeye in Johnstone Strait in 2014 even if food availability is commonly  
279 much lower there than in the Strait of Georgia (McKinnell et al. 2014; B. Hunt et al., Hakai  
280 Institute, unpublished data.). However, if the prey field was not limiting sockeye foraging rates  
281 then we might not expect to observe the differences in relative stomach fullness between  
282 infection categories that we did, since highly infected (and therefore less competitive (Godwin et  
283 al. 2015)) individuals would still have the opportunity to feed to satiation. It is also possible that  
284 the prey density estimates from our zooplankton collections did not represent the prey field

285 encountered by the fish when they were feeding, due to patchiness in time or space (Parsons et  
286 al. 1970) or the strong tidal currents known to occur in Johnstone Strait (Sutherland et al. 2007).  
287 Most of the sockeye in this study must have eaten in the preceding eight hours (see Appendix),  
288 which limits the potential effects of patchiness and currents on our results, but these remain  
289 possibilities that cannot be excluded. Perhaps the most likely explanation for our equivocal  
290 evidence of a relationship between prey density and relative stomach fullness was that the  
291 sample size of 11 collection sites was too small to detect an effect. While our study design was  
292 suitable for looking at consistent differences in relative stomach fullness within groups, the  
293 sample size was limited for investigating variation among collections.

294 The relationship that we found between sea louse infection and relative stomach fullness  
295 is correlative, but the weight of evidence is building that sea lice have sub-lethal effects on  
296 important determinants of sockeye salmon survival. Sea lice are associated with Pacific salmon  
297 population declines (Connors et al. 2010; Krkošek et al. 2011a), but these declines cannot be  
298 explained by direct mortality alone, which may only be significant at small host sizes (Jones et  
299 al. 2008). However, sea lice also appear to have sub-lethal effects that influence mortality  
300 through their hosts' ecological interactions, for example by reducing swimming endurance  
301 (Mages and Dill 2010), increasing risk-taking behaviours (Krkošek et al. 2011b), and elevating  
302 predation (Peacock et al. 2015). For juvenile sockeye salmon specifically, individuals that are  
303 heavily infected by sea lice, primarily *C. clemensi*, have lower competitive foraging ability  
304 (Godwin et al. 2015), reduced body growth (Godwin et al. 2017), and actively attempt to  
305 dislodge these parasites by leaping (Atkinson et al. In review). Nonetheless, laboratory studies  
306 utilizing experimental infections are needed to help differentiate two alternative interpretations  
307 of our results: 1) that sea lice abundance is a consequence rather than a cause of variation in

308 relative stomach fullness; or 2) that sea louse abundance and relative stomach fullness are both  
309 correlated with (signals of) fundamental underlying fitness variation among individuals. We  
310 consider these alternative explanations to be unlikely because they both require sustained  
311 differences in relative stomach fullness that would have led to a difference in body size between  
312 the two infection categories, which was not observed. It is also striking that the observed louse-  
313 associated differences in relative stomach fullness occurred in each of the 11 collections (Fig 3),  
314 so any correlation between an underlying condition and sea louse infection would have to be  
315 very strong indeed.

316 In addition to our main result that heavy sea louse infection is associated with reduced  
317 sockeye stomach fullness, we also found moderate evidence that relative stomach fullness  
318 increased with body size. This result runs counter to the negative exponential relationship  
319 between relative stomach fullness and body size reported by Brett (1971) for juvenile sockeye,  
320 suggesting that larger juvenile sockeye may have a foraging advantage due to their body size.  
321 The obvious potential mechanism for this is that smaller sockeye are prevented from foraging on  
322 larger (and possibly more abundant) prey due to gape limitation, which often, but not always,  
323 determines foraging success in young fish (Bremigan and Stein 1994; Devries et al. 1998;  
324 Hargreaves and LeBrasseur 1986; Scharf et al. 2000). Together with the relationship between  
325 infection status and relative stomach fullness, this potential effect of body size would be  
326 consistent with our previous findings that high infection intensities and smaller body sizes are  
327 associated with lower competitive foraging ability (Godwin et al. 2015) and reduced growth  
328 (Godwin et al. 2017) for juvenile sockeye. When considered together (Fig. 4), these  
329 interconnected relationships suggest that sea louse infection may not just be accompanied by a  
330 single, temporary effect for the duration of infection. Infection may instead have long-lasting

331 effects by initiating and/or intensifying divergent growth among individuals through differences  
332 in foraging success, which would create and reinforce intraspecific heterogeneity in body sizes  
333 and ultimately differential survival. To detect such differences in body size, the amount of time  
334 between sea louse exposure and fish collection would need to be greater than that of this study  
335 (3-10 days; Price et al. 2011; Welch et al. 2011), since the small amount of differential body  
336 growth that would occur between infection categories in that time (< 0.5 mm; Godwin et al.  
337 2017) would be statistically swamped by the individual-level variation in body size. This  
338 potential for lasting effects of sea lice on factors critical to sockeye survival highlights the need  
339 to consider the anthropogenic influence on the parasite burdens of these fish, and potentially  
340 reduce it through management actions when possible.

341 Over 98% of the motile sea lice infecting the juvenile sockeye salmon were *C. clemensi*,  
342 but although these infections have been linked to open net-pen salmon farms (Price et al. 2011),  
343 there are currently no management actions directed at regulating this louse species on farms in  
344 BC. *Lepeophtheirus salmonis*, the main species of sea louse that causes fish mortality and  
345 financial loss to salmon aquaculture in the northern hemisphere (Costello 2009a; Johnson et al.  
346 2004; Mustafa et al. 2001), is controlled on BC farms through application of in-feed parasiticide  
347 (emamectin benzoate; Saksida et al. 2010) when their abundance exceeds three motile lice per  
348 fish (Fisheries and Oceans Canada 2016). While emamectin benzoate also reduces *C. clemensi*  
349 numbers, *C. clemensi* abundance is not directly managed. Since *Caligus* spp. are considered less  
350 pathogenic than *L. salmonis* (Igboeli et al. 2014; Johnson et al. 2004) and most of the research  
351 into the effects of sea lice on wild salmon has focussed on *L. salmonis* (e.g., Connors et al. 2010;  
352 Johnson et al. 1996; Krkošek et al. 2005b), there has been little reason to target *C. clemensi* with  
353 treatments on farms until now. However, given the mounting evidence for sub-lethal effects of



354 *C. clemensi* on wild salmon, and the ability for *C. clemensi* to reach extreme abundances on  
355 farms without targeted treatment (e.g., 100% prevalence and 47.2 lice per fish (Di Cicco et al.  
356 2017)), it seems prudent to start considering *C. clemensi* in the fish health management plans of  
357 farmed salmon in BC.

358         There is increasing concern over the potential impacts of *C. clemensi* on wild Fraser  
359 River sockeye salmon (e.g., Moore et al. 2017), especially in the context of the record-low Fraser  
360 sockeye returns in 2009 and 2016 (Pacific Salmon Commission 2016). Unlike *L. salmonis*,  
361 which can only infect salmonids, the generalist *C. clemensi* may have multiple sea lice reservoirs  
362 along the juvenile sockeye migration route, including Pacific herring, which may amplify  
363 extinction risk for salmon by allowing parasite abundances to remain high when an imperilled  
364 host population declines (De Castro and Bolker 2005) and perhaps threaten herring stocks as  
365 well. Our results shed further light on the sometimes subtle interactions between parasites and  
366 wild Pacific salmon (Miller et al. 2014; Peacock et al. 2014), and underscore the need to study  
367 not only the direct mortality from parasites but their sub-lethal effects as well. The impacts of  
368 parasite-mediated intraspecific competition on host survival and recruitment may be particularly  
369 influential for fishes, which often experience intense food competition and growth-dependent  
370 mortality, but there has been little to no work in this area. Competition is a fundamental driver of  
371 populations, and identifying how and when parasites mediate the competitive interactions of  
372 their hosts may be essential to understanding the host-parasite dynamics of many systems.

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- 620

621 **Tables**

622 Table 1. Infection categories and sample sizes for each fish collection. The infection scale was  
 623 weighted such that one large chalimus louse was equal to one infection unit, one motile louse  
 624 was equal to two infection units, and copepodite and small chalimus lice were equal to zero  
 625 units. For each collection, a single fish pair was comprised of one fish from the highly infected  
 626 category and one from the lightly infected category.

Collection	Fish pairs	Lightly infected		Highly infected	
		Infection scale	Max. lice	Infection scale	Min. lice
1	5	0	3	4	6
2	6	0	1	3	2
3	7	0	1	4	5
4	7	0	2	4	4
5	6	0	3	4	4
6	7	0	3	4	7
7	6	0	3	4	6
8	5	0	3	5	7
9	5	0	3	5	4
10	6	0	3	5	9
11	5	0	3	5	10
<b>Average</b>	<b>5.9</b>	<b>0.0</b>	<b>2.5</b>	<b>4.3</b>	<b>5.8</b>

627

628 Table 2. Model selection results for the six models of relative foraging success that accounted for  
 629 at least 5% of model support. Relative stomach fullness was calculated as wet stomach content  
 630 weight divided by body weight. The models included combinations of infection category  
 631 (infection), body size (size; see description of principal component analysis), and prey density  
 632 fixed effects. Each model included a random effect on the intercept for collection number.  
 633 Interaction terms are distinguished with an asterisk symbol. See Supplementary Table S3 for the  
 634 full model set and selection results.

Rank	Model	$\Delta\text{AICc}^*$	$w_i^\dagger$	$R^{2\ddagger}$
1	infection	0	0.358	0.549
2	infection + size	1.24	0.192	0.530
3	infection + prey	1.66	0.156	0.542
4	infection + size + prey	2.66	0.095	0.510
5	infection*size	3.85	0.052	0.530
6	infection*prey	3.91	0.051	0.536

635 \* Difference from the top model AICc ( $\Delta\text{AICc}$ )

636 † Akaike model weight ( $w_i$ )

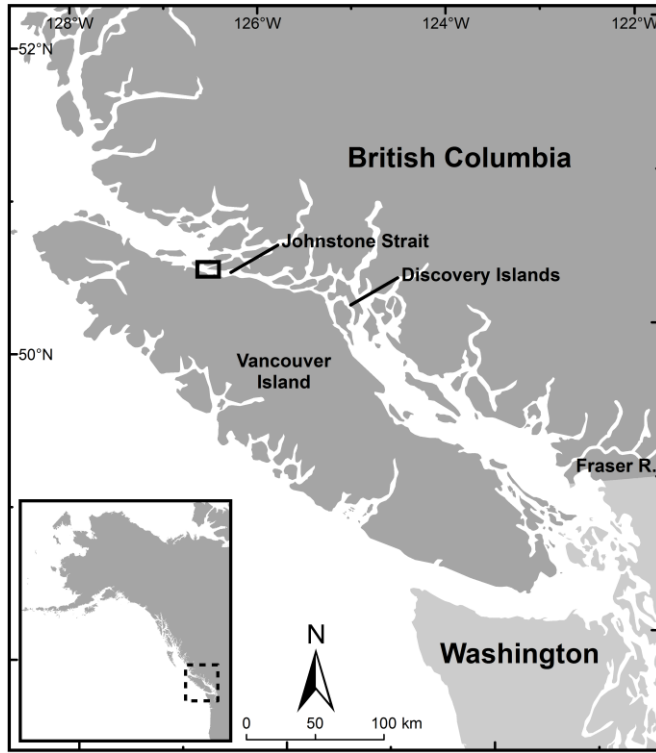
637 ‡  $R^2$  for mixed-effects models calculated using the method developed by Nakagawa and

638 Schielzeth (2013)

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### Figures



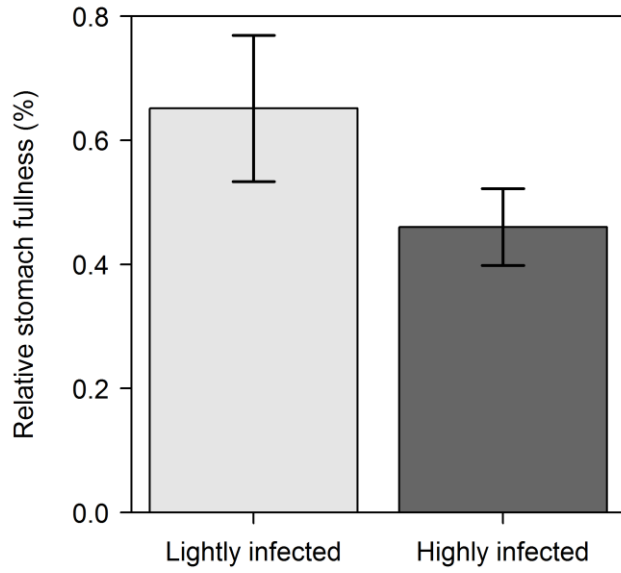
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Fig. 1. Map of study region. The solid black box indicates the area in which salmon collections occurred.





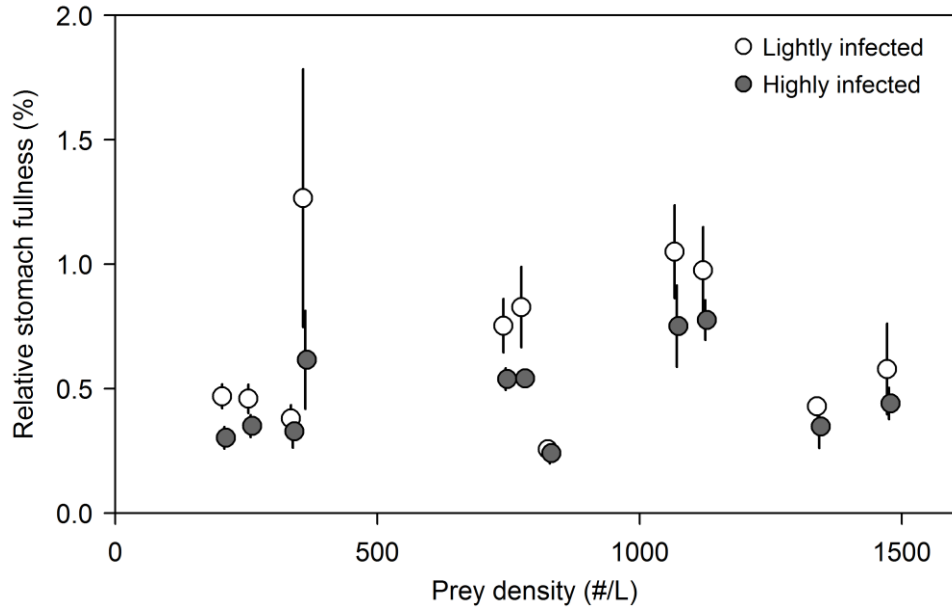
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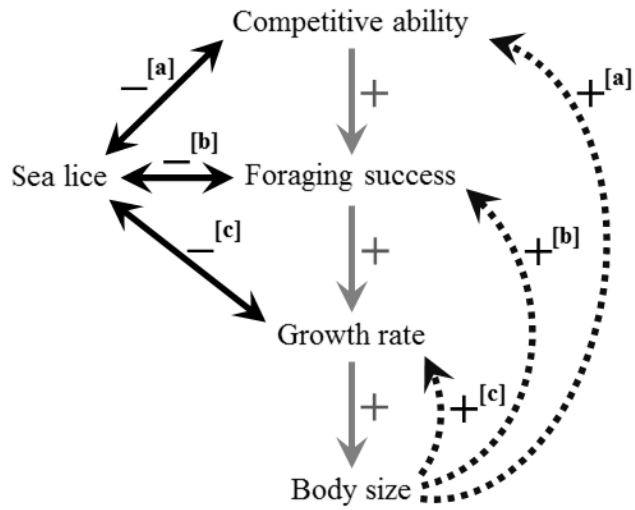
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Fig. 2. Relative stomach fullness of juvenile sockeye salmon for the two categories of sea louse infection. Error bars indicate the 95% confidence intervals around the relative stomach fullness for each infection category.



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 648 Fig. 3. Mean relative stomach fullness ( $\pm$  SE) for fish in both infection categories of each  
 649 collection. Each vertical pair of points (one grey, one white) comprises a single collection. The  
 650 relationship between relative stomach fullness and prey density had equivocal support in our  
 651 model selection results (see Table S3).



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Fig. 4. Relationships among juvenile sockeye salmon traits and sea louse infection. Solid double-ended arrows indicate established correlative sea louse relationships ([a] Godwin et al. 2015, [b] this paper, [c] Godwin et al. 2017). Dashed black arrows indicate established correlative body size relationships, and grey arrows indicate implicit mechanistic relationships.

## 1 **Appendix.** Juvenile sockeye salmon digestion experiment

2

### 3 *Methods*

4 To assess the extent to which our prey density estimates were representative of the prey  
5 field met by the juvenile sockeye salmon (*O. nerka*) when they had been feeding, we needed to  
6 determine how quickly juvenile sockeye digested their prey. To accomplish this, we performed a  
7 small feeding experiment at a floating field facility comprised of several floating docks and net  
8 pens. We collected fish at the same Johnstone Strait location used in the main study and  
9 transported them by boat for 1 h to the experimental facility (see Fig. 1 in Godwin et al. (2015)  
10 for map). During transport, the sockeye were again held in insulated fish totes with bubblers and  
11 ice packs. We did not collect temperature or salinity data for this experiment, but previous  
12 studies using the same experimental facility and juvenile salmon collection sites have indicated  
13 that their water temperatures and salinities are very similar (Atkinson et al. In review; Godwin et  
14 al. 2015).

15 Upon arrival at the facility, we transferred the fish to a large (2.8 m deep and 6.1 x 6.1 m  
16 across) net pen and weaned them onto frozen brine shrimp (Brine Shrimp Direct, Ogden, Utah,  
17 USA) over the next five days. Brine shrimp were thawed in freshwater and were fed to the fish  
18 by adding them to the center of the net pen. Medium-sized fish (between 107 and 120 mm) were  
19 removed for another study, leaving 31 smaller ( $104.1 \text{ mm} \pm 0.4 \text{ mm}$ ) and 37 larger ( $124.9 \pm 0.7$   
20 mm) fish. The fork length range of these experimental fish was 97 mm to 132 mm, which was  
21 fully within the fork length range of the fish from the main study (88 mm to 133 mm).

22 One hour after sunrise on their sixth day at the experiment facility, the 68 fish were fed to  
23 satiation and ten were immediately sacrificed with a lethal dose of MS-222. At half, one, two,

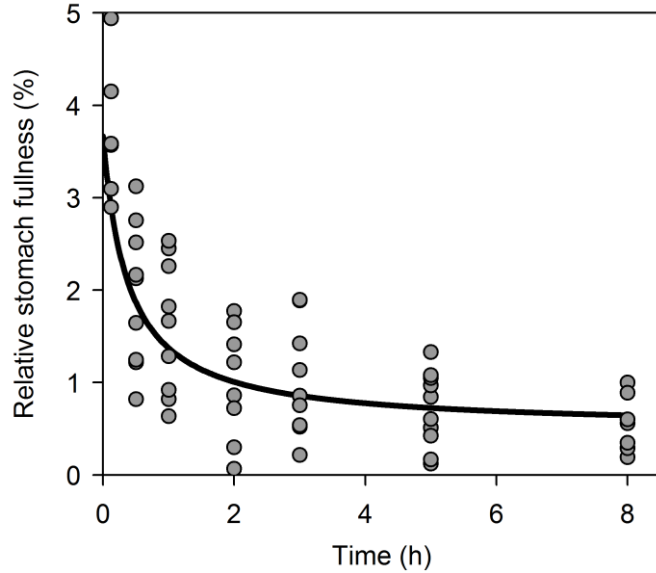
24 three, five hours after initial feeding, ten fish were again randomly removed and euthanized,  
25 leaving remaining fish. At eight hours, these eight fish were removed and euthanized. We  
26 weighed the wet stomach contents of the fish in the same manner as for those sacrificed in the  
27 field, and calculated relative stomach fullness by dividing the weight of each fish by the weight  
28 of its wet stomach contents.

29 We fit a Michaelis-Menten curve to the relative stomach fullness data and used these  
30 parameter estimates to calculate the amount of digestion that occurred between time points in the  
31 experiment.

32

### 33 *Results*

34 The digestion rate of the experimental fish began high and gradually slowed over time  
35 (Fig. A1). Six fish did not consume any brine shrimp and were therefore removed from the  
36 dataset. After one hour, 37% of the initial stomach contents remained, and after the final hour of  
37 the experiment (hour eight) only 18% remained. The predicted relative stomach fullness of the  
38 experimental fish at hour eight (0.6%) was similar to the mean relative stomach fullness of the  
39 main study's fish (0.6%), suggesting that most of the main study's fish must have eaten in the  
40 previous eight hours since not all of them would have fed to satiation like the experimental fish.



41

42 Fig. A1. Relative stomach fullness of juvenile sockeye salmon over the course of the digestion

43 rate experiment, with a Michaelis-Menten curve fit to the data (black line). Six fish were

44 removed from this dataset because they did not consume any food.

45

46 **References**

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