Response of the Sea Louse *Lepeophtheirus salmonis* Infestation Levels on Juvenile Wild Pink, *Oncorhynchus gorbuscha*, and Chum, *O. keta*, Salmon to Arrival of Parasitized Wild Adult Pink Salmon

ALEXANDRA MORTON[1] and ROB WILLIAMS[2]

[1] Raincoast Research Society, 13 Cramer Pass, Simoom Sound, British Columbia V0P 1S0 Canada email: wildorca@island.net

[2] Pearse Island, Box 193, Alert Bay, British Columbia V0N 1A0 Canada

Morton, Alexandra, and Rob Williams. 2006. Response of the sea louse *Lepeophtheirus salmonis* infestation levels on juvenile wild Pink, *Oncorhynchus gorbuscha*, and Chum, *O. keta*, salmon to arrival of parasitized wild adult Pink Salmon. Canadian Field-Naturalist 120(2): 199-204.

Recent recurring infestations of Sea Lice, *Lepeophtheirus salmonis*, on juvenile Pacific salmon (*Oncorhynchus* spp.) and subsequent annual declines of these stocks have made it imperative to identify the source of Sea Lice. While several studies now identify farm salmon populations as sources of Sea Louse larvae, it is unclear to what extent wild salmonid hosts also contribute Sea Lice. We measured Sea Louse numbers on adult Pink Salmon (*Oncorhynchus gorbuscha)* migrating inshore. We also measured Sea Louse numbers on wild juvenile Pink and Chum salmon (*Oncorhynchus keta*) migrating to sea before the adults returned, and as the two age cohorts mingled. Adult Pink Salmon carried an average of 9.89 (SE 0.90) gravid lice per fish, and thus were capable of infecting the adjacent juveniles. Salinity and temperature remained favourable to Sea Louse reproduction throughout the study. However, all accepted measures of Sea Louse infestation failed to show significant increase on the juvenile salmon, either in overall abundance of Sea Lice or of the initial infective-stage juvenile lice, while the adult wild salmon were present in the study area. This study suggests that even during periods of peak interaction, wild adult salmon are not the primary source of the recent and unprecedented infestations of Sea Lice on juvenile Pacific Pink and Chum salmon in the inshore waters of British Columbia.

Key Words: Sea Lice, *Lepeophtheirus salmonis* Pink Salmon, *Oncorhynchus gorbuscha* Chum Salmon, *O. keta,* salmon farm, British Columbia

The sea louse *Lepeophtheirus salmonis* is a common salmon-specific parasite (Nagasawa et al. 1993; Kabata 1973). While their preferred Pacific host is the Pink Salmon (*Oncorhynchus gorbuscha*) (Nagasawa 1987; Nagasawa et al. 1993), *L. salmonis* is found on all species of Pacific salmonids, as well as Atlantic Salmon (*Salmo salar*), Sea Trout (*Salmo trutta trutta*), Rainbow Trout (*Salmo gairdneri*) and Artic Charr (*Salvelinus alpinus*). Once considered benign (Boxshall 1974; Nagasawa 1987; Berland 1993), *L. salmonis* is now a significant problem species on farmed salmon (Pike and Wadsworth 1999; Johnson et al. 2004). Salmon farms are a series of floating net pens attached to the shoreline or anchored in the nearshore. Salmon arrive from hatcheries and are fed in these pens for 18-24 months, then harvested and sold as food. All farm salmon in our study area were Atlantic Salmon.

Optimal salinity for *L. salmonis* survivorship and reproduction is 30‰ (Johnson and Albright 1991b), with copepodids tolerating salinities as low as 15‰ (Pike and Wadsworth 1999). *L. salmonis* hatch into a free-swimming naupliar stage directly from egg strings attached to the female's body (Johnson and Albright 1991a). The interval from hatching to infective capability (copepodid stage) is approximately 4 d at 10ºC and 2 d at 15°C (Johnson and Albright 1991b). The copepodid stage is the first attached stage, thus abundant presence of this stage signals a local source of gravid Sea Lice and a host salmonid population. When wild salmon enter freshwater to spawn, the attached *L. salmonis* experience decay of life-processes leading to death (Hahnenkamp and Fyhn 1985; McLean et al. 1990; Johnson and Albright 1991b). As one would expect from an obligate parasite, there have been no reports of *L. salmonis* over-wintering off-host in the nearshore marine environment.

While early studies on juvenile wild Atlantic salmonids *Salmo salar* and *Salmo trutta* make no mention of parasitism by *L. salmonis* (Heuch and Mo 2001); Sea Lice are now reported in high numbers on wild European salmonids adjacent to farms (Tully et al. 1993; Birkeland 1996). Historically, researchers did not look specifically for *L. salmonis* on juvenile Pacific salmon in the inshore environment. However, the seminal works on juvenile Pink and Chum salmon (Healey 1978, 1982; Parker 1965; Parker and Vanstone 1966) did note the presence of the smaller sea louse, *Caligus clemensi* (Parker and Margolis 1964). *C. clemensi* is a generalist non salmon-specific parasite that has been reported on 13 species of fish (Jones and Nemec 2004*). It seems reasonable that if *Caligus* was noted, then the larger, more conspicuous *L. salmonis* would also have been reported had it been historically present on juvenile Pink salmon.

Today, Sea Lice are reported on juvenile Pink and Chum salmon in some areas of coastal British Colum-

bia and appear associated with salmon farming (Morton and Williams 2003; Morton et al. 2004; Morton et al. 2005; Krkosek et al. 2005; Krkosek et al. 2006). The impact of Sea Lice is host-size dependant (Grimnes and Jakobsen 1996; Bjørn and Finstad 1997) and this is critical to Pink and Chum salmon as they enter the marine environment at the smallest size of any salmonid. Pink and Chum Salmon weigh less than one gram in the study area (Broughton Archipelago) throughout March and April (Morton et al. 2005), and are without protective scales (A.M. personal observations). Juvenile Pink and Chum salmon exhibit prolonged inshore residency from March to September (Healey 1978). If some adult wild salmonids occur inshore year round, their numbers are low. The largest wild host population for *L. salmonis* are the mature Pink Salmon that enter coastal waters in July and run through September (Heard 1991).

Thus, in a natural setting, a system has evolved that isolates returning adult salmon from the most juvenile stage conspecifics. Juvenile Pink and Chum salmon do not share habitat with a significant *L. salmonis* host population until July, by which time they have grown to weigh several grams. Krkosek et al. (2005) report that after initial infection by salmon farms, juvenile salmon schools will re-infect themselves some weeks later as lice mature and being reproducing.

Salmon farming has altered this arrangement by siting 26 salmon farms in the nearshore environment of the Broughton Archipelago (Figure 1), each site holding potentially 1 million Atlantic Salmon (Naylor et al. 2003), a known host for *L. salmonis*. In July of 2003 there were approximately 6 million Atlantic Salmon among the 17 farm sites leased by Stolt Sea Farms with another nine sites leased by another company (Heritage) that did not report numbers (Orr *in press*). Orr (*in press*) reports an average of 2.2 – 9.2 gravid Sea Lice per salmon on the 6 million farm Atlantic Salmon for 2003-2004.

While salmon farms are now a recognized source of Sea Lice, this study further illuminates this subject by measuring the response in Sea Louse numbers on wild juvenile salmon to the arrival of a large population of this Sea Louse's preferred host, the adult Pink Salmon. We hypothesise that if wild adult salmon were a substantial source of Sea Lice on juvenile salmon in the study area, then the number of copepodid *L. salmonis* should rise in response to the arrival of in-migrating adult Pink Salmon. To test this, we first measured lice levels on juvenile Pink Salmon, then looked for evidence of copepodid Sea Louse recruitment subsequent to wild adult Pink Salmon arrival in the area.

Understanding the mechanisms of *L. salmonis* infestation of inshore juvenile wild salmon and the relative importance of both wild and farm lice sources has become crucial to both wild and farm salmon management. This study provides analysis on a previously unreported aspect of the dynamic between adult and juvenile Pacific salmon and Sea Lice.

Methods

This study took place in the 400 km^2 Broughton Archipelago in British Columbia. There are seven major Pink Salmon rivers and 26 Atlantic Salmon farm sites between the rivers and the open waters of Queen Charlotte Strait (Figure 1). The Broughton Archipelago's 200 km of inlets and 90 km of passages and small bays makes it ideal marine rearing habitat for juvenile Pink and Chum salmon (Healey 1978). Within this region, Fife Sound (Figure 1) through Tribune Channel is considered a primary route used by returning adult Pink Salmon (G. Neidrauer, Fisheries and Oceans Canada, Fisheries Patrolman, General Delivery, Simoom Sound, BC V0P 1S0 personal communication).

Juvenile Pink and Chum salmon were sampled once each week at the same sampling location from 1 June 2003 through 19 September 2003 (Figure 1). The salmon farm at this site was fallow, and without any farm salmon. A 50' × 4' beach seine of ⅛" mesh was used in June and a 120' × 8' beach seine with ¼" mesh and a ⅛" bunt was used for the remainder of the study. Sample size ranged from 20 to 30 fish per week. The juvenile salmon were placed individually in Whirlpak™ bags immediately after capture, laid on ice and then frozen. They were later examined under 30× magnification and the number of Sea Lice, their age-class and sex were determined and recorded using published taxonomic keys (Johnson and Albright 1991a). Adult female lice were classified as either virgin or gravid as per the Norwegian method of counting sea lice (Karin Boxaspen, Researcher, Institute of Marine Research, Bergen, Norway). Results are reported only for the salmon-specific Sea Louse, *L. salmonis*.

We used three independent methods to estimate the timing of the wild adult Pink Salmon return to the study area. First, we used measured Pink Salmon catch-per-unit directly at our juvenile salmon sampling site. We used two fishing rods with lures known to attract Pink Salmon in this area (A.M. personal observations). We fished for 166 hook-hours between 4 June and 19 September.

The second method compared our catch-per-unit-effort analysis with the timing of the adult return reported by Fisheries and Oceans Canada (DFO) as determined by their enumeration program on the known Pink Salmon-bearing streams nearby (Figure 1). The Fisheries and Oceans Pink Salmon enumeration flights began in the second week of August and continued through the end of October. Finally, a tourism operator in the Glendale River watershed (Figure 1) had guides on the river for 3 days in May, 11 days in June, 23 days in July, 28 days in August, and reported to us when Pink Salmon were first sighted.

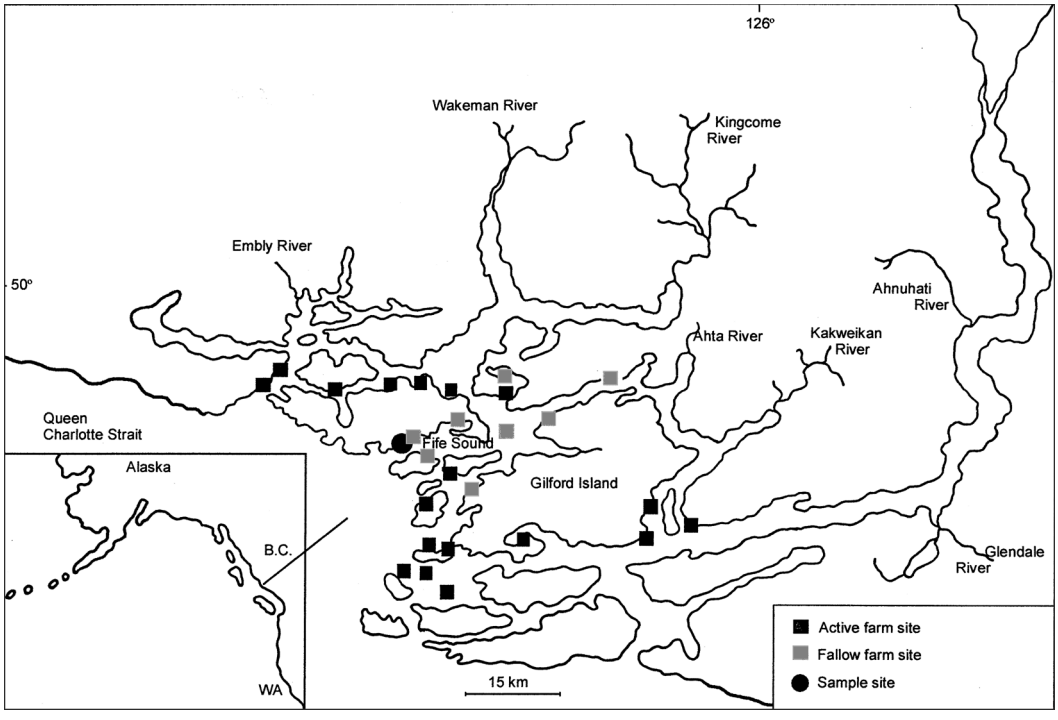

FIGURE 1. Study area, the Broughton Archipelago, showing major Pink Salmon rivers, salmon farm sites and status, and study site.

The adult salmon caught in this study were lifted from the water without a net and kept free from contact with any surface in order to reduce loss of lice. They were examined immediately for Sea Louse counts, stages and species identification using a hand lens. We estimated the infective capability of the returning adult salmon by counting gravid female sea lice per fish: a standard measure used to trigger de-lousing treatment of farm salmon to reduce infective capability and lower sea lice numbers on adjacent juvenile wild salmon (Heuch and Mo 2001).

Louse counts were not expected to follow a normal distribution. Rather than transforming the data, we made comparisons using Mann-Whitney U tests (MWU; the non-parametric equivalent of a two-sample t-test) in GraphPad version 3.05 by InStat (GraphPad Software Inc., 5575 Oberlin Drive, #110, San Diego, California 92121 USA).

We used the following standard measures of louse infestation rates (Margolis et al. 1982): prevalence = the proportion of fish infested with lice; intensity = the mean number of lice on each infected fish; and abundance = the mean number of lice on the entire sample.

Results

We fished for 47 "hook-hours" 4 June through July, without catching one adult Pink Salmon. We fished for 119 hook-hours in August until 19 September, and beginning on 4 August, caught 50 adult Pink Salmon at an average of 0.78 Pink Salmon/hook-hour (SE = 0.10, n = 17 fishing sessions, range 0-1.4 Pink Salmon/ hook-hour). Given that there was no variance in the 12 June/July fishing sessions (all 12 failed sessions to catch a fish), a Wilcoxon signed-rank test was conducted to assess whether the median catch-per-unit-effort in August and September differed significantly from the observed zero catch-per-unit-effort in June and July. The sum of positive ranks was 136, indicating that the median value was significantly greater than 0 ($P < 0.0001$).

Fisheries and Oceans Canada estimated that 188 730 Pink Salmon entered the Broughton Archipelago rivers from mid-August through September 2003 (G. McEachen, Fisheries and Oceans Canada, chief of conservation management for the central coast, Central Coast Area Office, 315-940 Alder Street, Campbell River, British Columbia V9W 2P8, personal commu-

TABLE 1. Mass, length, and sea lice infection of Pink and Chum salmon collected during the two sampling periods with average sea surface temperature and salinity for both time periods. "Total" signifies all *L. salmonis* and "cope" signifies copepodite *L. salmonis* only.

Period	n	Grams (SE)	Size cm (SE)	Salt % (SE)	Temp °C (SE)	Prevalence %		Abundance (SE) Range		Intensity (SE)	
						Total	Cope	Total	Cope	Total	Cope
June – July	623	6.94 (0.15)	8.47 (0.03)	29.1 (0.03)	12.1 (0.01)	43.0	7.2	1.20 (0.12) 0-42	0.079 (0.012) 0-2	2.79 (0.26)	1.09 (0.018)
August – 19 September	145	21.16 (0.57)	12.38 (0.10)	30.8 (0.11)	11.1 (0.05)	40.0	4.8	1.00 (0.25) 0-33	0.048 (0.018) 0-1	2.50 (0.58)	1 (0)

nication). This would indicate that Pink Salmon were present seaward of the rivers and within the study area for 2-3 weeks prior to the end of the second week of August, when they were first identified in the rivers, through September. We cannot be certain how many of these fish passed the sampling site, but Fife Sound is considered the primary migration corridor for adult Pink Salmon (Neidrauer, personal communication).

The tour operator and his guides looked for Pink Salmon on each of their tours, but did not see Pink Salmon in the largest Pink Salmon river in the study area, the Glendale River, until 20 August (H. Pattinson, owner/operator, Tide Rip Tours, 1660 Robb Avenue, Comox, British Columbia V9M 2W7 Canada, personal communication). Again, assuming that adults took two to three weeks to migrate through the Broughton Archipelago to reach the Glendale watershed, one would expect that the adults reached our sampling location in early August. In fact, these three methods show very good agreement, and all point to a best estimate return date for large numbers of wild adult Pink Salmon in the first days of August. Consequently, we estimate that juvenile Pink and Chum salmon were introduced to louse-infected adults around the first day of August.

We divided the pre- and post-exposure stages into two sampling periods: 1 June to 31 July, and 1 August to 19 September. As one would expect from a rapidly growing cohort, the juvenile salmon increased in both length and weight throughout the study (Table 1). The average seawater temperature and salinity varied slightly between the two sampling periods, but remained at all times within optimal range for *L. salmonis* (Table 1). The mean number of gravid lice on returning adult Pink Salmon was 9.31 (SE 0.93).

No measure of total Sea Louse occurrence varied between the sampling periods (Table 1) (abundance – MWU statistic: 43186, P = 0.4088; intensity – MWU statistic: 7153.5, P = 0.3412). As well, no measure of copepodite Sea Lice varied significantly (abundance – MWU 44072; P = 0.6448).

Given that there was no variance in the observed intensity of copepodid infection on juvenile salmon in the later sampling period (that is, all seven fish infected with copepodites carried a single copepodid louse), a Wilcoxon signed-rank test was used to assess whether the median early-season intensity differed from the observed intensity of 1 louse/fish in the later sampling season. The mean intensity of infection on the 45 fish infected with copepodites in the earlier sampling season was 1.09 (SE 0.043, median 1.00, range 1-2). This was not significantly greater than the 1 louse/infected fish observed in the later sampling season (sum of all signed ranks = 10, after correcting for ties; $P = 0.13$).

Discussion

The number of returning adult Pink Salmon carrying gravid Sea Lice was on the order of two hundred thousand, with approximately nine gravid Sea Lice per fish and thus we estimate that the juvenile Pink and Chum salmon in Fife Sound were exposed to the infective capability of close to two million gravid female Sea Lice. However no marked increase above the pre-existing background infection levels could be detected on juvenile salmon after the adult fish arrived in the area.

Even if the total number of Sea Lice failed to increase on juvenile salmon after the return of adult Pink Salmon, an increase in the proportion of lice at the copepodid stage would have indicated arrival of a source of Sea Lice that exceeded ambient levels. However, no increased copepodid settlement was observed. In fact, prevalence of copepodids was slightly lower after the adult Pink Salmon returned, which is as one would expect from an epizootic living out the course of its infestation. In the early, i.e., pre-exposure sampling period, 7.2% of juveniles sampled carried at least one copepodid, and after the adult Pink Salmon returned, 4.8% of juveniles sampled carried at least one copepodid. The juvenile salmon were traveling west out of an area where gravid Sea Lice occurred on farm salmon.

The decline we recorded in copepodite Sea Lice is contrary to what Krkosek et al. (2005) found where infected juvenile salmon re-infected each other as their farm-origin Sea Lice matured. The difference in

findings might be a result of geography. Krkosek et al. (2005) was conducted within the confined waterway of Tribune Channel, whereas this work occurred in an area of much greater flush at the archipelago edge. There are no juvenile Pink and Chum salmon in Tribune Channel in August. The juvenile Pacific salmon out-migrations and adult salmon in-migrations are generally timed such that interaction between the two cohorts occurs in open waters.

Ocean temperature and salinity were unlikely to have hindered parasite growth or transfer during August and September. Mean sea-surface temperature fell 1°C during the adult spawning in-migration, which had the potential to slow reproduction, but salinity increased, which favoured reproduction. Both values, however, were well within optimal range necessary for Sea Lice reproduction (Johnson and Albright 1991b; Boxaspen and Naess 2000; Tucker et al. 2000). Consequently, we conclude that the juvenile hosts in our study simply failed to respond measurably to exposure to a large influx of infested wild adult salmon.

We fully expected louse loads to increase when the adult Pink Salmon returned. We know that Sea Lice must be transmitted among wild salmon. The fact that Louse numbers did not increase in our study was surprising, and leads us to conclude that, compared to ambient levels of farm-origin parasitism in the Broughton Archipelago, the contribution of wild-source lice was negligible. We suspect the higher numbers of salmon-specific Sea Lice on juvenile Pink and Chum salmon in June and July originated from the population of several million, farmed Atlantic Salmon in the Broughton Archipelago in high-density open-net pens. Orr (*in press*) reports an average of several gravid sea lice per each of 6 million farm salmon during our study period, which translates into a very large number of copepodite sea lice occurring to the east of our study site area, but not at our study site itself which was adjacent to an empty salmon farm.

Why we did *not* find an increase in Sea Lice in August and September is perplexing. The mandatory 2-4 day dispersal term in the plankton layer likely limits Sea Louse recruitment rates to allow both parasite and host to thrive. Perhaps there were not enough wild adult Pink Salmon in the Broughton Archipelago for measurable Sea Lice transmission to the juvenile cohort in the face of such dispersal. Perhaps Sea Louse recruitment is an infrequent event between free-ranging salmon, and our sample size was too small to capture it. Perhaps the duration of exposure to adult Pink Salmon was not long enough or the dynamic of juvenile and adult salmon travelling in opposite directions with juveniles along the shoreline and adults mid-channel suppressed copepodid recruitment. Perhaps some small increase in parasite load did occur, but natural variability and small sample size left us with insufficient statistical power to detect this small effect above the ambient levels in the Broughton Archipelago. Morton et al. (2004) reported that in areas without salmon farms juvenile Pink Salmon were not infested with *L. salmonis*. Therefore, it is possible that in the absence of farm salmon the 4.8% prevalence we found on juvenile salmon in August and September could have been entirely or partially in response to arrival of the wild adult Pink Salmon.

Likely our inability to detect response in Sea Louse populations to returning adult Salmon was some combination of these. The lack of observed recruitment of new Sea Lice suggests that some mechanism has evolved to suppress transfer of lice from returning adults to out-migrating smolts in a naturally functioning ecosystem. Because Sea Louse pathogenicity is host-size dependant, protecting the smaller salmon from *L. salmonis* infestation would have clear evolutionary benefits, particularly for the Pink and Chum salmon that go to sea smaller than any other salmonid.

If exposure to abundant Sea Lice infested wild adults did not trigger a measurable increase in Sea Lice loads on juvenile Pink and Chum salmon, then this leaves the other, less abundant (if at all present), overwintering inshore wild salmon species poor candidates for explaining the enormous and recent spring *L. salmonis* outbreaks in the Broughton Archipelago.

Clearly, more extensive research is urgently needed. In the meantime, our study suggests that wild Pink Salmon do not appear to be the primary source of the high Sea Lice infestations reported on wild juvenile Pink and Chum salmon in the Broughton Archipelago. They may, however, be the primary source infecting the farm salmon and thus pose a risk to the industry. We conclude the most obvious source of *L. salmonis* on juvenile Pink and Chum salmon in the Broughton Archipelago is the stationary population of several million, farmed Atlantic Salmon.

Acknowledgments

This research was supported in part by Tides Canada. RW is supported by the Jane Marcher Foundation. Our thanks to Ron Turner for assistance in beach seining.

Documents Cited (marked * in text)

Jones, S., and **A. Nemec.** 2004. Pink Salmon Action Plan: sea lice on juvenile salmon and on some non-salmonid species in the Broughton Archipelago in 2003. Canadian Science Advisory Secretariat Research Document. Available from: http://www.dfo-mpo.gc.ca/csas/Csas/publications/ResDocsDocRech/2004/2004_105_e.htm.

Literature Cited

Berland, B. 1993. Salmon lice on wild salmon (*Salmo salar* L.) in western Norway. Pages 179-187 *in* Pathogens of wild and farmed fish: Sea Lice. *Edited by* G. A. Boxshall and D. Defaye. Ellis Horwood, London, United Kingdom.

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 Science 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., and **T. Naess.** 2000. Development of eggs and the Planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. Contributions to Zoology 69: 51-55.

Boxshall, G. A. 1974. Infections with parasitic copepods in North Sea marine fishes. Journal of Marine Biology Association. UK 54: 355-372.

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

Hahnenkamp, L., and **H. J. Fyhn.** 1985. The osmotic response of salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae), during transition from sea water to fresh water. Journal of Comparative Physiology B 155: 357-365.

Healey, M. C. 1978. The distribution, abundance and feeding habits of juvenile Pacific salmon in Georgia Strait, British Columbia. Fisheries Marine Service (Canada) Technical Report 78. 49 pages.

Healey, M. C. 1982. The distribution and residency of juvenile Pacific salmon in the Strait of Georgia, British Columbia, in relation to foraging success. *Edited by* B. R. Melteff and R. A. Neve. Proceedings of the North Pacific Aquaculture Symposium Alaska Sea Grant Report 82: 61-69.

Heard, W. 1991. Life history of pink salmon. Pages 121-230 *in* Pacific salmon life histories. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, British Columbia.

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.

Johnson, S. C., J. W. Treasurer, S. Bravo, K. Nagasawa, and **Z. Kabata.** 2004. A review of the impact of parasitic copepods on marine aquaculture. Zoological studies 43: 229-243.

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 Marine Biology Association U.K. 71: 425-436.

Kabata, Z. 1973. The species of *Lepeophtheirus* (Copepoda: Caligidae), a parasite of fishes from the Pacific coast of North America. Journal of Fisheries Research Board of Canada 30: 729-759.

Krkosek, M., M. A. Lewis, and **J. P. Volpe.** 2005. Transmission dynamics of parasitic sea lice from farm to wild salmon Proceedings of the Royal Society, Series B doi: 10.1098/rspb.2004.3027.

Krkosek, M., M. A. Lewis, A. B. Morton, L. N. Frazer, and **J. P. Volpe.** 2006. Epizootics of wild fish induced by farm fish. Proceedings of the National Academy of Sciences103: 15506-15510.

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.

McLean, P. H., G. W. Smith, and **M. J. Wilson.** 1990. Residence time of sea louse, *Lepeophtheirus salmonis* K., on the Atlantic salmon, *Salmo salar* L., after immersion in fresh water. Journal of Fish Biology 37: 311-314.

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 Science 61: 147-157.

Morton, A. B., R. Routledge, and **R. Williams.** 2005. Temporal patterns of sea lice infestation on wild Pacific salmon in relation to the fallowing of Atlantic salmon farms. North American Journal of Fisheries Management 25: 811-821.

Nagasawa, K. 1987. Prevalence and abundance of *Lepeophtheirus salmonis* (Copepod: Caligidae) on high-sea salmon and trout in the North Pacific Ocean. Bulletin of the Japanese Society of Scientific Fisheries 53: 2151-2156.

Nagasawa, K., Y. Ishida, M. Ogura, K. Tadokora, and **K. Hiramatsu.** 1993. The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on six species of Pacific salmon in offshore waters of the North Pacific Ocean and Bering Sea. Pages 166-178 *in* Pathogens of wild and farmed fish: Sea Lice. *Edited by* G. A. Boxshall and D. D. Defaye. Ellis Horwood, New York.

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

Orr, C. (*in press*). Estimated sea louse egg production from Marine Harvest Canada (Stolt) farmed salmon, Broughton Archipelago, British, Columbia, Canada, 2003-2004. North American Journal of Fisheries Management.

Parker, R. R. 1965. Estimation of sea mortality rates for the 1961 brood-year pink salmon of the Bella Coola area, British Columbia. Journal of Fisheries Research Board of Canada 22: 1523-1554.

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.

Parker, R. R., and **W. E. Vanstone.** 1966. Changes in chemical composition of central British Columbia Pink Salmon during early sea life. Journal of Fisheries Research Board Canada 23: 1353-1384.

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

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.

Received 17 April 2005
Accepted 9 February 2007