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Wild juvenile salmonids in Muchalat Inlet, British Columbia, Canada: factors associated with sea lice prevalence

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ABSTRACT: The Muchalat Inlet, British Columbia, is among the most westerly points at which aquaculture is practiced in Canada. In this paper, we summarise data from over 18 000 wild fish sampled at 16 sites over an 8 yr period, between 2004 and 2011. The most prevalent wild species was chum salmon *Oncorhynchus keta* (82.4 %), followed by Chinook *O. tshawytscha* (10 %) and coho *O. kisutch* (4.3 %). However, inter-annual and seasonal variation was evident, and smaller numbers of other Pacific salmon and stickleback species were sporadically observed. A high percentage of wild salmon (~95 %) had no sea lice parasites present, with less than 1 % of the fish hosting a mobile-stage sea louse. Of the data for which sea lice species were recorded, just over 96 % of samples were identified as *Lepeophtheirus salmonis*. Logistic regression models assessed the association between the presence of lice and a range of independent variables. These models indicated a significant degree of spatial variation, much of which could be explained in terms of salinity levels. There were also important variations through time, both over the season within a year and across years. In addition, coho salmon were significantly more likely (odds ratio = 1.65; 95 % CI = 1.20–2.3) to be infected than chum salmon. The protective effect of low salinity was most clearly seen at values lower than 15 psu, although this was dependent on fish species.

KEY WORDS: Ectoparasite · *Lepeophtheirus salmonis* · Chum salmon · Vancouver Island · Salinity · Epidemiology · *Oncorhynchus*

INTRODUCTION

Ectoparasitic copepods belonging to the family Caligidae, commonly referred to as 'sea lice', are endemic in many marine environments and infest both wild and farmed fish (Costello 2006, Revie et al. 2009). When considering salmonid hosts, the 2 copepod genera that are of primary interest are *Lepeophtheirus* and *Caligus*. In the Northern Atlantic Ocean, infestation with *L. salmonis* is a serious health concern affecting farmed Atlantic salmon *Salmo salar* L. (Lees et al. 2008a, Jansen et al. 2012, Jones et al. 2012), with a number of articles reporting impacts on wild Atlantic salmon (Krkošek et al. 2013) and sea trout (Tully et al. 1999, Middlemas et al. 2013). Although *C. elongatus* also affects farmed Atlantic

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salmon (Revie et al. 2002), the levels of infestation are typically lower and appear to be more easily controlled. By contrast, in Chile, the main copepod of concern is *C. rogercressyi* (Kristoffersen et al. 2013). In British Columbia (BC), Canada, both *L. salmonis* and *Caligus* spp., in particular *C. clemensi*, have been reported to infest farmed (Marty et al. 2010) and wild (Jones et al. 2006) hosts. However, the species of *L. salmonis* that occurs in the Pacific Ocean off BC genetically differs from that found in the Atlantic Ocean (Yazawa et al. 2008, Skern-Mauritzen et al. 2014). It is not clear to what extent this may be responsible for the much lower levels of infestations typically seen in Atlantic salmon farms in BC (Marty et al. 2010) or for the fact that sea lice resistance to the in-feed therapeutant emamectin benzoate has not thus far become a concern in this region (Saksida et al. 2010), in stark contrast to the situation in the North Atlantic farming regions (Lees et al. 2008b, Espedal et al. 2013, Jones et al. 2013). An association between levels of sea lice infestation on Atlantic salmon farms and those seen on out-migrating juvenile Pacific salmonids has been consistently reported (Krkošek et al. 2009, Marty et al. 2010), but the extent to which this may affect the robustness of the wild populations remains a matter of scientific dispute (Krkošek et al. 2011).

Muchalat Inlet, on the west coast of Vancouver Island, BC, is 55 km long with a maximum depth of 380 m, and is primarily influenced by the Gold River, which drains a 1010 km^2 watershed. Flow from the Gold River is bimodal, with heavy, but highly variable, winter precipitation and a later May–June flow attributed to melt water, as is common along the BC coast (e.g. see the river discharge summary reported for the Broughton Archipelago by Stucchi et al. 2011). Here we report on 8 consecutive years of sampling to assess sea lice infestation rates on juvenile salmonid and stickleback species captured in the Muchalat Inlet between 2004 and 2011. This study was undertaken to coincide with the commencement of finfish aquaculture in Muchalat Inlet and concerns that finfish aquaculture could impact sea lice infestation levels on wild juvenile salmonids (Butterworth et al. 2008). Initial site selection and sampling procedures were established by staff from Fisheries and Oceans Canada (DFO) in 2004. Subsequently, site selection and sample timings were occasionally altered, in consultation with DFO scientists, and sampling activities were carried out by Mainstream Biological Consulting on behalf of Grieg Seafood BC Ltd., the aquaculture company which operates the sites in this area. The first finfish aquaculture site approved in Muchalat Inlet had been recently stocked prior to the 2004 sampling period. Two additional sites became active during the 2005 and 2006 sampling periods, respectively. Between 2007 and 2011, 4 active finfish sites were operational during the annual sampling periods; in all cases, these sites were stocked with Atlantic salmon.

While the situation regarding sea lice infestation both on salmon farms and in wild juvenile stocks has been the subject of relatively extensive research in other parts of BC (Butterworth et al. 2008, Beamish et al. 2009, Gottesfeld et al. 2009, Saksida et al. 2011), in particular in the Broughton Archipelago (Jones & Hargreaves 2007, Marty et al. 2010, Patanasatienkul et al. 2013, Rogers et al. 2013), to date little has been published relating to the west side of Vancouver Island, and nothing, to our knowledge, has been published regarding the Muchalat Inlet. As will be shown, not only do the sea lice infestation dynamics appear to be very different from those reported in other regions of BC, the structure of wild Pacific salmon species present in the area is also somewhat different. Within the Muchalat Inlet samples, few, if any, pink salmon *Oncorhynchus gorbuscha* were observed, in stark contrast to the Broughton Archipelago (Patanasatienkul et al. 2013) or more northern areas of salmon farming in BC (Saksida et al. 2011), where pink salmon are common and indeed tend to dominate in many years. In addition to presenting for the first time a comprehensive breakdown of the numbers, sizes and timing of salmonid species migrating through the Muchalat Inlet, we also built a statistical model that helps elucidate the factors associated with sea lice infestation levels on these wild hosts.

Chum salmon *O. keta* begin out-migration from around early March as soon as they emerge from the gravel, at which point they are around 30–40 mm in length. They migrate downstream, usually at night and in the river systems draining into Muchalat Inlet, and will typically be out in the ocean within a few days. In contrast, Chinook salmon *O. tshawytscha*, after emerging from the gravel at a similar size, will spend 30 to 90 d in the stream or estuary before starting their out-migration. The case for coho salmon *O. kisutch* is quite different in that these fish will spend an entire year in the river before migrating. Their growth in fresh water is relatively slow, but as a result of this additional river time, they will typically be twice as large when they do migrate, any time from the spring freshet through June (Groot & Margolis 1991).

Here we provide spatial and temporal descriptive summaries of both the samples collected over the

8 yr period, as well as the levels of sea lice infestations observed. The modelling of spatial elements is relatively broad-scale and considers effects in terms of 4 zonal components in addition to salinity levels at the specific sampling site. No hydrodynamic flows or specific geo-location information are incorporated, nor are the sea lice loads that existed at active salmon farms in the area explicitly incorporated in the statistical modelling. It is our intention to explore the potential role of farm-origin sea lice, with the use of more finely-scaled spatial data in future studies; however, we believe that it is important to first describe the broad spatio-temporal patterns and variability in levels of sea lice infestation which had not been previously documented for this region.

MATERIALS AND METHODS

Salmon sampling

Weekly beach seine sampling was conducted to collect fish samples for sea lice analysis at sites in the Muchalat Inlet, BC (Fig. 1), between March and June from 2004 to 2011 (6 sites in 2004, 8 sites in 2005 and 2006, 16 sites in 2007 and 2008, 11 sites since 2009; Table 1). Sampling protocols were developed in consultation with the DFO. Briefly, a 45 m long by 3.7 m deep beach seine net was deployed in a consistent manner by a 3-person crew to collect fish in near-shore sites. The net consisted of 3 sections (each 15 m long): a centre bunt from which the fish were eventually retrieved consisting of 6 mm diamond mesh, and 2 side panels (wings) constructed from 12 mm mesh. The sites were selected so as to provide reasonable spatial coverage as well as proximity to finfish aquaculture sites in the area. Thirty fish from each host species (salmonids and sticklebacks) or all fish for a given species (when less than 30 were captured) were collected at each of the sites during weekly sampling. In practice, this maximum threshold was primarily of relevance for the case of chum salmon and was invoked in just under one-third of all sampling events; as far as all other species were concerned, more than 30 individuals of these species were caught in less than 0.5% of all the sampling events. Water quality measurements including seawater temperature and salinity were also recorded at the surface for each site (0.2 m). Sampled fish were individually packed into re-sealable bags, labelled with site number and date, and then placed into a portable freezer, kept at around −18°C, for transfer to a laboratory.

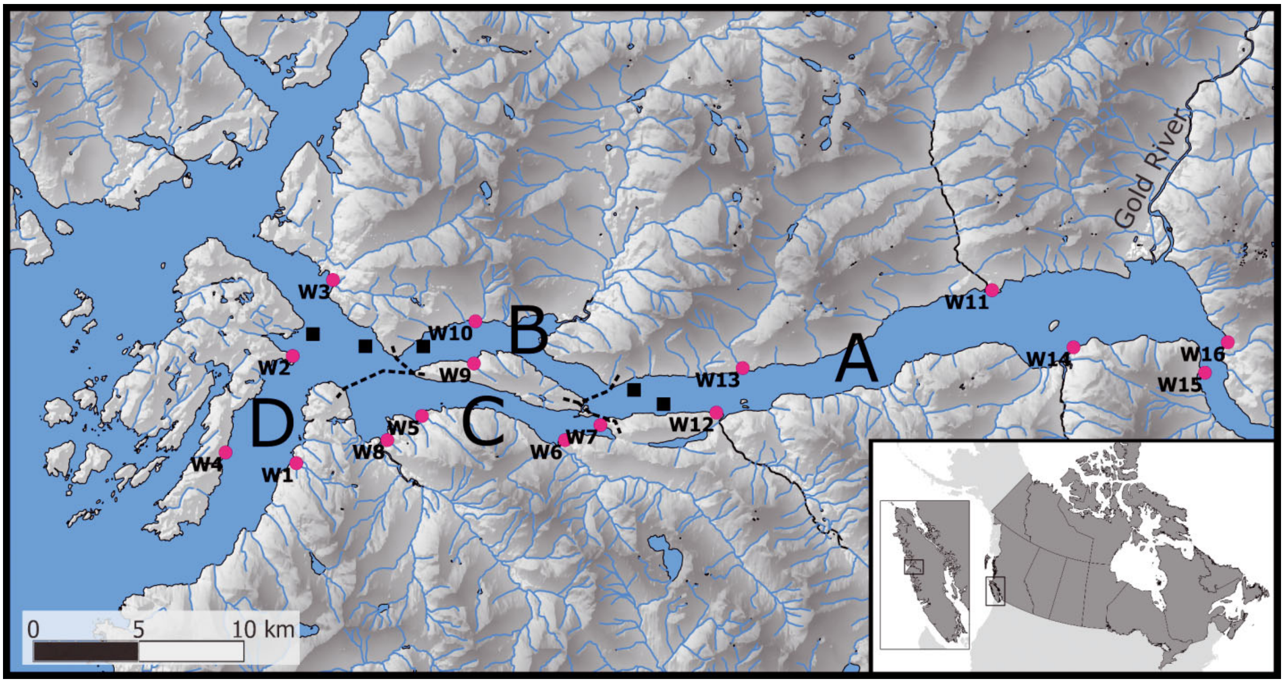

Fig. 1. Shore locations of the 16 sampling sites (pink circles: W1–W16) in 4 demarcated zones (A–D) within the Muchalat Inlet in British Columbia, Canada; the west of the inlet opens to the Pacific Ocean. Black squares: locations of 5 aquaculture sites in the region active at various points over the period 2004 to 2011

Table 1. Matrix indicating which of the 16 sites in Muchalat Inlet, British Columbia, Canada, was sampled in each of the 8 years covered by the study. ID labels match those shown in Fig. 1

Site	ID	Zone	2004	2005	2006	2007	2008	2009	2010	2011
Zuciarte Channel	W1	D	X	X	X	X	X	X	X	X
Concepcion Point South	W2	D				X	X	X	X	X
Hanna Channel	W3	D				X	X	X	X	X
Clerke Peninsula	W4	D				X	X			
East Mooyah Bay	W5	C	X	X	X	X	X	X	X	X
Silverado Creek	W6	C	X	X	X	X	X	X	X	X
Ous Point	W7	C	X	X	X	X	X	X	X	X
Mooyah Bay	W8	C	X	X	X	X	X			
North Gore Island	W9	B	X	X	X	X	X	X	X	X
Williamson Passage	W10	B				X	X	X	X	X
McCurdy Creek	W11	A		X	X	X	X	X	X	X
Houston River	W12	A		X	X	X	X	X	X	X
Muchalat North	W13	A				X	X	X	X	X
Jacklah River	W14	A				X	X			
Guaquina Point	W15	A				X	X			
Black Creek	W16	A				X	X			

Laboratory assessment

In the laboratory, the frozen fish were thawed, counted and identified to host species by DFO-trained staff. They were then scanned under a stereoscopic dissection microscope for the presence of sea lice. At the beginning of the study, the sea lice were only identified as being in the non-motile or motile stages of their life history. Non-motile lice were registered as 'chalimus' and were not identified to genus. Motile lice (pre-adults and adults) were identified as either *Lepeophtheirus* sp. or *Caligus* sp.; in addition, these motile lice were identified as male or female specimens. From 2007, the sea lice identification methodology was revised, identifying the species and detailed developmental stage of every louse (i.e. non-mobile lice were staged as copepodid or chalimus I to IV, based on the generally accepted morphological definition in effect at that time, and also identified to species). Individual fish specimens were measured, with length being recorded to the nearest millimetre (fork length for salmonids, total length for non-salmonids), while weight was recorded to the nearest tenth of a gram.

Descriptive statistics

A breakdown by species of the overall numbers of fish caught, together with their physical characteristics (summary statistics for length and weight) was carried out. In addition, an assessment of the relative contribution of the 5 wild host species, broken down by year, was made. This indicated that only 3 salmonid species (chum, Chinook and coho) were consistently observed, and for these host species a detailed annual summary of sea lice infestation (prevalence) by zone of capture (see Fig. 1 for zones) was carried out. An assessment as to how the size of the sampled fish varied across these 3 species was also made, using locally weighted scatterplot smoothing curves to show the relationship of fish length (mm) to the week of sampling.

Prevalence modelling

A mixed effects logistic regression modelling approach (Hosmer & Lemeshow 2004) was used to assess the association between the presence of lice and a range of independent variables. An initial univariable screening was carried out ($p < 0.20$) to identify candidate variables, which were then included in the full multivariable ($p < 0.05$) random effects logistic regression, where site was specified as the random effect to account for the repeated measures taken within sites. Two models were constructed: in the first, the 3 main salmonid species were considered, while in the second model, only data associated with chum salmon samples were considered (these comprised ~85% of the data from the first model). The following predictors were explored in the analyses: zone, year, month, fish species (in the first model only: chum, Chinook and coho), fish length and weight, as well as the environmental parameters seawater temperature and salinity. For salinity, a spline effect was included which expanded the variable to account for values greater than 15 psu and those below this value as 2 distinct estimates. The variable fish length, included only in the second model, was also included as a quadratic polynomial term for the chum salmon samples. All statistical summaries and analyses were carried out using Stata 13.0. The map was generated using QGIS (QGIS Development Team 2009) with freely available online datasets (http://geogratis.cgdi.gc.ca, Natural Resources Canada).

RESULTS

A map was created of the Muchalat Inlet region in which the sea lice surveillance took place (Fig. 1) and used to illustrate the 16 sites (W1–W16) at which the sampling of wild fish was carried out. Five Atlantic salmon farm sites are also present in the area, and while data from these farms were not directly included in the current study, their locations are shown on the map for completeness. In addition, the map indicates the 4 zones that were used to provide spatial categories over which the data were summarised and assessed. The delineation of these zones was based on detailed local knowledge, but also largely reflected the number of freshwater rivers/creeks draining into different parts of the inlet (from many in Zone A to almost none in Zone D). All data from sampling carried out over the period 2004 to 2011 were available. As the objective was to target wild juvenile salmonids, capture events took place from the beginning of March until around the end of June in each year. Table 1 indicates which of the sites were targeted for sampling in each year. The number of sites rose from 6 in 2004, up to 16 in 2007 and 2008, before falling back to 11 during the final 3 yr. This variation across years reflects an evolving protocol which attempted to balance sampling effort with the ability to provide a comprehensive picture of sea lice infestation across the region. In general, for each site included in a year, sampling was attempted on a weekly basis. Coverage tended to be a little more sporadic at the start of the sampling season (first 2 wk in March) and towards the end (after mid-June). Each zone used in the statistical comparisons was represented by at least 1 sampling site in each of the years considered, with the exception of 2004 where no sites from Zone A were included among the sampled locations. The mean and range of values associated with the seawater salinity and temperature across all sampling events, by zone, are given in Table 2. Zone A was typically associated with sites that were less saline (mean of 7.5 psu), whereas Zone D had the most saline conditions. There was less variability across zones when considering seawater temperature, although Zone A appeared to be slightly cooler (mean of 9.3°C), likely due to the effects of increased snow-melt entering the eastern end of the system during the sampled months.

On average, just over 2300 fish were sampled each year, though not unexpectedly, this tended to vary according to the number of sites targeted (Fig. 2). Of the 18 747 fish examined, 82.4% were chum salmon, 10.1% were Chinook salmon, and 4.3% were identified as coho salmon (Table 3). There was some variation in the proportions of these 3 main species, with Chinook, for example, accounting for just under 5% in 2 years (2006, 2009) to just over 25% in 2004. Less than 2% of the fish examined were sockeye salmon *Oncorhynchus nerka*, a number somewhat exaggerated by a single year, 2005, where sockeye comprised 11.4% of the samples; in other years, the percentage of sockeye salmon rarely exceeded 0.5%. In some samples, three-spined sticklebacks *Gasterosteus aculeatus* were identified; these varied over the years, but overall accounted for just under 1.5% of the samples (Table 3). Due to the low abundance of these species, as well as the sporadic appearance of the sockeye salmon, only the 3 main salmonid species that accounted for around 97% of all samples (i.e. chum, Chinook and coho) were included in the statistical analyses which follow. Before leaving these ~600 fish (i.e. the sockeye and stickleback samples) a few descriptive notes may be in order. Of the 336 sockeye sampled, just over half were captured in 2005. Of

Table 2. Statistical summary of salinity and seawater temperature data from 16 locations in Muchalat Inlet, British Columbia, Canada, by zone (A, B, C and D; see Fig. 1) over the duration of the study (2004 to 2011)

Zone	n	Range	Mean	Percentiles 25	Percentiles 50	Percentiles 75
Salinity (psu)						
A	341	0.2–27.1	7.5	2.9	5.5	11.2
B	161	2.5–27.5	15.4	10.8	15.4	20.1
C	313	1.3–28.8	14.7	9.6	14.7	19.9
D	231	3.5–30.0	17.8	13.3	17.5	23.5
Total	1046	0.2–30.0	13.2	6.9	13.2	18.9
Temperature (°C)						
A	345	2.6–18.0	9.3	6.8	9.0	11.7
B	163	3.8–15.7	9.6	7.5	9.7	12.0
C	316	4.4–17.5	10.2	8.0	9.9	12.7
D	234	4.8–16.7	9.7	7.5	9.6	12.0
Total	1058	2.6–18.0	9.7	7.4	9.5	12.1

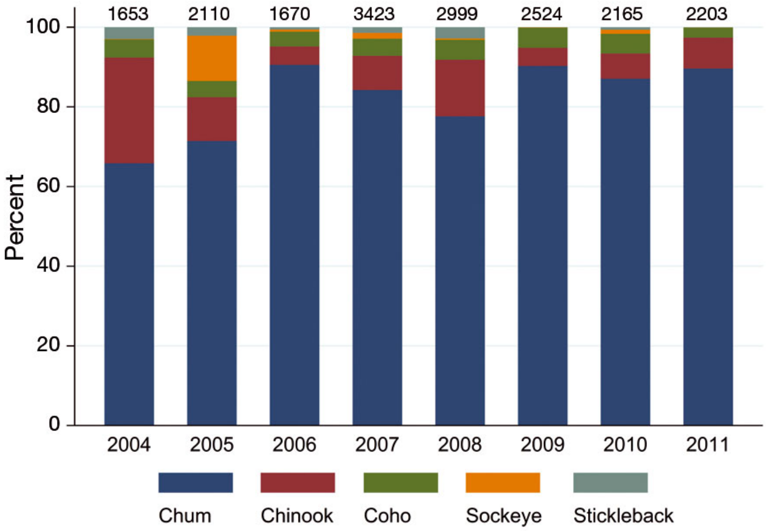

Fig. 2. Sampling distribution indicating the proportion of each fish species (chum *Oncorhynchus keta*, Chinook *O. tshawytscha*, coho *O. kisutch* and sockeye salmon *O. nerka*, and three-spined stickleback *Gasterosteus aculeatus*) caught in a particular year. The total number of fish sampled in that year is indicated at the top of each bar

Table 3. Summary of fish weight and length by various species (chum *Oncorhynchus keta*, Chinook *O. tshawytscha*, coho *O. kisutch* and sockeye salmon *O. nerka*, and three-spined stickleback *Gasterosteus aculeatus*) caught between 2004 and 2011

Species	n	Range	Mean	Percentiles		
				25	50	75
Weight (g)						
Chum	15455	0.1–23.3	0.8	0.4	0.5	0.7
Chinook	1891	0.3–24.7	2.7	0.7	1.1	2.9
Coho	810	0.2–57.7	9.2	4.9	7.4	11.3
Sockeye	336	0.7–15.7	3.8	2.1	3.0	4.5
Stickleback	255	0.1–5.4	2.3	1.0	2.5	3.2
Length (mm)						
Chum	15455	25–125	41	37	39	43
Chinook	1891	30–123	54	41	46	61
Coho	810	28–164	83	74	84	95
Sockeye	336	40–109	69	61	67	76
Stickleback	255	23–77	57	48	62	66

those 171 fish, 69 (28.8%) had at least 1 sea louse present on them, the highest annual prevalence level for any species, in any year. In comparison, among the 165 sockeye sampled over the other 7 years, only 1 fish was found to have a single sea louse. Of the 255 sticklebacks sampled over the entire period, 38 had a sea lice infestation. Prevalence was highest, at just over 20%, in 2004 and 2005, and decreased thereafter, although from 2009 onwards, very few sticklebacks were identified in the samples.

The remainder of the analysis considers only the 3 main species of Pacific salmonids observed (N = 18 156). While it is clear that chum were the dominant species observed throughout the study period (Fig. 2, Table 4), this dominance was most pronounced in the early part of the season, with chum typically representing over 90% of all fish in March and April. By June, chum typically represented only around half of the fish observed, while Chinook and coho were present at around 4 times their overall average proportions (data not shown). Fig. 3 shows that, unsurprisingly, the mean size of fish sampled increased as the season progressed. This increase is less obvious, particularly for coho salmon, in the early part of the season, possibly due to small sample sizes, but the larger lengths become very evident with fish of all species by the end of the sampling period. As would be expected, weight is highly correlated with fish length (with a mean rho of 0.9, see Table 6). In general, coho are significantly larger than the other 2 species, ranging from around 7 g in March up to around 14 g in June. At the opposite end of the size scale are the chum, which grow from around 0.5 g up to 2.5 g between March and June; Chinook follow a similar monthly pattern to chum but are on average almost twice their weight at each time point.

The presence of lice across the 3 main wild fish species, broken down by year, is indicated in detail in Table 4 and is summarised in Table 5 by the number of fish that were infested with sea lice in either the attached (non-motile) or motile stages. The first thing that is evident is that most of the wild salmonids did not have any infestation, and that where infestation did occur, it was more likely to be with a louse at an attached stage (3.8%) than with a motile louse (0.65%). On average over the 8 yr, the proportion of motile lice was about 15% of all lice observed. While the overall proportion of motile to attached lice was broadly similar across years, this proportion tended to rise from just 5% of all infestations in March to around 15% in May, before jumping steeply to account for around half of all infestations in June (data not shown). Another fairly obvious point from Table 5 is that a combination of fish having no infestation together with those having just a single louse accounts for the vast majority of all sampled fish, viz. 99.2% and 99.9% for the attached and motile stages,

Table 4. Breakdown by 3 main host species (chum *Oncorhynchus keta*, Chinook *O. tshawytscha* and coho salmon *O. kisutch*) across all years of the number of fish sampled (n) together with the number that were found to have a louse infestation (Inf.), which is also given as a percentage (%)

Zone	Fish species	Year 2004 Inf. / n (%)	2005 Inf. / n (%)	2006 Inf. / n (%)	2007 Inf. / n (%)	2008 Inf. / n (%)	2009 Inf. / n (%)	2010 Inf. / n (%)	2011 Inf. / n (%)	All years Inf. / n (%)
A	Chum	–	3 / 236 (1.3)	62 / 565 (11)	1 / 1166 (0.1)	6 / 944 (0.6)	16 / 821 (1.9)	14 / 329 (4.3)	14 / 587 (2.4)	116 / 4648 (2.5)
	Chinook	–	9 / 191 (4.7)	0 / 20 (0)	0 / 238 (0)	0 / 380 (0)	0 / 91 (0)	0 / 72 (0)	0 / 44 (0)	9 / 1036 (0.9)
	Coho	–	0 / 13 (0)	0 / 3 (0)	0 / 52 (0)	1 / 87 (1.1)	0 / 51 (0)	2/44 (4.5)	1/27 (3.7)	4 / 277 (1.4)
B	Chum	0 / 193 (0)	35 / 272 (12.9)	10 / 240 (4.2)	12 / 439 (2.7)	6 / 395 (1.5)	27 / 507 (5.3)	10 / 418 (2.4)	6 / 518 (1.2)	106 / 2,982 (3.6)
	Chinook	4 / 87 (4.6)	3 / 12 (25)	0 / 4 (0)	0 / 8 (0)	0 / 12 (0)	0 / 8 (0)	0 / 27 (0)	1 / 59 (1.7)	8 / 217 (3.7)
	Coho	0 / 7 (0)	1 / 7 (14.3)	1 / 2 (50)	0 / 12 (0)	6 / 18 (33.3)	3 / 17 (17.6)	4 / 8 (50)	0 / 3 (0)	15 / 74 (20.3)
C	Chum	8 / 696 (1.1)	55 / 769 (7.2)	46 / 611 (7.5)	4 / 535 (0.7)	21 / 323 (6.5)	25 / 355 (7)	20 / 448 (4.5)	9 / 182 (4.9)	188 / 3,919 (4.8)
	Chinook	18 / 351 (5.1)	7 / 29 (24.1)	0 / 53 (0)	0 / 31 (0)	0 / 1 (0)	0 / 12 (0)	0 / 3 (0)	0 / 16 (0)	25 / 496 (5)
	Coho	5 / 68 (7.4)	3 / 60 (5)	3 / 57 (5.3)	1 / 53 (1.9)	2 / 36 (5.6)	1 / 42 (2.4)	0 / 10 (0)	0 / 7 (0)	15 / 333 (4.5)
D	Chum	3/199 (1.5)	25 / 230 (10.9)	19 / 96 (19.8)	34 / 743 (4.6)	69 / 666 (10.4)	31 / 595 (5.2)	46 / 690 (6.7)	27 / 687 (3.9)	254 / 3906 (6.5)
	Chinook	0 / 1 (0)	–	–	1 / 17 (5.9)	3 / 33 (9.1)	1 / 4 (25)	12 / 35 (34.3)	0 / 52 (0)	17 / 142 (12)
	Coho	–	0 / 6 (0)	–	1 / 30 (3.3)	2 / 9 (22.2)	3 / 18 (16.7)	18 / 45 (40)	1 / 18 (5.6)	25 / 126 (19.8)
All zones	Chum	11 / 1088 (1)	118 / 1507 (7.8)	137 / 1512 (9.1)	51 / 2883 (1.8)	102 / 2328 (4.4)	99 / 2278 (4.3)	90 / 1885 (4.8)	56 / 1974 (2.8)	664 / 15455 (4.3)
	Chinook	22 / 439 (5)	19 / 232 (8.2)	0 / 77 (0)	1 / 294 (0.3)	3 / 426 (0.7)	1 / 115 (0.9)	12 / 137 (8.8)	1 / 171 (0.6)	59 / 1891 (3.1)
	Coho	5 / 75 (6.7)	4 / 86 (4.7)	4 / 62 (6.5)	2 / 147 (1.4)	11 / 150 (7.3)	7 / 128 (5.5)	24 / 107 (22.4)	2 / 55 (3.6)	59 / 810 (7.3)

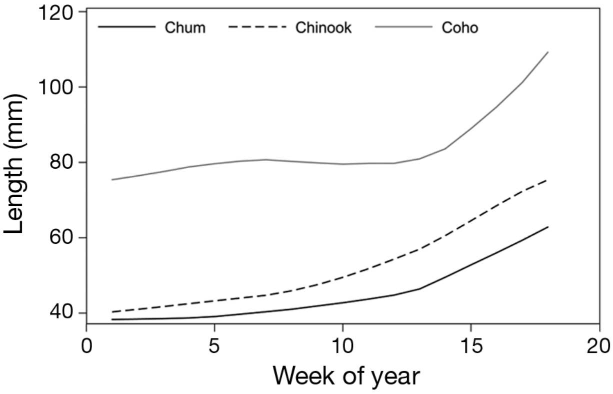

Fig. 3. Locally weighted scatterplot smoothing curves (with α = 0.8), showing the average progression of fish lengths (mm) over the sampling period, starting from the first week of March (Week 1) to the first week of July (Week 18). Fish lengths were recorded on the sampling day and averaged by week across all years for chum *Oncorhynchus keta*, Chinook *O. tshawytscha* and coho salmon *O. kisutch* samples (n = 18 156)

Table 5. Overall frequency distribution of number of fish with various lice count levels regardless of year or site for chum *Oncorhynchus keta*, Chinook *O. tshawytscha* and coho salmon *O. kisutch* combined (n = 18 156) by different sea lice life-cycle stages. The 'Any louse' column refers to the total lice count, regardless of stage

Lice count	Non-motile	Motile	Any louse
0	17472	18038	17374
1	541	99	609
2	110	15	131
3	23	4	30
4	8	–	8
5	2	–	4

respectively. This fact led to the adoption of a logistic regression statistical modelling approach when analysing the data, where the outcome of interest was whether a fish was infested with any louse. A detailed breakdown of fish sampled by species and year, using this simplified measure (i.e. any infestation) is given in Table 4. This output is included for completeness; it is clearly complex, and the detail is arguably more easily absorbed in the context of the modelled outcomes described below.

In terms of insights around the infestation patterns associated with various sea lice species, this data set can offer only limited insight. This is in part due to the fact that the attached stages, which as noted represent the largest proportion of all lice, were not identified to species during the period 2004 to 2006. In addition, when looking at the data from 2007 onwards, it was evident that the majority of infestations (96.5%) were putatively due to *Lepeophtheirus salmonis*. As a consequence, while the logistic regression model noted below specifies the presence of any louse as its outcome variable, in practice, the nature of the observed data means that the model is largely exploring factors associated with the presence of attached *L. salmonis* stages on chum, Chinook and coho salmon.

As part of the model-building process, it is important to know which, if any, variables might be strongly correlated. The matrix shown in Table 6 indicates that strong positive correlation values are seen when considering length and weight, as well as between month and seawater temperature, both of which would be expected. There is also a moderate negative correlation between month and salinity, likely due to the fact that a large amount of snowmelt places additional fresh water into the system in the later months. Moderate positive correlations also exist between month and the fish size variables (length and weight), again something that is not unexpected since fish will grow as the season progresses, and this trend was consistent across fish species. Based on these correlations, weight was excluded from the model with preference given to length. Seawater temperature was also excluded, as it was highly correlated with month of the year. The positive correlation between fish length and month was confounded by the fact that Chinook and coho (the larger species) were more likely to be observed later in the season. For this reason, only month was entered into the full logistic regression model which included all 3 fish species. In the model which considered only chum salmon, such confounding was not an issue, and so both length and month could be considered as candidate variables in the model.

The results of the final multivariable mixed effects model for the 3 main fish species are shown in Table 7, where the outcome was a fish with any louse infestation and the sampling site was modelled as a random effect. The model indicates that the likelihood of a fish being infested with a louse was significantly higher (odds ratio, OR = 7.5, p = 0.001) in Zone D as compared to Zone A. Year of observation was a significant (p < 0.001) factor in the model. In 2 years (2005 and 2006), significantly higher prevalence values were seen than in the baseline year (2004), while in 2007 and 2011, the prevalence was significantly lower. In terms of fish species, coho tended to be significantly more likely (OR = 1.7, p = 0.002) to be infested than chum salmon. For month of the year, prevalence was lowest at the start of the season, with May and June having significantly (p < 0.016) higher prevalence values than in March. Salinity also had an impact on the likelihood of being

Table 6. Correlation matrices among month (Mar–Jul = 3–7), weight (g), length (mm), salinity (psu) and temperature (°C)

	3 main host species (N = 17639)				
	Month	Weight	Length	Salinity	Temp.
Month	1.00				
Weight	0.37	1.00			
Length	0.46	0.90	1.00		
Salinity	−0.33	−0.07	−0.11	1.00	
Temperature	0.76	0.37	0.46	0.05	1.00

Table 7. Final multivariable mixed effects model showing variables associated with prevalence of sea lice in wild juvenile salmonids (chum *Oncorhynchus keta*, Chinook *O. tshawytscha* and coho salmon *O. kisutch*, N = 17052) captured at 16 sites in the Muchalat Inlet, British Columbia, Canada, over the period 2004 to 2011. OR: odds ratio; ICC: intra-class correlation coefficient

Variable	OR	95% CI	p
Fixed effects			
Intercept	0.003	0.001, 0.008	<0.001
Region			0.011
A	Baseline		
B	3.479	0.847, 14.287	0.084
C	2.967	0.920, 9.571	0.069
D	7.544	2.308, 24.652	0.001
Year			<0.001
2004	Baseline		
2005	2.617	1.782, 3.843	<0.001
2006	2.227	1.478, 3.355	<0.001
2007	0.463	0.285, 0.754	0.002
2008	1.249	0.817, 1.910	0.305
2009	1.230	0.812, 1.864	0.328
2010	1.444	0.957, 2.180	0.080
2011	0.632	0.401, 0.998	0.049
Fish species			0.009
Chum	Baseline		
Chinook	1.212	0.869, 1.692	0.258
Coho	1.651	1.196, 2.279	0.002
Month			0.006
March	Baseline		
April	1.051	0.858, 1.287	0.633
May	1.329	1.056, 1.674	0.015
June	1.709	1.204, 2.427	0.003
Salinity			<0.001
Salinity ≤15 psu	1.089	1.055, 1.123	<0.001
Salinity >15 psu	0.995	0.971, 1.019	0.686
Random effects			
Level	SD	SE	ICC
Site	0.793	0.203	0.160

infested, although this factor requires a little more attention when it comes to appropriate interpretation. At salinity values of ≤15 psu, the risk of having a sea louse increased significantly as salinity increased (OR = 1.09; 95% CI: 1.06 to 1.12). For example, the risk of detecting a sea louse on a fish was approximately 9% higher when salinity was 15 psu than when it was 14 psu, or similarly, the risk was approximately 2.34 times greater when salinity was 15 psu compared to 5 psu. However, no significantly increased risk of being infested with a sea louse was observed for salinity values in sampling sites with reported values >15 psu (p = 0.686).

The intra-class correlation coefficient (ICC), derived from the remaining variance that is unexplained by the model predictors, estimates the proportion of the total leftover variance that is explained by including sampling sites as a random effect. Therefore, the ICC partitions within-site and between-site variance. Given the variability in the number and locations of sampling sites over the 8 yr period, it was particularly important to select a model structure that could attempt to capture this potentially important clustering. When both salinity and region were removed from the model reported in Table 7, the ICC was 0.41 (model not shown), indicating that sampling sites explain approximately 41% of the variance, even after accounting for years, months and fish species. As seen in Table 7, when salinity and region were included in the model, the ICC decreased to 0.16, indicating that both salinity and region explain a large portion of the site-specific variability. More specifically, when only region was removed from the model, the ICC was 0.28, while when only salinity was removed, the ICC was 0.22 (models not shown), indicating that region explains a good portion of the site-specific variability, but not as much as the more finely spatially-scaled salinity variable.

Because chum salmon constituted around 85% of the data included in the multivariable model described above, we decided that it would be useful to carry out some additional analyses using only this subset of the samples. In particular, the inclusion of only 1 fish species could help clarify some of the interactions between month, fish size and species. The results for a similar multivariable mixed effects logistic model, but for only the chum samples, are shown in the Appendix (Table A1). Once again, the outcome variable was a chum sample with any louse infestation, and site was modelled as a random effect. These results are broadly in line with those found for the full model that included the 3 main fish species. However, in this case a quadratic polynomial fish length term provided a better fit than simply using month. The risk of having a sea louse infestation increased significantly as the length of the chum increased (OR = 1.22; 95% CI: 1.20 to 1.24). However, as length increased, the risk of having a sea louse was progressively less dramatic (squared-term OR = 0.996; 95% CI: 0.996 to 0.997). Care must be taken where comparing odds ratios between the 2 models, but it is interesting to note that the salinity effect is slightly stronger for the low salinity segment and much closer to being a significant effect for the higher salinity segment (Bricknell et al. 2006, Sutherland et al. 2012).

DISCUSSION

This communication represents the first attempt to provide quantitative insights into the nature of sea lice infestations on wild salmonids in this geographical region of BC. Repeated sampling at spatially representative locations in the Muchalat Inlet throughout the out-migration period over 8 consecutive years resulted in a robust data set to underpin these insights. One immediate observation is that the distribution of wild salmonid species appears to be very different from that seen in other regions of BC, with the absence of pink salmon being of particular note. In contrast, a study of the Kitasoo region (Saksida et al. 2011), slightly farther north on the BC coast, reported that an average of around 78% of the fish sampled over a 4 yr period were pink salmon. In the Broughton Archipelago, the dominant wild Pacific salmonid species were pink and chum salmon (Patanasatienkul et al. 2013). While the proportions varied over time, in only 1 year (2004) over a decade of observations did pink salmon fail to represent at least 40% of the total wild population sampled. However, in terms of sea lice across host species, the Broughton study indicated similar levels of infestation (Patanasatienkul et al. 2013), with chum exhibiting slightly higher levels in many years. In the case of the Kitasoo study (Saksida et al. 2011), chum exhibited significantly lower prevalence levels but only for *Caligus clemensi*. Considering the 3 species present in Muchalat, sea lice infestation levels are not significantly different on chum and Chinook. While coho salmon did tend to have significantly more sea lice than did chum, this result must be treated with caution. First, coho represent a very small proportion of the total fish sampled. Second, due to some issues of co-linearity, it was not possible to include both length and month in the main model, so part of the apparent 'coho' effect may in fact be due to the fact that these fish were significantly larger than the other 2 species. Finally, the migration behaviour of coho differs significantly from chum or Chinook, and it has been suggested that coho can exhibit elevated infestation levels due to the fact that these larger fish are preying on smaller chum or Chinook already infected with sea lice, which migrate during the predation event (Peacock et al. 2014). In summary, it seems unlikely that differences in the distribution of wild salmon species seen in the Muchalat Inlet is the key explanatory factor for explaining the relatively low sea lice infestation levels reported in this study, but it is important to remember these differences when comparing outcomes to those reported from other areas of BC.

An additional difference to other BC-focused studies was the fact that the sea lice that were identified to species were almost all *Lepeophtheirus salmonis*. While sea lice species identification was limited during the first 3 yr of this study, it is clear that the vast majority (>95%) of sea lice found on wild salmon in Muchalat were *L. salmonis*. A similar dominance of this species is also typical of infestations seen on the farmed fish in this area, in contrast to the more mixed observations that often include *Caligus* species from farms reporting in other areas of BC (e.g. DFO 2014). The exact proportions seen on wild salmonids in other BC studies is not always reported, but the Kitasoo study mentioned above indicated similar levels of *L. salmonis* and *C. clemensi* on chum salmon (Saksida et al. 2011). Probably the most extensive exploration of sea lice species distribution in BC is that reported from a decade of data collected in the Broughton Archipelago (Patanasatienkul et al. 2013) as part of the Broughton Archipelago Monitoring Plan initiative (www.bamp.ca). For 4 of the 10 years reported in that study, the proportions of each sea louse species were roughly equal, and in one year (2011), *C. clemensi* clearly dominated. While *L. salmonis* was the dominant sea louse species in the other 5 years, only in one of these (2004) did the extent of its dominance even begin to approach that seen in the Muchalat samples. It is known that some *Caligus* species tolerate low levels of salinity less well than is the case for *L. salmonis* (Landsberg et al. 1991), and thus salinity may be having a particularly strong effect in controlling *C. clemensi* in the Muchalat Inlet. In this context it is also worth noting that species identification of sea lice, particularly those in the early stages of development, can be prone to error (McBeath et al. 2006), and if resources permitted, it would be useful to cross-validate a sub-sample using molecular techniques.

It has been well established that the levels of sea lice typically found both on farmed fish and wild salmonids along the coast of BC are relatively low in comparison to those seen, for example, in the North Atlantic (Heuch et al. 2009, 2011, Jansen et al. 2012). However, even given that fact, the sea lice infestation rates on juvenile salmonids in the Muchalat Inlet between 2004 and 2011 were lower than previous studies have reported for other parts of BC, such as the Broughton Archipelago (Patanasatienkul et al. 2013), where prevalence values were typically 15 to 30%. A study in the Kitasoo region reported that the prevalence levels of *L. salmonis* ranged from 2 to 9%, 'which is lower than levels published for other areas without salmon farms' (Saksida et al. 2011, p. 193). However, the Kitasoo study indicated that the majority of sea lice observed were in the motile stage, so the most appropriate comparative figure from the current study would be the ~0.7% prevalence of motile sea lice. This is clearly a very low level, even by the standards of BC. While it should be acknowledged that the capture methods used can result in the loss of some sea lice and that the smaller stages can be more difficult to observe subsequent to the freeze/thaw process, it is also the case that many of the studies carried out within BC over the past decade have adhered to similar protocols and in many cases have been managed by the same contract research service (i.e. Mainstream Biological Consulting).

We do not understand the full set of reasons for this result, but it would appear that low salinity levels play an important role (Bricknell et al. 2006). Salinity is generally low across this region, and even in Zone D, the conditions are far from 'ideal' for sea lice. Within our model, entering the specific site-level salinity effect reduced the ICC. The impact of salinity on site-specific variability of sea lice infestation was larger than that achieved by considering only regional effects. This makes sense, as there were multiple sites within a zone, with varying levels of salinity that could individually influence the presence of sea lice. Additionally, there is likely a natural progression in the salinity gradient within zones, as the fish move away from freshwater sources, as well as among zones, as fish move toward the ocean. It seems intuitive that as fish pass through the zones (from A to D), they will spend more time exposed to potential infection and also progress towards waters with higher salinity that are more favourable to survival of sea lice (Heuch 1995). The fact that our salinity measurements were taken at a single depth may also have led to an under-estimation of the effect of this factor, which will vary within the water column and as the overall depths change in the various channels used by the migrating fish. However, juvenile salmonids tend to inhabit the first metre or so of the water column (Peacock et al. 2014).

Despite the fact that the statistical model quantitatively accounts for the confounding effects of time exposed (months) and salinity, there is still a significant regional effect, with a much stronger impact from being sampled in Zone D compared to Zone A (OR = 7.5). To determine the potential effect within and between the zones and along the salinity gradient, more finely scaled spatiotemporal analyses will be required. It may also be the case that the logistic approach used here, which only effectively models the prevalence of sea lice, should be supplemented by alternate analyses; other studies of sea lice infestation adopted a 2-part model, with one part relating to presence/absence and the other to estimates of abundance in cases of infestation (Kristoffersen et al. 2013, Rees et al. 2015). Also, given that the prevalence levels observed were at such low levels, it may be that a zero-inflated negative binomial modelling framework would be more appropriate. Moreover, aquaculture sites are present throughout the 4 zones, and these could be an additional source of unmeasured influence on the presence of sea lice, as they were not included in the current study. While sea lice on salmon farms can exhibit a 'spill-over' effect into wild populations (Tully et al. 1999, Marty et al. 2010, Middlemas et al. 2013, Peacock et al. 2013), it is not clear to what extent such an effect might be detectable here. For the duration of the study period each year (March to June), sea lice levels did not exceed the regulatory threshold of 3 motiles fish^{-1} at any farm site and on average tended to be <1 motile sea louse per farm in any given year (summary values can be found on the DFO site: www.pac.dfo-mpo.gc.ca/aquaculture/reporting-rapports/lice-pou-eng.html). Nevertheless, in future studies of this area, it would be interesting to explore interactions between farmed and wild salmon to ascertain the impacts, in both directions, on sea lice population dynamics.

While a number of differences from other regions in BC have been noted above, some trends appear to be similar. The proportion of motile sea lice that were observed on wild salmonids increased significantly over the season, as has been reported in other studies (Patanasatienkul et al. 2013, 2015). In addition, there was significant annual variation in the levels of sea lice observed, again a common theme of other studies in BC (Saksida et al. 2011, Patanasatienkul et al. 2013). It is not clear why 2005 and 2006, in particular, were associated with such an elevated risk of sea louse infestation, but once again it may be that more finely-grained spatio-temporal modelling will help uncover key drivers in these processes (Brooks 2005, Stucchi et al. 2011).

While limited comment has been made on the 'minor' host species encountered in this study, one unusual result was noted. In 2005, the level of sea lice infestation on sockeye salmon was around 29% (N = 171), while over all of the other years, only 1 of the 165 sockeye samples examined was found to have a sea louse present. We are not able to provide an explanation as to why this might have been the case, other than that 2005 was also the year of highest infestation risk to other salmon species. The data illustrate the importance of taking care not to draw conclusions from small and potentially unrepresentative samples. Had our sampling been confined to 2005, a very skewed and unrealistic picture of sea lice infestation on sockeye salmon would have emerged. As other studies of this wild species have indicated annual variation with some significant sea lice infestations (Price et al. 2011), there are clearly circumstances under which levels can become elevated, and it may be important to better understand the drivers of such events. In addition, the infestation levels seen on sticklebacks tended to be higher than was the case for the Pacific salmonids sampled in this study, with an annual median of around 12%, but the overall numbers sampled were too low to make general assertions or comparisons to other studies which have reported on sticklebacks in other areas of BC (Jones et al. 2006).

Despite these caveats as to the generalizability of our findings, for the main host and parasite species observed, we believe the trends and associations to be robust as they are based on a series of spatially repeated sampling events over 8 yr. We trust that these results are of interest in and of themselves, but also that they illustrate the value of careful long-term and consistent monitoring to gain a clearer understanding of the interactions in complex ecological community structures such as those that exist in these aquatic environments.

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Appendix

Table A1. Mixed effect logistic model showing association between lice prevalence on chum salmon *Oncorhynchus keta* by region, year and key continuous variables (n = 14 498). OR: odds ratio; ICC: intra-class correlation coefficient

Variable	OR	95% CI	p
Fixed effects			
Intercept	20.22×10^{-4}	$(8.28, 49.40) \times 10^{-4}$	<0.001
Region			0.020
A	Baseline		
B	1.941	0.765, 4.925	0.163
C	1.331	0.610, 2.904	0.472
D	3.298	1.478, 7.361	0.004
Year			<0.001
2004	Baseline		
2005	4.754	2.503, 9.032	<0.001
2006	3.446	1.790, 6.635	<0.001
2007	0.850	0.419, 1.726	0.654
2008	1.958	1.017, 3.769	0.044
2009	2.913	1.510, 5.619	0.001
2010	1.410	0.723, 2.748	0.313
2011	0.683	0.344, 1.358	0.277
Salinity			<0.001
Salinity ≤15 psu	1.100	1.061, 1.141	<0.001
Salinity >15 psu	1.027	1.000, 1.055	0.050
Length			<0.001
Length (mm)	1.220	1.196, 1.243	<0.001
Length^2 (mm)	0.996	0.996, 0.997	<0.001
Random effects			
Level	SD	SE	ICC
Site	0.476	0.154	0.064

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