

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

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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, British Columbia, 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 mass divided by body mass), 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 sublethal effects of parasites on salmonids and possibly other fish species.

Résumé : Les parasites peuvent moduler le succès d'approvisionnement, mais ce phénomène n'est pas bien compris en ce qui concerne les poissons marins, dont les groupements et la répartition parcellaire des proies créent des conditions favorables à une concurrence intraspécifique intense. Nous avons vérifié si les infections aux poux du poisson sont associées à la plénitude stomacale des saumons rouges (*Oncorhynchus nerka*) juvéniles sauvages dans le détroit de Johnstone (Colombie-Britannique) durant leur migration vers la mer à partir du fleuve Fraser. *Caligus clemensi* représente 98,6 % des poux du poisson préadultes et adultes et 86,5 % des copépodites (individus récemment fixés), alors que *Lepeophtheirus salmonis* constitue le reste. Nous avons constaté que l'état d'infection est un important prédicteur de la plénitude stomacale relative pour les saumons rouges juvéniles (masse humide du contenu stomacal divisée par la masse corporelle), comme l'indique la sélection de modèles à effets mixtes, et que la plénitude stomacale relative de poissons fortement infectés est de $17\% \pm 8\%$ inférieure à celle des poissons peu infectés. Cette réduction de la plénitude stomacale relative associée aux poux se produit au moment où les jeunes saumons rouges en migration passent par un milieu où la nourriture est restreinte et où la concurrence est probablement forte. Comme la croissance précoce en mer des saumons juvéniles est souvent une variable prédictive de la survie, nos résultats soulignent l'importance d'une bonne compréhension des effets sublétaux des parasites sur les salmonidés et possiblement d'autres espèces de poissons. [Traduit par la Rédaction]

Introduction

Foraging success is tightly linked to growth and survival of individuals, both of which are predictors of fitness and population dynamics (Crombie 1947; Sutherland 1996). Fish frequently experience patchy foraging opportunities and aggregate in large groups that intensify competition (see review by Ward et al. 2006), and consequently survival often depends on these competitive outcomes (e.g., Resetarits 1995; Welker et al. 1994). This is especially the case for juvenile fishes, whose early growth depends on food supply and often determines survival and recruitment (Anderson 1988; Bergenius et al. 2002; Houde and Hoyt 1987). Evidence suggests that parasites affect competitive foraging outcomes of hosts, thereby influencing host population dynamics, community structure, and biodiversity (see Hatcher et al. 2006). However, this evidence is primarily from terrestrial species (e.g., Grosholz 1992; Maksimowich and Mathis 2000; Schall 1992). Despite what is likely a

more competitive environment with food patchiness and consumer aggregation for fishes, there is little work in the fisheries literature on how parasites mediate competition in wild fishes and whether this translates to decreased survival through reduced foraging success and growth (but see Finley and Forrester 2003).

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

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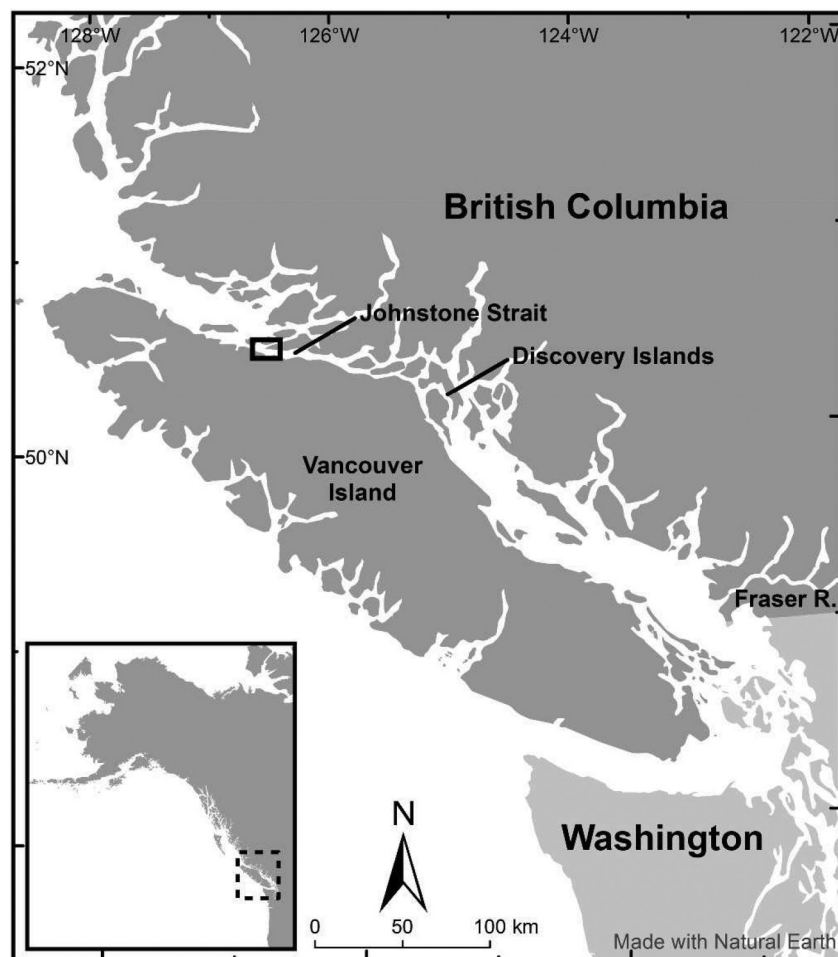
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Fig. 1. Map of study region. The black box in the main panel indicates the area in which salmon collections occurred.



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

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

In recent years, the generalist *C. clemensi* has infected over 98% of out-migrating juvenile sockeye salmon (*Oncorhynchus nerka*) from the Fraser River (Godwin et al. 2015, 2017), an iconic set of Pacific salmon populations that forms Canada's largest sockeye run. Juvenile sockeye salmon that experience high infection intensity by

C. clemensi exhibit reduced foraging success in a competitive and food-limited experimental setting (Godwin et al. 2015). Whether this translates to reduced foraging success in the wild is still unknown, but this is the focus of this work. Here, we tested whether the relative stomach fullness (wet stomach content mass divided by body mass) of wild juvenile sockeye is lower when sea louse infection intensity is higher, which has implications for our understanding of how parasites mediate competition in fishes and potentially for the management of *C. clemensi* in British Columbia.

Methods

Fish collection

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

We transferred captured fish from the net into an insulated fish tote (0.58 m deep and 0.97 m × 0.55 m across) filled with fresh seawater. We moved fish from the net into the tote by dipping them and their surrounding seawater into a 3.79 L container (an inverted milk jug with the top capped and bottom cut off). This transfer method minimized or prevented sea louse detachment as

fish were never exposed to air and there was minimal contact between the fish and sampling equipment (Godwin et al. 2015). All subsequent transfers were also performed using the same method. We used ice packs to regulate water temperature in the tote and aquarium bubblers to maintain adequate aeration. We transferred 50–100 sockeye into the tote during each capture event. See online Supplementary Table S1¹ for collection locations, catch sizes, and oceanographic data.

Infection status assessment

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

Larger, more developed sea lice have greater effects on their hosts (Jakob et al. 2013; Nendick et al. 2011; Wootten et al. 1982). We created infection categories that reflected this differential level of pathogenicity, so that small juvenile lice were not weighted equally to large adult lice (similar to Peacock et al. 2015). Sea lice initially attach to their host as copepodites, then develop through two (*L. salmonis*; Hamre et al. 2013) or four (*C. clemensi*; Kabata 1972) attached chalimus stages of increasing size before molting into their motile pre-adult and adult stages. Here, we consider individuals in their second *L. salmonis* chalimus stage or their third or fourth *C. clemensi* chalimus stages as “large chalimus” sea lice; we also consider pre-adult and adult individuals as “motile” sea lice. To weight the infection statuses of fish according to the development of lice infecting them, we defined a louse infection scale in which one large chalimus louse was equal to one infection unit, one motile louse was equal to two infection units, and copepodite and small chalimus lice were equal to zero. Because of the high infection prevalence observed (>98%), we were unable to create a category for uninfected fish. Instead, we created a “lightly infected” category in which all the fish had zero infection units and no more than three copepodite or small chalimus lice (Table 1). In all collections, the “lightly infected” and “highly infected” categories differed by a minimum of three infection units. See Supplementary Table S2¹ for the detailed sea louse infection data.

Approximately 1 h after capture, we released the remaining fish at the collection site. In each collection, we retained five to seven pairs of fish, each consisting of a lightly and highly infected sockeye. In total, we retained 130 juvenile sockeye salmon from across 11 collections to analyze stomach fullness in relation to infection status.

Zooplankton sampling and analysis

Immediately following the infection status assessments and subsequent release of fish, we collected zooplankton samples with a horizontal plankton tow at the fish capture site. Plankton tows were performed with a 0.5 m diameter plankton net with 250 µm mesh. The top of the net was kept 5–10 cm below the ocean surface, on average, and the tow lasted for 30 s. We attached

Table 1. Infection categories and sample sizes for each fish collection.

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
Mean	5.9	0.0	2.5	4.3	5.8

Note: The infection scale was weighted such that one large chalimus louse was equal to one infection unit, one motile louse was equal to two infection units, and copepodite and small chalimus lice were equal to zero units. For each collection, a single fish pair was composed of one fish from the highly infected category and one from the lightly infected category.

a calibrated flow meter (General Oceanics, Miami, Florida, USA) at the mouth of the net to measure the volume of water sampled. We used horizontal tows instead of vertical ones because plankton samples near the surface are more similar to sockeye diets than those from deeper in the water column (Landingham et al. 1998), and our field observations indicate that juvenile sockeye frequently occupy the surface waters at the collection sites.

Each plankton sample was placed in a glass jar containing 250 mL of 10% formalin–seawater solution. Within 3 days of the collection, the samples were poured into a 63 µm sieve and rinsed with distilled water. The samples were then halved repeatedly using a Folsom plankton splitter (Aquatic Research Instruments, Hope, Idaho, USA) until approximately 200–250 individuals remained, after which they were transferred to a Bogorov counting tray (Wildlife Supply Company, Yulee, Florida, USA). From these samples, we identified and enumerated individuals from the high-level taxa previously found in juvenile Fraser River sockeye salmon stomachs (Price et al. 2013); these were termed “sockeye prey”. These high-level taxa from Price et al. (2013) were Copepoda, Brachyura, Oikopleura, Euphausiacea, Cladocera, Pteropoda, Decapoda, Amphipoda, Insecta, Cumacea, fish, and eggs. We calculated sockeye prey density by multiplying the number of sockeye prey in the Bogorov tray by the reciprocal of the splitting fraction, then dividing by the volume of water that passed through the plankton net.

Determination of relative stomach fullness

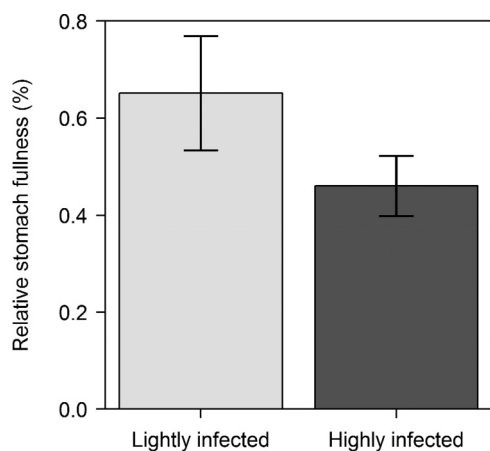
We used wet stomach content mass as our measure of stomach fullness and divided this by the fish’s body mass to calculate relative stomach fullness. Following the field collections, we transported the euthanized fish on ice to a laboratory facility 45 min away by boat. Upon arrival at the laboratory,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

Statistical analysis

To determine which biological variables best explained juvenile sockeye salmon relative stomach fullness, we fit a suite of

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0267>.

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.



13 mixed-effects models to our data (see Supplementary Table S3¹ for the full model set). Our models included the biologically relevant combinations of five fixed effects: infection status, body size, prey density, the two-way interaction between infection status and body size, and the two-way interaction between infection status and prey density. We included infection status as a fixed effect to test our main hypothesis that relative stomach fullness decreases with high intensities of sea louse infection. We included body size and its interaction with infection status to account for any additional benefit of a larger body size to relative stomach fullness and the potential decreasing effect of infection with body size (Godwin et al. 2015). Finally, we included prey density and its interaction with infection status to account for the probable association between relative stomach fullness and prey density and the possible decreasing effect of infection with increasing density of prey. Prey density and relative stomach fullness were centered and scaled by one standard deviation to allow the model-fitting optimizer to function correctly, since their variances were different by 10 orders of magnitude. Each model included a random effect of collection number on the intercept, which was determined a priori to account for the hierarchical structure of the sampling design, and a variance structure allowing for different variances in each collection to account for heteroscedasticity in the residuals. We performed model selection using Akaike information criterion corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989) as our measure of model parsimony. We calculated relative variable importance (RVI) values based on the AIC_c weights.

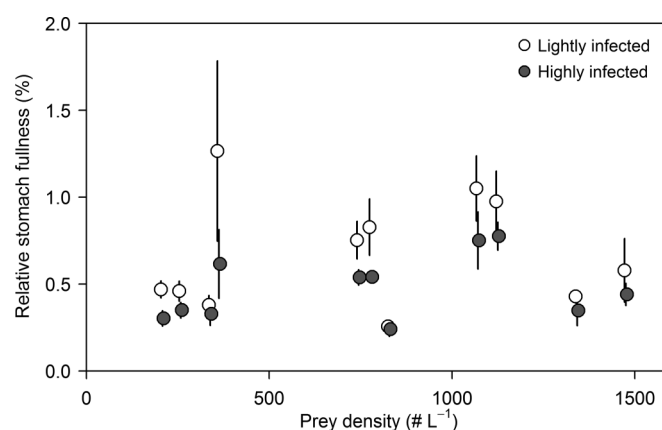
We derived our measure of body size from a principal component analysis using three highly correlated body metrics: fork length, body depth, and mass. The first principal component explained 98% of the original variation in these metrics, and so we used that as the variable representing body size in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

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

Results

The juvenile sockeye salmon in our highly infected category were primarily infected by *C. clemensi* rather than *L. salmonis*, with 98.6% of the motile sea lice and 86.5% of the copepodid lice infect-

Fig. 3. Mean relative stomach fullness (\pm SE) for fish in both infection categories of each collection. Each vertical pair of points (one grey, one white) constitutes a single collection. The relationship between relative stomach fullness and prey density had equivocal support in our model selection results (see Table S3¹).



ing these fish belonging to the former species. Neither motile abundance ($R^2 = 0.009$, $df = 63$, $p = 0.455$) nor overall louse abundance ($R^2 = 0.025$, $df = 63$, $p = 0.207$) increased with body size for fish in the highly infected category. Body size also did not differ between infection categories ($t = 0.282$, $df = 128$, $p = 0.779$). The mean (\pm SE) zooplankton density across all collections was 941 ± 141 individuals·L⁻¹, and sockeye prey density was 772 ± 134 individuals·L⁻¹, indicating that potential sockeye prey constituted 82% of the zooplankton community in the surface waters during our collections.

Lightly infected fish had higher relative stomach fullness than highly infected fish (Fig. 2), and this trend held in each of the 11 collections (Fig. 3). Infection status was the most important predictor of relative stomach fullness; of the 13 mixed-effects models, the top nine all included an infection status term, while none of the bottom four did (Supplementary Table S3¹). The importance of infection status to relative stomach fullness was corroborated by this predictor having the highest RVI (0.97), compared with body size (0.66), prey density (0.60), the interaction between infection status and prey density (0.16), and the interaction between infection status and body size (0.14). Regardless of their rank, all models with the relevant terms revealed that relative stomach fullness was higher for lightly infected fish, that it increased with body size, and that it increased with prey density. The top-ranked model included only an infection status term, but two other models were within 2 AIC_c units of the top model and therefore also had substantial support (Burnham and Anderson 2002; Table 2). One of these highly supported models included a body size term, while the other included a predictor for prey density (Table 2).

The highest-ranked model without an infection status predictor was 7.8 AIC_c units higher than the top model and accounted for only 0.7% of model support, as judged by AIC_c weights (Supplementary Table S2¹). The top-ranked model was 51 times more likely than the highest-ranked model without an infection status predictor, and its coefficients indicated that highly infected fish had $17\% \pm 8\%$ lower relative stomach fullness than lightly infected fish, on average.

Discussion

Theory and empirical evidence suggest that pathogens and parasites can influence host survival and population dynamics by modulating competitive foraging interactions (Hatcher et al. 2006). However, there is little evidence of parasite-mediated intraspecific competition in wild fishes, for whom intraspecific competi-

Table 2. Model selection results for the six models of relative foraging success that accounted for at least 5% of model support.

Rank	Model	ΔAIC_c^*	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 \times size	3.85	0.052	0.530
6	Infection \times prey	3.91	0.051	0.536

Note: Relative stomach fullness was calculated as wet stomach content mass divided by body mass. The models included combinations of infection category (infection), body size (size; see description of principal component analysis), and prey density fixed effects. Each model included a random effect on the intercept for collection number. Interaction terms are distinguished with a times symbol (\times). See Supplementary Table S3¹ for the full model set and selection results.

*Difference from the top model AIC_c (ΔAIC_c).

[†]Akaike model weight (w_i).

[‡] R^2 for mixed-effects models calculated using the method developed by Nakagawa and Schielzeth (2013).

tion may be particularly intense due to fish aggregation and food patchiness. Our results indicate that for wild juvenile sockeye salmon, high levels of sea louse infection are associated with reduced relative stomach fullness. The juvenile sockeye used in this study were captured during their early marine migration from their natal freshwater systems, which, based on the timing of capture and genetic analyses from previous studies (Godwin et al. 2017; Groot and Cooke 1987; Price et al. 2011), were mostly in the Fraser River watershed of British Columbia.

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

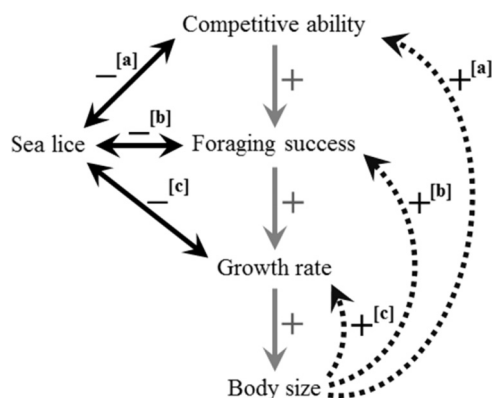
Animal migration is generally demanding metabolically, so managing energy gain and depletion is vital for most migrating animals to avoid starvation or the sublethal effects of depleted energy reserves (Sapir et al. 2011). Unlike some migratory species, juvenile sockeye salmon forage during their migration, but this foraging is temporally variable because feeding opportunities are patchy (McKinnell et al. 2014; Parsons et al. 1970). In regions with relatively high productivity, such as the northern Strait of Georgia, British Columbia (Masson and Peña 2009; Parsons et al. 1970), no evidence of food limitation has been observed (Price et al. 2013). By contrast, the region in which we captured fish for this study (i.e., Johnstone Strait) has a sparse prey field due to strong tidal mixing (B.P.V. Hunt, S. Godwin, L.A. Rogers, E. Pakhomov, and M. Krkošek, Hakai Institute, unpublished data), which may cause high mortality for juvenile sockeye that enter the Strait with insufficient energy reserves (McKinnell et al. 2014). Sea lice levels on juvenile sockeye are also considerably higher in Johnstone Strait than in the more productive southern regions (Godwin et al. 2015; Price et al. 2011). Hence, the potential effects of sea lice on sockeye salmon growth and survival in Johnstone Strait are likely to involve the elevated

abundances of the parasite itself, its effects on intraspecific competition, and the intensification of competition due to food limitation and the energy expenditure of migration.

Our results provide equivocal evidence for an association between prey density and the relative stomach fullness of juvenile sockeye. If food competition is indeed higher in Johnstone Strait for sockeye than in nearby regions and that contributed to our finding that relative stomach fullness is associated with heavy sea louse infection, then we might have expected to find a stronger relationship between prey density and relative stomach fullness. Only one of our three models with considerable support (as judged by AIC_c values; Burnham and Anderson 2002) contained a prey density predictor, which across our model set was our third most important predictor variable ($RVI = 0.60$). It is possible that prey density did not severely limit relative stomach fullness of sockeye in Johnstone Strait in 2014 even if food availability is commonly much lower there than in the Strait of Georgia (McKinnell et al. 2014; B.P.V. Hunt, S. Godwin, L.A. Rogers, E. Pakhomov, and M. Krkošek, Hakai Institute, unpublished data). However, if the prey field was not limiting sockeye foraging rates, then we might not expect to observe the differences in relative stomach fullness between infection categories that we did, since highly infected (and therefore less competitive; Godwin et al. 2015) individuals would still have the opportunity to feed to satiation. It is also possible that the prey density estimates from our zooplankton collections did not represent the prey field encountered by the fish when they were feeding, due to patchiness in time or space (Parsons et al. 1970) or due to the strong tidal currents known to occur in Johnstone Strait (Sutherland et al. 2007). Most of the sockeye in this study must have eaten in the preceding 8 h (see Appendix A), which limits the potential effects of patchiness and currents on our results, but these remain possibilities that cannot be excluded. Perhaps the most likely explanation for our equivocal evidence of a relationship between prey density and relative stomach fullness was that the sample size of 11 collection sites was too small to detect an effect. While our study design was suitable for looking at consistent differences in relative stomach fullness within groups, the sample size was limited for investigating variation among collections.

The relationship that we found between sea louse infection and relative stomach fullness is correlative, but the weight of evidence is building that sea lice have sublethal effects on important determinants of sockeye salmon survival. Sea lice are associated with Pacific salmon population declines (Connors et al. 2010; Krkošek et al. 2011a), but these declines cannot be explained by direct mortality alone, which may only be significant at small host sizes (Jones et al. 2008). However, sea lice also appear to have sublethal effects that influence mortality through their hosts' ecological interactions, for example by reducing swimming endurance (Mages and Dill 2010), increasing risk-taking behaviours (Krkošek et al. 2011b), and elevating predation (Peacock et al. 2015). For juvenile sockeye salmon specifically, individuals that are heavily infected by sea lice, primarily *C. clemensi*, have lower competitive foraging ability (Godwin et al. 2015), reduced body growth (Godwin et al. 2017), and actively attempt to dislodge these parasites by leaping (Atkinson et al., in press). Nonetheless, laboratory studies utilizing experimental infections are needed to help differentiate two alternative interpretations of our results: (i) that sea lice abundance is a consequence rather than a cause of variation in relative stomach fullness or (ii) that sea louse abundance and relative stomach fullness are both correlated with (signals of) fundamental underlying fitness variation among individuals. We consider these alternative explanations to be unlikely because they both require sustained differences in relative stomach fullness that would have led to a difference in body size between the two infection categories, which was not observed. It is also striking that the observed louse-associated differences in relative stomach fullness occurred in each of the 11 collections (Fig. 3), so any correlation between an

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.



underlying condition and sea louse infection would have to be very strong indeed.

In addition to our main result that heavy sea louse infection is associated with reduced sockeye stomach fullness, we also found moderate evidence that relative stomach fullness increased with body size. This result runs counter to the negative exponential relationship between relative stomach fullness and body size reported by Brett (1971) for juvenile sockeye, suggesting that larger juvenile sockeye may have a foraging advantage due to their body size. The obvious potential mechanism for this is that smaller sockeye are prevented from foraging on larger (and possibly more abundant) prey due to gape limitation, which often, but not always, determines foraging success in young fish (Bremigan and Stein 1994; Devries et al. 1998; Hargreaves and LeBrasseur 1986; Scharf et al. 2000). Together with the relationship between infection status and relative stomach fullness, this potential effect of body size would be consistent with our previous findings that high infection intensities and smaller body sizes are associated with lower competitive foraging ability (Godwin et al. 2015) and reduced growth (Godwin et al. 2017) for juvenile sockeye. When considered together (Fig. 4), these interconnected relationships suggest that sea louse infection may not just be accompanied by a single, temporary effect for the duration of infection. Infection may instead have long-lasting effects by initiating and (or) intensifying divergent growth among individuals through differences in foraging success, which would create and reinforce intraspecific heterogeneity in body sizes and ultimately differential survival. To detect such differences in body size, the amount of time between sea louse exposure and fish collection would need to be greater than that of this study (3–10 days; Price et al. 2011; Welch et al. 2011), since the small amount of differential body growth that would occur between infection categories in that time (<0.5 mm; Godwin et al. 2017) would be statistically swamped by the individual-level variation in body size. This potential for lasting effects of sea lice on factors critical to sockeye survival highlights the need to consider the anthropogenic influence on the parasite burdens of these fish and potentially reduce it through management actions when possible.

Over 98% of the motile sea lice infecting the juvenile sockeye salmon were *C. clemensi*, but although these infections have been linked to open net-pen salmon farms (Price et al. 2011), there are currently no management actions directed at regulating this louse species on farms in British Columbia. *Lepeophtheirus salmonis*, the main species of sea louse that causes fish mortality and financial loss to salmon aquaculture in the Northern Hemisphere (Costello

2009a; Johnson et al. 2004; Mustafa et al. 2001), is controlled on British Columbia farms through application of in-feed parasiticide (emamectin benzoate; Saksida et al. 2010) when their abundance exceeds three motile lice per fish (Fisheries and Oceans Canada 2016). While emamectin benzoate also reduces *C. clemensi* numbers, *C. clemensi* abundance is not directly managed. Since *Caligus* spp. are considered less pathogenic than *L. salmonis* (Igboeli et al. 2014; Johnson et al. 2004) and most of the research into the effects of sea lice on wild salmon has focussed on *L. salmonis* (e.g., Connors et al. 2010; Johnson et al. 1996; Krkošek et al. 2005b), there has been little reason to target *C. clemensi* with treatments on farms until now. However, given the mounting evidence for sublethal effects of *C. clemensi* on wild salmon and the ability for *C. clemensi* to reach extreme abundances on farms without targeted treatment (e.g., 100% prevalence and 47.2 lice per fish; Di Cicco et al. 2017), it seems prudent to start considering *C. clemensi* in the fish health management plans of farmed salmon in British Columbia.

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

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Appendix A. Juvenile sockeye salmon digestion experiment

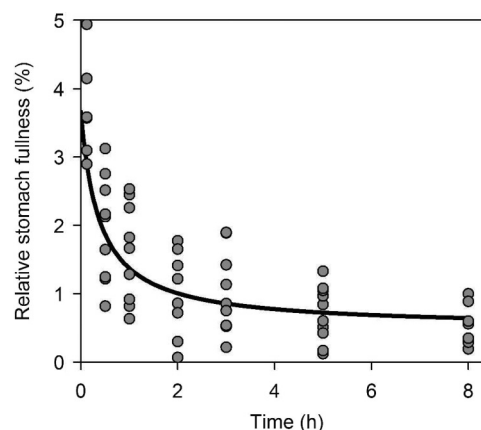
Methods

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

Upon arrival at the facility, we transferred the fish to a large (2.8 m deep and 6.1 m × 6.1 m across) net pen and weaned them onto frozen brine shrimp (Brine Shrimp Direct, Ogden, Utah, USA) over the next 5 days. Brine shrimp were thawed in fresh water and were fed to the fish by adding them to the center of the net pen. Medium-sized fish (between 107 and 120 mm) were removed for another study, leaving 31 smaller (104.1 ± 0.4 mm) and 37 larger (124.9 ± 0.7 mm) fish. The fork length range of these experimental fish was 97 to 132 mm, which was fully within the fork length range of the fish from the main study (88 to 133 mm).

One hour after sunrise on their sixth day at the experiment facility, the 68 fish were fed to satiation and 10 were immediately sacrificed with a lethal dose of MS-222. At 30 min and 1, 2, 3, and 5 h after initial feeding, 10 fish were again randomly removed and euthanized, leaving remaining fish. At 8 h, these eight fish were removed and euthanized. We weighed the wet stomach contents of the fish in the same manner as for those sacrificed in the field and calculated relative stomach fullness by dividing the mass of each fish by the mass of its wet stomach contents.

Fig. A1. Relative stomach fullness of juvenile sockeye salmon over the course of the digestion rate experiment, with a Michaelis–Menten curve fit to the data. Six fish were removed from this data set because they did not consume any food.



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

Results

The digestion rate of the experimental fish began high and gradually slowed over time (Fig. A1). Six fish did not consume any brine shrimp and were therefore removed from the data set. After 1 h, 37% of the initial stomach contents remained, and after the final hour of the experiment (hour 8) only 18% remained. The predicted relative stomach fullness of the experimental fish at

hour 8 (0.6%) was similar to the mean relative stomach fullness of the main study's fish (0.6%), suggesting that most of the main study's fish must have eaten in the previous 8 h, since not all of them would have fed to satiation like the experimental fish.

References

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- Godwin, S.C., Dill, L.M., Reynolds, J.D., and Krkošek, M. 2015. Sea lice, sockeye salmon, and foraging competition: lousy fish are lousy competitors. *Can. J. Fish. Aquat. Sci.* 72(7): 1113–1120. doi:10.1139/cjfas-2014-0284.