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Population Ecology and Epidemiology of Sea Lice in Canadian Waters

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Population ecology and epidemiology of sea lice in Canadian waters

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

Research documents are produced in the official language in which they are provided to the Secretariat.

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TABLE OF CONTENTS

ABSTRACT	IV
RÉSUMÉ	V
INTRODUCTION	1
POPULATION STRUCTURE AND EPIDEMIOLOGY OF SEA LICE IN ADULT WILD SALMO	
PACIFIC REGION	2
ATLANTIC REGION	4
POPULATION STRUCTURE AND EPIDEMIOLOLGY OF SEA LICE IN JUVENILE WILD SALMON POPULATIONS	5
PACIFIC REGION	5
ATLANTIC REGION	13
POPULATION STRUCTURE AND EPIDEMIOLOGY IN FARMED POPULATIONS	13
PACIFIC REGION	13
Farmed Pacific Salmon	14
Farmed Atlantic Salmon	15
ATLANTIC REGION	18
ROLE OF WILD SALMONID AND NON-SALMONID HOSTS AS RESERVIORS	19
PACIFIC REGION	19
ATLANTIC REGION	21
EVIDENCE FOR LINKAGE BETWEEN SEA LICE POPULATIONS ON FARMED SALMON AND WILD SALMON AND NON-SALMONID HOSTS	23
PACIFIC REGION	23
ATLANTIC REGION	23
MANAGEMENT THRESHOLDS FOR SEA LICE: SCIENTIFIC AND VETERINARIAN BASIS AND METRICS OF EFFECTIVENESS	
PACIFIC REGION	24
ATLANTIC REGION	27
REFERENCES	28

ABSTRACT

Sea lice are found on farmed and wild fish on both the west coast and east coast of Canada. The predominant species on both coasts is referred to as Lepeophtheirus salmonis but indications are that the two groups are genetically different. Caligus species are also found on both coasts, these too are different species: Caligus clemensi and C. elongatus, respectively. There has been extensive work on sea lice on both wild and farmed fish over the last decade. Research indicates that L. salmonis, commonly referred to as the salmon louse; may have a broader host range than commonly thought, infecting species such as the three-spine stickleback. The role of farmed salmon, particularly farmed Atlantic Salmon, as potential reservoirs of L. salmonis is accepted. What is still debated is the effect of sea lice infections on wild salmon populations, and whether the establishment of farm level treatment thresholds is the most appropriate method to manage the situation. There is indication that various Pacific salmon species have different tolerances to both L. salmonis and C. clemensi and the role of other non-salmon species in the ecology and epidemiology of sea lice still needs to be better researched. Published work on sea lice on farmed salmon on the East Coast is more limited: research on wild Atlantic Salmon even more so. This Research Document was presented and reviewed as part of the Canadian Science Advisory Secretariat (CSAS) National peer-review meeting, Sea Lice Monitoring and Non-Chemical Measures, held in Ottawa, Ontario, September 25-27, 2012. The objective of this peer-review meeting was to assess the state of knowledge and provide scientific advice on sea lice management measures, monitoring and interactions between cultured and wild fish.

Épidémiologie et écologie des populations de pou du poisson dans les eaux canadiennes

RÉSUMÉ

Les poux du poisson sont présents sur les poissons sauvages et d'élevage sur la côte ouest et la côte est du Canada. L'espèce prédominante sur les deux côtes est connue sous le nom de Lepeophtheirus salmonis, mais il semble que les groupes soient distincts sur le plan génétique. Deux différentes espèces de Caliqus sont aussi présentes sur les deux côtes : Caligus clemensi et C. elongatus, respectivement. D'importants travaux ont été réalisés au cours de la dernière décennie sur le pou du poisson chez les poissons sauvages et d'élevage. Les recherches indiquent que L. salmonis, communément appelé le pou du saumon, pourrait vivre sur un plus vaste éventail d'hôtes qu'on ne le pensait, infectant des espèces comme l'épinoche à trois épines. Le rôle du saumon d'élevage, surtout du saumon de l'Atlantique d'élevage, en tant que réservoir de L. salmonis est accepté. On débat encore de l'effet des infections par le pou du poisson sur les populations de saumon sauvage, et de la question à savoir si l'établissement de seuils de traitement dans les exploitations aquacoles constitue la méthode la plus appropriée pour gérer la situation. Il semble que les diverses espèces de saumon du Pacifique affichent différents niveaux de tolérance à L. salmonis et à C. clemensi, et le rôle des autres espèces que le saumon dans un contexte d'épidémiologie et d'écologie du pou du poisson doit être mieux étudié. Les travaux publiés sur le pou du poisson sur le saumon d'élevage sur la côte est sont plus limités; la recherche sur le saumon sauvage de l'Atlantique l'est encore davantage. Le présent document de recherche a été présenté et révisé lors d'une réunion nationale d'examen par les pairs du Secrétariat canadien de consultation scientifique (SCCS) sur le Suivi sur le pou du poisson et mesures sur les moyens non chimiques, qui s'est tenue à Ottawa du 25 au 27 septembre 2012. L'objectif de cette réunion d'examen par les pairs était d'évaluer l'état des connaissances et de fournir un avis scientifique sur les mesures de gestion du pou du poisson, la surveillance et les interactions entre le poisson d'élevage et le poisson sauvage.

INTRODUCTION

The occurrence of disease in cultured animals is obvious, as the sick and dead can be readily seen and entire populations are monitored. In contrast for wild populations, particularly salmon, which have large migratory ranges - often not seen for years - there are both serious and practical difficulties in detecting significant diseases and in measuring any impact that these may have on a population (McVicar 1997). As a consequence, wild fish research on the west coast of Canada has primarily been focused on detecting infectious agents rather than assessing for disease (Kent et al. 1998; Arkoosh et al. 2004). It must always be emphasized that the presence of an infectious agent does not equate to disease.

Epidemiology is the study of patterns of disease in populations and is concerned with detecting the existence of disease, identifying the causes of disease, measuring the patterns, the impact or the extent of the problem and finally, planning and evaluating possible disease control strategies (Baldock 2000). In order to understand disease in natural populations, it is important to understand the complexity of the ecology of disease; specifically the relationship among animals, pathogen and their environment in a natural situation without intervention. Very often this concept is represented as a Venn diagram (Figure 1). Table 1 outlines some of the components or factors belonging to each of the categories (revised from Baldock 2000).

Disease associated with sea lice infections is externally visible with damage to the integument of the salmon being observed. This is caused by the feeding activity of sea lice. Chalimus stages cause only mild and localized damage, although even this may have adverse effects on fish health. Pre-adult sea lice tend to cause the most damage, as these generally concentrate on the head region, which has no protective scales and is therefore more susceptible to damage. Integumental lesions can be quite severe, extending into the musculature or skeletal tissues. Severe dermal damage can cause osmotic distress or provide a portal for secondary infection, which may lead to death or other production related problems (i.e., poor growth, poor feed conversion ratio).

The following section primarily summarizes research on sea lice infection patterns and epidemiology observed on wild and farmed fish. Emphasis is on *Lepeophtheirus salmonis (L. salmonis)*, the salmon louse, since the majority of the research has focused on this species. Where available, information is also provided on *Caligus* spp. (*C. clemensi* in the Pacific region and *C. elongatus* or *C. curtus* in the Atlantic region). This section is not intended to be a literature review.

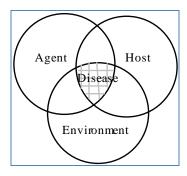


Figure 1: Venn diagram illustrating the complexity of the ecology of disease in the natural environment.

Table 1: A summarization of some of the components important in disease development.

Agent	Host	Environment
Pathogen load - concentration of pathogen	Species	Water quality (salinity, dissolved
Life stage	Age	oxygen, plankton)
Infectivity - proportion of susceptible individuals	Sex	Hydrography / oceanography
exposed that become infected	Nutritional status	Food
Pathogenicity - proportion of infected animals that develop disease	Physiological status	Distribution/abundance of alternative host species
Virulence - proportion of individuals with	Pathological status	Other infectious agents
disease that get seriously sick or die		Other infolious agents

POPULATION STRUCTURE AND EPIDEMIOLOGY OF SEA LICE IN ADULT WILD SALMON POPULATIONS

PACIFIC REGION

The population structure and epidemiology of sea lice on wild adult salmon in the Pacific (NW) region is one of the few areas where there has been information published. There are several reports describing large infections of *L. salmonis* (salmon louse) on adult Pacific salmon in coastal waters and high seas without lesions or any evidence of detrimental effects (Nagasawa et al. 1993; Johnson et al. 1996; Nagasawa 2001; Beamish et al. 2005; Trudel et al. 2007). Table 2 provides a brief summary of *L. salmonis* and *C. clemensi* levels reported on adult wild salmon.

Sea lice are found on all salmon species with infection levels varying with fish size, species, sampling season and year of sampling. In general, large salmon are more heavily infected than small salmon and infections increase over time, with lower values observed during the spring and higher values occurring in the following winter; although temperature has not been found to be a significant factor in determining infection levels (Nagasawa 1985; Trudel et al. 2007). It has been observed that Pink Salmon, which are at sea for only one year, are often the most heavily infected with *L. salmonis*. Chum Salmon had the second highest infection rates in the high seas studies (Nagasawa 1985, 2001) and nearshore (Trudel et al. 2007).

Spread and re-infection of Pacific salmon with *L. salmonis* likely occurs in the high seas since the prevalence of infection tends to increase with increased age (Nagasawa 1985, 2001). The presence of copepodids and chalimus on adult salmon returning to their natal river suggests that transmission of sea lice also occurs in coastal waters (Beamish et al. 2005). The intensity of the infections indicates that natural production of sea lice could be large during the coastal migration of adult Pacific salmon. Beamish et al. (2005) reported extensive levels of *C. clemensi*. It is possible that copepodids in this species are more commonly associated with coastal water or that the species is under-represented due to high motility of adults, which would allow them to guickly move off of captured fish.

There was no indication of detrimental effects for the intensity levels observed, which in some cases were high, with the exception of Johnson et al. (1996), where levels were very high and environmental conditions were poor (Table 2). Johnson et al. (1996) reported disease in adult Sockeye Salmon and attributed it to low water conditions, which forced a high percentage of salmon to remain in the inlet for a longer period than normal, exposing them to poor environmental conditions including high water temperatures, low dissolved oxygen and over-crowding.

Table 2: Abundance, prevalence and intensity of sea lice on adult wild Pacific salmon.

Pink	Chum	Chinook	Coho	Sockeye	Reference and Context
				Abundance of L. salmonis	Johnson et al. 1996
				1990 – 330 / fish (range 49-1372)	Sampled Sockeye Salmon returning to the west coast of Vancouver Island (Alberni).
				1991- 26.9 / fish (range 3- 59)	Reported high mortality and lesions in fish assessed in 1990 but not in 1991-92.
				1992- 16.5 / fish (range 3-64)	
75-100%	25-42%	56-100%	50-73%	2.3-10.9% prevalence	Nagasawa 2001
prevalence Intensity 4.7-8.6 / fish	prevalence Intensity 1.7-2.3 / fish	prevalence Intensity 3.0-9.7 / fish	prevalence Intensity 1.7-2.6 / fish	Intensity 1-2 /fish	Sampled offshore near Bering Sea and North Pacific between 1991-1997 (June-July) (only adult <i>L. salmonis</i> assessed).
71% prevalence	33% prevalence		100% prevalence		Wertheimer et al. 2003.
Intensity 4.1 / fish	Intensity 1.6 / fish		Intensity 3.7 / fish		Sampled adult salmon in marine waters in southeastern Alaska (June-August). Sea lice were predominantly <i>L. salmonis</i> (all stages).
100% prevalence	100% prevalence	98-99%	99-100%	100% prevalence	Beamish et al. 2005
Intensity 51-56 /fish	Intensity 17-43 / fish	prevalence Intensity 15-16 / fish	prevalence Intensity 18-19 / fish	Intensity 41-202 / fish.	Sampled near shore in coastal waters of central BC 2004 (June-July) - returning adult salmon (<i>L. salmonis</i> and <i>C. clemensi</i> combined - all stages).
80.4% prevalence	24.7% prevalence	19.4% prevalence	45.2% prevalence	15.5% prevalence	Trudel et al. 2007
					Looked at motile <i>L. salmonis</i> and <i>C. clemensi</i> (however very low numbers) in inshore waters between Oregon and Alaska (2002-2003). Overall level of infection ranged from 0-68 sea lice / fish.

ATLANTIC REGION

Sea lice have likely been associated with fish, such as early salmonids, for well over 1.5 million years (Selden et al. 2010); however, the first records in the Atlantic Ocean are only about 300 years old (Berland and Margolis 1983) from Norway. In the Bay of Fundy, the first formal observations for the salmon louse *Lepeophtheirus salmonis* were recorded in 1928 (Bere 1930), although it was described earlier in the USA (Wilson 1905). The species was formally described by the Danish scientist Krøyer in 1837. There are also records of two other species of sea lice, *Caligus elongatus* and *C. curtus* (Hogans and Trudeau 1989) being found on salmon in the Bay of Fundy.

General observations on outbreaks of *L. salmonis* in wild salmon populations in the Bay of Fundy were first recorded by A.G. Huntsman in 1930, and in 1931 by McGonagle (MacKinnon 1997). The earliest formal record for sea lice interactions with salmon on the east coast of Canada were from 1938 in the Moser River on the east coast of Nova Scotia (White 1940, 1942). This study showed that the Atlantic Salmon became infected with *L. salmonis* in early summer and reached a peak in mid-August where some fish had several hundred adult and pre-adult sea lice, ranging in size from 3 to 12 mm. Abrasions were readily apparent on most of the fish, and some of the fish also showed classic signs of infection with "red heads" where the vasculature in the dermal layer was exposed (Figure 2). Some fish mortalities were attributed to the sea lice by the author.

Interestingly, incidental observations were also made in the Apple River in the northern part of the Bay of Fundy and in the Margaree River in the Gulf of St. Lawrence on the west coast of Cape Breton. The author mentioned that sea lice on returning salmon were noted, but were not seen to be a serious problem. Indeed, many anglers believed that sea lice indicated a "fresh run" of fish that had returned to the rivers within the last week (Brandal et al. 1976). Observations from the Moser River showed that female copepods were slightly more abundant than males on returning fish (White 1940, 1942). This was at odds with observations from earlier taxonomic work through museum collections, which suggested that males were quite rare in the population (Wilson 1905). More recent research has suggested that the sex ratio in *L. salmonis* is approximately 1:1 (Heuch and Schram 1996; Connors et al. 2010). Females that were captured from the fish often had long egg strings (some up to 38 mm, each containing up to 250 eggs) which were often dark coloured, indicating that the enclosed embryos had begun developing their characteristic pigment patterns (Wilson 1905).



Figure 2: Atlantic Salmon post smolt showing a typical red lesion caused by sea lice (photo: I. Bricknell and S. Barker, University of Maine).

POPULATION STRUCTURE AND EPIDEMIOLOLGY OF SEA LICE IN JUVENILE WILD SALMON POPULATIONS

PACIFIC REGION

Most research on *L. salmonis* on wild juvenile salmon in BC has occurred over the last decade. Initially, considerable focus had been placed on Pink Salmon, likely due to their high abundance, their distinct and short lifecycle, and the relative small size of these fish when they enter the marine environment. Recently, the focus has broadened to include other salmon and sea lice species.

Similar to what has been reported in adult salmon, sea lice have been reported on all species of juvenile salmon in the marine environment (Table 3). Sea lice infections appear to vary among species (fish and sea louse), location, length of time in seawater and annually (Trudel et al. 2007). Sea lice have been reported on wild Pink and Chum Salmon shortly after emergence from the river, when they are as small as 0.2 grams. Annual and regional differences in both the predominant sea louse species and the prevalence have also been observed; for example Krkosek et al. (2007a) reported higher prevalence of *C. clemensi* than *L. salmonis* in the mid coast Pink and Chum Salmon; while in the South Coast (Broughton Archipelago) during most years, *L. salmonis* were more predominant than *C. clemensi* (Jones and Hargreaves 2007). Jones and Hargreaves (2007, 2009) also reported higher levels of *L. salmonis* on Pink and Chum Salmon sampled further down the migration route, which could

be a reflection of exposure time or a change in environment (i.e., higher salinity). They also found that prevalence varied significantly between years. For example, *L. salmonis* prevalence levels in 2004 were two fold higher than the other years examined. Price et al. (2011) reported that *C. clemensi* was the most common species of sea louse found on juvenile Sockeye Salmon in the Discovery Islands region and North Coast; which are areas with and without farms, respectively. It has been suggested that observed regional differences may be linked to environmental factors; including differences in temperature and salinity, prevalence, local hydrography (currents) and distribution of alternative hosts (Jones et al. 2006a). Sources of sea lice (reservoirs) include wild and farmed salmon and other fish species (Beamish et al. 2005; Jones and Hargreaves 2007; Trudel et al. 2007).

Research suggests that most initial infections on wild juvenile Pink Salmon are a consequence of attachment of the infective copepodid stage of *L. salmonis* (Jones and Hargreaves 2007, 2009; Saksida et al. 2012) with a low intensity of infection on these small fish - less than two sea lice / fish (Table 3). Jones and Hargreaves (2007) reported no evidence of re-infection during the first few months in seawater but rather found an increase in proportion of motile sea lice developmental stages over the sampling season (evidence of maturation of the parasite), particularly on juvenile Pink Salmon. Others have suggested that there might be direct transfer of motile stages from prey fish to its predator (i.e., Coho Salmon) during the act of predation (Connors et al. 2008).

There has been considerable debate about the health implications attributable to sea lice on individual juvenile salmon. For example, Morton and Williams (2003) observed bleeding at the base of fins on juvenile Pink Salmon infected with *L. salmonis* sampled in the Broughton Archipelago between June and August 2001. Jones et al. (2006a, 2008), however, reported that no similar lesions were observed in Pink Salmon exposed to *L. salmonis* under controlled laboratory trials, nor has this been observed in any other reports. Marty et al. (2010) suggested that reddening of fins may have been associated with some other pathogens (bacterial or viral) or some other unmeasured stressful environmental condition rather than a direct cause of sea lice infection. Saksida et al. (2012) reported only an increase in skin lesions and liver lesions associated with sea lice in their study in the Broughton Archipelago.

Controlled lab studies, the standard used to assess pathogen effect, have shown that the level of resistance to sea lice is species specific. For example, Pink Salmon have been reported to be highly resistant to disease from sea lice, while Chum Salmon are less so (see previous section for details). Based on these trials Jones et al. (2008) concluded that Pink Salmon above 0.7 gram are highly resistant to the effects of sea lice. Nendick et al. (2011) reported that the presence of sea lice did not have a significant effect on swimming performance in Pink Salmon over 1 gram. Jones et al. (2009) estimated that the lethal infection level for Pink Salmon averaging less than 0.7g) was 7.5 *L. salmonis /* gram. Above this size, Pink Salmon appear resistant. Others have suggested higher sea lice attributed mortality levels (Morton and Routledge 2005; Krkosek et al. 2006, 2009, 2011). Although these findings were based on field studies in which many factors may have contributed to the outcome of mortality, the authors attributed most or all the mortalities to sea lice. As no other cause was investigated, the causal link was poorly supported.

A similar debate has revolved around the effects of sea lice on a population scale. Many examples in the published literature provide evidence of associations but not necessarily causation (Morton et al. 2004, 2011; Krkosek et al. 2006, 2007b, 2011; Connor et al. 2010). For example, Krkosek et al. (2007b) reported that sea lice induced mortality of wild salmon in the Broughton Archipelago was commonly over 80%; this was based on their comparison of salmon catch and escapement data collected from two regions (with and without salmon farms). To apply the assumption that these areas were similar in all aspects except sea lice burden is an unwarranted weighting of a single factor in a multifactorial pathway.

Alternatively, when Jones and Hargreaves (2009) assessed sea lice data collected in the Broughton Archipelago and used mortality estimates derived from controlled exposure studies, they estimated that the sea lice specific induced mortality ranged between 0 and 4.5% in the Broughton Archipelago (2005 - 2008); thus making a relatively minor contribution to the estimated 55 - 77% mortality levels that have been suggested to occur during the first 40 days in the marine environment (Heard 1991). When Marty et al. (2010) examined wild / farmed and sea lice data over a 10 year period in the same area, they found that productivity of wild Pink Salmon is not negatively associated with sea lice. This illustrates not only the danger of magnifying the impact from single factors that may have only weak evidence in support of their estimated effect, but also the need to collect data over a long period to understand complex causal relationships.

There is general agreement that juvenile salmon, wild and farmed, are naturally exposed to sea lice in the marine environment. The consequence of these infections, however, varies depending on which species of fish is being examined, the species of sea louse infecting the fish and local environmental factors. Generalities cannot be made.

Table 3: Reported sea lice levels on juvenile wild salmon in the Pacific.

Pink	Chum	Chinook	Coho	Sockeye	Near Farms	Reference and Context
68 - 98 % prevalence <i>L.</i> salmonis					Yes	Morton and Williams 2003 Sampled (using a dip net) Pink
Intensity 2.7 - 12.5 sea lice / fish						Salmon in the Broughton Archipelago June/July 2001
(fish weight 2.2 - 2.9 g; length 59 – 64 mm)						
2.9% prevalence	4.2% prevalence	0% prevalence	53% prevalence	8.4% prevalence	No	Wertheimer et al. 2003.
Intensity 1.1 sea lice / fish	Intensity 1.3 sea	Intensity 0 sea	Intensity 2.6 sea	Intensity 1.5 sea lice / fish		Sampled juvenile and adult
(fish length 98 - 179 mm)	lice / fish	lice / fish	lice / fish	(fish length 118-253 mm)		salmon in marine waters in southeastern Alaska (suggested
	(fish length 115 – 138 mm)		(fish length 178- 237 mm)			predominantly <i>L. salmonis</i>) (June-August)
9.1% prevalence	0 - 0.52%	0.6 - 20%	0 - 1.6%	0 - 2.0% prevalence	No	Trudel et al. 2007
0.18 abundance	prevalence 0 - 0.005 abundance	prevalence 0.007 - 0.4 abundance	prevalence 0 - 0.02 abundance	0 abundance (?)		Looked at motile <i>L. salmonis</i> (mostly) and <i>C. clemensi</i> in inshore waters between Oregon and Alaska (2002-2003) on small and Y1 salmon (100-400 mm). (May-June)

Pink	Chum	Chinook	Coho	Sockeye	Near Farms	Reference and Context
Near Farm	Intensity ~1 sea				Yes /	Saksida et al. 2011b
1 - 9% prevalence for <i>L.</i> salmonis	louse per fish (mean fish				No	Assessed <i>C. clemensi</i> and <i>L. salmonis</i> on juvenile salmon in
2 - 20% prevalence for <i>C. clemensi</i>	weight 4.5 g; length 68.1 mm)					mid-coast during spring between 2005-2008 (late April-July)
Intensity ~1 sea louse						
Away from farm						
0 - 3% prevalence for <i>L.</i> salmonis						
1 - 6% prevalence for <i>C.</i> clemensi						
Intensity ~1 sea louse per fish						
(mean fish weight 3.5 -5.4 g; length 63 - 76.8 mm)						
2 - 3% prevalence for <i>L.</i> salmonis on juvenile Pink Salmon until July when prevalence increased to 50%					Yes / No	Krkosek et al. 2007a Assessed <i>C. clemensi</i> and <i>L. salmonis</i> on juvenile Pink Salmon in mid-coast during spring between 2004 -2006 (April-
8 - 20% prevalence for <i>C. clemensi</i>						August). In areas close to farms and a channel away with no
Intensity ~1 sea louse per fish						farms.
(fish weight 0.2 – 20 g; length 30 mm – 130 mm)						

Pink	Chum	Chinook	Coho	Sockeye	Near Farms	Reference and Context
97.1% prevalence (mostly <i>C. clemensi</i> although few <i>L. salmonis</i> recovered too) Intensity 3.5 (mean fish length 96 mm)	84.3% prevalence (mostly <i>C.</i> clemensi although few <i>L.</i> salmonis recovered too) Intensity 4.1 (mean fish length 104 mm)	74.4% prevalence (mostly <i>C.</i> clemensi although few <i>L.</i> salmonis recovered too) Intensity 3 (mean fish length 117 mm)		100% prevalence (Note only 1 fish examined) Intensity 2 (fish length 96 mm)	No	Beamish et al. 2009 Assessed wild fish in Gulf Islands for sea lice in 2008 (July)
	4.4 - 6.1% prevalence <i>L.</i> salmonis 0.3 - 1.3% for <i>C.</i> clemensi	0 - 9.8% prevalence <i>L.</i> salmonis 0 - 5.9% for <i>C.</i> clemensi			Yes	Clayoquot Sound Sea Lice Working Group (2012) sampled in Clayoquot Sound (March-June, 2007-2009)

Pink	Chum	Chinook	Coho	Sockeye	Near Farms	Reference and Context
59 - 63% prevalence <i>L.</i> salmonis (May-July 2004)	61 - 72% prevalence <i>L.</i>				Yes	Jones and Hargreaves (2007, 2009) sampled in the Broughton
24.4 - 27.1% prevalence <i>L.</i> salmonis (1.9 sea lice / fish) in 2005	salmonis (May- July 2004) (fish weight 3.8 -					Archipelago (March-June)
(fish weight 3.3 - 14.6 g)	28.7 g)					
13.9 -16.3% prevalence <i>L.</i> salmonis (1.5 sea lice /	2005 (23 - 29%)					
fish) in 2006	(fish weight 5.0 -					
(fish weight 2.5 - 13.2 g) 12.2 - 14.56% prevalence	27.6 g)					
L. salmonis (1.5 sea lice /fish) in 2007						
(fish weight 0.2 – 5 g (estimated))						
5.7 - 7.2% prevalence <i>L.</i> salmonis (1.4 sea lice / fish) in 2008						
(fish weight 0.2 – 5 g (estimated))						

Pink	Chum	Chinook	Coho	Sockeye	Near Farms	Reference and Context
				Discovery Islands prevalence 5 - 21% <i>L.</i> salmonis (intensity 1) 29 - 84% <i>C. clemensi</i> (intensity 2.6 - 5.7) (fish weight 3.9 – 12 g; length 72 – 103 mm) North Coast prevalence 1% <i>L. salmonis</i> (intensity 1) 9% prevalence <i>C. clemensi</i> (intensity 2) (fish weight 5.2 g; length 817 mm)	Yes / No	Price et al. 2011 sampled juvenile Sockeye Salmon in 2007 and 2008 (April-June) in Discovery Islands (near farms) and North Coast in 2007 (May-July) (away from farms). Different gear was used in each location

ATLANTIC REGION

There has been relatively little work on the interactions of sea lice and wild salmon in the north western Atlantic coast, partly due to the low abundances of stocks of salmon (Goode and Whoriskey 2003). One study on the early post-smolt stage was done in the Bay of Fundy and Gulf of Maine using surface trawls to capture the early salmon juveniles from 2001 to 2003 (Lacroix and Knox 2005). Both wild fish and those from hatchery origin were captured, but none showed any traces of sea lice and the fish were in excellent condition. They also took note of the incidental by-catch in the trawls and recorded that the prevalence of *C. elongatus* on lumpfish, *Cyclopterus lumpus*, was 8 to 53%, depending on the year with a mean intensity ranging from 2.2 to 4.4 sea lice per fish. The authors concluded that "the survey found no evidence to support the hypothesis that parasites or diseases found in salmon farms or hatcheries were affecting post-smolts leaving the Bay of Fundy" (Lacroix and Knox 2005).

Some observations were also made during salmon surveys in the Labrador Sea off the west coast of Greenland and east of Newfoundland in 1966 (from references in Chang et al. 2011). Their observations showed that 70 to 93% of the salmon captured were infected with *L. salmonis* with an average intensity between 2.7 and 7.5 per fish. Similar observations were reported by Urquhart et al. (2008, 2010) and Pert et al. (2009 a,b) on the prevalence and intensity of *L. salmonis* on returning salmonids in Scotland.

It cannot be inferred from the lack of observations or reports available for the East Coast, that sea lice do not have the potential to impact wild stocks in that area, particularly if those populations are very low in number. There are many published reports from Europe that have discussed impacts of sea lice on salmon and sea trout stocks, but even there, there is no consensus on the overall effects (Dawson et al. 1997, 1998; Mackenzie et al. 1998; McKibben and Hay 2004; McVicar 2004; Penston et al. 2004; Pert et al. 2006, 2009 a, b, 2012; Urquhart et al. 2008, 2010).

POPULATION STRUCTURE AND EPIDEMIOLOGY IN FARMED POPULATIONS

PACIFIC REGION

Serious health issues associated with *L. salmonis* infections on farmed salmon are frequently reported in salmon farming regions in Europe and Eastern North America, but not in Japan or on the BC coast (Johnson et al. 2004). Historically, damage as a result of infections with *L. salmonis* was not common in BC, and aquaculture veterinarians did not consider sea lice a serious health concern (Saksida et al. 2007a). Consequently, prior to 2003, enumeration of sea lice only occurred if there were health and / or welfare concerns at a farm site. Medicinal treatments for infection were not common (Figure 3) and limited data were maintained. In March 2003, routine sea lice monitoring began on Atlantic Salmon farms in the Broughton Archipelago (originally as part of the Broughton Archipelago Sea Lice Action Plan) (Saksida et al. 2007b). Monitoring and reporting in the other farming regions started in October 2003.

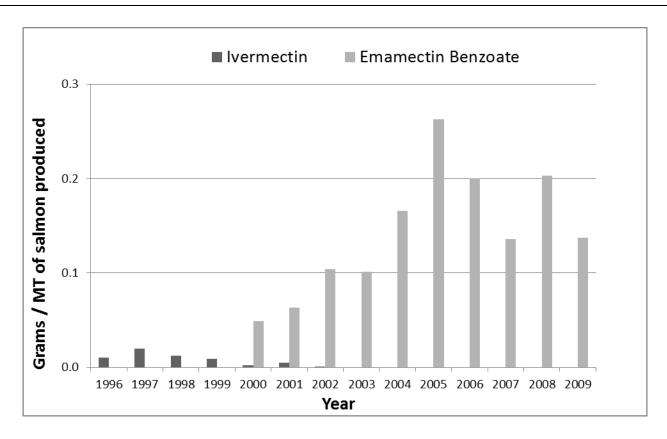


Figure 3: Sea lice treatments (grams of Ivermectin and Emamectin benzoate (SLICE®)) administered per metric tonne (MT) of salmon produced from 1996 to 2009 (Saksida et al. 2011b).

Farmed Pacific Salmon

In general, the abundance of sea lice on farmed Chinook and Coho Salmon in BC is low. Even without treatment, sea lice levels on farmed Pacific salmon were maintained at equal to or below those observed on farmed Atlantic Salmon (Saksida et al. 2006). Ho and Nagasawa (2001) also reported that Coho Salmon farmed in Japan had substantially lower sea lice levels than farmed Rainbow Trout. Even with low abundance levels, regional and seasonal variation has been observed. For example, those farmed on the east side of Vancouver Island have been reported to have higher mean abundance of motile *L. salmonis* than those farmed on the west side of the island (Saksida et al. 2006). Sea lice abundance on farmed Pacific salmon increases during the autumn, and is most likely associated with wild salmon returns, but declines soon after. For example, mean abundance of motile *L. salmonis* only reached 3.7 in the autumn but by spring, when sea lice on the salmon farms are required to maintain an abundance below three motile *L. salmonis*, the mean abundance reported on farms with Pacific salmon was 0.7 (Saksida et al. 2006).

Caligus clemensi levels on farmed Chinook and Coho Salmon in BC were even lower than those reported for *L. salmonis* with mean abundance ranging between 0 and 0.03 (Saksida, unpublished manuscript¹). As a consequence of the low abundance of sea lice on farmed Pacific salmon in BC, and

Saksida, S., Whelan D., Cusack R., Keith, I., Szemerda, M., and Beattie, M. (unpublished). Monitoring for Sea Lice on Farmed Salmon in Western and Eastern Canada. DFO Can. Sci. Advis. Sec. Working Paper.

due to the handling stress experienced by Pacific salmon, by the end of 2004, the provincial government stopped the required quarterly monitoring and reporting of sea lice abundance for these species. Continued monitoring was limited to opportunistic counts during routine handling events, and details of this monitoring were subject to audit. There continues to be no evidence that this approach has missed any unexpected increases in sea lice levels on Pacific salmon, and sea lice treatments have not been required.

Farmed Atlantic Salmon

Most of the research in BC pertaining to sea lice on farmed salmon has focused on Atlantic Salmon and the sea lice species *L. salmonis*; with almost all of this research conducted since the implementation of treatment thresholds, which may have modified the natural pattern of infection.

Lepeophtheirus salmonis are found on farmed Atlantic Salmon, with levels fluctuating both temporally and spatially. Levels generally rise as time spent in seawater increases. This trend was reported in both wild and cultured salmon and is likely attributable to increased duration of exposure (Nagasawa 1985; Bron et al. 1991; Revie et al. 2002; Tully and Nolan 2002; Heuch et al. 2003; Trudel et al. 2007). Saksida et al. (2006) reported that the abundance of *L. salmonis* on Atlantic Salmon more than one year in sea water was 2.5 times higher than on salmon that had been less than one year in sea water. The rate of increase of motile *L. salmonis* on farmed salmon in one study was calculated at 2% per month (Saksida et al. 2007b).

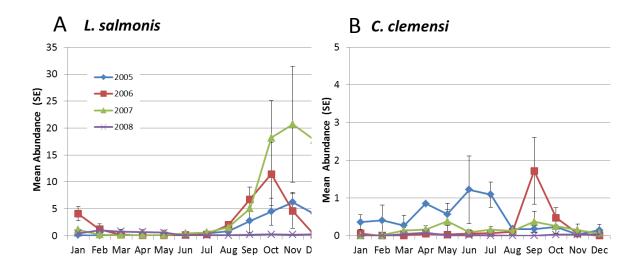
With very few exceptions, *L. salmonis* abundance increases in the autumn on farmed Atlantic Salmon in BC (Saksida et al. 2006, 2007a, 2007b, 2011a,b; Marty et al. 2010) and the lowest levels are most frequently reported in the summer. Beamish et al. (2006) reported that in the Broughton Archipelago, prevalence of sea lice on Atlantic Salmon ranged from 85% in February to 46% in August and the intensity of all sea lice stages was highest in February (21 sea lice / fish) and lowest in July (3.3 sea lice / fish). The increase in sea lice abundance on farmed salmon in the autumn is likely associated with the return of adult Pacific salmon to their natal rivers (Beamish et al. 2005; Saksida et al. 2006, 2007a; Marty et al. 2010). The decrease in abundance in the summer may be related to treatment or other factors (environmental, few sea lice in area). Infection by the copepodid stage is the most common mode of spread. Direct transfer of motile stages has been reported to occur in situations where host densities are high such as within salmon farms (Ritchie 1997; Tully and Nolan 2002) and from wild to farmed salmonids (Ho and Nagasawa 2001). Length of the "sea lice-free" period in BC following treatment (see below for details) suggests that re-infection from within a farm following a site-wide treatment is not common. This may be a reflection of water advection at the farm.

Annual variation in sea lice levels are also seen on farms in BC. For example, motile *L. salmonis* levels were four times higher in 2004 than in either 2003 or 2005 on farms operating in the Broughton Archipelago (Saksida et al. 2007a,b). In the mid-coast (Klemtu), 2007 mean abundance levels reached 20 motile *L. salmonis* in the fall, but in 2008 the levels were close to zero (Saksida et al. 2011a). Marty et al. (2010) suggested that this variation reflects the magnitude of the wild salmon returns. There is also considerable variation in abundance among and within the farming regions in BC (Saksida et al. 2007a). In 2004, the abundance of *L. salmonis* ranged from 0.47 to 3.29 among the regions (Saksida et al. 2006). A significant inter-zone variation for farms operating in the Broughton Archipelago was also observed (Saksida et al. 2007b).

The regional differences in the abundance of *L. salmonis* may be linked to environmental factors; including differences in temperature and salinity, or local hydrography (Jones et al. 2006a). For example, regions with the highest salinity reported the highest sea lice abundance levels on the farms (Saksida et al. 2006, 2007a). Salinity patterns vary considerably among the different BC regions. The

west coast regions as well as the Broughton Archipelago region show annual variation in surface (0 - 1 m) salinity. In these examples, however, the seasons of lowest salinity are different. Farms on the west coast of Vancouver Island report lowest salinity in the winter and highest in the summer with a mean difference of 4 mg/L (23 - 27 mg/L) (Saksida et al. 2006) and may be associated with precipitation, which is especially high during the fall and winter. Conversely, farms situated in the Broughton Archipelago report highest salinity levels in the winter and lowest in the summer with mean differences of almost 6 mg / L reported (range 23 – 29 mg / L) (Saksida et al. 2006). In this region, the freshwater run-off from snowmelt which occurs in the summer reduces surface salinity (Beamish et al. 2006; Foreman et al. 2006; Saksida et al. 2006, 2007 a, b). This can adversely impact sea lice infectivity (Bricknell et al. 2006). When Saksida et al. (2007b) used a generalized linear model to assess factors associated with *L. salmonis* abundance in the Broughton Archipelago, several factors such as salmon age, farm location and time of year were found to be significantly associated with L. salmonis abundance, but temperature and salinity were not. The dataset was relatively small, containing information collected over 3 years (2003-2005), and therefore may have been insufficient in quantity, quality or variation to be able to detect an association even if one were to exist. A longer time series would be useful to more fully understand the factors contributing to L. salmonis abundance on farmed Atlantic Salmon.

Caligus clemensi is also reported on farmed Atlantic Salmon but in general, is less common than *L. salmonis* (Marty et al. 2010; Saksida et al. 2011a) (Figure 4). Although, in 2003 *C. clemensi* made up 42% of the motile sea lice observed on farmed Atlantic Salmon (Saksida et al. 2007a), and Beamish et al. (2006) reported a similar proportion (40.6% between February and July) from their study in the same area (the Broughton Archipelago), suggesting that there is annual variation.



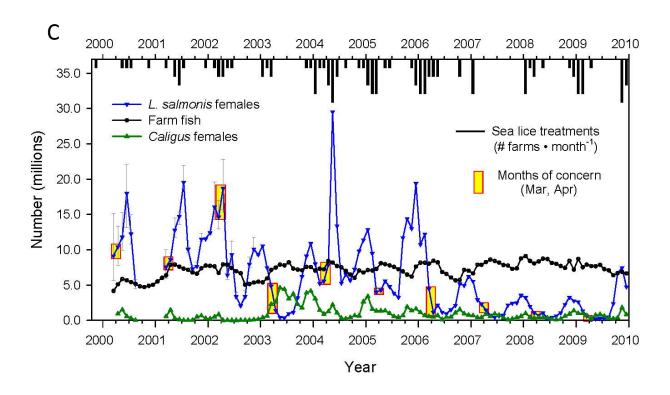


Figure 4: The abundance of Caligus clemensi and Lepeophtheirus salmonis on farmed Atlantic Salmon in Klemtu (A and B) (from Saksida et al. 2010) and Broughton Archipelago (C) (from Marty et al. 2010, British Columbia). Note differences in abundance scale for each parasite.

There also exists a significant difference in abundance of *C. clemensi* between farming regions: the highest abundance occurs in the Campbell River and Port Hardy regions and the lowest in the Sunshine Coast (Saksida et al. 2011b). Unlike the abundance of *L. salmonis*, which increases on

farmed and wild salmon with increased ocean residency times, that of motile *C. clemensi* tends to be higher on younger farmed salmon populations (Saksida et al. 2011a).

As stated earlier, treatment for sea lice prior to the establishment of threshold levels in 2003 was not common. Ivermectin was the only therapeutant used with any frequency for the treatment of sea lice on farmed salmon in BC prior to 2000 (Figure 4). Another tool used in the management of sea lice was to move the salmon through a fish pump (i.e., SILKSTREAMTM, ETI, Washington USA) to dislodge the motile sea lice from the fish. The discharge water would sometimes be filtered to collect the detached sea lice. Although this method was very labour intensive and resulted in stress and physical injury to the fish, it was often preferred to using Ivermectin, which has a very low margin of safety.

In 1999, SLICE® (Emamectin benzoate (EMB), Merck Animal Health) became available to veterinarians under an emergency drug release (EDR) issued by Health Canada (Saksida et al. 2011a). Soon after, it became the only therapeutant used for sea lice treatment in BC. There has been an increase in the use of SLICE® after the introduction of the threshold limits with quantities in 2005 over 2.5 times greater than levels that existed prior to implementation of the BC Sea Lice Management Strategy in October 2003. Peak use of SLICE occurred in 2005 (~0.25 g / metric ton (MT) of salmon produced) and usage since has been at or below 0.2 g / MT. During the first two years of the program (2004, 2005) the total number of SLICE® treatments for Atlantic Salmon ranged from zero to three per production cycle (i.e., smolt entry to harvest) (Saksida et al. 2006). The average number of treatments per production cycle was estimated to be 1.6 in the Broughton Archipelago, with the average farmed salmon residing in the ocean almost nine months before receiving its first treatment (Saksida et al. 2007a). More recent analysis of the data suggests that frequency of treatment has not changed over the five years since the establishment of the maximum threshold levels and every year there are farms that do not need to treat for sea lice (Saksida et al. 2010). Almost 75% of SLICE® treatments occurred in populations of Atlantic Salmon during their second year in seawater, between October and March (Saksida et al. 2007a, 2010). This is likely the result of trying to reduce the mean motile *L. salmonis* abundance levels to below three for the start of the spring wild juvenile Pacific salmon migration in March and to adhere to required SLICE® treatment withdrawal periods prior to scheduled harvest dates.

SLICE® remains effective in the treatment of sea lice in BC with no evidence of change in efficacy between 2003 and 2008 (Saksida et al. 2010). This study found that by one month (26-34 days) post-treatment, sea lice levels had fallen to below 20% of pre-treatment levels and remained at or below 10% of pre-treatment levels for at least another month - the time-period assessed. Bioassay results suggest that adult female *L. salmonis* are significantly more sensitive to EMB than males (Saksida et al. 2013). However, an immediate concern for the BC salmon farming industry continues to be the inherent limitation of having only one sea lice treatment product available for use. Other agricultural industries in comparison, utilize integrated pest management; a rotation of treatments in addition to the inclusion of other non-chemical management methods, such as fallowing, to prevent or delay development of resistance in a pathogen.

ATLANTIC REGION

Salmon farming on the east coast of Canada started in 1978 off Deer Island in the Bay of Fundy. Initially, farms were quite small but by the mid-1980s, expansion of the industry happened quickly, particularly in the Limekiln Bay, Bliss Harbour and Back Bay areas (Chang et al. 2011).

Some of the first studies on the interactions between sea lice and cultured salmon were done in the late 1980s (Hogans and Trudeau 1989). Cages of salmon were monitored for sea lice in 1988-89. Three species were found: *Caligus curtus, Caligus elongatus* and *L. salmonis. Caligus elongatus* was

the most abundant species and reached a prevalence of 100% in some populations with a maximum intensity of 47 parasites per fish (mean of 18). Sea lice intensity peaked in October. A generation time of 5 weeks in lab experiments was a little longer than that reported by Johnson and Albright (1991a, b) but within the development range seen by Boxaspen and Naess (2000). *Lepeophtheirus salmonis* was uncommon on the salmon, with 8% prevalence and an intensity not exceeding 3 sea lice per fish. Reproduction and developmental rates increased for all species as temperature rose. The authors suggested that "The eggs extruded in late fall apparently remain dormant and unharmed during the winter months, being eventually released in spring". The authors also suggested that *L. salmonis* may not die in winter, but may remain dormant on bottom until optimal water temperatures are reached in spring. Although the overwintering strategies of *L. salmonis* remain poorly understood, this hypothesis is not supported by the majority of research.

Although there were reports of sea lice on farmed salmon in the late 1980s (Chang et al. 2011), the first major outbreak started in 1994 in the Limekiln and Back Bay areas (Hogans 1995). Intensity of sea lice on the fish increased from approximately 2 per fish in September to about 85 per fish in November prior to treatments (Hogans 1995). Cages monitored during the fall and winter of 1994-95 showed large and sudden increases in sea lice on salmon farms in the Limekiln and Back Bay areas in October 1994. As many as 317 L. salmonis were found on individual fish on the most heavily infected sites (Hogans 1995). The two sites had a much higher intensity than any of the other areas outside Limekiln and Back Bay, but the prevalence of infection outside Limekiln and Back Bay was also high (97%). There was an increase in the intensity level from January to March. Re-infection rates were low over the winter and there did not appear to be any moulting of the chalimus or pre-adult stages. Laboratory studies indicated that nauplii II rarely moulted successfully into copepodids below 3°C. The number of females with egg strings increased over the winter. Although fecundity often increased in the winter months, this was offset by a smaller mean egg size and reduced nauplii and copepodid survival (Stien et al. 2005). The authors felt that unusually prolonged high water temperatures in fall 1994 and winter 1995 were probably responsible for the fall epidemic and the high residual infection found on cultured salmon at all sites examined through the winter of 1995. Laboratory studies showed that egg strings were produced over the entire winter with the most eggs produced per string in the coldest months (0.8°C). Nauplii were found during all months studied. See Jones and Johnston (2014) for a general overview of sea louse biology.

The sea lice outbreak from 1994 to 1995 was ultimately controlled with the use of hydrogen peroxide and ivermectin (Hogans 1995; Chang et al. 2011). In 2010, another outbreak of *L. salmonis* occurred in the same general regions as before (M. Beattie, New Brunswick Department of Agriculture, Aquaculture and Fisheries, pers. comm.). High mortality rates were experienced on the newly introduced smolts as the dermal lesions on the smolts (Figure 2) caused an osmoregulatory failure. Interestingly, although *L. salmonis* was the predominant species during 2010 and 2011, observations suggested that *C. elongatus* became the dominant sea louse infecting salmon early in 2012, but then *L. salmonis* became dominant later in the season (M. Beattie, New Brunswick Department of Agriculture, Aquaculture and Fisheries, pers. comm.).

ROLE OF WILD SALMONID AND NON-SALMONID HOSTS AS RESERVIORS

PACIFIC REGION

It has been suggested that the variation in sea lice abundance between the different farming regions may be partly related both to the species of wild salmon found in a zone and to their respective abundances (Saksida et al. 2006; Marty et al. 2010). Another source of variation in sea lice abundance

between the different farming regions may be related to the presence of non-salmonid fishes (Jones et al. 2006b). The relative importance of alternate hosts will depend on their abundance, infection level and the probability of having sufficient direct contact with the host of interest to allow for spread of the sea lice, or alternatively contact with the free swimming nauplii and copepodid stages which would be released from the egg strings of sea lice attached on the alternate hosts. The aquatic environment with its currents and tides means that transport and movement of unattached infective stages can be fairly significant from the original source of the infection (Murray 2009).

The BC coast has many more wild salmon than other salmon farming regions in the world, with a ratio of wild to farmed salmon in BC estimated at 1000:1. Although most of the salmon stocks are migratory, leaving the nearshore regions of BC for feeding grounds offshore, there are a few stocks (particularly Coho Salmon) that spend their entire marine lifecycle in the local waters, although the populations are not large (Beamish et al. 2007). The largest numbers of wild salmon are found in the spring / summer period during the seaward migration of juvenile salmon and summer / fall, when the adult salmon return to the coastal waters heading back to their natal rivers. Beamish et al. (2005) suggested that in some years there could be between 10 and 40 million Pacific salmon in the Queen Charlotte Strait. There is, however, considerable variation in the species and abundance of salmon in the different farming regions of BC. For example, Pink Salmon and Chum Salmon are very abundant along the east coast of Vancouver Island and the mid-coast region (Klemtu), but Pink Salmon are not common on the west coast of the Island. The mid-coast region has very few Chinook Salmon while the Broughton Archipelago has few Sockeye Salmon. Very little information about the specific migratory routes taken by the stocks is available; particularly for juvenile salmon (See Johnson and Jones 2014). It has been suggested, however, that natural transmission of L. salmonis to the next host generation is maximized in late summer or early autumn when out-migrating juvenile Pink, Chum, and Sockeye Salmon encounter returning adult salmon. Lepeophtheirus salmonis on younger juvenile Coho and Chinook Salmon that remain in nearshore habitats after adult salmon enter freshwater may help to carry the infections over the winter and into the following year (Jones and Beamish 2011).

The role that these alternate species may play in the natural infection patterns of the salmon louse on wild and farmed salmon has not been fully determined. Non-salmonid species of fish have also been reported to harbor sea lice, including the three-spined stickleback, Gasterosteus aculeatus L. - a very abundant nearshore species found in BC. In fact, three-spined stickleback were one of the four most common wild non-salmonid species netted or hooked in a survey of fish near salmon farms (Kent et al. 1998) and were commonly found to cohabit with juvenile salmon in the nearshore of the Broughton Archipelago (Jones et al. 2006a, 2006b; Jones and Prosperi-Porta 2011). This species has been found to harbour L. salmonis and C. clemensi, and could act as reservoir hosts (Table 4) although L. salmonis have only been found to the pre-adult stage. Lepeophtheirus salmonis may be incapable of maturing on this species of fish (i.e., die or leave) or are perhaps eaten. Pert et al. (2009a) suggested successful settlement and feeding on non-salmonids could allow L. salmonis to use other species as peripatetic (or paratenic/transport) hosts to improve survival and to aid dispersion until a salmonid host is encountered. Pacific herring, another very common coastal species has been found to host C. clemensi (Krkosek et al. 2007a; Beamish et al. 2009). Virtually all young-of-the-year, and spawning herring concurrently sampled from this area were infected with *C. clemensi* at abundances almost twice those measured for the infections on the salmon (Jones and Beamish 2011). However, overall abundance and migration patterns for these non-salmonid species is not known, particularly for the species not fished commercially.

Table 4: Sea lice reported on non salmonid species.

Comment	Reference and Context		
C. clemensi on Pacific Sandfish, Pacific Herring and	Krkosek et al. 2007a		
sticklebacks L. salmonis on sticklebacks	Assessed <i>C. clemensi</i> and <i>L. salmonis</i> on juvenile Pink Salmon in mid-coast during spring between 2004-2006 (April-August)		
94% prevalence Pacific Herring (all C. clemensi)	Beamish et al. 2009		
Intensity 4.6	Assessed wild fish in Gulf Islands for sea lice in 2008 (June-July)		
83.6% prevalence with Lepeophtheirus sp. and	Jones et al. 2006b		
42.8% prevalence with <i>C. clemensi</i> on Three-spined Stickleback in 2004	1,309 sticklebacks examined – 22,300 sea louse specimens examined.		
Prevalence ranged 51% (2005) to 11% (2008) of	Jones and Prosperi-Porta 2011		
Lepeophtheirus sp. (estimated 71% of these to be L. salmonis).	Evaluated over 7500 sticklebacks collected between 2005 and 2008 during spring (March-June) in the Broughton		
Prevalence ranged 56% (2007) to 24%(2008)	Archipelago; counted over 25,000 sea lice		

ATLANTIC REGION

There are not a lot of data available from monitoring programs for sea lice on wild salmon. Probably the best example is a 10 year study (1992 - 2002) in Passamaquoddy Bay which examined wild returning salmon to the Magaguadavic River (Carr and Whoriskey 2004). They noted that the prevalence of sea lice on wild salmon was approximately 20% from 2000 to 2006 after which it increased to about 90%. Farmed fish that had escaped from cages and migrated to the river also showed very similar patterns. In addition to these observations, the authors showed that acoustically-tagged salmon left the river, spent some time in close proximity to salmon cages and then returned some showing signs of damage from sea lice. These results suggest that wild salmon can come in close proximity to salmon aquaculture cages and some interactions may result. Of course, it is impossible to say if the tagged fish became infected with *L. salmonis* before they moved into the region around the farm or after they had spent some time around the farm.



Figure 5: Lumpfish (Cyclopterus lumpus) with attached sea lice (Caligus elongatus) taken at a salmon aquaculture site in Back Bay, New Brunswick (photo credit: Shawn Robinson).

There is a good possibility that the lumpfish, *Cyclopterus lumpus*, may be an alternate host for some sea lice parasites, particularly *C. elongatus* that could transfer to salmon (see Table 1, in Jones and Johnson 2014). As mentioned above, lumpfish captured with surface trawls in conjunction with juvenile salmon showed moderate infection rates with sea lice. Lumpfish are often found near salmon aquaculture cages living on the infrastructure associated with the operation (S. Robinson, pers. obs.) (Figure 5). However, the numbers of lumpfish on the salmon sites are limited and it is not clear how the lumpfish abundance could initiate significant increases in the sea lice populations on the salmon.

Lumpfish have also been shown to be a host for *C. elongatus* (Oeines et al. 2006; Oeines and Heuch 2007) in Europe and Scandinavia, and appear to host at least two genetically and morphologically distinct varieties that have different host preferences (Oines and Heuch 2007). They could act as an intermediate or peripatetic host for *C. elongatus* and possibly *Lepeophtheirus* species, although no observations have been reported for this genus. There is also evidence that *C. elongatus* infections increase when migratory fish, such as herring or mackerel, enter the area close to a salmon farm. *Caligus elongatus* is considered to be far more mobile (i.e., move actively on and off fish) than *L. salmonis*, and have a greater host range (including Atlantic Salmon). Adult *C. elongatus* also migrate from the migratory fish where prevalence and parasite intensity are high to exploit a host with a lower prevalence and intensity (Bron et al. 1993; Revie et al. 2002; Oeines et al. 2006; Oines and Heuch 2007; Lees et al. 2008; Oeines and Schram 2008).

EVIDENCE FOR LINKAGE BETWEEN SEA LICE POPULATIONS ON FARMED SALMON AND WILD SALMON AND NON-SALMONID HOSTS

PACIFIC REGION

Three potential sources of sea lice for wild juvenile salmon have been proposed: farmed salmon, wild salmonids, and wild non-salmonids. Farmed salmon are year-round residents of the BC nearshore environment. Evidence suggests that farmed fish most likely derive *L. salmonis* sea lice from wild returning salmon (primarily Pink and Chum Salmon) and may be an important source of sea lice to out-migrating salmon in the spring when adult salmon or alternative hosts are not in the area. For example, Marty et al. (2010) found that the number of Pink Salmon returning to spawn in the fall predicts the number of female *L. salmonis* sea lice on farmed fish the next spring, which, in turn, accounts for 98% of the annual variability in the prevalence of sea lice on out-migrating wild juvenile salmon in the Broughton Archipelago. Wild salmon populations (productivity), however, were not negatively impacted by either farm sea lice numbers or farmed fish production. The authors concluded that *L. salmonis* sea lice on farms are not good predictors of wild salmon survival in the Broughton Archipelago. This conclusion is not consistent with other reports (i.e., Krkosek et al. 2004, 2011) which did find an association and illustrates the complexity of effectively studying and understanding the effects of single factors on natural populations.

This trend is not apparent with *C. clemensi* where studies exist. For example, *C. clemensi* on wild Pink Salmon downstream from farms operating in the midcoast (Klemtu) had higher prevalence of *C. clemensi* than *L. salmonis*. On farmed salmon, *L. salmonis* were more abundant than *C. clemensi* (Saksida et al. 2011a). This suggests that factors other than farmed salmon influence the prevalence of *C. clemensi* on wild populations. The source of variation in sea lice abundance between the different farming regions may be linked to prevalence of non-salmonid hosts such as the Three-spined Stickleback and Pacific Herring (Jones et al. 2006b; Beamish et al. 2009). The role that these alternate species may play in the natural infection patterns of sea lice on wild and farmed salmon remains unclear.

ATLANTIC REGION

The current thought on migration routes of Atlantic Salmon is that the salmon use cues from the Saint John River system to return to their natal rivers in the Bay of Fundy (Chang et al. 2011). As a result, it would be expected that most of the salmon would bypass commercial aquaculture areas. However, recent hydrographic modeling shows that some of the tidal excursions from some of the farms in the southeastern Grand Manan area could extend several kilometers offshore (Chang et al. 2011) and therefore potentially carry sea lice larvae in the water masses. It could be reasonably anticipated that there would be a fair amount of dilution of larvae over this distance. The infection rates of sea lice produced from aquaculture farms on distant populations of wild salmon remains unknown in the Atlantic region.

There is a strong possibility that salmon farms themselves may be the cause of the magnification of the sea lice infections on their sites. Higher densities of larvae were found on salmon sites in Passamaquoddy Bay in 1996-1997 (Hogans 1997) than on reference sampling sites distant from them. Overall numbers of larvae were low. Hogans (1997) felt that the combination of reasonably heavily fouled nets in conjunction with low flows were responsible for the re-infection of fish within the cage. These results are consistent with a more recent study in the same area of the Bay of Fundy that found

sea lice nauplii (*L. salmonis*) were located primarily at salmon sites in low numbers and were virtually absent from all other reference sites (Bjorn et al. 2011). In Europe and Scandinavia, several studies have confirmed similar patterns of larval sea lice distribution where higher numbers of sea lice larvae are found near salmon cages (Costello et al. 1998; Penston et al. 2008; Penston and Davies 2009). When active salmon farming sites were fallowed for a year, significantly lower infection rates of sea lice were found in the early stages of the next culture cycle (Bron et al. 1993).

MANAGEMENT THRESHOLDS FOR SEA LICE: SCIENTIFIC AND VETERINARIAN BASIS AND METRICS OF EFFECTIVENESS

PACIFIC REGION

Sea lice monitoring was part of the Broughton Archipelago Sea Lice Action Plan initiated in early 2003 (Saksida et al. 2007a). In October 2003, the monitoring program was expanded to include all BC salmon farms as part of a provincial management plan known as the Sea Lice Management Strategy. Atlantic Salmon farms were expected to assess 3 pens (one index (usually first entered), plus 2 others) at least once a month for sea lice - 20 fish per pen. Most often, fish were captured using a seine, removed from the seine with a dip-net, anesthetized and assessed. The number of motile L. salmonis, adult female L. salmonis, motile C. clemensi and chalimus stages (species not distinguished) were counted per fish. All detached sea lice in the anesthetic tote were also counted, and farm level abundance was calculated. Farms were required to report their results to a central database. A summary of the mean abundance, on a monthly basis, was submitted to the provincial authorities, which was then posted on the provincial government website. In January 2004, the provincial government started to visit farms and audit the sea lice counts to verify the levels. Provincial fish health biologists routinely audited 25% of the farms operating during any quarter; and during the spring quarter (April-June), 50% of the farms were audited. In 2011, this authority moved to Fisheries and Oceans Canada (DFO) and the frequency of monitoring was increased to twice a month between March and June.

Mandated management of sea lice has been entirely based on mean motile *L. salmonis* abundance (average number / fish). The Sea Lice Management Strategy stipulates that during the period of juvenile Pink Salmon migration out of the nearshore (March to July), *L. salmonis* are to be below a mean of three motile sea lice per fish (including all preadult and adult male and female *L. salmonis* stages). Mean abundance levels are calculated and used to determine threshold. Distribution of sea lice, however, is similar to other parasites – it is normally skewed to the right - suggesting that median values are more appropriate to use to when determining a threshold (Saksida et al. 2007a). During this period (March to July), if sea lice levels exceed this threshold, the fish must either be treated (SLICE® was the only therapeutant available) or be harvested. Management options during the rest of the year remain at the discretion of the farmer and the attending veterinarian. The same threshold was set for all the regions even though there are significant differences between regions in relation to environmental (temperature, salinity, hydrography) and biological (types of salmon species, other fish species) factors. Management is normally conducted as needed on a farm-wide basis but in some areas (where sites are in close proximity) there have been agreements between farms to synchronize treatments (i.e., Okisollo Channel).

The BC sea lice threshold, however, is not based on scientific evidence but instead was determined by government and industry as a level that would allow precautionary management while more scientific data were gathered to better inform the issues - specifically the effect sea lice had on wild juvenile salmon. This precautionary level was an acknowledgement of: 1) the lack of serious disease occurring

on BC farmed salmon compared to other jurisdictions that had *L. salmonis*, and 2) the large populations of wild salmon in BC that are known to carry sea lice and thus influence the sea lice abundance on the farmed salmon, particularly during the autumn months. By comparison, in Europe where serious problems with sea lice infections had been reported on farmed salmon since the 1970's (Brandal and Egidius 1979; Wootten et al. 1982), the maximum thresholds in Norway had been set at two adult female *L. salmonis* during spring and summer until 2000 when the levels were decreased to 0.5 adult female *L. salmonis* (or six motile *L. salmonis*) (Heuch et al. 2003). The threshold level in BC (3 motile *L. salmonis*) was in fact lower than that prescribed in Norway (6 motile *L. salmonis*) during the same time. It has been almost 10 years since the thresholds have been established in BC.

At this point, establishing metrics (a standard methodology) to assess the suitability of the levels would be appropriate. For instance, the threshold in BC was set as a precautionary no- or minimal-effect level for the protection of juvenile salmon; particularly Pink Salmon. This allowed for laboratory studies to be conducted on the effects of sea lice on wild Pacific salmon. During this time, Jones et al. (2006a, 2008) were able to show that juvenile Pink Salmon quickly developed resistance to *L. salmonis* and were likely only susceptible when less than 1 gram, or during the first few weeks in the sea. A similar conclusion was reached by Nendick et al. (2011). Therefore, if the concern was regarding sea lice on Pink Salmon then this threshold should only apply to areas with known Pink Salmon runs (i.e., not west coast of Vancouver Island) and for only the period of susceptibility (i.e., one month following outmigration, rather than 3 months). Furthermore, Chum Salmon were found to be more susceptible to *L. salmonis*. Other research showed that juvenile Coho and Chinook had good tolerance to *L. salmonis* and recent controlled laboratory trials show that the response of juvenile Sockeye Salmon to *L. salmonis* is similar to that of Chinook Salmon (Jakob et al. 2013). How these findings affect the thresholds should be considered.

Prior to 2002, when the concern of sea lice on juvenile Pacific salmon was raised, there was little to no data with regards to natural sea lice levels on juvenile salmon populations. After this time, surveillance programs were established to assess sea lice on migrating wild juvenile salmon in the regions where salmon farms operate such as Tofino, Gold River, Campbell River, the Broughton Archipelago and Midcoast (Klemtu). Routine surveillance also occurred in areas without farms such as the Strait of Georgia (Salish Sea). This data as discussed in the earlier sections showed that the distribution of not only sea lice, but also juvenile Pacific salmon, other potential hosts and the environment varied both spatially and temporally. This suggests that BC sea lice threshold (levels and time line) applied equally across all regions may not be appropriate for all areas since seaward migrations for the different stocks can vary considerably.

Ultimately, the concern was what effects sea lice infections were potentially having on population survival. The initial surveillance programs on wild juvenile salmon focused on sea lice; a few programs were expanded to include fish health parameters when it became evident that factors other than sea lice were likely more important in survival of the populations. Initially, most of the programs concentrated on Pink and Chum Salmon, some also assessed other salmon and non-salmonid species, but this was less consistent between programs. Recently, some surveillance programs have ceased due to new knowledge gained on the effects of sea lice on juvenile salmon and the loss of public interest (i.e., Clayoquot surveillance program). The fact that public interest has driven much of the research and the surveillance programs as well as funding opportunities (i.e., Pacific Salmon Forum, Cohen Commission) in BC, rather than scientific—based policy, is a concern.

Fisheries and Oceans Canada have maintained the collection of catch (fish captured in fisheries) and escapement (fish that reach rivers to spawn) data for many of the stocks in BC for many years. In assessing for sea lice impacts, most assessment has been on Pink Salmon returns simply because this species spends the least amount of time in the sea (1+ years), has distinct cohorts (even / odd

years) and are very small when they enter the sea (~0.2 g). Research discussed above has shown that there is no association between the current sea lice levels on farms / sea lice on juvenile salmon and impacts on returns. Marty et al. (2010) went further to suggest that even prior to the establishment of regular reporting and monitoring, the level of impact on the wild populations as a consequence of sea lice (from farms) was likely very low or non-existent. This research, however, would not have been possible without data collected through these surveillance programs. Another smaller study examined juvenile Pink Salmon health in the field. It found no evidence that sea lice infection increased prevalence in infections with other parasites, viruses or bacteria (i.e., no secondary infection) in naturally sea lice infected juvenile Pink Salmon (Saksida et al. 2012). With the exception of sea lice, there was very little similarity between infections found on the wild salmon and those on the salmon farmed in the same area (Gary Marty, pers. comm.).

Industry compliance has also been measured with the information provided to the public. Farms have been expected to report sea lice and treatment information on a monthly basis to government authorities which are then summarized on a quarterly basis on the DFO website². The province and now DFO conduct audits year round with increased surveillance during the second quarter (April-June) to verify the sea lice levels being reported. In addition, two of the three Atlantic Salmon farming companies also directly provide sea lice data on their websites³. The level of compliance by the aquaculture industry verified by the government audits has been high (I. Keith, pers. comm.) with most farms maintaining sea lice below the threshold level during the period. However, this raises the question of the ease at which compliance was achieved.

In BC, this has been assessed by evaluating treatment frequency, efficacy and assessing for resistance. Currently emamectin benzoate (SLICE®) is the only product available for use in BC. It is only available by veterinary prescription and since 1999. This is an in-feed product and the dosage is fish size dependent (0.05 mg / kg fish / day for 7 days). Subsequent to the establishment of the thresholds, there has been an increase in use of SLICE® with quantities in 2005 over 2.5 times greater than levels that existed prior to implementation of the program.

Saksida et al. (2010) suggests that frequency of treatment has not changed over the first five years since the establishment of threshold levels and that every year there are farms that do not need to be treated for sea lice. Treatment efficacy and bioassays directly on adult *L. salmonis* have also been conducted. The data suggest that sea lice continue to be susceptible to the product (Saksida et al. 2010; Saksida et al. 2013) although regional differences are seen. Without other products, however, sea lice treatments and the requirement to treat because of an inflexible arbitrary threshold could lead to increased tolerance or even resistance.

An argument could be made that a better model for determining a threshold could involve establishing separate thresholds for specified areas / regions (either based on sea lice levels or biomass) rather than a per farm limit (Table 5). This could result in a more prudent use (avoid misuse or overuse) of the therapeutant and overall better management of an area.

² Fisheries and Oceans Canada, Pacific Region, Public Reporting on Aquaculture - Sea Lice

³ Cermaq Canada's Website and Marine Harvest Canada's Website

Table 5: An illustration of the change in treatment requirements if area based management was implemented rather than by farm thresholds.

Area consisting of three farms	No. of fish on a farm	Average size of fish (kg)	Abundance of <i>L.</i> salmonis	Scenario 1 – current farm level threshold	Scenario 2 – area based thresholds (3 / fish / area) but now abundance only 1.7 / fish / area
1	500,000	5	3	Treatment required	No treatment required
2	500,000	1	1	No treatment required	No treatment required
3	500,000	1	1	No treatment required	No treatment required

ATLANTIC REGION

Initially in 1995, the Province of New Brunswick set up 10 sea lice management zones based on local knowledge of the water currents on the site interactions. This became too unwieldy to manage, particularly with the onset of the viral disease infectious salmon anemia (ISA) and the switch to single year-class farming in defined management zones. Currently, there are three major Aquaculture Bay Management Areas (ABMAs), which are much larger and are based on a much stronger understanding of the oceanography and potential for disease spread in the area. ABMAs 2 and 3 have two geographic areas to accommodate rotation of year-classes on Grand Manan. There are also two very small ABMAs that represent a buffer area between ABMA 1 and 2a and a small area off the east coast of Grand Manan (ABMA 5a).

Mandatory fallowing is required, with each farm to have a minimum 4 month fallow period, with a minimum synchronized bay-wide fallow period of two months between successive year-classes. Fallowing has been shown to be effective in helping to initially reduce the severity of infections in successive year classes (Bron et al. 1993).

Monitoring for sea lice occurs in protocols outlined in the New Brunswick Integrated Pest Management Plan for Sea Lice. Currently, there are no fixed thresholds on the number of sea lice required for treatment. Thresholds are also not used in Newfoundland and Labrador or Nova Scotia. (See Saksida et al. 2014 for monitoring details.)

REFERENCES

- Arkoosh, M.R., Clemons, E., Kagley, A.N., Stafford, C., Glass, A.C., Jacobson, K., Reno, P., Myers, M.S., Cassillas, E., Loge, F., Johnson, L.L., and Collier, T.K. 2004. Survey of pathogens in juvenile salmon *Oncorhynchus* spp. migrating through Pacific Northwest estuaries. J. Aquat. Anim. Health 16: 186-196.
- Baldock, C. 2000. Epidemiology Notes. University of Tasmania AusVet Animal Health Services. 23-27 July 2000.
- Beamish, R.J., Jones, S., Neville, C.M., Sweeting, R., Karreman, G., Saksida, S., and Gordon, E. 2006. Exceptional marine survival of pink salmon that entered the marine environment in 2003 suggests that farmed Atlantic salmon and Pacific salmon can coexist successfully in a marine ecosystem on the Pacific coast of Canada. ICES J. Mar. Sci. 63: 1326-1337.
- Beamish, R.J., Neville, C.M., Sweeting, R.M., and Ambers, N. 2005. Sea lice on adult Pacific salmon in the coastal waters of central British Columbia. Fisheries Research 76: 198-208.
- Beamish, R.J., Neville, C.M., Sweeting, R.M., Jones, S.R.M., Ambers, N., Gordon, E.K., Hunter, K.L., and McDonald, T.E. 2007. A proposed life history strategy for the salmon louse, *Lepeophtheirus salmonis* in the subarctic Pacific. Aquaculture 264: 428-440.
- Beamish, R., Wade, J., Pennell, W., Gordon, E., Jones, S., Neville, C., Lange, K., and Sweeting, R. 2009. A large, natural infection of sea lice on juvenile Pacific salmon in the Gulf Islands area of British Columbia, Canada. Aquaculture 297: 31-37.
- Bere, R. 1930. The parasitic copepods of the fish of the Passamaquoddy region. Contribution to Canadian Biology and Fisheries 13: 423-430.
- Berland, B., and Margolis, L. 1983. The early history of 'lakeselus' and some nomenclatural questions relating to copepod parasites of salmon. Sarsia 68: 281-288.
- Bjorn, P.A., Sivertsgard, R., Finstad, B., Nilsen, R., Serra-Llinares, R.M., and Kristoffersen, R. 2011. Area protection may reduce salmon louse infection risk to wild salmonids. Aquaculture Environment Interactions 1: 233-244.
- Boxaspen, K., and Naess, T. 2000. Development of eggs and the planktonic stages of salmon lice (*Lepeophtheirus salmonis*) at low temperatures. Contrib. Zool. 69: 51-55.
- Brandal, P.O., and Egidius, E. 1979. Treatment of salmon lice (*Lepeophtheirus salmonis* Krøyer, 1838) with Neguvon® Description of method and equipment. Aquaculture 18: 183-188.
- Brandal, P.O., Egidius, E., and Romslo, I. 1976. Host blood-major food component for parastic copepod *Lepeophtheirus salmonis* Krøyer, 1938 (Crustacea- Caligidae). Norwegian Journal of Zoology 24: 341-343.
- Bricknell, I.R., Dalesman, S.J., O'Shea, B., Pert, C.C., and Luntz, A.J.M. 2006. Effect of environmental salinity on sea lice *Lepeophtheirus salmonis* settlement success. Dis. Aquat. Organ. 71: 201-212.
- Bron, J.E., Sommerville, C., Jones, M., and Rae, G.H. 1991. Settlement and attachment of early stages of the salmon louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae) on the salmon host, *Salmo salar*. J. Zool. 224: 201-212.
- Bron, J.E., Sommerville, C., Wootten, R., and Rae, G.H. 1993. Fallowing of marine Atlantic salmon, *Salmo salar* L., farms as a method for the control of sea lice, *Lepeophtheirus salmonis* (Krøyer, 1837). J. Fish Dis. 16: 487-493.

- Carr, J., and Whoriskey, F. 2004. Sea lice infestation rates on wild and escaped farmed Atlantic salmon (*Salmo salar* L.) entering the Magaguadavic River, New Brunswick. Aquac. Res. 35: 723-729.
- Chang, B.D., Page, F.H., Beattie, M.J., and Hill, B.W.H. 2011. Sea louse abundance on farmed salmon in the southwestern New Brunswick area of the Bay of Fundy. *In* Salmon Lice: an Integrated Approach to Understanding Parasite Abundance and Distribution. S. Jones, and R. Beamish (Eds.). Wiley Blackwell, Oxford, UK. pp. 83-115.
- Clayoquot Sound Sea Lice Working Group (CSSLWG). 2012. Patterns of sea lice (*L. salmonis*) infections in juvenile chum salmon (*Oncorhychus keta*) in Clayoquot Sound, 2007-2009.
- Connors, B., Krkosek, M., and Dill, L.M. 2008. Sea lice escape predation on their host. Biology Letters 4: 455-457.
- Connors, B., Krkosek, M., Ford, J., and Dill, L. 2010. Coho salmon productivity in relation to direct and trophic transmission of sea lice from salmon aquaculture. J. Appl. Ecol. 47: 1372-1377.
- Costelloe, M., Costelloe, J., O'Donohoe, G., Coghlan, N.J., Oonk, M., and Van Der Heijden, Y. 1998. Planktonic distribution of sea lice larvae, *Lepeophtheirus salmonis*, in Killary Harbour, west coast of Ireland. J. Mar. Biol. Assoc. U.K. 78: 853-874.
- Dawson, L.H.J., Pike, A.W., Houlihan, D.F., and McVicar, A.H. 1997. Comparison of the susceptibility of sea trout (*Salmo trutta* L.) and Atlantic salmon (*Salmo salar* L.) to sea lice (*Lepeophtheirus salmonis* (Krøyer, 1837)) infections. ICES J. Mar. Sci. 54: 1129-1139.
- Dawson, L.H.J., Pike, A.W., Houlihan, D.F., and McVicar, A.H. 1998. Effects of salmon lice Lepeophtheirus salmonis on sea trout Salmo trutta at different times after seawater transfer. Dis. Aquat. Organ. 33: 179-186.
- Foreman, M.G.G., Stucchi, D.J., Zhang, Y., and Baptista, A.M. 2006. Estuarine and tidal currents in the Broughton Archipelago. Atmos. Ocean 44: 47-63.
- Goode, A., and Whoriskey, F. 2003. Finding resolution to farmed salmon issues in eastern North America. *In* Salmon at the Edge. D. Mills (Ed.). Blackwell Science, Oxford, UK. pp. 144-158.
- Heard, W.R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). *In Pacific Salmon Life Histories*. C. Groot and L. Margolis (Eds.). UBC Press, Vancouver, BC. pp. 121-230.
- Heuch, P.A., Revie, C.W., and Gettinby, G. 2003. A comparison of epidemiological patterns of salmon lice, *Lepeophtheirus salmonis*, infections on farmed Atlantic salmon, *Salmo salar* L., in Norway and Scotland. J. Fish Dis. 26: 539-551.
- Heuch, P.A., and Schram, T.A. 1996. Male mate choice in a natural population of the parasitic copepod *Lernaeocera branchialis* (Copepoda: Pennellidae). Behaviour 133: 221-239.
- Ho, J.S., and Nagasawa, K. 2001. Why infestation by *Lepeophtheirus salmonis* (Copepoda: Caligidae) is not a problem in the coho salmon farming industry in Japan. J. Crustacean Biol. 21: 954-960.
- Hogans, W.E. 1995. Infection dynamics of sea lice, *Lepeophtheirus salmonis* (Copepoda: Caligidae) parasitic on Atlantic salmon (*Salmo salar*) cultured in marine waters of the lower Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 2067: 10 p.
- Hogans, W.E. 1997. Planktonic density and dispersion of larval sea lice (*Lepeophtheirus salmonis*) (Copepoda: Caligidae) and its relationship to infection dynamics and sea cage site location in the lower Bay of Fundy, New Brunswick. Report to the Department of Fisheries and Oceans, St. Andrews, N.B. 31 March 1997, 18 p.

- Hogans, W.E. and Trudeau, D.J. 1989. Preliminary studies on the biology of sea lice, *Caligus elongatus*, *Caligus curtus* and *Lepeophtheirus salmonis* (Copepoda: Caligoida) parasitic on cage-cultured salmonids in the lower Bay of Fundy. Can. Tech. Rep. Fish. Aquat. Sci. 1715: 14 p.
- Jakob, E., Sweeten, T., Bennett, W., and Jones, S.R.M. 2013. Development of the salmon louse, Lepeophtheirus salmonis and its effects on juvenile sockeye salmon *Oncorhynchus nerka*. Dis. Aquat. Organ. 106: 217-227.
- Johnson, S.C., and Albright, L.J. 1991a. Development, growth and survival of *Lepeophtheirus salmonis* (copepoda, caligidae) under laboratory conditions. J. Mar. Biol. Assoc. U.K. 71: 425-436.
- Johnson, S.C., and Albright, L.J. 1991b. The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda, Caligidae). Can. J. Zool. 69: 929-950.
- Johnson, S. C. and Jones S.R.M. 2015. Monitoring for sea lice on wild salmon in western and eastern Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/060.
- Johnson, S.C., Blaylock, J., Elphick, J., and Hyatt, K.D. 1996. Disease induced by the sea louse (*Lepeophtheirus salmonis*) (Copepoda: Caligidae) in wild sockeye salmon (*Oncorhynchus nerka*) stocks of Alberni Inlet, British Columbia. Can. J. Fish. Aquat. Sci. 53: 2888-2897.
- Johnson, S.C., Treasurer, J.W., Bravo, S., Nagasawa, K., and Kabata, A. 2004. A review of the impact of parasitic copepods on marine aquaculture. Zool. Stud. 43: 229-243.
- Jones, S., and Beamish, R. 2011. *Lepeophtheirus salmonis* on salmonids in the Northeast Pacific Ocean. *In* Sea Lice: An integrated approach to understanding Parasite Abundance and Distribution. S. Jones and R. Beamish (Eds.). Wiley Blackwell, Oxford, UK. pp. 307-329.
- Jones, S., Kim, E., and Bennett, W. 2008. Early development of resistance to the salmon louse Lepeophtheirus salmonis (Krøyer) in juvenile pink salmon Oncorhynchus gorbuscha (Walbaum). J. Fish Dis. 31: 591-600.
- Jones, S.R.M., and Hargreaves, N.B. 2007. The abundance and distribution of *Lepeophtheirus* salmonis (Copepoda: Caligidae) on pink (*Oncorhynchus gorbuscha*) and Chum (*O. keta*) salmon in coastal British Columbia. J. Parasitol. 93: 1324-1331.
- Jones, S.R.M., and Hargreaves, N.B. 2009. Infection threshold to estimate *Lepeophtheirus salmonis*-associated mortality among juvenile pink salmon. Dis. Aquat. Organ. 84: 131-137.
- Jones, S., and Johnson, S. 2014. Biology of sea lice, *Lepeophtheirus salmonis* and *Caligus* spp., in western and eastern Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/019. iv + 18 p.
- Jones, S.R.M., and Prosperi-Porta, G. 2011. The diversity of sea lice (Copepoda: Caligidae) parasitic on three-spined stickleback (*Gasterosteus aculeatus*) in coastal British Columbia. J. Parasitol. 97: 399-405.
- Jones, S.R.M., Prosperi-Porta, W., Kim, E., Callow, P., and Hargreaves, N.B. 2006b. The occurrence of *Lepeophtheirus salmonis* and *Caligus clemensi* (Copepoda: Caligidae) on three-spine stickleback *Gasterosteus aculeatus* in coastal British Columbia. J. Parasitol. 92: 473-480.
- Jones, S.R.M., Wosniok, W., and Hargreaves, N.B. 2006a. The salmon louse *Lepeophtheirus salmonis* on salmonid and non-salmonid fishes in British Columbia. Proceedings of 11th International Symposium on Veterinary Epidemiology and Economics. p 1331.
- Kent, M.L., Traxler, G.S., Kieser, D., Richard, J., Dawe, S.C., Shaw, R.W., Prosperi-Porta, G., Ketcheson, J., and Evelyn, T.P.T. 1998. Survey of Salmonid Pathogens in Ocean-Caught Fishes in British Columbia, Canada. J. Aquat. Anim. Health. 10: 211-219.

- Krkosek, M., Connors, B.M., Morton, A., Lewis, M.A., Dill, L.M., Hilborn, R. 2011. Effects of parasites from salmon farms on productivity of wild salmon. P. Natl. Acad. Sci. 108: 14700-14704.
- Krkosek, M., Gottesfeld, A., Proctor, B., Rolston, D., Carr-Harris, C., and Lewis, M.A. 2007a. Effects of host migration, diversity and aquaculture on sea lice threats to pacific salmon populations. Proc. R. Soc. B. 274: 3141-3149.
- Krkosek, M., Ford, J.S., Morton, A., Subhash, L., Ransom, A.M., and Lewis, M.A. 2007b. Declining wild salmon populations in relation to parasites from farm salmon. Science 14: 1772-1775.
- Krkosek, M., Lewis, M.A., Morton, A., Frazer, L.N., and Volpe, J.P. 2006. Epizootics of wild fish induced by farm fish. Proc. Natl. Acad. Sci. 103: 15506-15510.
- Krkosek, M., Lewis, M.A., and Volpe, J.P. 2005. Transmission dynamics of parasitic sea lice from farm to wild salmon. Proc. R. Soc. B. 272: 689-696.
- Krkosek, M., Morton, A., Volpe, J.P., and Lewis, M.A. 2009. Sea lice and salmon population dynamics: effects of exposure time migratory fish. Proc. R. Soc. B. 276: 2819-2828.
- Lacroix, G.L., and Knox, D. 2005. Distribution of Atlantic salmon (*Salmo salar*) postsmolts of different origins in the Bay of Fundy and Gulf of Maine and evaluation of factors affecting migration, growth, and survival. Can. J. Fish. Aquat. Sci. 62: 1363-1376.
- Lees, F., Gettinby, G., and Revie, C.W. 2008. Changes in epidemiological patterns of sea lice infestation on farmed Atlantic salmon, *Salmo salar* L., in Scotland between 1996 and 2006. J. Fish Dis. 31: 259-268.
- Mackenzie, K., Longshaw, M., Begg, G.S., and McVicar, A.H. 1998. Sea lice (Copepoda: Caligidae) on wild sea trout (*Salmo trutta* L.) in Scotland. ICES J. Mar. Sci. 55: 151-162.
- MacKinnon, B.M. 1997. Sea lice: a review. World Aquaculture 28: 5-10.
- Marty, G.D., Saksida, S.M., and Quinn, T. 2010. Relationship of farm salmon, sea lice, and wild salmon populations. P. Natl. Acad. Sci. 107: 22599-22604.
- Mckibben, M.A., and Hay, D.W. 2004. Distributions of planktonic sea lice larvae *Lepeophtheirus* salmonis in the inter-tidal zone in Loch Torridon, Western Scotland in relation to salmon farm production cycles. Aguac. Res. 35: 742-750.
- McVicar, A.H. 1997. Disease and parasite implications of the coexistence of wild and cultured Atlantic salmon populations. ICES J. Mar. Sci. 54: 1093-1103.
- McVicar, A.H. 2004. Management actions in relation to the controversy about salmon lice infections in fish farms as a hazard to wild salmonid populations. Aquac. Res. 35: 751-758.
- Morton, A.B., and Routledge, R. 2005. Mortality rates for juvenile pink *Oncorhynchus gorbuscha* and chum *O. keta* salmon infested with sea lice *Lepeophtheirus salmonis* in the Broughton Archipelago. Alaska Fishery Research Bulletin 11(2): 146-152.
- Morton, A., Routledge, R., Peet, C., and Ladwig, A. 2004. Sea lice (*Lepeophtheirus salmonis*) infection rates on juvenile pink (*Oncorhynchus gorbuscha*) and chum (*Oncorhynchus keta*) salmon in the nearshore marine environment of British Columbia, Canada. Can. J. Fish. Aquat. Sci. 61(2): 147-157.
- Morton, A., Routledge, R., McConnell, A., and Krkosek, M. 2011. Sea lice dispersion and salmon survival in relation to salmon farm activity in the Broughton Archipelago. ICES Journal of Marine Science. 68: 144-156.

- Morton, A.B., and Williams, R. 2003. First report of sea louse, *Lepeophtheirus salmonis*, infestation on juvenile pink salmon, *Oncorhynchus gorbuscha*, in nearshore habitat. Can. Field Nat. 117: 634-641.
- Murray, A.G. 2009. Using simple models to review the application and implications of different approaches used to simulate transmission of pathogens among aquatic animals. Prev. Vet. Med. 88: 167-177.
- Nagasawa, K. 1985. Comparison of the infestation levels of *Lepeophtheirus salmonis* (Copepoda) on Chum salmon captured by two methods. Jpn. J. Ichthyol. 32: 68-370.
- Nagasawa, K. 2001. Annual changes in the population size of the salmon louse *Lepeophtheirus* salmonis (Copepoda: Caligidae) on high-seas Pacific salmon (*Oncorhynchus* spp.), and the relationship to host abundance. Hydrobiologia 453/454: 411-416.
- Nagasawa, K., Ishida, Y., Ogura, M., Tadokoro, K., and Hiramatsu, K. 1993. The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on six species of Pacific salmon in offshore waters of the North Pacific Ocean and Bering Sea. *In* Pathogens of Wild and Farmed Fish: Sea Lice. G.A. Boxshall and D. Defaye (Eds.). Ellis Horwood, Chichester, UK. pp. 166-178.
- Nendick, L., Sackville, M., Tang, S., Brauner, C.J., and Farrell, A.P. 2011. Sea lice infection of juvenile pink salmon (*Oncorhynchus gorbuscha*): effects on swimming performance and postexercise ion balance. Can. J. Fish. Aquat. Sci. 68: 241-249.
- Oines, O., and Heuch, P.A. 2007. *Caligus elongatus* Nordmann genotypes on wild and farmed fish. J. Fish Dis. 30: 81-91.
- Oines, O., and Schram, T. 2008. Intra- or inter-specific difference in genotypes of *Caligus elongatus* Nordmann 1832. Acta Parasitol. 53: 93-105.
- Oines, O., Simonsen, J.H., Knutsen, J.A., and Heuch, P.A. 2006. Host preference of adult *Caligus elongatus* Nordmann in the laboratory and its implications for Atlantic cod aquaculture. J. Fish Dis. 29: 167-174.
- Penston, M.J., and Davies, I.M. 2009. An assessment of salmon farms and wild salmonids as sources of *Lepeophtheirus salmonis* (Krøyer) copepodids in the water column in Loch Torridon, Scotland. J. Fish Dis. 32(1): 75-88.
- Penston, M.J., McKibben, M.A., Hay, D.W., and Gillibrand, P.A. 2004. Observations on open-water densities of sea lice larvae in Loch Shieldaig, Western Scotland. Aquac. Res. 35: 793-805.
- Penston, M.J., Millar, C.P., Zuur, A., and Davies, I.M. 2008. Spatial and temporal distribution of Lepeophtheirus salmonis (Kroyer) larvae in a sea loch containing Atlantic salmon, Salmo salar L., farms on the north-west coast of Scotland. J. Fish Dis. 31(5): 361-371.
- Pert, C.C., Luntz, A.J.M., Fryer, R.J., O'Shea, B., and Bricknell, I.R. 2009a. The settlement and survival of the salmon louse, *Lepeophtheirus salmonis* (Kroyer, 1837) on atypical hosts. Aquaculture 288: 321-324.
- Pert, C.C., Mordue, A.J., O'Shea, B., and Bricknell, I.R. 2012. The settlement and reproductive success of *Lepeophtheirus salmonis* (Krøyer 1837; Copepoda: Caligidae) on atypical hosts. Aquac. Res. 43: 799-805.
- Pert, C.C., Raffell, J., Urquhart, K., Weir, S.J., Kantola, K.M.H., and Bricknell, I.R. 2009b. The pathogen burden of early returning sea trout (*Salmo trutta* L.) infected with *Lepeophtheirus* salmonis (Krøyer, 1837), in the River Shieldaig, Scotland. Bull. Euro. Assn. Fish P. 29: 210-216.

- Pert, C.C., Urquhart, K., and Bricknell, I.R. 2006. The sea bass (*Dicentrarchus labrax* L.): a peripatetic host of *Lepeophtheirus salmonis* (Copepoda: Caligidae)? Bull. Euro. Assn. Fish P. 26: 163-165.
- Price, M.H.H., Proboszcz, S.L., Routledge, R.D., Gottesfeld, A.S., Orr, C., and Reynolds, J.D. 2011. Sea louse infection of juvenile Sockeye salmon in relation to marine salmon farms on Canada's west coast. PLoS ONE 6: e16851. doi:10.1371/journal.pone.0016851.
- Revie, C.W., Gettinby, G., Treasurer, J.W., Rae, G.H., and Clark, N. 2002. Temporal, environmental and management factors influencing the epidemiological patterns of sea lice (*Lepeophtheirus salmonis*) infestations on farmed Atlantic salmon (*Salmo salar*) in Scotland. Pest Manag. Sci. 58: 576-584.
- Ritchie, G. 1997. The host transfer ability of *Lepeophtheirus salmonis* (Copepoda: Caligidae) from farmed Atlantic salmon, *Salmo salar* L. J. Fish Dis. 20: 153-157.
- Saksida, S., Constantine, J., Karreman, G.A., and Donald, A. 2007b. Evaluation of sea lice abundance levels on farmed Atlantic salmon (*Salmo salar*) located in the Broughton area of British Columbia from 2003-2005. Aquac. Res. 38: 219-231.
- Saksida, S., Constantine, J., Karreman, G.A., Neville, C., Sweeting, R., and Beamish, R. 2006. Evaluation of sea lice, *Lepeophtheirus salmonis*, abundance levels on farmed salmon in British Columbia, Canada. Proceedings of the 11th International Symposium on Veterinary Epidemiology and Economics.
- Saksida, S.M., Greba, L., Morrison, D., and Revie, C.W. 2011a. Sea lice on wild juvenile Pacific salmon and farmed Atlantic salmon in the northernmost salmon farming region of British Columbia. Aquaculture 320: 193-198.
- Saksida, S., Karreman, G.A., Constantine, J., and Donald, A. 2007a. Differences in *Lepeophtheirus* salmonis abundance levels on Atlantic salmon farms in the Broughton Archipelago British Columbia, Canada. J. Fish Dis. 30: 357-366.
- Saksida, S.M., Marty, G.D., Jones, S.R.M., Manchester, H.A., Diamond, C.L., Bidulka, J., and St-Hilaire, S. 2012. Parasites and hepatic lesions among juvenile pink salmon (*Oncorhynchus gorbuscha*) during early seawater residence. J. Fish Dis. 35: 137–151.
- Saksida, S.M., Morrison, D., McKenzie, P., Milligan, B., Downey, E., Boyce, B., and Eaves, A. 2013, Use of Atlantic salmon, *Salmo salar* L., farm treatment data and bioassays to assess for resistance of sea lice, *Lepeophtheirus salmonis*, to emamectin benzoate (SLICE®) in British Columbia, Canada. J. Fish Dis. 36: 515-520.
- Saksida, S.M., Morrison, D., and Revie, C.W. 2010. The efficacy of emamectin benzoate against infestations of sea lice, *Lepeophtheirus salmonis*, on farmed Atlantic salmon *Salmo salar* L., in British Columbia. J. Fish Dis. 33: 913-917.
- Saksida, S., Morrison, D., Sheppard, M., and Keith, I. 2011b. Sea lice management on salmon farms in British Columbia, Canada. *In* Sea lice: An integrated approach to understanding parasite abundance and distribution. S. Jones and R. Beamish (Eds.). Wiley-Blackwell, Oxford, UK. pp. 235-278.
- Selden, P.A., Huys, R., Stephenson, M.H., Heward, A.P., Taylor, P.N. 2010. Crustaceans from bitumen clast in Carboniferous glacial diamictite extend fossil record of copepods. Nature Communications 1 (50): 1-6.
- Stien, A., Bjorn, P.A., Heuch, P.A., and Elston, D.A. 2005. Population dynamics of salmon lice *Lepeophtheirus salmonis* on Atlantic salmon and sea trout. Mar. Ecol. Prog. Ser. 290: 263-275.

- Trudel, M., Jones, S., Thiess, R.M., Morris, M.E., John, F.T., Welch, D.W., Sweeting, R.M., Moss, J.H., Wing, B.L., Farley, E.V. Jr., Murphy, J.M., Baldwin, R.E., and Jacobson, K.C. 2007. Infestations of motile salmon lice on Pacific salmon along the west coast of North America. American Fisheries Society Symposium 57: 1-25.
- Tully, O., and Nolan, D. 2002. A review of the population biology and host-parasite interactions of the sea louse *Lepeophtheirus salmonis* (Copepoda: Calgidae). Parasitology 124: S165-S182.
- Urquhart, K., Pert, C.C., Fryer, R.J., Cook, P., Weir, S., Kilburn, R., Mccarthy, U., Simons, J., Mcbeath, S.J., Matejusova, I., and Bricknell, I.R. 2010. A survey of pathogens and metazoan parasites on wild sea trout (*Salmo trutta*) in Scottish waters. ICES J. Mar. Sci. 67: 444-453.
- Urquhart, K., Pert, C.C., Kilburn, R., Fryer, R.J., and Bricknell, I.R. 2008. Prevalence, abundance, and distribution of *Lepeoptheirus salmonis* (Krøyer, 1837) and *Caligus elongatus* (Nordmann, 1832) on wild sea trout *Salmo trutta* L. ICES J. Mar. Sci. 65: 171-173.
- Wertheimer, A.C., Fergusson, E.A., Focht, R.L., Heard, W.R., Orsi, J.A., Sturdevant, M.V., and Wing, B.L. 2003. Sea lice infection of juvenile salmon in the marine waters of the northern region of southeastern Alaska, May-August, 2003. (NPAFC Doc. 706) 13 p. Auke Bay Lab., Alaska Fish. Sci. Cen., Nat. Mar. Fish. Serv., NOAA, U.S. Dept. Commerce, 11305 Glacier Highway, Juneau, AK 99801-8626, USA.
- White, H.C. 1940. Sea lice (*Lepeophtheirus*) and death of salmon. Journal of the Fisheries Research Board of Canada 5: 172-175.
- White, H.C. 1942. Life history of *Lepeophtheirus salmonis*. Journal of the Fisheries Research Board of Canada 6: 24-29.
- Wilson, C.B. 1905. North American parasitic copepods belonging to the family Caligidae. Proceedings of the United States National Museum 28: 479-672.
- Wootten, R., Smith, J.W., and Needham, E.A. 1982. Aspects of the biology of the parasitic copepods Lepeophtheirus salmonis and Caligus elongatus on farmed salmonids, and their treatment. Aquaculture 81: 185-197.