

1 **Sea lice infestation of wild juvenile salmon and herring associated with fish farms off the**
2 **east central coast of Vancouver Island, BC**

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5 Alexandra Morton¹, Rick Routledge² and Martin Krkošek³

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8 ¹Raincoast Research Society, Simoom Sound, BC, Canada, V0P 1S0

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10 ²Department of Statistics and Actuarial Science, Simon Fraser University

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12 ³Centre for Mathematical Biology, Department of Biological Sciences, University of Alberta

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15 **Abstract**

16 Reports of sSea lice (*Lepeophtheirus salmonis* and *Caligus clemensi*) infestations of juvenile
17 salmonids in Pacific Canada have been restricted to pink (*Oncorhynchus gorbuscha*) and chum
18 (*O. keta*) salmon from one salmon farming region only – the Broughton Archipelago, British
19 Columbia. Here, we report on two years of sea lice field surveys of wild juvenile pink, chum,
20 and sockeye (*O. nerka*) salmon and wild larval herring (*Clupea harengus pallasii*) in another
21 salmon farming region, the Discovery Islands region of British Columbia. For pink and chum
22 salmon we tested for dependency of sea lice abundance on temperature, salinity, sampling period,
23 host species, and farm exposure category. For both species of lice, farm exposure was the only
24 consistently significant predictor of sea lice abundance. Fish exposed to salmon farms were
25 infected with more sea lice than those in the peripheral category. Sea lice abundance on sockeye
26 and herring followed the same trends, but sample sizes were too low (148 for sockeye and 322
27 for herring) to support formal statistical analysis. Herring were translucent and lacked scales and
28 were primarily parasitized by *C. clemensi*. These results suggest the association of salmon farms
29 with sea lice infestations of wild juvenile fish in Pacific Canada extends beyond juvenile pink
30 and chum salmon in the Broughton Archipelago to juvenile pink, chum, and sockeye salmon, as
31 well as, larval herring in the Discovery Islands. Canada’s most abundant and economically
32 valuable salmon populations, as well as, BC’s most valuable herring stock migrate through the
33 Discovery Islands, and hence so parasite transmission from farm to wild fish in this region may
34 have important economic and ecological implications.

35

36 **Introduction**

37 Salmon farming is associated with sea lice (*Lepeophtheirus salmonis* and *Caligus* spp.)
38 infestations of wild juvenile salmonids in Norway (Bjorn and Finstad 2002), Scotland
39 (MacKenzie et al. 1998), Ireland (Tully et al. 1999), and Canada (Morton et al. 2004). In Pacific
40 Canada, farm salmon have been identified as a primary determinant of sea lice infection patterns
41 on wild juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon (Morton et al 2004;
42 Krkošek et al. 2005a), with farm salmon initiating population growth and spread of the parasites
43 in wild juvenile salmon populations (Krkošek et al. 2005a). Physical factors such as temperature
44 and salinity may also be important (Brooks 2005; Brooks and Stucchi 2006), but may not be
45 significant predictors of sea lice abundance (Morton et al. 2004; Krkosek et al. 2005b). Low
46 abundances of *L. salmonis* are lethal to juvenile pink and chum salmon (Morton and Routledge
47 2005), sea lice transmission from farm salmon can cause high mortality in wild juvenile salmon
48 (Krkošek et al. 2006), and pink salmon populations have collapsed following infestations
49 (Morton and Williams 2003; PFRCC 2002). Following a migration route in one year reduced sea
50 lice abundances (Morton et al. 2005) and those cohorts experienced high marine survival
51 (Beamish et al. 2006). These types of associations have long been controversial (McVicar 1997;
52 McVicar 2004; Hilborn 2006), and it remains unknown whether increased abundances of sea lice
53 on wild juvenile salmon are associated with salmon farms in regions outside the Broughton
54 Archipelago in Pacific Canada.

55 The migratory paths of many of the most abundant and economically important Canadian
56 salmon populations are constricted through a region of intensive salmon aquaculture between the
57 Strait of Georgia and Johnstone Strait (Groot and Margolis 1991), known as the Discovery
58 Islands (Figure 1). Susceptible salmon populations include those from the Fraser River, east

59 coast Vancouver Island, and mainland inlet stocks that migrate north between Vancouver Island
60 and mainland BC. These include pink, chum, sockeye (*O. nerka*), steelhead (*O. mykiss*), coho (*O.*
61 *kisutch*) and chinook (*O. tshawytscha*) salmon. In addition, this region may be important early
62 juvenile rearing habitat for Strait of Georgia herring (*Clupea harengus pallasii*), BC's largest
63 herring stock. Sea lice on juvenile herring are unreported for the Pacific and extremely rare in the
64 Atlantic (Tolonen and Karlsbakk 2003). We report on sea lice infestations of wild juvenile pink
65 and chum salmon, with observations of sea lice on juvenile sockeye salmon, and juvenile
66 herring, all associated with salmon farms in the Discovery Islands.

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68 **Field Methods**

69 The study area comprised the waters of the Discovery Islands, a region just north of the Strait of
70 Georgia (Figure 1). We organized the sample sites into two categories – exposed and peripheral
71 – based on the proximity of the collection site to salmon farms. Exposed sites were in among the
72 channels with one or more salmon containing several active farms located in both directions from
73 the sample site. The wild juvenile salmon must therefore have been directly exposed to at least
74 some of the farms to reach these sites. Peripheral sites were outside these narrow channels in
75 places where juvenile salmon and herring need not have been directly exposed to any the salmon
76 farms. Some peripheral sites were near salmon farms, but depending on direction of migration
77 wild salmon sampled at these sites may or may not have passed the farm. We determined the
78 production status of farms (Table 1) by collecting information directly from the salmon farm
79 companies in 2005 and by observing the salmon farms from a boat in 2006. There were four 2-3
80 day bi-weekly surveys in each year, over the time period April 19-June 5 in 2005 and April 3-
81 June 9 in 2006, when we sampled 50 juvenile pink and/or chum salmon from each of 15 sites (in

82 2005) and 16 sites (in 2006) during each survey using a 30m x 1.8m beach seine net with 1.6 cm
83 knotless mesh. There were approximately 25 individuals of pink and chum in each sample
84 collection in 2005 and higher abundance of chum than pink in 2006. We occasionally collected
85 some juvenile herring and sockeye salmon as by-catch and also examined these fish for lice. All
86 sampled fish were placed in individual bags and temporarily stored on ice and then quickly
87 frozen within hours. The fish were subsequently weighed, measured (fork length), and identified
88 to species. Sea lice were identified using a dissecting microscope, and categorized by species,
89 age-class and sex using Galbraith (2005). Additionally, we collected some juvenile sockeye and
90 herring with a 30m x 3m beach seine with 1.6 cm knotless mesh during one survey in June 2005
91 of sites labeled h and s in Figure 1. For these fish we used the non-lethal assay described in
92 Krkošek et al. (2005b) to measure fish fork length and count and identify the sea lice. We did not
93 survey sockeye and herring in 2006 except those collected as by-catch in the pink/chum surveys.

94

95 **Statistics**

96 We analyzed abundances of each louse species on pink and chum salmon for dependence on
97 exposure category (peripheral or exposed; Figure 1) and on the following factors: sampling trip,
98 salinity, temperature, and host species. Separate analyses were conducted for each of the two
99 years. We treated site-to-site differences within the exposure categories as random, and also
100 included random effects associated with each sampling occasion at each site. To handle (i) the
101 mixture of fixed and random effects, (ii) unequal variances and (iii) possible nonlinear effects,
102 we used the SAS procedure, GLIMMIX for handling generalized linear models with mixed
103 effects. We specified a log link (implying multiplicative as opposed to additive effects) (Limpert
104 et al. 2001) with a Poisson distribution for the counts on individual fish given the random effects

105 mentioned above. (Note that these random effects will introduce extra-Poisson variation with a
106 correlation structure.) In addition, when the GLIMMIX algorithm did not converge, and
107 elsewhere as a check, we used the more traditional expedient (e.g., Steel and Torrie 1980, pp.
108 168 & 235) of transforming the abundances (y) to $\log_e(y+.5)$, and then applying a linear model.
109 To account for the mixture of fixed and random effects, we used the SAS procedure, MIXED,
110 for this analysis. In both instances, we calculated denominator degrees of freedom with a
111 Satterthwaite approximation. We fit the models in a backward stepwise fashion by first fitting
112 the full model and then sequentially dropping the insignificant factor with the largest p -value and
113 refitting the simplified model until only significant factors remained. (The MIXED analysis on
114 the transformed data was needed for convergence only in the initial stages of these some of these
115 analyses.) We generated least squares estimates for the exposure category means and associated
116 standard errors using the SAS GLIMMIX procedure. Since both the generalized linear modeling
117 and linear modeling on log transformed data produced similar final results, we present results for
118 the more modern (GLIMMIX) methodology only, for which the troublesome issue of back-
119 transformations and associated biases does not arise.

120

121 **Results**

122 Over the two years we examined 4,699 fish for sea lice infections. . In 2005, most of the salmon
123 farms indicated in Figure 1 were stocked with farm salmon more mature than smolts
124 (information provided in 2005 by Pan Fish, Stolt and Heritage) Table 1. In 2006, only Church
125 House was fully stocked with older salmon. All other sites were empty, partially empty or
126 stocked with smolts only (based on observation and pervious year's data). In 2005, we found a
127 total of 4,232 *Lepeophtheirus salmonis* and 2,408 *Caligus clemensi* summed over all 2,432 fish

128 that we lethally examined for sea lice. In 2006, we found 680 *Lepeophtheirus salmonis* and 857
129 *Caligus clemensi* summed over all 2,267 fish examined. The number of samples for each species,
130 mean fork length, weight, salinity and temperature are given for each year in Tables 2. There was
131 little variation between exposure categories in salinity and temperature (Tables 3-4), but
132 substantial increases in sea lice prevalence, intensity, and abundance in exposed sites relative to
133 peripheral sites (Tables 5-8).

134 Results of the statistical model fitting are summarized in Table 9. For both years and both
135 sea lice species, abundances on pink and chum salmon declined significantly from the exposed to
136 the peripheral sites (Figure 2). For both *L. salmonis* and *C. clemensi*, the decline was significant
137 in 2005 ($p < 0.0001$ and $p = 0.0002$, respectively) and in 2006 ($p = 0.0086$ and 0.047 ,
138 respectively). In addition, each of sampling trip and salmon species (pink vs. chum) was
139 significant in one instance only. Salmon species was significant for *C. clemensi* in 2006 ($p =$
140 0.011); sampling trip, for *L. salmonis* in 2005 ($p = 0.0045$). *C. clemensi* in 2006 was about 20%
141 less abundant on pink vs. chum salmon. Sea lice abundance was greater in 2005 than in 2006.
142 For pink and chum salmon in 2005, sea lice abundance peaked on 23 May at a mean of 10.5 lice
143 per fish ($3.4 \text{ lice} \cdot \text{g}^{-1}$ host weight). There was not a clear peak in sea lice abundance in 2006.

144 Samples sizes for sockeye salmon and herring were too small to support formal statistical
145 analyses, but trends indicate abundances of sea lice on sockeye salmon followed the same pattern
146 (Figure 3). Louse abundance on sockeye salmon in 2005 was highest at the Church House site at
147 8.8 lice per fish that averaged 2.4 g host weight. On herring, *C. clemensi* were elevated at the
148 exposed sites, whereas *L. salmonis* was essentially absent (Figure 3). None of the herring had
149 scales.

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Discussion

Sea lice infestations of wild juvenile salmonids have been associated with salmon farms in several countries (Bjorn and Finstad 2002; MacKenzie et al. 1998; Tully et al. 1999; Morton et al. 2004). This study provides further evidence that this pattern is widespread, and it is the first observation of this association in Pacific Canada outside the Broughton Archipelago, where all previous observations of high *L. salmonis* abundances on juvenile salmon have occurred (Morton and Williams 2003; Morton et al 2004; Morton et al. 2005; Krkošek et al. 2005; Krkošek et al. 2006). Similar to these other findings, our analysis shows that farm salmon were the most likely cause of the increased sea lice abundance observed on juvenile salmon in areas exposed to salmon farms relative to areas peripheral to salmon farms in the Discovery Islands. Exposure category was the only consistently significant factor explaining the data and other factors such as salinity and temperature were not significant. The difference in sea lice abundance between 2005 and 2006 can be explained by a decrease from 2005 to 2006 in the abundance of adult farm salmon; abundance of sea lice is known to be lower on wild salmon juveniles near salmon farms that are empty or stocked with smolts, than near salmon farms stocked with older salmon (Morton et al. 2004, Morton et al. 2005). It is useful to note that the prevalence of sea lice on juvenile salmon in regions of British Columbia without salmon farms is less than 0.05 (Morton et al. 2004; Peet 2007; Allen Gottesfeld, Skeena Fisheries Commission, pers. com.). If 0.05 is taken to be the natural baseline prevalence of sea lice on juvenile pink and chum salmon then the data in this study suggest that salmon farms may also have increased sea lice abundance on juvenile salmon in the peripheral area relative to baseline levels. However, the true natural baseline abundance of sea lice on juvenile pink and chum salmon in the Discovery Islands is unknown

174 because no sea lice surveys of juvenile pink and chum salmon were conducted in this area before
175 salmon farming began.

176 We did not detect a significant effect of temperature or salinity on sea lice abundance on
177 juvenile pink and chum salmon and only observed sporadic significance for two factors other
178 than salmon farms. The significant effect of sampling trip for *L. salmonis* in 2005 could be due
179 to temporal progression in sea lice development and/or fish migration. The significant effect of
180 host species for *C. clemensi* abundance in 2006 could be due to interspecific differences in
181 migration or resistance to sea lice. Other studies of sea lice dynamics on salmon farms and/or
182 experiments rearing larval lice in laboratory conditions have shown temperature and salinity can
183 influence lice survival (Johnson and Albright 1991) and epidemiology (Heuch et al. 2003; Revie
184 et al. 2003). Based on these studies on salmon farms and in lab conditions others have argued,
185 without testing their predictions with field surveys, that temperature and salinity have a large
186 effect on the spatial distribution of sea lice in the natural environment in the Broughton
187 Archipelago (Brooks 2005; Brooks and Stucchi 2006). Meanwhile other studies in British
188 Columbia based on field surveys on the spatial distribution of sea lice on juvenile salmon have
189 considered, but not detected salinity and temperature as alternate explanatory factors to salmon
190 farm proximity in explaining sea lice abundance data on juvenile salmon (Morton and Williams
191 2003; Morton et al. 2004). This discrepancy may be explained by behavior of sea lice larvae,
192 where copepodids position themselves vertically in the water column and may therefore seek out
193 and track suitable temperature and salinity regimes (Heuch 1995; Heuch et al. 1995). The
194 discrepancy may also be explained by a strong effect of salmon farms that obfuscates the
195 influence of these environmental factors on the spatial distributions of sea lice.

196 Although there are hosts other than farm salmon that can contribute to sea lice
197 abundances on wild juvenile salmon in the Discovery Islands, it is unlikely that these hosts
198 caused the increased abundance of sea lice on wild juvenile salmon in the exposed area relative
199 to the peripheral area. Immature Chinook salmon in these waters may transmit sea lice to
200 juvenile salmon in exposed and peripheral areas, but they are probably a negligible source
201 relative to farm salmon and wild adult pink, chum, and sockeye salmon, which are likely orders
202 of magnitude more abundant. Further, wild adult pink, chum, and sockeye salmon are situated
203 off-shore during our surveys (Groot and Margolis 1991). Stickleback and other hosts for *C.*
204 *clemensi* could also contribute to *C. clemensi* abundances observed on juvenile pink and chum
205 salmon. We consider it doubtful that stickleback are a prominent source of *L. salmonis*, because
206 the occurrence of gravid *L. salmonis* on stickleback, in other areas than the Discovery Islands,
207 has only been observed at very low abundances (Jones et al. 2006; Allen Gottesfeld, Skeena
208 Fisheries Commission, pers. com.). Aside from the difficulties described above in attributing
209 increased sea lice abundance in the exposed area relative to the peripheral area, these other host
210 species for sea lice must also occupy a spatial distribution that is similar to that of the salmon
211 farms and is sustained for at least two months. We consider this last possibility unlikely.

212 These results suggest sea lice infestations of wild juvenile salmon are not limited to
213 juvenile pink and chum salmon, for which there are now several reports from the Broughton
214 Archipelago (Morton and Williams 2003; Morton et al 2004; Morton et al. 2005; Krkošek et al.
215 2005; Krkošek et al. 2006). The data on juvenile sockeye and herring suggest that farm salmon
216 may transmit sea lice to these species as well. This latter evidence, though less definitive and
217 preliminary, is important. Sea lice on juvenile herring are unreported for the Pacific and
218 extremely rare in the Atlantic (Tolonen and Karlsbakk 2003). The herring were young-of-the-

219 year, translucent, and lacked scales, suggesting high vulnerability to mechanical damage of
220 surface tissues caused by sea lice. Fraser River sockeye salmon are thought to migrate through
221 the most infested areas of this study (Groot and Margolis 1991). Together, Fraser sockeye and
222 Strait of Georgia herring are British Columbia's most important commercial fish stocks –
223 contributing a total of \$50 million dollars (landed value) to the annual provincial economy.
224 Ecologically, herring are a valuable forage fish for many other species and sockeye, pink, and
225 chum salmon are the most abundant Pacific salmonids. Declines in these species and populations
226 would likely have severe economic and ecological effects. We did not have opportunity to
227 examine steelhead, chinook or coho and this does not imply these salmonid species remain
228 unaffected. These results underscore an urgent need to develop and implement conservation
229 policy that protects wild salmon from sea lice.

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Table 1. Status of salmon farms within study area.

	Site	Year	Species	Age
A	Brougham Pt.	2005	Chinook	Growers
		2006	?	Smolts
B	Owen Pt.	2005		Empty
		2006	?	?
C	Venture Pt.	2005	Atlantic	Growers
		2006	?	Smolts
D	Philips	2005	Atlantic	Smolts
		2006	Atlantic	½ Harvested
E	Church House	2005	Atlantic	Smolts
		2006	Atlantic	Growers
F	Conville B.	2005	?	Growers
		2006	?	Smolts
G	Raza I.	2005	Atlantic	Growers
		2006		Empty
H	S. Thurlow	2005	Atlantic	Growers
		2006	Atlantic	½ Harvested
I	Sonora Pt.	2005	Chinook	Brood/Growers
		2006		Empty
J	Brent I.	2005	Atlantic	Growers
		2006	Atlantic	Smolts
K	Cyrus	2005	Chinook	Growers
		2006		Empty
L	Young Pass	2005	Atlantic	Empty
		2006		Empty

Table 2. A summary of salinity and temperature, the number of each species caught (*n*) with fork length and weight by year.

Year	Salinity ‰	Temperature °C	Species	<i>N</i>	Length mm (range)	Weight g (range)
2005	28.3	10.9	Pink	982	61.2 (27.8-115)	3.07 (0.10-77)
			Chum	980	52.7 (27.8-1070)	1.93 (0.16-15.1)
			Sockeye	148	88.3 (54-124)	n/a
			Herring	322	45.1 (34-57)	0.87* (0.5-1.4)
2006	29	10.6	Pink	726	54.8 (21-132)	2.72 (0.17-31.5)
			Chum	1534	57.0 (30-142)	3.21 (0.17-34.3)
			Sockeye	7	69.9 (30-96)	5.93 (0.28-12.7)

*based on a lethal sample of 23 fish.

Table 3. Mean fork length (L) and mean body weight (W) of juvenile pink and chum salmon, as well as, sea surface salinity (S) and temperature (T) measured at each collection in 2005. Fork length is measured in mm, body weight is measured in grams, salinity is measured in parts per thousand, and temperature is measured in degrees centigrade.

Category	Site	19-20 Apr				5-7 May				23-24 May				4-5 Jun			
		L	W	S	T	L	W	S	T	L	W	S	T	L	W	S	T
Exposed	1	43.6	0.83	29	9.5	53.9	1.71	30	10.1	54.9	1.80	33	10.2	73.5	4.49	29	11.5
	2	64.1	2.72	30	10.2	-	-	-	-	53.0	1.67	30	10.5	61.2	2.61	31	10.8
	3	50.0	1.39	29	10.1	38.3	0.57	33	10.3	-	-	-	-	82.6	6.53	29	10.2
	4	40.5	0.66	30	10.1	56.4	2.06	30	10	72.4	4.52	31	10.5	73.1	4.65	29	10.5
	5	-	-	-	-	65.4	3.30	34	10	56.7	1.97	30	10.8	72.3	4.55	29	10.8
	6	-	-	-	-	-	-	-	-	65.0	3.24	30	11.2	86.0	7.44	29	11
Peripheral	7	35.5	0.45	20	10	38.2	0.52	28	11.1	56.4	1.96	27	10.4	66.1	2.96	11	12.5
	8	31.9	0.27	20	10.2	41.5	1.46	26	10	34.3	0.29	27	10	-	-	-	-
	9	40.3	0.58	27	9.7	-	-	-	-	-	-	-	-	-	-	-	-
	10	43.1	0.74	28	9.7	45.1	0.98	29	11.4	58.6	2.59	28	11.5	-	-	-	-
	11	59.2	2.50	30	10.5	62.9	3.04	32	10	71.7	4.44	28	11.4	-	-	-	-
	12	45.1	0.86	30	9.8	41.4	0.83	30	10.1	52.4	1.63	31	10.1	-	-	-	-
	13	-	-	-	-	64.1	3.33	30	10	70.2	4.23	34	10	-	-	-	-
	14	-	-	-	-	48.9	1.42	31	12	56.7	2.17	26	12	-	-	-	-
	15	-	-	-	-	-	-	-	-	61.3	3.07	24	11.1	75.6	5.05	26	11.5

Table 4. Mean fork length (L) and mean body weight (W) of juvenile pink and chum salmon as well as sea surface salinity (S) and temperature (T) measured at each collection in 2006. Fork length is measured in mm, body weight is measured in grams, salinity is measured in parts per thousand, and temperature is measured in degrees centigrade.

Category	Site	3-4 Apr				14-15 Apr				10-11 May				8-9 Jun				
		L	W	S	T	L	W	S	T	L	W	S	T	L	W	T	S	
Exposed	1	35.2	0.48	28	9.2	39.6	0.68	31	9.5	52.8	1.76	30	10	-	-	-	-	
	2	39.2	0.63	30	9.5	39.8	0.65	30	9.6	-	-	-	-	73.4	4.56	30	10.5	
	3	-	-	-	-	-	-	-	-	59.3	2.53	30	10.4	-	-	-	-	
	4	36.6	0.47	34	9.6	43.9	1.03	34	9.8	56.0	2.16	30	10	75.6	5.80	31	10.5	
	5	37.9	0.50	31	9.5	-	-	-	-	56.7	2.02	31/30	11.2/1	0	-	-	-	
	6	-	-	-	-	-	-	-	-	60.9	2.75	31	10.4	-	-	-	-	
Peripheral	16	-	-	-	-	-	-	-	65.7	3.82	29	11.2	68.2	5.04	31	12.9		
	7	35.7	0.42	27	9.2	-	-	-	50.3	1.61	27	10.8	74.2	6.75	25	11		
	8	40.3	0.67	32	9.5	-	-	-	50.0	1.60	30	10	64.9	3.31	29	10.8		
	9	-	-	-	-	-	-	-	-	-	-	-	109.	16.1	-	-		
	10	37.0	0.50	30	9.5	44.6	1.03	28	9.5	56.5	2.20	27	11.5	1	8	26	15	
	17	50.2	1.52	28	9.5	30.6	0.90	28	9.8	61.8	2.95	26	11	80.3	6.72	27	14	
	18	40.1	0.65	31	9.6	46.9	1.55	30	9.8	69.5	4.16	27	10	77.6	5.98	32	10.2	
	19	35.2	0.39	32	9.5	38.9	0.61	26	9.8	47.5	1.18	24	11	-	-	-	-	
	20	37.5	0.53	27	10	-	-	-	-	-	-	-	-	66.7	3.58	26	15.8	
	21	-	-	-	-	59.5	2.85	25	9.5	-	-	-	-	-	-	-	-	
	-	-	-	-	51.9	1.58	28	7.5	63.3	3.46	29	11	124.	23.1	8	2	27	15.8

Table 5. *L. salmonis* prevalence (P), intensity (I), and abundance (A) on juvenile pink and chum salmon for each collection in 2005.

Category	Site	19-20 Apr			5-7 May			23-24 May			4-5 Jun		
		P	I	A	P	I	A	P	I	A	P	I	A
Exposed	1	0.55	1.50	0.82	0.75	2.81	2.10	0.96	5.44	5.22	0.83	3.65	3.04
	2	0.75	4.47	3.35	-	-	-	0.74	3.59	2.64	0.76	3.21	2.45
	3	0.38	1.53	0.58	0.90	2.95	2.67	-	-	-	0.57	2.59	1.49
	4	0.10	2.00	0.20	0.47	2.39	1.12	0.69	3.45	2.38	0.63	6.76	4.26
	5	-	-	-	0.76	3.38	2.55	0.96	10.28	9.88	0.66	3.29	2.17
	6	-	-	-	-	-	-	0.98	5.96	5.85	0.71	3.42	2.41
Peripheral	7	0.02	1.00	0.02	0.02	1.00	0.02	0.15	1.38	0.21	0.02	6.00	0.12
	8	0.66	1.32	0.87	0.40	1.62	0.65	0.64	2.06	1.32	-	-	-
	9	0.20	1.30	0.25	-	-	-	-	-	-	-	-	-
	10	0.40	1.35	0.54	0.72	3.12	2.24	0.93	8.59	7.95	1.00	5.67	5.67
	11	0.85	3.73	3.19	0.57	2.83	1.60	0.62	6.84	4.24	-	-	-
	12	0.04	1.00	0.04	0.57	1.56	0.89	0.74	2.54	1.89	-	-	-
	13	-	-	-	0.22	1.18	0.26	0.40	3.21	1.27	-	-	-
	14	-	-	-	0.53	1.78	0.94	0.23	2.67	0.62	-	-	-
	15	-	-	-	-	-	-	0.48	4.55	2.17	0.35	1.58	0.56

Table 6. *C. clemensi* prevalence (P), intensity (I), and abundance (A) on juvenile pink and chum salmon for each collection in 2005.

Category	Site	19-20 Apr			5-7 May			23-24 May			4-5 Jun		
		P	I	A	P	I	A	P	I	A	P	I	A
Exposed	1	0.39	2.15	0.84	0.31	1.47	0.46	0.18	1.33	0.24	0.60	2.07	1.25
	2	0.50	3.88	1.94	-	-	-	0.55	3.45	1.89	0.49	2.44	1.20
	3	0.50	1.60	0.80	0.76	1.94	1.48	-	-	-	0.36	1.24	0.45
	4	0.00	0.00	0.00	0.22	1.64	0.37	0.79	5.61	4.40	0.57	2.42	1.37
	5	-	-	-	0.53	2.46	1.31	0.83	6.95	5.75	0.60	2.57	1.53
	6	-	-	-	-	-	-	0.58	3.03	1.75	0.29	1.20	0.35
Peripheral	7	0.00	0.00	0.00	0.02	1.00	0.02	0.02	1.00	0.02	0.06	1.00	0.06
	8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-	-
	9	0.02	1.00	0.02	-	-	-	-	-	-	-	-	-
	10	0.02	1.00	0.02	0.30	1.21	0.37	0.78	4.32	3.35	0.33	1.00	0.33
	11	0.69	2.64	1.81	0.36	1.58	0.57	0.46	7.13	3.28	-	-	-
	12	0.08	1.25	0.10	0.14	2.00	0.29	0.06	1.50	0.09	-	-	-
	13	-	-	-	0.14	1.14	0.16	0.10	1.00	0.10	-	-	-
	14	-	-	-	0.41	2.38	0.98	0.08	1.25	0.10	-	-	-
	15	-	-	-	-	-	-	0.48	3.36	1.61	0.02	1.00	0.02

Table 7. *L. salmonis* prevalence (P), intensity (I), and abundance (A) on juvenile pink and chum salmon for each collection in 2006.

Category	Site	3-4 Apr			14-15 Apr			10-11 May			8-9 Jun		
		P	I	M	P	I	M	P	I	M	P	I	M
Exposed	1	0.24	1.42	0.34	0.58	1.59	0.92	0.38	1.68	0.64	-	-	-
	2	0.36	1.50	0.54	0.24	1.25	0.30	-	-	-	0.34	1.50	0.51
	3	-	-	-	-	-	-	0.26	1.46	0.38	-	-	-
	4	0.10	1.00	0.10	0.22	1.09	0.24	0.14	1.00	0.14	0.22	1.55	0.34
	5	0.10	1.00	0.10	-	-	-	0.35	1.40	0.49	-	-	-
	6	-	-	-	-	-	-	0.06	1.00	0.06	-	-	-
	16	-	-	-	-	-	-	0.46	1.57	0.72	0.19	1.35	0.26
Peripheral	7	0.00	-	0.00	-	-	-	0.00	0.00	0.00	0.00	0.00	0.00
	8	0.40	1.60	0.64	-	-	-	0.12	1.00	0.12	0.12	1.00	0.12
	9	0.06	1.00	0.06	0.26	1.23	0.32	0.28	1.21	0.34	0.00	0.00	0.00
	10	-	-	-	0.42	1.85	0.77	0.37	1.26	0.46	0.10	1.00	0.10
	17	0.19	1.20	0.23	0.22	1.36	0.30	0.66	1.55	1.02	0.18	1.11	0.20
	18	0.00	0.00	0.00	0.00	0.00	0.00	0.15	1.00	0.15	-	-	-
	19	0.06	1.00	0.06	-	-	-	-	-	-	0.12	1.17	0.14
20	-	-	-	0.52	1.42	0.74	-	-	-	-	-	-	
21	-	-	-	0.12	1.00	0.12	0.20	1.30	0.27	0.04	1.00	0.04	

Table 8. *C. clemensi* prevalence (P), intensity (I), and abundance (A) on juvenile pink and chum salmon for each collection in 2006.

Category	Site	3-4 Apr			14-15 Apr			10-11 May			8-9 Jun		
		P	I	M	P	I	M	P	I	M	P	I	M
Exposed	1	0.04	1.00	0.04	0.20	1.30	0.26	0.50	1.60	0.80	-	-	-
	2	0.08	1.00	0.08	0.44	1.68	0.74	-	-	-	0.20	1.45	0.29
	3	-	-	-	-	-	-	0.32	1.31	0.42	-	-	-
	4	0.08	1.00	0.08	0.38	1.16	0.44	0.10	1.00	0.10	0.38	1.47	0.56
	5	0.15	1.00	0.15	-	-	-	0.36	1.36	0.49	-	-	-
	6	-	-	-	-	-	-	0.22	1.36	0.30	-	-	-
Peripheral	16	-	-	-	-	-	-	0.54	1.70	0.92	0.54	1.56	0.84
	7	0.00	-	0.00	-	-	-	0.15	1.14	0.17	0.00	0.00	0.00
	8	0.02	1.00	0.02	-	-	-	0.08	1.00	0.08	0.33	1.38	0.45
	9	0.63	1.58	1.00	0.78	2.62	2.04	0.20	1.10	0.22	0.00	0.00	0.00
	10	-	-	-	0.35	1.59	0.56	0.23	1.58	0.37	0.26	1.00	0.26
	17	0.02	1.00	0.02	0.20	1.50	0.30	0.46	1.39	0.64	0.04	1.00	0.04
	18	0.00	0.00	0.00	0.10	1.00	0.10	0.02	1.00	0.02	-	-	-
	19	0.00	0.00	0.00	-	-	-	-	-	-	0.22	1.27	0.28
	20	-	-	-	0.30	2.27	0.68	-	-	-	-	-	-
	21	-	-	-	0.26	1.38	0.36	0.33	1.31	0.43	0.40	2.05	0.82

Table 9. Summary of significance for effects remaining in each model.

Louse Species	Year	Effect	<i>p</i> -value
<i>L. salmonis</i>	2005	Exposure Category	< 0.0001
		Sampling Trip	0.0045
	2006	Exposure Category	0.009
<i>C. clemensi</i>	2005	Exposure Category	0.0002
		2006	Exposure Category
		Salmon Species	0.011

Figure Headings

Figure 1. The study area, with arrows showing migration directions for young salmon, sample sites for all species (numbered for pink and chum), salmon farms (identified by letters) and the contour that groups sample sites as peripheral (outside the oval ring) and exposed (inside the oval ring). Site categorization (salmon and herring) was based on proximity to salmon farms and probable migration routes (salmon). The salmon farms, indicated by capital letters in square boxes, correspond to descriptions in Table 1. The sample sites, indicated by numbers in ovals, correspond to sample site numbers in Tables 3 and 4.

Figure 2. Mean abundance of sea lice on juvenile pink and chum salmon at exposed (light grey) and peripheral (dark grey) sites in 2005 (a) and 2006 (b). Error bars are standard errors. Note difference in y-axis scale.

Figure 3. Mean abundance of *Lepeophtheirus salmonis* (a) and *Caligus clemensi* (b) infecting juvenile sockeye and herring in 2005. Error bars were not computed for sockeye and herring due to small sample sizes. See *Statistics* section for methods on mean and standard error calculations.

Figure 1.

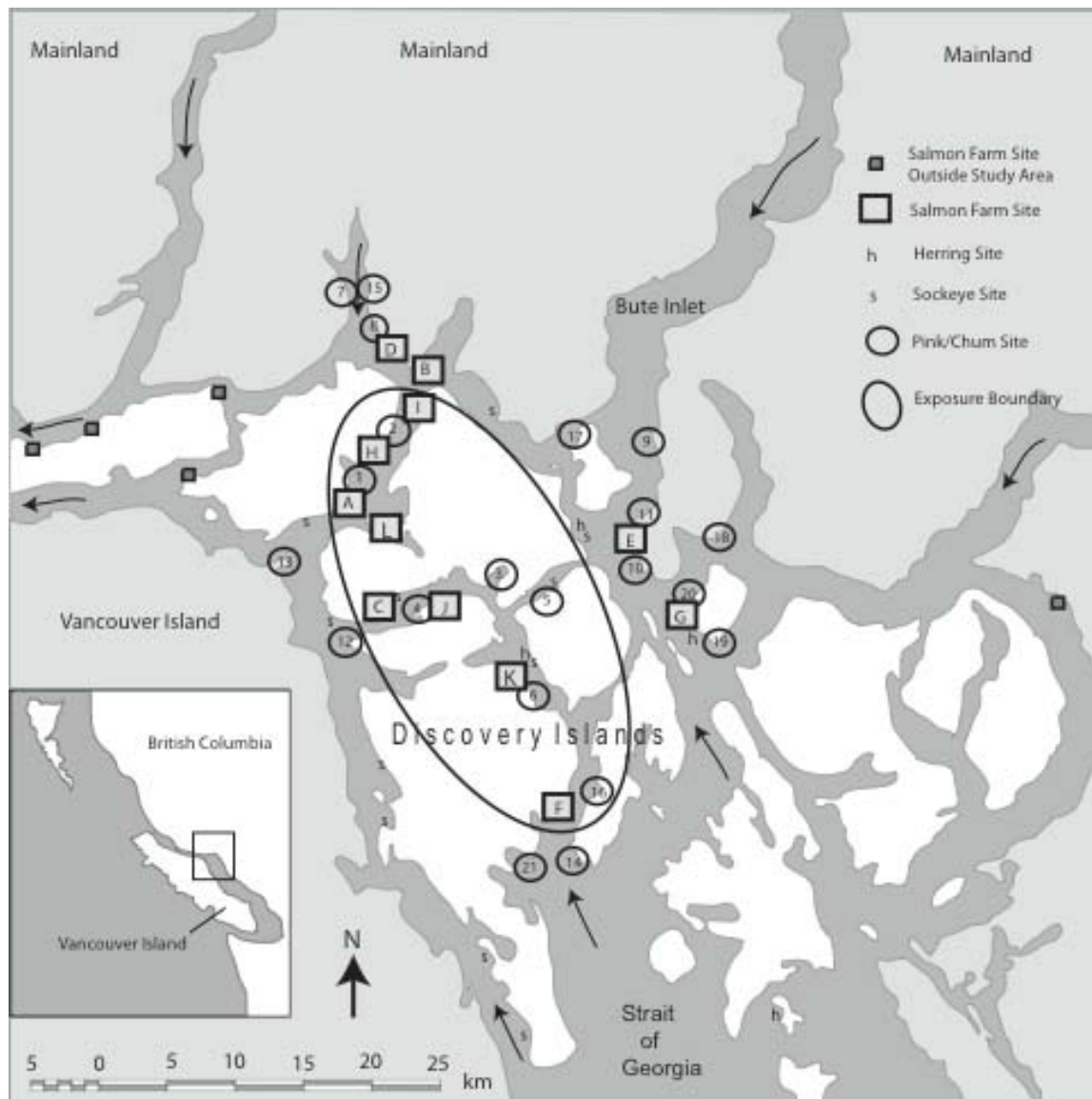


Figure 2.

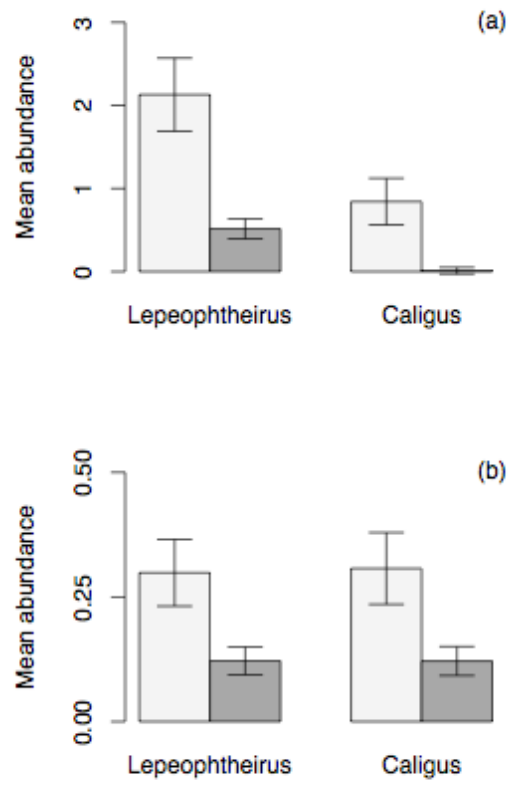


Figure 3.

