

THE ABUNDANCE AND DISTRIBUTION OF *LEPEOPHTHEIRUS SALMONIS* (COPEPODA: CALIGIDAE) ON PINK (*ONCORHYNCHUS GORBUSCHA*) AND CHUM (*O. KETA*) SALMON IN COASTAL BRITISH COLUMBIA

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ABSTRACT: In total, 23,750 specimens of the salmon louse, *Lepeophtheirus salmonis*, were collected from 3,907 juvenile pink and 3,941 chum salmon caught within the Broughton Archipelago during a 2-yr survey. The prevalence on pink salmon was significantly higher than on chum salmon in 2004 (62.3% and 58.6%, respectively) and in 2005 (26.4% and 23.1%, respectively). The mean abundance on chum salmon was significantly higher than on pink salmon in 2004 (7.0 ± 0.3 and 2.8 ± 0.2 , respectively), whereas in 2005 the mean abundance did not differ between species (0.6 ± 0.1 and 0.5 ± 0.0 , respectively). The mean intensity on chum salmon was significantly higher than on pink salmon in 2004 (12.0 ± 0.4 and 4.5 ± 0.2 , respectively) and in 2005 (2.5 ± 0.2 and 1.7 ± 0.1 , respectively). The prevalence, intensity, and abundance of *L. salmonis* were significantly higher on salmon belonging to both host species in 2004 compared with 2005. In both years, a majority of pink and chum salmon had 2 or fewer lice. In general, a decline in abundance of *L. salmonis* over the 3 collection periods in each year coincided with an increased percentage of motile developmental stages. The abundance was lowest on fish collected from zones in which the seawater surface salinity was also lowest. Seawater surface temperature was higher and salinity was lower in 2004 compared with 2005. The spatial and temporal trends in the abundance of *L. salmonis* in relation to host size, infestation rates, and seawater salinity and temperature, evident in both years, must be considered in future studies assessing the role of farmed salmon in the epizootiology of this parasite on juvenile salmon in this area.

The marine ecosystem of the Broughton Archipelago in coastal British Columbia, Canada (Fig. 1), is hydrographically and biologically complex. The area supports numerous populations of Pacific salmon (*Oncorhynchus* spp.), and there are 28 sites for the production of farmed Atlantic salmon (*Salmo salar*), of which 15 to 18 are typically active at any time. There are few studies of the relationships among the physical and biological components of this region (e.g., see Brooks, 2005; Foreman et al., 2006). The Broughton Archipelago has been the focus of recent scientific debate because of concerns that juvenile pink (*O. gorbuscha*) and chum (*O. keta*) salmon migrating from natal streams in the area toward the open ocean are vulnerable to infestations with the salmon louse, *Lepeophtheirus salmonis* (Morton et al., 2004; Krkošek et al., 2005, 2006). These studies concluded that the spatial and temporal patterns of mixed infestations with *L. salmonis* and a related parasite, *Caligus clemensi*, are consistent with proximity of the pink and chum salmon to salmon farms. Furthermore, the studies concluded that the farmed salmon serve as reservoirs of the salmon louse. However, despite the presence of salmon farms and infestations with *L. salmonis*, measurements made in 2003 and 2004 indicated that pink salmon in this area experienced high marine survival (Beamish et al., 2006).

Lepeophtheirus salmonis is a common parasite of salmonids in seawater in the Northern Hemisphere. The parasite undergoes direct development, which includes planktonic (2 nauplii), infective (1 copepodid), and parasitic (4 chalimus, 2 preadult, 1 adult) stages (Johnson and Albright, 1991). In the Broughton Archipelago, *L. salmonis* and *C. clemensi* were found to infest a high proportion of three-spine stickleback (*Gasterosteus aculeatus*) (Jones, Prosperi-Porta et al., 2006), which was a previously unrecognized host species for *L. salmonis*. Furthermore, the abundance of these parasites was lower on sticklebacks collected from zones in which the seawater salinity was also low (Jones, Prosperi-Porta et al., 2006). This observation is consistent with the adverse effect of low salinity on the survival and

settlement of *L. salmonis* (Pike and Wadsworth, 1999; Boxaspen, 2006; Bricknell et al., 2006). Thus, the relative roles of oceanographic processes and the availability of nonsalmonid and salmonid (farmed and nonfarmed) hosts in influencing the epizootiology of *L. salmonis* in the Broughton Archipelago remain unclear. The objective of this study was to describe patterns of *L. salmonis* infestation, salmon size, water temperature, and salinity over 2 yr in the Broughton Archipelago.

MATERIALS AND METHODS

The study area, including its stratification into 11 zones, and the methods by which salmon were collected using beach and purse seine gear were described previously (Jones, Prosperi-Porta et al., 2006). Data were collected during 6 periods, 3 in each of 2004 and 2005 (see Table 1 for the corresponding dates). Fish were collected from approximately 10 sites per zone in all periods. Fish were confined into a small volume of water within the net, individually bagged directly from the net, labelled, and immediately frozen. The first 30 specimens of each salmon species to be bagged were selected for examination. The frozen specimens were transported to the laboratory for species confirmation and microscopic examination. Wet weight and fork length were determined for each fish, and all lice, including those free in the bag, were counted, and identified to species and to developmental stage according to published criteria (Kabata, 1988; Johnson and Albright, 1991). After identification, lice were stored in 70% ethanol for future reference. Salinity and temperature data were obtained from samples of surface seawater collected from most sites in each period. Salinity was estimated from conductivity using a salinometer as described previously (Jones et al., 2006), and temperature was measured using a hand-held thermometer.

Prevalence, mean intensity, and mean abundance of *L. salmonis* were defined according to Bush et al. (1997). The significance of differences in these parameters was tested using the chi-square and Kruskal–Wallis tests. The significance of log-transformed weights was tested using Bonferroni-adjusted 2-sample *t*-tests. The significance of differences in mean salinity and mean temperature was tested using the Kruskal–Wallis test. In all cases, differences were considered significant when $P \leq 0.05$.

RESULTS

Over 2 yr, 3,907 pink and 3,941 chum salmon were examined, and 23,750 *L. salmonis* in total were collected. Approximately 80% of all fish samples were obtained from 6 of the 11 zones surveyed, i.e., D, E, F, G, H, and K (see Fig. 1; Tables

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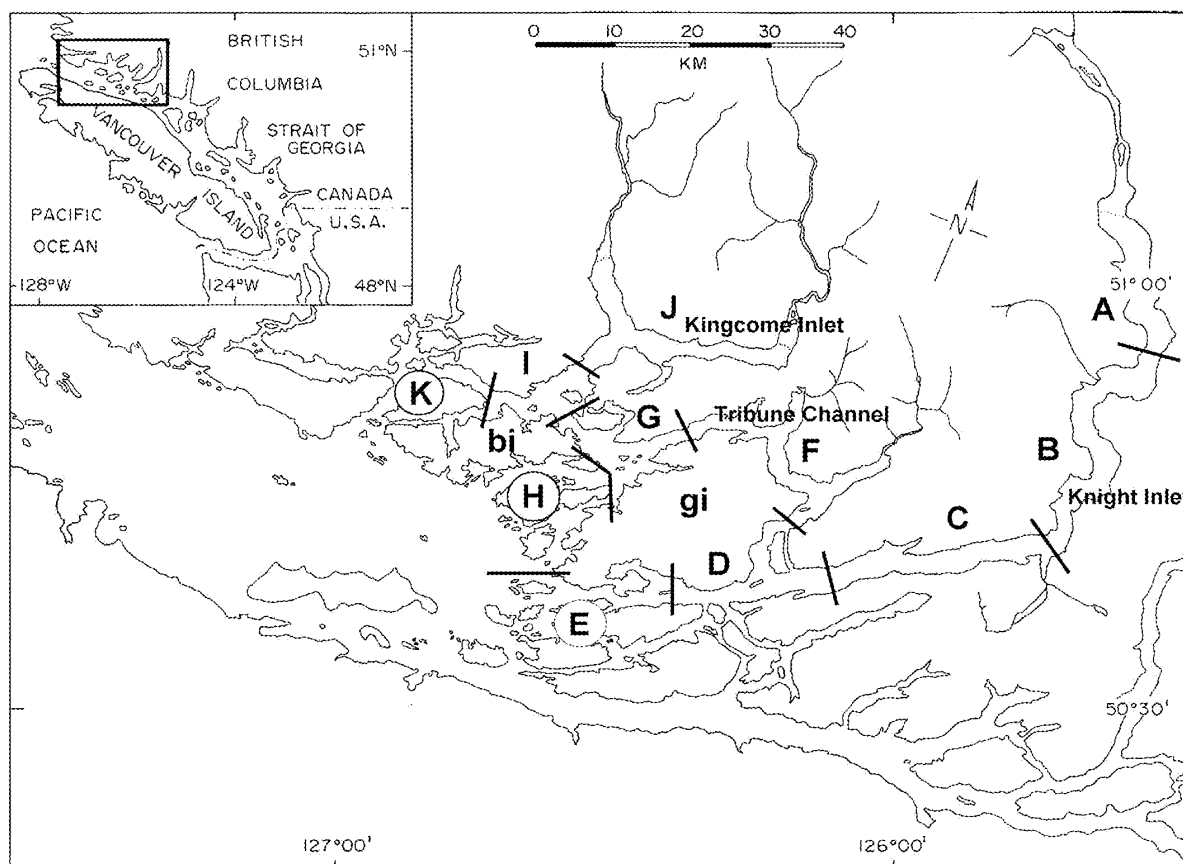


FIGURE 1. Map of study area showing major water bodies and zone designations. bi, Broughton Island; gi, Gilford Island. Reproduced from Jones et al. (2006). *Journal of Parasitology* 92: 473–480 (with permission).

TABLE I. Infestations with *Lepeophtheirus salmonis* on pink salmon (*Oncorhynchus gorbuscha*) collected from the Broughton Archipelago, British Columbia.

Zone*	2004			2005		
	1†	2	3	1	2	3
A	0/1‡	0/8	0/0	0/10	0/3	0/0
B	1/1	0/2	0/0	0/3	0/2	0/0
C	0/0	0/0	0/0	1/13	0/0	0/0
D	33/85	35/64	0/0	7/101	15/58	1/55
E	49/98	64/107	1/2	21/120	20/109	5/67
F	222/285	63/112	36/56	11/59	47/124	15/103
G	61/111	24/37	5/8	82/234	14/48	5/57
H	142/214	133/208	34/44	95/188	50/175	10/115
I	1/4	9/9	0/0	19/71	6/23	5/32
J	0/1	0/3	0/0	0/3	1/1	0/0
K	10/18	15/24	0/0	72/183	98/315	34/133

* See Figure 1 for locations of zones.

† Collection period (2004): 1 = 25 May–1 June, 2 = 22–29 June, 3 = 20–26 July; (2005): 1 = 23 May–1 June, 2 = 20–29 June, 3 = 18–27 July.

‡ Number infested/number examined.

I, II). Similarly, 45.9% of samples were collected in period 1, whereas 18.7% were collected in period 3 (Table III). The weight of pink and chum salmon increased significantly during the surveys in both years (Table III), and this trend was evident in most zones, although the salmon tended to be smallest in zones A, B, C, and J.

In both years, the overall prevalence of *L. salmonis* on pink salmon was significantly higher than on chum salmon (62.3% vs. 58.6% in 2004; 26.4% vs. 23.1% in 2005; $P = 0.02$ both years). A significantly higher overall prevalence was observed on both species in 2004 ($P < 0.01$). In contrast, the overall mean abundance of *L. salmonis* on chum salmon in 2004 (7.0 ± 0.3) was significantly higher than on pink salmon (2.8 ± 0.2) ($P < 0.01$), whereas in 2005, there was no significant difference in overall mean abundance between the host species (0.6 ± 0.1 and 0.5 ± 0.0 , respectively) ($P = 0.10$). The overall abundance on both species was significantly higher in 2004 ($P < 0.01$). In both years, the overall mean intensity on chum salmon was significantly higher than on pink salmon (12.0 ± 0.4 vs. 4.5 ± 0.2 in 2004; 2.5 ± 0.2 vs. 1.7 ± 0.1 in 2005) ($P < 0.01$ both years). The overall mean intensity on both species was significantly higher in 2004 ($P < 0.01$).

TABLE II. Infestations with *Lepeophtheirus salmonis* on chum salmon (*Oncorhynchus keta*) collected from the Broughton Archipelago, British Columbia.

Zone*	2004			2005		
	1†	2	3	1	2	3
A	0/39‡	0/5	0/0	0/34	0/4	0/0
B	6/26	0/6	0/0	2/95	0/25	0/3
C	2/2	0/0	0/0	2/23	1/6	0/2
D	98/127	56/104	0/5	15/123	1/20	5/40
E	32/36	57/134	6/60	11/47	7/51	0/5
F	212/218	48/64	25/61	17/64	5/19	2/23
G	81/94	36/46	31/124	21/29	2/3	0/9
H	169/180	157/218	27/68	50/59	39/121	14/58
I	39/72	26/62	13/98	36/63	1/3	1/100
J	11/140	6/70	2/47	16/83	0/42	0/2
K	166/202	156/181	10/21	26/40	53/165	3/70

* See Figure 1 for locations of zones.

† Collection period (see Table 1 for dates).

‡ Number infested/number examined.

In 2004, the maximum number of *L. salmonis* observed was 175 on a chum and 79 on a pink salmon, whereas in 2005 the maxima were 30 and 17, respectively. In 2004, 2, or fewer, lice were observed on 69.4% of pink and 53.2% of chum salmon, whereas in 2005, these values were 95.8% and 93.8% (Fig. 2). A category of >10 lice per fish was notable in 2004 (5.7% of pink and 19.9% of chum salmon) but not in 2005 (0.04% and 0.6%, respectively) (Fig. 2). In 2004, copepodids predominated on pink and chum salmon, whereas in 2005 the predominant stages were preadults on chum and adults on pink salmon (Fig. 2). In both years, all 4 chalimus stages were more abundant on chum salmon than on pink salmon.

Significant declines in the mean abundance of *L. salmonis* over the 3 collection periods occurred on chum salmon in both years and on pink salmon in 2005 (Table III). The mean abundance on pink salmon increased between periods 2 and 3 such that the significantly lower mean abundance of *L. salmonis* on pink compared with chum salmon described above for 2004 was only evident in periods 1 and 2. The prevalence on chum salmon decreased significantly over the 3 periods in both years and on pink salmon in 2005 (Table III). Parasite development was estimated by calculating the percentage of motile (preadult and adult) stages. Percentage of motile stages on pink salmon increased to 95% in both years. On chum salmon, percentage of motiles only increased significantly by period 3 in 2004 (Table III). Significant reductions in the proportion of copepodids were observed on pink salmon in both years and on chum salmon in 2004.

Similar spatial patterns in the abundance of *L. salmonis* were observed for both host species and in both years. Mean abundance tended to be greatest in those zones within Tribune Channel (F, G, and H), lower Knight Inlet (E), and Well's Passage (K) (Fig. 3). Conversely, mean abundance was consistently lowest in the zones furthest inland (A, B, and J), and these patterns were most pronounced in periods 1 and 2. A decline in mean abundance was evident in most zones, resulting in a spatial pattern of mean abundance in period 3 that was less conspicuous than in earlier periods. Nevertheless, in period 3, differences in mean abundance among zones in which lice were

TABLE III. Temporal changes in *Lepeophtheirus salmonis* infestations on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon from the Broughton Archipelago, British Columbia.

Year	P*	No. fish	Pink					Chum				
			Weight (g)	Abund*	Prev* (%)	Cop* (%)	Motile (%)	No. fish	Weight (g)	Abund*	Prev* (%)	Cop* (%)
2004	1	818	3.3 ± 0.1	3.8 ± 0.3	63.4	43.7	26.0	1,136	3.8 ± 0.1	9.8 ± 0.5	71.8	30.5
	2	574	6.8 ± 0.1†	1.6 ± 0.1†	59.2	13.6†	82.3†	890	9.6 ± 0.2†	6.8 ± 0.5†	61.0†	23.7†
	3	110	14.6 ± 0.5‡	2.0 ± 0.2‡	69.1‡	3.3‡	94.9‡	484	28.7 ± 0.6‡	1.0 ± 0.2‡	23.6‡	5.4‡
2005	1	985	2.5 ± 0.0	0.6 ± 0.0	31.3	21.9	47.4	660	5.0 ± 0.1	0.8 ± 0.1	29.7	14.4
	2	858	7.0 ± 0.1†	0.5 ± 0.0	29.3	4.6†	87.5†	459	14.2 ± 0.3†	0.5 ± 0.1	23.7†	8.2†
	3	562	13.2 ± 0.2‡	0.2 ± 0.0‡	13.3‡	1.0†	95.0‡	312	27.6 ± 0.8‡	0.1 ± 0.0†	8.0‡	11.4

* P, collection period (see Table 1 for dates); Abund, mean abundance (± SE); Prev, prevalence; Cop, copepodid.

† Significantly different from collection period 1.

‡ Significantly different from collection period 2.

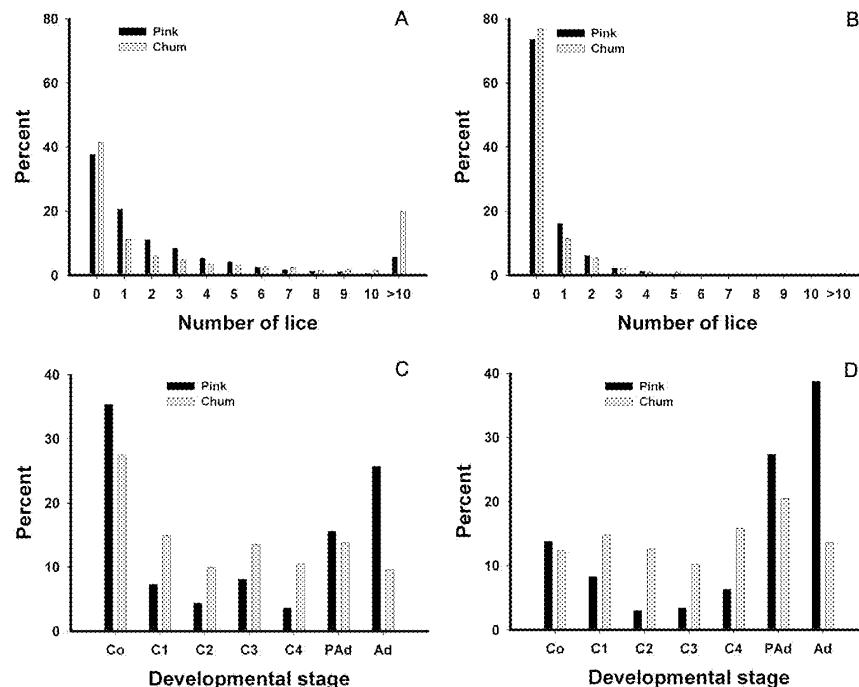


FIGURE 2. Distribution and developmental stages of *Lepeophtheirus salmonis* on juvenile pink and chum salmon in the Broughton Archipelago. Percentage of salmon with salmon lice in 2004 (A) and 2005 (B). Percent of developmental stages in 2004 (C) and 2005 (D). Co, copepodid; C1–C4, chalimus I to IV; PAd, preadult (both stages and sexes); Ad, adult (both sexes).

detected were still significant ($P < 0.01$) on chum salmon in both years and on pink salmon in 2005. The prevalence on both salmon species also varied among zones and followed a trend similar to that described for abundance (Tables I, II).

The mean surface salinity was 15.1 parts per thousand (ppt) (range, 0.02–30.5) in 2004 and 20.2 ppt (range, 0.05–30.9) in 2005. Salinity decreased significantly between the first and third periods in both years (Table IV). In all periods, salinity was significantly lower in 2004 compared with 2005 ($P < 0.01$). Significant variation in salinity was observed among zones in both years (Fig. 4). Salinity was greatest in zones closest to the open ocean (E, H, and K) and least in zones furthest inland (A, B, and J). The significant decline in salinity among periods described above was most evident in those zones furthest from the open ocean (zones A, B, C, I, and J) (Fig. 4).

The mean surface temperature was 14.6 C (range, 6.8–23.2 C) in 2004 and 12.8 C (range, 8.5–19.8 C) in 2005. In both years, temperatures increased significantly between the first and second periods (Table IV), and a trend of increasing temperature was evident in most zones (Fig. 4). In all periods, the temperature was significantly higher in 2004 compared with 2005 ($P < 0.01$) (Table IV). Significant differences in temperature were evident among zones, and these differences were most pronounced in period 3 (Fig. 4). With the exception of zones A and B, temperatures were higher throughout the study area in 2004 compared with 2005. The warmest water occurred in Kingcome Inlet (zones I and J) in both years. The water was coolest in upper Knight Inlet (zone A) in 2004 and in lower Knight Inlet (zone E) in 2005.

DISCUSSION

Infestations with *L. salmonis* were observed on 2.5- to 28.7-g pink and chum salmon from the Broughton Archipelago in British Columbia, Canada, collected over 2 yr. All measures of *L. salmonis* infestation in 2005 were significantly lower than in 2004, and in neither year were infestations uniform throughout the study area. In addition, distinct patterns of infestation were observed on pink and chum salmon in both years. The present study confirmed earlier work documenting year-to-year differences in the abundance of *L. salmonis* on juvenile salmon in the Broughton Archipelago. Significantly higher abundances of *L. salmonis* were reported on juvenile pink and chum salmon in 2004 compared with 2002 and 2003 (Morton et al., 2005). The latter study reported an overall abundance of 9.75 for 2004, but it did not report infestations on pink and chum salmon separately. Relatively low abundances were also reported for 2003, and in that year, *C. clemensi* was approximately 3 times more abundant than *L. salmonis* on both salmon species (Jones and Nemec, 2004). The abundance of *L. salmonis* on juvenile pink and chum salmon in the study area in 2006 was similar to that observed in 2003 (S. Jones, unpubl. obs.). Together, these studies support a significantly higher abundance of *L. salmonis* in 2004 compared with the adjacent years. This pattern of interannual variability with peak abundance occurring in 2004 was also evident on three-spine sticklebacks collected from the same area (Jones and Nemec, 2004; Jones, Prosseri-Porta et al., 2006; S. Jones, unpubl. obs.). Interannual differences in the abundance of *L. salmonis* on wild migrating salmon smolts have

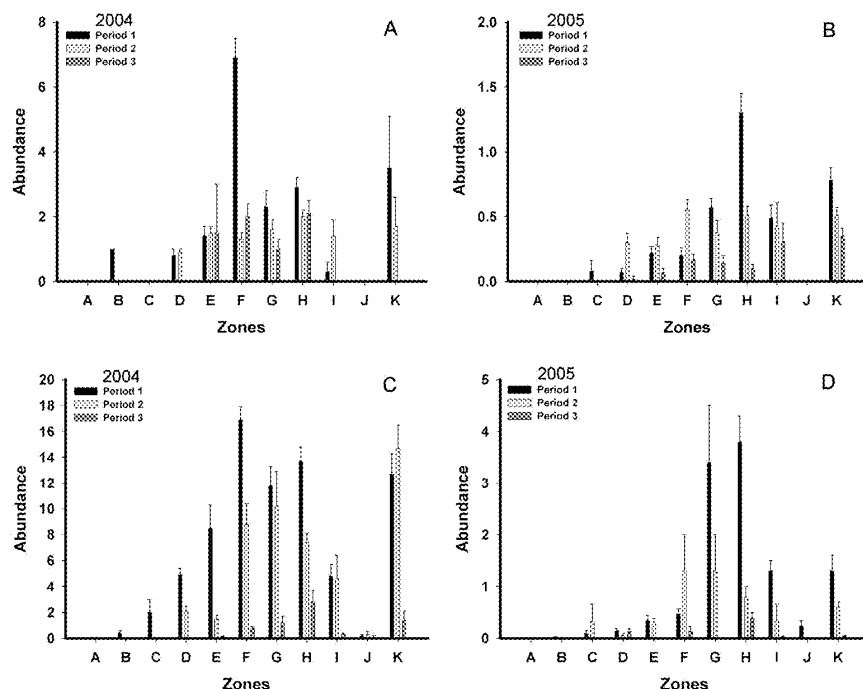


FIGURE 3. Mean abundance of *Lepeophtheirus salmonis* on juvenile pink salmon (*Oncorhynchus gorbuscha*) (A–B) and chum salmon (*Oncorhynchus keta*) (C–D), from zones within the Broughton Archipelago in 2004 and 2005. Error bars are SEM. See Figure 1 for locations of zones and Table I for dates of collection periods.

also been reported from Norway (Heuch et al., 2005). Morton et al. (2005) concluded that the relatively low abundance observed in 2003 was the result of a coordinated fallow of several salmon farms along Tribune Channel coincident with the migration of the juvenile salmon. The absence of coordinated fallows in 2002 and 2004 was said to have resulted in the elevated abundances observed in those years. However, the 4-fold reduction in abundance reported here for most zones and on both salmon species in 2005 also occurred in the absence of a coordinated fallow of farm sites in Tribune Channel (J. Constantine and S. Saksida, pers. comm.). Furthermore, the abundance of *L. salmonis* on juvenile salmon in Tribune Channel was amongst the highest observed in each of 2003, 2004, and 2005,

regardless of whether salmon farms were held fallow along this watercourse (Jones and Nemec, 2004). It is possible that treatment of farmed salmon for sea lice infestations may explain the patterns of variation in *L. salmonis* abundance on the juvenile salmon. A fall in the abundance of caligid planktonic stages was observed in Loch Shieldaig shortly after farmed salmon in the loch were treated for *L. salmonis* infestations (Penston et al., 2004). However, there were no significant differences in annual sea lice treatment rates of farmed salmon in the Broughton Archipelago between 2003 and 2005 (Saksida et al., 2007), suggesting treatment alone does not explain the year-to-year variation in abundance. Variation in the capacity of seawater to support the development, survival, and retention of the planktonic nauplii in the study area requires consideration as an alternative explanation. Temperature was significantly higher in 2004 compared with 2005. The seawater temperature reported by Jones and Nemec (2004) for the equivalent of period 1 in 2003 was lower than that of 2004 and 2005. Similarly, Morton et al. (2005) reported cooler water temperatures in 2003 compared with 2002 and 2004. Laboratory studies support a role of temperature in controlling developmental rates and promoting settlement success of larval *L. salmonis* (Tucker et al., 2000). The apparent association of the abundance of *L. salmonis* and seawater temperature over several years requires closer examination. Future research should also focus on salinity and temperature during the weeks preceding the juvenile salmon migration, because these factors may be informative in understanding the occurrence of infective copepodids when the salmon first encounter seawater.

TABLE IV. Salinity and temperature of surface seawater within the Broughton Archipelago, British Columbia, in 2004 and 2005.

Year	Period	Sample size	Salinity (‰)	Temperature (°C)
2004	1*	144	15.0 ± 0.7	13.1 ± 0.1
	2	147	17.2 ± 0.8†	15.3 ± 0.2†
	3	144	13.2 ± 0.7‡	15.6 ± 0.2†
2005	1	149	22.1 ± 0.7	12.0 ± 0.2
	2	151	19.8 ± 0.8†	13.0 ± 0.2†
	3	149	18.8 ± 0.9†	13.4 ± 0.2†

* See Table I for dates.

† Significantly different from collection period 1.

‡ Significantly different from collection period 2.

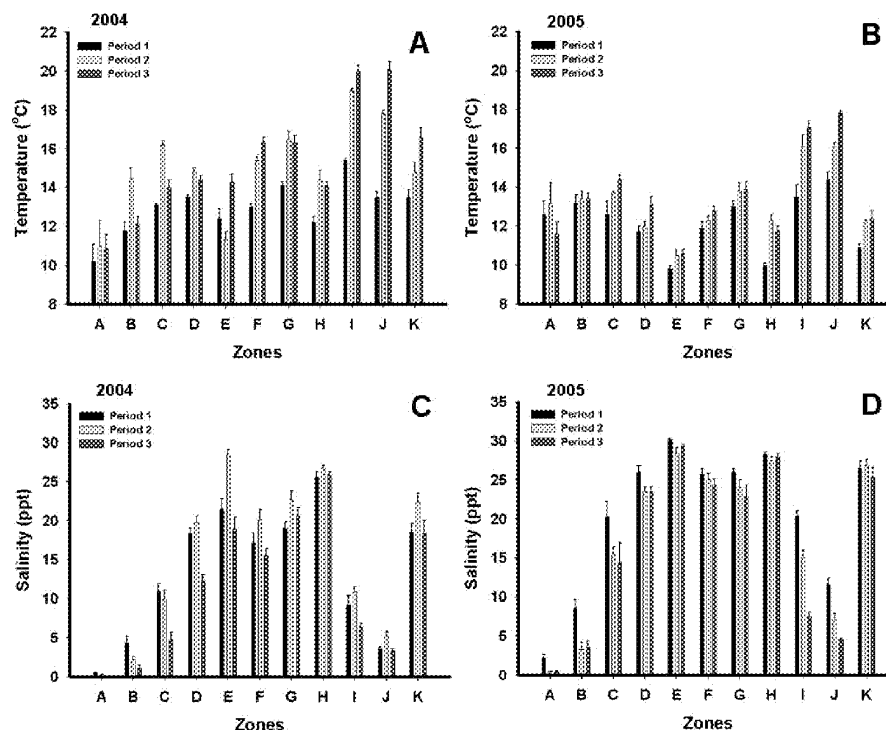


FIGURE 4. Mean surface seawater temperatures and salinities collected within the Broughton Archipelago in 2004 and 2005. Error bars are SEM. See Figure 1 for locations of zones and Table 1 for dates of collection periods.

In neither 2004 nor 2005 were *L. salmonis* infestations uniformly distributed within the study area. Despite the differences in overall abundance between years, the parasite was most commonly found on salmon from Tribune Channel (zones F, G, and H), lower Knight Inlet (zone E), and Well's Passage (zone K). This is similar to the distribution of *L. salmonis* and *C. clemensi* observed on pink and chum salmon in 2003 (Jones and Nemec, 2004) and on sticklebacks in 2004 (Jones, Prosperi-Porta et al., 2006). Generally, juvenile salmon enter the sea from rivers within the study area and migrate westerly toward the open ocean. During this migration, they grow and move from areas of lower to higher salinity. The relatively low numbers of pink salmon collected from zones A, B, C, and J indicated that most salmon from rivers in the headwaters of Knight and Kingcome Inlets had already migrated from these regions when collections were made. In contrast, in period 1 of both years, chum salmon were still relatively abundant in these zones. Low abundances of *L. salmonis* were associated with zones in which the salmon were smallest and had the least opportunity for exposure to *L. salmonis*. In addition, the low salinities in these zones may have further impaired the viability and developmental potential of planktonic stages of the parasite, consistent with laboratory observations (Bricknell et al., 2006). A relatively low level of infestation in zones B and C was evident from the reduced proportions of copepodids on sticklebacks (6.7% and 2.6%, respectively) (Jones, Prosperi-Porta et al., 2006). Interestingly, copepodids accounted for 33.6% of developmental stages on sticklebacks from another area of low salinity (zone J, <10 ppt)

(Jones, Prosperi-Porta et al., 2006), raising the possibility that the sticklebacks had migrated into this zone from areas of higher salinity or that the *L. salmonis* in the study area are more tolerant of reduced salinity than expected (see Pike and Wadsworth, 1999). However, until salinity depth profiles are more adequately characterized within the study area, it is prudent to use the surface salinity values reported here as indicators of spatial trends in the abundance of *L. salmonis*, rather than as predictors of its presence or absence. Other studies have concluded that local elevations in the abundance of *L. salmonis* and *C. clemensi* resulted from the proximity of the captured fish to salmon farms (Morton et al., 2004; Krkošek et al., 2005, 2006). Although the conclusions drawn in the latter studies remain controversial (e.g., Brooks and Stucchi, 2006), it is well established from coastal regions of Scotland, Norway, and Ireland that the local abundance of planktonic and parasitic stages of *L. salmonis* is elevated when farmed salmon populations that occupy the same water body are known to be infested with egg-producing female *L. salmonis* (McKibben and Hay, 2004; Penston et al., 2004; Heuch et al., 2005). Thus, the present work is consistent with earlier studies in identifying spatial patterns in the variation of *L. salmonis*. The variation was shown here to occur on a population of rapidly growing juvenile salmon as they migrated through a coastal habitat of variable salinity and temperature. The significant spatial and temporal variations in abundance of *L. salmonis* on farmed salmon in this area (Saksida et al., 2007) raises the possibility that common environmental processes play a role in regulating the abundance of the

parasite on captive and wild populations. Thus, we are presently modeling the significance of environmental, host, and farm parameters as sources of variation in *L. salmonis* infestations on juvenile Pacific salmon.

Temporal trends evident during each of the 2 yr included a decrease in salinity, an increase in temperature, and an increase in the weight of salmon in both species. The changes in salinity and temperature are seasonal and related to the estuarine flow resulting from increased summer melting of snow and ice in adjacent mountains (Foreman et al., 2006). Similarly, the rapid growth of pink and chum salmon after entry into the ocean is well documented (Heard, 1991; Salo, 1991). Coincident with these trends was a decreasing abundance of *L. salmonis* on both species; however, trends in other measures of infestation were not consistent between pink salmon and chum salmon. For example, the prevalence of *L. salmonis* increased on pink salmon but decreased on chum salmon in 2004, whereas prevalence decreased on both species in 2005. The occurrence of new infestations was estimated from the proportion of copepodids. As the percentage of copepodids decreased, motile stages became more abundant, increasing to approximately 95% on pink salmon in both years and to 71% on chum salmon in 2004. On chum salmon in 2005, however, the percentage of neither copepodids nor motile stages changed over time. A smaller proportion of motile *L. salmonis* was consistently observed on chum compared with pink salmon throughout the study. The distinct pattern of *L. salmonis* development, in addition to the overall higher level of infestation on chum compared with pink salmon, was similar to laboratory studies. Infestations in these studies were lower on juvenile pink salmon as a result of a more rapid rejection of *L. salmonis* from pink compared with chum salmon after controlled exposures (Jones, Kim, and Dawe, 2006; Jones et al., 2007). The trends suggested that, in general, infestations were acquired early during the seaward migration of pink salmon and that parasite development coincided with salmon growth. This agrees with a life history strategy in which *L. salmonis* infestations on salmon that overwinter in coastal habitats serve as a reservoir for infestations on juvenile salmon that have recently entered the ocean (Beamish et al., 2007). The possibility that sticklebacks serve as a reservoir of *L. salmonis* infestations that establish on juvenile salmon by the settlement of motile preadult stages requires further investigation. Prevalence on pink salmon remained between 60 and 70% in 2004, indicating most infested fish remained in the population. In contrast, the declining prevalence on chum salmon in 2004 indicated a proportion of infested fish failed to remain in the population. In 2005, declining prevalences on both species suggested infested fish did not remain in the population or that *L. salmonis* was rejected from the salmon. Although there are insufficient data to distinguish between these scenarios, the laboratory studies cited above, in combination with the relatively low level of infestation observed in 2005, support the possibility that rejection by the host accounted for some of the reduced prevalence.

The present study has documented significant spatial and temporal trends in *L. salmonis* infestation on juvenile pink salmon and chum salmon over 2 yr, coincident with trends in salmon size, and in the temperature and salinity of surface seawater. Ongoing research seeks to establish the relative magnitude of these environmental and biological variables, relative to

that of farmed salmon, in influencing the epizootiology of *L. salmonis*.

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