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The Effects of Water Temperature, Salinity, and Currents on the Survival and Distribution of the Infective Copepodid Stage of Sea Lice (*Lepeophtheirus Salmonis*) Originating on Atlantic Salmon Farms in the Broughton Archipelago of British Columbia, Canada

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Recent reports claim that pink salmon fry are heavily infected by Lepeoptheirus salmonis *as they pass salmon farms in the Broughton Archipelago. Hydrodynamic studies reveal that the top 25 to 40 m of water generally flows seaward through the archipelago under the influence of freshwater, reducing surface salinity from 15–25% from June through November of most years. Sea lice larvae do not consistently develop to an infectious stage at salinities <30‰—providing a natural control in the archipelago. The larvae require 4.2–5.8 days to develop to the infective stage at the temperatures typical during the time that pink salmon fry are migrating. Net current speeds measured at 15 salmon farms are predicted to carry most sea lice nauplii 7.3–10.0 km downcurrent and out of the archipelago before they become infective. A particle-tracking model predicts that nauplii released in the vicinity of two farms located deep in the archipelago are carried 10–40 km from the farms before they become infective. These predictions are consistent with the European experience and suggest little potential for salmon farms to be self-infecting or to infect migrating wild fish in their immediate vicinity, except where net current vectors are zero. A clearer picture of sea lice epizootics requires detailed knowledge of site-specific oceanographic characteristics and the affects these have on sea lice survival and dispersal during development to the infectious copepodid stage.*

Keywords Atlantic salmon, sea lice, dispersal, pink salmon, British Columbia

Introduction

Sea lice have not presented a significant challenge to Atlantic salmon producers in the Pacific Northwest (Johnson, 2004). Morton et al. (2004) reported higher abundance and intensity of sea lice (*Lepeophtheirus salmonis*) on juvenile pink salmon (*Oncorhynchus gorbuscha*) collected within 250 m of salmon farms containing fish in their second year of growth when compared with those collected at further distances during 2001 and 2002. Krkosek et al. (2005) asserted that sea lice infections on pink salmon were 73 times greater than ambient rates adjacent to a salmon farm in the Broughton Archipelago. Pink salmon

have a 2-year life cycle and juveniles migrating out of the Broughton Archipelago in the spring of 2001 returned as adults in the summer and fall of 2002. The number (3, 621, 049) of pink salmon returning in 2000 declined dramatically to 122, 924 in 2002 (BCMAFF, 2005) and concern has been expressed that sea lice infections associated with salmon aquaculture were responsible. The purpose of this report is to examine the importance of water temperature, salinity, and currents on sea lice dynamics and to review recent data describing the epizootiology of sea lice in pink salmon fry migrating through the archipelago.

Background

European Sea Lice Studies

Cultured salmon are introduced to the marine environment from freshwater, free of sea lice. At some point after entering the growout phase, they become hosts to sea lice, which are ubiquitous in temperate marine environments. Sea lice, particularly *L. salmonis*, have adversely affected cultured Atlantic salmon production in Scotland, Ireland, and Norway for decades (Brandal and Egidius, 1979). The control of sea lice and their damage to farmed salmon have been estimated to cost producers £15–30 million in Scotland each year (Pike and Wadsworth, 1999). Sea lice epizootics also affect wild populations of Atlantic salmon (Grimnes and Jakobsen, 1996), sea trout, *Salmo trutta*, (Tully et al., 1993a, 1993b) and sockeye salmon in British Columbia (Johnson et al., 1996). The importance of Atlantic salmon cultured in marine net-pens as sources of caligid copepodids and their effects on wild stocks has been studied in Europe without reaching a consensus among authors. Tully and Whelan (1993) concluded that over 95% of the larval *L. salmonis* produced in some areas on the west coast of Ireland during 1991 originated on Atlantic salmon farms. The authors asserted that, "Because the copepodid of *L. salmonis* is obliged to find a host within days of molting from nauplius II, its transmission must occur close to the location where nauplii are produced." Penston et al. (2002) reported highest nauplius:copepodid ratios near an Atlantic salmon farm with reductions in the ratio as a function of distance from the farm and hypothesized that the farm was the source of the larvae. Supporting the thesis that salmon farms are significant contributors of sea lice found on wild fish, McKibben and Hay (2002) reported higher densities of copepodids near river mouths when local salmon farms were in their second year of production (i.e., nearing harvest).

Costelloe et al. (1996) took plankton samples from within, and at distances of 10 m to 1 km from commercial salmon cages and found highest densities of larvae within the cages (maximum of 66.1/m^3). The numbers of nauplii decreased from 4.8/m^3 at 10 m to 0.4/m^3 at 1.0 km. Costelloe et al. (1998) studied the interaction between salmon farms, sea lice, and wild stocks of Atlantic salmon for several years in Killary Harbour on the west coast of Ireland. Their research included drogue studies to evaluate seston transport vectors from a salmon farm located at the mouth of the harbor. They concluded that sea lice nauplii hatched at the farm were swept out of the harbor into the open ocean and found no evidence of sea lice transport from the farm into the inner harbor where large numbers of *L. salmonis* copepodids were observed. The intensity of lice infections on wild salmon were higher than on farmed salmon and Costelloe et al. (1998) concluded that the high numbers of copepodids observed in the inner harbor, waiting to infect out-migrating salmon smolts, originated from wild fish—not farmed salmon. Marshall (2003) assessed sea lice infestations on sea trout in Laxford Bay on the west coast of Scotland during Atlantic salmon production and a 1-year fallow period. During production, she found that wild lice abundance did not lag the production of nauplii on the fish farm, which would be expected if the farm were the

source of lice and she concluded that, "it would appear from this study that the abundance of lice on wild fish is not directly related to that on the neighboring farm." Her study found high lice abundance in the spring when sea trout and salmon were migrating to sea, even when the salmon farm was fallow; suggesting that the spring increase in sea lice infections of wild fish was a natural event. In contrast to the assertion by Krkosek et al. (2005) that Costelloe et al. (1998) and Marshall (2003) reported a link between lice parasitizing wild salmonids and the presence of salmon farms, both of these authors actually concluded that the source of the infective copepodids was most likely wild fish—not farmed fish.

Life History of Lepeophtheirus Salmonis

Fecundity. Tully and Whelan (1993) and Wooten et al. (1982) reported that *L. salmonis* parasitizing wild Atlantic salmon were larger and carried approximately twice as many eggs as those found on farmed Atlantic salmon. Pike and Wadsworth (1999) noted that female lice on wild salmon from the west of Ireland produced 965 ± 30.1 eggs/louse compared with 758 ± 39.4 eggs/louse on untreated farmed salmon and 297 ± 19.1 eggs/louse on Atlantic salmon that were routinely treated to control lice. Several authors were cited reporting increases in fecundity during cold winter months (246–315 in January to March) with a decline in summer (107–175 eggs/louse in August). Generations of *L. salmonis* are produced continuously in series with new ovipositioning occurring within 24 h of hatching of the previous brood.

Brood generation time as a function of temperature. Tully (1992) used regression analysis to estimate *L. salmonis* generation times equal to $345-273*\text{Log}_{10}$ (temperature in °C). At a typical early spring temperature of 7.5°C in the Broughton Archipelago, the generation time is 106 days. During Broughton summers, when surface temperatures may reach 14–15°C, the generation time is reduced to 32 days.

Temperature affects on nauplius development to the copepodid stage. Tully (1992) summarized data describing the length of time that *L. salmonis* remains in the noninfective nauplius I and II stages as varying between 223.3 h at 5°C; 87.4 h at 10°C; and 50.0 h at 15°C. Tucker et al. (2000) showed that a larger proportion of copepodids fail to establish themselves on a host at 7°C than at 12°C.

Salinity affects on the development and life span of sea lice. Pike and Wadsworth (1999) summarized information indicating that adult lice die rapidly at salinities <12‰ and that while eggs hatched successfully at salinities as low as 15‰, survival was negligible. Survival improved at 20–25‰, but development to the copepodid stage remained low at salinities <30‰. Information measuring the survival of chalimus stages, as a function of salinity, was not found. However, the cited sensitivity of copepodids to salinities <30‰ suggests that the chalimus may also be sensitive to low salinity. Pike and Wadsworth (1999) summarized information indicating that 50% of *L. salmonis* were lost from infected fish entering freshwater within 24 h and that <10% survived more than 48 h. These references also indicate that a few adult sea lice can survive for up to 21 days in fresh water.

Life-span and survival of L. salmonis larvae. The nauplius and copepodid stages of *L. salmonis* are nonfeeding lecithotrophic larvae that drift imbedded in surface waters as part of the seston. They depend on yolk reserves to supply their energy needs until the copepodid finds a suitable host. This gives them a finite life span, which is dependent on temperature (Pike and Wadsworth, 1999; Tully, 1992). Survival of *Caligus elongatus* from hatching to the copepodid stage declined from 90% at 15°C to 60% at 5°C. Copepodids remain viable and capable of intercepting new hosts for between 4 days (Wootten et al., 1982) and 6 days (Voth, 1972) for *L. hospitalis*. Johannessen (1978) suggested that copepodids remain

infective for up to 30 days. However, Pike and Wadsworth (1999) questioned that value. For purposes of this analysis, copepodids will be assumed to be competent for an average of 5 days.

Behavior of L. salmonis larvae. The copepodid stage is positively phototactic and nonfeeding. The process of host location and attachment is energetically demanding, so depleted reserves at this point in their life cycle are critical, and reduced competency near the end of the copepodids' life span is expected. Copepodid larvae move to the surface during daylight and downward at night. Heuch et al. (1995) hypothesized that crossing over, as *L. salmonis* copepodids migrate upwards and salmon move downwards at daybreak, facilitates finding a host. Based on laboratory studies, they concluded that copepodids aggregated in steep salinity gradients. In single-step gradients of 2, 5, 15, and 34‰, 80% of copepodids accumulated at the bottom of the halocline in 34‰ water. Heuch and Karlsen (1997) observed a short-term burst swimming speed of 9 cm/sec for 1 second followed by a more prolonged speed of 2 cm/sec when stimulated to swim. The literature suggests that sea lice larvae remain at relatively shallow depths and the limited energy reserves of the nonfeeding nauplius makes long vertical migrations problematic. However, vertical migration patterns for sea lice have not been determined.

Migration of Pink Salmon Fry in the Broughton Archipelago

Pink salmon are found around the Pacific Rim from Washington State to North Korea at latitudes between 40 and 70°N. Small numbers have been reported occasionally from rivers as far south as North Central California. They are the smallest (1.0 to 2.5 kg/fish) of the Pacific salmon species. They are also the most abundant and represent 40% by weight and 60% in abundance of all commercially caught salmon in the North Pacific region. Pink salmon are anadromous and different stocks return in either odd or even years to complete a 2-year life cycle.

Pink salmon fry migrate to salt water more quickly than most salmonids at a size of ca. 35 mm. In British Columbia, downstream migrations begin in mid-March; peak in mid to late April; and may extend to the end of May (Heard, 1991). During their first few weeks of marine residence, the majority of fry are found in shallow water along shorelines. However, Heard (1991) noted that early age schools have been observed well offshore in British Columbia and Karpenko (1987) reported pink salmon fry in three hydrological zones during their first 3 to 4 months of marine residency. These included: (1) the littoral zone up to 150 m from shore; (2) open parts of inlets and bays from 150 m to 3.2 km from shore; and (3) open parts of Karaginskiy Gulf at distances of 3.2–96.5 km from shore. Distribution within these regions was related to the size of the fish, with larger fry more prevalent offshore in August and September. Following a few weeks to a few months in estuaries and nearshore habitats, pink salmon generally migrate to sea for 12–16 months (Heard, 1991). However, pink salmon in British Columbia and Washington State often spend 2 to 3 months in nearshore marine environments (Heard, 1991) and some pink salmon remain in Puget Sound and/or Hood Canal, Washington State, during their entire marine phase (NMFS, 1996). This trait has not been documented in British Columbia, but that may be associated with a lack of studies specifically addressing this issue.

Results of 2003 Sea Lice Monitoring Programs in British Columbia

The Canadian Department of Fisheries and Oceans examined Pacific salmon and several other species of marine fish for caligid infections during 2003 (Jones and Nemec, 2004).

The fish were collected by beach and purse seine (Hargreaves et al., 2004) from March 2 until June 8, 2003. Juvenile pink salmon were caught throughout the study. However, the peak catches in beach seines occurred from mid-April until the third week in May. Purse seine catches of larger juveniles in deeper water were near zero until the first week of May. Sporadically high purse seine catches were then reported until the studies termination on June 8, 2003. In general, their study suggested that pink salmon fry were most abundant in near shore environments during late April and May of 2003 and that the catch of juveniles in deeper water increased about a month later.

Sea lice were identified and enumerated on 11,271 chum (*Oncorhynchus keta*) salmon, 7,438 pink salmon and 2,815 three-spine sticklebacks (*Gasterosteus aculeatus*). Three species of lice were observed. *Lepeoptheirus salmonis* was found only on salmon and *Caligus clemensi* on salmon and sticklebacks. *Lepeophtheirus sp.* was frequently found on sticklebacks, which had the highest prevalence of infection (60–100% of fish) until near the end of the study when surface salinity in the archipelago declined quickly and prevalence was reduced to 20–35%. The louse from stickleback resembles *L. salmonis* but its identity is currently under review. Louse prevalence on chum and pink salmon was nearly identical for *Lepeophtheirus* and *Caligus*, but variable over the course of the study. Prevalence of caligid copepods increased as the pink and chum salmon migrated from east to west through the archipelago, but was <50% of pink salmon fry as they exited the archipelago. Infection intensity (lice/infected fish) was 2.18 on chum; 1.65 on pink salmon and 5.95 on sticklebacks with >10 lice/infected stickleback observed in over 10% of the population. The abundance of lice/pink salmon fry was <1.0 at most stations within the Broughton Archipelago, but reached 1.15 lice/fish in zone H as the fish exited the archipelago. The same general trend was seen for three-spine sticklebacks except that the intensity was ≥6 in four of the 11 areas examined. Initially, *L. salmonis* chalimus stages represented 50 to 90% of the lice on juvenile pink and chum salmon. However, as the juvenile fish migrated through the archipelago and the intensity of infection increased, the proportion of *C. clemensi* increased and by week 15 of the study (early June), *Caligus sp.* represented 85 to 90% of the lice infecting juvenile pink or chum salmon. At the low observed infection rates (all louse species and stages), no adverse effects on growth (weight or length) of pink or chum salmon were observed as a function of time. The infected fish had slightly higher Fulton's condition factor than uninfected pink or chum salmon, but the differences were not statistically significant.

Jones and Nemec (2004) concluded that sea lice were not uniformly distributed within the archipelago. They found that juvenile host weight and salinity were factors most important in determining the level of lice infection. Because pink and chum salmon fry weight increases rapidly with time in the marine environment, it is possible that residence time was the actual factor affecting infection intensity rather than weight of the host. Increased sea lice infection intensity appeared associated with increased abundance of *C. clemensi* on pink and chum salmon rather than increased numbers of *L. salmonis*. The authors found no evidence that the low levels of infection were affecting growth rates or condition factors of juvenile pink or chum salmon.

Krkosek et al. (2005) collected juvenile pink and chum salmon from locations east of Sargeaunt Pass in Knight Inlet westward to Doctor Islets and then northward around Tribune Channel between April 17–27 and from 9–23 May, 2003 (see Figure 1). A total of 552 copepodids, 2,078 chalimi, and 1,015 motile lice were observed on 5,514 juvenile pink and chum salmon giving an overall abundance of 0.66 lice/fish. Only 65 of the lice were identified to species and no quality assurance was undertaken for the identifications. The authors reported low lice abundance east of Doctor Islets. Peak abundance was observed at the Doctor Islets farm followed by low abundance adjacent to the Humphrey Rocks farm.
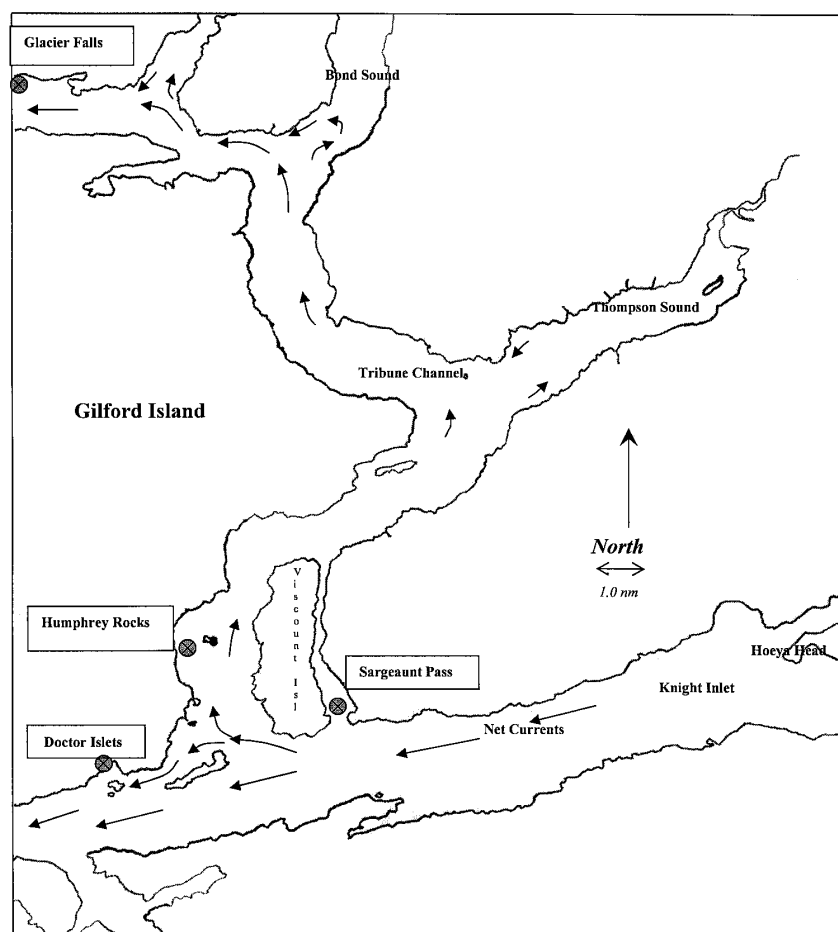
Figure 1. Eastern portions of the Broughton Archipelago with the relative magnitude and direction of net near surface current vectors generated by Stucchi et al. (2005) indicated together with the location of all salmon farms in this area.

The authors did not report either Sargeaunt Pass or Humphrey Rocks as active salmon farms and may have been unaware that cultured salmon were present at both sites. Based on the peak infection rate observed adjacent to Doctor Islets, the authors concluded that the source of the infective copepodids was the farmed salmon. Doctor Islets was being harvested in the spring of 2003 and it was fallow on and after May 19, 2003. Therefore, there were no farmed fish containing gravid sea lice in this area during their final sample period when Krkosek et al. (2005) again reported peak abundance adjacent to the farm. The authors calculated that the infection pressure on juvenile wild salmon passing the farm was four orders of magnitude higher than ambient pressure and that copepodids infecting the wild fry matured and producing a new generation of nauplii that reinfected the same cohort

20–40 km north of the Doctor Islets farm. Ambient surface temperatures were reported as 8–10°C and salinity was 27.6–0.3%.

Currents, Salinity, and Temperature in the Broughton Archipelago

Salmon Farm Location and Net Current Vectors. Figure 1 describes the eastern portions of the archipelago including Tribune Channel, Knight Inlet, and licensed salmon farms. Near surface current vectors were interpreted from Stucchi et al. (2005). Freshwater moves from east to west down Knight Inlet. A portion of this water enters Tribune Channel at Viscount Island and moves counterclockwise, eventually flowing west into Queen Charlotte Straits through Fife Sound where net current speeds have been measured at 8 to 14 cm/sec (Stucchi et al. 2005). Net current speeds were predicted to be slow in Thompson and Bond Sounds but this has not been field verified.

Temperature and Salinity in the Upper 20 m of Water. Canadian Institute of Ocean Sciences (IOS) (2004) data indicates that surface temperatures and salinities in the Broughton are affected by large quantities of freshwater originating from the Klinaklini and Franklin rivers at the head of Knights Inlet and the Wakeman and Kingcome Rivers in Kingcome Inlet. Surface salinity in the archipelago is reduced by rain and snow melts in the late winter and spring and by glacial melt in mid to late summer. Figure 2 describes surface salinity and temperature at depths ≤2.0 m at various locations in Knight Inlet west of Hoeya Head between 1951 and 2001 (IOS, 2004). Even lower near-surface salinities are reported to the
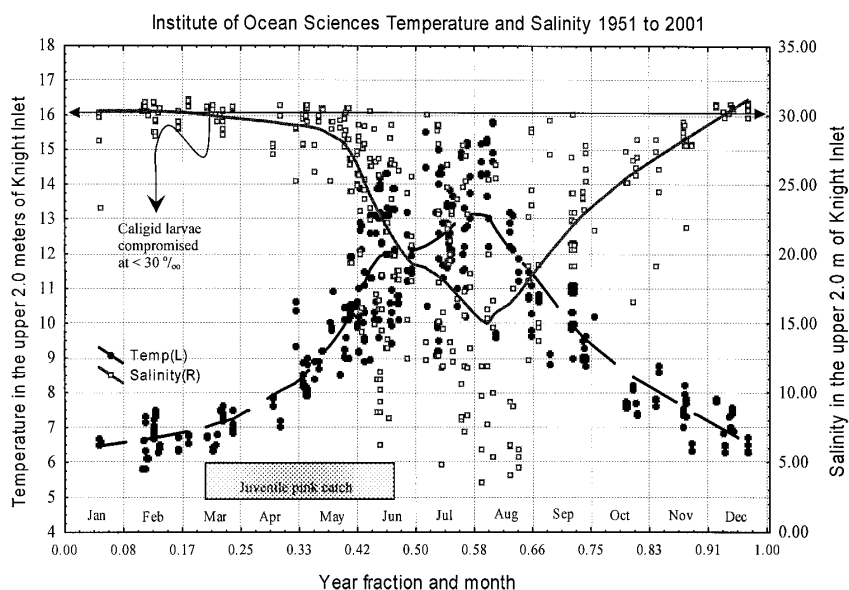

Figure 2. Surface salinity and temperature at depths ≤2.0 m in Knight Inlet, Broughton Archipelago between 1951 and 2001 (IOS, 2004). Lowess smoothing creates a local regression model fit for each datum and points close to it; providing a clearer picture of the overall shape of the relationship between the x and y variables.
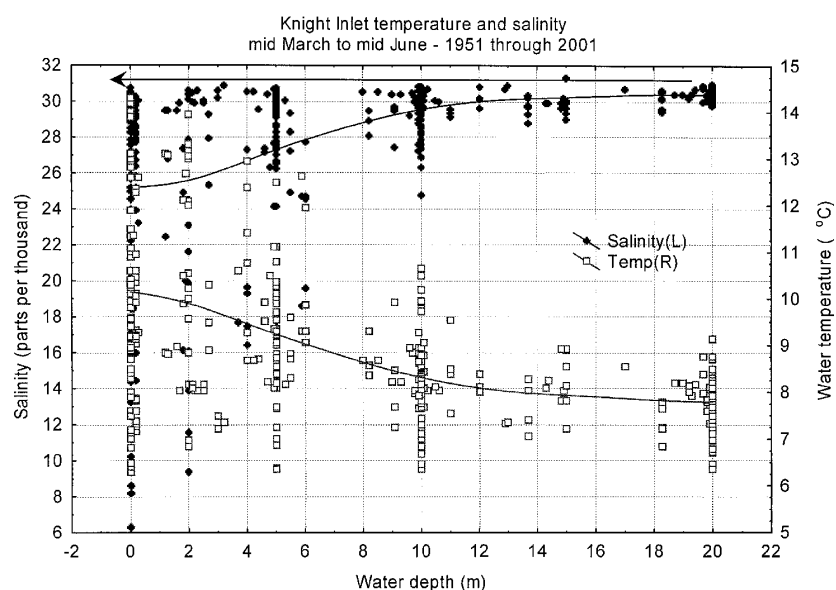
Knight Inlet temperature and salinity
mid March to mid June - 1951 through 2001

Figure 3. Salinity and temperature of Knight Inlet water as a function of depth between March 15 and June 15 during the period 1951 to 2001. Data from IOS (2004).

east of Hoeya Head. The salinity (30 $^o/_{oo}$), below which consistent *L. salmonis* development to the copepodid stage does not occur, is indicated. These data demonstrate that in an average year, salinity is <30‰ from mid-March until the end of November. The period during which pink salmon juveniles are migrating through the area is highlighted with a shaded bar. Figure 3 describes temperature and salinity as a function of depth in Knight Inlet between April 15 and June 15 in all years between 1951 and 2001. Distance weighted least squares fits are provided for both variables. The high variability in salinity and temperature and the slope of the distance weighted least square fits suggests strong mixing in the upper 10 m of water with shallow thermoclines and haloclines ending at 10 and 12 m depth.

A portion of the variability in Figures 2 and 3 is associated with interannual differences. An example of this is provided in Figure 4, describing salinity in Viner Sound (Figure 9) near the western boundary of the archipelago (Stolt Sea Farm, 2004). This sound is influenced by low salinity water entering from the east and higher salinity, Queen Charlotte Strait, water flushing into the archipelago from the west on flood tides. The winter of 2000–2001 was exceptionally dry (Table 1) with an accumulated deficit with respect to long-term average rainfall of −37.6 cm up to April 2001 (Environment Canada, 2003). This likely resulted in reduced snow pack and early spring runoff. In response, salinity in the upper 2.0 m of the water column remained above 30‰ in the western portions of the Broughton during the spring of 2001. The winter of 2001–2002 was also dry and salinity remained high in Viner Sound until the first week in July. More normal rainfall occurred in 2003 and excepting the first week in May, surface salinity was ≤30‰ from the beginning of April. The lack of rain did not affect summer glacial runoff and salinities were low from July through October in all years. It should be emphasized that salinity in Viner Sound on the western edge of the
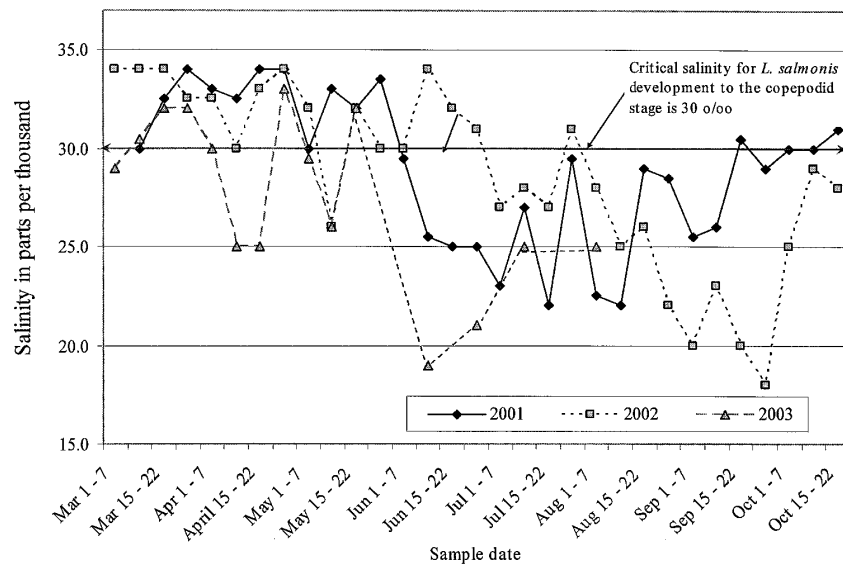
Figure 4. Sea surface (1.0 meter depth) salinity recorded in Viner Sound, British Columbia during the spring and summer of 2001, 2002 and 2003. Data from Stolt Sea Farm (2004).

Broughton was likely higher than in most other areas of the archipelago. Figure 2 suggests that mean surface salinity in the Broughton was <30‰ from early March until November in an average year but that this pattern can be disrupted, at least in the western portions of the archipelago, during years of low rainfall (Figure 4).

Discussion

Few studies have included a thorough assessment of the influence of temperature, salinity, and hydrodynamics on the survival and dispersal of sea lice during development to an infective stage. Monitoring at salmon farms, archived Institute of Ocean Sciences temperature and salinity data, computer modeling and current meter data provided by Stucchi et al. (2005), and the report of Jones and Nemec (2004), allow a semi-quantitative assessment of lice population dynamics in the Broughton Archipelago.

Sources, Survival, and Distribution of Caligid Larvae in the Broughton

New hosts are not infected by the sea lice's naupliar stage. The nauplius does not feed and has limited energy reserves, which inhibits its mobility over long distances. Typical of most lecithotrophic larvae, sea lice nauplii are most likely part of the seston and as such, currents heavily influence their dispersion. Costelloe et al. (1996, 1998), Penston et al. (2002), and McKibben and Hay (2002) all recognized the importance of larval development time and wind, tidal and freshwater (riverine) driven currents in determining the spatial distribution of the nauplius larvae and infective copepodid stages. In the Broughton Archipelago, freshwater inputs force strong seaward flowing surface currents in the main channels that likely

Table 1
Rainfall (millimeters) reported by Environment Canada (2003) at Port Hardy from September 2000 until April 2001

	September 2000	October 2000	November 2000	December 2000	January 2001	February 2001	March 2001	April 2001
Normal Port Hardy (mm)	104.6	261.6	300.2	280.8	237.3	146.3	155.2	125.1
Recorded Port Hardy (mm)	103.0	225.7	185.5	140.2	159.8	81.2	195.9	144.2
Difference (mm)	−1.6	−35.9	−114.7	−140.6	−77.5	−65.1	+40.7	+19.1
Percent of normal (±)	98.5	86.3	61.8	49.9	67.3	55.5	126.2	115.3
Accumulated Difference since September 2000 (mm)	−1.6	−37.5	−152.2	−292.8	−370.3	−435.4	−394.7	−375.6

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carry imbedded sea lice larvae significant distances during their development to an infective stage.

Sources of Larval Sea Lice. At least seven non-salmonid and six salmonid hosts have been identified for *C. clemensi* (McDonald and Margolis, 1995). The non-salmonid hosts include several species common in the archipelago such as rockfish (*Sebastes sp.*), ratfish (*Hydrolagus colliei*), three-spine stickleback (*Gasterosteus aculeatus*), and herring (*Clupea pallasi*). In addition, commonly occurring cutthroat trout (*Oncorhynchus clarki*) are host to *L. salmonis*. The dominance of *C. clemensi* on pink and chum salmon fry in the Broughton Archipelago during 2003 suggests that this species may have significant ecological and economic importance and it bears further study. For purposes of this discussion, the life history of all of these species of sea lice will be assumed to be consistent with the preceding discussion. However, it should be emphasized that growth and survival of *Lepeophtheirus sp.* and *Caligus sp.* as a function of temperature and salinity have not been studied in the Northeast Pacific and future studies elucidating these factors will be beneficial in refining this discussion.

Identification of Sea Lice. Morton et al. (2004) reported that 4338 *L. salmonis* (92% of total) and 364 *Caligus sp.* (8% of total) were identified on pink salmon fry caught using a dip net between April 16 and the end of June 2002 in the Broughton Archipelago. No quality assurance procedures were presented by the authors to confirm their identifications. The authors concluded that the persistent *L. salmonis* infections could not occur in the absence of a substantial salmonid host population and that while juvenile salmon of several species might have been present in the Broughton, the only known adult salmon present during the spring fry migration were farmed Atlantic salmon. In contrast, Jones and Nemec (2004) examined 11,204 chum and 7,411 pink salmon and 2,561 three-spine sticklebacks between March 3, 2003 and June 13, 2003. Their identifications were confirmed by inter-laboratory quality assurance procedures. *Lepeophtheirus salmonis* was observed on salmon and possibly on sticklebacks. Sticklebacks carried *Caligus clemensi* and an unconfirmed species of *Lepeophtheirus*. Sticklebacks had the highest overall prevalence (59% of fish) and abundance of lice (4.0 to 6.0/fish) observed during the study. *Lepeophtheirus hospitalis* was observed on herring (*Clupea pallasi*) but statistics were not reported for these infections. In contrast to the report of Morton et al. (2004), these authors observed a steady increase in the ratio of *Caligus* to *Lepeophtheirus* on pink salmon fry as their study progressed. During the final month of the study (June 2003) 80 to 90% of the chalimus stages on pink salmon were *Caligus sp.* The report of Jones and Nemec (2004) demonstrated that sea lice infections of pink salmon fry in the Broughton Archipelago during 2003 were associated with at least two species of lice having a broad range of readily available hosts. Krkosek et al. (2005) identified 65 of the 3645 lice counted on 5,514 juvenile salmon sampled. The samples were then returned to the sea and it is not possible to compare their data with other data sets or to confirm their identifications. The importance of proper identification to at least genus is particularly important in the Broughton Archipelago because the lice load on pink salmon is comprised of both *Caligus* and *Lepeophtheirus* and as previously noted *C. clemensi* has many hosts in the archipelago.

Survival of Lice as a Function of Temperature and Salinity. The algorithm of Tully (1992), predicts a louse generation time of 106 days at 7.5°C and 84 days at 9.0°C for *L. salmonis*. Survival of *Caligus elongatus* from hatching to the copepodid stage declined from 90% at 15°C to 60% at 5°C. Their data suggests that 68% of *L. salmonis* hatched in the Broughton

during March to the end of May, when sea surface temperatures are 7.5 to 9°C, will survive to the copepodid stage. Surface water in the Broughton can reach 15°C during July and August (Figure 2) resulting in a louse generation time of only 32 days. However, survival of sea lice larvae at the recorded summer salinities of 15 to 20‰ is problematic (Pike and Wadsworth, 1999). Stratification may play an important role in larval sea lice survival. Heuch et al. (1995) reported that L. salmonis larvae tended to aggregate at the base of the halocline where salinity was 34‰. Salinity >31.5‰ has not been reported in the upper 20 m of Knight Inlet. However, it seems reasonable to assume that larvae will be vertically mixed, but may attempt to maintain themselves at the base of the halocline located at ca. 10 m depth (Figure 3). Salinity at and below this depth is fairly stable at 30 to 31‰ suggesting some development to the copepodid stage. Reduced survival might therefore be expected during periods of significant stratification characterized by low tidal exchange, weak winds, plentiful spring rainfall, and high snow melts. These circumstances appear regularly in Knight Inlet (Figure 2) and were widely documented by Jones and Nemec (2004) in 2003 when mean surface salinity at 11 Broughton stations was 21.9‰ in mid May declining to 14.9‰ by June 15, 2003. Increased louse survival could be anticipated during years with little rainfall and snow-pack, such as occurred in the winter and spring of 2001–2002 when surface salinity in Viner Sound remained above 30‰ until July (Figure 3). The vertical distribution of sea lice in the Northeast Pacific and their survival at salinities of 15–30‰ has not been documented. However, the available information suggests reduced survival to an infective copepodid stage in the long-term average salinity recorded for this area.

Natural salinity controls on lice in the Broughton Archipelago could explain the absence of significant effects on cultured Atlantic salmon during the last decade. In compliance with the British Columbia Broughton Archipelago Sea Lice Action Plan (BCMAFF, 2003), 20 cultured salmon from each of three randomly selected netpens have been examined monthly for sea lice since 2002 at each active farm. The abundance of the chalimus stages of all species of lice and of pre-adult, male, female, and gravid female L. salmonis were recorded as well as the abundance of all motile stages of C. clemensi. Figures 5 and 6 were constructed using raw lice count data, provided by Stolt Sea Farm (2004). Figure 5 describes lice counts on untreated Atlantic salmon at Sargeaunt Pass, which is located up current from Doctor Islets. Juvenile Atlantic salmon were introduced to this site, free of sea lice, in late March of 2003. There are no salmon farms east (up current) from Sargeaunt Pass and the Caligus and Lepeophtheirus infections documented at this site in the spring of 2003 were likely associated with copepodids hatched from wild fish hosts. Spring infections at this farm were dominated by Caligus, whose abundance decreased during the summer. No cause-and-effect relationships were investigated in this review, but it is hypothesized that the decreased lice load was caused by reduced salinity in Knight Inlet and the hosts' immune response. The immune response of pink and/or chum salmon to sea lice is unknown. However, Johnson and Albright (1992) have shown varying responses in other salmon species. The farmed fish were reinfected with primarily Lepeophtheirus during the fall return of Pacific salmon late in 2003 as the archipelago's salinity increased. No gravid female sea lice were observed on cultured fish at Sargeaunt Pass until the end of October 2003 when a total of two gravid females were observed on 60 cultured fish (Abundance = 0.03). Figure 6 describes the abundance of sea lice at the Humphrey Rocks salmon farm located in Tribune Channel upcurrent and approximately three nm north of the Doctors Islets farm. Gravid female lice were not observed at Humphrey Rocks until October 28, 2003 when four were counted on 60 fish (abundance = 0.07). The abundance of gravid females at Humphrey Rocks was 0.1 to 0.15 in November 2003 (one in 6 to 10 Atlantic salmon had a single gravid female).
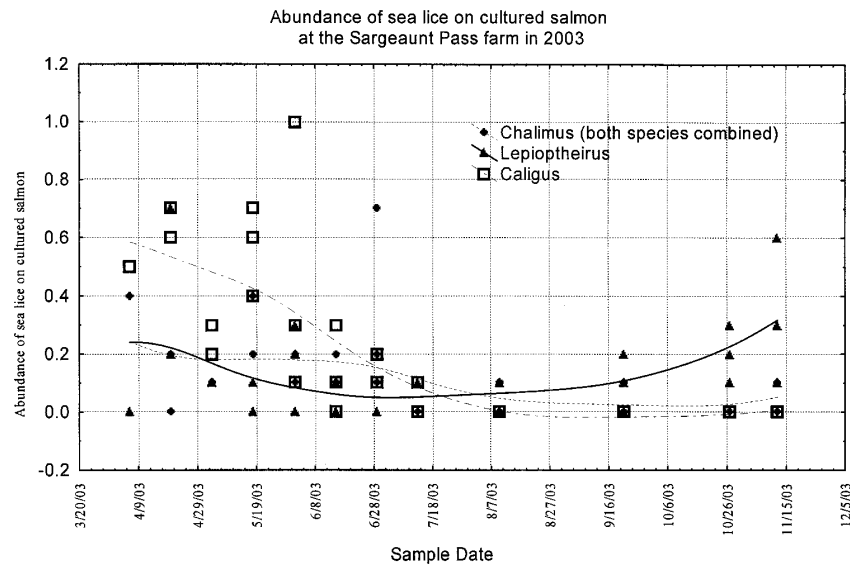
Abundance of sea lice on cultured salmon
at the Sargeaunt Pass farm in 2003

Figure 5. Abundance (mean number of lice/cultured fish) at the Sargeaunt Pass salmon farm in 2003. The regression lines were derived using the least square fitting routine in Statistica?™ Version 6 software. Data from Stolt Sea Farm (2004).

Abundance of sea lice on cultured salmon
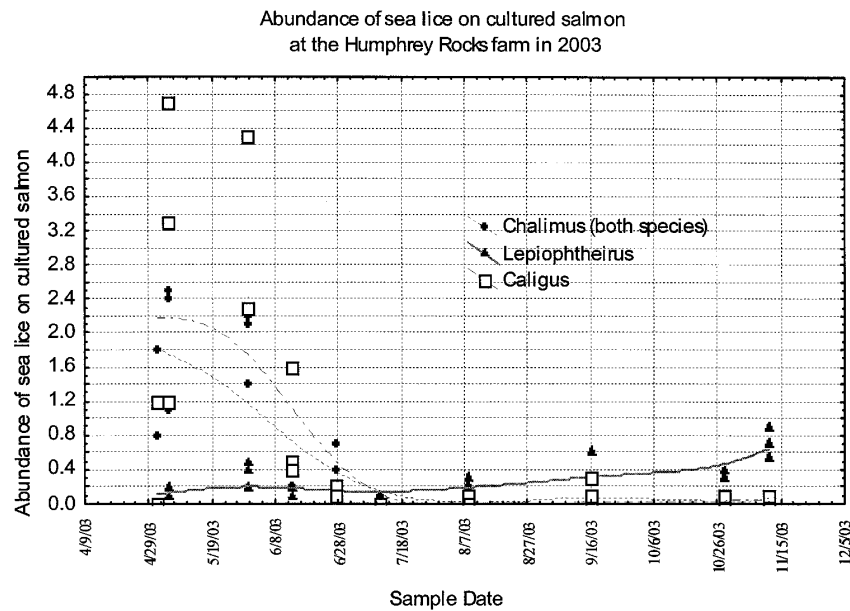at the Humphrey Rocks farm in 2003

Figure 6. Abundance (mean number/fish) of sea lice on cultured Atlantic salmon at the Humphrey Rocks salmon farm located in Tribune Channel, British Columbia. Data from Stolt Sea Farm (2004).

The pattern at this farm was similar to that seen at Sargeaunt Pass with significant spring infections of both lice species. The abundance of lice declined in summer followed by steadily increasing infections in the fall. Like Sargeaunt Pass, the spring infections were dominated by *Caligus* and the fall infections by *Lepeophtheirus*.

Caligus and *Lepeophtheirus* infected naïve fish at both of these farms shortly after their introduction in March and April of 2003. The only other source of copepodids originating on farmed salmon was at Doctor Islets where the abundance of gravid female lice was 1.5 on April 18, 2003. This farm was harvested between February and the beginning of May 2003 and it was fallow on and after May 19, 2003. Doctor Islets is located down current from Sargeaunt Pass and it is unlikely that larvae released at the former farm could move against the strong westerly currents in Knight Inlet to infect salmon at Sargeaunt Pass. Under some conditions of wind and tide, it is possible that surface water originating at Doctor Islets could be backed against the prevailing westerly currents to enter Tribune Channel contributing to wild lice vectors at Humphrey Rocks. However, based on long-term current meter studies, that is not the prevailing flow. It is hypothesized that the spring *Caligus* infections were caused by the multiple wild hosts available to this louse. The fall increase in the abundance of *Lepeophtheirus* on the cultured fish was likely associated with returning Pacific salmon (Beamish et al., 2004). In both cases, it appears that reduced summer salinity resulted in the loss of most sea lice from cultured salmon at these farms.

Dispersal of Larval Lice in the Broughton Archipelago. Figure 7 provides a polynomial fit predicting larval development time from hatching to the infective copepodid stage based

Development of naupliar stages of *L. salmonis* to the copepodid stage (Data from Johnson and Albright (1991), Johannesson (1978), Wootten *et al.* (1982) and Taylor (1987)

Days from hatching to copepodid stage = $19.95 - 2.58 \times \text{Temp} + 0.092 \times \text{Temp}^2$
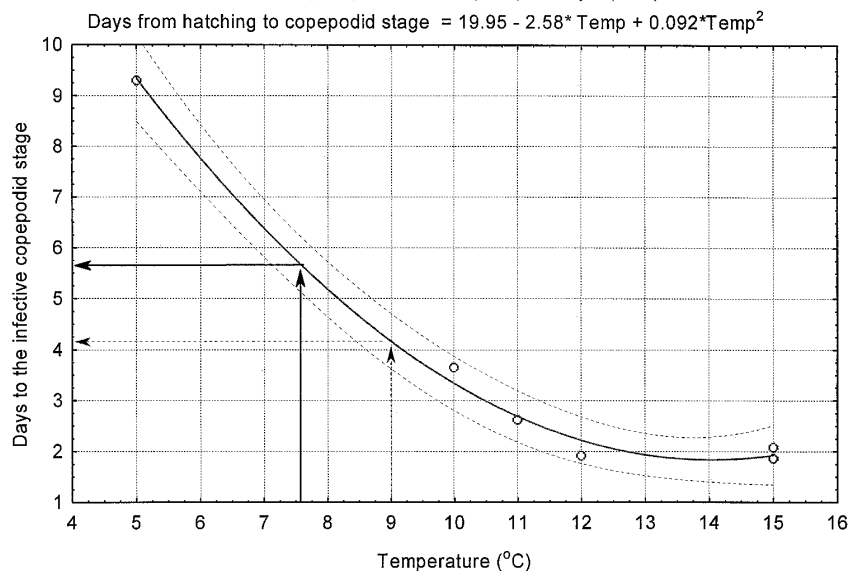

Figure 7. Estimated development times for newly hatched nauplii to reach the infective copepodid stage as a function of temperature. 95% confidence intervals are provided.

on data summarized by Tully (1992). The regression suggests that *L. salmonis* larvae will be resident in the seston for between 4.2 and 5.8 days at the minimum (7.0) and maximum (9.0°C) surface water temperatures observed during the juvenile pink salmon migration.

Several European researchers have searched for correlations between distance from salmon farms and sea lice infection parameters on wild sea trout. The data provided by MacKenzie et al. (1998) indicated low abundance and prevalence of sea lice on wild fish caught 0.5 km from salmon farms. Increased infection rates were found at distances of 2.0 to 12.0 km from the farms. Distance-weighted least squares best fits are provided in Figure 8 summarizing data presented by Butler et al. (2001) describing the abundance, prevalence, and intensity of sea lice on wild sea trout as a function of distance from the nearest salmon farm. These data are similar to that of MacKenzie et al. (1998) in that they demonstrate relatively low infection rates near farms with increasing abundance, prevalence, and intensity of infection at distances ≥2.0 km.

Net current vectors are defined as the vector sums of the instantaneous current speeds and directions. Mean current speed is the average magnitude of the instantaneous current vectors averaged over the period of observation. Assuming that sea lice nauplii are part of the seston and that their dispersal is largely dependent on net current vectors provides a basis for defining *zones of infection* where copepodids are competent to infect new hosts. These zones are site-specific and cannot be applied generally. The net current vectors summarized for 15 Broughton Archipelago salmon farms in Table 2 were developed from 15 m depth current meter data collected over one full lunar cycle at each tenure as part of the tenure
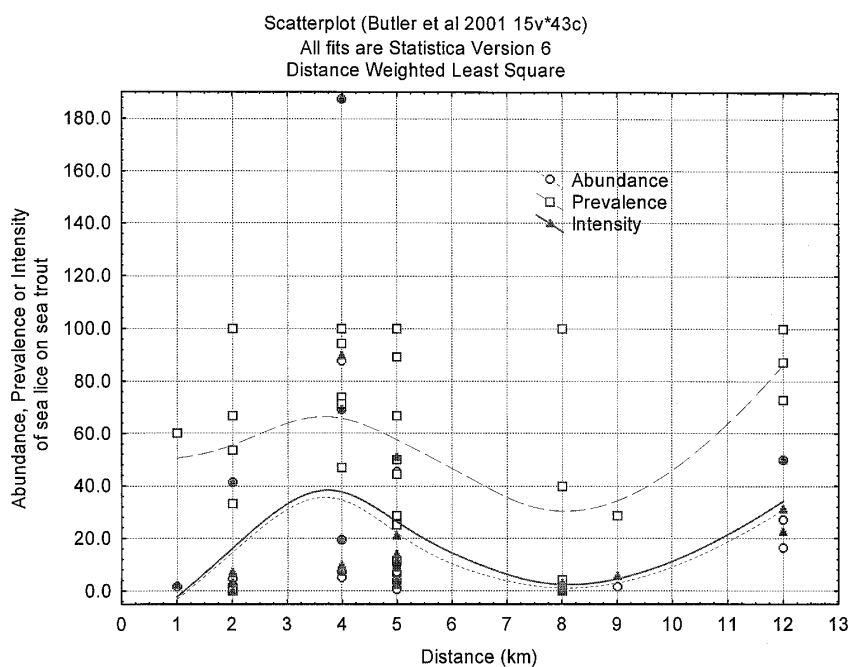

Figure 8. Abundance, prevalence and intensity of sea lice (*L. salmonis*) on the west coast of Scotland as a function of distance from Atlantic salmon farms. Data from Butler et al. (2001).

Table 2

Net surface (15 m depth) current vectors at 15 salmon farms in the Broughton Archipelago. The net current vectors are the vector sums of the instantaneous current vectors measured at each site. They indicate the direction and speed at which seston (including lice nauplii) would be displaced from each farm as a function of time. Average current speed is the mean of the magnitude of the instantaneous current vectors. The minimum distance at which nauplii molt to the infective copepodid stage is provided for a temperature of 9.0°C (4.2 days) and the maximum typical distance at which copepodids die if they don't find a new host (10.8 days) is provided assuming a larval development time of 5.8 days at 7.5°C. Distances are in km from each farm. Distances in nautical miles are provided in parentheses

	Net speed Cm/sec	Net direction degrees true	Average speed cm/sec	Minimum distance to copepodid (4.2 d)	Maximum distance (copepodids die in 10.8 d)
Arrow Pass	2.0	193	3.9	7.3 (3.9)	18.7 (10.1)
Blunden Pass	0.2	251	2.2	0.7 (0.4)	1.9 (1.0)
Bocket Point	2.2	024	4.5	8.0 (4.3)	20.5 (11.1)
Deep Harbor	1.2	210	1.2	4.4 (2.4)	11.2 (6.0)
Doctor Islets	1.4	261	5.6	5.1 (2.8)	13.1 (7.1)
Eden	1.6	077	7.0	5.8 (3.1)	14.9 (8.0)
Glacier Falls	4.3	082	6.7	15.6 (8.4)	40.2 (21.7)
Humphrey Rock	3.1	041	6.6	11.2 (6.0)	28.9 (15.6)
Midsummer Island	1.6	283	4.3	5.8 (3.1)	14.9 (8.0)
Port Elizabeth	2.6	073	4.3	9.4 (5.1)	24.3 (13.1)
Sargeaunt Pass	1.8	126	6.4	6.5 (3.5)	16.8 (9.1)
Smith Rock	2.0	085	8.4	7.3 (3.9)	18.7 (10.1)
Swanson Island	1.9	264	7.7	6.9 (3.7)	17.7 (9.6)
Upper Retreat	2.2	036	4.8	8.0 (4.3)	20.5 (11.1)
Wicklow	0.5	166	10.5	1.8 (1.0)	4.7 (2.5)
All farms	1.8			6.5 (3.5)	16.8 (9.1)

application process (Stolt Sea Farms, 2004). They integrate the influence of tides, winds, and freshwater inputs on currents. It is possible for seston, such as sea lice nauplii, to be driven inshore from well-flushed areas where salmon farms are located and to be trapped in lower energy intertidal areas. Macroalgal beds, eelgrass meadows, rock outcroppings, etc. could then slow the drift of larvae. The proportion of larvae potentially released from a farm that reach the shore and survive in that environment is unknown and very difficult to model. The net currents provided in Table 2 are near-shore speeds that represent a compromise between main channel speeds and current speeds in the intertidal. Net current speeds, describing the movement of imbedded seston, varied between 0.5 and 5.4 cm/sec with an overall mean for the 15 farms of 1.8 cm/sec. The long-term (several months) average east-west component of the current is strongest near the surface and decreases with depth. The depth of the zero crossing or thickness of the out-flowing surface layer varies, but is in the range of 25 to 40 m (Stucchi et al. 2005). This westward surface flow is balanced by inflowing water at depths >25 to 40 m. Assuming that the distribution of nauplii can be characterized as seston that is not extensively trapped in intertidal areas and that their mobility is limited, Table 2 includes the minimum distance in km that sea lice nauplii are carried as they develop to the infective copepodid stage at 9.0°C and the maximum distance at which copepodids remain viable when the water temperature is 7.5°C. Distances in nautical miles (nm) are provided in parentheses.

The data in Table 2 indicates that sea lice larvae released from salmon farms located in the western portions of the archipelago are generally carried into the Queen Charlotte Straits before reaching an infectious stage. However, this simplified analysis indicated that larvae released from the Glacier Falls and Doctor Islets farms (see Figure 1) were capable of infecting other salmon farms and/or migrating pink and chum salmon fry. Stucchi et al. (2005) provides a more robust methodology for assessing these two farms. A computer-based, three-dimensional model describing circulation within the Broughton Archipelago was used together with the DROG3D program (Blanton, 1995) to track particles simulating sea lice larvae released from the Doctor Islets and Glacier Falls salmon farms. The hydrodynamic model was shown to be reasonably consistent with long-term (several month long) data collected using acoustic Doppler current profilers located in Fife Sound and near Glacier Falls in Tribune Channel. However, the Stucchi et al. (2005) model does not include the influence of wind on surface currents, which might be significant at times. In addition, the model *captures* particles that intercept the shoreline and holds them until a change in tide predicts movement offshore. The model appears accurate with respect to predicting main circulation patterns in the archipelago, but it is not particularly robust with respect to shoreline effects. Particles simulating sea lice larvae were released into this hydrodynamic model hourly over a 25-hour period and tracked for 10 days. The 25-hour release period was chosen to account for the initial movement of particles released into ebb and flood stages of the semi-diurnal tides typical of this area. The 10-day track was chosen because that appears to be the sum of the development time of the larvae to an infective stage (4.2–5.8 days) plus the expected life span of the copepodids (4–6 days). Separate exercises were undertaken to track particles during both spring (maximum tidal exchange) and neap (minimal exchange) tidal series. Predicted larval dispersal patterns during neap tides are reported here as they represent the worst case with respect to potential for infection of pink or chum salmon stocks migrating through the archipelago. Figure 9 describes the predicted location of sea lice nauplii released from the Doctor Islets salmon farm at 5 days post-hatching as they molt to the infective copepodid stage. Due to the strong westward flowing surface currents in Knight Inlet, the noninfective nauplii released at Doctor Islets were swept out of the archipelago into Queen Charlotte Strait before molting to an infective
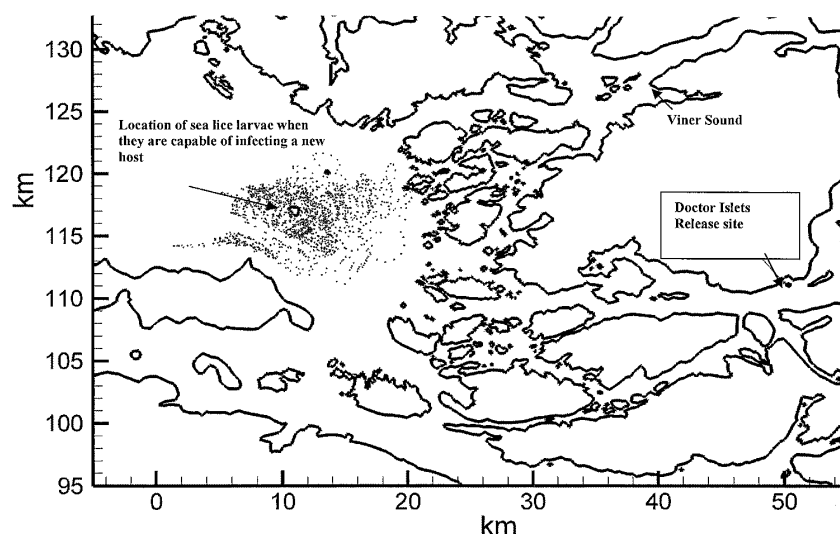
Figure 9. Location of sea lice larvae released from the Doctor Islets salmon farm five days after release when they are predicted to molt to the infective copepodid stage at temperatures characteristic of those found in the Broughton Archipelago during the migration of pink and chum salmon (Stucchi et al., 2005).

stage. Krkosek et al. (2005) argued that because salmon farms are potentially a continuous source of sea lice, the infectious stages would be continuously distributed from the farm to a distance downstream determined by the lifespan of the copepodids. However, the results presented in Figure 9 apply to any cohort of larvae released during any 25-hour neap tide period and few if any of the larvae released from Doctor Islets were predicted to remain in the Broughton Archipelago as they developed to an infective stage. Nauplii released from the Glacier Falls salmon were predicted to travel westward in Tribune Channel. Rather than exiting through Fife Sound, the prediction carried the larvae southwest through Hornet and Retreat Passages. Some of the larvae were predicted to exit the archipelago into Queen Charlotte Straits before they matured to an infective stage. However, a portion of the larvae matured in Hornet and Retreat Passages and these copepodids could infect five salmon farms as they pass into the straits. Migratory routes of pink and chum salmon are unknown in this area. If the fry pass along the northern shore of Tribune Channel, they might exit through Fife Sound and not be sympatric with the Glacier Falls lice. If pink or chum fry migrate down Retreat Passage, they would be exposed to increased infection pressure from the surviving copepodids hatched at Glacier Falls. Because *Caligus clemensi* has many abundant wild hosts in the archipelago and because the population of resident salmonids carrying *Lepeophtheirus salmonis* is unknown, the natural population of sea lice in the archipelago cannot be estimated. Therefore, the relative magnitude of the farmed salmon contribution is also unknown.

Other Factors Affecting Potential Sea Lice Infections of Pink Salmon Fry

Modeling Sea Lice Epizootics. Heuch and Mo (2001) provided a model describing the contribution of sea lice larvae from farmed fish, escaped farm fish, and wild fish in Norway.

Benchmarks, based on the number of *Lepeophtheirus salmonis* produced pre-salmon farming, were estimated and used to define allowable numbers of gravid females on farmed Atlantic salmon. In an environment where there are few alternative hosts, this approach is manageable. The authors emphasized that defining *sustainable louse egg levels* requires knowledge of the possible hosts and their parasites' abundance, the tolerance levels of potential hosts, and the factors causing changes in lice levels. In the Broughton Archipelago, rainfall and snow pack strongly influence salinity and therefore survival of sea lice. It should be emphasized that it is not just the overall abundance of sea lice larvae that is important, but also the density of infective agents as they interact with potential new hosts. In areas where net transport vectors are not null vectors, that interaction will occur at some distance from the point of larval release. As emphasized by Heuch and Mo (2001), differences in physicochemical and hydrographic factors affecting sea lice epizootiology require local models. The vectors along which horizontally transmitted etiological agents are carried are but one factor in determining the potential for disease. The degree and extent of disease in fish is problematic and depends on a complicated suite of environmental, parasite and host factors (Brooks, 1991; McVicar, 1997). Understanding potential or real epizootics in open marine environments is a complex task and there are few examples where definitive answers have been achieved (Elston et al., 1992).

Host–Parasite Density. The horizontal transmission of parasites, such as sea lice, is in part dependent on the density of hosts and parasites. Given the predicted dispersion of lice larvae from Doctor Islets and Glacier Falls (Figures 9 and 10), the density of infective copepodids would be low and not likely to result in epizootic disease. However, recent studies do indicate that some portion of pink and chum salmon fry are being infected with
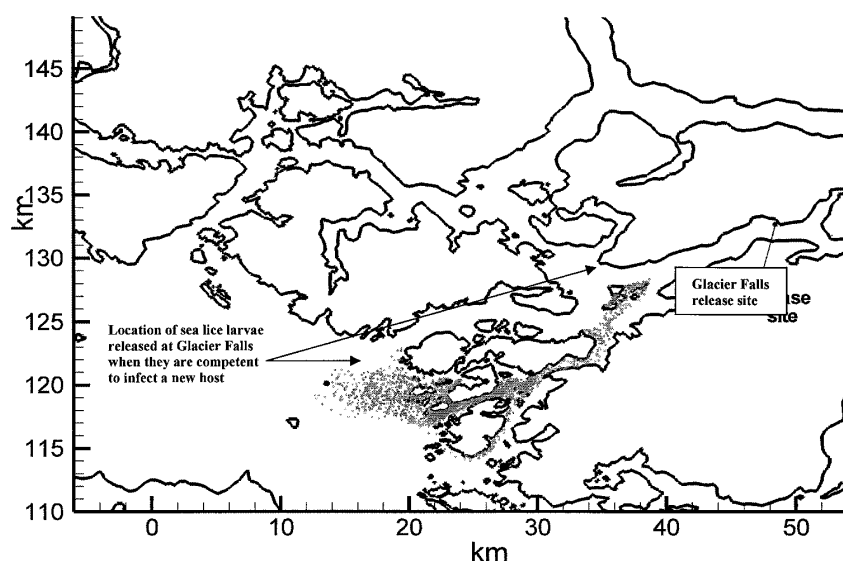

Figure 10. Predicted location of particles (sea lice nauplii) five days after release from the Glacier Falls salmon farm when they molt to the copepodid stage and can infect new hosts (Stucchi et al., 2005). This model is based on neap tides.

lice during their residence in the archipelago. The question then becomes where are these infections most likely to occur? Jones and Nemec (2004) have shown high abundance of *Caligus* on three-spine sticklebacks. This euryhaline species lives in fresh and saltwater and is common in intertidal and shallow subtidal areas (Hart, 1973). Stucchi et al. (2005) suggests slow net current vectors in Thompson Sound and Bond Sound (see Figure 1). Pink salmon fry pass through and likely reside in these sounds for extended periods as they leave the Kakweiken and Ahta Rivers. Extensive estuaries are also found in association with the Wakeman, Kingcome, and Klinaklini Rivers. All of these rivers are identified by BCMAFF (2005) as major pink salmon spawning systems. Pink salmon fry would likely be at their highest densities as they exit these rivers. One would also expect to find high densities of three-spine sticklebacks in these estuaries. The combination of high host density and potentially high parasite density together with slow net transport vectors provides a more suitable environment for significant host parasite interactions and disease than occurs in the open waters of the Broughton's major channels. These apparently poorly circulated areas should be investigated as potential sites of infection.

Pink Salmon Response to Sea Lice Infections. Bjorn and Finstad (1997) reported that sea trout post smolts weighing 60 g would succumb to *L. salmonis* copepod infections of 90 chalimus/fish held in 34‰ seawater at 9.7°C. Their assessment assumed a chalimus survival rate of 63% to the motile stage at the stated temperature and salinity. Based on this report Morton et al. (2004) asserted that 1.6 chalimus/gram of host would result in the death of juvenile pink salmon fry weighing 1.07 to 2.7 g. Johnson and Albright (1992) demonstrated significant differences in the immune response of salmonids with the coho's (*Oncorhynchus kisutch*) response more effective in killing or shedding the chalimus stages of *L. salmonis* than the chinook's (*O. tshawytscha*) response. No studies were found describing the lethality of sea lice to pink salmon or to one to three gram salmon fry of any species. Nor were studies documenting survival as a function of intensity of infection found for salinities of 25 to 30‰ that are typical of the upper 10 m of water where pink salmon fry are likely to be found as they migrate through the Broughton. Jones and Nemec (2004) found no evidence that the low levels of louse infection observed on juvenile pink and chum salmon in the Broughton Archipelago during 2003 were affecting growth rates or condition factors. While louse intensity was generally low in 2003, approximately 1.4% of chum and 1.2% of pink salmon were infected with two or more motile *L. salmonis*. Some juvenile pink salmon had up to 12 lice/fish and chum carried as many as 25 lice/fish. These results suggest that the health of pink and chum salmon fry is not compromised at an infection rate of 1.6 chalimus/g. However, the immune and physiological response of pink or chum salmon to sea lice infections has not been described.

History of Pink Salmon Returns and Farmed Salmon Production in the Broughton

Figure 11 describes the relationship between odd and even year pink salmon returns to Broughton Archipelago watersheds (bars) and the production of Atlantic salmon through 2004 (BCMAFF, 2005). In common with previous sharp declines in pink salmon returns, the population, which was depressed in 2002, rebounded in 2004 when escapement exceeded the long-term average. The data for cultured Atlantic salmon was shifted 1 year backward with respect to the pink salmon return data so that the analysis is between the biomass of cultured Atlantic salmon in the year of pink salmon fry migration and the return of each year-class.
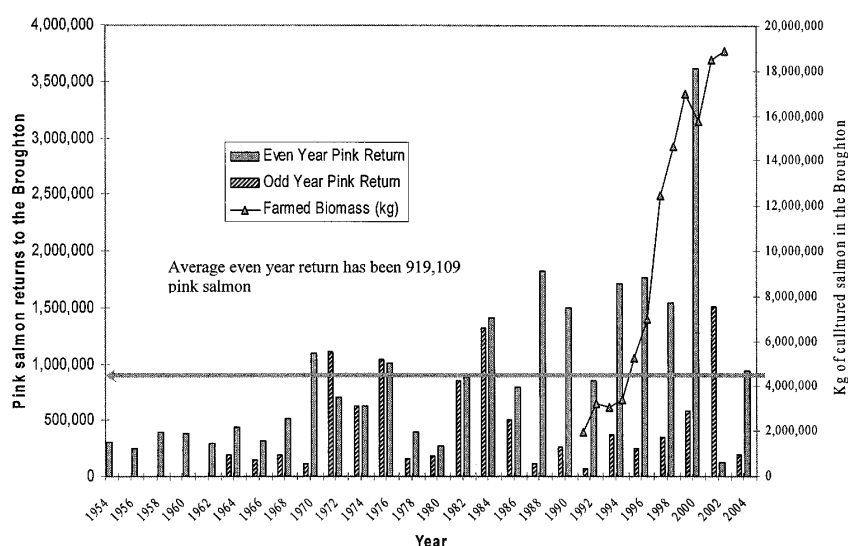
Figure 11. Odd and even year pink salmon returns (vertical bars) and Atlantic salmon production (line) in the Broughton Archipelago from 1962 through 2002.

Interpretation of Previous Sea Lice Studies in the Broughton Archipelago

Morton et al. (2004) and Krkosek et al. (2005) observed increased abundance of sea lice on pink salmon in the immediate vicinity of salmon farms, which they concluded were the most likely source of the infections. The analysis presented herein suggests that infection of new hosts at the site of naupliar hatching occurs only when net vectors are null vectors. Both Glacier Falls and Doctor Islets, which are sites sampled by these authors, lie alongside major channels where seston, including sea lice larvae, are quickly swept downcurrent toward the Queen Charlotte Strait. Therefore, the source of copepodids infecting pink salmon fry at either of these farms would have been located 10 to 15 km upcurrent than the farms.

Based on data collected between April 17 and April 27, 2003, Krkosek et al. (2005) concluded that copepodids infecting pink salmon adjacent to the Doctor Islet salmon farm matured on the pink salmon fry and produced a second generation of lice, which reinfected the cohort at distances of 0 to 60 km, with a modal peak at 30 km downcurrent from the farm. The generation time described by Tully (1992) at the mean temperature of 9°C measured by Krkosek et al. (2005) is 84.5 days. Secondary infections observed in early April 2003 could only have resulted from initial infections occurring between January 22 and February 1, 2003, which is a month or more before pink salmon begin their migration. Therefore, the conclusion of Krkosek et al. (2005) does not appear plausible and is likely a result of the way in which the data was analyzed.

Krkosek et al. (2005) did not report that Sargeaunt Pass (see Figure 1) was stocked with a new year-class of Atlantic salmon in March of 2003. These Atlantic salmon were infected with abundances of 0.4 ± 0.8 combined chalimus (*Lepeophtheirus* and *Caligus*) and 0.5 ± 0.7 motile *Caligus* when first examined on April 6, 2003 (total abundance = 0.9 lice/fish). Gravid female lice of any species were not observed at Sargeaunt Pass until October 27, 2003 and there are no salmon farms upcurrent from this farm. Therefore, self-infection did

not occur in the spring of 2003 at Sargeaunt Pass and these infections were almost certainly derived from wild hosts. Several of the upcurrent stations examined by Krkosek et al. (2005b) were in close proximity to Sargeaunt Pass. The near absence of sea lice reported by Krkosek et al. (2005) on pink salmon at these stations is very different from the abundance of 0.9 lice/cultured fish documented on the farm. Differences in immune response, residence time in the marine environment, spatial heterogeneity of the distribution of copepodids, or in sampling techniques could explain the differing abundances reported in the two datasets.

The need for careful evaluation of current vectors when investigating sea lice infections is evident in the report of Krkosek et al. (2005). These authors did not consider either the magnitude or direction of local currents in the area of Doctor Islets and assumed that larvae released from the farm were carried north into Tribune Channel. Long-term current meter data from Doctor Islets indicates that the net current vector is to the west, which is consistent with the report of Stucchi et al. (2005). There was a new year-class of Atlantic salmon at the Humphrey Rocks salmon farm located in Tribune Channel north of Doctor Islets (Figure 1), but no gravid females were observed there until October of 2003 and the source of the observed pink salmon infections in this area of Tribune Channel was most probably wild hosts.

Summary, Recommendations, and Conclusions

More questions have been asked by this analysis and review than have been answered. It appears incontrovertible that infections of new hosts by copepodids occur at distances of at least several kilometers from the source of larvae in areas where net transport vectors are not null vectors. *Zones of infection*, with respect to the source of larvae, depend primarily on water temperature and net water transport vectors. This analysis suggests that salmon farms contribute an unknown and presently unpredictable number of copepodids to the parasite population. However, it appears that infections of pink salmon fry in the Broughton are associated with at least two lice species, which have numerous hosts within the archipelago. An understanding of the relative contribution by farmed Atlantic salmon cannot be made without understanding the contribution from these other hosts and a more detailed understanding of the archipelago's low salinity environment on the development and survival of at least *L. salmonis* and *C. clemensi*. This study concludes that oceanographic conditions in the Broughton Archipelago naturally control lice populations during years of normal rainfall but that increased infections might occur during years with below average precipitation. The following specific summary statements bear emphasis and the recommendations are made to help direct future research in all regions where sea lice epizootics are of interest.

Summary

The literature describing the contribution of sea lice from Atlantic salmon farms to wild stocks of fish in the northeast Atlantic remains contradictory with some reports showing significant correlations and other reports concluding that copepodids originating on wild stocks were primarily responsible for new infections of other wild stocks. These apparent contradictions may have their roots in differences in temperature, salinity, and currents at the study sites. The European literature has documented increased densities of nauplii near salmon farms. It has not documented an increase in the prevalence or intensity of lice on wild stocks in the immediate vicinity of these farms. Increased infections are apparent at distances ≥ 2.0 km.

At typical spring Broughton surface water temperatures of 7.5 to 9.0°C, caligid larvae are transported up to 40 km while developing to an infective copepodid stage. Copepodids remain viable for another 4 to 6 days while they are transported another 7.8 km. Larval transport vectors and corresponding zones of infection will vary from one region to another. However, except where net transport vectors are null vectors, copepodids will not infect new hosts within 250 m of the source of nauplii as asserted by Morton et al. (2004). A large portion of the nauplii released at salmon farms located near the western boundary of the archipelago are swept into Queen Charlotte Straits and highly dispersed before reaching an infective stage. However, lice released from the Glacier Falls farm during periods of high salinity are capable of infecting several other farms and wild stocks of fish migrating in the western area of the archipelago.

The literature suggests significant stress and a failure to develop to the copepodid stage when sea lice larvae are subjected to salinities <30‰. During years of normal rainfall, surface water salinity in the Broughton Archipelago is reduced to well below 30‰ by snow melt and rainfall during spring and more dramatically by glacial melt in the summer and early fall. Salinity appears too low in normal years to support larval development to the copepodid stage from April through November. The record of sea lice infections at Sargeaunt Pass and Humphrey Rocks supports the existence of this natural control mechanism. However, interannual differences are apparent and salinities of 30 to 31‰ have been recorded in some areas of the archipelago during years of abnormally low rainfall. Snow pack and spring rainfall may be important factors for predicting the risks of sea lice infections on both farmed and wild fish in this as well as other regions;

Caligus clemensi appears to dominate spring infections of both migrating juvenile pink and farmed Atlantic salmon. *Lepeophtheirus salmonis* infections increased at two Atlantic salmon farms coincident with increasing late fall salinities and the return of adult Pacific salmon, which typically carry high lice loads. *Caligus clemensi* is hosted by at least seven nonsalmonid and six salmonid species, many of which are common at all times of year in the Broughton Archipelago. In addition *L. salmonis* is hosted by all salmonids, including cutthroat trout (*Oncorhynchus clarki*), which is also abundant in the archipelago. Censuses of the numerous lice hosts such as three-spine sticklebacks and resident salmon have not been made and their contribution of lice to the Broughton cannot be estimated.

Salmon farms in British Columbia are generally located in well-flushed environments over relative deep water (30 to >50 m). Their distance from shore varies, but is typically >25 to several hundred meters. Net current speeds at these farms are likely higher than found in nearshore environments where current speeds may be reduced by macroalgae beds, eelgrass meadows, and shallow reefs. The report of Jones and Nemec (2004) is important because they found *Caligus sp.* were the dominant lice on pink salmon fry during the later stages of their migration. *Caligus sp.* has many hosts including the three-spine stickleback (*Gasterosteus aculeatus*) and the authors reported a high prevalence and intensity of *Caligus* on this species. Hart (1973) notes that *G. aculeatus* is euryhaline and is frequently found in schools in nearshore environments. This is an environment where current speeds are frequently slowed resulting in reduced dispersal of copepods and an area where juvenile salmon are also likely to be found. From this, it appears reasonable to assume that pink and chum salmon fry are most exposed to sea lice infection as they migrate through shallow nearshore waters where slow currents are expected and where there is likely reduced dispersal of copepodids from sympatric hosts carrying high intensities and prevalence of *Caligus sp.* Many of the pink salmon spawning rivers empty into sounds and estuaries where water circulation is slow and high densities of hosts carrying sea lice might be anticipated. These sounds and estuaries should be investigated as important zones of infection.

No studies describing the immune or physiological response of pink salmon or any species of salmon fry were found in this review. Nor were studies documenting host survival as a function of lice intensity at salinities of 25–30‰ found. There is no credible basis for assuming that 1.6 chalimus stage *L. salmonis*/g of host represents a lethal infection for pink salmon weighing 1 to 3 g migrating in water of <30‰ salinity. The report Jones and Nemec (2004) suggest that the growth and health of pink and chum salmon was not compromised at infection intensities much greater than this.

The population of pink salmon returning to Broughton watersheds grew exponentially to historically unprecedented numbers in 2000 and 2001. This growth occurred over a 7-year period during which the biomass of cultured Atlantic salmon increased from 3,241 to 18,862 tonnes/year. The positive correlation in abundance between these two groups suggests that salmon farming, in and of itself, does not adversely affect the abundance of pink salmon. Pink salmon populations have suffered repeated significant declines throughout their documented history, which extends to times before salmon aquaculture was initiated in the archipelago. Consistent with the history of this species, their numbers rebounded to above the long-term average in 2004 and the population appears healthy.

Recommendations

The uncertainties revealed in this review and analysis can only be reduced with well-focused studies that consider at least the following questions. While these suggestions are made specific to conditions in the Broughton Archipelago, they likely apply to all areas where sea lice are of interest. These recommendations are ranked in the order of easiest implementation. The need to better understand sea lice life history, host response, and the contribution of larvae from all potential hosts cannot be overemphasized.

Physicochemical Monitoring. Farmed salmon producers should be encouraged to continuously monitory meteorological data, particularly rainfall at several locations in the Broughton Archipelago. In addition, it appears that surface salinity varies around a critical value of 30‰ in some areas of the archipelago during drought years. Accurate and continuously recording rain gauges and salinity and temperature probes should be maintained on several salmon farms. This information will help predict years in which increased salinity and sea lice larval survival should be anticipated.

Monitoring of Sea Lice on Cultured Atlantic Salmon. Anecdotal evidence suggests that sea lice have not historically been a significant factor in the production of Atlantic salmon in the Broughton Archipelago. Continued monitoring of sea lice on cultured fish with emphasis on correct identifications will provide valuable data elucidating the sources of infection and the influence that salinity and temperature have on sea lice transmission vectors.

Management of Lice on Cultured Fish. It is in the best interest of the environment and the producer to manage lice on farmed fish. Regardless of the relative contribution of lice by farmed fish, they can and should be managed using approved methods. The refinement of hydrodynamic models coupled with a better understanding of the response of sea lice larvae to salinity and temperature will allow for more accurate predictions of zones of infection and the identification of those farms where control of sea lice will be most beneficial and those where control is only necessary to protect the quality of the farmed product.

Alternate Hosts. An assessment of the relative contribution of larvae from their various hosts is required before the contribution from aquaculture can be assessed relative to natural infection pressures. This is considered important because sea lice infections most likely occur at some distance from their source. Studies suggesting increased infection pressure in the immediate vicinity of a source of larvae in dynamic marine environments must reconsider their findings in light of the known development times of larvae to an infective stage and local net current vectors.

Careful Identification of Lice to Genus and/or Species. Taxonomic identifications are tedious and identification to genus or species can be difficult requiring rigorous training and quality assurance procedures—especially when dealing with larvae and chalimus stages. It is easy for taxonomists and technicians to assume that chalimus stages are *L. salmonis* because the lice are from salmon. The report of Jones and Nemec (2004) emphasizes the need for care in these identifications and for rigorous quality assurance procedures to include interlaboratory or interexpert verification of some subset of the enumerated sample.

Sea Lice Life History. The development and survival of both *C. clemensi* and *L. salmonis* larvae at temperatures of 5–10°C and salinity in the 15–30‰ range must be determined if the population dynamics of sea lice in the Broughton Archipelago are to be understood.

Larval Transport. Hydrodynamic models for the Broughton Archipelago have been developed and field testing has begun. These models are necessary to better predict the zones of infection for sea lice larvae and other etiological agents released from salmon farms or other sources. These models need to be improved to better understand larval transport in complex nearshore environments. The potential for sea lice to create disease in fish is more a function of the density of copepodids and the density of new hosts than it is of the total number of lice larvae released. Because salmon farms are located in well-flushed environments, it is likely that larvae released from them are widely dispersed before reaching an infective stage. Higher densities of copepodids might be maintained in shallow near-shore areas where net transport vector speeds are reduced. This hypothesis would explain why *C. clemensi*, hosted by three-spine sticklebacks, were primarily responsible for the increased prevalence and intensity of lice on pink and chum salmon as they migrated through the archipelago. Near shore current vectors are likely site-specific and no literature was identified describing their behavior along the major pink and chum salmon fry migration routes. However, the archipelagos sounds and lagoons should be investigated as potential sites of increased infection.

The vertical distribution of nauplii during development should be determined for the Broughton Archipelago and other areas. This information is important for fully understanding their transport in vertically stratified marine waters and modeling parasite density at the point where they molt to an infective stage.

Conclusion

The emerging picture of sea lice associated disease in the Broughton Archipelago is likely applicable to many areas of the world. This analysis indicates that contrary to other published reports, there is no basis for expecting an increase in wild fish infections in the immediate vicinity of any source of lice larvae—including those hatched from lice at Atlantic salmon farms. However, it should be emphasized that this analysis is area specific and zones of potential sea lice infection will vary from one region to another. Understanding and predicting

epizootic disease associated with caligid lice in wild or cultured stocks of fish requires an expanded understanding of the life history of the lice and of the hydrodynamic and physic-ochemical characteristics of the specific environments of concern. As noted by Heuch and Mo (2001), development of local or regional models including the factors described above would provide the necessary tools for optimal management of coastal systems with re-gard to sea lice infections in salmon. Ongoing monitoring by the Canadian Department of Fisheries and Oceans indicates that the health of pink salmon fry is not compromised at low to moderate levels of sea lice infection. Pink salmon returns to the Broughton Archipelago in 2004 were above their historical average and the population appears healthy despite the decline observed in 2002.

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