

Differential infestation of juvenile Pacific salmon by parasitic sea lice in British Columbia, Canada

Cole B. Brookson, Martin Krkošek, Brian P.V. Hunt, Brett T. Johnson, Luke A. Rogers, and Sean. C. Godwin

Abstract: Fraser River Pacific salmon have declined in recent decades, possibly from parasitism by sea lice (*Caligus clemensi* and *Lepeophtheirus salmonis*). We describe the abundance of both louse species infesting co-migrating juvenile pink (*Oncorhynchus gorbuscha*), chum (*Oncorhynchus keta*), and sockeye (*Oncorhynchus nerka*) salmon over 5 years in the Discovery Islands and Johnstone Strait, British Columbia. The generalist louse, *C. clemensi*, was 5, 7, and 39 times more abundant than the salmonid specialist, *L. salmonis*, on pink, chum, and sockeye salmon, respectively. *Caligus clemensi* abundance was higher on pink salmon (0.45, 95% CI: 0.38–0.55) and sockeye (0.39, 95% CI: 0.33–0.47) than on chum salmon. *Lepeophtheirus salmonis* abundance was highest on pink salmon (0.09, 95% CI = 0.06–0.15). *Caligus clemensi* had higher abundances in Johnstone Strait than in the Discovery Islands. These results suggest differences in host specialization and transmission dynamics between louse species. Because both lice infest farmed salmon, but only *C. clemensi* infests Pacific herring (*Clupea pallasii*), conservation science and management regarding lice and Fraser River salmon should further consider *C. clemensi* and transmission from farmed salmon and wild herring.

Résumé : Les saumons du Pacifique du fleuve Fraser ont subi un déclin au cours des récentes décennies, possiblement en raison du parasitisme de poux de mer (*Caligus clemensi* et *Lepeophtheirus salmonis*). Nous décrivons l'abondance des deux espèces de poux de mer qui infestent des saumons roses (*Oncorhynchus gorbuscha*), kéta (*Oncorhynchus keta*) et sockeyes (*Oncorhynchus nerka*) juvéniles qui migrent en même temps, sur une période de 5 ans, dans les îles Discovery et le détroit de Johnstone (Colombie-Britannique). Le pou généraliste *C. clemensi* était 5, 7 et 39 fois plus abondant que le pou spécialiste des salmonidés *L. salmonis* chez les saumons roses, kéta et sockeyes, respectivement. L'abondance de *C. clemensi* était plus grande chez les saumons roses (0,45, IC 95 % : 0,38–0,55) et sockeyes (0,39, IC 95 % : 0,33–0,47) que chez les saumons kéta. L'abondance de *L. salmonis* était la plus grande chez les saumons roses (0,09, IC 95 % : 0,06–0,15). *Caligus clemensi* était présent en plus grande abondance dans le détroit de Johnstone que dans les îles Discovery. Ces résultats indiqueraient des différences sur le plan de la spécialisation par rapport aux hôtes et de la dynamique de transmission entre espèces de poux de mer. Comme les deux poux infestent les saumons d'élevage, mais que seul *C. clemensi* parasite le hareng du Pacifique (*Clupea pallasii*), la recherche scientifique sur la conservation et la gestion visant les poux et les saumons du fleuve Fraser devraient accorder une attention accrue à *C. clemensi* et à la transmission à partir de saumons d'élevage et de harengs à l'état sauvage. [Traduit par la Rédaction]

Introduction

Parasitism can influence fish recruitment and population growth via direct mortality and potentially through parasite-mediated sublethal effects on host behaviour, growth, predation risk, and reproductive success (Williams 1964; Barber et al. 2000; Longshaw et al. 2010; Krkošek et al. 2013b). Many fish parasites are generalists, infecting multiple host species, which can lead to apparent competition — indirect competition via some shared natural enemy (Hudson and Greenman 1998) — among host populations. Generalist parasites can persist even when the abundance of a focal host species is low by infesting a reservoir host

species, leading to spill-over and spill-back dynamics that are relevant for management of farmed and wild stocks (Hedrick 1998; de Castro and Bolker 2005). Such is the case in the coastal waters of British Columbia (BC), Canada, where a specialist parasite, *Lepeophtheirus salmonis* (Johnson and Albright 1991), infects wild Pacific salmon (*Oncorhynchus* spp.) and farmed Atlantic salmon (*Salmo salar*), while these salmon along with Pacific herring (*Clupea pallasii*) share a generalist fish parasite, *Caligus clemensi* (Parker and Margolis 1964). Both of these parasites are ectoparasitic copepods broadly called “sea lice”. All of the host fish species are commercially important, and numerous populations of wild salmon and

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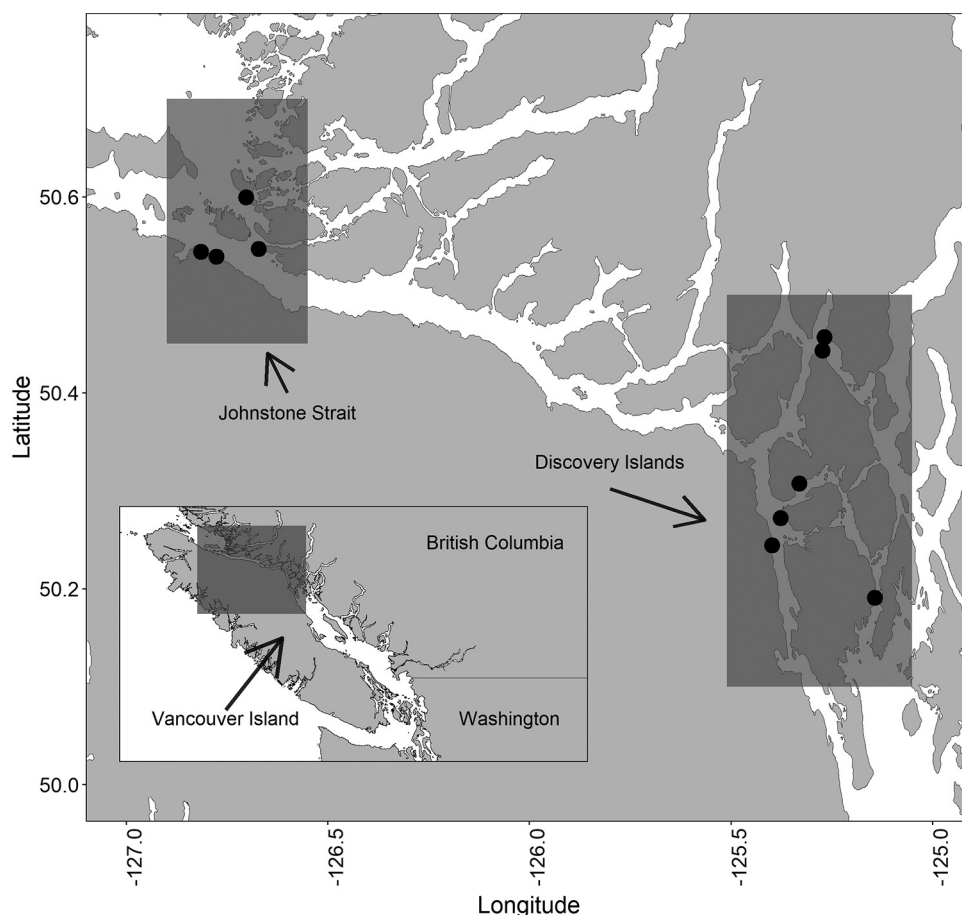
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Fig. 1. Our study region on the west coast of British Columbia, Canada. All collection sites were in the sampling areas of Discovery Islands or Johnstone Strait, wedged between the western coast of the mainland and the east coast of Vancouver Island. The Discovery Islands is a hotspot of salmon farming in British Columbia. Map was created in R, version 4.0.1 (R Core Team 2020). Base map data was pulled from the ggplot2 package (Wickham 2016), and site locations are available from the Juvenile Salmon Program database (Johnson et al. 2020).



herring are also a focus for conservation. Prevalence of *L. salmonis* and *C. clemensi* on wild juvenile salmon is positively correlated with the presence of Atlantic salmon farms in BC (Marty et al. 2010; Price et al. 2011). How the dynamics of *L. salmonis* and *C. clemensi* vary among Pacific salmon species, however, is not well resolved, nor is the role of herring in this host–parasite system, which may serve as a natural reservoir host population for *C. clemensi* (Morton et al. 2008; Beamish et al. 2009).

Pacific salmon support some of the most important fisheries in Canada and are of ecological, cultural, and historical importance (Hilderbrand et al. 2004; Scheuerell et al. 2005; FAO 2015). Populations of Pacific salmon have experienced major declines in recent decades, for example, sockeye salmon (*Oncorhynchus nerka*) from the Fraser River, whose decline triggered a CAN\$37 million federal judicial inquiry (Cohen 2012). This inquiry identified the early marine phase as a potentially critical life stage for overall survival and recruitment of Fraser River salmon populations and specifically called for investigation into the interactions between migrating wild juvenile salmon and sea lice (Peterman et al. 2010; Cohen 2012). Sockeye, pink (*Oncorhynchus gorbuscha*), and chum (*Oncorhynchus keta*) salmon from the Fraser River enter the marine environment in the Strait of Georgia and primarily migrate through the Discovery Islands and Johnstone Strait, before passing through Queen Charlotte Sound to the open ocean (Fig. 1). When juvenile salmon leave their natal freshwater systems for their early marine migration, they experience multiple stressors, including variable prey availability, predators, and parasites (Hunt et al. 2018).

The sea lice *C. clemensi* and *L. salmonis* are native to BC, and both feed on the surface tissues, musculature, and blood of their host fish (Costello 1993; Krkošek et al. 2009). Sea lice are unable to survive in freshwater environments (Bricknell et al. 2006), but naturally infest juvenile salmon at low intensities after the fish migrate into the marine environment in spring. The abundances of sea lice observed on juvenile salmon in spring are a result of transmission from other wild fish species and farmed salmon, with most migratory adult salmon not having returned yet to coastal waters (Groot and Margolis 1991; Krkošek et al. 2005a). Juvenile sockeye in the Discovery Islands and Johnstone Strait are infected primarily by *C. clemensi* (Price et al. 2011; Godwin et al. 2015), but there are no estimates comparing infestation by both *C. clemensi* and *L. salmonis* among co-migrating juveniles of sockeye, pink, and chum salmon in the Discovery Islands and Johnstone Strait — an area with high density of salmon farms and wild herring (Beamish et al. 2009) (Fig. 1).

In this paper we compare *L. salmonis* and *C. clemensi* abundance from co-migrating groups of juvenile pink, chum, and sockeye salmon in the Discovery Islands and Johnstone Strait, BC, over 5 years of field surveys. We investigate possible sources of variation between louse species in their specialization among Pacific salmon species by focusing on the relative abundances of the two louse species on the three salmon species in our study. We also characterize the dynamics of sea lice on wild salmon relative to other areas with salmon farming in BC and the North Atlantic. While many systems are typically dominated by *L. salmonis* associated with farmed salmon (Mustafa and MacKinnon 1999; Marty

et al. 2010; Krkošek et al. 2013b), we explore the possibility of this particular region and species set being characterized more by *Caligus* from wild herring and farmed salmon reservoir host populations.

Methods

Data collection and preparation

The data used in this study originate from the Hakai Institute's Juvenile Salmon Program (JSP; Johnson et al. 2020). The JSP has conducted annual surveys of out-migrating juvenile salmon in the Discovery Islands and Johnstone Strait areas of BC since 2015, with the overarching aim to determine the drivers of early marine mortality in juvenile sockeye, pink, and chum salmon. These surveys include sampling sea louse abundances on juvenile sockeye, pink, and chum salmon. Detailed sampling methods for the JSP are described in Hunt et al. (2018). Briefly, we collected juvenile salmon via a hand-retrieved purse seine (bunt: 27 m × 9 m with 13 mm knotless mesh; tow: 46 m × 9 m with 76 mm knotless mesh) at sites in the two sampling areas, once or twice weekly during May–July when juvenile salmon migrate through the area. Our sites were located at the entry points to the Discovery Islands from the Strait of Georgia and the exit points from Johnstone Strait to Queen Charlotte Strait (Fig. 1). We deployed the purse seine nets from open, 6–8 m twin-outboard research vessels to capture heterospecific schools composed of juvenile pink, chum, sockeye, Chinook (*Oncorhynchus tshawytscha*), and coho (*Oncorhynchus kisutch*) salmon, along with Pacific herring. Visual survey transects of surface activity were used to identify areas with juvenile salmon, with the purse-seine net only being deployed if juvenile salmon were observed.

Once we deployed the seine, it was used to corral the fish beside the boat in a submerged section of the bunt end of the net so that the captured fish remained in the water and had space to swim freely within the net. A subset of each species were individually and haphazardly captured from different depths and locations of the seine net in the standard manner (Krkošek et al. 2005a; Peacock et al. 2016), but using an inverted 4 L plastic jug with the end cut off instead a dipnet to prevent louse detachment (as in Atkinson et al. 2018; Godwin et al. 2018; Hunt et al. 2018). They were then transferred to a sample bag (532 mL Whirl-Pak Write-On sample bag), euthanized with a 250 mg·L⁻¹ concentration of tricaine methanesulfonate (TMS), then drained and transferred to a liquid nitrogen-cooled (−196 °C) dry-shipper, where they were flash-frozen for future analyses. We retained up to 30 sockeye and 10 of each other species from every collection, and all remaining fish were released. In 2015 and 2016, sea lice were enumerated and their species and life stage identified using a dissecting microscope. In 2017 and 2019, only the motile-stage lice (i.e., pre-adults and adults) were enumerated under a 16× hand lens in the field using methods described in Krkošek et al. (2005b). Owing to the contrasting louse assessment protocols, we analyzed only the motile-stage *L. salmonis* and *C. clemensi* data, since motile-stage lice are easy to find and identify even by the naked eye, and the data are therefore likely comparable across enumeration methods. We also collected muscle tissue for genetic stock identification of 673 sockeye salmon in our study (all from 2015–2017) to determine their watershed of origin. Genetic stock identification compared genotypic variation at 14 microsatellite loci and one major histocompatibility complex with a baseline genotypic library of known populations (Beacham et al. 2004). Each fish was assigned a probability of stock of origin using CBAYES, a computer program that uses Bayesian prior knowledge of baseline population's genotypic variation and compares the genotype of

individuals in the unknown mixture using Monte Carlo Markov chains (Neaves et al. 2005).

To facilitate comparisons of louse abundance among the salmon species, we filtered our data for collections in which we retained at least five individuals each of pink, chum, and sockeye salmon. This was done to guarantee that we only included schools of fish with all three species co-migrating together and to ensure that no bias was introduced into our analysis by under-representing a given species within and among collections. All fish in a collection were retained for analysis, so no bias was introduced by filtering data within collections, which is the level at which the comparisons were made. While a higher cut-off would have reduced species under-representation even further, a five-fish cut-off struck the best balance because increasing it any more would have drastically reduced the number of collections available to analyze (e.g., using a ten-fish cut-off would have resulted in an overall sample size of 1217 instead of 2262). We specifically targeted these species with our field methodology, and therefore they were by far the most commonly captured fishes in our collections; coho were captured often but generally in low numbers and Chinook were caught infrequently (see online Supplementary material, Fig. S1¹). Our final dataset was composed of sea louse assessments for 2262 fish across 65 collections over 5 years and 10 sites.

Statistical analyses

To investigate potential differences in sea louse parasitism between sampling areas and among pink, chum, and sockeye salmon, we fit a suite of generalized linear mixed-effects models (GLMMs) with louse abundance per fish as the response variable. The models employed a negative binomial (type II) error distribution with a logarithmic link function to account for overdispersion in the parasite counts. The models involved six fixed effects: salmon species, sampling year, sampling area (Discovery Islands or Johnstone Strait), and the two-way interactions between these three predictors. In accordance with the hierarchical nature of our data, every model included both the sampling area and year as fixed effects. We therefore fit ten models for each louse species. All our models included a random effect on the intercept for collection number to allow for group-level variation among collections arising from local conditions, such as time held in the net, sea state, and fish density in the net, all of which could affect the abundance of motile-stage lice that can easily detach from a fish. We attempted including an additional fixed effect for fork length, but fork length measurements were not taken for every fish; therefore, we chose to exclude this predictor to draw on a larger number of observations.

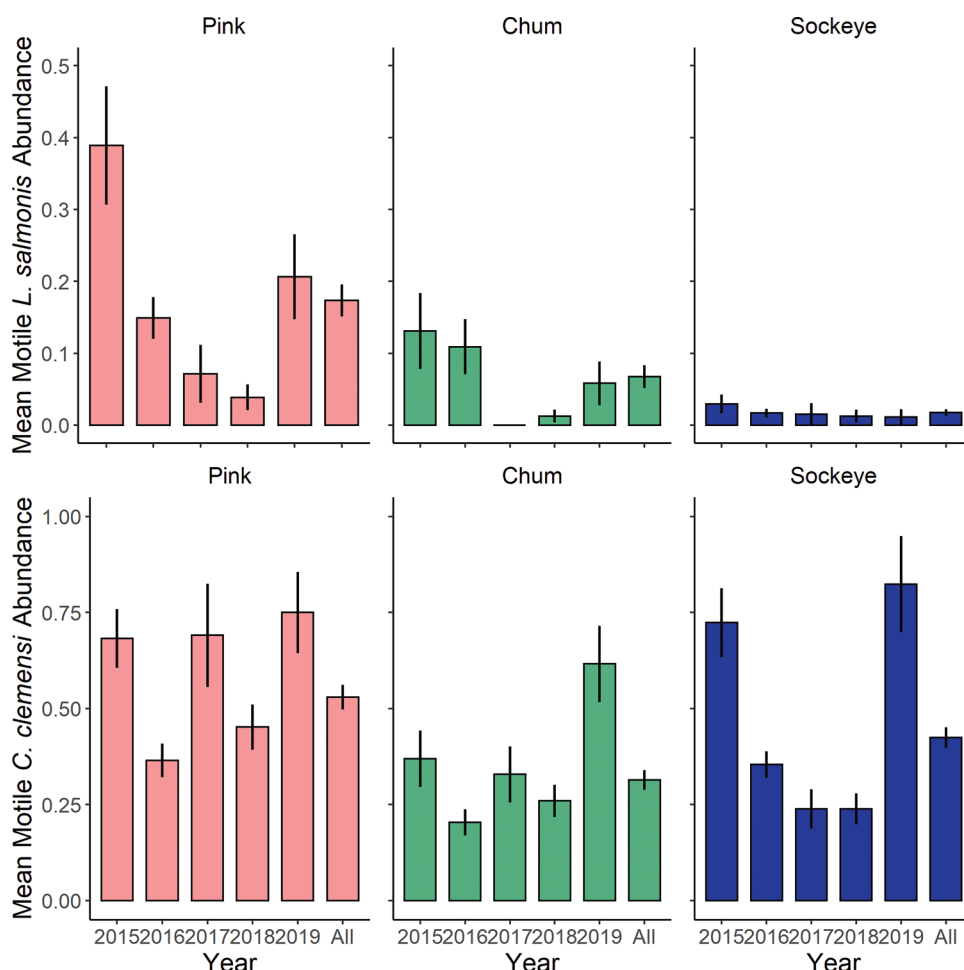
We conducted model selection using Akaike's information criterion (AIC; Akaike 1974). Since several of our models had similar AIC values, we kept all models with nonzero weights and calculated model-averaged predicted values on the scale of the response (hereinafter termed "predictions") of sea louse abundance from these (Burnham and Anderson 2004; Cade 2015) with 95% confidence intervals (CIs) that were calculated by bootstrapping the data 10 000 times, hierarchically structuring the resampling procedure so that it was consistent with the nested structure of the data. We performed our analysis in R using the glmmTMB (Brooks et al. 2017) and ggeffects packages (Lüdtke 2018) in R version 4.0.1 (R Core Team 2020). The code for this analysis, including a static version of the JSP database, is available in an open-access Github repository (Brookson 2020).

Results

Motile-lice abundance was highly variable among individuals, with the majority of fish having no attached lice but several hav-

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2020-0160>.

Fig. 2. Observed mean abundance and standard error of *L. salmonis* (top panels) and *C. clemensi* (bottom) on pink (left), chum (centre), and sockeye (right) salmon in 2015–2019. Note that the figures have different y-axis ranges.



ing more than 10. The overall predicted motile *L. salmonis* abundance across all years was 0.09 (95% CI = 0.06, 0.15) lice per fish for pink salmon, 0.04 (0.02, 0.06) for chum, and 0.01 (0.006, 0.02) for sockeye, while the mean motile *C. clemensi* abundance for the same salmon species was 0.45 (0.38, 0.55), 0.28 (0.23, 0.35), and 0.39 (0.33, 0.47), respectively. For all three salmon species, *C. clemensi* reached their highest abundance in 2019, and *L. salmonis* reached their highest abundance in 2015 (Fig. 2). The year-to-year trends in *L. salmonis* abundance were consistent for all three salmon species, though abundance on sockeye were low throughout our sampling period. Year-to-year trends were also consistent in *C. clemensi* abundance for both chum and sockeye salmon (Fig. 2); these were characterized by a decrease between 2015 and 2017 and an increase in 2018 and 2019. Pink salmon exhibited entirely different and highly variable temporal patterns of louse abundance for *C. clemensi* (Fig. 2), with a large spike in 2017. All three species of salmon were of comparable size in our study; of the fish for which we had measurements, the mean fork lengths (\pm SE) were 109.3 (\pm 16.3), 111.3 (\pm 15.8), and 107.1 (\pm 14.3) mm for pink, chum, and sockeye, respectively.

The models that received the most support from the data differed between the two louse species (Tables 1 and 2, Supplementary Table S1¹). The highest ranking model for *C. clemensi* included fixed effects for year, sampling area, salmon species, the interaction between salmon species and sampling area, the interaction between sampling area and year, and the interaction between salmon species and year. The top model for *L. salmonis* was similar but did not include the interaction between sampling area and

year, nor the interaction between salmon species and year. For both the *C. clemensi* and *L. salmonis* model sets, salmon species had the highest relative variable importance (RVI) value of 1.0, as it was present in all eight of the nonzero weighted models, indicating it was the most important explanatory variable for both louse species. RVI values for the other fixed effects differed between the two model sets (Tables 1 and 2). Despite the support for an effect of salmon species on louse abundance, there was no one “best” model for either louse species. Instead, there were eight models within 13 AIC units of the top *L. salmonis* model, and eight models within 12 AIC units for *C. clemensi*. To capture maximum variation, we performed model-averaging over all nonzero weight candidate models, rather than using a delta-AIC threshold to denote which models were considered.

Our model-averaged predictions for *L. salmonis* and *C. clemensi* were consistent with observed abundances and showed obvious differences among salmon species, years, and sampling areas (Figs. 3 and 4). *Caligus clemensi* were more than five times as abundant as *L. salmonis*, on average, and our mean predictions for *C. clemensi* were higher than *L. salmonis* for every combination of salmon species, year, and sampling area. Generally, pink salmon had the highest *L. salmonis* abundance of any salmon species (Fig. 3). For *L. salmonis*, by far the highest abundance occurred on pink salmon in the Discovery Islands in 2015 (0.59, 95% CI = (0.31, 0.73)). Sampling area patterns were not consistent across years for *L. salmonis*; in 2015, all salmon species experienced higher *L. salmonis* abundances in the Discovery Islands compared with Johnstone Strait, while the opposite pattern generally occurred

Table 1. Selection statistics for the full *L. salmonis* model set.

Sampling area	Year	Salmon species	Sampling area × salmon species	Sampling area × year	Salmon species × year	Negative log-likelihood	ΔAIC	Akaike model weights
+	+	+		+		−487.8097	0.00	0.5023
+	+	+	+	+		−486.4150	1.26	0.2667
+	+	+	+	+	+	−479.0541	2.84	0.1215
+	+	+		+	+	−481.3206	3.29	0.0971
+	+	+				−496.0730	8.44	0.0074
+	+	+	+			−495.0862	10.50	0.0026
+	+	+			+	−489.6456	11.79	0.0014
+	+	+	+		+	−488.0149	12.60	0.0009
+	+			+		−524.0823	68.50	0.0000
+	+					−532.9370	78.13	0.0000
RVI		1.0	0.39	0.99	0.22			

Note: All models employ a negative binomial error distribution and a random effect on the intercept for collection number. Each model contained a different combination of six fixed effects: sampling area (Johnstone Strait or Discovery Islands), year (2015–2019), salmon species (pink, chum, and sockeye), and the three two-way interactions between these three predictors (as indicated by the “×” symbol). ΔAIC is the difference in AIC value between the given model and the top model. Akaike model weights can be interpreted as the probability that the candidate model is the best model (Bolker 2008). In addition, we calculated the relative variable importance (RVI) for each of the four fixed effects that did not appear in every model. They are displayed as a summary in the bottom row.

Table 2. Selection statistics for the full *C. clemensi* full model set.

Sampling area	Year	Salmon species	Sampling area × salmon species	Sampling area × year	Salmon species × year	Negative log-likelihood	ΔAIC	Akaike model weights
+	+	+	+	+	+	−1853.623	0.00	0.4187
+	+	+		+	+	−1856.025	0.72	0.2921
+	+	+	+	+		−1862.461	1.38	0.2099
+	+	+		+		−1865.751	3.91	0.0594
+	+	+			+	−1863.737	8.00	0.0077
+	+	+	+		+	−1861.726	8.04	0.0075
+	+	+	+			−1870.655	9.67	0.0033
+	+	+				−1873.460	11.24	0.0015
+	+			+		−1876.974	22.30	0.0000
+	+					−1884.350	28.98	0.0000
RVI		1.0	0.64	0.98	0.73			

Note: All models employ a negative binomial error distribution and a random effect on the intercept for collection number. Each model contained a different combination of six fixed effects: sampling area (Johnstone Strait or Discovery Islands), year (2015–2018), salmon species (pink, chum, and sockeye), and the three two-way interactions between these three predictors (as indicated by the “×” symbol). ΔAIC is the difference in AIC value between the given model and the top model. Akaike model weights can be interpreted as the probability that the candidate model is the best model (Bolker 2008). In addition, we calculated the relative variable importance (RVI) for each of the six fixed effects. They are displayed as a summary in the bottom row.

during 2016–2019. Our model-averaged predictions indicated that pink and sockeye salmon experienced similar *C. clemensi* abundances. In terms of sampling area, the abundance of *C. clemensi* on sockeye salmon was higher in the Discovery Islands than in Johnstone Strait, and pink salmon experienced higher *C. clemensi* abundance in Johnstone Strait than in the Discovery Islands. Chum salmon harboured the fewest *C. clemensi* in both areas.

Most of the sockeye salmon in our study were from the Fraser River. Of the 673 sockeye salmon that were genetically identified to stock, 89% were from the Fraser River, just over half the fish originating from Chilko (26%), Lower Adams (12%), and Lower Shuswap (12%) stocks. In total, 38 separate stocks were represented in our subsample of sockeye from 2015 to 2017 (Table S2¹).

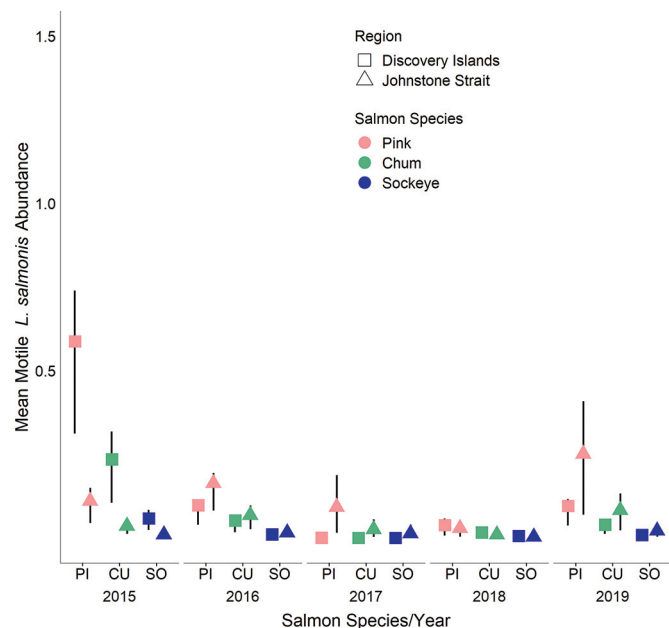
Discussion

Our results indicate that *C. clemensi* and *L. salmonis* differ in their contribution to the total sea louse burden on juvenile Pacific salmon in the Discovery Islands and Johnstone Strait areas of BC. For a given salmon species, *C. clemensi* was generally more abundant than *L. salmonis* across years, and particularly so for sockeye. With respect to salmon species, our results indicate that pink salmon may be a more competent host for both species of louse than sockeye or chum salmon, in contrast with previous estimates of louse abundance on juvenile Pacific salmon (Beamish et al. 2009), which report higher abundances and prevalence of

lice on chum salmon. While laboratory studies have shown that pink salmon are relatively resistant to infestation from *L. salmonis* after some initial growth in the marine environment (Jones et al. 2007; Braden et al. 2012; Sutherland et al. 2014), pink salmon nonetheless had the highest abundances of *L. salmonis* and *C. clemensi*. Pink salmon are therefore likely to host the majority of sea lice on wild juvenile salmon in this system; this is in contrast with findings from a nearby region, the Broughton Archipelago, where in 9 of the 10 years data were collected, juvenile chum salmon showed higher louse abundances than juvenile pink salmon (Patanasatienkul et al. 2013). Sockeye salmon also experienced the largest difference in infestation rates among species are unlikely to be confounded by environment–species correlations unless there are large differences in species-specific migration speeds.

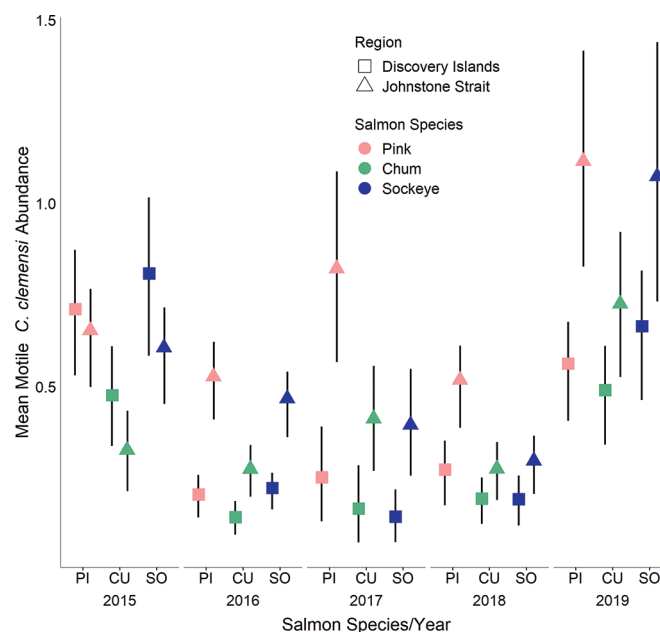
Our results indicate that there are differences in specialization of *C. clemensi* and *L. salmonis* among pink, chum, and sockeye that could arise via the initial infection process, survival of attached parasites, or parasite-induced host mortality. During the initial

Fig. 3. Model-averaged estimates for *L. salmonis* abundance (number of individuals) on pink (PI), chum (CU), and sockeye (SO) salmon in the Discovery Islands and Johnstone Strait in 2015–2018. Points represent the mean estimates and error bars represent bootstrapped 99% confidence intervals. Negative binomial aggregation (shape) parameter = 1 for the top *L. salmonis* model. [Colour online.]



infection process, free-swimming copepodites (juvenile-stage lice) use both physical and chemical cues to locate and pursue a potential host (MacKinnon 1998; Hevroy et al. 2003). Although little is known about how these cues differ among salmon species, it is possible that host characteristics such as odour, swimming speed, body shape, and surface roughness, as well as swimming hydrodynamics (Bailey et al. 2006; Mordue and Birkett 2009), could influence the reception of these cues by lice and, ultimately, attachment rates. Once sea lice have attached, host fish mount an immune response to rid themselves of infestation, and these responses vary among salmon species (Jones et al. 2007; Sutherland et al. 2014; Vargas-Chacoff et al. 2016). Direct mortality from sea lice is unlikely at the host sizes we observed (Jones et al. 2008; Sutherland et al. 2011), and specifically for sockeye and *C. clemensi*, previous studies suggest direct mortality is quite low (Jakob et al. 2013; Godwin et al. 2015). However, indirect or “sublethal” effects of sea lice (e.g., slower growth, reduced foraging success, and increased predation risk) may play an important role in reducing host survival, and these effects likely differ according to each species’ foraging strategies and predator interactions (Costello 2009; Peacock et al. 2015; Godwin et al. 2017). The stress response of the salmonids to sea louse infestation typically involves an increase in plasma cortisol levels for both *Oncorhynchus* and *Salmo* species (Fast et al. 2006; Jones et al. 2007), along with an inflammatory response resulting from elevated expression of proinflammatory genes (Johnson and Albright 1992; Fast 2014). However, there are likely differences in immune response within the *Oncorhynchus* genus, and species-specific immune responses likely work in concert with foraging strategies and predator interactions to mediate direct and indirect effects of infestation. If any of these effects on initial infection, attached-lice survival, or host mortality vary with host species, this could explain the differences we observed in *C. clemensi* and *L. salmonis* abundances among salmon species. Perhaps most notably, if any of these species have a higher propensity to experience mortality (indirect or direct) as a consequence of louse infection, there would be fewer infected fish of

Fig. 4. Model-averaged estimates for *C. clemensi* abundance (number of individuals) on pink (PI), chum (CU), and sockeye (SO) salmon in the Discovery Islands and Johnstone Strait in 2015–2018. Points represent the mean estimates and error bars represent bootstrapped 99% confidence intervals. Negative binomial aggregation (shape) parameter = 1.92 for the top *C. clemensi* model. [Colour online.]



that species in the co-migrating school and therefore in our dataset as well.

Spatial and temporal variation in temperature and salinity, as well as the interaction between the two, could play a role in explaining the differences we see in parasite abundance among years and sampling areas. *Lepeophtheirus salmonis* has higher rates of development (Hayward et al. 2011), settlement (Tucker et al. 2000), and survival (McEwan et al. 2019) with increased water temperatures. Settlement and survival of *L. salmonis* also decreases with lowered salinity (Bricknell et al. 2006; Sutherland et al. 2014; Rittenhouse et al. 2016). As juveniles migrate into the Discovery Islands from the Strait of Georgia, they transition to a region of deep tidal mixing that is characterized by colder, more saline water than the stratified Strait of Georgia. These cold and saline tidally mixed conditions persist through Johnstone Strait, before warming again as the fish pass northward into Queen Charlotte Strait (Dosser et al. 2019). These temperature and salinity patterns also vary among years (Riche et al. 2014; Chandler 2018). Looking forward, with a warming climate and resulting increase in coastal water temperatures, sea louse abundance on migrating juvenile salmon is likely to increase, as has been seen in the Broughton Archipelago, BC (Bateman et al. 2016). Climate-driven changes in environmental conditions could also influence survival rates of host fish. However, it is unclear from our current data how environmental drivers interact with other relevant factors to shape infestation patterns as a whole. If salinity and temperature were the only factors influencing infestation, we would expect coherence of infestation patterns among salmon and louse species. The lack of this coherence suggests a more complex relationship between the various drivers of infestation. Further work is needed to gain a more complete understanding of this multi-host–parasite system not only as it currently stands, but how further environmental change will alter its dynamics in the future.

One reservoir host population for sea louse infection pressure on the fish in this study is domesticated Atlantic salmon from salmon farms along the wild salmon migration routes. The link

between sea louse counts on salmon farms and sea louse abundance on wild juvenile salmon is well documented for *L. salmonis* (Krkošek et al. 2007; Morton et al. 2008; Bateman et al. 2016), but has been largely ignored for *C. clemensi*, the dominant louse species in this study. Management of sea lice on salmon farms is targeted at *L. salmonis* rather than *C. clemensi* and involves government-mandated harvest or a delousing treatment when louse abundance exceeds three motile *L. salmonis* per fish (Fisheries and Oceans Canada 2019). When treatments do occur, they are effective at removing both species of lice (Godwin et al. 2020), but high numbers of *C. clemensi* themselves do not trigger management action. Industry counts of sea lice on salmon farms show generally low levels of *C. clemensi* in BC, with occasional very high abundances (Di Cicco et al. 2017). However, recent work has indicated that the true *C. clemensi* abundance on Atlantic salmon farms is approximately 2.55 times the reported counts (cf. 1.17 for *L. salmonis*), due to a combination of louse detachment during counts and systematic underestimation when counts are not being audited by Fisheries and Oceans Canada (Godwin et al. 2020). In fact, the true *C. clemensi* abundance on salmon farms during the wild juvenile salmon migration is roughly equivalent to that of *L. salmonis* (Godwin et al. 2020). However, while salmon farms may well be a source of *C. clemensi* for juvenile Pacific salmon, they are unlikely to be the only source or even the dominant source given their generalist nature.

The other main source of *C. clemensi* in this region is likely Pacific herring, which had high abundances in our study region during the years of our study (2015–2019; DFO 2019) and have been known to carry large abundances of *C. clemensi* (Morton et al. 2008; Beamish et al. 2009). The abundance of motile-stage *C. clemensi* on fish in the Discovery Islands and the fast migration speed of sockeye salmon suggests that many of the lice may have been acquired in the Strait of Georgia — the area that supports the largest spawning biomass of Pacific herring in BC (DFO 2019) — before the fish arrived in the salmon farming area of the Discovery Islands. According to Welch et al. (2009), the average residence time of juvenile Fraser River sockeye in the Strait of Georgia is 26–34 days, and while there are no published development rate data for *C. clemensi*, the development timing of other sea louse species indicates that copepodid lice acquired in the Strait of Georgia would have time to mature into motiles by the time the fish reached the Discovery Islands (Hogans and Trudeau 1989; Piasecki and MacKinnon 1995; Hamre et al. 2019); in contrast, lice acquired in the Discovery Islands would not likely have moulted into motiles by the time of sampling.

The potential of herring to be a primary source of *C. clemensi* on juvenile salmon is further supported by our sampling area-level results. With the exception of 2015, *C. clemensi* was present at higher levels in Johnstone Strait relative to the Discovery Islands (Figs. 3 and 4), especially for pink salmon. This rise in abundance between the two sampling areas was not observed for *L. salmonis*, with the exception of pink salmon in 2017. Since most *L. salmonis* likely originate from farmed salmon (Krkošek et al. 2007; Marty et al. 2010) and *C. clemensi* are subject to the same parasiticide treatments on farms, the relative magnitude of the increase in abundance between Discovery Islands and Johnstone Strait should be the same for *C. clemensi* and *L. salmonis* in the absence of other wild reservoir hosts. That these sampling area patterns differ between louse species indicates the source pathway may also differ.

Pacific salmon from the Fraser River support some of the most important fisheries in Canada, but many populations are seeing declines and are the focus of considerable conservation concern. In 2019, Fraser River sockeye, which represented almost 90% of the genetically identified sockeye in our study, experienced the worst adult return on record, just 8 years after the conclusion of a CAN\$37 million federal inquiry into their decades-long decline in productivity (Cohen 2012; Grant et al. 2019). For sockeye salmon and other threatened species, generalist parasites like *C. clemensi* —

whose abundance on sockeye salmon was on average 39-fold higher than *L. salmonis* in our study — are of particular concern because their additional reservoir host populations can maintain high levels of parasite abundance in the environment even when focal host abundance is low (de Castro and Bolker 2005; Krkošek et al. 2013a). In our study area, the main reservoir host population for *L. salmonis* is likely farmed Atlantic salmon (Price et al. 2011; Godwin et al. 2015) and wild Pacific herring for *C. clemensi* (Morton et al. 2008; Beamish et al. 2009). Our results show that *C. clemensi* is the dominant louse species infesting out-migrating pink, chum, and sockeye salmon in the most important salmon migration corridor in BC, in contrast with other salmon-farming areas in BC and the North Atlantic where *L. salmonis* is the dominant species (Glover et al. 2005). Conservation science and management of salmon populations vulnerable to sea louse infestation, like those from the Fraser River, should therefore shift some focus to *C. clemensi* and its transmission dynamics among farmed salmon, wild herring, and wild juvenile salmon.

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References

- Akaike, H. 1974. A new look at the statistical model identification. In *Selected papers of Hirotugu Akaike*. Springer. pp. 215–222.
- Atkinson, E.M., Bateman, A.W., Dill, L.M., Krkošek, M., Reynolds, J.D., and Godwin, S.C. 2018. Oust the louse: leaping behaviour removes sea lice from wild juvenile sockeye salmon *Oncorhynchus nerka*. *J. Fish Biol.* 93(2): 263–271. doi:10.1111/jfb.13684. PMID:29956312.
- Bailey, R.J., Birkett, M.A., Ingvarsdóttir, A., Mordue, A.J., Mordue, W., O'Shea, B., et al. 2006. The role of semiochemicals in host location and non-host avoidance by salmon louse (*Lepeophtheirus salmonis*) copepodids. *Can. J. Fish. Aquat. Sci.* 63(2): 448–456. doi:10.1139/f05-231.
- Barber, I., Hoare, D., and Krause, J. 2000. Effects of parasites on fish behaviour: a review and evolutionary perspective. *Rev. Fish Biol. Fish.* 10(2): 131–165. doi:10.1023/A:1016658224470.
- Bateman, A.W., Peacock, S.J., Connors, B., Polk, Z., Berg, D., Krkošek, M., and Morton, A. 2016. Recent failure to control sea louse outbreaks on salmon in the Broughton Archipelago, British Columbia. *Can. J. Fish. Aquat. Sci.* 73(8): 1164–1172. doi:10.1139/cjfas-2016-0122.
- Beacham, T.D., Lapointe, M., Candy, J.R., McIntosh, B., MacConnachie, C., Tabata, A., et al. 2004. Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. *Trans. Am. Fish. Soc.* 133(5): 1117–1137. doi:10.1577/T04-001.1.
- Beamish, R., Wade, J., Pennell, W., Gordon, E., Jones, S., Neville, C., et al. 2009. A large, natural infection of sea lice on juvenile Pacific salmon in the Gulf Islands area of British Columbia, Canada. *Aquaculture*, 297(1–4): 31–37. doi:10.1016/j.aquaculture.2009.09.001.
- Bolker, B.M. 2008. Ecological models and data in R. Princeton University Press.
- Braden, L.M., Barker, D.E., Koop, B.F., and Jones, S.R.M. 2012. Comparative defense-associated responses in salmon skin elicited by the ectoparasite *Lepeophtheirus salmonis*. *Comp. Biochem. Physiol. Part D Genom. Proteomics*, 7(2): 100–109. doi:10.1016/j.cbd.2011.12.002. PMID:22244883.
- Bricknell, I.R., Dalesman, S.J., O'Shea, B., Pert, C.C., and Mordue Luntz, A.J. 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. *Dis. Aquat. Organ.* 71: 201–212. doi:10.3354/dao071201. PMID:17058601.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., et al. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R Journal*, 9(2): 378–400. doi:10.3929/ETHZ-B-000240890.
- Brookson, C. 2020. Juv-Pacific-Salmon-Seallice v1.0. Zenodo. doi:10.5281/zenodo.4005400.

- Burnham, K.P., and Anderson, D. 2004. Model selection and multi-model inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag New York.
- Cade, B.S. 2015. Model averaging and muddled multimodel inferences. *Ecology*, **96**(9): 2370–2382. doi:10.1890/14-1639.1. PMID:26594695.
- Chandler, P.C. 2018. Temperature and salinity observations in the Strait of Georgia and Juan de Fuca strait in 2017. In State of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems in 2017. Fisheries and Oceans Canada.
- Cohen, B.I. 2012. Commission of Inquiry into the Decline of Sockeye Salmon in the Fraser River (Canada) The uncertain future of Fraser River sockeye. Final report — October 2012 [online]. Available from <http://www.npafc.org>, http://publications.gc.ca/collections/collection_2012/bcp-pco/CP32-93-2012-1-eng.pdf.
- Costello, M.J. 1993. Review of methods to control sea lice (Caligidae: Crustacea) infestations on salmon (*Salmo salar*) farms [online]. Available from [https://books.google.ca/books?hl=en&lr=&id=e9KP0mkBuTAC&oi=fnd&pg=PA219&dq=Review+of+methods+to+control+sea+lice+\(Caligidae,+Crustacea\)+infestations+on+salmon+farms.&ots=tOx0Ckrn1&sig=3xvMhhMLh_jiM0rV3XV7DFnpp4](https://books.google.ca/books?hl=en&lr=&id=e9KP0mkBuTAC&oi=fnd&pg=PA219&dq=Review+of+methods+to+control+sea+lice+(Caligidae,+Crustacea)+infestations+on+salmon+farms.&ots=tOx0Ckrn1&sig=3xvMhhMLh_jiM0rV3XV7DFnpp4).
- Costello, M.J. 2009. How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. *Proc. R. Soc. B Biol. Sci.* **276**(1672): 3385–3394. doi:10.1098/rspb.2009.0771. PMID:19586950.
- de Castro, F., and Bolker, B. 2005. Mechanisms of disease-induced extinction. *Ecol. Lett.* **8**(1): 117–126. doi:10.1111/j.1461-0248.2004.00693.x.
- DFO. 2019. Stock Assessment and Management Advice for BC Pacific Herring: 2018 Status and 2019 Forecast [online]. DFO Can. Sci. Advis. Sec. Sci. Resp. Available from http://www.dfo-mpo.gc.ca/csas-sccs/Publications/SCR-RS/2019/2019_001-eng.pdf.
- Di Cicco, E., Ferguson, H.W., Schulze, A.D., Kaukinen, K.H., Li, S., Vanderstichel, R., et al. 2017. Heart and skeletal muscle inflammation (HSMI) disease diagnosed on a British Columbia salmon farm through a longitudinal farm study. *PLoS ONE*, **12**(2): e0171471. doi:10.1371/journal.pone.0171471. PMID:28225783.
- Dosser, H.V., Jackson, J., Hunt, B., Waterman, S., and Hannah, C.G. 2019. Queen Charlotte Strait to the Strait of Georgia: Distinct regional differences in physical properties and nutrients. State of the Pacific Ocean Meeting, Sidney, B.C., 18 and 19 March 2019.
- FAO. 2015. FAO Global Capture Production database updated to 2013 — Summary information [online]. Available from <http://www.fao.org/3/a-i4883e.pdf>.
- Fast, M.D. 2014. Fish immune responses to parasitic copepod (namely sea lice) infection. *Dev. Comp. Immunol.* **43**(2): 300–312. doi:10.1016/j.dci.2013.08.019. PMID:24001580.
- Fast, M.D., Muise, D.M., Easy, R.E., Ross, N.W., and Johnson, S.C. 2006. The effects of *Lepeophtheirus salmonis* infections on the stress response and immunological status of Atlantic salmon (*Salmo salar*). *Fish Shellfish Immunol.* **21**(3): 228–241. doi:10.1016/j.fsi.2005.11.010. PMID:16483797.
- Fisheries and Oceans Canada. 2019. Industry sea lice counts at BC marine finfish aquaculture sites [online]. Fisheries and Oceans Canada. Available from <https://open.canada.ca/data/en/dataset/3cafb89-c98b-4b44-88f1-594e8d28838d> [accessed 11 August 2019].
- Glover, K.A., Aasmundstad, T., Nilsen, F., Storset, A., and Skaala, Ø. 2005. Variation of Atlantic salmon families (*Salmo salar* L.) in susceptibility to the sea lice *Lepeophtheirus salmonis* and *Caligus elongatus*. *Aquaculture*, **245**(1–4): 19–30. doi:10.1016/j.aquaculture.2004.11.047.
- Godwin, S.C., Krkošek, M., Reynolds, J.D., and Bateman, A.W. 2020. Bias in self-reported parasite data from the salmon farming industry. *Ecol. Appl.* e2226.
- 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.
- Godwin, S.C., Dill, L.M., Krkošek, M., Price, M.H.H., and Reynolds, J.D. 2017. Reduced growth in wild juvenile sockeye salmon *Oncorhynchus nerka* infected with sea lice. *J. Fish Biol.* **91**(1): 41–57. doi:10.1111/jfb.13325. PMID:28556094.
- Godwin, S.C., Krkošek, M., Reynolds, J.D., Rogers, L.A., and Dill, L.M. 2018. Heavy sea louse infection is associated with decreased stomach fullness in wild juvenile sockeye salmon. *Can. J. Fish. Aquat. Sci.* **75**(10): 1587–1595. doi:10.1139/cjfas-2017-0267.
- Grant, S.C., MacDonald, B.L., and Winston, M.L. 2019. State of the Canadian Pacific salmon: response to changing climate and habitats. Fisheries and Oceans Canada.
- Groot, C., and Margolis, L. 1991. Pacific salmon life histories. UBC Press.
- Hamre, L.A., Bui, S., Oppedal, F., Skern-Mauritzen, R., and Dalvin, S. 2019. Development of the salmon louse *Lepeophtheirus salmonis* parasitic stages in temperatures ranging from 3 to 24°C. *Aquacult. Environ. Interact.* **11**: 429–443. doi:10.3354/aei00320.
- Hayward, C.J., Andrews, M., and Nowak, B.F. 2011. Introduction: *Lepeophtheirus salmonis* — a remarkable success story. In *Salmon lice: an integrated approach to understanding parasite abundance and distribution*. John Wiley and Sons, Chichester, UK. pp. 1–28.
- Hedrick, R.P. 1998. Relationships of the host, pathogen, and environment: implications for diseases of cultured and wild fish populations. *J. Aquat. Anim. Health*, **10**(2): 107–111. doi:10.1577/1548-8667(1998)010<0107:ROTHPA>2.0.CO;2.
- Høyev, E.M., Boxaspen, K., Oppedal, F., Taranger, G.L., and Holm, J.C. 2003. The effect of artificial light treatment and depth on the infestation of the sea louse *Lepeophtheirus salmonis* on Atlantic salmon (*Salmo salar* L.) culture. *Aquaculture*, **220**(1–4): 1–14. doi:10.1016/S0044-8486(02)00189-8.
- Hilderbrand, G.V., Farley, S.D., Schwartz, C.C., and Robbins, C.T. 2004. Importance of salmon to wildlife: implications for integrated management. *Ursus*, **15**(1): 1–10. doi:10.2192/1537-6176(2004)015<0001:IOSTWI>2.0.CO;2.
- Hogans, W.E., and Trudeau, D.J. 1989. Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda: Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. Canadian Technical Report of Fisheries and Aquatic Sciences (1715).
- Hudson, P., and Greenman, J. 1998. Competition mediated by parasites: biological and theoretical progress. *Trends Ecol. Evol.* **13**(10): 387–390. doi:10.1016/S0169-5347(98)01475-X. PMID:21238357.
- Hunt, B.P.V., Johnson, B.T., Godwin, S.C., Krkošek, M., Pakhomov, E.A., and Rogers, L.A. 2018. The Hakai Institute Juvenile Salmon Program: Early life history drivers of marine survival in sockeye, pink and chum salmon in British Columbia [online]. Available from <http://www.npafc.org>.
- Jakob, E., Sweeten, T., Bennett, W., and Jones, S.R.M. 2013. Development of the salmon louse *Lepeophtheirus salmonis* and its effects on juvenile sockeye salmon *Oncorhynchus nerka*. *Dis. Aquat. Org.* **106**(3): 217–227. doi:10.3354/dao02642. PMID:24191999.
- Johnson, B.T., Gan, J.C.L., Godwin, S.C., Krkošek, M., and Hunt, B.P.V. 2020. Hakai juvenile salmon program time series. Hakai Institute, Quadra Island Ecological Observatory, Heriot Bay, British Columbia, Canada. doi:10.21966/1.566666.
- Johnson, S.C., and Albright, L.J. 1991. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. *J. Mar. Biol. Assoc. U.K.* **71**(2): 425–436. doi:10.1017/S0025315400051687.
- Johnson, S.C., and Albright, L.J. 1992. Comparative susceptibility and histopathology of the response of naive Atlantic, chinook and coho salmon to experimental infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Dis. Aquat. Org.* **14**(3): 179–193. doi:10.3354/dao014179.
- Jones, S.R., Fast, M.D., Johnson, S.C., and Groman, D.B. 2007. Differential rejection of salmon lice by pink and chum salmon: disease consequences and expression of proinflammatory genes. *Dis. Aquat. Org.* **75**: 229–238. doi:10.3354/dao075229. PMID:17629118.
- Jones, S., Kim, E., and Bennett, W. 2008. Early development of resistance to the salmon louse, *Lepeophtheirus salmonis* (Krøyer), in juvenile pink salmon, *Oncorhynchus gorbuscha* (Walbaum). *J. Fish Dis.* **31**(8): 591–600. doi:10.1111/j.1365-2761.2008.00933.x. PMID:18482380.
- Krkošek, M., Lewis, M.A., and Volpe, J.P. 2005a. Transmission dynamics of parasitic sea lice from farm to wild salmon. *Proc. R. Soc. B Biol. Sci.* **272**(1564): 689–696. doi:10.1098/rspb.2004.3027.
- Krkošek, M., Morton, A., and Volpe, J.P. 2005b. Nonlethal assessment of juvenile pink and chum salmon for parasitic sea lice infections and fish health. *Trans. Am. Fish. Soc.* **134**(3): 711–716. doi:10.1577/T04-133.1.
- Krkošek, M., Ford, J.S., Morton, A., Lele, S., Myers, R.A., and Lewis, M.A. 2007. Declining wild salmon populations in relation to parasites from farm salmon. *Science*, **40**: 1772–1775. doi:10.1126/science.1149887.
- Krkošek, M., Morton Volpe, J.P., and Lewis, M.A. 2009. Sea lice and salmon population dynamics: effects of exposure time for migratory fish. *Proc. R. Soc. B Biol. Sci.* **276**(1668): 2819–2828. doi:10.1098/rspb.2009.0317.
- Krkošek, M., Ashander, J., Frazer, L.N., and Lewis, M.A. 2013a. Allee effect from parasite spill-back. *Am. Nat.* **182**(5): 640–652. doi:10.1086/673238. PMID:24107371.
- Krkošek, M., Revie, C.W., Gargan, P.G., Skilbrei, O.T., Finstad, B., and Todd, C.D. 2013b. Impact of parasites on salmon recruitment in the Northeast Atlantic Ocean. *Proc. Biol. Sci.* **280**(1750): 20122359. doi:10.1098/rspb.2012.2359. PMID:23135680.
- Longshaw, M., Frear, P.A., Nunn, A.D., Cowx, I.G., and Feist, S.W. 2010. The influence of parasitism on fish population success. *Fish. Manage. Ecol.* **17**: 426–434. doi:10.1111/j.1365-2400.2010.00741.x.
- Lüdecke, D. 2018. ggeffects: tidy data frames of marginal effects from regression models. *J. Open Source Softw.* **3**(26). doi:10.21105/joss.00772.
- MacKinnon, B.M. 1998. Host factors important in sea lice infections. *ICES J. Mar. Sci.* **55**(2): 188–192. doi:10.1006/jmsc.1997.0361.
- Marty, G.D., Saksida, S.M., and Quinn, T.J. 2010. Relationship of farm salmon, sea lice, and wild salmon populations. *Proc. Natl. Acad. Sci. U.S.A.* **107**(52): 22599–22604. doi:10.1073/pnas.1009573108.
- McEwan, G.F., Groner, M.L., Cohen, A.A., Imsland, A.K., and Revie, C.W. 2019. Modelling sea lice control by lumpfish on Atlantic salmon farms: interactions with mate limitation, temperature and treatment rules. *Dis. Aquat. Org.* **133**(1): 69–82. doi:10.3354/dao03329. PMID:31089004.
- Mordue, A.J., and Birkett, M.A. 2009. A review of host finding behaviour in the parasitic sea louse, *Lepeophtheirus salmonis* (Caligidae: Copepoda). *J. Fish Dis.* **32**(1): 3–13. doi:10.1111/j.1365-2761.2008.01004.x. PMID:19245627.
- Morton, A., Routledge, R., and Krkošek, M. 2008. Sea louse infestation in wild juvenile salmon and Pacific herring associated with fish farms off the east-central coast of Vancouver Island, British Columbia. *N. Am. J. Fish. Manage.* **28**(2): 523–532. doi:10.1577/M07-042.1.
- Mustafa, A., and MacKinnon, B.M. 1999. Genetic variation in susceptibility of Atlantic salmon to the sea louse *Caligus elongatus* Nordmann, 1832. *Can. J. Zool.* **77**(8): 1332–1335. doi:10.1139/z99-096.

- Neaves, P.I., Wallace, C.G., Candy, J.R., and Beacham, T.D. 2005. CBayes: computer program for mixed stock analysis of allelic data. Version v4.02.
- Parker, R.R., and Margolis, L. 1964. A new species of parasitic copepod, *Caligus demensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. *J. Fish. Res. Board Can.* **21**(5): 873–889. doi:10.1139/f64-085.
- Patanasatienkul, T., Sanchez, J., Rees, E.E., Krkošek, M., Jones, S.R., and Revie, C.W. 2013. Sea lice infestations on juvenile chum and pink salmon in the Broughton Archipelago, Canada, from 2003 to 2012. *Dis. Aquat. Org.* **105**(2): 149–161. doi:10.3354/dao02616. PMID:23872858.
- Peacock, S.J., Krkošek, M., Bateman, A.W., and Lewis, M.A. 2015. Parasitism and food web dynamics of juvenile Pacific salmon. *Ecosphere*, **6**(12): 1–16. Wiley Online Library.
- Peacock, S.J., Bateman, A.W., Krkošek, M., Connors, B., Rogers, S., Portner, L., et al. 2016. Sea-louse parasites on juvenile wild salmon in the Broughton Archipelago, British Columbia, Canada. *Ecology*, **97**(7): 1887–1887. doi:10.1002/ecy.1438. PMID:27859168.
- Peterman, R.M., Marmorek, D., Beckman, B., Bradford, M., Mantua, N., Riddell, B.E., et al. 2010. Synthesis of evidence from a workshop on the decline of Fraser River sockeye. A report to the Pacific Salmon Commission, Vancouver, B.C.
- Piasecki, W., and MacKinnon, B.M. 1995. Life cycle of a sea louse, *Caligus elongatus* von Nordmann, 1832 (Copepoda, Siphonostomatoida, Caligidae). *Can. J. Zool.* **73**(1): 74–82. doi:10.1139/z95-009.
- Price, M.H.H., Probošcz, S.L., Routledge, R.D., Gottesfeld, A.S., Orr, C., and Reynolds, J.D. 2011. Sea louse infection of juvenile sockeye salmon in relation to marine salmon farms on Canada's west coast. *PLoS ONE*, **6**(2): e16851. doi:10.1371/journal.pone.0016851. PMID:21347456.
- R Core Team. 2020. R: a language and environment for statistical computing [online]. R Foundation for Statistical Computing, Vienna, Austria. Available from <https://www.R-project.org/>.
- Riche, O., Johannessen, S.C., and Macdonald, R.W. 2014. Why timing matters in a coastal sea: Trends, variability and tipping points in the Strait of Georgia, Canada. *J. Mar. Syst.* **131**: 36–53. doi:10.1016/j.jmarsys.2013.11.003.
- Rittenhouse, M.A., Revie, C.W., and Hurford, A. 2016. A model for sea lice (*Lepeophtheirus salmonis*) dynamics in a seasonally changing environment. *Epidemics*, **16**: 8–16. doi:10.1016/j.epidem.2016.03.003. PMID:27663786.
- Scheuerell, M.D., Levin, P.S., Zabel, R.W., Williams, J.G., and Sanderson, B.L. 2005. A new perspective on the importance of marine-derived nutrients to threatened stocks of Pacific salmon (*Oncorhynchus* spp.). *Can. J. Fish. Aquat. Sci.* **62**(5): 961–964. doi:10.1139/f05-113.
- Sutherland, B.J., Jantzen, S.G., Sanderson, D.S., Koop, B.F., and Jones, S.R. 2011. Differentiating size-dependent responses of juvenile pink salmon (*Oncorhynchus gorbuscha*) to sea lice (*Lepeophtheirus salmonis*) infections. *Comp. Biochem. Physiol. D Genomics Proteomics*, **6**(2): 213–223. doi:10.1016/j.cbd.2011.04.001.
- Sutherland, B.J., Koczka, K.W., Yasuike, M., Jantzen, S.G., Yazawa, R., Koop, B.F., and Jones, S.R. 2014. Comparative transcriptomics of Atlantic *Salmo salar*, chum *Oncorhynchus keta* and pink salmon *O. gorbuscha* during infections with salmon lice *Lepeophtheirus salmonis*. *BMC Genomics*, **15**: 200. doi:10.1186/1471-2164-15-200. PMID:24628956.
- Tucker, C.S., Sommerville, C., and Wootten, R. 2000. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon, *Salmo salar* L. *J. Fish Dis.* **23**(5): 309–320. doi:10.1046/j.1365-2761.2000.00219.x.
- Vargas-Chacoff, L., Muñoz, J.L.P., Hawes, C., Oyarzún, R., Pontigo, J.P., Saravia, J., et al. 2016. Atlantic salmon (*Salmo salar*) and Coho salmon (*Oncorhynchus kisutch*) display differential metabolic changes in response to infestation by the ectoparasite *Caligus rogercresseyi*. *Aquaculture*, **464**: 469–479. doi:10.1016/j.aquaculture.2016.07.029.
- Welch, D.W., Melnychuk, M.C., Rechisky, E.R., Porter, A.D., Jacobs, M.C., Ladouceur, A., et al. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. *Can. J. Fish. Aquat. Sci.* **66**(5): 736–750. doi:10.1139/F09-032.
- Wickham, H. 2016. ggplot2: elegant graphics for data analysis [online]. R. Available from <https://ggplot2.tidyverse.org> [accessed 31 August 2020].
- Williams, H.H. 1964. Some observations on the mass mortality of the freshwater fish *Rutilus rutilus* (L.). *Parasitology*, **54**(1): 155–171. doi:10.1017/S0031182000074448. PMID:14124280.