

The Effects of Water Temperature, Salinity and Currents on the Survival and Distribution of the Infective Copepodid Stage of the Salmon Louse (*Lepeophtheirus salmonis*) Originating on Atlantic Salmon Farms in the Broughton Archipelago of British Columbia, Canada (Brooks, 2005)—A Response to the Rebuttal of Krkošek et al. (2005a)

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Introduction

The following comments are offered in response to the rebuttal of Krkošek et al. (2005a) to Brooks (2005). The response has required a closer look at the model of Krkošek et al. (2005b) in order to unravel why the results of the model are *counter-intuitive* as acknowledged by the authors.

Conclusions Reached by Brooks (2005)

Contrary to the assertion made by Krkošek et al. (2005a), Brooks (2005) did not argue that “these effects combine to prevent the transmission of lice from farm salmon to sympatric wild juvenile pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon.” The purpose of Brooks (2005) was to review the effects of salinity, temperature, and net current vectors on the survival and dispersion of sea lice larvae (*Caligus* sp. or *Lepeophtheirus* sp.) with specific emphasis on the Broughton Archipelago of British Columbia, Canada. The primary conclusion reached in the article was that infection of new hosts by copepodid larvae does not occur in the immediate vicinity of the source of the nauplius I larvae, except where net current vectors are null vectors. Brooks (2005) clearly demonstrated the potential for larvae released from the Glacier Falls farm to reach the infective copepodid stage within the archipelago and to infect Atlantic salmon being cultured in the western portions of the Archipelago or to infect wild stocks of salmon migrating through that area.

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Salinity Effects on Sea Lice in the Broughton Archipelago

Existing data suggests that reduced salinity in the Broughton Archipelago during late spring and summer may naturally control sea lice. In 2003, Jones and Nemec (2004) documented variable salinity ranging between 3.6‰ in eastern areas of the archipelago to 28.6‰ in areas adjacent to Queen Charlotte Strait. The data was collected during a 15-week period between March and June 2003. Mean salinities ≥ 30 ‰ were not observed anywhere within the Archipelago during this period. Historical data collected since 1951 in Knight Inlet and presented in Figure 2 of Brooks (2005) indicates high temporal and spatial variability in both temperature and salinity. However, mean salinities have been below 25‰ from the beginning of June until the middle of October during the 50-year period of observation. Furthermore, the near elimination of sea lice on farmed Atlantic salmon at the Sargeant Pass and Humphrey Rocks salmon farms in July and August of 2003, with increased infections during late fall, winter, and early spring supports this hypothesis of a natural control (Figures 5 and 6 in Brooks (2005)). If confirmed, this hypothesis will explain why sea lice have not presented a challenge to Atlantic salmon producers in the Archipelago as they have in the Northeast Atlantic. In their rebuttal, Krkošek et al. (2005a) fail to acknowledge that Johnson and Albright (1991) reported that $< 0.01\%$ of the nauplii developed to an active (competent) copepodid stage at 25‰ salinity and an average (static and flowing water tests) of only 31% of the nauplii developed to competent copepodids at 30‰. Pike and Wadsworth (1999) reviewed the work of Johnson and Albright (1991) and similar to Brooks (2005), they concluded that "Complete development was only achieved at salinities ≥ 30 ‰ and, even then, it varied widely." The absence of competent copepodids at salinities < 30 ‰ was confirmed by Dr. Stewart Johnson (personal communication, October 29, 2005). In his *Recommendations*, Brooks (2005) noted that there is a need for additional information describing the development and survival of *C. clemensi* and *L. salmonis* larvae at temperatures of 7.5 to 12°C and salinities of 15 to 31‰ typical of the Broughton Archipelago during the March-to-June migration of pink and chum salmon fry. The response of organisms to environmental stressors, such as osmoregulatory stress created by higher or lower than optimal salinities, are typically continuously distributed. With this assumption of continuity, it is possible to obtain a sense of the effects of salinity on sea lice larvae by using the data provided in Johnson and Albright (1991). This was accomplished by assuming that survival to a competent copepodid can be modeled as $N_{\text{Copepodids}} = N_{\text{Nauplius}} \cdot \exp(-\Sigma \mu_i - \mu_{\text{salinity}}) \cdot \text{time}$. Where N is the number of animals hatched in a cohort during some period of time, Δt and $\Sigma \mu_i$ is the instantaneous mortality associated with all causes other than that associated with salinity (μ_{salinity}). Mortality associated with all effects other than salinity ($\Sigma \mu_i$) was estimated by assuming that there were no salinity effects at 30‰ and forcing μ_i to produce a mean survival of 31% at the end of 5 days of development to the copepodid stage at 30‰, corresponding to a mean temperature $\sim 8.2^\circ\text{C}$. This gave a value for $\Sigma \mu_i$ of 0.0088. The instantaneous total mortality equal to $0.0088 + \mu_{\text{salinity}}$ was then fit to the data for survival time and numbers of copepodids given in Johnson and Albright (1991) at salinities of 15, 20, 25, and 30‰ using linear regression to obtain a statistical model describing μ_{salinity} as a function of salinity (Figure 1). The resulting model ($\mu_{\text{salinity}} = 0.4404 - 0.01484 \cdot \text{salinity}$) explained 99% of the variation in the dataset and the coefficient on salinity was significant ($p < 0.01$). This continuously distributed model for μ_{salinity} was then used together with $\mu_i = 0.0088$ to predict the proportion of competent copepodids at some time t after hatching ($N_t = N_0 \exp^{-(0.0088 - 0.4404 + 0.01484 \cdot \text{salinity}) \cdot t}$) to construct the family of curves in Figure 2.

Figure 2 suggests significant reductions in competent copepodid production at all salinities < 30 ‰. It is emphasized that this model assumes no salinity effect at 30‰ and that the stress response is continuously distributed. A more definitive description of reductions

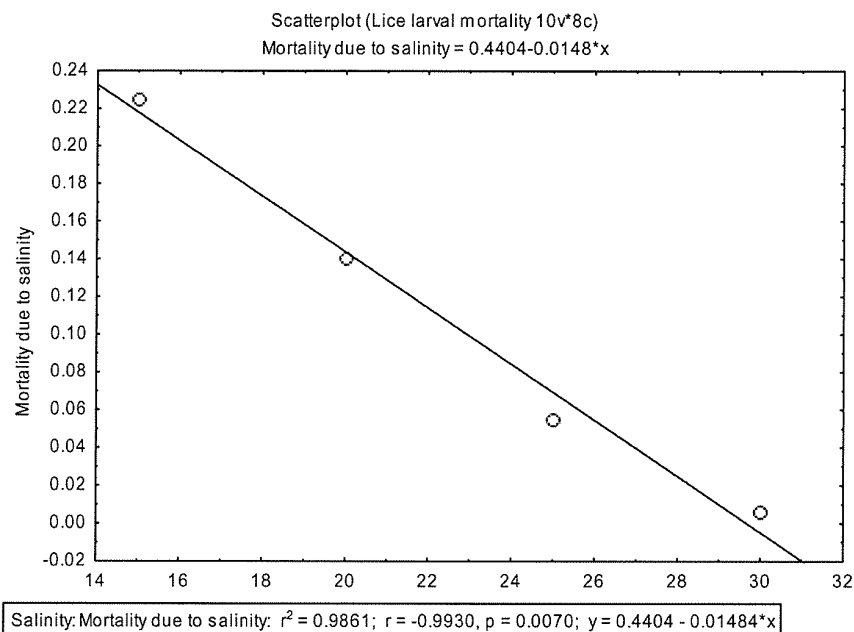


Figure 1. Results of a linear regression model predicting the loss of competent sea lice copepodids as a function of salinity using data presented in Johnson and Albright (1991).

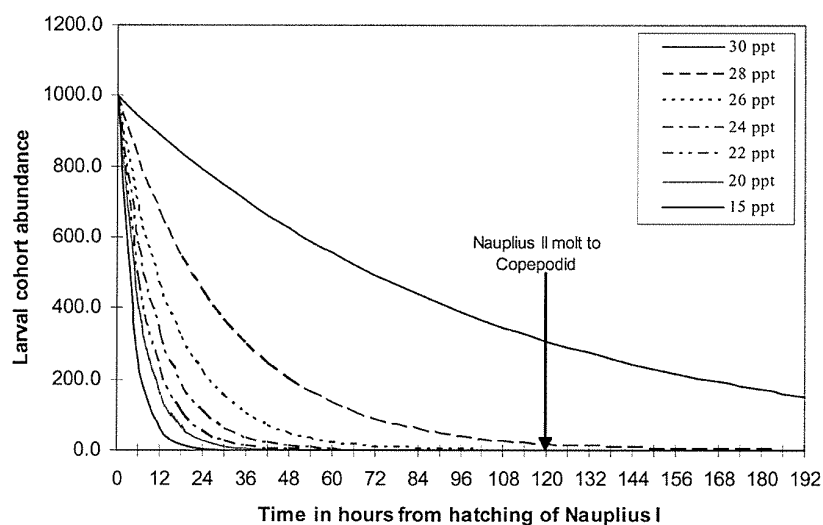


Figure 2. Abundance of larval *Lepeophtheirus salmonis* as a function of time and ambient salinity. Data from Johnson and Albright (1991) was used to estimate instantaneous mortality rates.

in competent copepodid production as a function of salinity must await the production of appropriate data. As mentioned previously, survival data to the copepodid stage should be obtained for both *Caligus clemensi* and *Lepeophtheirus salmonis* at salinities between 15 and 31‰ and temperatures between 7.5 and 12°C, which are typical of conditions in the Broughton Archipelago during the springtime out-migration of pink and chum salmon fry. The data should be collected in a two-by-two matrix design because there is likely an interaction between temperature and salinity. The conclusions of Johnson and Albright (1991) and this analysis do not support the assertion of Krkošek et al. (2005b) that “Rather these data suggest salinities ranging 25–30 ppt are suitable for copepodid development and survival.” Even without this analysis, that assertion is difficult to understand in light of the <0.01% competent copepodid production reported by Johnson and Albright (1991) at 25‰ and the average copepodid production of only 31% at 30‰.

Models of Larval Transport and Dispersion

Krkošek et al. (2005b) predicted the dispersal of sea lice larvae using an advection–diffusion model. In planning their pink salmon fry collections, Krkošek et al. (2005b) incorrectly interpreted data presented by D. Stucchi in 2003. Those preliminary results did not show any counter-clockwise current around Gilford Island that would significantly advect water from the Doctor Islets farm into the Tribune Channel as asserted by Krkošek et al. (2005a, 2005b). The model predictions of Foreman et al. (in press) clearly showed a significant seaward flow in Knight Inlet with some of this flow bifurcating into the Tribune Channel east (upcurrent) of the Doctor Islets farm. Diagrams of model output showing the seaward surface flow in the Knight Inlet were sent in 2003 to one of the authors of Krkošek et al. (2005b). This misinterpretation led the authors to analyze pink salmon fry in the Tribune Channel rather than downcurrent from Doctor Islets in Knight Inlet. Krkošek et al. (2005b) used this data to estimate diffusion and advection coefficients in their model. The result is that they estimated a seaward advective flow in Knight Inlet of -0.0056 cm/sec (counter-clockwise around Gilford Island) in April 2003 and 4.64 cm/s (seaward down Knight Inlet) in May 2003. Krkošek et al. (2005a) challenged a Knight Inlet mean advective flow rate of 9.3 cm/sec because it was thought to be inconsistent with the 30-day net current vector of 1.4 cm/sec at 261° True (seaward down Knight Inlet from Doctor Islets), which was also reported in Brooks (2005). Brooks (2005) was originally written in 2004. It was reviewed by 17 scientists in North America and Europe before submission for publication. The original manuscript did not include the particle-tracking exercise, but it relied on net current speeds measured over full lunar cycles at Broughton salmon farms (Table 2 in Brooks, 2005). Several reviewers emphasized the articles caveat that these site-specific net current vectors were likely not representative of the net currents transporting nauplii during the 4.2 to 5.8 days required for development to the copepodid stage. Publication of Brooks (2005) was delayed 6 months in order to include the more refined particle-tracking approach to understanding the advection of sea lice larvae from their source in the archipelago presented in Stucchi et al. (2005). The particle-tracking simulations in Brooks (2005) were based on the currents computed in a numerical circulation model of the region. A more complete description of the model used in our study and comparisons of its results with observations are detailed in Foreman et al. (in press), which is also an advection–diffusion model, but in this case the diffusion is explicit (rather than parameterized) in that it includes tidal motions directly. Furthermore, the average seaward flow γ is not a parameter in the model but a variable that is spatially dependant (x, y, z), and whose value is a direct consequence of the physics and forcing. In contrast, the diffusion coefficient D and the advective velocity γ are constants in Krkošek et al. (2005a and 2005b). The use of constants makes the solution

of the advective-diffusion equation tractable but ignores the important spatial variations in diffusion and advection. Krkošek et al. (2005b) failed to recognize that currents at Doctor Islet are not representative of the much faster net current speeds encountered just to the west of the site. In fact, the 1.4 cm/sec value for the mean seaward flow measured at the Doctor Islets (Brooks, 2005) site is not representative of the seaward flow across the breadth of Knight Inlet nor is it representative of seaward flow along the length of the inlet. We know from the observations of Baker and Pond (1995) in Knight Inlet that the surface mean-flow in mid-channel near Protection Point (9 km east of Doctor Islets) was about 14 cm/sec in May–June 1989 or about 10 times larger than the measured mean-flow at Doctor Islets. In addition, the net seaward flowing current speed of 1.4 cm/sec at Doctor Islets (Brooks, 2005) was measured using a current meter moored at a 15m depth and not at the surface. Observations from Knight Inlet (Baker and Pond, 1995) and in Tribune Channel and Fife Sound (Foreman et al., in press) show a vertically sheared seaward surface flow, which was strongest at the surface and diminished with depth. Thus the surface seaward flow at Doctor Islets was likely larger than the 1.4 cm/sec value measured at a depth of 15m. Clearly, spatial variability in the mean flow is an important characteristic of the flow, and it is not captured in the simple 1D model of Krkošek et al. (2005a, 2005b). We acknowledge that our model appears to overestimate the mean seaward surface flow in Knight Inlet (Foreman et al., in press), but using a constant value of 1.4 cm/sec in their 1D model, Krkošek et al. (2005a) have underestimated the seaward advection of the planktonic sea lice larvae. Furthermore, the predicted counter-clockwise flow around Gilford Island is not substantiated by any available oceanographic data. Because Krkošek et al. (2005a, 2005b) used sea lice data to predict diffusion and advection rates, the proper test of their model is a comparison of their diffusion and advection coefficients with empirical data. The estimation of the Krkošek et al. (2005a, 2005b) model parameters from field data of sea lice infecting juvenile pink and chum salmon produced essentially a zero value for the April 2003 mean-surface flow in Knight Inlet (Krkošek et al., 2005a, 2005b). This is a physically unrealistic value that, in part, may be explained by an overly simplistic advective-diffusion model that does not account for the spatial and temporal variability in the currents.

Larval Development and Mortality

In Krkošek et al. (2005a), equation 2 defines development of nauplii into copepodids at a constant rate μ such that mean duration of the naupliar stages of the louse is μ^{-1} . The laboratory experiment of Johnson and Albright (1991) and others have demonstrated that the development times of the naupliar stages of *Lepeophtheirus salmonis* are controlled by seawater temperatures. For example, at 10°C the average time taken from hatching to the copepodid stage was 3.6 days with a standard deviation of 0.2 days. Thus, at 10°C, there is a time lag of about 3.6 days after hatching when the nauplii do not moult to the copepodid stage. During that time lag, the currents transport the larvae seaward a distance that is dependant on the speed of the mean seaward flow γ . The development of the nauplii into the infective copepodid is age (time)-dependant and does not occur at a constant rate. Using a constant μ in Krkošek et al. (2005a), equation (2) has the biologically problematic effect of permitting development of the nauplii into copepods irrespective of age. A 1-day-old nauplius has the same probability of moulting into a copepodid as does a 3.6- or 6-day-old nauplius. This is a severe limitation of the model and the constant μ in Krkošek et al. (2005a) equation (2) should be replaced with a time-dependant function that represents the known age dependence of the naupliar to copepodid development.

Krkošek et al. (2005a, 2005b) assert that including mortality (ϕn) and a term defining loss of nauplii due to molting of the nauplius II to the copepodid stage (μn) explains their finding of high copepodid densities near the farm. Based on the report of Johnson and Albright (1991), the authors conclude that “larvae are three times more likely to die than survive and so $\phi = 3\mu$.” Since μ represents the rate of molting to the copepodid stage, the authors are asserting that mortality results in the molting rate increasing from μn to $4\mu n$. They continue with the assertion that “Perhaps surprisingly, this brings the expected distribution of copepodids nearer to the source.” The actual reason this “brings the copepodids nearer to the source” is that in equation (4), the rate of molting to the copepodid stage is now expressed as $(-\mu n + 3\mu n) = -4\mu n$, which more quickly depletes the naupliar population resulting in increased copepodid abundance. Incorrectly modeling the copepodid abundance, based on the loss of nauplii due to all causes, results in predicting copepodid creation near the point of naupliar hatching because mortality occurs at a constant rate ($-4\mu n$ in the Krkošek et al. (2005a, 2005b) model) and thus it begins as soon as the nauplii are hatched. It is emphasized that nauplii lost from the population due to mortality do not contribute to the copepodid population. As will be seen in the following section, one cannot predict the spatial distribution of copepodids by convolving the scaled (PDF) version of equation 3 with itself once until the minimum time to development of the copepodid stage is reached (3.6 days at 8.2°C). The result is that the model of Krkošek et al. (2005a, 2005b) is irreconcilably flawed. The molting of nauplius II to the copepodid stage does not occur at a constant rate beginning at hatching. This event in the larvae’s life cycle occurs following development through two naupliar stages at a time that is primarily dependent on water temperature. These problems occur because the authors have ignored the biology of the parasite.

A Biologically Based Conceptual Model of Larval Transport and Dispersion

Figure 3 provides a conceptual model based on the known life history of sea lice larvae. The cohort of larvae is assumed to have been released during some incremental period of time (Δt). Each cohort of larval lice released from a source would behave in a way similar to that described in Figure 3. The continuous and constant hatching of larvae from a source would simply maintain the given distribution of larvae—it would not change the shape of, or displace in time or space, the distribution of the developmental events. The temporal variances associated with the curves in Figure 3 are based on standard deviations provided in Johnson and Albright (1991). Mortality of the nauplius larvae in Figure 3 results in the production of 60% competent copepodids and therefore represents full strength sea water (34‰). Figure 3 includes advective transport of the larvae from a source, mortality as a function of time, identification of the predicted time at which Nauplius II molts to the copepodid stage, and further transport of the infective copepodids. A second ordinate, scaled to represent a constant current speed of 2.0 cm/sec, is provided. The temporal scale would not be affected by changes in current speed. However, the spatial ordinate would be expanded or contracted to represent faster or slower net current speeds. Diffusion causes an initially leptokurtic Gaussian spatial distribution to become more platykurtic with time. However, diffusion is a random process and it does not affect the location in time or space of the modes of the distributions of the larvae. The approach taken by Krkošek et al. (2005a, 2005b) of convolving the naupliar population on itself to define the copepodid population is only appropriate at the time that the cohort of Nauplius II larvae are molting to the copepodid stage. At a temperature of 8.2°C, this occurs 3.6 days after hatching. This approach would ignore the increased natural mortality associated with ecdysis, which is a period of high stress and mortality in most crustaceans. In Figure 3, this excess mortality is described at the molt

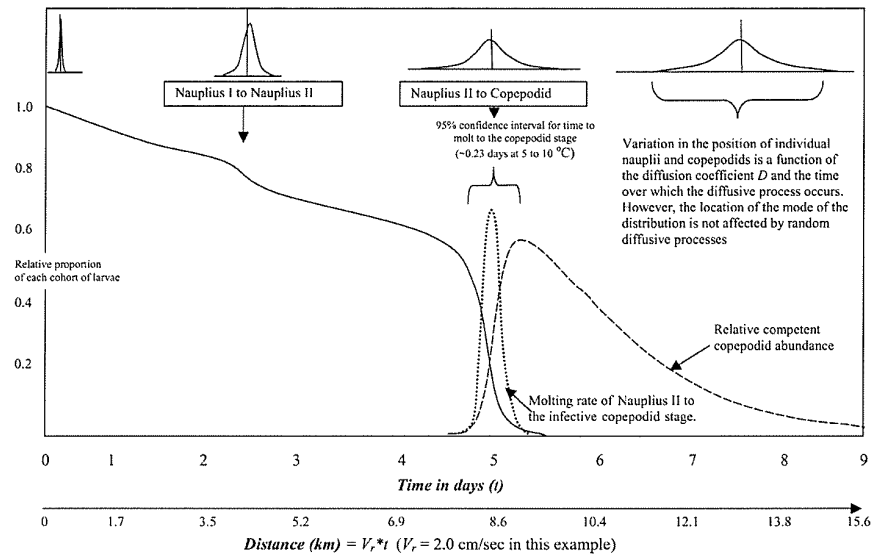


Figure 3. Conceptual model describing the life history of sea lice larvae and their dispersion using an advection–diffusion model. Diffusion, described at the top of the figure, is a random process that does not influence the location of the modes of the advecting population. Survival is a function of time and not of the number of larvae as described by Krkošek et al. (2005a, 2005b). The distance scale in this example assumes a net current speed of 2.0 cm/sec.

from Nauplius I to Nauplius II. In an area where the average net current speed is 2.0 cm/sec, Nauplius II does not molt to the infective copepodid stage until a minimum distance of ca. 7.75 km from the point at which the larvae hatched is reached. Peak rate of molting to the copepodid stage occurs at 8.6 km. The population of copepodids is described by integrating the molting rate over the period of time this event is predicted to occur. Ignoring ongoing mortality, including the expected mortality associated with ecdysis during the Nauplius II to copepodid molt, this is the time (8.6 ± 0.23 days) during which the naupliar population could be convolved upon itself to estimate the population of copepodids. As pointed out earlier, the Krkošek et al. (2005a, 2005b) procedure of convolving the naupliar population upon itself from the point of hatching from the egg is one of the errors that resulted in predicting peak pink salmon fry sea lice infection rates in the vicinity of the source of Nauplius I.

Interpretation of the European Literature

Krkošek et al. (2005a) cite the genetic similarity of sea lice on farmed and wild salmon reported by Todd et al. (2004). This is not surprising as Atlantic salmon enter the marine environment free from sea lice and are initially infected by copepodids originating on wild hosts. This was illustrated by Brooks (2005) with reference to the infection of a new cohort of Atlantic salmon at the Sargeant Pass farm, which is located upcurrent from any source of larval lice released at other salmon farms. Infections here and at the Humphrey Rocks farm were seen to have been associated with wild sources of copepodids. Beamish et al. (2005)

found that virtually all adult salmon returning to Central British Columbia watersheds in 2004 were infected with sea lice. Pink, chum, and sockeye salmon had average intensities ranging from 41.5 to 52.0 lice/infected fish. Significant differences in sea lice infection parameters were not found between fish returning to the Smith and Rivers Inlets, where there were no salmon farms and the Queen Charlotte Strait adjacent to the Broughton Archipelago where there were salmon farms. Returning adult pink salmon held an average of 3.4 gravid female lice/fish. Assuming that 965 nauplius larvae were hatched from each gravid female (Pike and Wadsworth, 1999), it is reasonable to hypothesize that the 3,621,049 pink salmon returning to the Broughton Archipelago watersheds in 2000 brought 11,880,660,000 lice larvae with them into the archipelago—at a time (fall) when rising surface salinities are typically more conducive to survival of all life stages of *L. salmonis*. Revie et al. (2003) found that sea lice levels in the preceding 6 months were an important factor describing sea lice infection endpoints on Atlantic salmon farms in Scotland. The finding of high intensities of sea lice, including *L. salmonis*, on three-spine stickleback (*Gasterosteus aculeatus*) in the Broughton Archipelago suggests that there is an abundant resident host capable of carrying at least a portion of this infusion of sea lice into the following spring when Morton et al. (2004) reported sea lice infections on out-migrating juvenile pink salmon.

Krkošek et al. (2005a, 2005b) continue to confuse the noninfective nauplius stage of sea lice with the infective copepodid stage. In their review of the European literature they assert that Costelloe et al. (1998) found higher densities of sea lice larvae near the Killary Salmon Farm and that this is consistent with their finding of higher infection rates of pink salmon fry in the Tribune Channel near salmon farms. The fact is that Costelloe et al. (1998) observed fewer larval *L. salmonis* larvae near the Killary Salmon Farm (station K12) in comparison with higher densities near the Bundorragha and Erriff rivers located 8 and 14 km from the farm. For instance, in 1995 Costelloe et al. (1998) collected a total of 11 larvae at stations K7 to K12 located in the Outer Harbour where the farm is located. Of these, four were nauplii recovered beside a cage at the Killary Salmon Farm and seven were copepodids collected at the mouth of the Bundorragha River (K8 and K9) and at station K7 located approximately 9 km from the farm. In 1996, Costelloe et al. (1998) summarized their collections near the salmon farm by stating that, “Larvae were recovered on most sampling dates, the majority being at the naupliar stage of development with few copepodids being recovered in any of the samples.” Costelloe et al. (1998) did not find any copepodids near the farm in 1995 and very few in 1996. High concentrations of infective copepodids were observed in nearshore areas adjacent to the natal streams from which outgoing sea trout were migrating. Hydrodynamic studies by Costelloe et al. (1998) led them to conclude that the nauplii released from the salmon farm, located near the mouth of the harbor, were swept out to sea before they developed to the infective stage and that the source of the copepodids infecting the sea trout smolts were most likely wild fish—not the farmed salmon.

Ongoing Studies in the Broughton Archipelago

The Canadian Department of Fisheries and Oceans (Beamish et al., 2005; Jones and Nemec, 2004; Jones et al., in press) have been conducting intensive studies describing the prevalence, intensity, and abundance of sea lice on pink and chum salmon in the Broughton Archipelago since 2003. These studies have resulted in the recent publication of a series of *Fact Sheets* regarding their findings. These are available at http://www.dfo-mpo.gc.ca/media/infocus/2005/20051011b/info_e.htm#3. Perhaps Krkošek et al. omitted a discussion of these papers because after 3 years of study, the Canadian Department of Fisheries has concluded the following, which are direct quotes from the *Fact Sheets*:

- Sea lice are very common on all Pacific salmon adults during their return to the freshwater lakes and streams in which they were born. Commercial fishermen and First Nations people, both accustomed with handling salmon, have for generations reported seeing sea lice on wild adult Pacific salmon.
- The presence of sea lice in the ocean is a broader marine ecosystem puzzle than simply pointing at salmon farms. It emphasizes the need for additional information on sea lice biology and abundance. It is true that sea lice and wild salmon have been an issue in many areas of the world involved with salmon farming. However, no direct cause-and-effect has been determined in these areas.
- Sea lice populations are affected by environmental conditions and thrive in warm water temperatures and high salinity levels. Ocean temperatures and lower levels of freshwater runoff from reduced annual rainfall along the British Columbia coast may currently be contributing to higher levels of sea lice.
- Our results show that, despite higher levels of sea lice observed on pink and chum salmon throughout the study area in 2004 than what we observed in 2003, there was no evidence on the fish sampled that showed this had a negative effect on the growth and condition of infected fish. It is our view that salmon farms and wild stocks can co-exist.
- Pink salmon returns to the Broughton Archipelago and Knight Inlet returned to average levels in 2004—approximately one million—consistent with what had been observed during the last 50 years. This is noteworthy because many opponents to salmon farms predicted poor returns given the presence of sea lice on wild salmon in 2003.
- Since 1987—the introduction of salmon farms to the area—average returns of pink salmon have been higher than the 50-year average. The chart previously discussed (see the DFO website or Brooks (2005)) and our research to date, does not support allegations that there are collapses in pink salmon populations in this area. (The responding author's note that returns of pink salmon to the Broughton Archipelago in 2005 are similar to those recorded in 2003, when some salmon farms were fallowed. While still incomplete, 2005 returns appear to be above the 50-year average odd-year return.)

Conclusions

Neither this response, nor Brooks (2005) assesses the contribution of sea lice from farmed salmon to natural levels found in the Broughton Archipelago. The results of ongoing and planned investigations by a multidisciplinary team of scientists from several parts of the world will provide the information that is necessary to make that assessment. These articles simply point out the importance of considering the biology of sea lice and oceanographic conditions such as net current vectors, salinity, and water temperature in predicting appropriate *zones of infection*.

Morton et al. (2004) concluded that pink salmon fry collected within 250 m of salmon farms in their second year of production carried 8.8 times as many sea lice as did fry collected from areas distant from salmon farms. As firmly as ever, the responding authors believe that infection of new hosts by sea lice copepodids does not occur near the point of larval hatching—except where net current vectors are null vectors. We believe that there are significant basic flaws in the model of Krkošek et al. (2005a and 2005b). These flaws exist because the authors did not include important biological factors describing the life

history of sea lice in their model and they did not consider empirical evidence describing the hydrodynamics of Knight Inlet and Tribune Channel. These omissions and significant modeling errors, such as assuming that Nauplius II molts to the copepodid stage at a constant rate beginning at the point of hatching and the authors' procedure of combining molting and mortality followed by convolving the naupliar population on itself to estimate the copepodid population, have led to a model that is seriously flawed and that is, as acknowledged by the authors, "counterintuitive." The advection and turbulent diffusion of a cohort of sea lice released during some time interval (Δt) is like a puff of smoke in the wind. A continuous release of larvae is simply a stream of cohorts, each of which develops in a similar manner. When was the last time you tracked a puff of smoke released into a 5 km/hr wind and after an hour found that it was still at the smoke stack?

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