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[Article]

Temporal Patterns of Sea Louse Infestation on Wild Pacific Salmon in Relation to the Fallowing of Atlantic Salmon Farms

ALEXANDRA MORTON*

Raincoast Research,
Simoom Sound, British Columbia V0P 1S0, Canada

RICHARD D. ROUTLEDGE

Department of Statistics and Actuarial Science, Simon Fraser University,
8888 University Drive, Burnaby, British Columbia V5A 1S6, Canada

ROB WILLIAMS

Raincoast Conservation Society,
Pearse Island, British Columbia V0N 1A0, Canada

Abstract.—We report on a 3-year study of the infestation rates of the sea louse, *Lepeophtheirus salmonis*, on wild juvenile pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* in the Broughton Archipelago, British Columbia. In 2002, the British Columbia Ministry of Agriculture, Fisheries, and Food ordered farm fallowing (i.e., the removal of farmed Atlantic salmon *Salmo salar* from net-cages) along the presumed migration route of wild juvenile Pacific salmon in this area. The goal was to protect wild juvenile fish from sea louse infestation. We assessed the effectiveness of this decision by comparing sea louse infestation rates on wild juvenile salmon near three Atlantic salmon farm sites prior to, during, and after fallowing. Overall, *L. salmonis* levels were significantly reduced ($P < 0.0001$) at the study sites during fallowing but returned to the original level after fallowing. The decline was age specific. While the abundance of the earliest attached sea louse phase (the copepodid stage) declined by a factor of 42, the mean abundance of adult *L. salmonis* did not decline significantly. Changes in salinity and temperature could not account for the decline. This study provides evidence that the fallowing of Atlantic salmon farms during spring juvenile salmon migrations can be an effective conservation and management tool for protecting wild salmon. While this correlation adds to the increasing weight of evidence linking Atlantic salmon farms to increased parasite loads on wild salmon, greater cooperation between researchers and farmers will be necessary to isolate the causal mechanisms and provide safe seaward passage to wild juvenile salmon.

The farming of Atlantic salmon *Salmo salar* is correlated with infestation of the sea louse *Lepeophtheirus salmonis* on juvenile salmon in Europe (Tully et al. 1993; Birkeland 1996; Heuch et al. 2005) and Canada (Morton and Williams 2003; Morton et al. 2004). While other nonsalmon-specific sea louse species have been recorded on salmon, they are not known to have pathogenic effects on salmonid hosts.

Lepeophtheirus salmonis is a salmon-specific marine sea louse endemic to the Northern Hemisphere (Pike and Wadsworth 1999). Its naupliar larvae are free-swimming for approximately 4 d at 10°C before attaining infective capability (copepodid stage) (Johnson and Albright 1991a). Copepodid-stage sea lice can survive without a host for approximately 5 d at 10°C (Boxaspen and Næss 2000). *Lepeophtheirus salmonis* molts through eight stages from attachment to adulthood at approximately 4 weeks of age, permitting uncomplicated approximation of age within this period (Johnson and Albright 1991a, 1991b). Optimal salinity for *L. salmonis* survivorship and reproduction is 30‰ (Johnson and Albright 1991b), and copepodids can tolerate salinity levels as low as 15‰ (Pike and Wadsworth 1999). Sustained temporal presence of the earliest attached juvenile stages (copepodid and chalimus I) of sea lice on a population of fish indicates chronic re-infestation and a local source of gravid female sea lice. This characteristic is specific to infestations found on wild salmon near salmon farms (Pike and Wadsworth 1999).

Prior to salmon farming, *L. salmonis* was not observed on the early juvenile seawater phases of wild Atlantic salmon and sea-run brown trout *Sal-*

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* Corresponding author: wildorca@island.net

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mo trutta (also known as sea trout) (Heuch and Mo 2001). *Lepeophtheirus salmonis* was also not observed on wild juvenile Pacific salmon in the first weeks after seawater entry, although infestation by a smaller, generalist sea louse species, *Caligus clemensi*, has been reported (Parker and Margolis 1964). *Lepeophtheirus salmonis* infestation occurs on farmed salmon (Håstein and Bergsjo 1976; Wootten et al. 1982; Tully and Whelan 1993), and pathogenic infestations appear on wild juvenile salmonids (Atlantic salmon and sea trout) captured in areas adjacent to salmon farms (Tully et al. 1993; Birkeland 1996; Heuch et al. 2004).

The first report of *L. salmonis* infestation on juvenile Pacific salmon came from the Broughton Archipelago, British Columbia (BC), in 2001 (Morton and Williams 2003). Morton et al. (2004) found that pink salmon *Oncorhynchus gorbuscha* and chum salmon *O. keta* were equally infested by sea lice in the Broughton Archipelago and that sea louse infestation on wild fish was three times higher in areas adjacent to Atlantic salmon farms holding the older growers than in areas near farms that held smolts.

Butler and Watts (2002) found that wild salmon stocks in sea lochs containing salmon farms suffered high infestations of sea lice and severe population declines, while wild salmon in lochs without salmon farms did not. Similar abundance patterns are beginning to emerge in the Broughton Archipelago. In 2001, sea louse prevalence on juvenile pink salmon was estimated at 98.1% (Morton and Williams 2003), and the adult return of the 2001 pink salmon cohort was 99% below that of the parental generation (PFRCC 2002). In 2002, sea louse prevalence was estimated at 91.8%, and the adult return of this stock in 2003 was 89% below that of the parental generation (Canada Department of Fisheries and Oceans, http://www-sci.pac.dfo-mpo.gc.ca/mehsd/sea_lice/2003/freshwater_reports/2003_escapement_e.htm).

In 2002, the Pacific Fisheries Resource Conservation Council (PFRCC), a government-appointed advisory group, concluded that in the absence of absolute scientific proof, the evidence linking Atlantic salmon farms to the decline of the Broughton Archipelago pink salmon stock was strong enough to warrant the fallowing of farms throughout the entire archipelago to reduce the prevalence of sea lice. This strong, risk-averse recommendation was accompanied by a second, higher-risk option that included strategic fallowing of farms on the major salmon migration route and the use of chemotherapeutants to kill sea lice on all active Atlantic salmon farms over and beyond husbandry requirements.

The seven most productive rivers of the Broughton Archipelago (Figure 1) have annually produced over 3 million wild adult pink salmon (PFRCC 2002). Atlantic salmon farming was introduced to BC in the late 1970s and to the Broughton Archipelago in 1984 (A. Morton, unpublished data). There are currently 129 Atlantic salmon farm tenures in BC, and 26 of those tenures are sited in the 400-km^2 Broughton Archipelago (Figure 1). While we could not establish the number of fish per farm in this area, Naylor et al. (2003) reported the presence of up to 1 million fish per farm in BC.

It has been suggested that salmon farms can act as ''pathogen culturing facilities'' (Bakke and Harris 1998) because the nets used to contain farmed salmon allow the free flow of microorganisms between the wild and farmed environments. No evidence exists to indicate that sea louse larvae are not moving through the net pens in both directions between transitory wild stocks and high-density, stationary farm stocks.

In response to the PFRCC recommendations, the BC Provincial Ministry of Agriculture, Fisheries, and Food applied a fragment of the second, higher-risk option in their Sea Lice Action Plan (MAFF 2003). Eleven Atlantic salmon farms were fallowed, and chemical treatment was applied to other undisclosed farms. Our purpose herein was to assess the impact of the fallowing component of the Sea Lice Action Plan.

We compared sea louse infestation rates on wild juvenile pink salmon and chum salmon schooling together near three Atlantic salmon farm sites over 3 years (prior to, during, and after the implementation of the Sea Lice Action Plan) and at one farm site during its first 2 years of operation. The null hypotheses were that (1) the number of sea lice per individual wild salmon was no lower during the single year (2003) of fallowing than during the two control years and (2) the number of sea lice per wild salmon did not increase in the second year of operation at the new farm site.

Methods

We selected four fixed locations to describe the interannual variation in sea louse counts. Three sites (1–3 [Glacier, Burdwood, and Licklow, respectively]) were sampled weekly, and one site (H) was sampled once per year (Figure 1). Our sites were selected as the closest locations, outside the farm lease boundaries, where schooling pink salm-

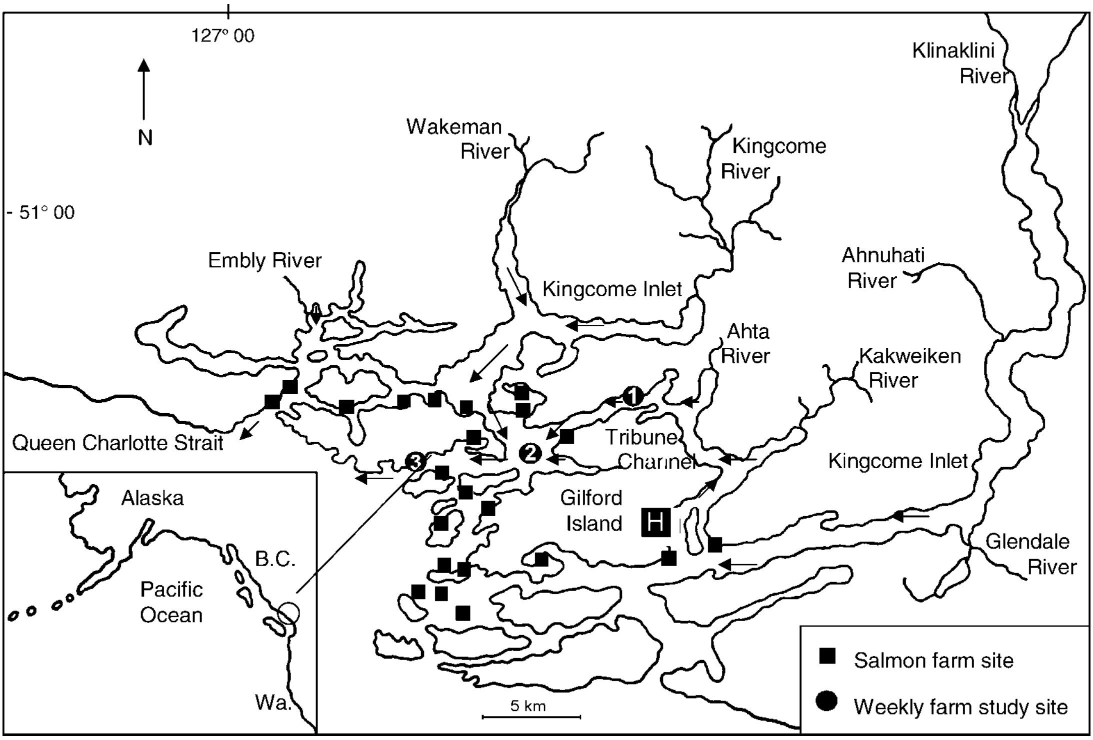

FIGURE 1.—Map of the Broughton Archipelago, British Columbia, showing all major pink salmon−producing rivers, the general direction and course of juvenile pink salmon and chum salmon migration, study sites 1–3 (sampled weekly during 2002–2004) adjacent to three Atlantic salmon farms, study site H (sampled annually in 2003 and 2004) adjacent to a newly established Atlantic salmon farm, and other salmon farm tenures in the area.

on and chum salmon could be reliably found. The weekly sites were 930 m east of farm 1, 830 m south of farm 2, and 610 m west of farm 3 (Figure 1). Farmed Atlantic salmon were present at all the weekly sites in 2002 and 2004, but none were present in 2003. In all years, 20–30 pink salmon and/or chum salmon were collected at each site once per week for 10 weeks from 16 April through 22 June. In 2003, sampling continued through September 13 at site 3, the only site where wild fish persisted at that date. The annual site (Figure 1, H) was 520 m south of an Atlantic salmon farm established in 2003 and 28.2 km east of site 3. Site H was positioned ‘‘upstream’’ of all the other sites in terms of the direction of travel by the juvenile wild salmon. One sample of 70 wild salmon was taken at site H within days of stocking at farm H in 2003, and a second equivalent sample was taken there 1 year later.

A dip net (45-cm diameter; 5-mm knotless mesh) on a 2.45-m pole (after Bailey et al. 1975) was used in 2002 and 2003 to capture the fish from a 6.7-m shallow-draft vessel. Although use of a dip net can introduce bias, such as selecting for weaker fish, this bias would have remained constant throughout the first 2 years (Morton and Williams 2003; Morton et al. 2004). A 15.2 × 1.8 m, 0.63-cm-mesh beach seine was used in 2004 to further ensure that healthy fish were not omitted from our sample. No attempt was made to sample fish from deeper strata of the water column, because juvenile salmon less than 5.6 cm inhabit only near-surface waters (Groot and Margolis 1991). The fish were put immediately into individual Whirlpak bags, placed on ice, and then frozen within hours. The fish were weighed, measured (fork length), and identified to species. Sea lice were observed by means of a dissecting microscope and were categorized by species, age-class, and sex based on the work of Johnson and Albright (1991a). Only *L. salmonis* sea lice were included in this study because this species is of particular concern elsewhere and is of primary concern in this instance as well. The relative length of affixing filament and the occurrence of single or double eyespots were used to distinguish between juvenile

L. salmonis and *Caligus* spp. (as per Schering Plough [www.spaquaculture.com/assets/3–28 sealcfinal.pdf] and Johnson and Albright 1991a). We used the following standard measures of sea louse infestation rates (Margolis et al. 1982): prevalence was the proportion of fish infested with sea lice; intensity was the number of sea lice on each infested host; and abundance was the mean number of sea lice on all potential hosts.

Statistical methods.—The formal analysis was restricted to those sampling weeks for which there were results from each of the weekly sites in 2002–2004. This approach minimized any reliance on restrictive model assumptions that would otherwise have been needed to perform the mathematical equivalent of filling in missing data records.

Abundance data were primarily analyzed by linear mixed models applied to data transformed by the standard transformation $\log_e(y + 0.5)$. Effects associated with individual sampling events at each weekly site (i.e., location × year × week interactions) were included in the model and were specified as random. The resulting inferences treated these items as the primary sampling units. In addition, denominator degrees of freedom were calculated by use of Satterthwaite approximations (Gaylor 1988). Other terms were specified as fixed. Hence, inferences should not be extended to other sites or years. This is appropriate because the sites were chosen specifically for their proximity to farms that were active in 2002, fallowed in 2003, and reactivated in 2004. Calculations were performed by means of the MIXED procedure in the Statistical Analysis System (SAS; SAS Institute 2005).

The modeling procedure used in the analysis was as follows: First, a reasonably full model was fit to the transformed overall sea louse abundances (summed over all sea louse life stages). The model included effects for year, week, location, and all interactions among these three factors. Temperature and salinity, as measured for each sampling location and time, were also included as covariates. Some of these terms were not significant at the 0.05 level. The term with the highest *P*-value was dropped from the model, and the model was then refit to the data. This backward elimination procedure was repeated until all remaining terms in the model were significant at the 0.05 level. In addition, when the year term was retained in the model, specific pairwise comparisons between years were tested. This would normally call for adjustments to statistical decision rules to control experimentwise error rates. However, since only three such comparisons were contemplated for each analysis and since all *P*-values were either less than 0.0001 or greater than 0.2, no decisions required alteration.

TABLE 1.—The number, weight, and fork length of wild pink and chum salmon sampled in the Broughton Archipelago, British Columbia, 2002–2004. Values in parentheses are SEs.

Month	*n*	Weight (g)	Length (cm)
Mar	287	0.37 (0.01)	3.27 (0.02)
Apr	670	0.53 (0.01)	3.85 (0.02)
May	738	1.34 (0.04)	4.85 (0.04)
Jun	631	2.26 (0.06)	5.74 (0.05)

We used a generalized linear model with a logarithmic link and Poisson error variance structure for the fitting of the final model. The generalized linear model was more sophisticated but computationally less stable than the linear mixed modeling procedure. The generalized linear model obviated the need for transforming the data with the arbitrary term (0.5) and served as a useful check on potential inadequacies of the less-sophisticated methodology. The calculations were performed by the SAS macro, GLIMMIX. We present results only for the former model, because our check did not reveal any notable discrepancies between the two approaches.

The analysis was repeated for transformed copepodid abundance and transformed adult abundance data. For the latter analysis, one notable change was made: the year term was forced to remain in the model in case its effect was masked by some other variable that was subsequently removed.

Data from site H were tested independently from other samples. A Mann–Whitney *U*-test was conducted to assess whether median counts of copepodid- and chalimus-I-stage sea lice differed between the year in which Atlantic salmon smolts were reared at farm H (2003) and the year in which adult Atlantic salmon were present (2004).

Escapement numbers for adult pink salmon were provided by Fisheries and Oceans Canada (P. VanWill, Pacific Biological Station, Nanaimo, BC, personal communication).

Results

The overall average weight of pink salmon and chum salmon during March and April of all years combined was 0.37 and 0.53 g, respectively (Table 1). The overall abundance of *L. salmonis* on juvenile pink salmon and chum salmon declined sig-

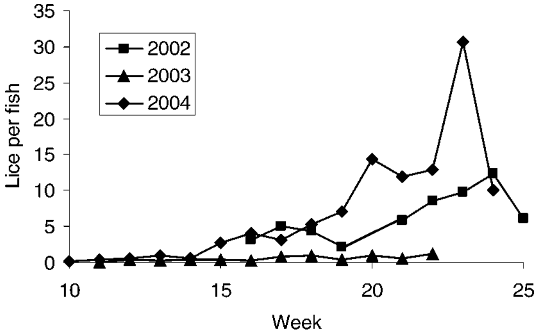

FIGURE 2.—Abundance (mean number/fish) of sea lice *Lepeophtheirus salmonis* (all life stages) on wild pink and chum salmon in the Broughton Archipelago, British Columbia, by week for 2002, 2003, and 2004.

nificantly at the weekly sites between the 2002 and 2003 samples ($P < 0.0001$) and increased again in 2004 ($P < 0.0001$) to a level that was not significantly different from 2002 abundance ($P = 0.27$). These changes were substantial (Figure 2). According to least-squares mean estimates, abundance declined by a factor of 8.9 (95% confidence limits = 5.6 and 14.8) and subsequently increased by a factor of 7.2 (95% confidence limits = 4.4 and 12.4). In addition to the abundance decline in 2003, two other factors were significant (Table 2): week-to-week differences ($P = 0.013$) and surface water temperature ($P < 0.0001$).

The intensity and prevalence of sea lice were also substantially lower in 2003 than in 2002 and 2004 (Table 3). Mean salinity and temperature in all years were within the range favorable to sea louse survival and reproduction (Table 3). At site 1, salinity ranged from 22‰ to 34‰ and temperature ranged from 8.4°C to 16°C. At site 2, salinity ranged from 23‰ to 35‰ and temperature ranged from 8.3°C to 16°C. At site 3, which was furthest from the rivers, salinity ranged from 27‰ to 35‰ and temperature ranged from 8.5°C to 15°C).

Copepodid abundance also declined significantly from 2002 to 2003 ($P < 0.0001$) and rebounded in 2004 ($P < 0.0001$) to a level that was not significantly different from that in 2002 ($P = 0.71$). Although two significant interaction terms (year × location and year × week; Table 2) indicated that year-to-year fluctuations varied among locations and over weeks, the overall year-to-year differences dominated these relatively minor deviations (Figures 3, 4).

There were no significant year-to-year fluctuations in adult sea louse abundance ($P = 0.51$; Table

TABLE 2.—Summary of the primary model fitting for data on sea louse abundance on wild pink and chum salmon in the Broughton Archipelago, British Columbia. For each of the three abundance categories (total, copepodid, and adult) the table provides an ordered list of the factors that were dropped from the model and a list of the variables included in the final model.

Category	Factor	df		*F*	*P*-value	Included?
		Numerator	Denominator			
All sea louse stages	Salinity	1	140	0.01	0.926	No
	Location	2	18.0	0.21	0.815	No
	Week × location	10	17.8	0.71	0.706	No
	Year × location	6	27.5	1.06	0.411	No
	Year × week	10	33.4	1.29	0.274	No
	Week	5	45.0	3.29	0.013	Yes
	Temperature	1	892	57.4	<0.0001	Yes
	Year	2	45.3	62.8	<0.0001	Yes
Copepodids	Week × location	10	18.0	0.64	0.761	No
	Salinity	1	57.3	0.44	0.511	No
	Temperature	1	119	7.05	0.009	Yes
	Year	2	37.8	161	<0.0001	Yes
	Week	5	35.1	14.4	<0.0001	Yes
	Location	2	32.4	5.15	0.011	Yes
	Year × week	10	32.7	5.88	<0.0001	Yes
	Year × location	4	32.1	3.49	0.018	Yes
Adult sea lice	Week × location	10	16.3	1.05	0.449	No
	Year × location	4	25.0	1.58	0.211	No
	Year × week	10	28.6	1.61	0.155	No
	Salinity	1	56.4	1.18	0.283	No
	Location	2	36.5	1.36	0.268	No
	Year	2	39.8	0.68	0.510	No
	Temperature	1	143	33.8	<0.0001	Yes
	Week	5	38.0	15.0	<0.0001	Yes

TABLE 3.—Standard measures of annual sea louse infestation rates on wild salmon in the Broughton Archipelago, British Columbia. Salinity and temperature are also presented. All life stages of sea lice were included in the infestation variables.

Variable	2002	2003	2004
Abundance (sea lice/fish)	6.8	0.64	9.75
Intensity (sea lice/infected fish)	7.4	1.78	10.2
Prevalence (% of fish infected)	91.8	36.1	94.5
Pink salmon, chum salmon (*n*)	491, 68	366, 305	535, 540
Sea surface temperature (°C)	10.9	9.9	12.2
Salinity (‰)	28.6	29.9	30.3

2; Figure 5). More complete results of the model fitting are summarized in Table 2. Unfortunately, the smaller adult abundances were inadequate to generate estimates that were as reliable as those of the other analyses, especially when the generalized linear modeling approach was used. The number of adult sea lice per fish was simply too small. Hence, any marginally significant results should be viewed with caution. Fortunately, the *P*-values associated with year-to-year differences were never marginal, and hence the validity of these key inferences is insensitive to all but the most severe inadequacies in the approximations associated with these tests.

At site H, sea louse abundance rose significantly ($P < 0.0001$) by a factor of 23.8 over farm H's first full year of operation, 2003–2004 (Table 4). Because the two samples were taken at the same time of year, there was no need to use least-squares methods to adjust the raw means. It is possible, nonetheless, that the increase could be attributable to between-sample variation, since only one sample was taken in each year. However, between-sample variation at the other sites was estimated to be less than the fish-to-fish variation within a sample (ratio of variance components = 0.32). Any test for significance based on fish-to-fish variation would therefore have to be only marginally significant for its validity to be suspect. The Mann–Whitney *U*-test was not at all marginal. Hence, we found strong evidence of a substantial increase in sea louse abundance on nearby juvenile pink salmon and chum salmon over the farm's first year of operation.

Fisheries and Oceans Canada estimated the escapement of adult pink salmon to the Broughton Archipelago in 2004 at approximately 900,000 fish, which translates to a greater than 10-fold increase from the parental generation (70,000 fish) (http://wwwsci.pac.dfompo.gc.ca/mehsd/sea_lice/2004/Bulletins/Bulletin3/area12_bulletin3_e.htm). This is in stark contrast to the cohorts that emigrated as juveniles in 2001 and 2002, which experienced 99% and 89% declines in escapement relative to their respective parental generations.

Discussion

Sea louse numbers on juvenile pink and chum salmon were significantly higher at our weekly sites in both years when farmed salmon were present than in the 1 year in which farmed salmon were

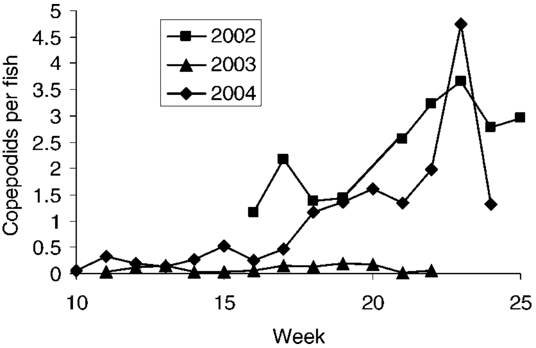

FIGURE 3.—Abundance (mean number/fish) of copepodid-stage sea lice *Lepeophtheirus salmonis* on wild pink and chum salmon in the Broughton Archipelago, British Columbia, by week for 2002, 2003, and 2004.

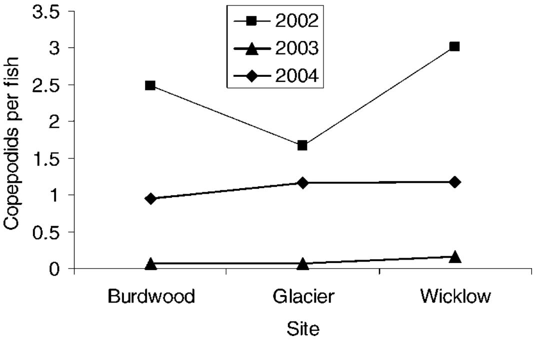

FIGURE 4.—Abundance (mean number/fish) of copepodid-stage sea lice *Lepeophtheirus salmonis* on wild pink and chum salmon collected in the Broughton Archipelago, British Columbia, near three Atlantic salmon farms in 2002, 2003, and 2004.

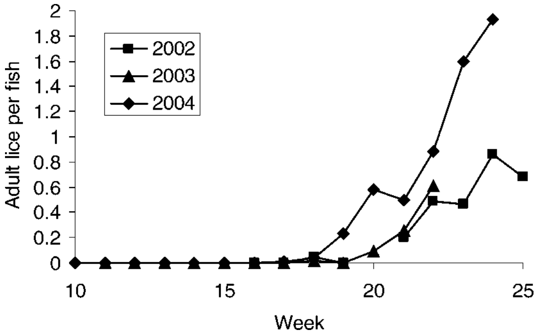

FIGURE 5.—Abundance (mean number/fish) of adult-stage sea lice *Lepeophtheirus salmonis* on wild pink and chum salmon collected in the Broughton Archipelago, British Columbia, by week for 2002, 2003, and 2004.

absent. The high abundance of sea lice on juvenile pink salmon sampled in this area in 2001 (Morton and Williams 2003) was also consistent with our results. Sea louse numbers on wild juvenile salmon at site H were also higher in farm H's second year of operation than in the first year of operation. Sea louse populations did not simply increase when the adjacent farms were stocked; the increase was particularly strong for the earliest attached sea louse phase (copepodid stage) but was absent for the adult phase. This evidence suggests a relationship between stocked Atlantic salmon farms and a source of newly molted sea louse copepodids.

While the presence or absence of farmed Atlantic salmon appears to be the most obvious potential factor related to sea louse abundance, there are other factors to consider. The two most relevant environmental candidate covariates are temperature and salinity. Temperature and salinity remained within the range conducive to sea louse survivorship in all years (Johnson and Albright 1991b; Boxaspen 1997; Tucker et al. 2000). However, the average temperature in 2003 was 1°C colder than that of 2002 and 2°C colder than that of 2004. A temperature fluctuation of this magnitude is large for this area, where the maximum oscillation is 14.2°C (mean = 9.28°C; range = 6.68–20.93°C; 1953–2003) (Dario Stucchi, Pacific Biological Station, personal communication); sea louse abundance appeared to be correlated with the fluctuating temperature. The stepwise modeling procedure indicated that temperature had an effect but could not account for the anomalously low sea louse abundance in 2003. If temperature was responsible for this phenomenon, then we should have seen within-season variation in sea louse numbers, as temperature varied within seasons. Furthermore, within-season variability should have been consistent with the between-year variability. However, sea louse abundance did not increase in 2003, when the temperature increased to 11.8°C (SE = 0.06) from 1 July 1 to 13 September. At site 3, the only site where juvenile pink salmon and chum salmon remained present beyond the month of June, sea louse intensity declined during this time period to 1.15 sea lice/infected fish (SE = 0.16, n = 346). Hence, although temperature was an influential environmental factor, it could not explain key aspects of sea louse dynamics, specifically the anomalously low abundance in 2003, when the farms were fallowed.

Similarly, the higher salinity values recorded in 2003 than in 2002 should have promoted faster population growth of sea lice (Johnson and Albright 1991b; Tucker et al. 2000), but they did not. The stepwise modeling procedure dropped salinity as a candidate covariate.

Knowledge of the prevalence and incidence of sea louse infestation at each Atlantic salmon farm during all study years would have allowed for more detailed, conclusive analyses. However, these data were not available. Currently, data on sea louse infestation for Atlantic salmon farms in BC is limited to single averaged values by area for 2003 and averages for two of the three farms in 2004. Therefore, although we know that the farmed Atlantic salmon were consistently infected with sea lice over this time period, we could not compare data among the farms.

TABLE 4.—Sea louse abundance (sea lice/fish) on wild pink and chum salmon fry sampled in 2003 immediately after first stocking of a new Atlantic salmon farm (H) in the Broughton Archipelago, British Columbia, and abundance 1 year later in 2004. Salinity and temperature are also presented.

Variable	2003	2004
Abundance of all sea lice stages (SE)	0.4 (0.08)	9.6 (1.59)
of copepodids, chalimus I and II (SE)	0.3 (0.07)	7.61 (1.37)
Abundance range	0–2	0–78
Salinity (‰)	31	26
Temperature (°C)	9.3	10.4

Sustained dominance of copepodid-stage *L. salmonis* is symptomatic of infestations near salmon farms (Pike and Wadsworth 1999). When the farmed Atlantic salmon were removed from the farms adjacent to our weekly sites in 2003, the abundance of this infective stage declined 42-fold. By contrast, absolute abundance of adult sea lice did not change significantly from year to year. This would suggest that, coincident with the presence of farmed Atlantic salmon in seawater for a year, a large population of gravid female sea lice must have existed in close proximity to all our weekly sites in 2002 and 2004 and to site H in 2004. When the farmed Atlantic salmon were removed in 2003, evidence of a gravid sea louse population was no longer present.

The earliest attached sea louse phase (copepodid stage) did not dominate the sampled population in 2004. However, at site H (located to the east of our weekly sites), copepodid levels were much higher in 2004 than in 2003. The high contribution of copepodids (78% of total sea lice at site H) would have translated to an increased percentage of the next-oldest stage as the fish sampled at site H moved westward to the closest weekly site. Indeed, this corresponding rise in the chalimus-I and chalimus-II phases was evident in 2004 at site 1, where 51.2% of sea lice were at these stages.

It is valuable to examine why we found 36% prevalence of *L. salmonis* in 2003, when another study (Morton et al. 2004) found virtually no sea lice on juvenile pink and chum salmon sampled beyond the range of farm-origin sea louse larvae (75–400 km from Atlantic salmon farms). Although some farms were fallowed under the Sea Lice Action Plan, there were active Atlantic salmon farms completely encircling our study area, and a passively suspended particle can travel 10 km during one tidal cycle (6 h) in the Broughton Archipelago (Dario Stucchi, Pacific Biological Station, personal communication). Therefore, at distances of 5.3, 18.5, and 33.3 km from active Atlantic salmon farms, none of our three weekly sites were effectively outside the range of salmon previously exposed to farm-origin sea lice and none were beyond the range of farm-origin, drifting, larval-stage sea lice. It is reasonable to expect that a foraging salmon with a fork length of less than 4 cm would require several days to travel 5.3–33.3 km. Therefore, the majority of sea lice acquired at active farm sites upstream should have outgrown the copepodid phase before arriving at our sample sites; we found this to be the case. This would suggest that the few sea lice we did record on wild salmon smolts during the fallow period originated from the active Atlantic salmon farms. Control measures may have been more effective if all farms linked hydrographically were fallowed, as per the area management strategies used elsewhere (Grant and Treasurer 1993; Boxaspen 1997; Jackson et al. 1997).

Our correlational study cannot identify the key component of the Sea Lice Action Plan that resulted in the drastically lower sea louse levels we observed on wild salmon in 2003. While the results indicate that fallowing was a successful mitigation measure, it is difficult to estimate how much of this efficacy was due to fallowing and how much might be attributable to additional actions taken by farmers, such as increased chemical treatment of farmed fish. Potential confounding factors in 2003 include (1) fallowing; (2) chemotherapeutant treatment; (3) an archipelago-wide reduction in the farmed Atlantic salmon population as a result of infectious hematopoietic necrosis outbreaks, as reported by the industry; (4) a potentially smaller wild salmon population caused by the precipitous decline of the parent generation; (5) independent environmental factors; and (6) some combination of these.

We lacked access to essential auxiliary information, including (1) which sites beyond the fallow corridor were not treated and could therefore have served as experimental controls; (2) how many farmed Atlantic salmon were present in each active farm; and (3) the infective capability (i.e., abundance of gravid sea lice) of each farm. This left us with only the imperfect method of comparing sea louse abundance on wild salmon sampled at the same sites among years. As a result, our study can only suggest that fallowing of the Atlantic salmon farms reduced sea louse numbers. What we can say with certainty is that a substantial decline in sea lice occurred when farmed Atlantic salmon were removed from the farms, and no evidence analyzed to date points to any other factor that outcompetes fallowing as the leading potential cause.

If pathogenicity of sea lice is host-size dependent (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997), then the sea louse abundances of 6.8 and 9.7 sea lice/fish, which were recorded in the years when all farms were active, should trigger concern for the survival of fish of the extreme diminutive size in our samples. Indeed, even the lower infestation levels we recorded during implementation of the Sea Lice Action Plan may still have had lethal and sublethal impacts.

FIGURE 6.—Photograph of two wild pink salmon (7.7 and 5.9 cm) captured on 31 May 2003 from site 3 (near Wicklow Point Salmon Farm) at the west end of Fife Sound, British Columbia. The black pinprick-sized marks are holes or ‘‘tracks’’ of gravid female sea lice *Lepeophtheirus salmonis*; gravid *L. salmonis* are also visible (the translucent ‘‘tails’’ are the egg strings).

In addition to known pathogenicity levels, we observed an unreported effect of *L. salmonis*. Paired pinprick ruptures in the skin were associated with the presence of gravid female *L. salmonis* (Figure 6). As each female sea louse was pried from the fish, a pair of the sea louse’s appendages could be seen exiting these holes or tracks. The effect of this tissue damage remains to be studied; indeed, it has not even been reported for the larger Atlantic salmon (Karin Boxaspen, Institute of Marine Research, Norway, personal communication). The skin of juvenile pink salmon and chum salmon may simply be too delicate to support infestation by any mature *L. salmonis*.

Atlantic salmon farms first appeared in the Broughton Archipelago in 1987 (A. Morton, unpublished data). Sea louse infestation was not noted until 2001, and the decline of pink salmon did not occur until 2002. Increases in farmed Atlantic salmon stocking density, farm size, and farm density may be linked to sea louse infestations (Heuch et al. 2005). Farmed Atlantic salmon production in BC rose from 16 metric tons in 1995 to 58 metric tons in 2001 during a moratorium that prevented development of new sites (British Columbia Salmon Farmers Association, unpublished data; MAFF 2004). The stocking density at each site must therefore have increased. Heuch and Mo (2001) reported that the number of farmed Atlantic salmon per unit area has a direct effect on the number of sea lice infesting wild salmon.

Evaluation of potential interactions between sea lice on farmed Atlantic salmon and wild salmon in the North Pacific is needed urgently. High sea louse infection rates in juvenile pink salmon were followed by drastic declines in the number of returning adults in both 2002 and 2003, and these declines did not persist in 2004 for the cohort that experienced a lower sea louse infection rate as juvenile migrants in 2003. Currently, all BC Atlantic salmon farm sites exist exclusively (and are expanding) in habitat utilized by wild salmon during their most vulnerable (i.e., juvenile) life stage. Recently emerged criteria suggest that some coastal areas are inherently unsuitable for salmon farming (Djupvik and Skjelvan 1999). Holst et al. (2000) noted that the common practice of siting salmon farms in confined coastal waters can aggravate both farm infections and wild salmon stock collapse through sea louse amplification on farm stocks. One siting criterion could be based on the size of wild juvenile salmon migrating past the existing or proposed salmon farm sites so as to maximize the separation of juvenile wild salmon from the large farmed salmon populations.

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References

Bailey, J. E., B. L. Wing, and C. R. Mattson. 1975. Zooplankton abundance and feeding habits of fry of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *Oncorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. Fishery Bulletin 73:846–861.

Bakke, T. A., and P. D. Harris. 1998. Diseases and parasites in wild Atlantic salmon (*Salmo salar*) populations. Canadian Journal of Fisheries and Aquatic Sciences 55(Supplement 1):247–266.

Birkeland, K. 1996. Consequences of premature return by sea trout (*Salmo trutta*) infested with the salmon louse (*Lepeophtheirus salmonis* Krøyer); migration, growth, and mortality. Canadian Journal of Fisheries and Aquatic Sciences 53:2808–2813.

Bjørn, P. A., and B. Finstad. 1997. The physiological effects of salmon lice infection on sea trout post smolts. Nordic Journal of Freshwater Research 73: 60–72.

Boxaspen, K. 1997. Geographical and temporal variation in abundance of salmon lice (*Lepeophtheirus salmonis*) on salmon (*Salmo salar* L.). ICES Journal of Marine Science 54:1144–1147.

Boxaspen, K., and T. Næss. 2000. Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. Contributions to Zoology 69:51–55.

Butler, J. R. A., and J. Watts. 2002. Assessing and managing the impacts of marine salmon farms on wild Atlantic salmon in western Scotland: identifying priority rivers for conservation. Pages 93–118 *in* D. Mills, editor. Salmon at the edge. Blackwell Science, Oxford, UK.

Djupvik, H. O., and A. Skjelvan. 1999. Produksjon av laksefisk l Hardangerfjorden: Kva er mogeleg innafor ei berekraftlg ramme? [Farming of salmonids in the Hardangerfjord: what is the potential within a sustainable framework?] Norsk Fiskeoppdrett 18/ 99:30–31.

Gaylor, D. W. 1988. Satterthwaite's formula. Pages 261–262 *in* S. Kotz, N. L. Johnson, and C. B. Read, editors. Encyclopaedia of statistical sciences, volume 8. Wiley-Interscience, New York.

Grant, A. N., and J. W. Treasurer. 1993. The effects of fallowing on caligid infestations on farmed Atlantic salmon (*Salmo salar* L.) in Scotland. Pages 255–260 *in* G. A. Boxshall and D. Defaye, editors. Pathogens of wild and farmed fish: sea lice. Ellis, Horwood, Ltd. Chichester, UK.

Grimnes, A., and P. J. Jakobsen. 1996. The physiological effects of salmon lice infection on postsmolt of Atlantic salmon. Journal of Fish Biology 48:1179–1194.

Groot, C., and L. Margolis. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Håstein, T., and T. Bergsjo. 1976. The salmon lice *Lepeophtheirus salmonis* as the cause of disease in farmed salmonids. Rivista Italiana di Piscicultura e Ittiopatologia A11:3–4.

Heuch, P. A., and T. A. Mo. 2001. A model of salmon louse production in Norway: effects of increasing salmon production and public management measures. Diseases of Aquatic Organisms 45:145–152.

Heuch, P. A., P. A. Bjørn, B. Finstad, J. C. Holst, L. Asplin, and F. Nilsen. 2005. A review of the Norwegian national action plan against salmon lice on salmonids: the effect on wild salmonids. Aquaculture 246:79–92.

Holst, J. C., P. Jakobsen, F. Nilsen, and M. Holm. 2000. Sea lice kill the wild salmon: measures ahead! Institute of Marine Research, Aquaculture Report 2000, Bergen, Norway.

Jackson, D., S. Deady, Y. Leahy, and D. Hassett. 1997. Variations in parasitic caligid infestations on farmed salmonids and implications for their management. ICES Journal of Marine Science 54:1104–1112.

Johnson, S. C., and L. J. Albright. 1991a. The development stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). Canadian Journal of Zoology 69:929–950.

Johnson, S. C., and L. J. Albright. 1991b. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. Journal of the Marine Biology Association of the United Kingdom 71:425–436.

Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology: report of an ad hoc committee of the American Society of Parasitologists. Journal of Parasitology 68:131–133.

MAFF (British Columbia Ministry of Agriculture, Fisheries, and Food). 2003. Sea lice achon plan. Available: http://www2.news.gov.bc.ca/nrm_news_releases/ 2003AGF0004-000137-Attachment1.htm.

MAFF (British Columbia Ministry of Agriculture, Fisheries, and Food). 2004. Aquaculture statistics. Available: http://www.agf.gov.bc.ca/fisheries/index.htm. (June 2005.)

Morton, A., and R. Williams. 2003. First report of the sea louse, *Lepeophtheirus salmonis*, infestation on juvenile Pink Salmon, *Oncorhynchus gorbuscha*, in nearshore habitat. Canadian Field-Naturalist 117: 634–641.

Morton, A., R. Routledge, C. Peet, and A. Ladwig. 2004. Sea lice *Lepeophtheirus salmonis* infection rates on juvenile pink *Oncorhynchus gorbuscha* and chum salmon *Oncorhynchus keta* in the nearshore marine environment of British Columbia, Canada. Canadian Journal of Fisheries and Aquatic Sciences 61: 147–157.

Naylor, R. L., J. Eagle, and W. L. Smith. 2003. Salmon aquaculture in the Pacific Northwest: a global industry with local impacts. Environment 45(8):18–39.

Parker, R. R., and L. Margolis. 1964. A new species of parasitic copepod, *Caligus clemensi* sp. nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. Journal of the Fisheries Research Board of Canada 21:873–889.

PFRCC (Pacific Fisheries Resource Conservation Council). 2002. 2002 advisory: the protection of Broughton Archipelago pink salmon stocks, appendix 1, annex 2. Report to the Minister of Fisheries and Oceans and the British Columbia Minister of Agriculture, Food, and Fisheries. Available: www.fish.bc.ca. (June 2005.)

Pike, A. W., and S. L. Wadsworth. 1999. Sea lice on salmonids: their biology and control. Advanced Parasitology 44:234–337.

SAS Institute. 2005. SAS OnlineDoc 9.1.3. SAS Institute, Cary, North Carolina. Available: http://support.sas.com/onlinedoc/913/docMainpage.jsp.

Tucker, C. S., C. Sommerville, and R. Wooten. 2000. The effect of temperature and salinity on the settlement and survival of copepodids of *Lepeophtheirus salmonis* (Krøyer, 1837) on Atlantic salmon *Salmo salar* L. Journal of Fish Diseases 23:309.

Tully, O., W. R. Poole, and K. F. Whelan. 1993. Infestation parameters of *Lepeophtheirus salmonis* (Kroyer) (Copepod: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquaculture and Fisheries Management 24:545–555.

Tully, O., and K. F. Whelan. 1993. Production of nauplii of *Lepeophtheirus salmonis* (Krøyer) (Copepoda: Caligidae) from farmed and wild salmon and its relation to the infestation of wild sea trout (*Salmo trutta* L.) off the west coast of Ireland in 1991. Fisheries Research 17:187–200.

Wootten, R., J. W. Smith, and E. A. Needham. 1982. Aspects of the biology of parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongates* on farmed salmonids and their treatment. Proceedings of Royal Society of Edinburgh, Section B 81:185–197.