

# Evidence of farm-induced parasite infestations on wild juvenile salmon in multiple regions of coastal British Columbia, Canada

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**Abstract:** Salmon farms are spatially concentrated reservoirs of fish host populations that can disrupt natural salmonid host–parasite dynamics. Sea lice frequently infect farm salmon and parasitize sympatric wild juvenile salmonids, with negative impacts on survival in Europe and Pacific Canada. We examined louse parasitism of wild juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*Oncorhynchus gorbuscha*) from three salmon farming regions in British Columbia (Finlayson, Broughton Archipelago, and Georgia Strait). We compared sites of low and high exposure to farms and included an area without farms (Bella Bella) to assess baseline infection levels. Louse prevalence and abundance were lowest and most similar to natural baseline levels at low-exposure sites and highest at high-exposure sites in all farm regions. A significantly greater proportion of the lice were *Lepeophtheirus salmonis* at high-exposure sites. Exposure to salmon farms was the only consistently significant factor to explain the variation in prevalence data, with a secondary role played by salinity. Our results support the hypothesis that salmon farms are a major source of sea lice on juvenile wild salmon in salmon farming regions and underscore the importance of using management techniques that mitigate threats to wild stocks.

**Résumé :** Les élevages de saumons sont des réservoirs concentrés dans l'espace de populations de poissons hôtes qui peuvent perturber la dynamique naturelle des saumons hôtes et de leurs parasites. Les puces de mer infectent fréquemment les saumons d'élevage et parasitent les jeunes salmonidés sauvages sympatriques, ce qui a des impacts négatifs sur la survie en Europe et la région pacifique du Canada. Nous avons étudié le parasitisme par les puces de mer chez les saumons keta (*Oncorhynchus keta*) et roses (*Oncorhynchus gorbuscha*) dans trois régions d'élevage de saumons en Colombie-Britannique (Finlayson, archipel de Broughton et détroit de Géorgie). Nous avons comparé les sites fortement et faiblement exposés aux élevages, ainsi qu'une région sans élevages (Bella Bella), afin d'évaluer les niveaux d'infection de base. La prévalence et l'abondance des puces de mer sont minimales et le plus semblables aux niveaux de base naturels aux sites de faible exposition, et maximales aux sites de forte exposition dans toutes les régions d'élevage. Aux sites de forte exposition, une proportion significativement plus élevée des puces de mer appartient à l'espèce *Lepeophtheirus salmonis*. L'exposition aux élevages de saumons est le seul facteur explicatif constamment significatif dans les données de prévalence avec la salinité qui joue un rôle secondaire. Nos résultats appuient l'hypothèse selon laquelle les élevages de saumons sont une source importante de puces de mer pour les jeunes saumons sauvages dans les régions d'élevage de saumons et ils soulignent l'importance d'utiliser des techniques de gestion qui réduisent les menaces aux stocks sauvages.

[Traduit par la Rédaction]

## Introduction

Disease outbreaks are an increasing threat to wildlife, exacerbated by increases in the human population and domesticated animals (Macdonald and Laurenson 2006; Thirgood 2009). The most common route of transmission to wildlife is from artificial reservoirs of host populations (McCallum and Dobson 1995; Daszak et al. 2000). Marine salmon farms located along near-shore wild salmon migration routes provide spatially concentrated host populations that can serve as reservoirs and perturb the dynamics of natural salmonid

host–parasite systems (Krkošek et al. 2006, 2010; Costello 2009). Sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.) frequently infect farm salmon, and many studies in Europe have identified farm-origin lice as those that parasitize sympatric wild salmonids (MacKenzie et al. 1998; Tully et al. 1999; Bjorn and Finstad 2002). Moreover, parasite outbreaks from salmon farms have been implicated in the collapse of wild sea trout (*Salmo trutta*) and Atlantic salmon (*Salmo salar*) populations in Norway, Scotland, and Ireland (McVicar 1997, 2004).

Received 16 October 2009. Accepted 04 August 2010. Published on the NRC Research Press Web site at cjfas.nrc.ca on 9 November 2010.

J21472

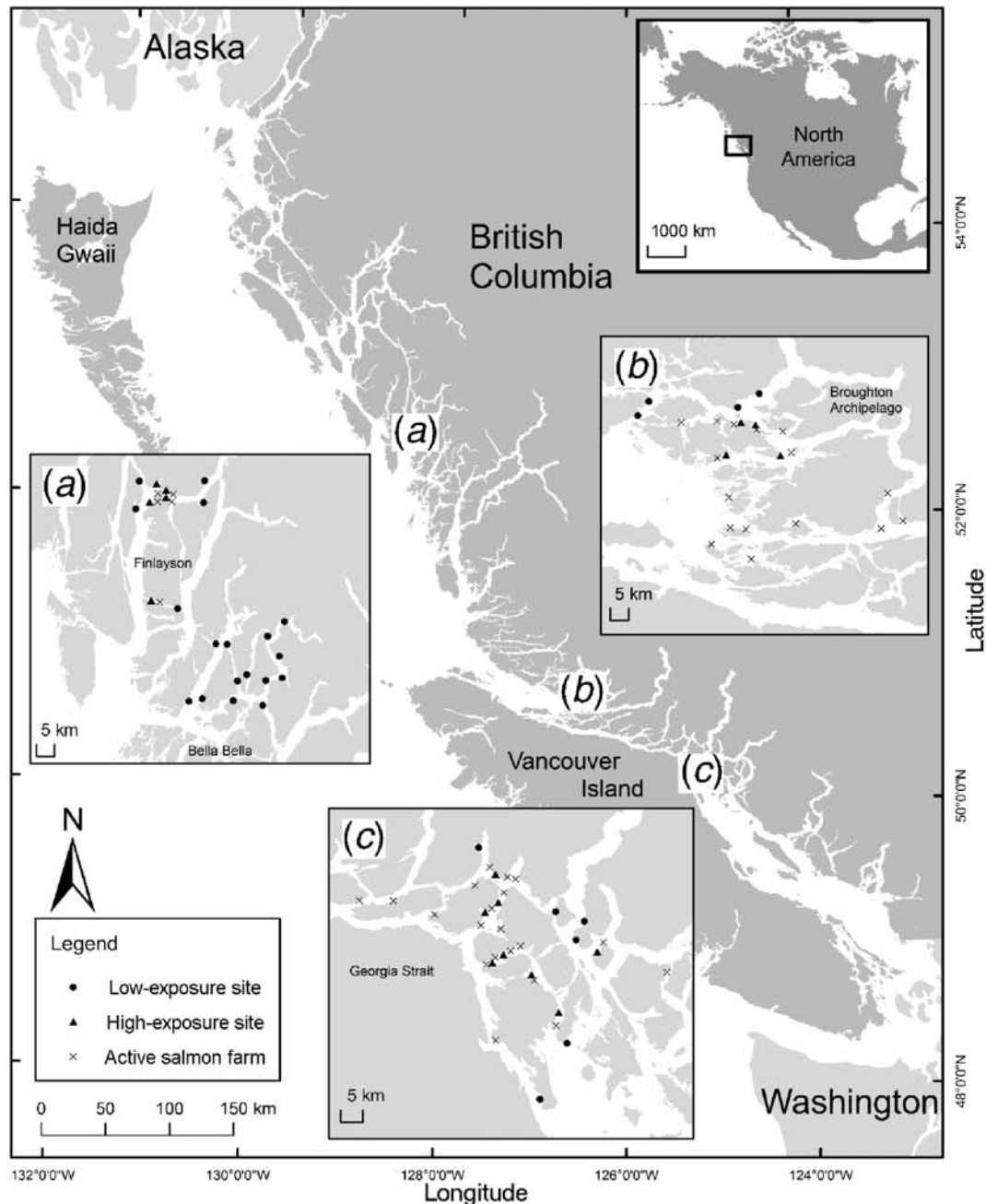
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**Fig. 1.** Study area, including three salmon farm regions (a–c), the non-salmon farm area of Bella Bella, and all associated sampling sites for juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined for sea lice in British Columbia, Canada, in 2007 and 2008.



In Pacific Canada, recurrent parasite infestations transmitted from farms to wild juvenile pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) have been well documented in the Broughton Archipelago (Krkošek et al. 2005a, 2006; see our Fig. 1), where the first epizootic in British Columbia was observed (Morton and Williams 2003). Pink salmon populations have shown a general decline in this region, and there is evidence that farm-origin lice may be partly responsible (Pacific Fisheries Resource Conservation Council 2002; Krkošek 2007a; Ford and Myers 2008). Additionally, a recent investigation has shown parasite outbreaks on wild salmon in a salmon farm

region south of the Broughton, in nearby Georgia Strait (Morton et al. 2008). Given the current intensity of farmed salmon produced in British Columbia, and the proposed expansion of the industry, there is concern that lice outbreaks and negative impacts on wild salmon populations could occur elsewhere.

Alternative explanations have been suggested for the origins of sea lice on wild juvenile salmon in fish farming regions (Brooks 2005; Beamish et al. 2007; Jones and Hargreaves 2007). Factors such as temperature, salinity, and presence and abundance of wild fish hosts have been cited. Adding to this uncertainty is a paucity of information on lice

**Table 1.** Summary of mean capture site and biological data values for juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined in coastal British Columbia in 2007 and 2008.

| Location              | Exposure | Salinity (‰) | Temperature (°C) | Species | Fork length (cm)* | Mass (g)*   |
|-----------------------|----------|--------------|------------------|---------|-------------------|-------------|
| Bella Bella           | Low      | 20.1         | 10.6             | Chum    | 4.79 (0.02)       | 1.28 (0.02) |
|                       |          |              |                  | Pink    | 4.68 (0.03)       | 1.21 (0.04) |
| Finlayson             | Low      | 25.2         | 9.4              | Chum    | 4.75 (0.05)       | 0.70 (0.00) |
|                       |          |              |                  | Pink    | 4.34 (0.03)       | 1.20 (0.16) |
|                       | High     | 26.3         | 9.5              | Chum    | 5.23 (0.07)       | 2.27 (0.22) |
|                       |          |              |                  | Pink    | 4.80 (0.05)       | 1.18 (0.10) |
| Broughton Archipelago | Low      | 27.6         | 10.4             | Chum    | 4.19 (0.17)       | —           |
|                       |          |              |                  | Pink    | 3.76 (0.24)       | —           |
|                       | High     | 21.5         | 9.5              | Chum    | 4.48 (0.31)       | —           |
|                       |          |              |                  | Pink    | 3.92 (0.26)       | —           |
| Georgia Strait        | Low      | 24.9         | 10.4             | Chum    | 5.41 (0.45)       | 2.19 (0.08) |
|                       |          |              |                  | Pink    | 5.87 (0.76)       | 2.54 (0.17) |
|                       | High     | 27.6         | 12.1             | Chum    | 5.93 (0.39)       | 2.71 (0.08) |
|                       |          |              |                  | Pink    | 5.61 (0.67)       | 2.19 (0.07) |

\*Standard error is in parentheses.

**Table 2.** Mean prevalence (P), abundance (A), and intensity (I) of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined in 2007 and 2008 among four coastal regions of British Columbia and exposure (low or high) of these wild fish species to salmon farms.

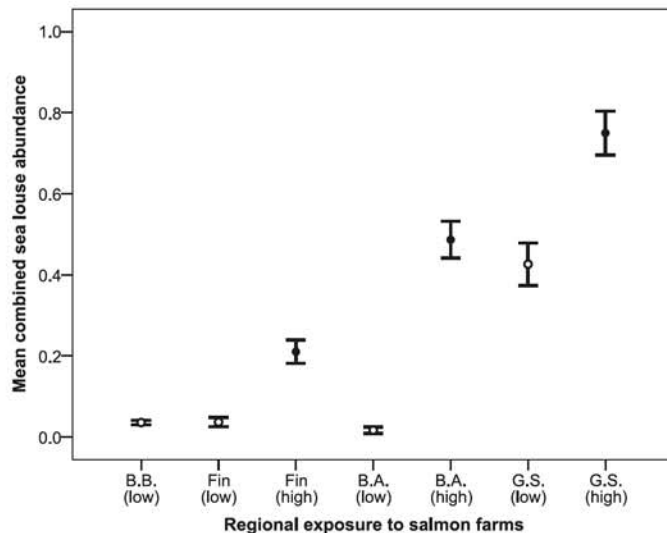
| Location              | Year | Exposure | No. of fish | <i>L. salmonis</i> |     |     | <i>C. clemensi</i> |     |     | Combined prevalence* | Combined abundance |
|-----------------------|------|----------|-------------|--------------------|-----|-----|--------------------|-----|-----|----------------------|--------------------|
|                       |      |          |             | P                  | A   | I   | P                  | A   | I   |                      |                    |
| <b>Chum</b>           |      |          |             |                    |     |     |                    |     |     |                      |                    |
| Bella Bella           | 2007 | Low      | 1504        | 2.1                | 0.0 | 1.0 | 2.2                | 0.0 | 1.1 | 4.2                  | 0.0                |
|                       | 2008 | Low      | 1916        | 0.5                | 0.0 | 1.0 | 2.5                | 0.0 | 1.0 | 2.9                  | 0.0                |
| Finlayson             | 2008 | Low      | 317         | 0.0                | 0.0 | 0.0 | 1.3                | 0.0 | 1.0 | 1.3                  | 0.0                |
|                       |      | High     | 372         | 3.2                | 0.1 | 2.0 | 16.1               | 0.2 | 1.0 | 19.1                 | 0.3                |
| Broughton Archipelago | 2007 | Low      | 910         | 0.5                | 0.0 | 1.0 | 1.3                | 0.0 | 1.2 | 1.8                  | 0.0                |
|                       |      | High     | 717         | 13.5               | 0.2 | 1.2 | 15.1               | 0.2 | 1.4 | 25.9                 | 0.4                |
| Georgia Strait        | 2007 | Low      | 674         | 15.6               | 0.2 | 1.4 | 19.9               | 0.3 | 1.4 | 29.8                 | 0.5                |
|                       | 2008 | Low      | 169         | 7.1                | 0.1 | 1.3 | 10.1               | 0.1 | 1.4 | 15.4                 | 0.2                |
|                       | 2007 | High     | 884         | 18.4               | 0.3 | 1.6 | 24.8               | 0.3 | 1.4 | 37.3                 | 0.6                |
|                       | 2008 | High     | 635         | 23.6               | 0.6 | 2.4 | 17.2               | 0.4 | 1.9 | 37.2                 | 1.0                |
| <b>Pink</b>           |      |          |             |                    |     |     |                    |     |     |                      |                    |
| Bella Bella           | 2007 | Low      | 479         | 1.3                | 0.0 | 1.0 | 2.3                | 0.0 | 1.1 | 3.5                  | 0.0                |
|                       | 2008 | Low      | 955         | 0.4                | 0.0 | 1.0 | 2.7                | 0.0 | 1.0 | 3.1                  | 0.0                |
| Finlayson             | 2008 | Low      | 774         | 0.3                | 0.0 | 1.0 | 4.3                | 0.0 | 1.0 | 4.5                  | 0.0                |
|                       |      | High     | 741         | 3.5                | 0.1 | 4.6 | 14.7               | 0.2 | 1.0 | 18.5                 | 0.2                |
| Broughton Archipelago | 2007 | Low      | 473         | 0.8                | 0.0 | 1.0 | 0.2                | 0.0 | 1.0 | 0.8                  | 0.0                |
|                       |      | High     | 697         | 20.4               | 0.2 | 1.2 | 24.2               | 0.4 | 1.5 | 37.7                 | 0.6                |
| Georgia Strait        | 2007 | Low      | 82          | 20.7               | 0.3 | 1.3 | 15.9               | 0.2 | 1.5 | 32.9                 | 0.5                |
|                       | 2008 | Low      | 79          | 8.8                | 0.1 | 1.1 | 11.4               | 0.1 | 1.1 | 19.0                 | 0.2                |
|                       | 2007 | High     | 538         | 37.4               | 0.7 | 1.8 | 20.3               | 0.3 | 1.4 | 48.9                 | 1.0                |
|                       | 2008 | High     | 510         | 12.7               | 0.2 | 1.4 | 18.0               | 0.3 | 1.7 | 27.3                 | 0.5                |

\*Combined prevalence includes *L. salmonis*, *C. clemensi*, and unidentified chalimus A and B stages.

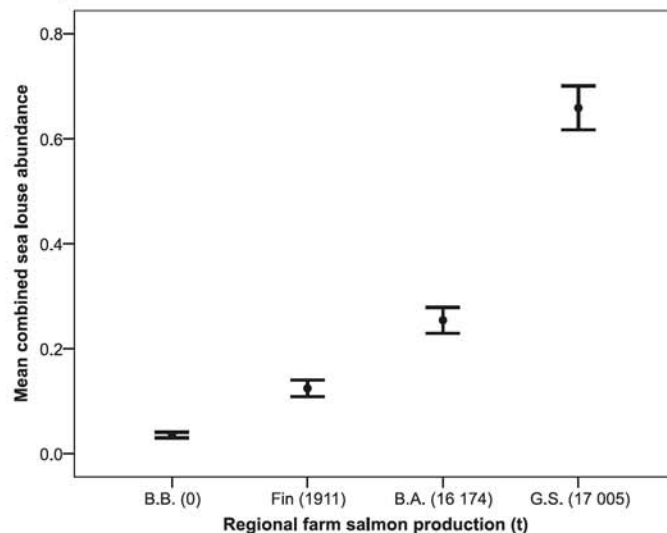
levels in farm regions beyond the Broughton Archipelago. Additionally, there is a lack of information on lice levels in regions without salmon farms, which could be compared with concurrent data gathered in active farm regions. Moreover, no investigation has examined the relationship between lice levels on wild juveniles and the total amount of salmon produced on farms in a region.

In this study we examine multiple potential causes and correlates of lice infections on juvenile chum and pink salmon from four regions in British Columbia. We extend our comparative investigation beyond the Broughton Archipelago to include Bella Bella (an area without salmon farms) and the salmon farming regions of Finlayson to the north and Georgia Strait to the south.

**Fig. 2.** The 95% confidence intervals of combined mean sea louse (*Lepeophtheirus salmonis* and *Caligus clemensi*) abundance on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined at sites of low (open circle) or high (filled circle) exposure to salmon farms for all years combined. B.B., Bella Bella; Fin, Finlayson; B.A., Broughton Archipelago; G.S., Georgia Strait.



**Fig. 3.** The 95% confidence intervals of combined mean sea louse (*Lepeophtheirus salmonis* and *Caligus clemensi*) abundance on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined among four areas of coastal British Columbia and their associated farm salmon production in tonnes (t). B.B., Bella Bella; Fin, Finlayson; B.A., Broughton Archipelago; G.S., Georgia Strait.



## Materials and methods

We collected early marine phase juvenile chum and pink salmon from four regions along the British Columbia coast from March to June 2007 and 2008 (Fig. 1). Capture locations were selected based on the probability of exposure of juvenile salmon to active salmon farms, categorized as high (<1 km from active farms) or low (4–40 km upstream from farms; Fig. 1). Some low-exposure sites were relatively near

an active salmon farm (4 km). However, these sites were situated along migration corridors upstream of the predominant flow from farms or across large channels that juveniles at the time of capture are known not to cross. Thus, we considered the exposure probability at those sites to be low. This way of categorizing exposure matches that in similar studies within the Broughton Archipelago and Georgia Strait (Morton et al. 2004, 2005, 2008). It would not have been appropriate to treat probability of exposure as a continuous variable based on distance from the nearest farm, because that would have ignored the movements of fish from upstream (pre-exposure) to downstream (post-exposure) of farms. We determined the activity status of farms (i.e., active or fallow) and annual production harvest during the years of study from the Oceans and Marine Fisheries Branch of the British Columbia Ministry of Environment (British Columbia Ministry of the Environment 2009; Fig. 1). Sites near farms that were fallow in a given year were considered low exposure. Dates and frequency of surveys varied slightly between regions: Finlayson, 23 April – 22 June (bi-weekly); Bella Bella, 17 April – 15 June (weekly); Broughton Archipelago, 20 March – 15 May (biweekly); Georgia Strait, 22 April – 14 June (biweekly).

At each site, juveniles were corralled by beach seine (50 m long, 6 mm mesh) from a boat, and in all regions except Georgia Strait, subsets of 30–100 juveniles per site were haphazardly selected and live-sampled for sea lice using methodology described by Krkošek et al. (2005b). Because this technique broadly categorizes chalimus stages of lice into only two stages and not according to species, we modified this approach in Finlayson and Bella Bella by euthanizing and collecting only those juvenile salmon that hosted a louse. All infected juveniles were frozen and sent to a lab for louse and host species identification, as well as fork length and mass measurements, as described by Morton et al. (2008). To assess observer accuracy during nonlethal sampling, we also euthanized three juveniles per sampling day in Finlayson and Bella Bella ( $n = 100$ ) that were judged to be louse-free and later assessed them for louse presence using a dissecting microscope; no fish had lice. Only adult and copepodid stages of sea lice were identified in the Broughton Archipelago (for reasons explained above; but all lice were counted), and fish species and fork length were recorded without taking mass measurements according to nonlethal field assessment methods (Krkošek et al. 2005b). In Georgia Strait, entire subsets of juveniles (30–50 per site per week) were euthanized and lethally assayed for sea lice as described above. We recorded sea surface salinity and temperature at each collection site per sampling event among all regions using a calibrated YSI 85 multifunction meter (YSI Inc., Yellow Springs, Ohio). Measures of lice infection rates are as follows: prevalence is the number of hosts infected with lice (expressed as a percentage), abundance is the total number of lice divided by the total number of hosts (infected and uninfected), and intensity is the mean number of lice per infected host (Margolis et al. 1982).

We were interested in which factors most influence sea louse infection levels on juvenile salmon in British Columbia. Accordingly, based on the literature cited in the Introduction, we formulated a priori hypotheses relating fish capture sites to the prevalence of sea lice on juveniles cap-



**Table 3.** Percentages of sea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) at different life stages infecting juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*) examined among three coastal regions of British Columbia and exposure (low or high) of these wild fish species to salmon farms.

| Location       | Exposure | <i>L. salmonis</i> |               |                |                |              | <i>C. clemensi</i> |             |               |                |                |           |
|----------------|----------|--------------------|---------------|----------------|----------------|--------------|--------------------|-------------|---------------|----------------|----------------|-----------|
|                |          | No. of lice        | Copepodid (%) | Chalimus A (%) | Chalimus B (%) | Preadult (%) | Adult (%)          | No. of lice | Copepodid (%) | Chalimus A (%) | Chalimus B (%) | Adult (%) |
| Bella Bella    | Low      | 68                 | 8.3           | 33.3           | 16.7           | 8.3          | 33.3               | 135         | 12.8          | 53.2           | 17.0           | 17.0      |
|                | Low      | 2                  | 0.0           | 0.0            | 33.3           | 33.3         | 33.3               | 38          | 17.4          | 65.2           | 8.7            | 8.7       |
| Finlayson      | High     | 61                 | 23.5          | 48.2           | 14.1           | 7.1          | 7.1                | 171         | 11.6          | 44.2           | 11.6           | 32.6      |
|                | Low      | 189                | 10.2          | 37.1           | 18.4           | 14.7         | 19.6               | 236         | 10.2          | 47.6           | 28.2           | 14.0      |
| Georgia Strait | High     | 1046               | 8.0           | 38.7           | 20.0           | 17.0         | 16.2               | 840         | 8.0           | 38.9           | 30.8           | 22.3      |

**Note:** Broughton Archipelago is not included because of unidentified species in chalimus stages during live sampling.

tured at those sites. Specifically, we hypothesized that fish from locations that were more exposed to farms would have higher louse prevalence and that high temperature and salinity would also be correlated with high lice loads (because sea louse growth in lab-based trials depends strongly on temperature and salinity; Pike and Wadsworth 1999; Costello 2006).

We used linear mixed-effects modelling to account for the hierarchical nature of the sampling, where multiple sampling events at a given location were treated as random factors nested within location, which itself was a random factor nested within a region. We included exposure category (low or high) nested within region, temperature, salinity, and fork length as fixed factors to examine their influence on sea louse infection levels on juvenile salmon. Our initial model selection included analyses for each louse and host species, respectively; however, because results were broadly similar for each analysis, we combined louse prevalence and host species for simplification of presentation (minor differences are discussed in the Results). Thus, for the model, we averaged prevalence for combined sea louse species (*L. salmonis* and *Caligus clemensi*) for all host individuals (pink and chum) within a sampling event (i.e., replicate;  $n = 296$ ) and transformed prevalence data using an arcsine square-root function to correct for unequal variances and nonnormality. We tested a set of candidate models using Akaike's information criterion (AIC) and then evaluated  $\Delta AIC$  to select the best approximating model(s). We made appropriate inference using  $\Delta AIC < 4$  to describe the top model set. Finally, we summed Akaike weights ( $\omega_i$ ) across the top model set for each variable to rank them by importance (Burnham and Anderson 1998; Anderson et al. 2001).

We performed a  $\chi^2$  test to examine whether the ratio of louse species abundances changed in accordance to a given salmon farm region and associated differences in farm salmon production. We performed all statistical tests using SPSS 16.0 for Mac (SPSS 2007).

## Results

We assessed a total of 13 426 juvenile chum and pink salmon over 296 sampling episodes for sea louse parasitism across the four regions in 2007 and 2008. Juvenile salmon were largest in Georgia Strait and smallest in the Broughton Archipelago, and both pink and chum salmon were larger, on average, at high-exposure sites in all farm regions except pink salmon in Georgia Strait, where they were larger at low-exposure sites (Table 1). Sea surface salinity and temperature were higher on average at sites of high exposure than at sites of low exposure.

Louse prevalence and abundance were lowest for both chum and pink salmon in all farm regions at sites of low exposure and most similar to Bella Bella, where there are no farms (Table 2; Fig. 2). In a comparison among the four regions, combined louse abundance was highest in Georgia Strait, where salmon production is greatest (Fig. 3). Increases in combined louse abundance between sites of low and high exposure ranged from a 2.4-fold increase at Georgia Strait, to a 7.1-fold increase at Finlayson, to a 30.5-fold increase in the Broughton Archipelago. A greater proportion of the lice were *L. salmonis* at sites of high exposure ( $\chi^2 =$

**Table 4.** List of candidate models and resulting Akaike's information criterion (AIC) scores used to determine which factors most influence sea louse prevalence on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*).

| Model  | K | AIC      | $\Delta$ AIC | $\omega_i$ |
|--|---|----------|--------------|------------|
| Exposure + salinity*                                     | 4 | -255.069 | 0.000        | 0.394      |
| Exposure*  | 3 | -254.660 | 0.409        | 0.321      |
| Exposure + temperature*                                  | 4 | -254.231 | 0.838        | 0.259      |
| Exposure + length  | 4 | -248.094 | 6.975        | 0.012      |
| Length   | 3 | -221.4   | 33.674       | 0.000      |
| Salinity   | 3 | -213.52  | 41.551       | 0.000      |
| Temperature  | 3 | -212.54  | 42.535       | 0.000      |
| Salinity + temperature                                   | 4 | -205.107 | 49.962       | 0.000      |
| Salinity + temperature + (salinity $\times$ temperature) | 5 | -194.39  | 60.680       | 0.000      |

**Note:** Model structure, number of parameters + intercept + covariance structure (K), AIC,  $\Delta$ AIC, and Akaike weight ( $\omega_i$ ) are included; exposure is fish exposure to farms (low or high), salinity is sea surface salinity, temperature is sea surface temperature, and length is host fork length.

\*A model of the top model set.

3.814,  $df = 1$ ,  $p \leq 0.001$ ), and lice at all locations were dominated by larval stages (copepodid and chalimus; Table 3).

Model selection and multimodel inference suggested that exposure plus salinity was the best predictor of louse prevalence on juvenile salmon, given the set of candidate models (Table 4). Specifically, louse prevalence increased at sites of high exposure to salmon farms, and this was most prominent in the regions with the highest salmon production (Fig. 3); three of three models in the top model set (0–4  $\Delta$ AIC) contained exposure. Summing the Akaike weights ( $\Sigma\omega_i = 0.974$ ) across the top models ranked the variable exposure higher than salinity and temperature by factors of 2.5 and 3.8, respectively (Table 5). Although mixed-effects modelling results were broadly similar for each louse and host species, an exception was an increase in the effect of chum salmon host length on the prevalence of *C. clemensi*.

## Discussion

Our study shows associations between salmon farms and infestations of sea lice on wild juvenile salmon across a large area of coastal British Columbia. Specifically, we show regional differences in parasitism of juvenile salmon between areas with and without salmon farms, as well as within-regional differences between sites of differing exposure levels. Within salmon farmed regions, juveniles at low-exposure sites hosted fewer sea lice and were most similar in infection levels to regions without salmon farms. Overall, exposure to farms was the most important factor explaining louse prevalence. Finally, the proportion of *L. salmonis* infection increases in concert with farm salmon production.

Because louse parasitism of juvenile salmon at low-exposure sites in active farm regions is most similar to levels in a region that lacks salmon farms, this suggests a "baseline" designation that can enable regional comparisons. Juvenile chum and pink salmon examined at sites of low exposure in Finlayson and the Broughton Archipelago hosted spatially uniform louse prevalence averaging less than 5%. These rates are most similar to that at Bella Bella, where farms are absent (3.5%), and correspond with those

**Table 5.** Summed Akaike's information criterion (AIC) weights ( $\Sigma\omega_i$ ) across the top model set to rank parameters by relative importance in predicting sea louse prevalence on juvenile chum salmon (*Oncorhynchus keta*) and pink salmon (*O. gorbuscha*).

| Parameter   | $\Sigma\omega_i$ | Direction of highest louse prevalence |
|-------------|------------------|---------------------------------------|
| Exposure    | 0.974            | High exposure to salmon farms         |
| Salinity    | 0.394            | Higher salinity                       |
| Temperature | 0.259            | Higher temperature                    |

**Note:** Exposure is fish exposure to farm influence (low or high), salinity is sea surface salinity, and temperature is sea surface temperature.

reported elsewhere in coastal British Columbia without farms (Morton et al. 2004; Krkošek et al. 2007b; Gottesfeld et al. 2009). However, juveniles at low-exposure sites in Georgia Strait hosted higher louse levels than those in all other peripheral areas, though levels were significantly lower than those in high-exposure locations within the region. The large number of farms in this area, the high complexity of waterways, and evidence of long-distance transmission capability of farm-origin lice (>30 km; Krkošek et al. 2006; Costello 2009) suggest that louse transmission in this region confounds point sources as previously described (Morton et al. 2008).

The consistent relationship between elevated louse levels near salmon farms over all regions examined strongly suggests farm-induced parasite transmission to wild fish. Farm fish hosting even small numbers of lice can collectively produce large numbers of louse eggs and infectious larvae (Heuch and Mo 2001; Heuch et al. 2005; Orr 2007). Both juvenile chum and pink salmon hosted elevated levels of lice in all regions and years at sites of high exposure compared with lice levels at sites of low exposure. These results are consistent with previous research in farm areas of Europe (Tully et al. 1999; Bjorn and Finstad 2002) and locally in the Broughton Archipelago and Georgia Strait (Krkošek et al. 2005a, 2006; Morton et al. 2008). We add to this evidence a 7.1-fold increase in louse abundance near farms in the northern region of Finlayson compared with that of sites of low exposure. Although this is the first demonstration of elevated lice levels on British Columbia's north-central coast, the lower parasitism compared to that of other farm areas is most likely due to low salmon production in the region.

Although environmental parameters have been considered as contributors to elevated louse parasitism of juvenile salmon, the data we present here suggest they are not the primary factors predicting prevalence levels in areas that are exposed to open net-pen salmon farms. Other work has shown that sea louse growth is strongly dependent on, and positively correlated with, salinity and temperature (Pike and Wadsworth 1999; Costello 2006). However, we found only moderate positive associations between salinity and louse prevalence, and only at sites of high exposure to salmon farms. Size (length) of juveniles also did little to predict louse prevalence. Instead, our analyses show that exposure to farms was the most important factor explaining louse prevalence. Moreover, louse abundance is coupled with the amount of salmon produced in a given farm region. For example, regional louse abundance (combined low- and high-exposure sites) increased from 0.13 at Finlayson, to

0.24 in the Broughton Archipelago, to 0.65 in Georgia Strait, with associated farmed salmon production of 1911, 16 174, and 17 005 metric tonnes, respectively.

A comparison of infections by the two louse species provides further insights into the potential for salmon farms to alter natural parasite dynamics. Juvenile salmon at sites of low exposure in all regions were most infected by *C. clemensi*, which is consistent with observations in other British Columbia areas where farms are absent (Morton et al. 2004; Krkošek et al. 2007b; Gottesfeld et al. 2009). This species is not salmon specific, unlike *L. salmonis*. However, parasitism by *L. salmonis* increased in all regions at sites of high-farm exposure and became the dominant louse infecting juveniles near Broughton and Georgia Strait farms, where farmed salmon production is highest. This proportional shift may contribute to the relationship between increased fish aquaculture intensity and decreasing wild salmon populations observed in Europe and eastern and western Canada by Ford and Myers (2008). *Lepeophtheirus salmonis* are locally associated with juvenile chum and pink salmon mortality (Morton and Routledge 2005; Krkošek et al. 2006) and have been implicated in contributing to the population collapse of pink salmon in the Broughton Archipelago (Pacific Fisheries Resource Conservation Council 2002; Krkošek et al. 2007a). Accordingly, these data should alert managers to the potential for high mortality of juvenile salmonids and associated population level impacts on numerous wild salmon stocks migrating through the high-intensity farm salmon production region of Georgia Strait.

### Conservation implications

Sea lice from salmon farms threaten vulnerable wild salmon populations in British Columbia, heightening the urgency required for Canada to develop an effective conservation-based salmon aquaculture policy. Infection levels are correlated with the amount of salmon produced in a given farm region; the alternative explanations beyond farm-origin lice that we tested here have less support. These findings should concern resource managers, as current wild salmon populations on the coast of British Columbia are under multiple human stressors, and many populations are at low levels (English et al. 2006; Price et al. 2008). Moreover, salmon farms have been specifically implicated in the decline or collapse of several local wild salmon populations (Krkošek et al. 2007a; Ford and Myers 2008). Given the increased production and site expansion proposed by the salmon farm industry, associated effects from farms may intensify and ultimately challenge the sustainability of ecosystems and economies along British Columbia's entire coast (Krkošek 2010). Threats from salmon farms to wild salmon can be mitigated by reducing the number of fish per farm, limiting the number of farms in a region, and moving farms from migration routes and juvenile salmon habitats, as has been implemented in some wild salmon sensitive areas of Norway (Heuch et al. 2005; Krkošek 2010). Ultimately, a switch to land-based aquaculture offers the best solution to the problem of transmission of diseases to wild fish.

### Acknowledgements

We are grateful to the Heiltsuk, Homalco, Kitasoo, and MTTC Nations, in whose traditional territories the research

occurred; S. Bergh, J. Eriksson, H. Humchitt, D. Kwaii, K. Poppe, I. Reid, and A. Woods for technical assistance; D. Braun and M. Hocking for analytical advice; Redden Net and Raincoast Conservation Foundation for in-kind support; and B.M. Connors, C.T. Darimont, and W.J. Palen for review. This work was supported by The B.C. Pacific Salmon Forum, Coastal Alliance for Aquaculture Reform, David and Lucille Packard Foundation, Gordon and Betty Moore Foundation, Ritchie Foundation, Sandler Foundation, Vancouver Foundation, Tom Buell Endowment Fund, a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to J.D.R., and an NSERC Industrial Postgraduate Scholarship to M.H.H.P.

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