Supporting Information

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SI Introduction

Wild pink salmon and farmed Atlantic salmon are hatched in freshwater but move to salt water at different times. Adult pink salmon spawn in gravel substrate of coastal rivers in the fall, eggs hatch and larvae (alevins) develop during the winter, and juveniles (fry) emerge from the substrate and move directly to the ocean, usually in March and April (1). Juvenile pink salmon in the Broughton Archipelago feed in the near shore area for 2–3 mo, growing rapidly to about 10 g in July (2) before leaving the region to return to their natal stream to spawn 2 y after their parents (1). Farmed Atlantic salmon are hatched and reared in fresh water for up to 1 y, after which they are transferred to salt water as smolts (~100 g); fish are usually harvested after 18–24 mo at sea (Dataset S1).

The sea louse life cycle includes multiple stages of development but no intermediate hosts. Adult female sea lice release eggs that hatch into planktonic nauplii. Nauplii develop into a copepodid that attaches to a fish and becomes a chalimus. Chalimus stages are nonmotile, but lice soon develop into motile preadults and adults. Depending on water temperature, the generation time for an egg to develop into an infectious copepodid stage is about 3–4 wk, and it takes another 4 wk for a copepodid to develop into an egg-laying female (3). Juvenile pink salmon are free of sea lice when they migrate from freshwater streams to the ocean in March and April. Although sea lice sometimes attach as soon as fish enter marine waters, most juvenile pink salmon migrate out of the Broughton Archipelago before these sea lice mature and produce eggs (4). Therefore, infested juvenile pink salmon are not a significant source of sea lice for other juvenile pink salmon (5), and sea lice on juvenile pink salmon must come from farm fish or other species of wild fish.

When veterinarians identified a need for sea lice treatment of farm salmon in the early 1990s, ivermectin was shown to be effective (6); however, it was rarely used, because it has a very low safety threshold: drug concentrations needed to kill lice often kill some medicated fish (7). If fish are not treated with antiparasiticides, sea lice numbers in the Broughton Archipelago tend to increase until fish are harvested about 2 y after entering saltwater (8). In the 1990s, sea lice infestation of farm fish was diagnosed without quantification, and therefore, specifics of sea lice infestations during that time are unknown. In the 2000s, sea lice counts were standardized and became common after emamectin benzoate (Slice) became available in Canada through an Emergency Drug Release program to treat farm fish for sea lice. Emamectin benzoate has a high safety threshold (9), and its use increased after it became available in 1999. Since 2009, Slice has been approved for use in Canada by regular veterinary prescription.

SI Methods

Farm Sea Lice Abundance Estimates. For analysis of sea lice abundance on farm fish, we used numbers most relevant to the potential of lice to produce progeny that infest wild fish: (*i*) the number of adult female *Lepeophtheirus salmonis* and (*ii*) 40% of the number of motile *Caligus clemensi* (standard counts do not differentiate *C. clemensi* gender or motile stage, but the 40% value provides a liberal estimate of the numbers of mature female *C. clemensi*). Since October 2003, the British Columbia Provincial Government has required each Atlantic salmon farm to conduct lice assessments on a monthly basis and report that monthly data (in an aggregated form) from each subzone. At each farm, monthly assessments are conducted using three pens; 20 live fish per pen are anesthetized and examined (farm total = 60 fish) (10). Pens chosen for assessment include one reference or index pen (i.e., the first pen stocked at the farm or the pen with the highest likelihood of having lice based on historical counts). The reference pen is sampled each month. Two additional pens may be selected by farm staff, either by rotation or convenience. Counts are not required for farms with less than or equal to three pens of fish or when handling would unduly stress the fish (e.g., during a toxic algal bloom or low dissolved oxygen conditions). The number of lice on each farm was determined by multiplying the mean number of lice per sampled fish times the total number of fish on the farm.

We filled most small gaps in the data using estimates from available data before and after a gap (11). In all, we report actual mean counts of adult female *L. salmonis* from 1,199 farm-mo and estimated mean counts from 227 farm-mo (16% of the total). Several types of estimates were used based on fish or site history:

Smolt entry (57 counts): Because smolts enter the marine environment free of lice, estimates for newly entered smolts were 0; if more than 1 mo was missing, counts were increased in a regular progression to the first available count.
Transfer (24 counts): These estimates were based on the closest available count at the donor or recipient site.
Missing values between counts (54 estimates fill the 1-mo gaps, 10 estimates fill five 2-mo gaps, and 9 estimates fill three 3-mo gaps): These estimates were based on the counts before and after the gap. They were either an arithmetic mean (1-mo gap) or a progression based on counts before and after the gap.
Harvest (67 counts): These estimates were based on counts before the gap and always increased; the magnitude of the increase was based on salinity/season and history of the site.
Other (6 counts): The bases for these estimates are explained in comments in Dataset S1.

Counts before 2003 were less standardized, but veterinarians requesting an Emergency Drug Release for Slice from the Canadian Bureau of Veterinary Drugs were required to provide lice counts both pre- and posttreatment. Veterinarians normally assessed three pens of fish, with 10–20 fish per pen. For the first counts in April 2000, the farm counts exceeded these minimum requirements:

(*i*) Farm #3: Lice counted on fish from four pens = 20 + 20 + 10 + 7 = 57 fish counted.
(*ii*) Farm #4: Lice counted on fish from four pens = (20 × 3) + 18 = 78 fish counted.
(*iii*) Farm #8: Lice counted on fish from six pens = (20 × 4) + 16 + 22 = 118 fish counted.

Methods for estimating the monthly total number of adult female sea lice on all farm fish in the Broughton Archipelago varied depending on whether lice numbers were estimated on all farms. From 2003 to 2009, the Broughton-wide total was determined by adding the estimated number of adult female lice on every farm. Before 2003, the Broughton-wide total was determined by adjusting the available farm total (e.g., from 6 of 17 active farms in April 2001) based on patterns of lice distribution among farms from 2003 to 2008. Most counts before 2003 occurred on farms with the greatest number of sea lice per fish (i.e., to support treatments with emamectin benzoate); the main exception was that fish >600 d in the ocean were rarely counted, because they rarely required treatment. Although older (and larger) fish tend to have greater infestation levels than younger fish, they often handle these infestations without need for treatment. From 2003 to 2008, the three most infested farms accounted for ≥60% of the Broughton-wide total number of adult female *L. salmonis* during 62 of 72 mo. Data from 2009 were not used here, because most treatments during 2009 were applied independent of sea lice counts, and 2009 counts were not likely to be representative of variability before 2003 (when treatments were applied only at farms with high counts).

Whenever monthly estimates of adult female *L. salmonis* numbers were available from at least three farms, the total of these estimates was adjusted in two ways to estimate the total number of sea lice on all farms in the Broughton Archipelago: (*i*) a proportion adjustment based on the number of farms that were estimated and (*ii*) an old fish adjustment to account for higher numbers of sea lice on older fish (>600 d in the ocean). For the proportion adjustment, we assumed that the ratio of adult female *L. salmonis* numbers on farms with the most lice vs. all Broughton farms was the same before and after January 2003, when count estimates first became available from all farms. For example, in April 2001, the total number of adult female *L. salmonis* on the six counted pretreatment farms (7.15 million) was divided by 0.917 (the average ratio of the top six counts among all farms from April 2003 to 2008) for a subtotal estimate of 7.80 million adult female *L. salmonis* (Dataset S1). For the old fish adjustment, the subtotal adult female *L. salmonis* estimate was increased by adding the product of (*i*) the number of farm fish >600 d at sea and (*ii*) the average number of adult female *L. salmonis* on pretreatment counted fish during the month. For April 2001, farms held 421,370 fish >600 d at sea, and the average adult female *L. salmonis* load on the counted fish was 1.94 lice per fish; therefore, 819,318 *L. salmonis* (421,370 × 1.94) were added to the subtotal (7.80 million) for a final April 2001 estimate of 8,618,401 adult female *L. salmonis* on all Broughton farms (Dataset S1). Two types of counts were omitted from both adjustments: counts not used for treatments (e.g., for training personnel) and posttreatment counts.

Error bars for Broughton-wide estimates were calculated for all months before 2003 using the range of ratios for the most infested fish vs. all fish for each month from 2003 to 2008. For example, this ratio for the six most infested farms in April varied from 0.894 (in 2005) to 0.960 (in 2008); therefore, the first adjustment for the April 2001 sum of farm counts/estimates (7.15 million) was divided by 0.960 (7.4 million) and 0.894 (8.0 million), and then, the old fish (>600 d at sea) adjustment (0.8 million) was added, yielding a range estimate from 8.3 to 8.8 million. Actual formulas are included in Dataset S1.

We assessed the accuracy of our adjustments for incomplete farm counts (2000–2002) using complete October counts from 2003 to 2009 (Dataset S1). We chose October, because sea lice distribution among farms during October (2003–2009) was probably fairly close to what occurred before 2003. From 2003 to 2009, only three sea lice treatments were applied to farms during July, August, or September (i.e., in most years, no treatments were applied during these months); therefore, the influence of treatments on October sea lice numbers was low. We began our assessment using estimates derived from the three greatest farm lice counts among fish <600 d in the ocean (during October), and we ignored counts from all other farms. We calculated a proportional adjustment for October data from 2003 to 2009 using the same formulas that were used for each October before 2003. The adjustment that used the standard old fish adjustment (i.e., the average of the three greatest sea lice counts for the month) yielded a final total estimate that averaged 5.5% greater than the actual counts (range = 28% less than to 73% greater than the actual counts) (Dataset S1). An alternate old fish adjustment—using the greatest counts for the month—yielded a final total estimate that averaged 22% greater than the actual estimates (range = 22% less than to 113% greater than the actual counts) (Dataset S1). We conclude that our standard adjustment yielded an acceptable estimate of the total number of adult female *L. salmonis* on all Broughton farms combined; the alternative old fish adjustment was inferior, and it was not used.

To estimate the monthly total number of female *C. clemensi* on Broughton farm fish before 2003, available pretreatment estimates were adjusted using *C. clemensi*-specific ratios derived from the most infested farms from 2003 to 2008. Species-specific ratios were used, because *C. clemensi* tended to be more concentrated on a few farms than *L. salmonis*. For example, the three most-infested farms accounted for ≥60% of the female *C. clemensi* on all Broughton farm fish during 71 of 72 mo from 2003 to 2008. In April 2001, the total of pretreatment *C. clemensi* counts or estimates from six farms (1.38 million) was divided by 0.945 (the average ratio of the top six counts for April 2003–2008; range = 0.857–1.00) for a total estimate of 1.46 million female *C. clemensi*. Because *C. clemensi* counts were not clearly associated with fish age, further adjustment for uncounted old fish was not done for *C. clemensi*.

We believe that farm sea lice counts from 1999 to 2002 are reliable, because (*i*) the expense of Slice treatments (e.g., about $70,000 to treat a farm of 500,000 2.5-kg fish) provided farms with a financial incentive to ensure accurate counts, (*ii*) all 20 treatments during this period occurred before pink salmon population decline was first documented in fall 2002, and (*iii*) counts supporting all 18 Slice treatments during this period were recorded by licensed veterinarians and reported to the Canadian Bureau of Veterinary Drugs. We believe that farm sea lice counts since October 2003 are reliable, because they were audited by government fish health personnel and confirmed accurate (8).

Pink Salmon Population Data. We obtained pink salmon escapement estimates for 1950–2009 from the Canadian Department of Fisheries and Oceans (DFO) for nine rivers in the Broughton Archipelago (DFO management area 12) and 64 rivers in a northern reference region (DFO management areas 7, 8, 9, and 10). DFO provided several caveats for these data:

(*i*) Escapement estimates were derived through visual (aerial and foot inspections) observations, typically resulting in a peak count with several visits.

(*ii*) Many historical, nonenvironmental events (e.g., changes in basic enumeration method or annual effort) affecting year to year changes in the reliability of escapement estimates are not stored in the database. Thus, comparison of annual estimates at face value within and between streams must be approached with caution, depending on the application under consideration.

(*iii*) In general, all numeric estimates are useful for determinations of presence or absence of pink salmon. Similarly, comparison of mean abundance values by decade is certainly more reliable than comparison of pairs of single year values.

(*iv*) In addition, the larger the difference between annual estimates for a particular stream, the greater the likelihood that they are biologically meaningful and require no further verification.

(*v*) For example, large differences (changes of fivefold or greater) in estimates may be assumed to be generally useful as indicators of trends in spawner abundance. Users wishing to attach biological significance to values that differ by less than this or users wishing further information about the estimate are advised to seek additional expert advice from appropriate Stock Assessment Division personnel regarding the relative accuracy and consistency of a given set of abundance estimates.

(*vi*) Harvest has occurred in the past on these stocks with various levels of exploitation. It would be difficult to look at the escapement data closely to determine production without including catch estimates.

To address item *vi* above, we obtained catch estimates for the Broughton Archipelago from the Canadian DFO. These estimates are updated from ref. 10 based on fishery location and escapement proportions.

To minimize effects of these data limitations, our analysis focused on general trends and summed escapement for several rivers within each region. To enhance comparisons with previous analyses, our analysis of nine Broughton Archipelago rivers (Fig. S1) included the same rivers used in studies of pink salmon abundance in midcoastal British Columbia (10, 12). Differences included our use of (*i*) Embly Creek, which contributed up to 10% of the nine-river sum (e.g., in 1988) (Dataset S1) and (*ii*) Glendale Creek—used in ref. 10 but not in ref. 12—which contributed 90% of the nine-river odd-year escapement summed for all years 1997, 1999, 2001, 2003, 2005, and 2007 (Dataset S1). Among the nine rivers, spawning channels were added to Glendale Creek (1988) and the Kakweiken River (1989) (10). The Broughton Archipelago has several other creeks and rivers that support pink salmon spawning, but escapement estimates for these rivers are incomplete (i.e., many years have no estimates). The rivers that we used usually account for >90% of the Broughton escapement totals (10).

For comparisons of regional escapement trends over the past decade, we used 12 of 64 rivers from the northern reference region that were used in previous analysis (12). We report available escapement estimates for the other 52 rivers (Dataset S1), but these estimates were not used for our analysis, because those rivers have too many missing values over the past decade. Only six rivers in the reference region have DFO escapement estimates for each of the 10 y from 2000 to 2009. Another six rivers are missing only 1 y of data during this period, and all missing estimates are from the even-year run. Each of these missing estimates is designated by DFO as “Adults Present: inspected and species present, but no estimate of escapement available.” To include these rivers in our analysis, we replaced each missing value with an estimate that contributed the same ratio to that year’s 12-river escapement total as that river’s contribution during the parental generation. Addition of these six rivers doubled the number of rivers that were used; the additional six rivers accounted for up to 30% of the 12-river total from 2000 to 2009 and up to 81% of the 12-river total in earlier years, but the six single-year replacement estimates comprised only 0.5% (2004), 2.7% (2006), and 7.0% (2008) of total 12-river escapement those years.

Farm Production and *L. salmonis* vs. Wild Salmon Adult Returns. To test the relationship of farm-source *L. salmonis* and wild pink salmon adult returns, we used a variation of the classic Ricker model. In the classic Ricker model, instantaneous mortality Z during the early life history phase (for brevity, the juvenile phase) is assumed to be a density-dependent function of the spawning stock (S) that produced the year-class. If $J(x)$ is the abundance of pink salmon juveniles from the egg stage (age $x = 0$) until the year-class returns (at age $x = 2$), then the change in juvenile abundance can be expressed as the differential equation $\frac{dJ}{dx} = -Z(x)J(x)$. The simplest assumption is that instantaneous mortality is linear or $Z(x) = a + bS$. This leads to the classic Ricker equation $R \equiv J(2) = \alpha S \exp(-\beta S)$, where R is the number of returning salmon at age 2 and S is the number of spawners 2 y earlier (13). Parameter α is the density-independent productivity parameter, and parameter β is the density-dependent parameter that produces declines in returns at high spawning levels (termed overcompensation). The number of returning salmon in year t is denoted as R_t. If the stock is subject to a fishery that catches C_t fish, then these fish will not become part of the spawning stock. The escapement (or spawning stock) is calculated by subtracting the catch from the number of returns or $S_t = R_t - C_t$. Because of the 2-y life cycle, juvenile mortality for salmon that return in year t is then $Z(x) = a + bS_{t-2}$.

The first hypothesis that we wish to test is that sea lice from fish farms affect the returns of wild pink salmon by increasing their juvenile mortality. The hypothesis is that lice from adult salmon the previous fall (year $t - 2$) multiply over winter on the farm fish, and then, farm-source sea lice causes mortality of sea-going wild juvenile salmon in year $t - 1$. If a simple linear relationship is assumed, then $Z(x) = a + bS_{t-2} + cL_{t-1}$, where L is the number of farm-source sea lice in the year before return. The solution of this differential equation is (Eq. **S1**)

$$R_t = \alpha S_{t-2} \exp(-\beta S_{t-2} - \gamma L_{t-1}). \qquad \textbf{[S1]}$$

A linearized form of this equation is (Eq. **S2**)

$$\ln(R_t/S_{t-2}) = \ln(\alpha) - \beta S_{t-2} - \gamma L_{t-1}, \qquad \textbf{[S2]}$$

showing that parameters can be estimated through linear regression (13). The null hypothesis of no sea lice effect is H_0: $\gamma = 0$. This equation is essentially identical to previous analysis of these populations (12), except that previous analysis covered only years when the fishery was small (that is, $R_t = S_t$). Similarly, the significance of the density-dependent parameter can be tested as H_0: $\beta = 0$. We report analysis using the number of adult female *L. salmonis* on all Broughton farms in March; this gives the best estimate of exposure of wild salmon in April, when most juvenile pink salmon have entered the marine environment but are still small enough to be susceptible to lice infestation. An alterative analysis using April farm lice numbers is included in Dataset S1.

A variant of this hypothesis is that, regardless of sea lice, farm fish production has a deleterious effect on wild salmon because of other unconfirmed causes. Instead of using the number of sea lice, farm fish production, P_{t-1}, is substituted for sea lice counts in Eq. **S2**, resulting in (Eq. **S3**)

$$\ln(R_t/S_{t-2}) = \ln(\alpha) - \beta S_{t-2} - \gamma P_{t-1}. \qquad \textbf{[S3]}$$

As before, the null hypothesis is H_0: $\gamma = 0$. Farmed fish production and numbers of wild salmon escapement and catch data are available from 1990 to 2009.

Another hypothesis of interest is that the total number of sea lice (adult female *L. salmonis*) on all Broughton fish farms in April is related to the number of wild fish returning the previous fall. This is because returning pink salmon bring sea lice with them in year $t - 2$, and at least some of these sea lice move to fish farms (8, 14, 15). If the relationship is assumed to be linear, then (Eq. **S4**)

$$L_{t-1} = \alpha_2 + \beta_2 S_{t-2}. \qquad \textbf{[S4]}$$

The null hypothesis is H_0: $\beta_2 = 0$. It is tested by performing a linear regression of wild returns the previous year vs. April farm sea lice counts and testing the slope for significance (16). Although counts of salmon and/or lice often have a lognormal distribution, we did not find a major departure from normality and therefore, used the simple linear regression procedure. Because odd- and even-year pink salmon seem to carry different loads of lice (Fig. 3), separate analyses were conducted for the two runs, as needed. We also tested alternative regressions using March farm sea lice data (instead of April) (Dataset S1). Estimates of March and April farm sea lice numbers are available from 2000 to 2009.

SI Results and Discussion

Pink Salmon Population Data. Pink salmon population abundance in the Broughton Archipelago is highly variable, with periods of consecutively high or low abundance. Trends in abundance over time are not similar for even- and odd-year populations (Fig. S2), and a large decline in returns after 1 y of high escapement is common. Among the odd-year runs in the Broughton Archipelago, the dominant river changed from the Kakweiken River in the mid-1970s and mid-1980s to Glendale Creek since the mid-1990s (Fig. S2 and Dataset S1). In contrast, even-year runs have been more uniformly distributed among the rivers. Among the odd- and even-year populations in each of the seven Broughton rivers previously identified as exposed to farm-source sea lice since 2001 (12), escapement peaks during the period 1950–1999 were followed by next-generation decline of >85% for 8 of 14 populations. Five of these peak–decline cycles occurred even before fish farms were established in the area (Dataset S1).

Broughton Archipelago pink salmon populations in 2002 and 2003 declined markedly compared with unexposed reference populations, but since 2003, escapement trends in the two regions have either been similar (for the even-year runs) or become similar (odd-year runs) (Fig. S3). For the even-year populations, 60-y escapement peaks occurred in the Broughton Archipelago in 2000 (Fig. S2) and the reference area in 2002 (Dataset S1); however, a 97% collapse in escapement occurred in both regions over the next three or four salmon generations (Fig. S3 and Dataset S1). For the odd-year populations, 60-y escapement peaks occurred in both regions in 2001, followed in 2003 by population decline that was greater in the Broughton Archipelago than in the reference region (88% vs. 40% generational decline) (Fig. S3 and Dataset S1). Since 2003, populations in the reference area declined each generation until increasing in 2009 (Fig. S3), whereas Broughton populations increased each generation (Fig. S3) until commercial fishing was opened there in 2009 for the first time since 2001. Population trends in relationship to a single variable like the presence of fish farms need to be interpreted with caution. For example, from 1975 to 1977, pink salmon escapement declined 85% for the Broughton populations but increased 72% for the reference populations (Dataset S1); however, these differences occurred more than a decade before fish farms were established in the area.

Fish Farms in the Broughton Archipelago. In the Broughton Archipelago since January 2000, 26 farm tenures have held Atlantic salmon (*Salmon salar*) at some time (Fig. S1 and Dataset S1), but within any month, several of the tenures were empty (fallow). The number of stocked farms varied from 11 (Oct 2003) to 18 (April 2005). Annual farm fish production in the Broughton Archipelago first approached 1 Gg in 1990 and increased rapidly to about 17 Gg by 1999; thereafter, production during odd years remained about the same, whereas production during even years was greater than 20 Gg (Fig. S2). Production from 1990 to 1992 included a mixture of Chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and Atlantic salmon, but production since 1992 has been exclusively Atlantic salmon (Dataset S1). Maximum farm fish production in the Broughton in 2006 was followed in 2007 by escapement of wild pink salmon that was greater than the 60-y median for the odd-year run and 21% greater than the parent generation in 2005 (Fig. S2).

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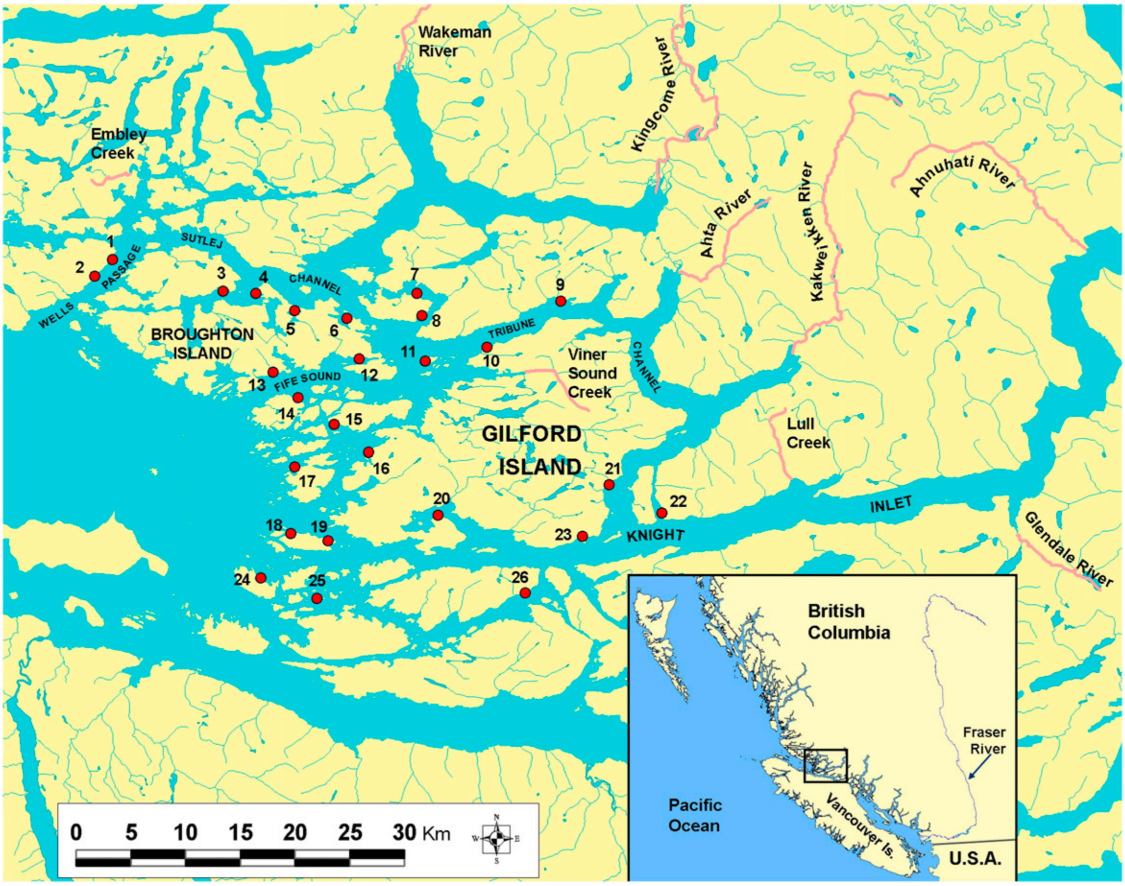


Fig. S1. Map of the Broughton Archipelago with fish farm tenures (red dots) and major pink salmon rivers. Farm tenure numbers correspond to Dataset S1.

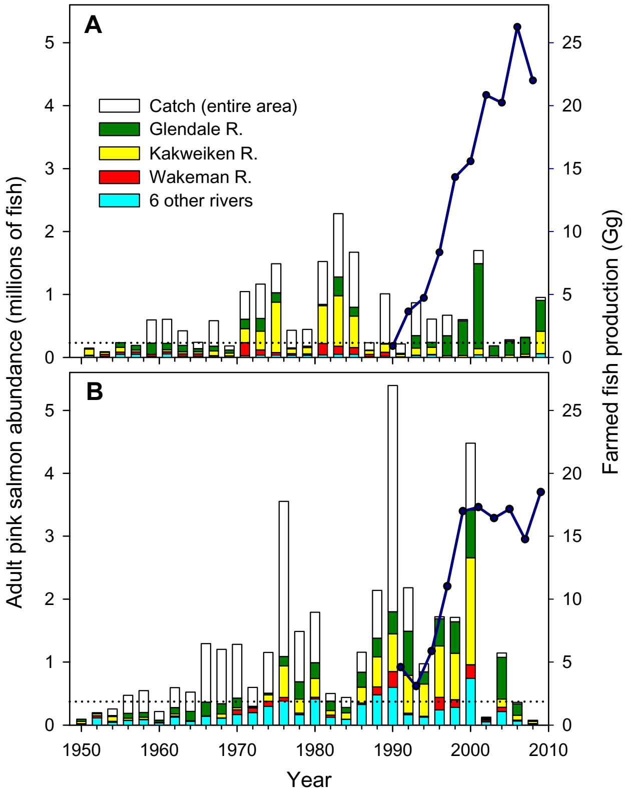


Fig. S2. Broughton Archipelago adult pink salmon abundance (stacked bars designate the same source for each graph) for odd-year populations (*A*) and even-year populations (*B*). Because farm salmon production (dark blue line and black symbols) is most likely to affect marine survival of wild pink salmon when they are juveniles (1 y before they return to spawn), farm fish production is shown during even years (*A*) and odd years (*B*). The dotted reference line on each graph signifies the 60-y median escapement for each population.

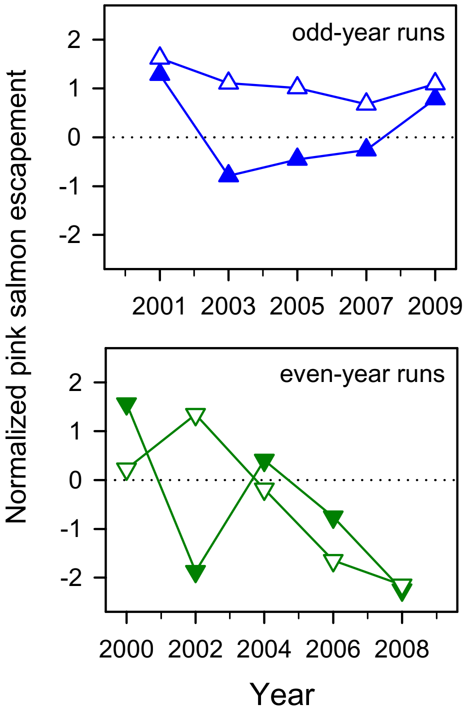


Fig. S3. Time series of normalized deviances of summed pink salmon populations ($\ln[S_i(t)/m_i]$, where $S_i(t)$ is the summed escapement estimate for populations i in year t and m_i is the time-series mean abundance for summed populations i from 1950 to 2008 for the even-year run and from 1951 to 2009 for the odd-year run) for 9 populations exposed to salmon farms in the Broughton Archipelago (solid triangles) and 12 populations not exposed to salmon farms in the northern reference region (open triangles). The dotted reference line on each graph signifies the 60-y mean escapement for each group of populations.

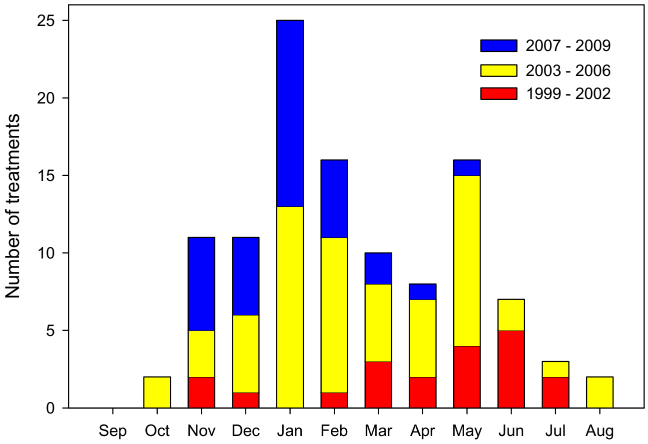


Fig. S4. Stacked bar graph with the number of sea lice treatments per month for different periods over the past decade.

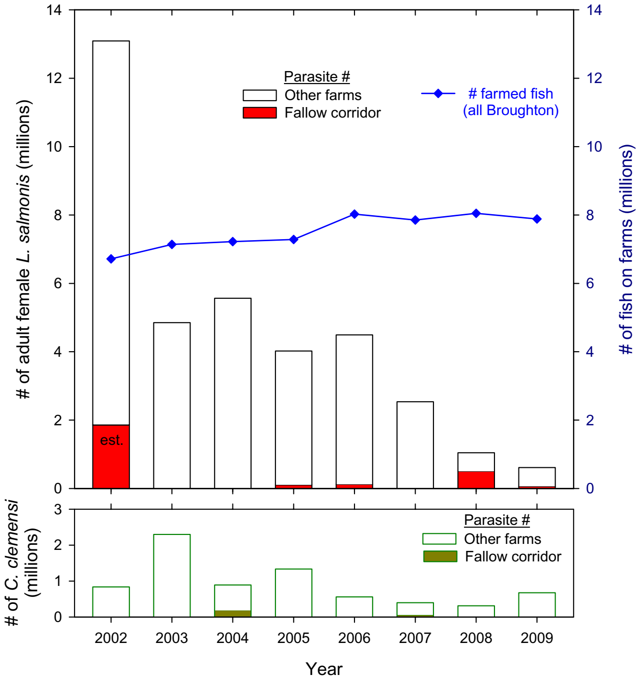
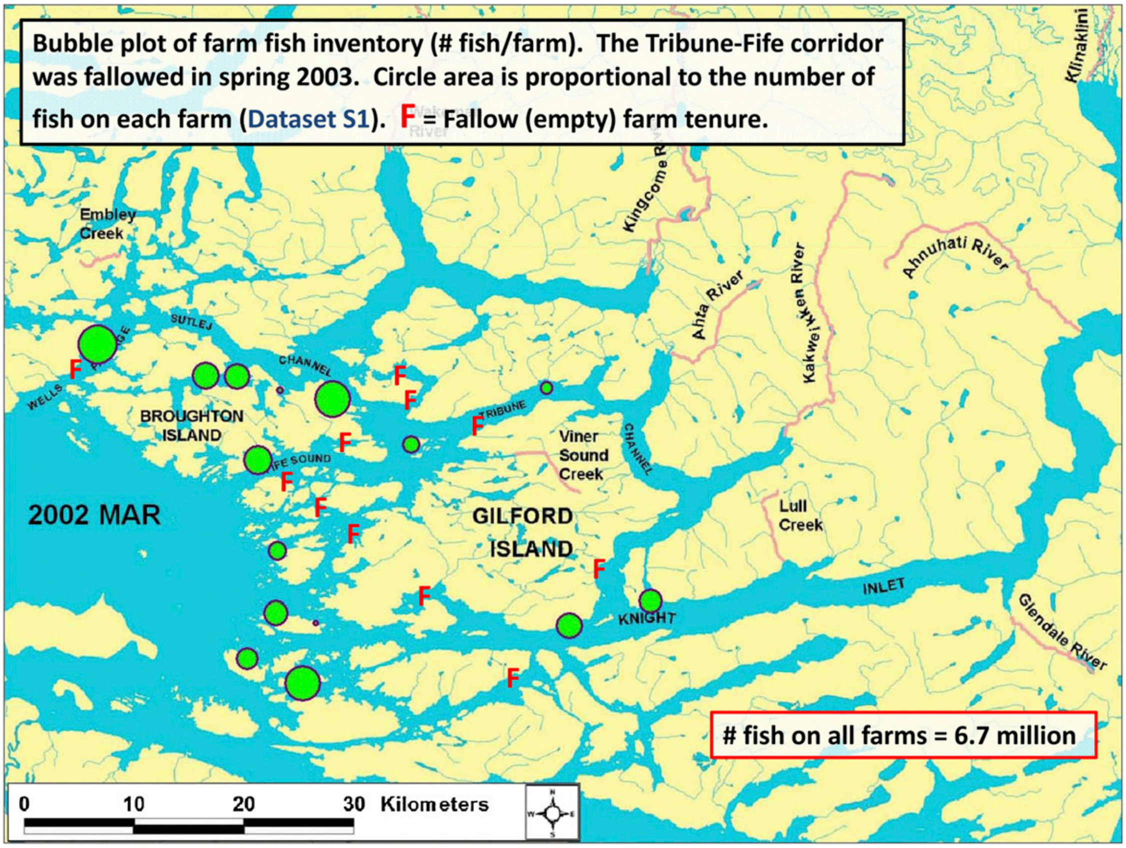


Fig. S5. Stacked bar graph with the number of farm fish and number of adult female sea lice on farm fish during March, the month of greatest concern during juvenile pink salmon outmigration. For each species of sea lice, plots include total numbers of adult female sea lice on farm fish in (*i*) the Tribune-Fife corridor that was fallowed in spring 2003 and (*ii*) the remainder of the farm fish in the Broughton Archipelago. The Tribune-Fife corridor was not fallowed before or after 2003.



Movie S1. Bubble plot of farm fish inventory (number of fish × farm^{-1}). The Tribune-Fife corridor was fallowed in spring 2003. The circle area is proportional to the number of fish on each farm (Dataset S1). F, fallow (empty) farm tenure.

Movie S1

Other Supporting Information Files

Dataset S1 (XLSX)