Sea lice and salmon in Pacific Canada: ecology and policy

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The spread of sea lice (*Lepeophtheirus salmonis*) from salmon farms probably contributes to declines of some native Pacific salmon populations. Migration normally protects juvenile wild Pacific salmon from the marine ectoparasite in coastal waters by separating juvenile salmon from infected wild adults that are located offshore. Farmed salmon populations dwarf natural coastal host populations, particularly in winter, leading to biomagnification of louse populations. By spring, there may be large numbers of lice on farmed salmon, and this is associated with recurrent parasite infestations of wild juvenile salmon and depressed wild salmon stocks. Abiotic (eg temperature and salinity), biotic (eg predator abundance and food availability), and management (eg periodically emptying farms and applying chemical parasiticides) factors are thought to mediate the louse threat, but none have been well studied. Policy is needed that protects undeveloped juvenile salmon habitats and that supports long-term study of salmon ecosystems, to evaluate the sustainability of wild and farmed salmon.

Ocean fisheries and ecosystems are likely affected by the spread of infectious disease from industrial fish farms. Industrial salmon aquaculture is associated with depressed sympatric wild salmon stocks, as a result of disease interactions, competition, and interbreeding (Ford and Myers 2008). Possibly the best studied parasite of fish is the salmon louse (*Lepeophtheirus salmonis*), a marine copepod that parasitizes wild and farmed salmonids (Boxaspen 2006; Costello 2006; Figures 1 and 2). Lice feed on host surface tissues (skin, muscle, and blood), causing morbidity and mortality (Pike and Wadsworth 2000). The louse has been economically damaging to the salmon aquaculture industry (Johnson *et al.* 2004), and is a threat to wild salmonid populations (Heuch *et al.* 2005; Krkošek *et al.* 2007a).

In Pacific Canada, recurrent parasite infestations of wild juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon have been well studied.

> ### In a nutshell:
> - Pacific salmon migrations normally protect juvenile salmon from sea lice; salmon farms can increase the exposure of wild juvenile salmon to sea lice
> - Sustained high exposure to lice can lead to parasite outbreaks among wild juvenile salmon; annually recurrent infestations are associated with depressed wild salmon stocks
> - Abiotic, biotic, and anthropogenic factors are thought to mediate the sea louse threat
> - Policy is needed that supports conservation, monitoring, and adaptive management

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Recent work from the Broughton Archipelago (located along the central coast of British Columbia) and elsewhere (Figure 3) offers insights into how salmon farms affect sea lice and salmon ecology (eg Morton *et al.* 2004; Beamish *et al.* 2005; Jones *et al.* 2006b; Krkošek *et al.* 2007a). I looked for convergence of evidence among differing perspectives on the origin and impact of sea lice infestations; some studies identify salmon farms as the primary cause, whereas others emphasize biotic and abiotic correlates. A clearer understanding of sea lice ecology is emerging, with important messages for policy and management, as well as future research directions.

◼ Natural ecology of sea lice and Pacific salmon

The transmission cycle of *L salmonis* in the eastern Pacific is closely linked to the migration of Pacific salmon. When juvenile salmon first enter the Pacific Ocean in spring (March–May; Groot and Margolis 1991; Quinn 2005), they are uninfected, because lice do not occur in freshwater (Johnson and Albright 1991a; Bricknell *et al.* 2006). The juvenile salmon remain in coastal waters for several months, where they feed and grow; however, most adult salmon remain in offshore waters (Groot and Margolis 1991; Quinn 2005). This spatial separation between adults and juveniles protects the juveniles from parasites that infect adults, an ecological characteristic called *migratory allopatry* (Krkošek *et al.* 2007b).

There is much recent evidence for migratory allopatry, particularly among pink salmon. Juvenile salmon enter the sea when they are about 30 mm in fork length (length from the tip of the snout to the fork of the tail), or about 0.3 g in weight, and lack scales. During the spring, for 2–3 months following marine emergence, *L salmonis* are rare (< 5% prevalence; Wertheimer *et al.* 2003; Morton *et al.* 2004;
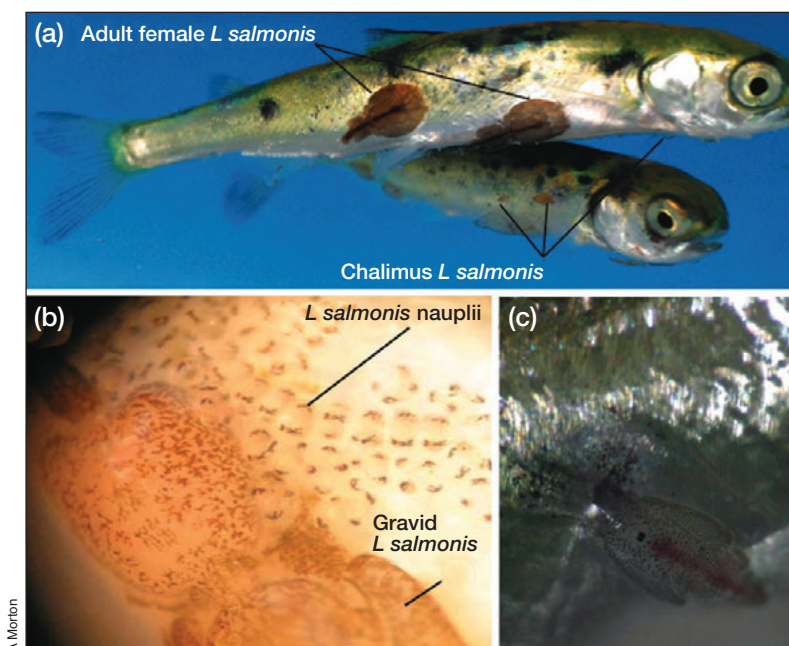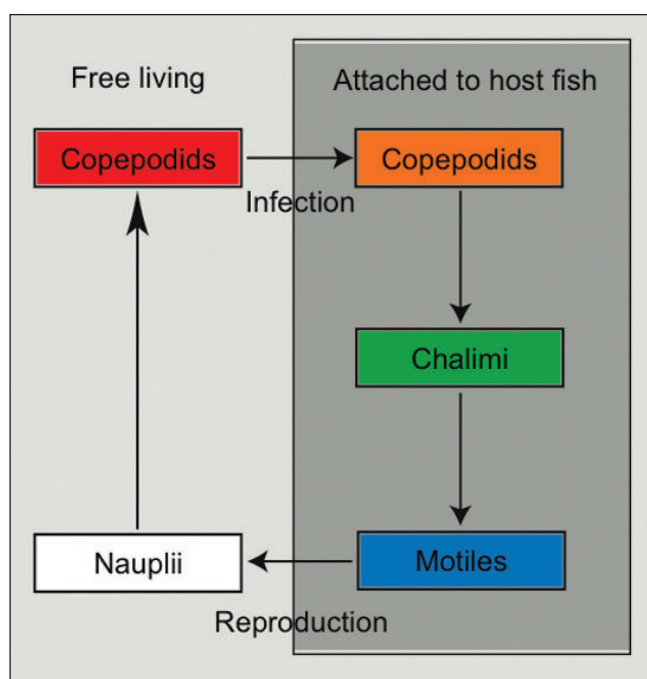
Figure 1. *Salmon lice* (L salmonis) *on juvenile pink salmon. (a) Chalimus and adult female* L salmonis *on juvenile pink salmon, (b) gravid* L salmonis *with newly hatched nauplii, and (c) an* L salmonis *chalimus larva on a juvenile pink salmon. The red coloration in (c) is likely fish blood in the gut of the larval louse. Note the lack of scales and damage to surface tissues on the 50–60 mm fork length juvenile pink salmon.*

Krkošek *et al.* 2007b; Peet 2007). The lice observed during this time probably come from local native hosts, such as subadult coho (*Oncorhynchus kisutch*) and Chinook (*Oncorhynchus tshawytscha*) salmon. These host populations are orders of magnitude less abundant than populations of adult pink, chum, sockeye (*Oncorhynchus nerka*), coho, and Chinook salmon, all of which are located offshore during this time (Groot and Margolis 1991).

Figure 2. *Salmon louse life cycle. Free-swimming, noninfectious nauplii hatch from gravid, motile female lice and then moult into copepodids, which infect a host fish or die. Once attached to a host fish, copepodids develop through chalimus stages and then ultimately motile stages, which include sexually mature adults, thereby completing the life cycle. There are nauplii I and II substages, chalimus I–IV substages, and pre-adult I and II and adult motile substages (Johnson and Albright 1991b).*

Migratory allopatry ends when large populations of adult salmon begin returning to coastal waters in the summer, during their spawning migration. These wild adult Pacific salmon support large populations of *L salmonis* in offshore waters (Nagasawa 2001) and then bring the lice back to the coastal waters (Beamish *et al.* 2005), where they become sympatric with larger juvenile salmon. *L salmonis* abundance on the juveniles then increases correspondingly (Krkošek *et al.* 2007b). By this time, the juvenile salmon have developed scales, have grown by one or two orders of magnitude (Krkošek *et al.* 2007b), and display a high level of resistance to sea lice in experimental conditions (Jones *et al.* 2006a).

While the adult salmon occupy coastal marine waters, the lice may spread naturally to small populations of overwintering subadult coho and Chinook salmon (Beamish *et al.* 2007). In late summer and autumn, adult salmon migrate into freshwater to spawn and their associated lice either die as a result of the low salinity or disperse (motile lice only) into the marine environment in search of another host (life cycle is shown in Figure 2). There are no known resting stages for lice that would allow them to survive the winter without a host. Meanwhile, during summer, the newly infected juvenile salmon carry the parasite to offshore waters, where they support the majority of the *L salmonis* population (Nagasawa 2001) until the following summer, when adult salmon return to coastal waters, completing the transmission cycle among salmon generations.

Louse transmission occurs either via the infectious copepodid stage or as a result of the movement of preadult and adult lice among fish hosts (Ritchie 1997; Hull *et al.* 1998; Figure 2). Both transmission routes from adult to juvenile salmon are evident during summer sympatry (Krkošek *et al.* 2007b). Copepodid and chalimus lice have very low survival rates (Morton and Routledge 2005; Jones *et al.* 2006a; Figure 2), yet pink salmon carry fewer lice when leaving coastal waters as juveniles than when they return as adults (Beamish *et al.* 2005; Krkošek *et al.* 2007b). Transmission of motile lice may therefore be important to compensate for chalimus mortality and reconcile observations of low larval survival and louse population growth within a salmon generation.

■ Effects of salmon farms on sea lice transmission

Farmed salmon are raised in net pens that are open to the larger marine ecosystems in which they are embedded. The farmed fish are therefore exposed to the pathogens that infect wild fish and vice versa. In British Columbia, farms are typically stocked with several hundreds of thousands of fish (Orr 2007), usually Atlantic salmon (*Salmo salar*), but sometimes Chinook salmon. Salmon farms occur in regional clusters, leading to regional abundances of farmed salmon that dwarf sympatric wild salmon stocks, especially during the winter months. This change in host population structure has important implications for parasite transmission.

Farmed salmon enter the ocean from freshwater hatcheries and so are initially uninfected with sea lice. Sea lice on farmed salmon therefore originate from wild salmon, with possible further transmission among farms. From mid-summer to mid-autumn, farmed salmon probably experience high exposure to *L salmonis* copepodids originating from the returning wild adult salmon populations (Beamish *et al*. 2005). Salmon farms experience louse population growth during winter (Orr 2007; Saksida *et al*. 2007), probably as a result of high transmission rates associated with high host densities (Anderson and May 1978; Grenfell and Dobson 1995).

Figure 3. *British Columbia salmon farms (black dots) and areas where sea lice have been studied on juvenile wild salmon (boxes). Sources – Chatham Sound: Morton et al. (2004); Krkošek et al. (2007b). Bella Bella: Morton et al. (2004); Peet (2007). Rivers and Smith Inlets: Morton et al. (2004). Muchalat Inlet: B Hargreaves (pers comm). Discovery Islands: Morton et al. (2008). Clayoquot Sound: K Beach (pers comm). Broughton Archipelago: Morton and Williams (2003); Morton et al. (2004, 2006); Krkošek et al. (2005, 2006, 2007a); Jones et al. (2006); Jones and Hargreaves (2007).*

In spring, the louse population on farmed salmon may be an important source of larvae in the environment (Orr 2007). In contrast, natural overwintering coastal host populations are considerably less abundant than farmed salmon populations. In a natural system, louse transmission and subsequent total parasite population size the following spring would be low, because of low host abundance. Correspondingly, during the spring, wild juvenile salmon experience < 5% prevalence of *L salmonis* in areas without salmon farms (Krkošek *et al*. 2007b). Near salmon farms, *L salmonis* abundance on wild juvenile salmon is much greater (Morton and Williams 2003; Morton *et al*. 2004; Krkošek *et al*. 2005,

2006a; Morton *et al*. 2008).

Mathematical modeling has made it possible to quantify sea lice transmission from farmed salmon relative to wild host populations (Krkošek *et al*. 2005, 2006a). The approach applies mathematical models to field data regarding sea lice on juvenile salmon migrating past salmon farms (Figure 4). Studies suggest that salmon farms are the primary contributors of lice during the spring out-migration season, with farm-origin lice exceeding natural levels for over 30 km of migration route per farm. An exchange in *Reviews in Fisheries Science* highlights disagreement and misunderstandings among scientists, clarifies some details of the modeling
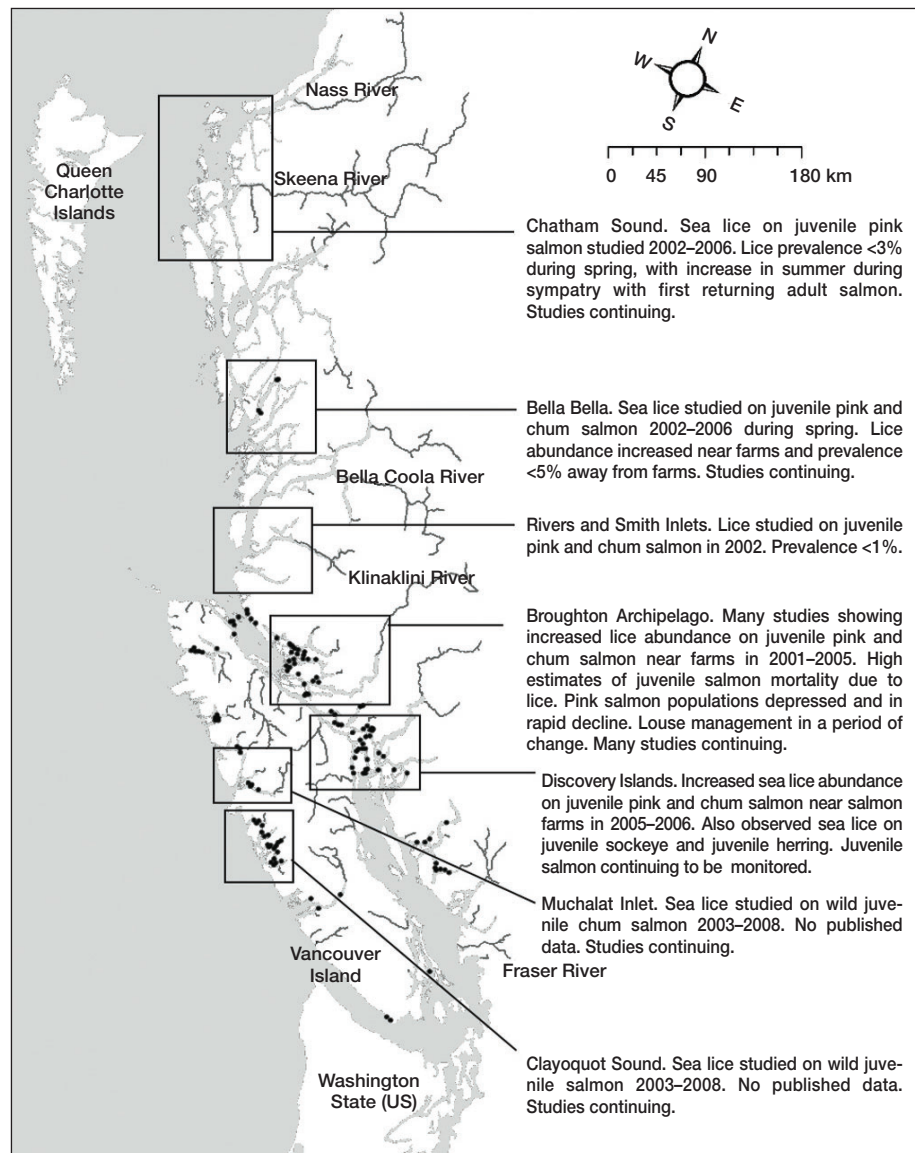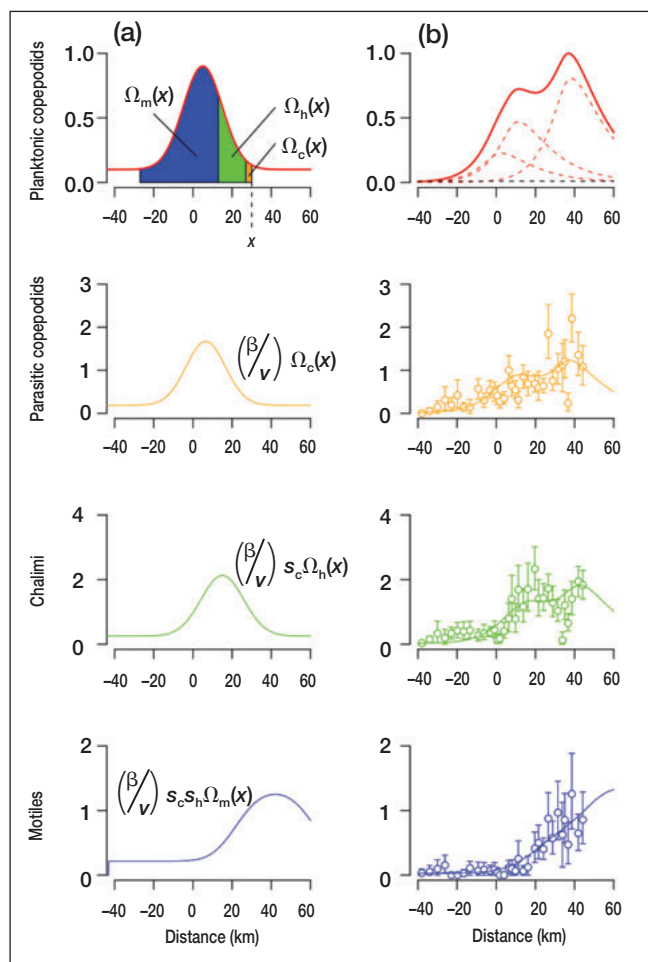
Figure 4. *Measuring sea louse transmission from farmed to wild salmon in (a) theory and (b) practice. (a) Top panels represent the spatial distribution of planktonic copepodids along the length of an inlet. The copepodids come from a spatially uniform distribution, representing natural sources of lice and an advection–diffusion model for the spread of nauplii and copepodids from a farm at kilometer 0. Juvenile salmon migrate seaward (left to right) at average velocity, v. At any location x, the number of parasitic copepodids, chalimi, and motiles on a fish are related to the total number of infectious larvae previously encountered, shown by the shaded regions. The width of each region is the distance the juvenile salmon travel during each louse developmental stage. The number of planktonic copepodids that appear as parasitic stages is mediated by the rate copepodids capture fish (β/v), and then survive copepodid (s_c), and chalimus (s_h) stages. (b) The model can be fit to data on sea lice infecting juvenile salmon migrating past salmon farms using maximum likelihood (curved lines). The parameter estimates reveal the overall spatial distribution of copepodids (solid red line), the spatial distribution of copepodids originating from each farm (dotted red lines for three farm sources), and the uniform distribution from natural hosts (dotted black line). Data are for chum salmon in dataset TR-II from Krkošek* et al. *(2006).*

approach, and discusses abiotic correlates (Brooks 2005; Brooks and Stucchi 2006; Krkošek *et al.* 2006b). Krkošek *et al.* (2006a) have since replicated the modeling approach extensively.

Other factors affecting infestations

Three-spined stickleback (*Gasterosteus aculeatus*) are abundant in the Broughton Archipelago and are infested with sea lice, and so may play a role in louse epizootiology (Jones *et al.* 2006b; Brooks and Jones 2008). Lice do not reach reproductive age on sticklebacks (Jones *et al.* 2006a, 2006b), so they die before reproducing and/or pre-adult lice move to another host species. Because there are many copepodids and chalimi on wild juvenile salmon near farms (Morton and Williams 2003; Morton *et al.* 2004; Krkošek *et al.* 2006a), egg-bearing female lice must have been present nearby, but these are not observed on sticklebacks (Figure 2). Further work is needed to determine whether sticklebacks function as a source or a sink for louse populations.

Wind and larval louse behavior may be important in louse dispersal. Oceanographic models omitting these features (Brooks 2005; Brooks and Stucchi 2006; Foreman *et al.* 2006) overestimate seaward flow and louse dispersal (Krkošek *et al.* 2006a). Oceanographic models from Europe that have similar characteristics to models of British Columbia inlets seem to indicate that wind can retain copepodids near farms and salmon streams (Murray and Gillibrand 2006). Active vertical positioning in the water column by larval lice may result in many dispersion patterns, including those observed in the Broughton Archipelago (Gillibrand and Willis 2007). Further work is needed to include these features in oceanographic models of sea lice dispersal in Pacific Canada.

There are natural variations in salinity in coastal waters, and this may mediate sea louse infestation of juvenile wild salmon (Brooks 2005; Jones and Hargreaves 2007). In laboratory conditions, low salinity is associated with poor louse survival and settlement on host fish (Johnson and Albright 1991a; Bricknell *et al.* 2006). Distinguishing the role of salinity in infestations is difficult, because as juvenile salmon migrate past farms they also transition from low salinity surface waters near rivers to high salinity in surface waters nearer the open ocean. Furthermore, larval lice migrate vertically in the water column each day (Heuch *et al.* 1995), and so may simply avoid low salinity surface waters.

Field studies typically measure sea-surface salinities, and some have found spatial associations between salinity and louse abundance (Jones *et al.* 2006b; Jones and Hargreaves 2007). These papers are difficult to interpret because salmon farms were excluded from the analysis. Analyses that included farms found weak or no association between salinity and sea louse abundance and strong association with the presence of farms (Morton *et al.* 2004; Morton *et al.* 2008). Re-examination of sea lice and salinity data by Krkošek *et al.* (2006a) showed that sea-surface salinity cannot explain the infestations (Figure 5). Sea-surface salinity is probably an important factor in sea louse survival, but may not be an explanation of the infestations. Alternatively, larval production on farms may compensate for louse mortality in low salinity waters.

Temperature may influence sea louse infestations

Figure 5. *Temporal progression in the spatial distribution of sea-surface salinity and sea lice abundances on juvenile chum salmon migrating through Tribune Channel in spring 2004. The three time periods correspond to 10–14-day sampling trips, conducted in early April, late April and early May, and late May, that collected the data used to generate the figure. Black lines are models of parasitic copepodids (C), chalimi (H), and motiles (M) fit to the sea louse data and the thick blue line represents sea-surface salinities measured at each site (data and models from Krkošek et al. 2006). The farm-to-wild transmission pattern is evident early in the season, before a freshwater plume moved down Knight Inlet, causing the landward drop in salinity observed in late April. By late May, sea louse abundances peaked (note change in scale) when salinity declined in Knight Inlet as well as Tribune Channel. Salinities < 25 parts per thousand (ppt) are considered hostile to sea lice.*

(Brooks 2005; Jones and Hargreaves 2007). In laboratory conditions, increasing temperature accelerates louse developmental rates (Stien *et al.* 2005), which could increase louse population growth rates and intensify infestations. At the temperatures observed in the field, louse developmental rates estimated in transmission models are related to laboratory studies by the juvenile salmon migration speed, estimated to be ~1 km per day in the Broughton Archipelago (Krkošek *et al.* 2006a). There are no known changes in temperature unique to the Broughton Archipelago that could explain the infestations. It is likely that increasing temperature due to global climate change may exacerbate sea louse infestations in the future (Costello 2006).

■ Effects of lice on juvenile salmon survival

Sea lice may affect juvenile salmon survival directly or indirectly via predation risk, secondary pathogen exposure, competitive fitness, or other interactions. Only direct mortality has been investigated for juvenile pink and chum salmon, in both experimental and field conditions. Experimental studies looked at survival of initially uninfected fish held in laboratory conditions after being exposed to infectious copepodids (Jones *et al.* 2006a, 2007). Field studies observed the survival of fish in ocean enclosures after they were collected from the field with existing infections (Morton and Routledge 2005; Krkošek *et al.* 2006a).

Both field and experimental studies report high mortality of lice on juvenile salmon (Morton and Routledge 2005; Jones *et al.* 2006a; Krkošek *et al.* 2006a; Jones *et al.* 2007). Naturally infected fish, 0.3–1 g in weight, held in ocean enclosures showed low survival rates among those carrying motile lice (Morton and Routledge 2005; Krkošek *et al.* 2006a). Experimentally infected fish showed high survival rates (Jones *et al.* 2006a, 2007), but the fish weighed over 10 g and were fully scaled, whereas infestations in the Broughton Archipelago involve scaleless fish weighing less than 1 g (Morton *et al.* 2004).
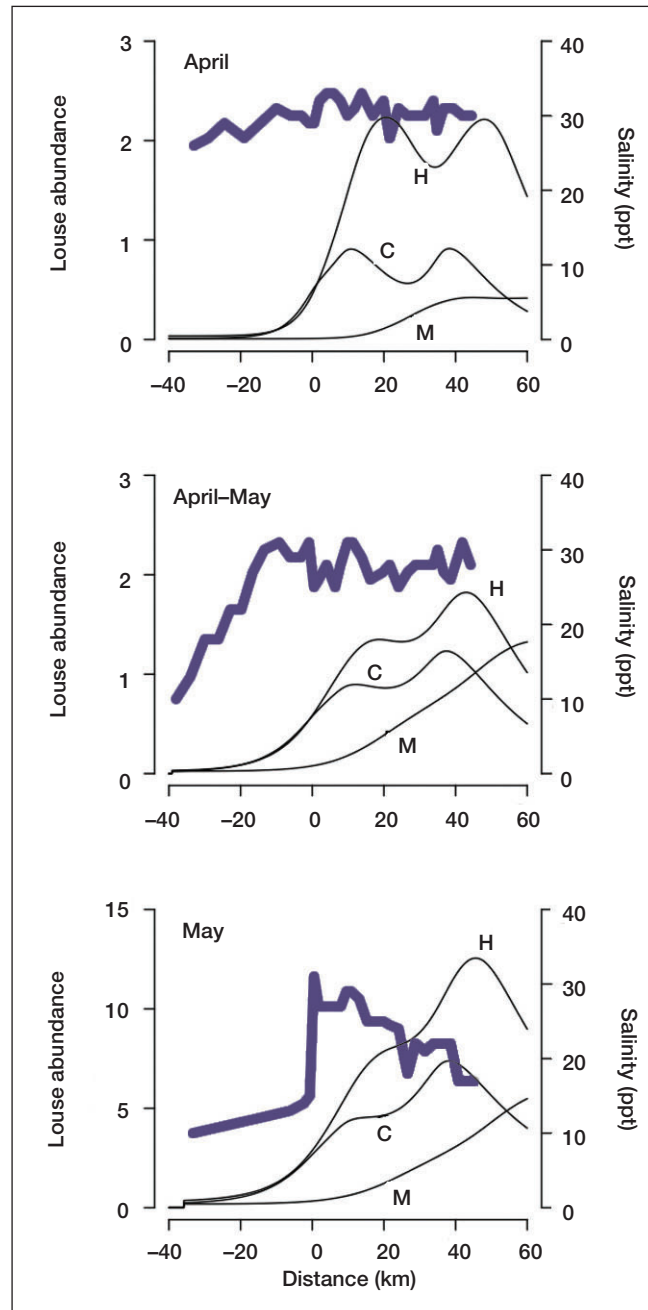
Further experimental work has reported that juvenile salmon weighing < 0.7 g die as a result of lice, whereas larger fish showed increased resistance to lice (Jones *et al.* 2008). Further data and analyses are needed to estimate survival of juvenile and adult lice, as well as survival of salmon within the 0.3–10 g range.

The experimental and field survival studies point to an interesting situation involving both high host rejection and high pathogenicity of lice. This suggests that juvenile salmon (pink and chum, at least) may be able to survive sea louse exposure under certain conditions – when infection pressure is low and brief. The recurrent infestations observed in the Broughton Archipelago (Morton and Williams 2003; Morton *et al.* 2004; Krkošek *et al.* 2006a) and other areas of British Columbia (Morton *et al.* 2008)

indicate that epizootics can emerge when infection pressure is high and sustained (about 2 months in the Broughton Archipelago). Further work on juvenile salmon at various sizes is needed to confirm and expand upon these findings.

■ Effects of infestations on salmon population dynamics

The most critical question for policy makers is whether sea louse infestations threaten wild salmon stocks. Juvenile salmon, particularly pink and chum, naturally experience high mortality, mostly due to predation (Heard 1991). It is therefore debatable whether increased exposure to sea lice among juvenile salmon results in a decrease in salmon survival and threats to wild salmon populations. In other words, if most of the juvenile salmon are going to die anyway, does it matter if some are infected with sea lice? Several recent studies have shed light on these issues, using theoretical and empirical approaches (Beamish *et al.* 2006; Krkošek *et al.* 2007a, 2007b; Ford and Myers 2008).

The first study on wild Pacific salmon survival in relation to sea lice reported high marine survival for one pink salmon cohort from the Broughton Archipelago (Beamish *et al.* 2006). Because the juvenile salmon migrated to the sea when salmon farms operated at average regional abundance, the study concluded that wild and farmed salmon can coexist. While the regional abundance of farmed salmon may have been average, the primary wild salmon migration corridor was fallowed (farms were emptied of fish) as part of the provincial government's Broughton Archipelago Sea Lice Action Plan to protect wild juvenile salmon from lice. Morton *et al.* (2006) found that louse abundance decreased significantly during the fallow treatment. Another interpretation of Beamish *et al.* (2006) is therefore that fallowing reduces louse abundance and improves pink salmon survival.

Predators may mediate the relationship between sea lice and pink salmon population dynamics. If predators selectively remove infected prey, parasitism may have little effect on prey populations (Hudson *et al.* 1992; Packer *et al.* 2003). By extending a standard fisheries model, Krkošek *et al.* (2007a) evaluated the sensitivity of pink salmon populations to sea louse exposure with and without selective predation. Without selective predation, salmon populations quickly decline and collapse when exposure increases to about two motile lice per juvenile salmon for 2 months. Under selective predation, there is a threshold motile louse abundance of about 0.75 per fish, below which there are no effects on salmon populations and above which salmon numbers decline followed by population collapse at approximately three motile lice per fish for 2 months.

The prediction of high sensitivity to sea lice among pink salmon populations was empirically tested by Krkošek *et al.* (2007a), by comparing the population growth rate, r, for stocks in the Broughton Archipelago before and during sea lice infestations as compared with those of stocks located just to the north, where there are no salmon farms. By using a comparative approach, they controlled for other, potentially confounding factors (eg climate). The sea lice infestations were associated with a significantly reduced r, despite the closure of the fishery (Figure 6). Because r is significantly negative, the infestations threaten the viability of pink salmon at a rate of 99% collapse per four salmon generations. The analysis indicates declining trends may be reversed and recovery initiated if lice are reduced to less than approximately 1.3 motile lice per juvenile pink salmon.

A review by Brooks and Jones (2008) disagrees with Krkošek *et al.* (2007a), emphasizing that many factors contribute to high variation in pink salmon population dynamics and claiming that negative effects of sea lice infestations are not evident. In their response, Krkošek *et al.* (2008) explain how alternate factors (density dependence and environmental stochasticity) were controlled by using a stochastic non-linear model in a comparative analysis. Krkošek *et al.* (2008) further show that the claims in Brooks and Jones (2008) lack support when the data and statistics are more closely scrutinized. Neither Brooks and Jones (2008) nor Krkošek *et al.* (2008) were subjected to peer review during the publication process in *Reviews in Fisheries Science*.

Using a global dataset, Ford and Myers (2008) evaluated whether the production of farmed salmon was associated with salmonid declines, by comparing populations exposed to farms with nearby, unexposed populations. They did not isolate the effects of lice relative to other pathogens, or to genetic and competitive interactions with escaped salmon. Genetic introgression (infiltration of the genes of one species into the gene pool of another through repeated backcrossing of an interspecific hybrid with a parent) and competition are probably minor in British Columbia, particularly for pink and chum salmon, and so the mechanism of impact is probably lice and other pathogens. Ford and Myers' meta-analysis confirms the declines in pink salmon observed by Krkošek *et al.* (2007b) for the Broughton Archipelago and suggests similar effects for pink salmon populations in the Discovery Islands (British Columbia; Figure 3).

Results from Ford and Myers (2008) indicate that chum salmon populations in the Broughton Archipelago and Discovery Islands may also be affected, although the trend of declining survival with increasing aquaculture intensity was not statistically significant. Like pink salmon, chum salmon may be threatened due to their small size during marine entry. Further, experimental work indicates that juvenile chum salmon are more susceptible to lice than pink salmon (Jones *et al.* 2007). Because chum salmon have a longer life cycle than pink salmon (3–5 years versus 2 years, respectively; Groot and Margolis 1991), evidence for the effects of lice on chum salmon will be slower to accumulate than for pink salmon, so the current evidence may be weak.

The studies discussed above suggest that sea lice infestations affect wild pink salmon populations, and possibly chum salmon as well. Salmonids that feed on juvenile pink and chum salmon, such as coho salmon and cutthroat trout (*Oncorhynchus clarkii*), may also be at risk, due to the accumulation of motile lice from prey onto predators (Connors *et al.* 2008). More work is needed to empirically and theoretically identify the mechanisms by which sea lice infestations affect wild Pacific salmon populations. Further investigation is also needed to evaluate whether, and how, sea lice infestation interacts with other ecological factors, such as food availability, predation, exposure to other pathogens, and abiotic factors, to affect salmon population dynamics.

■ Toward conservation policy in Pacific Canada

Canada's Policy for Conservation of Wild Pacific Salmon specifies a mandate to "restore and maintain diverse salmon populations and their habitats" and places "conservation of wild salmon and their habitat [as] the highest priority for resource management-decision making" (DFO 2005). This provides a strong basis for developing a sea lice policy in Canada. Because of scientific uncertainty as well as environmental, anthropogenic, and biotic change, a policy structure is needed that not only protects wild Pacific salmon from sea lice, but that is also adaptive to new scientific information. Policy development on sea lice in British Columbia has been complex, because salmon aquaculture has been regulated by the provincial Ministry of Agriculture and Lands, whereas salmon conservation rests with the federal Department of Fisheries and Oceans (DFO). A recent ruling by the British Columbia Supreme Court has transferred regulatory authority of salmon aquaculture from provincial to federal governments, thereby placing responsibility for managing wild salmon and salmon aquaculture within DFO.

As the Canadian federal government drafts policy on salmon aquaculture, they could heed lessons learned from Europe. European policy is well developed and includes legal limits on sea louse abundance on farmed fish, mandatory reporting of lice data to regulators, and protection of coastal waters that support some of the remaining wild Atlantic salmon populations. The protected zones include the Norwegian National Salmon Fjords, which seek to protect wild salmon by prohibiting and/or restricting salmon aquaculture activity (www.fisheries.no). There is debate as to what constitutes acceptable risk to wild salmon and how policy can achieve this (Heuch *et al.* 2005). The threat to wild salmon depends not only on the number of lice per farmed fish, but also on the number of fish per farm, the number of farms in a region, the location of the farms, and prevailing environmental and biotic factors.

Management options available to mitigate sea lice threats to wild salmon include chemical treatment, fallowing, reduction of farmed salmon abundance, closed containment technology that treats farm effluent, and
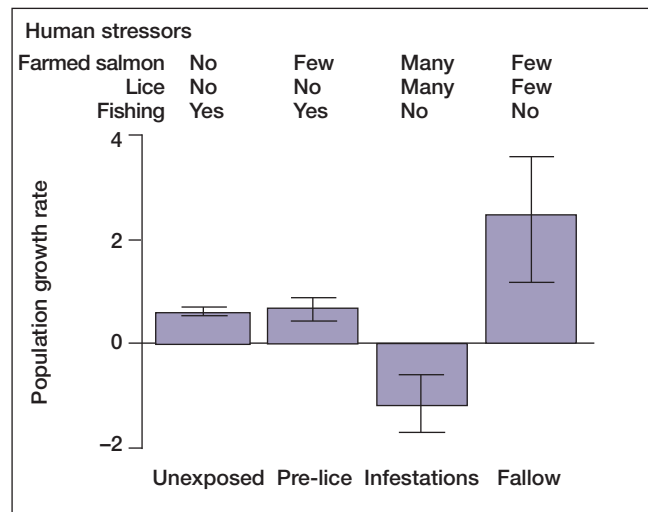

Figure 6. *Pink salmon population growth rates (and 95% confidence intervals) in relation to farmed salmon abundance, sea lice infestation, and fishing. The population growth rates were estimated by fitting a stochastic Ricker model to escapement data for populations unexposed to salmon farms (Unexposed), and populations exposed to salmon farms before infestations (Pre-lice), during recurrent infestations (Infestations), and for a fallowing treatment applied in one year (Fallow) (Krkošek* et al. *2007a).*

moving farms away from migration routes and juvenile salmon habitats. Chemical treatment reduces lice on farmed fish (Orr 2007), but may impact non-target crustaceans (Waddy *et al.* 2002) and lice may evolve resistance (Lees *et al.* 2008). Fallowing reduces louse abundance (Morton *et al.* 2005), but cannot be conducted annually, because the production cycle of farmed salmon exceeds 1 year. The economic and ecological viability of closed containment technology or reducing farmed salmon density is unknown. However, while no single management option is without flaws, a coordinated application of several options may prove fruitful.

Sea lice policy in Canada developed by the British Columbia provincial government is limited to monitoring lice on farms. There are no corresponding regulations to respond to monitoring data. However, industry has a fish health management plan that calls for harvesting farmed fish or applying chemical therapeutants when louse abundance reaches three motile lice per fish. While the threshold level lacks a scientific basis for protecting wild salmon, it does provide a starting point for evaluation and modification. However, evaluation and modification of management have been slow to develop. Government scientists have excluded farms from analyses (Jones and Hargreaves 2007), whereas independent and academic scientists have proceeded without access to farm data (Krkošek *et al.* 2006a).

The Pacific Salmon Forum (PSF; www.pacificsalmonforum.ca) was an initiative of the British Columbia government, to study and resolve threats posed by salmon farms to wild salmon. It progressed in terms of funding and coordinating science, but lacked legislative support

to implement and evaluate management actions according to basic scientific principles of control, treatment, randomization, and replication. The PSF mandate has now ended, meaning there is no long-term support, which is needed to understand and respond to management (eg treatment), environmental (eg temperature), and biological (eg louse evolution of chemical resistance) changes. The PSF final report to the British Columbia provincial government recommended major changes to governance structures responsible for managing salmon ecosystems and the salmon farming industry. However, none of the PSF recommendations are binding, and the provincial government has lost regulatory authority over salmon farms.

One recent policy change implemented by the provincial government is aligned with the precautionary principle: a moratorium on industry expansion in northern coastal British Columbia. This action was taken to ensure that some areas of coastal British Columbia remain protected, while the sustainability of wild Pacific salmon stocks and salmon aquaculture is evaluated. The policy change implies precautionary management but also reflects strong public opposition to expansion of the salmon aquaculture industry in British Columbia – opposition that could affect electoral outcomes (Winram and Hong 2007). The increase in public opposition and its influence on conservation policy is likely due to a combination of a cultural tradition with wild salmon, vocal wild salmon interests, and publicity of scientific publications.

There is opportunity for Canadian policy to follow that of Europe. Most salmon farming regions and the provincial government's moratorium are encompassed in the Pacific North Coast Integrated Management Area (PNCIMA). The planning and implementation of PNCIMA have not yet begun but have been promised to Canadians by the Federal government in the Oceans Act (DOJ 1996). The PNCIMA should involve zoning for multiple user groups, which could prohibit salmon farming in waters supporting wild salmon populations of ecological, economic, or cultural importance. In areas with farms, policy should depend on scientific evaluation to set and revise legal limits on sea lice abundance on farmed salmon. This requires a coordinated area management perspective to accommodate salmon migration, distribute stocking and harvesting schedules, and apply chemical treatment. Management options, ranked by efficacy, immediacy, and sustainability, might be: relocating farms away from rivers, relocating farms away from constricted migration corridors, fallowing during spring, reducing stocking density, applying chemical treatment, and using closed containment technology.

■ Acknowledgements

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