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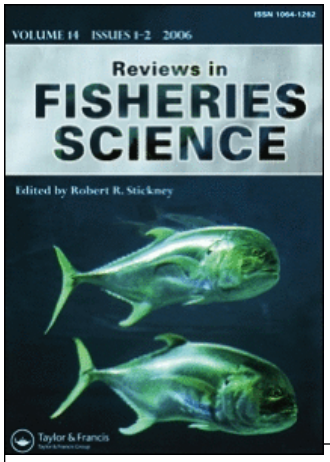

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Sea Lice and Pink Salmon Declines: A Response to Brooks and Jones (2008)

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Sea Lice and Pink Salmon Declines: A Response to Brooks and Jones (2008)

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In this article, we respond to concerns raised by Brooks and Jones (2008) about recent advances in sea lice and salmon population dynamics in the Broughton Archipelago, British Columbia. We show that the assessment by Brooks and Jones (2008) is thoroughly mistaken and that their conclusions are based on a combination of obfuscation, misrepresentation, and fundamental misunderstandings. The extinction hypothesis is not actually a hypothesis at all, but rather an inevitable consequence of sustained population decline. Local extinction of Broughton Archipelago pink salmon can be prevented if population declines are turned around, and the data and models suggest this can be achieved if the infestations are stopped. We have organized our responses in an itemized manner according to the headings and subheadings in Brooks and Jones (2008).

Keywords aquaculture, conservation, population dynamics, transmission, salmon, sea lice

1. THE VARIABILITY OF PINK SALMON RETURNS THROUGHOUT THE NORTH PACIFIC WITH PARTICULAR EMPHASIS ON THE BROUGHTON ARCHIPELAGO

a. Understanding the Variability of Pink Salmon Returns in the North Pacific is Important to Predicting Future Escapement

Brooks and Jones (2008) emphasize that pink salmon population dynamics are naturally variable. We fully agree and point out that the variation is due to many factors—both biotic and environmental—and that the variability is clearly represented in both Figures 2 and 3 of Krkošek et al. (2007a). We do not claim that sea lice are the only factors that affect salmon population dynamics; rather, in Krkošek et al. (2007a), we have shown that sea lice are one key factor that affects the population dynamics of pink salmon. To accommodate the natural variability of pink salmon population dynamics in the analysis, we used the stochastic Ricker model (Dennis and Taper, 1994), which is a nonlinear stochastic model that explicitly models density-dependent mortality and environmental variation in pink salmon population dynamics. This quantitative framework is well known and well established for analyzing the population dynamics of fish (Myers et al., 1999; Hilborn and Walters, 2001) as well as many other species (Brook and Bradshaw, 2006). To control for other factors that affect pink salmon population dynamics and isolate the effects of sea lice on pink salmon population dynamics, we used a comparative analysis of exposed pre-infestation, exposed infested, and unexposed populations. The exposed pre-infestation populations and exposed infested populations are in the vicinity of salmon farms prior to and after the sea lice infestations, which were first observed in 2001. The unexposed populations are far from salmon farms, with no known sea lice infestations. The exposed pre-infestation and unexposed populations share the many factors that affect pink

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salmon population dynamics, evidenced by their similar population growth rates (Krkošek et al., 2007a) and synchronous population dynamics (Pyper et al., 2001). The exposed infested populations have a markedly depressed growth rate, which is isolated to the exposed infested populations. This statistical design, similar to the matched case-control study design in epidemiology (Rothman, 1986), indicates sea lice are the factor driving the difference in population growth rates.

Brooks and Jones (2008) present pink salmon escapement data from the Klinaklini River as an example of natural variation in pink salmon population dynamics. Their assessment suggests pink salmon disappeared from this river in even years between 1974 and 1990 and then abruptly returned to abundances in the tens of thousands in 1998 and subsequent years. We checked the validity of their assessment against information held in the Fisheries and Oceans Canada Pacific salmon escapement database using the Mapster program (http://www-heb.pac.dfo-mpo.gc.ca/maps/maps-data_e.htm). Most of the data portrayed as showing zero abundance between 1974 and 1990 in Figure 2 of Brooks and Jones (2008) correspond to entries of "no data" or "not inspected" in the Pacific salmon escapement database, rather than "zero abundance." There is also a problem with their interpretation of the increased abundance in this river in 1998. The rise in pink salmon escapement estimates in the Kliniklini following 1998 coincides with a change in escapement estimation from overhead flights and river walks (1996 and earlier) to mark-recapture programs that used a fishwheel to capture fish (1998 and afterward). The Klinaklini is a large glacier-fed and heavily-silted river, making visibility of fish and escapement estimates based on overhead flights very difficult. A fishwheel-based mark-recapture approach would be enhanced by silted water because the low visibility will limit the salmon's vision during capture. The data from the two escapement methods have not been calibrated (Pieter van Will, Fisheries and Oceans Canada, personal communication). These limitations of the Klinaklini River data suggest that the extinction-colonization dynamics that Brooks and Jones (2008) described did not actually occur and are rather the spurious result of a poor quality data set. The Klinaklini data were not used in the analysis in our *Science* report (Krkošek et al., 2007a).

b. Exclusion of Glendale Creek Data is Inappropriate

Brooks and Jones (2008) expressed concern about Krkošek et al. (2007a) excluding the Glendale populations but including the Kakweiken populations. In Krkošek et al. (2007a), it was statistically necessary to exclude rivers that recently had spawning channels constructed. As stated in the paper, this was done systematically for rivers in the Broughton as well as the unexposed area to the north. The objective of spawning channel construction is to improve spawning habitat quantity and spawning gravel quality. If the spawning channels are effective, the increased productivity due to spawning channels prevents evaluation of recent trends relative to historical abundance, which is the basis of analysis in the paper. The Kakweiken was included in the analysis because its spawning channel has not been successfully utilized (usually less than 7% and frequently 0% of the run use it; Glen Neidrauer, Fisheries and Oceans Canada, personal communication). In contrast, the Glendale spawning channel has been well utilized (typically 70,000 fish use it; Pieter van Will, Fisheries and Oceans Canada, personal communication) and has greatly increased the escapement in this system since its construction. It is straightforward to reanalyze the data with Glendale included and Kakweiken excluded, despite the biases. The population growth rate, r, with 95% confidence intervals for Broughton pink salmon populations during the sea lice infestations are:

With Glendale

$$\mathrm{r} = -1.002, 95\%\mathrm{CI} : -1.52 \text{ to } -0.52$$

Without Glendale and Kakweiken

$$\mathrm{r} = -1.23, 95\%\mathrm{CI} : -1.80 \text{ to } -0.62$$

The population growth rate for Broughton pink salmon populations during the infestations as reported in our study are:

$$r = -1.17, 95\% \quad , \mathrm{CI} : -1.71 \text{ to } -0.59$$

All of these analyses show that Broughton pink salmon populations were depressed and rapidly declining during the sea lice infestations.

2. CLAIMS THAT PINK SALMON FRY WILL SUFFER UP TO 97% MORTALITY FOLLOWING INFECTION WITH SEA LICE ARE NOT SUBSTANTIATED

The estimates of annual pink salmon mortality due to salmon lice in Krkošek et al. (2007a) are not based on previous experimental work as Brooks and Jones (2008) claim. Rather, the mortality estimates in Krkošek et al. (2007a) are based on a direct analysis of pink salmon escapement data and annual average salmon lice abundances. The estimates for mortality ranged from 16% to over 97%, and were commonly over 80%. However, the pathogenicity of motile *L. salmonis* on juvenile pink salmon, estimated in Krkošek et al. (2007a) from escapement data, gives similar values to those estimated independently from survival experiments of infected juvenile salmon held in ocean enclosures (Krkošek et al., 2006). The reduction in wild salmon survival from these two studies is also similar to the observed decline in wild pink salmon in Ford and Myers (2008) meta-analysis. The studies by Jones et al. (2006a, 2007) evaluated the effect of salmon lice on the survival of juvenile pink salmon at sizes over 10 times larger than the juvenile salmon infested each spring in the Broughton Archipelago (Morton and Williams, 2003; Morton et al., 2004, 2005). Jones et al. (2006a, 2007) used juvenile salmon that weighed over 10 g and were fully scaled, whereas the juvenile pink salmon studied in the

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Broughton Archipelago weigh less than 1 g and do not have scales (Morton and Williams, 2003; Morton et al., 2004, 2005). The effect of salmon lice on salmon survival is host size dependent (Pike and Wadsworth, 2000; Boxaspen, 2006), and so the studies by Jones et al. (2006a, 2007) likely underestimate the impact of sea lice on juvenile salmon survival at the size relevant to the infestations in the Broughton Archipelago. The study by Webster et al. (2007) tested for the effect of salmon lice on juvenile pink salmon behavior, not survival. Webster et al. (2007) examined the juvenile pink salmon after 14 days and found most of the lice were gone before the lice reached their pathogenic motile stages. Studies that have reared salmon lice to motile stages on juvenile pink salmon weighing less than 1 g have observed high mortality of the infected juvenile pink salmon (Morton and Routledge, 2005; Krkošek et al., 2006). In addition, all experimental work on pink salmon mortality from sea lice does not reflect the sustained rate of new infections characteristic of the Broughton Archipelago as the fish migrate past multiple farms.

3. *NO CAUSE AND EFFECT RELATIONSHIP HAS BEEN DEMONSTRATED BETWEEN SEA LICE INFECTING PINK SALMON FRY AND LARVAL LICE RELEASED FROM SALMON FARMS*

Many studies have demonstrated spatial or temporal associations of sea lice infestation of wild juvenile Pacific salmon with salmon farming operations (Morton and Williams, 2003; Morton et al., 2004, 2005, 2007; Krkošek et al., 2005, 2006). Some of these studies have shown excellent agreement between models of sea lice dispersion and infection with field data of sea lice infecting juvenile pink and chum salmon migrating past salmon farms (Krkošek et al., 2005, 2006). These studies have allowed for significant sources of lice other than salmon farms. In fact, two of these studies statistically detected and quantified the transmission of sea lice from non-farm sources to wild juvenile pink and chum salmon (Krkošek et al., 2005, 2006). The estimated transmission from non-farm hosts has been consistently very low and overwhelmed by transmission from farm salmon (Krkošek et al., 2005, 2006; Orr, 2007).

a. *The "Fallow Route" Described in Krkošek et al. (2007) was Not Entirely Fallow in 2003*

The Broughton Archipelago is a system of linear inlets and channels. Because the juvenile pink salmon migrate from their natal stream to the open ocean, they have to migrate down the inlets and channels. Primary migration routes in a system like this do not require empirical evidence. Rather the migration routes are obviously based on the topography of the Archipelago. Krkošek et al. (2007a) clearly identified the fallow route as Tribune Channel and Fife Sound. The Doctor Islet farm, which was stocked with adult salmon in the spring of 2003, is not located in Tribune Channel, but rather in Knight Inlet. Krkošek et al. (2007a) clearly identified that some of the lice observed on the juvenile pink salmon in 2003 could have originated from salmon farms located outside this fallowed migration corridor, and this is known based on previous work documenting the spread of lice from the Doctor Islet farm (Krkošek et al., 2005). It is true that Sergeants Pass and Humphrey Rock salmon farms were stocked with smolts later in the spring of 2003. These farms could not have been a source of lice because the stocked smolts enter the ocean without lice, and there was insufficient time for sea lice to colonize the smolts, reproduce, and become a significant source of lice to infect the wild juvenile salmon migrating past these farms.

b. *There is No Evidence that a "Pre-Infestation Period" Actually Existed*

There is a strong basis for assuming an *L. salmonis* pre-infestation period existed. In areas without salmon farms, the prevalence of salmon lice on juvenile pink salmon during their first 1–3 months of marine life is less then 5% (Wertheimer et al., 2003; Morton et al., 2004; Krkošek et al., 2007b; Peet, 2007). The low prevalence of salmon lice on juvenile pink salmon in these areas during this time is because the vast majority of the adult wild Pacific salmon that carry the parasite are located offshore when the juvenile salmon enter sea (Groot and Margolis, 1991; Krkošek et al., 2007b). In this way, salmon migration protects juvenile pink salmon from salmon lice during early marine life (Krkošek et al., 2007b). Salmon lice infestations of juvenile pink salmon have only been observed in areas with salmon farms, and the primary source of salmon lice has been consistently identified to be salmon farms (Morton and Williams, 2003; Morton et al., 2004, 2005, 2007; Krkošek et al., 2005). Salmon lice infestations of juvenile pink salmon are conspicuous, and because the Broughton Archipelago is inhabited by biologists, fishermen, and First Nations people, it is unlikely that the infestations occurred before 2001 without notice. The sudden occurrence of the infestations could be explained by farmed salmon regional density in the Broughton Archipelago exceeding a host density threshold that previously suppressed outbreaks. Such thresholds are common in epidemiology (May and Anderson, 1991; Grenfell and Dobson, 1995) and are the basis for culling as a means for disease control in domestic and wild animals. Such thresholds, however, may be difficult to predict and identify (Lloyd-Smith et al., 2005).

c. *Farmed Salmon are Not the Only Source of Either* **C. clemensi** *or* **L. salmonis** *in the Broughton Archipelago*

The infestations associated with the rapid decline in Broughton Archipelago pink salmon populations are *L. salmonis*, not *C. clemensi* (Morton and Williams, 2003; Morton et al., 2004, 2005; Krkošek et al., 2006). Much previous work by

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some of the authors has examined the sources of sea lice infesting juvenile salmon in the Broughton Archipelago (Morton and Williams, 2003; Morton et al., 2004, 2005; Krkošek et al., 2005, 2006). None of this work has ignored the presence of alternate hosts for sea lice in the Broughton Archipelago. In fact, some of the studies have specifically tested for the presence of natural origin sea lice in the Broughton Archipelago and quantified how many lice are coming from these natural hosts (Krkošek et al., 2005, 2006). These analyses have indicated that the vast majority of sea lice infecting wild juvenile salmon in the Broughton Archipelago have originated from farm salmon. It is simply not true that sea lice commonly infest juvenile pink salmon everywhere in the Northeast Pacific. The studies examining salmon lice infections on juvenile pink salmon during their first 1–3 months of marine life in areas without salmon farms in the Northeast Pacific have found salmon lice on less than 5% of the juvenile pink salmon when the salmon are less than 80 mm fork length (Wertheimer et al., 2003; Morton et al., 2004; Krkošek et al., 2007b; Peet, 2007). Three-spine stickleback cannot be the origin of salmon lice infestations because stickleback are distributed throughout the North Pacific coastal waters, whereas *L. salmonis* infestations of wild juvenile Pacific salmon occurred only in areas with salmon farms (Morton and Williams, 2003; Morton et al., 2004, 2005, 2007; Krkošek et al., 2005, 2006), and infestations of juvenile salmon near salmon farms are dominated by larval copepodid and chalimus lice, whereas salmon lice do not survive to reproductive age on stickleback (Jones et al., 2006a, 2006b).

d. The Effects of Salinity and Temperature on Development and Survival of Sea Lice Larvae are Poorly Documented

In our *Science* report (Krkošek et al., 2007a), we did not investigate the effects of salinity and temperature on sea lice larvae as Brooks and Jones (2008) suggest. Rather, we investigated the relationship between salmon returns and measured levels of sea louse infection on juvenile pink salmon. However, it is known that abiotic factors such as temperature and salinity affect salmon lice survival and developmental rates (Stien et al., 2005; Bricknell et al., 2006). In our earlier work examining salmon lice infestations of wild juvenile salmon (Krkošek et al. 2005, 2006), the louse developmental rates estimated at the observed ocean temperatures were related to those expected from experimental data (Stien et al., 2005) by the average juvenile salmon migration speed, ∼1 km per day (Krkošek et al., 2006). In other work, the effects of salinity on sea lice abundance on wild juvenile Pacific salmon were insignificant (Morton et al., 2004, 2007), possibly because of louse behavior. Salinity is vertically distributed in the water column and larval lice have a diel vertical migration (Heuch et al., 1995) and can select locations suitable for their survival and/or transmission (Heuch, 1995). The behavior of lice can combine with these physical variables including tides, currents, and wind to generate spatial distributions of nauplii and copepodids from a point source of release that take a variety of forms, including those observed in the Broughton Archipelago (Gillibrand and Kate, 2007).

e. The Dispersion of Sea Lice between Hatching and Molting to the Infective Copepodid Stage are Not Considered in the Models of Krkošek et al. (2007)

In our *Science* report (Krkošek et al., 2007a), we did not investigate sea lice dispersion as Brooks and Jones (2008) suggest. Rather, Krkošek et al. (2007a) investigated the effects of *L. salmonis* infestations on wild pink salmon population dynamics. However, in some of our previous work, we have used a model of sea lice dispersion as part of the analyses of sea lice infecting juvenile salmon migrating past salmon farms (Krkošek et al., 2005, 2006). This model tracked sea lice development through nauplii and then copepodid stages, and was parameterized by data on the current speeds measured in the Broughton Archipelago (Krkošek et al., 2006). This constrained model, which represents the simplest possible model of sea lice dispersal, explains the data very well and has been spatially, temporally, and taxonomically replicated (Krkošek et al., 2005, 2006). The predictions cited by Brooks and Jones (2008) of sea lice larvae being dispersed from the Broughton Archipelago before the lice reach infectious stages (Brooks, 2005) are probably overestimated because the models overestimate advective flow, do not include the effects of wind on sea surface water flow, and they do not represent the behavioral ecology of planktonic larval sea lice. Inclusion of these factors can give rise to a wide range of dispersion patterns for sea lice larvae, including those observed in the Broughton Archipelago (Gillibrand and Kate, 2007). The theoretical oceanographic model of Gillibrand and Kate (2007) does not refute the connections between sea lice and salmon farms in the Broughton Archipelago, but rather shows sea lice infestation patterns observed in the Broughton Archipelago are within the range of those predicted by their model.

f. Prophylactics and Sea Lice Dispersion

Our *Science* report (Krkošek et al., 2007a) tested for and quantified the effects of *L. salmonis* infestations of wild juvenile pink salmon on wild pink salmon population dynamics in the Broughton Archipelago. Contrary to Brooks and Jones (2008) interpretation of Krkošek et al. (2007a), we did not model sea lice dispersion, assume a steady state dispersion model, estimate the production of sea lice nauplii on salmon farms, or investigate the effects of prophylactic treatment on sea lice abundances on farm salmon. Brooks and Jones (2008) claim the prophylactic treatments have reduced sea lice abundance on salmon farms, which may be the case, but they provide no supporting evidence for their claim. The effects of prophylactic use on sea lice control on salmon farms and sea lice transmission from farm to wild salmon is an important line of future research,

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but was not the focus of our *Science* report (Krkošek et al., 2007a).

4. ANALYSIS OF THE ENTIRE PINK SALMON DATABASE SUPPORTS CONCLUSIONS OPPOSITE TO THOSE REACHED BY KRKOŠEK ET AL. (2007)

a. Misleading Regression Analysis

In our *Science* report (Krkošek et al., 2007a), we did not conduct a regression analysis. Rather, we fit the stochastic Ricker model to estimates of the number of pink salmon returning annually to rivers on the Central Coast of British Columbia. The Ricker model is well established in fisheries science (Hilborn and Walters, 2001) and is the preferred method for estimating population growth rates (Myers et al., 1999) and testing for density dependence in time series data of population abundances (Dennis and Taper, 1994; Mueter et al., 2002). Brooks and Jones (2008) place high emphasis on the coefficients of determination in their regression analysis, but these statistics are meaningless in this context because of the problem of non-independence between $x$and $y$variables. Because of the dependence of $\ln[n(t+2)/n(t)]$ on $n(t)$ in the Ricker model, the variation in the data must be represented by parametric bootstrapping (Dennis and Taper, 1994). Brooks and Jones (2008) advocate using non-linear regression to analyze the data, but fail to describe how the variation in the data can be correctly represented in such an analysis. More fundamentally, they fail to explain the biological significance of such an analysis.

b. Incomplete Model

Brooks and Jones (2008) suggest the stochastic Ricker model used in Krkošek et al. (2007a) was inadequate to model pink salmon population dynamics. The stochastic Ricker model is a nonlinear stochastic model that captures density-dependent mortality as well as stochastic environmental variation (Dennis and Taper, 1994). The Ricker model may be the most fundamental model in fisheries science and is used widely in fisheries and ecology (Dennis and Taper, 1994; Myers et al., 1999; Hilborn and Walters, 2001; Brook and Bradshaw, 2006). The Ricker model directly models overcompensation - the cycle of population crash following high brood-year abundance (Kot, 2001) and so fully accommodates the high spawner abundance in 2000. The population growth rate, r, is estimated as the intercept, and density-dependent mortality is estimated as the slope when fitting the stochastic Ricker model (Dennis and Taper, 1994), meaning that these two parameters are well distinguished. Figure 3 in Krkošek et al. (2007a) shows that a common slope parameter (strength of density dependence) fit all the data well, including the data from the Broughton Archipelago during the sea lice infestations. This indicates at least two things. First, the sea lice infestations have affected the population growth rate but not density-dependent mortality, which is expected from theory (Krkošek et al., 2007a, 2007b). Second, and importantly, the density-dependent parameter estimated from all the data represents well the high spawner density and subsequent collapse that occurred for Broughton pink salmon populations in 2002. This latter point can be seen by the fact that there are no major outliers in the data from the model fit in panel C relative to the model fits in panels A and B in Figure 3 in Krkošek et al., 2007a. Brooks and Jones (2008) introduce a new alternative model that supposedly tracks fresh and marine water quality, predation, and several density-dependent factors such as food availability, horizontally transmitted disease agents, and random disease effects. The model looks interesting, but Brooks and Jones (2008) provide no quantitative basis for its validity, nor any empirical evidence that it is a suitable alternative model. It is not clear how the Brooks and Jones (2008) model accounts mechanistically for the effects they list, and it is difficult to imagine a suitable dataset that contains sufficient information to estimate all the parameters.

c. Selective Use of Data

Brooks and Jones (2008) combine all the pink salmon populations as though they were one population. The problem with this approach is that the functional unit in the pink salmon metapopulation structure is the odd- or even-year lineage in each individual river, not the regional summation of many rivers. Figures 2 and S1 in Krkošek et al. (2007a) show clearly that there is substantial variation in the data at the individual river level. This variation and the information it contains about the processes underlying it is lost when simply summing the escapement estimates. The natural periodic declines in the summed escapement data do not provide an alternate explanation to our results in Krkošek et al. (2007a). A more careful examination of the variation in the individual populations of Figure 2 in Krkošek et al. (2007a) shows that the catastrophic event currently affecting Broughton pink salmon populations is unprecedented, rather than common. Table 1 shows that all the periods of decline in summed escapement estimates identified by Brooks and Jones (2008) do not yield negative growth rates and extinction predictions when applying our analytical approach. This is because trends in summed escapement data reflect trends in only the largest populations, and, while the largest populations may have declined due to nonlinear density dependence, the smaller populations did not. Similar obfuscation of ecological processes by analyzing data at the stock complex level rather than the individual river level is known elsewhere in fisheries, where simulation models show that evidence for depensation is lost at the stock complex level when it is in fact present at the individual population level (Frank and Brickman, 2000). With the analysis that Brooks and Jones (2008) conduct, some populations could go extinct, and that may not be statistically detectable or even evident in the data if other populations were healthy, declining less rapidly, or equally declining but starting with higher abundance. Because the Glendale populations had recently increased due

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to the spawning channel, this hides the trends happening in the other populations. By analyzing the data at a level that permits examination of all the variation it contains, it becomes clear that all the populations, including Glendale, had significantly negative population growth rates during the sea lice infestations (Krkošek et al., 2007a).

d. Incomplete Analysis

The alternate analysis in this section of Brooks and Jones (2008) involves fitting arbitrary polynomials to log-transformed summed escapement and log-transformed time variables. Brooks and Jones (2008) do not provide a biological basis for the analysis or discuss the associated scientific inference. It is not clear to us what can be learned about the effects of sea lice on pink salmon population dynamics by fitting a cubic function to seven data points on log-transformed summed escapement and log-transformed year axes. The presentation by Brooks and Jones (2008) of the stochastic Ricker model as a linear regression through a plot of log escapement vs log year is not correct. The correct method for fitting the stochastic Ricker model and comparing parameter estimates is conducted by linear regression of $\ln[n(t+2)/n(t)]$ vs $n(t)$ to obtain the point estimates of the parameters and then parametric bootstrapping to construct the 95% confidence intervals on the parameter estimates (Dennis and Taper, 1994).

e. Current Trends in Pink Salmon Returns

Brooks and Jones (2008) suggest that recent trends in Broughton Archipelago pink salmon populations are increasing rather than decreasing (their Figure 8). Their analysis is based on regionally summed escapement estimates, and we have already explained how this obfuscates the variation and processes in the underlying data. But there are more fundamental flaws in their analysis. Odd- and even-year pink salmon lineages are independent populations that commonly have different abundances, population dynamics, and divergent genetics. It can be appropriate to pool data from odd- and even-year lineages if the data are first scaled by odd- and even-year mean abundances to make the data comparable (Krkošek et al., 2007a). The data must then be analyzed on $n(t+2)$ vs $n(t)$ or $\ln[n(t+2)/n(t)]$ vs $n(t)$ axes to represent the autocorrelation in the time series correctly. In their Figure 8, Brooks and Jones (2008) analyze the data as though the data points are all independent, which they are not, and the odd- and even-year lineages are not comparable because they have not been scaled appropriately. After excluding the year following the fallow for outmigrating juveniles (2004), there is only one valid $n(t+2)$ and $n(t)$ data pair present in their analysis (2003 and 2005). Despite these fundamental flaws, we attempted to verify the analysis in Figure 8 of Brooks and Jones (2008) using summed escapement data from the seven rivers in our *Science* report (Krkošek et al., 2007a) plus Glendale Creek. We found that the increasing trend claimed by Brooks and Jones (2008) in unscaled summed escapement data in the years 2002–2006 (excluding 2004) is not statistically significant ($t = 2.87$, $df = 2$, $p = 0.103$), and when the data are appropriately scaled the statistical results are further weakened ($t = 1.38$, $df = 2$, $p = 0.302$). This means that Brooks and Jones (2008) conclusion that Broughton Archipelago pink salmon are recovering is based on a statistically insignificant result from a flawed analysis. A careful examination of all the variation in the individual populations of Figures 2 and 3 in Krkošek et al. (2007a) indicates steep and unprecedented declines in Broughton Archipelago pink salmon populations during the sea lice infestations. This is confirmed by examination of Table 2, which shows that the survival of pink salmon populations during the infestation years was negative overall, with some underlying variation. The underlying variation is expected due to the high stochasticity in the data and model. While the populations decline overall, there are temporary exceptions due to the stochastic process (Figure 1).

Table 1 Point estimates of the population growth rate, r, for subsets of the Broughton Archipelago pink salmon escapement database suggested by Brooks and Jones (2008) to be periods of natural decline

Data period	Population growth rate, r
Odd years 1959–1969	0.45
Odd years 1983–1991	0.39
Odd years 2001–2003	Sea lice infestation years
Even years 1976–1984	0.12
Even years 1990–1996	0.64
Even years 2000–2006	Sea lice infestation years

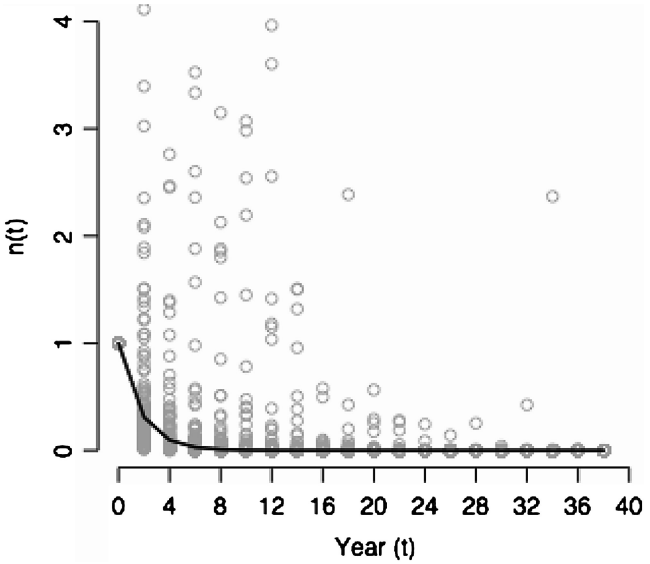

Figure 1 Simulation of the stochastic extinction model $n(t+2) = n(t) \cdot \exp(r + Z_t(0,v))$ described and parameterized in Krkošek et al. (2007a). Parameters are r, the population growth rate ($r = -1.17$), and v, the variance ($v = 1.91$). The environmental stochasticity term, Z, is a normally distributed random variable with mean 0 and variance v, which is drawn each generation. There are 100 stochastic simulations shown (grey open circles), all starting at historical mean abundance $n(t = 0) = 1$. The solid black line is the decline predicted by the deterministic model $n(t+2) = n(t) \cdot \exp(r)$.

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Table 2 Annual survival estimates, $\ln[n(t)/n(t-2)]$ per pink salmon population in the Broughton Archipelago during 2002–2006

	2002	2003	2004*	2005	2006
Ahta	−4.48	−3.16	3.40	1.05	−2.73
Kakweiken	−5.03	−1.93	2.46	0.75	−0.55
Kingcome	−3.79	−1.08	2.63	−1.94	−1.93
Wakeman	−2.54	1.02	0.86	−3.65	−1.55
Viner	−0.51	−2.10	1.57	−1.05	−3.02
Lull	−6.73	−5.31	4.28	3.55	−3.16
Ahnuhati	−4.11	0.40			
a2.82	−0.01	−2.54			
Glendale	−3.73	−2.12	3.59	0.32	−1.29
Average	−3.87	−1.79	2.70	−0.12	−2.10

*This year corresponds to the pink salmon cohort whose juvenile outmigration occurred during the fallow year 2003.

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