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Biology of sea lice, *Lepeophtheirus salmonis* and *Caligus* spp., in western and eastern Canada

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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.

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ABSTRACT

Five species of sea lice (*Lepeophtheirus salmonis, L. cuneifer, Caligus elongatus, C. clemensi, C. curtus*) are reported from net pen-reared salmonids in Canada. Of these, *L. salmonis* is the largest and most aggressive species and is the primary focus of management activities and regulations. Sea louse biology is broadly divisible into free-living and parasitic phases. The development and survival of sea lice during both phases of development are regulated by the ambient seawater temperature and salinity. In addition, free-living stages possess numerous adaptations that permit sensing of environmental gradients of light, substances secreted by fish (semiochemicals) and mechanical energy (vibrations derived from fish movements). These adaptations enhance larval survival by optimising host-detection and settlement behaviour. The high fecundity of adult female sea lice further optimises parasite survival. There is a wide range of susceptibilities to *L. salmonis* among salmonid host species in Canada indicating that sea lice survival is also mediated by host factors. Infestations tend to be of lower intensity and of shorter duration on less susceptible species. There are significant genetic differences between the varieties of *L. salmonis* that occur on the Pacific and Atlantic coasts of Canada. Further research is required to determine the biological significance of the genetic differences and to better understand the mechanisms responsible for host resistance to sea lice. 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.

Biologie du pou du poisson *Lepeophtheirus salmonis* et des espèces du genre *Caligus* dans l'ouest et l'est du Canada

RÉSUMÉ

Cinq espèces de pou du poisson (*Lepeophtheirus salmonis, L. cuneifer, Caligus elongatus, C. clemensi, C. curtus*) sont déclarées comme présentes chez les salmonidés élevés en parc en filet au Canada. Étant l'espèce caractérisée par la plus grande taille et la plus grande agressivité parmi ces espèces, *L. salmonis* constitue l'espèce la plus souvent visée par les activités de gestion et la règlementation. Le cycle biologique du pou du poisson se divise sommairement en stade libre et en stade parasitaire. Le développement et la survie du pou du poisson pendant ces deux stades dépendent de la température ambiante et de la salinité de l'eau. De plus, les stades libres ont de nombreuses adaptations qui leur permettent de reconnaître des gradients environnementaux tels que la lumière, les substances sécrétées par le poisson (substances sémiochimiques) et l'énergie mécanique (vibrations provenant du déplacement des poissons). Ces adaptations ont pour effet d'accroître le taux de survie des larves en optimisant la détection des poissons-hôtes et le comportement d'établissement. La fécondité élevée des femelles adultes optimise également le taux de survie du parasite. Le large éventail de sensibilités à l'infestation par *L. salmonis* chez les espèces-hôtes de salmonidés au Canada indique que des facteurs attribuables à l'hôte peuvent également avoir un effet sur le taux de survie du pou du poisson. Les infestations tendent à être de moindre durée et de moindre intensité sur les espèces les moins vulnérables. Il existe des différences génétiques importantes entre les variétés de *L. salmonis* sur les côtes du Pacifique et de l'Atlantique du Canada. D'autres recherches doivent être effectuées afin de déterminer l'importance biologique de ces différences génétiques et de mieux comprendre les mécanismes responsables de la résistance de l'hôte au pou du poisson. Le présent document de recherche a été présenté et révisé lors d'une réunion nationale d'examen par les pairs (*Surveillance du pou du poisson et mesures non chimiques*) du Secrétariat canadien de consultation scientifique (SCCS) tenue à Ottawa du 25 au 27 septembre 2012. L'objectif de cette réunion d'examen par les pairs était d'évaluer la qualité 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

Sea lice is the term used collectively for copepods in the genera *Lepeophtheirus* and *Caligus* that are parasites of marine fishes. There are 245 recognized species of *Caligus* and 129 recognized species of *Lepeophtheirus*: copepods belonging to both genera share a cosmopolitan geographic distribution and a broad range of host species (Kabata 1988, World of Copepods 2012). In several parts of the world, sea lice species have proliferated on the relatively high densities of susceptible fish hosts provided by open net pen aquaculture. In eastern Canada, only Atlantic salmon are produced in marine net pen aquaculture whereas in Pacific Canada, Atlantic salmon represent approximately 95% of the biomass and Chinook salmon most of the remainder. The salmon louse, *Lepeophtheirus salmonis*, occurs throughout the North Pacific and Atlantic Oceans, the marine native range of salmonids belonging to the genera *Salmo*, *Oncorhynchus* and *Salvelinus*. In the northeastern Pacific Ocean, *L. salmonis* also occurs on 3-spine sticklebacks *Gasterosteus aculeatus* (Jones et al. 2006a, Jones and Prosperi-Porta 2011). Section C of this report (Saksida et al. 2015) describes in more detail the epizootiology of *L. salmonis* on its wild and farmed hosts in Canada. This species of parasitic copepod is the largest, most abundant and potentially the most damaging of the sea lice to affect Atlantic salmon aquaculture on both coasts of Canada. In contrast, much lower abundances of *L. salmonis* are reported from pen-reared Chinook salmon. Damage caused to the host by *L. salmonis* is principally due to its feeding behaviour, particularly that of the larger, mobile preadult and adult stages. The parasites feed on mucus and skin and when left untreated, high intensity infections cause skin erosion with varying degrees of invasiveness and associated haemorrhage (Brandal and Egidius 1979, Johnson et al. 2004). The combined effects of the parasite can include reduced growth; the loss of mucus and scales provides an opportunity for secondary pathogens to become established and more severely damage the fish (Copley et al. 2001). It is now clear that sub-lethal effects in Atlantic salmon, including increased stress and reduced swim performance, are also important consequences of *L. salmonis* infection on the susceptible host (Wagner et al. 2008, Brauner et al. 2012).

Other species of sea lice are also pests of Atlantic salmon aquaculture in Canada. On the Pacific coast, *Caligus clemensi* occurs on a wide range of salmonid and non-salmonid hosts and is reported from farmed Atlantic salmon. Similarly, *Lepeophtheirus cuneifer* also occurs on non-salmonids and on wild and cultured salmonid species (Kabata 1974, Johnson and Albright 1991a, Jones and Prosperi-Porta 2011), however this species is less well studied and its importance to salmon aquaculture is poorly documented. On the Atlantic coast, *Caligus elongatus* and *Caligus curtus* have been reported from cultured Atlantic salmon. The known host ranges of sea lice affecting cultured salmon in Canada are listed in Table 1. A majority of the literature concerning the biology of sea lice in Canada focuses on *L. salmonis*. Despite this, it is occasionally possible to extrapolate from our knowledge of *L. salmonis* to help understand the biology of other species affecting salmonids, particularly those belonging to the genus *Caligus*.

This Section summarises the biology of sea lice, particularly *L. salmonis*, and emphasises those features of the parasite that are amenable to its control or management.

GEOGRAPHIC VARIATION AMONG *LEPOEPHTHEIRUS SALMONIS*

The salmon louse occurs on cultured Atlantic salmon in Atlantic and Pacific Canada, and while the Atlantic salmon is indigenous to the Atlantic Ocean, it is an exotic species in the Pacific Ocean. This is an important distinction because although *L. salmonis* occurs on both coasts of Canada, genetically distinct variants of the species occur in the Atlantic and Pacific Oceans. Microsatellite data from six loci revealed significant variations between one population from the

Pacific Ocean and Atlantic forms (Todd et al. 2004). Similarly, Tjensvoll et al. (2006) reported differences in the mitochondrial genome between a population of *L. salmonis* from Japan and Atlantic forms. Subsequently, Yazawa et al. (2008), based on samples obtained from nine populations throughout the Pacific Ocean, found that nuclear genes differ, on average, by 3.2% and the mitochondrial genome by 7.1% between Pacific and Atlantic forms of the parasite. This finding is consistent with the geographic isolation and divergence of salmon belonging to *Oncorhynchus* and *Salmo* 11 to 24 million years ago (McKay et al. 1996) and suggests that the Pacific and Atlantic variants are distinct species of *Lepeophtheirus* (Yazawa et al. 2008). Similar genetic variants have also been observed for *C. elongatus* and *L. cuneifer* (Øines and Heuch 2005, Øines and Schram 2008, Jones and Prosperi-Porta 2011) although these occurred over much smaller geographic ranges than for *L. salmonis*. Further research is needed to fully document and compare the biological consequences, including reproductive potential, responses to environmental variables and virulence, of the genetic variation between and Atlantic and Pacific Ocean forms of *L. salmonis*. The recent availability of novel genomics tools to complement functional studies on *L. salmonis* and related copepods will support this objective (Yasuike et al. 2012).

THE LIFE CYCLE OF SEA LICE

The developmental cycle is similar for copepods belonging to *Lepeophtheirus* and *Caligus*: generally, all life cycles include 10 developmental stages. First stage nauplii released from egg strings extruded from adult females moult to second stage nauplii then to copepodids, which are infective to the fish host. Despite possessing a rudimentary gut, the preceeding stages are non-feeding and possess a finite endogenous energy reserve. A decline in energy reserves has been associated with reduced infectivity among copepodids aged 3 to 7 days old (Tucker et al. 2000b). Mean endogenous lipid content was shown to decrease by approximately 95% in copepodids between 7 and 20 days post hatch (Cook et al. 2010). Thus, the viability and longevity of infectivity among free-swimming copepodids will depend closely on the rate of consumption of endogenous lipids. Following settlement on the host, the copepodid moults to the first of four chalimus stages that are tethered to one site on the host by the frontal filament. The fourth chalimus stage moults to the first of two preadult stages followed by a moult to the reproductive adult stage. In some species of *Caligus*, additional chalimus stages occur and preadults may be absent or reduced to one stage. The sexes can be distinguished in the fourth stage chalimus and later stages. The morphology of the developmental stages of *Lepeophtheirus salmonis* and of *Caligus* spp. important to salmon aquaculture in Canada have been illustrated in earlier publications (Kabata 1972, 1988, Johnson and Albright 1991b, Piasecki and MacKinnon 1995). Therefore, the biology of sea lice involves two distinct life history patterns: an earlier free-living phase and a later parasitic phase. A thorough understanding of the factors influencing development, survival and dispersal in both phases will assist in the formulation of management strategies.

REPRODUCTIVE BIOLOGY OF SEA LICE

Mating and oviposition among sea lice has been reviewed in Pike and Wadsworth (1999). Adult male *L. salmonis* mature approximately 1 day earlier than adult females on Atlantic salmon. The male *L. salmonis* is attracted to pheromones secreted by preadult II females (Ingvarsdóttir et al. 2002a) and will guard the female until the final moult, after which mating occurs. In *C. elongatus*, males are believed to die following mating (Piasecki and MacKinnon 1995). Heuch et al. (2000) reported that the fertilised female *L. salmonis* will produce 11 pairs of egg strings following a single mating, and Ritchie et al. (1996) indicated that a single mating is sufficient to fertilise all the eggs produced in the lifetime of a female *L. salmonis*. Occasionally, fertilised female *L. salmonis* may lose one or both spermatophores and in these cases matings with multiple males have been confirmed (Todd et al. 2005). Female *L. salmonis* have survived in the laboratory for 191 days (Heuch et al. 2000), although the authors suggested a greater longevity may be possible during natural infections.

The length of the egg string is directly related to the number of developing embryos in the string. Factors that appear to regulate the length of eggs strings (numbers of embryos) include batch number: egg string length increased with batch number following mating (Pike and Wadsworth 1999, Heuch et al. 2000); whether the lice are attached to wild (longer egg strings) or farmed salmon (shorter egg strings) (Jackson and Minchin 1992) – although this finding was not confirmed by Heuch et al. (2000); whether sea lice are attached to susceptible (longer eggs strings on Atlantic salmon) or resistant salmon species (shorter egg strings on Chinook salmon) (Johnson 1993) and whether the samples were collected in winter (longer egg strings) or summer (shorter egg strings) and therefore related to temperature (Tully 1989). Heuch et al. (2000) agreed with (Ritchie et al. 1993) in suggesting that the inverse relationship between egg string length and temperature was weakly supported and that the earlier observations were because of differences in photoperiod. Differences in the proportion of viable embryos are frequently observed among sequentially extruded egg strings and the reasons for these differences are not understood (Pike and Wadsworth 1999, Heuch et al. 2000).

EFFECTS OF TEMPERATURE ON SEA LICE DEVELOPMENT

Temperature profiles differ between those regions of Pacific and Atlantic coastal Canada in which salmon aquaculture occurs. In the Bay of Fundy Rates of development and metabolism in sea lice are directly linked to temperature. The time from infection to production of the first egg string was 20 days at 12.2 °C and 79 days at 7.1 °C (Heuch et al. 2000). The rate of embryonic development development is also affected by temperature. At 2°C, 3°C, 4°C and 5°C, the hatching of nauplii takes 45.1, 35.2, 27.6 and 21.6 days, respectively, compared with 8.7 days at 10°C (Boxaspen and Naess 2000). The number of days to first hatching was fitted to a polynomial function (Table 2, equation 1). The effects of temperature on the rate of development and therefore the generation time of *L. salmonis* has been described in earlier reviews (Pike and Wadsworth 1999, Brooks 2005, Hayward et al. 2011). The generation time of *L. salmonis* ranges from 4 weeks at 18 °C to 8-9 weeks at 6 °C (Hayward et al. 2011). Tully (1992) used previously published work (Tully 1989) to refine the relationship between generation time and temperature (Table 2, equation 2). The rate of development and the generation times for *C. elongatus* are also strongly temperature dependent (Tully 1992) and although this research has not been conducted, similar relationships with temperature are to be expected for *C. clemensi*.

Based on previously published work, Stien et al. (2005) showed that a modified Belehrádek function provided the best fit for the relationship between temperature and the minimum time for egg development to hatching (Table 2, equation 3) and the minimum time for development from hatching to the infective copepodid (Table 2, equation 4). In a related paper, Brooks (2005) fit a polynomial relationship to the relationship between development time from hatching to the infective copepodid (Table 2, equation 5), based on the same data set used by Tully (1992). Brooks (2005) estimated *L. salmonis* larvae require 4.2 to 5.8 days to develop to infective copepodid stages at temperatures found in the Broughton Archipelago, British Columbia.

The development and survival of parasitic stages of *L. salmonis* is also governed by temperature. Sex-specific rates of development to chalimus or preadult stages according to temperature were estimated by Stien et al. (2005) and summarised in equations 6-9 (Table 2). These data suggest that preadult males develop more rapidly than preadult females, consistent with earlier observations of *L. salmonis* on Atlantic salmon (Johnson and Albright 1991c). The effects of temperatures >15 °C and <7 °C on the development of *L. salmonis* require additional research (Stien et al. 2005). In addition to the effects of temperature on growth rate, *L. salmonis* and *C. elongatus* were both found to be larger and more fecund in colder water (Tully 1989, Hogans 1995). However, moult success was reduced at 2 °C and few copepodids were recovered in winter field samples from the Bay of Fundy (Hogans 1995). Infectivity is compromised at reduced temperatures as fewer copepodids settled onto laboratory-reared Atlantic salmon at 7 °C compared with 12 °C (Tucker et al. 2000a). Water temperatures at salmon farms in the Bay of Fundy temperatures range from approximately 2 °C to 14 °C, although extremes of 0.1 °C and 16.1 °C have been reported (Chang et al. 2011). Infections with *L. salmonis* persist over-winter on farmed salmon in the Bay of Fundy, albeit at reduced prevalence and intensity (Hogans 1995, Chang et al. 2011). In British Columbia, surface (1 m) seawater temperatures range from approximately 6 °C to 13 °C and unlike in the Bay of Fundy, temperature does not appear to influence the seasonal abundance of *L. salmonis*, whether in the Broughton Archipelago or elsewhere on the coast (Saksida et al. 2007a, b).

EFFECTS OF SALINITY ON SEA LICE DEVELOPMENT

The salmon louse is a stenohaline copepod whose larval stages in particular, possess limited capacity for osmoregulation. Survival and development of *L. salmonis* is optimal in high salinity seawater although numerous field and laboratory reports, summarised in Pike and Wadsworth (1999), illustrate the capacity for adult *L. salmonis* to survive several days in fresh water. Survival in freshwater however, is enhanced for those adult copepods residing on host fish, presumably because feeding on host tissues replenishes ions lost to the hypo-osmotic environment (Hahnenkamp and Fyhn 1985). In a laboratory study, eggs of the Pacific variety of *L. salmonis* failed to develop at 10‰ whereas eggs developed but the nauplii did not hatch at 15‰ (Johnson and Albright 1991c). When salinity ranged from 20 to 30‰, viable nauplii were produced but these moulted to copepodids only when salinity was 30‰. However, a copepodid survival beyond one day only occurred when salinity was greater than 10‰ (Johnson and Albright 1991c). Thus, larvae derived from ovigerous parasites carried into freshwater by adult salmon are unlikely to be viable. In addition to reduced survival, lowered salinity is also associated with poor infectivity: settlement of *L. salmonis* copepodids onto Atlantic salmon was significantly improved at 34‰ salinity compared with 24‰ (Tucker et al. 2000a). When presented with continuous or step-wise salinity gradients in a laboratory mesocosm, *L. salmonis* copepodids aggregated in zones of rapidly changing salinity that were at or above 20‰ (Heuch 1995). Heuch (1995) argued that by aggregating in steep haloclines, opportunities for host detection by *L. salmonis* copepodids is enhanced because salmon tend to forage in areas of steep haloclines. Bricknell et al. (2006) found that survival of free-swimming copepodids was markedly reduced at salinities less than 29‰ and that the copepodid altered its behaviour to avoid zones of reduced salinity. Infectivity of copepodids was also reduced at lower salinity, confirming the findings of Tucker et al. (2000a). Bricknell et al. (2006) suggested that in reduced salinity seawater, the increased sinking rate imparts a metabolic cost to the copepodid in addition to the increased physiological costs of osmoregulation. Sutherland et al. (2012) characterised the significantly elevated expression of stress-associated genes in *L. salmonis* copepodids maintained in 27‰ seawater compared with 30‰. In addition to limiting its viability and infectivity, the reduction of endogenous lipids in aging copepodids (Cook et al. 2010) may also determine the salinity at which the animal is neutrally buoyant. In stratified water, the depth at which a copepodid is neutrally buoyant may influence its dispersal in water currents.

SENSORY ADAPTATIONS OF *L. SALMONIS* COPEPODIDS

Location of and attachment to the host by the infective *L. salmonis* copepodid is facilitated by numerous adaptive physiological and behavioural traits (Mordue and Birkett 2009). Copepodids display positive phototaxis (Wootten et al. 1982, Bron et al. 1993, Flamarique et al. 2000) resulting in a diurnal migratory behaviour in which they reside high in the water column during daylight and deeper at night (Heuch et al. 1995). Photoreceptors in the copepodid are sensitive both to visible (400 to 700 nm) and ultraviolet light (313 nm) (Bron et al. 1993, Aarseth and Schram 1999). The greatest response was elicited by light with a wavelength of 550 nm (Bron et al. 1993). Visible light, along with salinity and host velocity, also influences the initial phases of settlement onto Atlantic salmon (Genna et al. 2005), but not the intensity of infection 20 days after exposure (Browman et al. 2004). Bron et al. (1993) reported mechanical vibrations in water generated by the host elicit a burst swimming response by copepodids. Heuch and Karlsen (1999) showed that the water-borne vibration to which the copepodid responds are generated within centimetres of a swimming fish. In a laboratory study, a non-parasitic copepod was repelled by the hydrodynamic oscillations generated by a simulated fish whereas *L. salmonis* copepodids displayed an attack response that was equally significant in lighted or dark conditions (Heuch et al. 2007).

Chemicals secreted by fish (i.e., semiochemicals) are another category of environmental stimuli that elicit a host-seeking behavioural response in *L. salmonis* copepodids (Devine et al. 2000, Ingvarsdóttir et al. 2002b). The highly setate second antennae contain chemoreceptors (Gresty et al. 1993) that respond to semiochemicals, thus triggering host finding behaviour and may also facilitate settlement on the appropriate host (Bron et al., 1993). Kinetic responses among *L. salmonis* copepodids are triggered by semiochemicals from host and non-host species, whereas kinetic and rheotactic responses are triggered specifically by semiochemicals from hosts species (Bailey et al. 2006). The finding of Pacific and Atlantic Ocean varieties of *L. salmonis* settling and developing on non-salmonid fishes (Bruno and Stone 1990, Lyndon and Toovey 2001, Jones et al. 2006a, Pert et al. 2009, Jones and Prosperi-Porta 2011) indicates that certain host-marker semiochemicals may occur widely among fish species.

Host location and settlement by *L. salmonis* copepodids therefore functions over several scales: phototaxis triggers diurnal vertical migrations thought to increase the chance of encountering a host, rheotaxis in the proximity of fish triggers a burst swimming response and semiotaxis fine-tunes the behavioural response and provides some capacity to discriminate between an appropriate and inappropriate host during settlement. The initial phase of settlement onto the skin of the host is reversible until the attachment of the copepodid into the epidermis by means of the second antennae (Bron et al. 1991).

HOST FACTORS ASSOCIATED WITH *L. SALMONIS* DEVELOPMENT AND ABUNDANCE

The abundance of *L. salmonis* and its ability to develop into reproductively active adults will also depend on defence responses mounted by the host. Differential susceptibility to *L. salmonis* occurs among salmon species. On salmon farms in Ireland, rainbow trout (*Oncorhynchus mykiss*) carried fewer *L. salmonis* than did Atlantic salmon (Jackson et al. 1997) and in Japan, fewer *L. salmonis* occurred on coho salmon (*Oncorhynchus kisutch*) compared with rainbow trout, despite concurrent exposures to the parasite from wild chum salmon (*Oncorhynchus keta*) (Ho and Nagasawa 2001). While the mean abundance of lice declined both on sea trout (*Salmo trutta*) and Atlantic salmon, a higher mean abundance was maintained on the sea trout eight weeks following a laboratory exposure, suggesting greater susceptibility (Dawson et al. 1997). Similarly, parasites were lost more rapidly from coho salmon compared with Atlantic salmon or rainbow trout (Johnson and Albright 1992, Fast et al. 2002) and matured more slowly on coho salmon than on Atlantic salmon or rainbow trout (Fast et al. 2002). Naturally infected juvenile chum salmon had higher intensities of infection with *L. salmonis* compared with pink salmon (*Oncorhynchus gorbuscha*) (Jones and Hargeaves 2007, 2009). The latter pattern was repeated in laboratory exposures in which the parasite was rapidly rejected from juvenile pink compared with juvenile chum salmon (Jones et al. 2006b, 2007). While the Pacific variety of *L. salmonis* occurs on 3-spine sticklebacks throughout coastal British Columbia, field and laboratory observations confirm that development rarely proceeds beyond the chalimus 4 stage on this host as evidenced by the lack of preadult and adult stages (Jones et al. 2006a, b). The fate of later developmental stages, if they occur, is not known.

Although Atlantic salmon are highly susceptible to infection with *L. salmonis* (Johnson and Albright 1992, Fast et al. 2002, Fast et al. 2006b), there is an interest in the application of selective breeding programmes for resistance to *L. salmonis* (Jones et al. 2002). Intraspecific heterogeneity in susceptibility to *L. salmonis* occurs among distinct spawning stocks (Glover et al. 2004) and among full-sib families (Glover et al. 2005, Kolstad et al. 2005, Gjerde et al. 2011). The heritability of sea lice counts in the latter studies ranged from 0.07 to 0.33, indicating some genetic basis for the differences observed among families. Similarly, a heritability of 0.22 was calculated for counts of the related copepod *Caligus elongatus* among full-sib Atlantic salmon families (Mustafa and MacKinnon 1999). Susceptibility to *L. salmonis* in Atlantic salmon has been linked to a major histocompatibility (MH) class II genotype (Sasa-DAA-3UTR) (Glover et al. 2007). However, a subsequent QTL analysis provided only weak support for this relationship (Gharbi et al. 2009) and suggested a better understanding of innate mechanisms of resistance to *L. salmonis* is necessary to explain differential susceptibility. Previous exposure to *L. salmonis*, severity of the exposure and co-infection with *C. elongatus* can influence susceptibility to *L. salmonis*. Thus, the importance of reproducible controlled challenges for assessing the genetic basis for susceptibility to *L. salmonis* in Atlantic salmon has been emphasised (Kolstad et al. 2005, Wagner et al. 2008).

The capacity to mount a local inflammatory response has been a known mechanism of host resistance to *L. salmonis* for some time and the rate with which copepodid and chalimus stages of *L. salmonis* are rejected is directly related to the severity of the inflammatory response, particularly in coho salmon or immunostimulant-treated Atlantic salmon (Johnson and Albright 1992). Dietary immunostimulants (e.g. CpG oligodeoxynucleotide [ODN]) caused greater than 40% reduction in parasite intensity in Atlantic salmon seven to 10 days after exposure to *L. salmonis* (M. Fast, personal communication). The magnitude of the host response is related to recognition of and modulation by *L. salmonis* secretory/excretory products (SEP), including proteases and prostaglandin E_2 (Fast et al. 2003, 2004, 2007). Similar to other parasitic arthropods, the feeding salmon louse secretes SEP into the wound and this promotes local proteolytic activity which increases the availability of host peptides and amino acids as a source of nutrients for the parasite and reduces the magnitude of the defense-related inflammatory response to the parasite. In the Atlantic salmon, elevation in the expression of proinflammatory- or immune-related genes, such as cyclo-oxygenase-2 interleukin 1ß, tumour necrosis factor α, and major histocompatibility class I and II (Fast et al. 2006a, Skugor et al. 2008, Tadiso et al. 2011), indicates that defense-associated pathways are activated even in this relatively susceptible salmon species. Resistance to *L. salmonis* is therefore not only related to the activation of inflammatory pathways, but to the speed of activation and the ability of this response to elicit a localised and functional cellular infiltrate (Jones et al. 2007, Braden et al. 2012).

Vaccination is a well established disease management strategy against diseases caused by some bacteria or viruses in salmon aquaculture. In contrast, there are few experimental vaccines against parasitic diseases of importance to aquaculture and none that are commercially available (Sommerset et al. 2005). Specific antibodies against *L. salmonis* were detected in caged rainbow trout following a natural infection. In contrast, antibodies from pen-reared Atlantic salmon, exposed to a relatively severe (~ 200 *L. salmonis* per fish) infection, recognised only five *L. salmonis* antigens compared with over 38 parasite antigens recognised by immunised rabbits or fish (Grayson et al. 1991, Reilly and Mulcahy 1993). The relatively poor immune response mounted by salmonids to *L. salmonis* likely results from limited exposure of the salmon immune system to copepod antigens during attachment and feeding (Grayson et al. 1991, Roper et al. 1995). However, salmon immunised with a crude extract of *L. salmonis* were found to be infected with fewer ovigerous parasites and those present carried fewer developing embryos compared with non-immunised controls following a laboratory exposure (Grayson et al. 1995). While earlier evidence did not support the development of protective immunity in salmon as a result of a previous infection with *L. salmonis* or immunization with parasite antigens (Raynard et al. 2002), it is possible that effective vaccination may interfere with parasite reproduction, similar to that seen in the freshwater gourami *Helostoma temmincki* infected with the copepod *Lernea cyprinacea* (Woo and Sharif 1990). The recent sequencing of the *L. salmonis* genome has identified approximately 22,000 genes (Torrissen et al. 2013) and some of these may be shown to encode candidate vaccine antigens. For example, the my32 antigen was recently shown to reduce the number of *C. rogercresseyi* in vaccinated salmon compared with controls (Carpio et al. 2011). As with any vaccine used in aquaculture, the benefit of a salmon louse vaccine will be maximised when coordinated with other disease management husbandry strategies.

CONCLUSIONS AND FUTURE RESEARCH

Sea louse biology is broadly divisible into free-living and parasitic phases. Fluctuations in environmental temperature and salinity regulate developmental and survival in both phases. Free living stages have numerous adaptations that recognise and respond to physical and chemical environmental gradients eliciting behavioural responses by the larval copepod to optimise host finding and settlement.

There is a wide range of susceptibilities to *L. salmonis* among salmonid host species in Canada, and this is particularly apparent among juveniles (post-smolts) of Pacific salmon species. Infections tend to be of reduced duration and of lower intensity on the less susceptible species. In addition, there are significant genetic differences between the varieties of *L. salmonis* that occur on the Pacific and Atlantic coasts of Canada.

The following non-prioritized aspects of sea lice biology are identified in the context of Canadian requirements, as needing further research:

L. SALMONIS

- Determine the longevity of viability of *L. salmonis* egg strings under sub-optimal temperatures (Atlantic and Pacific regions);
- Compare and contrast responses to salinity and temperature gradients of Atlantic and Pacific varieties of *L. salmonis*;
- Compare and contrast virulence (capacity to cause disease) of Atlantic and Pacific varieties of *L. salmonis*;
- Determine whether *L. salmonis* copepodids are differentially attracted to various species of Pacific salmon or other commercially or ecologically important fish inhabiting Canadian coastal waters (Pacific region);
- Determine whether *L. salmonis* that have developed to fourth stage chalimus on sticklebacks, migrate to and continue development on salmonid hosts (Pacific region).

CALIGUS SPP.

- Determine effects of temperature and salinity on development rates, survival and infectivity of species of *Caligus*.
- Determine the reproductive output of *Caligus* species under different environmental and host conditions.
- Determine the relative importance of the copepodid and preadult and adult stages in establishing infections on wild and farmed salmonids.
- Determine why *Caligus* species have broader host ranges than *L. salmonis*.
- Determine whether *Caligus* species produce secretory/excretory products and if so determine the makeup of secretory/excretory products and effects on hosts.

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Table 1. Known hosts for species of sea lice (Copepoda: Caligidae) reported from netpen-reared salmonids in Canada

Lice species	**Host species**	**Common name**	**Ocean**
Lepeophtheirus salmonis (P)[1]	*Salmo salar*	Atlantic salmon	Pacific
	Oncorhynchus gorbuscha	Pink salmon	Pacific
	Oncorhynchus keta	Chum salmon	Pacific
	Oncorhynchus nerka	Sockeye salmon	Pacific
	Oncorhynchus kisutch	Coho salmon	Pacific
	Oncorhynchus tshawytscha	Chinook salmon	Pacific
	Oncorhynchus mykiss	Rainbow trout	Pacific
	Salvelinus malma	Dolly Varden charr	Pacific
	Salmo clarki	Cutthroat trout	Pacific
	Gasterosteus aculeatus	3-spine stickleback	Pacific
Lepeophtheirus salmonis (A)[1]	*Salmo salar*	Atlantic salmon	Atlantic
	Oncorhynchus mykiss	Rainbow trout	Atlantic
	Salvelinus fontinalis	Brook charr	Atlantic
Lepeophtheirus cuneifer	*Salmo salar*	Atlantic salmon	Pacific
	Oncorhynchus mykiss	Rainbow trout	Pacific
	Gasterosteus aculeatus	3-spine stickleback	Pacific
	Clupea harengus pallasi	Pacific herring	Pacific
	Raja binoculata	Big skate	Pacific
	Hexagrammos lagocephalus	Rock greenling	Pacific
Caligus clemensi	*Salmo salar*	Atlantic salmon	Pacific
	Gasterosteus aculeatus	3-spine stickleback	Pacific
	Oncorhynchus gorbuscha	Pink salmon	Pacific
	Oncorhynchus keta	Chum salmon	Pacific
	Oncorhynchus nerka	Sockeye salmon	Pacific
	Oncorhynchus kisutch	Coho salmon	Pacific
	Oncorhynchus tshawytscha	Chinook salmon	Pacific
	Oncorhynchus mykiss	Rainbow trout	Pacific
	Hexagrammos spp.	Greenling species	Pacific
	Sebastes spp.	Rockfish species	Pacific
	Theragra chalcogramma	Alaska pollock	Pacific
	Trichodon trichodon	Pacific sandfish	Pacific
	Hydrolagus colliei	Spotted ratfish	Pacific
Caligus elongatus	*Salmo salar*	Atlantic salmon	Atlantic
	Clupea harengus harengus	Atlantic herring	Atlantic
	Oncorhynchus mykiss	Rainbow trout	Atlantic
	Alosa sapidissima	American shad	Atlantic
	Conger oceanius	Conger eel	Atlantic
	Cyclopterus lumpus	Lumpfish	Atlantic
	Gadus morhua	Atlantic cod	Atlantic
	Melanogrammus aegelfinus	Haddock	Atlantic
	Merlucius bilinearis	Silver hake	Atlantic
	Microgadus tomcod	Tomcod	Atlantic
	Pollachius virens	Pollock	Atlantic
	Urophycis tenuis	White hake	Atlantic
	Hippoglossus hippoglossus	Atlantic halibut	Atlantic
	Macrozoarces americanus	Ocean pout	Atlantic
	Raja laevis	Barndoor skate	Atlantic
	Raja sp.	Skate	Atlantic

Lice species	**Host species**	**Common name**	**Ocean**
Caligus curtus	*Salmo salar*	Atlantic salmon	Atlantic
	Gadus morhua	Atlantic cod	Atlantic
	Melanogrammus aegelfinus	Haddock	Atlantic
	Merlucius bilinearis	Silver hake	Atlantic
	Microgadus tomcod	Tomcod	Atlantic
	Pollachius virens	Pollock	Atlantic

1. *(P) and (A) indicate genetically distinct Pacific and Atlantic Ocean varieties of L. salmonis, respectively*

Table 2. Equations describing relationships between temperature and generation time or developmental rates of various life history stages of Lepeophtheirus salmonis (see text).

Equation Number	Equation
1	$\tau_H = 0.6638t^2 – 12.492t + 67.116$
2	$\tau_G = 345 – 273 \times \log_{10}t$
3	$\tau_H = [ß_1/(t – 10 + ß_1ß_2)]^2$; *where* $ß_1 = 41.98 \pm 2.85$ *and* $ß_2 = 0.338 \pm 0.012$.
4	$\tau_{PI} = [ß_1/(t – 10 + ß_1ß_2)]^2$; where $ß_1 = 24.79 \pm 1.43$ and $ß_2 = 0.525 \pm 0.017$.
5	$\tau = 19.95 - 2.58 \times t + 0.092 \times t^2$
6	$\tau_{CHm} = [ß_1/(t – 10 + ß_1ß_2)]^2$; where $ß_1 = 24.79 \pm 1.43$ and $ß_2 = 0.525 \pm 0.017$
7	$\tau_{CHf} = [ß_1/(t – 10 + ß_1ß_2)]^2$; *where* $ß_1 = 24.79 \pm 1.43$ *and* $ß_2 = 0.525 \pm 0.017$
8	$\tau_{PAm} = [ß_1/(t – 10 + ß_1ß_2)]^2$; *where* $ß_1 = 24.79 \pm 1.43$ *and* $ß_2 = 0.525 \pm 0.017$
9	$\tau_{PAf} = [ß_1/(t – 10 + ß_1ß_2)]^2$; *where* $ß_1 = 24.79 \pm 1.43$ *and* $ß_2 = 0.525 \pm 0.017$

τ_H *is hatch time (days),* τ_G *is generation time (days),* τ_{PI} *time (days) to development of infective copepodid,* τ_{CHm} *and* τ_{CHf} *are times (days) to*

References (by equation) are: 1, Boxaspen and Naess (2000); 2, Tully (1992); 3-4, Stien et al. (2005); 5, Brooks (2005); 6-9, Stien et al. (2005).