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Exceptional marine survival of pink salmon that entered the marine environment in 2003 suggests that farmed Atlantic salmon and Pacific salmon can coexist successfully in a marine ecosystem on the Pacific coast of Canada

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Juvenile pink salmon that entered a marine ecosystem along the eastern margin of Queen Charlotte Strait in 2003 and returned as adults in 2004 had very high marine survival. The early seaward migration and midsummer rearing in 2003 were in an area containing 16 active Atlantic salmon farms. Two species of sea louse, *Lepeophtheirus salmonis* and *Caligus clemensi*, were commonly found on farmed salmon and juvenile Pacific salmon during the early rearing period of the pink salmon. Mobile *L. salmonis* and *C. clemensi* were most abundant on farmed Atlantic salmon from February to May and on pink salmon in June. Chalimus stages were the dominant stages on pink salmon to the end of May. Mobile stages of *C. clemensi* were the dominant stages and species of sea louse on farmed Atlantic salmon and pink salmon at about the same time in June. DNA studies showed that local juvenile pink salmon were in the area until August. The exceptional returns of the brood year suggest that pink salmon populations and farmed Atlantic salmon coexisted successfully during 2003 within an environment that included sea lice and farmed Atlantic salmon. The processes responsible for the high marine survival cannot be identified with certainty, but they could include increased freshwater discharge in 2003, which may have resulted in lower salinity less favourable to sea louse production, increased inflow of nutrient-rich water to the study area, and the introduction of a Provincial Action Plan that required mandatory louse monitoring and established a fallowed migration corridor for pink salmon.

Keywords: management, marine survival, pink salmon, salmon farms, sea lice.

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Introduction

Farmed Atlantic salmon (*Salmo salar*) is currently British Columbia's largest agricultural export with an average annual production of 61 000 t between 1998 and 2004. This compares with an annual average catch of all species of wild Pacific salmon of 24 000 t for the same period. Salmon farming in British Columbia is also a contentious issue (Hume *et al.*, 2004; Morton *et al.*, 2004). Some researchers have proposed that salmon farms in British Columbia are a source of sea lice that infect juvenile (first marine year) pink salmon (*Oncorhynchus gorbuscha*) with such intensity that the productivity of the population is threatened (PFRCC, 2002; Morton *et al.*, 2004; Krkošek *et al.*, 2005; Morton *et al.*, 2005). In 2002, concern was expressed that the low return of pink salmon was the result of sea louse infestations during the spring 2001 outmigration from the Broughton Archipelago (http://www.agf.gov.bc.ca/fisheries/health/sealice_BA_monitoring.htm). The controversy over salmon farms in the study area prompted a Provincial Action Plan that fallowed a number of farms in the northern Tribune Channel and Fife Sound corridor for the entire smolt migration period from March to the end of June 2003 and that required mandatory monitoring of sea lice, a programme that remains active. Although some farms were fallowed, the biomass of farmed salmon reared in the Broughton Archipelago has remained almost constant since 1999.

In the North Atlantic, sea lice are a concern to the salmon farming industry because of damage to farmed fish and the cost of control (Boxshall and Defaye, 1993; Pike and Wadsworth, 1999). Sea lice on farmed salmon in the North Atlantic have also been linked to damage to wild salmonids such as sea trout, *Salmo trutta* (Tully *et al.*, 1993; Heuch *et al.*, 2005). However, evidence of these associations remains unclear (ICES, 1997). Despite the difficulty of scientifically defining the impact of sea lice on farmed salmon and on the health of wild salmonids, it is recognized that sea louse production on salmon farms should be controlled (Anon., 1998; Heuch and Mo, 2001).

The public controversy surrounding salmon farming in British Columbia has stimulated a number of continuing impact studies (Morton *et al.*, 2004; Brooks, 2005). Laboratory studies that measure the impact of sea lice provide information at the individual fish level for conditions specific to the experiment. Usually, researchers are careful to report that such results should not be used to define responses in the natural environment, particularly at the population level (Bjorn and Finstad, 1997; Bjorn, 2002). Assessing the impact of sea louse parasitism on juvenile pink salmon by studying the population dynamics of pink salmon provides information at the population level, but the lack of controls makes it difficult to define the important linkage between levels of sea lice infestation and salmon survival. Therefore, examinination of the impact of sea lice on pink salmon and other species of salmon should include both laboratory studies and studies in the natural environment. This study provides information about the marine survival and population dynamics of pink salmon juveniles that were in an area of salmon farms in 2003.

Our study focused on the 2002 brood year of pink salmon. Adults that produced this brood year spawned in 2002, and fry entered the ocean in spring 2003. These juveniles were in the area of salmon farms before moving into the open ocean. The migration timing of the juvenile pink salmon out of the coastal areas is not known, and we demonstrate in this paper that some juveniles remained through the summer. Mature adult pink salmon returned to their spawning rivers in late summer 2004.

Pink salmon life cycle

Pink salmon are the most abundant of Pacific salmon. They have a fixed age-at-maturity of two years and one year class. The two-year life cycle results in distinct populations spawning in odd-numbered or even-numbered years. These odd- and even-year lines may or may not both occur in the same river system. Usually, one line is dominant, but the dominance can switch. Pink salmon numbers can build gradually to a very large abundance and then drop suddenly to a very small abundance (Bugaev, 2002; Gritsenko, 2002). The dominant odd-year line in western Kamchatka, for example, collapsed abruptly in 1983 and switched to even years (Bugaev, 2002). There was a 97% reduction in the odd-year line from an average of about 60 million fish, apparently as a consequence of overcrowding on spawning grounds and density-related effects in the ocean (Gritsenko, 2002). In general, the escapements of the odd-year line (excluding the Fraser River) have declined in the general area from Queen Charlotte Sound to southern Vancouver Island (Riddell and Beamish, 2003). At the same time, there have been large increases in the even-year lines. Riddell and Beamish (2003) reported that in the 1990s there was an increase of approximately 500% in the escapements of the even-year lines, while there was a decrease of about 40% in the odd-year lines. This indicates that there have been recent large-scale natural changes in pink salmon populations that occur in trends, although the mechanisms responsible are not understood.

Life cycle of sea lice

Until recently, few published studies provided reliable estimates of the numbers, species, and stages of sea lice on Pacific salmon. Chalimus stages of *Lepeophtheirus salmonis* and *Caligus clemensi* were first reported on pink salmon fingerlings in the Central Coast area by Parker and Margolis (1964). Higher levels of *L. salmonis* were first reported on juvenile pink salmon in the Broughton Archipelago in 2001 by Morton and Williams (2003) and every year since (Morton *et al.*, 2004, 2005; Krkošek *et al.*, 2005; Morton and Routledge, 2005). Beamish *et al.* (2005) contributed to our understanding of sea lice in the nearshore environment with the first comprehensive assessment of sea louse abundances on five species of adult Pacific salmon in a coastal ecosystem. In the study area, two species of sea lice are commonly found on the farmed Atlantic salmon and on Pacific salmon (*Oncorhynchus* sp.). The developmental stages of *L. salmonis* were reported by Johnson and Albright (1991) and of *C. clemensi* by Kabata (1972). The life cycles consist of ten stages not including the egg, which hatches into a nauplius. There are two free-swimming nauplius stages followed by the infective copepodid stage. If the copepodid finds a host, it develops into the chalimus, which has four stages and is tethered to the fish by a frontal filament. The sea louse becomes mobile on the fish after it develops into the first pre-adult stage and then, after a second pre-adult stage, develops into the adult stage.

Study area

The study area includes Queen Charlotte Strait and the Broughton Archipelago. Queen Charlotte Strait is the body of water between the northern end of Johnstone Strait and Queen Charlotte Sound (Figure 1). The coast of British Columbia has 58 inlets of 18.5 km or more in length (Pickard, 1961). East of Queen Charlotte Strait, two inlets, Knight and Kingcome inlets, extend from braided waterways into the Pacific Range of the Coastal Mountain Range. The area was unofficially designated as the "Broughton Archipelago" (Figure 1b) in the 1960s. All but one salmon farm in our study are in the Broughton Archipelago (Figure 1b and c). We define the study area as extending through the Broughton Archipelago to the eastern margin of Queen Charlotte Strait (as shown in Figure 3), but not into Queen Charlotte Strait as shown in Figure 1b.

Salmon farms were first established in the area in 1987. In the mid-1990s, there were 13 active farms, and by 2000 there were approximately 20 active farms (Figure 1c). We use the standard definition of an active farm as a site that is stocked with salmon at any time. The production year for the salmon farms is 1 July−30 June. These farm sites produced approximately 19 000 t (dressed, head on) of Atlantic salmon in the production year 2002/2003, and 18 950 t in 2003/2004.

Methods

Adult pink salmon returns and marine survival

The assessment of the number of adult pink salmon returning to spawning rivers (escapement) was made by government employees or contractors who visually counted fish during flights over the rivers or on foot surveys beside the rivers,

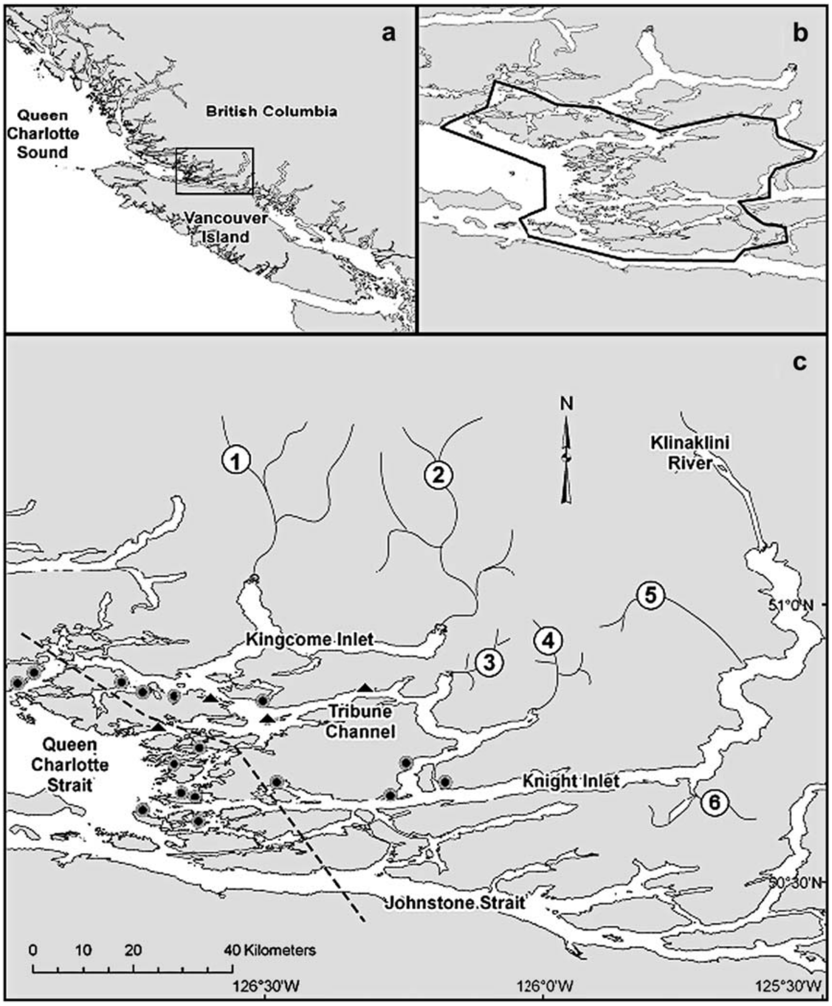

Figure 1. Maps showing (a) location of the study area on the British Columbia coast; (b) location of the area referred to as the Broughton Archipelago; (c) study area showing the location of the six major populations of pink salmon (1 = Wakeman River, 2 = Kingcome River, 3 = Ahta River, 4 = Kakweiken River, 5 = Ahnuhati River, and 6 = Glendale Creek), and the 16 active farm sites (◉) and four fallowed farm sites (▲) in early 2003 (http://www.agf.gov.bc.ca/fisheries/health/sealice_BA_monitoring.htm). The dashed line provides a separation between coastal and inland salmon farm sites.

or both. Error estimates are not available. Escapement estimates, therefore, are useful indices of the number of adult salmon that potentially spawn in their natal rivers. There are 27 rivers and streams containing pink salmon in the fish farm area. The main populations of pink salmon originate in a small number of these rivers (Figure 1c). We estimate that the six populations associated with the six rivers used in this study accounted for approximately 95% of the total pink salmon entering the ocean in 2003 and 92% of the pink salmon returning to spawn from 1990 to 2004 (Table 1). Accurate assessment of marine survival requires that the catch and escapement be determined. Pink salmon catches in regional fisheries were separated into areas of origin by the Department of Fisheries and Oceans (DFO), using stock identification techniques or in proportion to escapements. We reassigned the catches for the combined populations in the study area to the six major populations as a percentage of their escapement (Table 1). The catch ranged from 2% to 53% of the escapement. Since 2000, the percentage ranged from 7% to 16%. Data used in these calculations are available from DFO at sweetingr@pac.dfo-mpo.gc.ca.

The comparison of marine survival began with adults returning in 1990, because two of the major populations, Glendale Creek and Kakweiken River, had artificial spawning channels added in 1988 and 1989, respectively, which presumably improved freshwater production, making it problematic to compare escapement estimated before and after this date. In all calculations, 1999 estimates were excluded because data were incomplete. The exclusion of 1999 escapement data prevents calculation of marine survival estimates for the 1997 and 1999 brood years. Marine survival was calculated using the brood year escapement and assuming an equal number of male and female adults. Some adults would not spawn and some would be eaten by predators, such as bears. Estimates of this mortality for pink salmon were not available, so we assigned a conservative estimate of pre-spawn mortality of 5%, which reduced the number of females by 2.5%. Average fecundity was estimated using the observations of Hunter (1959). Hunter (1959) also estimated an egg retention rate of 1.5%, which we applied to determine the total number of eggs. We reviewed the range of egg-to-fry survival estimates in Heard (1991) and selected a mid-range estimate of 5.6% to calculate the number of fry that entered the ocean. Marine survival for a brood year was the resulting production in the following year divided by the calculated number of fry that entered the ocean. The calculation for the 2002 brood year that entered the ocean in 2003 and returned in 2004 is shown in Table 2. Calculations for the other years followed the procedure in Table 2.

Sea lice on farmed Atlantic salmon

Monitoring of sea lice on farmed Atlantic salmon became mandatory in 2003 under the Provincial Action Plan, and sampling was conducted according to the general guidelines identified in http://www.agf.gov.bc.ca/fisheries/health/sealice_BA_monitoring.htm. Monitoring was bimonthly from March to June in 2003 and monthly in

Table 1. Escapements, catch, and production (escapement plus catch) estimates for pink salmon from the six reference populations (rivers) in the study area, and 21 other populations (rivers) in the study area for 1990–2004. Escapement data were not available for 1999. Escapement and catch estimates are recorded as numbers of fish. Individual river escapements have been rounded to the nearest hundred fish, while total escapement for the six populations has been rounded to the nearest thousand fish. Escapement information for the 21 other populations was not available for 2004.

	Escapements									
Return Year	Ahnuhati River	Glendale Creek	Ahta River	Kakweiken River	Kingcome River	Wakeman River	Total escapement for six populations	Estimated catch for six populations	Production for six rivers	Escapement for remaining 21 populations
1990	250 000	350 000	40 000	600 000	200 000	250 000	1 690 000	1 876 000	3 566 000	137 000
1991	4 000	17 500	3 000	37 175	3 000	1 300	66 000	56 000	122 000	8 000
1992	85 700	700 000	17 150	600 000	31 500	24 000	1 458 000	681 000	2 140 000	41 000
1993	25 000	200 000	5 400	112 000	125	4 700	347 000	356 000	703 000	24 000
1994	70 000	192 000	27 000	510 000	20 500	13 600	833 000	131 000	964 000	18 000
1995	35 000	80 000	5 800	114 000	1 450	2 700	239 000	118 000	357 000	7 000
1996	75 000	430 000	60 000	816 000	45 600	198 000	1 625 000	38 000	1 663 000	96 000
1997	3 500	320 000	800	18 000	500	30	343 000	151 000	494 000	24 000
1998	80 000	500 000	64 000	737 000	111 750	170 000	1 663 000	57 000	1 720 000	108 000
1999	—	—	—	—	—	—	—	—	—	—
2000	500 000	760 000	55 000	1 700 000	76 000	369 600	3 461 000	968 000	4 429 000	175 000
2001	2 800	1 350 000	22 000	9 600	1 100	900	1 386 000	266 000	1 652 000	25 000
2002	8 200	18 200	600	11 100	1 200	29 300	69 000	8 000	77 000	61 000
2003	4 200	161 900	900	16 600	400	2 600	187 000	17 000	203 000	10 000
2004	78 400	662 200	13 000	65 000	23 700	69 400	912 000	66 000	978 000	—

Table 2. Example of the method used to estimate the marine survival of the pink salmon returning in 2004.

	Number
The 2002 escapement for six major pink salmon populations	68 568
Female escapement assuming a 50:50 male:female ratio	34 285
Predation and other prespawning mortality in freshwater estimated at 5% (no source)	1 714
Effective female escapement	32 570
Average fecundity (Hunter, 1959)	1 593
Egg retention (Hunter, 1959)	1.5%
Total number of eggs spawned	51.1 million
Average egg-to-fry survival (Heard, 1991)	5.6%
Total number of fry entering the ocean in 2003	2.86 million
The 2004 escapement for six major pink salmon populations*	911 662
The 2004 commercial catch of six major pink salmon populations*	66 368
Marine survival of the pink salmon returning in 2004* ((911 662 + 66 368/ 2 860 000) × 100)	34.2%

*http://www-sci.pac.dfo-mpo.gc.ca/mehsd/sea_lice/2004/2004_intro_e.htm.

January, February, and from July to September. Twenty fish from each of three pens were caught in a box-seine and individually anaesthetized in MS222. Two pens were selected randomly, and one pen was standard. Independent audits checked the monitoring conducted by industry staff. Each fish was examined on all sides in a shallow, water-filled container. Magnification was not used, and copepodids were not recorded. The number of chalimi was recorded without identifying the species. The numbers of mobile *L. salmonis* and mobile *C. clemensi* were recorded. Any lice in the sampling containers were identified and added to the total counts according to the percentages of the two sea louse species observed on the fish. Fish were returned to the original pen after examination. There was some variation in the procedure early in 2003 because this was the beginning of the programme. For example, ten fish could have been selected from the ten pens or more than 20 fish from one pen. There was also more frequent sampling on some farms requiring only one monthly sample. In some cases, the provincial protocol exempted the farm from taking a sample if it would cause the fish excessive stress. Because of the variation in sampling periods, we averaged the results and report the results monthly. The theoretical number of samples during our study is 152. The actual sample consists of 130 samples or 86% of the theoretical number.

Sea lice on juvenile pink salmon

Jones *et al.* (2006) and Jones and Nemec (2004) reported on a study of sea lice on juvenile pink salmon in the fish farm area. From 3 March to 13 June 2003, they examined 7124 pink salmon for sea lice. Pink salmon were captured at more than 115 sites throughout the area using a beach-seine and adjacent sets with a purse-seine. These Broughton Archipelago samples were collected each week for 15 weeks. In this paper, we compare the monthly averages of sea louse prevalence, intensity, and abundance from their study with those from farmed salmon. The criteria used to identify skin damage caused by sea lice on trawl-caught juvenile pink salmon were not applied to juvenile pink salmon captured in seines.

Trawl survey for older juvenile pink salmon

Juvenile pink salmon were caught in August 2003 in Queen Charlotte Strait and the fish farm area using a large trawl (Beamish and Folkes, 1998). Trawl studies were conducted primarily to determine if pink salmon from the study area remained and reared in the study area during summer and to examine fish for skin damage caused by sea lice. All sets lasted 30 min during daylight. Catch per unit effort (cpue) of juvenile pink salmon was calculated and standardized at 1 h. Large floats were attached to the headrope to ensure that the net fished at the surface. All salmon in the catch were identified to species and examined for skin lesions resulting from sea lice. Skin lesions were defined as areas where skin was removed and muscle exposed or skin was partially removed, exposing necrotic tissue and haemorrhaging at the margins of the lesions. The total catch was sampled when the catches were small. For larger catches, samples were taken from the top of a container without selection. Subsamples were measured for length, examined for sea lice, and tissue samples for DNA analyses were collected.

DNA sampling and analysis

An opercular punch was taken from juvenile pink salmon in the trawl catches and placed in 70% ethanol for DNA analysis. The stock of origin of the pink salmon was estimated using the techniques described in Withler *et al.* (2004). Previous studies using allozymes showed that it was possible to detect population structure in pink salmon (Beacham *et al.*, 1985, 1988). Recent DNA techniques provide a method for determining more fine-scale structure (Beacham *et al.*, 2005, 2006). It follows that DNA methods provide more resolution than allozyme estimates, and it is DNA estimates that are used to distinguish the populations of Broughton Archipelago region pink salmon from pink salmon of other regions. The number of samples analysed was limited by the cost of the analysis. Baseline samples of pink salmon from the odd-year line were also collected in the rivers.

River discharge

The major rivers flowing into the Broughton Archipelago are Wakeman River, Kingcome River, Kakweiken River, Glendale Creek, Ahnuhati River, and Klinaklini River. Maximum river discharge is during summer because most water originates from melting glaciers and snow. Complete records of discharge are available only for the Klinaklini River, which is the largest river in the salmon farm area. Flow data were obtained from the Water Resources Branch (Station #08GE002) of Environment Canada. We include river discharge in our study because changes in discharge can affect surface salinities, which affect sea louse production (Brooks, 2005).

Results

Adult pink salmon returns and marine survival

Pink salmon returned to the six rivers in both even- and odd-numbered years from 1992 until 2004. The even-year line was dominant during the study period and remained dominant in all years except for 2002 in Glendale Creek (Table 1). The largest catch and escapement of 3 566 000 and 4 429 000 occurred in the return years 1990 and 2000, respectively (Table 1). The smallest catches and escapements of 122 000, 77 000, and 203 000 occurred in the 1991, 2002, and 2003 return years, respectively (Table 1). Marine survival (Figure 2) was high at 25.5% and 34.2% for the return years 1993 and 2004, respectively. Marine survival was low at 0.1% and 0.4% in the return years 2002 and 2003, respectively. Marine survival in the remaining years, 1990–2004, ranged from 1.2% to 6.6%. There was a large increase in pink salmon marine survival in all six populations in 2004 compared with 2002. The increase in the marine survival of pink salmon returning in 2004 compared with those returning in 2002 was 0.19%–5.68% in the Wakeman River, 0.02%–14.01% in the Kakweiken River, 0.04%–23.01% in the Ahnuhati River, 0.04%–48.46% in the Kingcome River, 0.03%–49.83% in the Ahta River, and 0.06%–87.13% in Glendale Creek. The average percentage increase in marine survival for the six populations was 1480%.

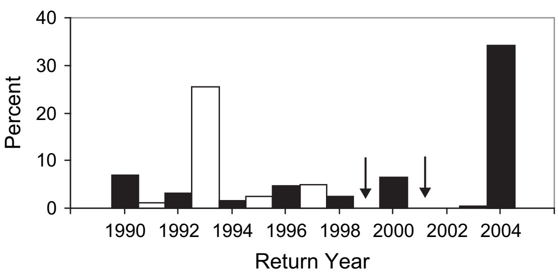

Figure 2. Average marine survival percentages for the combined six reference populations of pink salmon (*O. gorbuscha*) in the Broughton Archipelago. Solid bars are the even-year lines and open bars are the odd-year lines. The brood year is two years earlier than the return year shown. Data were not complete for 1999, so marine survival in 1999 and 2001 (arrows) could not be estimated for the six populations.

Sea lice on farmed salmon

The number of farms in which Atlantic salmon were sampled for sea lice in 2003 increased from nine in February to 12 in March, remained constant at 13 from April to the end of July, and declined to eight in September (Table 3). The percentage of farms sampled changed as farms were fallowed or previously fallowed farms received fish. Salmon farms actively harvest fish, move fish, add smolts, treat with Slice, and on occasion, will fallow a site. For example, in March 2002, three of 19 farms were fallow. Three other farms had received treatment for sea lice from January to February. In March 2003, four of 20 routinely active farms were fallow. Three of these farms were treated with Slice between January and the end of February, and three more were treated in March. In March 2004, four of 20 normally active farms were fallow. Four farms had been treated with Slice in February 2004. In summary, there were 16 active farms in March in each year from 2002 to 2004, but the location of the stocked farms was not constant.

The percentage of farms sampled for sea lice averaged 86% and ranged from 56% to 100% between February and September. In all, 8630 fish were sampled. The mean prevalence of sea lice was 64.4%, ranging from 46.4% to 85.3%. Prevalence declined gradually from 85.3% in February to 46.4% in August, then increased in September to 58.0%. The intensity also declined from 21.0 in February to between 3.3 and 4.8 from June to September (Table 3). In February, 64% of the sea lice were in the chalimus stage, declining to 19% in August. In September, the proportion of chalimi increased to 42%. The average abundance of all mobile sea lice declined steadily from 6.5 in February to 1.2 in July, with a small increase in August and September. At the same time, there was a change in the dominant species of mobile sea lice, from *L. salmonis* in February and March to *C. clemensi* in June, July, and August. There were 11 samples that, when averaged monthly, had average sea louse intensities greater than ten in one month. These came from six different farms located throughout the coastal area, and one was inland of the dashed line (Figure 1c). If only mobile stages were considered, there were 11 samples from the same six coastal farms and one inland farm with an average intensity of more than five mobile sea lice of both species in the monthly assessment.

Sea lice on juvenile pink salmon from the nearshore and purse-seine survey

Sea lice were observed on approximately 24% of pink salmon from mid-March to mid-June, and the infestations were caused by *C. clemensi* and *L. salmonis*. Pink salmon ranged in fork length from 3.1 to 7.3 cm over the study period (Jones and Nemec, 2004). Chalimus stages were dominant on juvenile pink salmon in March and April, accounting for approximately 93% of sea louse abundance

Table 3. The prevalence, intensity, and abundance of sea lice on Atlantic salmon in farms in 2003.

Month	Number of active farms	Number of samples from farms	Number of fish sampled	Prevalence (%)	Intensity	Average number of sea lice (abundance)	Chalimus Total Abundance	Chalimus Total %	Mobile Total Abundance	Mobile *L. salmonis* Abundance	Mobile *L. salmonis* %	Mobile *C. clemensi* Abundance	Mobile *C. clemensi* %
Feb	16	9	516	85.3	21.0	17.9	11.4	63.8	6.5	6.3	35.3	0.2	0.9
Mar	16	19	1 260	72.1	12.5	9.0	4.4	49.5	4.6	3.5	38.3	1.1	12.2
Apr	17	24	1 364	72.4	7.1	5.2	1.1	21.0	4.1	2.1	40.0	2.0	39.0
May	15	23	1 720	69.9	7.0	4.9	1.5	30.1	3.4	1.9	39.0	1.5	29.9
Jun	13	19	1 530	59.9	4.8	2.8	0.8	29.0	2.0	0.3	11.1	1.7	59.9
Jul	14	15	980	47.7	3.3	1.6	0.4	22.8	1.2	0.5	30.6	0.7	46.6
Aug	13	13	820	46.4	4.8	2.2	0.4	19.1	1.8	0.5	24.3	1.3	56.6
Sep	12	8	440	58.0	4.4	2.3	1.0	41.7	1.3	0.8	37.3	0.5	21.0
Average				64.4	8.1	5.2	2.1	40.0	3.1	1.8	34.7	1.3	25.3
Total		130	8 630										

(Table 4). The intensity of infestation was almost constant during the study. There was an increase in the percentage of mobile stages in June, when they represented approximately 73% of sea louse abundance. Mobile *C. clemensi* were almost 50% more abundant than mobile *L. salmonis* at this time (Table 4). Overall, copepodids represented approximately 30% of all non-mobile *L. salmonis* stages on pink salmon. The average prevalence and intensity of mobile *L. salmonis* were 6.2 and 1.2 (range 1−5), respectively. The average prevalence and intensity of mobile *C. clemensi* were 4.1 and 1.2 (range 1−6), respectively. Mobile *L. salmonis* were observed on pink salmon from mid-April to June and primarily from samples collected in Tribune Channel and west towards Queen Charlotte Strait (Figure 1).

Juvenile pink salmon trawl survey

The catches were separated into the Broughton Archipelago, including some areas farther up the inlets, and Queen Charlotte Strait, west of a boundary just outside the eastern margin of the strait, as shown in Figure 3. From 30 July to 8 August, 28 sets were conducted in Queen Charlotte Strait and 44 sets in the Broughton Archipelago, including waters farther up the inlets. In the Broughton Archipelago and Queen Charlotte Strait, 674 and 449 juvenile pink salmon were caught, respectively. The cpue of pink salmon was highest in the Broughton Archipelago (Figure 3). The average fork length of pink salmon was similar in Queen Charlotte Strait (12.9 cm) and the associated mainland inlets (13.4 cm).

All pink salmon were examined for skin lesions, and no fish had any wounds that exposed muscle. A subsample of 628 pink salmon collected from both areas was examined for sea lice using magnification. The prevalence of all species of sea louse was 10.4%, and the intensity was 1.25 (range 1−5). Chalimus stages represented 28.8% and copepodid stages 7%. Mobile stages represented 64.2% of all sea lice, and 90% of all sea lice stages were *L. salmonis* and 10% were *C. clemensi*.

DNA analysis

DNA analysis was conducted on 278 juvenile pink salmon collected from Queen Charlotte Strait ($n = 50$) and the Broughton Archipelago ($n = 228$). The baseline data for DNA included stocks from four of the major rivers (Glendale Creek, Kakweiken River, Wakeman River, and Ahnuhati River). The Kingcome River and Ahta River stocks were not in the baseline. Thus, the percentage of pink salmon determined to be from the study area probably would have been larger if the other two main stocks were in the baseline. The DNA analysis determined that at least 65.4% ± 10.8 s.d. of the pink salmon from the Broughton Archipelago catches were from Glendale Creek, Kakweiken River, Wakeman River,

Table 4. The prevalence, intensity, and abundance of sea lice on juvenile pink salmon in 2003.

Month	Number of fish	Number infested	Total sea lice	Prevalence (%)	Intensity	Average number of sea lice (abundance)	Chalimus Total Abundance	%	Mobile *L. salmonis* Abundance	%	Mobile *C. clemensi* Abundance	%
3–29 Mar	1 296	170	282	13.1	1.7	0.22	0.20	94	0.01	6	0.00	1
30 Mar–26 Apr	1 793	388	744	21.6	1.9	0.42	0.39	93	0.03	6	0.00	1
27 Apr–31 May	3 218	883	1 385	27.4	1.6	0.43	0.29	67	0.10	24	0.04	9
1–13 Jun	1 131	343	541	30.3	1.6	0.48	0.13	26	0.14	30	0.21	43

and Ahnuhati River, four of the six rivers used in our study. The sample in Queen Charlotte Strait was from the single large catch shown in Figure 3. Pink salmon from the Ahnuhati River, Glendale Creek, Kakweiken River, and Wakeman River constituted 52.2% ± 12.1 s.d. of the sample.

River flow

There was a pattern in the January–June discharge from 1977 to 2003 (Figure 4). The period 1977–1990 was characterized by low flows, followed by continuous high flows from 1991 to 1998 (Figure 4). Beginning in 1999, they were low, with the average flow anomaly for the six-month period about two times lower than that for the years 1991–1998 (Figure 4). The flow was larger in 2003 and more typical of flows in the mid-1990s.

Discussion

The six populations used in our analysis demonstrated high marine survival between the time they entered the study area in spring 2003 and their return in autumn 2004. Heard (1991) reported a range of marine survival percentages from 1.7% to 4.7% for five North American stocks. For pink salmon in the Fraser River, catches and escapement

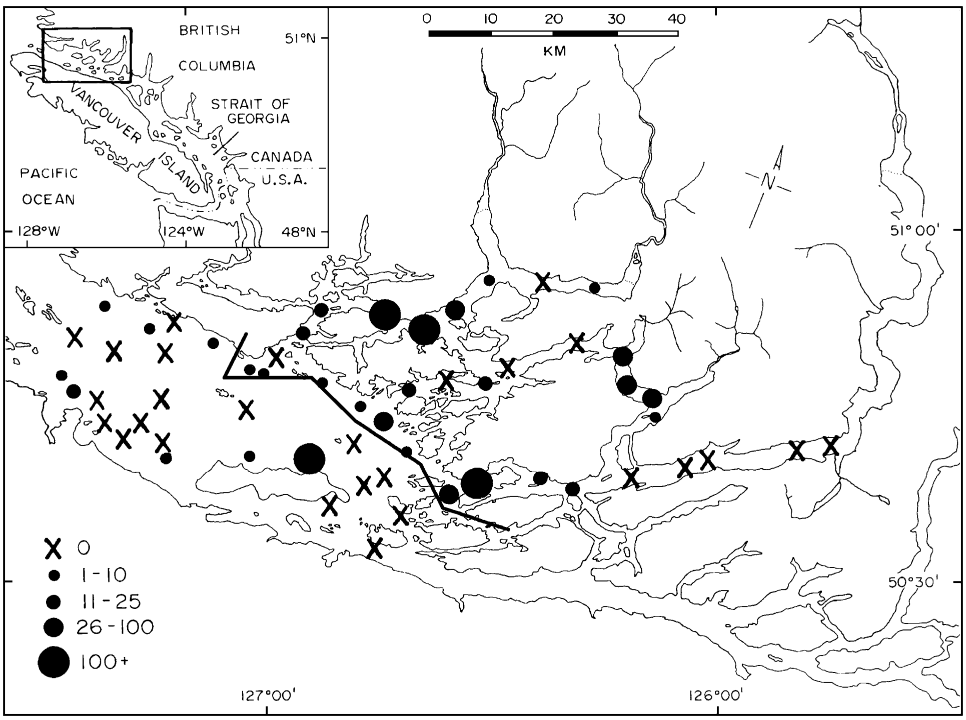

Figure 3. Catches of juvenile pink salmon in the August 2003 trawl survey. The index of catch is shown in the bottom left of the figure. In some areas, trawl catches are the average of several sets. The line partitions catches within the study area and along the immediate coast of the study area from Queen Charlotte Strait.

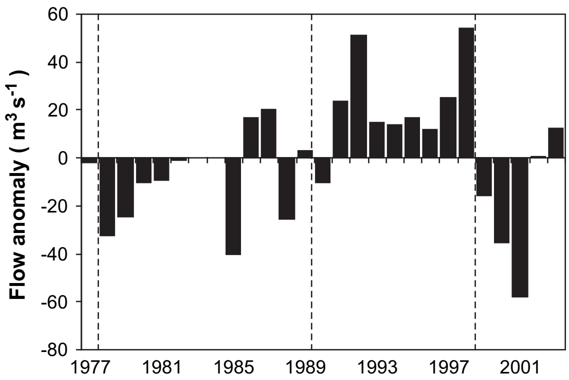

Figure 4. Anomaly of average January–June flow for the Klinaklini River, 1977–2003. The vertical dashed lines identify the regime shift years in 1977, 1989, and 1998 (Latif and Barnett, 1994; Hare and Francis, 1995; Zhang *et al.*, 1997; Beamish *et al.*, 1999).

data were combined to provide estimates of marine survival ranging from 0.8% to 5.4% (Heard, 1991). The combined estimate of 34.2% marine survival for this brood year is exceptional compared with the estimates in Heard (1991), and may be the highest marine survival of pink salmon recorded. The estimate is so large that it is logical to question its validity. An obvious source of error is the escapement estimates in 2002 and 2004. Perhaps the 2002 estimate was too low and the 2004 estimate too high. It is impossible to confirm these estimates, but the determinations were made by persons experienced at estimating escapements. The estimated catch was small in both years, representing 6.8% and 10.8% of the total returns in 2004 and 2002, respectively, so would not be a major source of error. We conclude that the marine survival estimate of 34.2% is an index of very high marine survival, but probably not an accurate measurement.

Mobile *L. salmonis* and *C. clemensi* were commonly found on farmed salmon from February to May. The intensity of all species of sea louse on farmed salmon declined from February to May and remained at 2–3 sea lice per fish until September. Chalimus stages declined from February to April, remaining at one sea louse per fish or less until September. The species composition of mobile sea lice changed from primarily *L. salmonis* in February and March to *C. clemensi* from June to August. A decline in the non-mobile stage of sea lice on wild Pacific salmon in June corresponded to a decline in non-mobile and mobile sea lice on farmed salmon in June.

In 2003, no farms were treated with Slice after March or before the end of September, so changes in abundance or species composition of the sea lice after the treatments corresponded with decreasing salinity during peak glacier run-off into the rivers. In September, there was an increased percentage of chalimus stages that was probably a result of the large numbers of sea lice transported into the area by adult Pacific salmon (Beamish *et al.*, 2005). In general, the greatest abundances of sea lice were in farms situated along the eastern margin of Queen Charlotte Strait, and not inland. The increased abundances could be the result of higher salinity in this area or the transport of nauplii seawards down the inlets, as reported by Brooks (2005).

Two species of sea louse occurred on farmed salmon. *C. clemensi* is also commonly found on about 14 other species of fish in the area (Parker and Margolis, 1964), and immature *L. salmonis* was reported recently on the stickleback, *Gasterosteus aculeatus* (Jones *et al.*, 2006), although very few were gravid. Recognizing that there are other sources of both species of sea louse besides farmed salmon (Kabata, 1979; Jones *et al.*, 2006), it becomes apparent that infestations of sea lice on farmed and wild Pacific salmon can come from a number of sources.

Beginning in March, juvenile pink salmon entered the ocean free of lice (Jones *et al.*, 2006). As expected, their initial infestation at that time was dominated by chalimus stages, which were also abundant on farmed salmon, with an additional average of 6.5 mobile lice, which included gravid females. The dominance of chalimus stages persisted on pink salmon until June, indicating that the source of the two species of sea louse remained in the area. Mobile stages were the dominant stages on farmed salmon from February until April and May, with about equal representation of each species. It was not until June that mobile stages dominated on pink salmon. At this time, *C. clemensi* was the most abundant mobile stage on both pink and farmed salmon. Understanding the association between sea lice produced on farmed salmon and observed on pink salmon is confounded by the dominance of *C. clemensi*, because it is also found on a number of species in the area (Parker and Margolis, 1964). However, as mobile *C. clemensi* are better adapted to free swimming than *L. salmonis*, it is more difficult to track the host source.

Sea lice counts from trawl-caught fish may be underestimates because of the capture method, but the prevalence of 10.4% shows that sea lice remain on juvenile pink salmon in the coastal areas and most probably are carried into the open ocean when these pink salmon migrate from the coast in late summer and autumn. Transport of sea lice into the open ocean may ensure that sea lice abundance increases following the reduction in Pacific salmon abundance in the previous year, when adults returned to spawn. Even though there are no published studies comparing sea louse abundances on juvenile Pacific salmon caught in trawls with those caught individually, counts of sea lice from fish caught in trawls are useful indicators of the distribution of sea lice throughout the Subarctic Pacific (Wertheimer *et al.*, 2003; Bugaev, 2005).

The trawl survey in early August and the results of the DNA analysis showed that pink salmon from the six populations in our study were in the Broughton Archipelago area and in Queen Charlotte Strait. A survey in late September 2003 showed that reduced abundances of juvenile pink salmon and other Pacific salmon were still present (RJB, unpublished data), confirming that the study area was an important rearing area for pink salmon through August.

River discharge affects surface salinity in the study area, and sea louse survival to the infective stage is poor at low salinity (Johnson and Albright, 1991; Pike and Wadsworth, 1999). Beginning in 1999, there were reduced freshwater discharges into the study area, as indicated by the discharge pattern from the Klinaklini River. The change in flow patterns is consistent with the large-scale change in climate and ocean patterns in 1998 that affected marine ecosystems beginning about 1999 (Hare and Mantua, 2000; McFarlane *et al.*, 2000; Beamish *et al.*, 2004; King, 2005). The pattern of river discharge is consistent with the pattern of decadal-scale, north–south oscillations in British Columbia's precipitation reported by Moore and McKendry (1996). The regime shift in 1998 that appears as reduced flows in 1999 would improve the ocean conditions for sea louse production in early spring by reducing freshwater discharge and increasing sea surface salinity (Johnson and Albright, 1991; Pike and Wadsworth, 1999). Thus, it is possible that the productivity of many species of sea louse improved in the study area after the 1998 regime shift that reduced flows beginning in 1999. Brooks (2005) reviewed the potential effects of salinity on the development of *L. salmonis* to the copepodid stage in waters around the salmon farms in the Knight Inlet area and concluded that naturally low salinity below 30 psu could explain the absence of significant effects of sea lice on farmed Atlantic salmon in the 1990s. In 2003, there was an increase in flow, which we considered part of the variability expected within a regime. However, this increase in flow could have resulted in lower salinity, reduced sea louse production, and an increased flow of nutrient-rich bottom water into the study area. It is not possible to associate the increased flow in 2003 with the very high marine survival of pink salmon because reliable salinity measurements are not available. The possibility of a relationship indicates the importance of monitoring salinity levels throughout the study area in future.

A report by Krkošek *et al.* (2005) identified salmon farms as a source of the sea lice found in the study area in 2003. These authors and Morton *et al.* (2004) linked the decline in escapements and marine survival of pink salmon brood years in 2000 and 2001 (return years 2002 and 2003) to sea-louse-induced mortality. Morton *et al.* (2004) also said that 1.6 sea lice per g of fish are lethal to juvenile pink salmon. However, Bjorn and Finstad (1997), who determined the level, wrote that 1.6 chalimus larvae per g of fish weight that could be lethal in laboratory experiments cannot be applied directly to wild migrating smolts. Therefore, the caution of Bjorn and Finstad (1997) and the observations from this study indicate that it is important to associate sea lice counts on juvenile salmon in their natural environment with natural mortality in years when marine survival is high, as well as when it is low.

We conclude that the ocean ecosystem in the study area in 2003 resulted in high marine survival of pink salmon. It is clear from these observations in 2003 and from the numbers of adult pink salmon returning in 2004 that farmed Atlantic and pink salmon coexisted successfully in this ecosystem in 2003. The processes responsible for the high marine survival cannot be readily identified, but they could include increased freshwater discharge in 2003, which may have resulted in lower salinity less favourable to sea louse production, increased inflow of nutrient-rich water to the study area, and the introduction of a Provincial Action Plan that required mandatory louse monitoring and established a fallowed migration corridor for pink salmon.

Morton *et al.* (2005) found sea louse abundance and prevalence to be lowest on juvenile pink salmon during the fallowed period, and other studies in the area found a similar trend (SJ, unpublished). However, production of farmed salmon in 2003 remained at levels similar to those in 2001 and 2002 when pink salmon survival was low. This is a significant finding because active and viable salmon farming continued even as wild salmon showed high marine survival. Levels of sea lice on farmed salmon and pink salmon could not have been harmful at the population level for the observed high marine survivals to have been achieved. Furthermore, it is possible that the current abundance of sea lice is recent and may have resulted from a climate shift in 1998 that reduced river flows into Knight and Kingcome inlets beginning in 1999, causing increased salinity in the Broughton Archipelago, which is favourable to sea louse production. If this is true, it is possible that the next regime shift will increase river flows, which would decrease salinities and reduce sea lice production. Reduced sea louse production would also reduce sea louse abundance on farmed salmon.

Regardless of the accuracy of these speculations, conditions in the marine ecosystem around salmon farms in the study area in 2003 suggest that it is possible to have sustainable wild and farmed salmon in a common ecosystem.

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