The Winter Infection of Sea Lice on Salmon in Farms in a Coastal Inlet in British Columbia and Possible Causes

R. Beamish*, E. Gordon†, J. Wade‡, B. Pennell§, C. Neville†, K. Lange*, R. Sweeting and S. Jones

1Fisheries & Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo BC V9T 6N7
2Fundy Aqua Services, 1619 Venlaw Rd, Nanaimo BC V9S 1J3
3Vancouver Island University, 900 Fifth Street, Nanaimo BC V9R 5S5

Abstract

An increase in infections with two species of sea lice occurred on farmed salmon farthest up an inlet in the Broughton Island area of British Columbia during the winter of 2005/2006. The increase in the chalimus stage started at the end of November 2005 at a rate of 0.03 lice/day for Lepeophtheirus salmonis and 0.015 lice/day for Caligus clemensi. The increase in the infection started at a time of high salinity and low sea surface temperatures with very few gravid sea lice detected on the farmed fish. The mobile stages increased in early January about one month after the increase in the chalimus stage. Gravid lice increased in abundance about the time the farmed fish were treated with SLICE® in early February. This pattern of an increase in infection in the winter was similar in two nearby farms.

In January of 2008 the three farms in the study area were either treated with SLICE® or the fish were harvested. Despite the reduced capacity of the salmon farms to produce sea lice, the juvenile stages remained abundant on sticklebacks (Gasterosteus aculeatus) around the farms in February and March of 2008. Sticklebacks were heavily infected with sea lice but were not a host of gravid lice. Trawl studies in the vicinity of the farms did not find an abundance of hosts except for sticklebacks. Some of the infection on the sticklebacks could originate from a low level of gravid lice on the farmed fish in the study area. However, we speculated that a major source of the winter infection on the sticklebacks could result from the transport of infectious stages in the deeper water that flows into the area as a consequence of the estuarine circulation. The source of these lice and the lice in the 2005/2006 study could be natural or from untreated fish farms farther down the inlet or both. Continued research is needed to understand the biology and population ecology of both species of sea lice in order to manage their production.

Keywords: Salmon farms; Sea lice; Broughton Island area; Winter infection; Estuarine circulation

Introduction

Salmon farming in British Columbia is an important and controversial industry. It is important because the industry provides direct full time employment to about 2800 people [1] and is valued at $406.1 million (cultured value in Canadian dollars in 2008) [2] which may be compared to a value of $20.3 million for the commercial wild Pacific salmon industry (landed value in Canadian dollars in 2008) [2].

Salmon farming provides employment in coastal communities and it reduces the pressure on Pacific salmon (Oncorhynchus spp.) stocks at a time when a warming climate is complicating the management of wild Pacific salmon stocks [3]. Salmon farming is also part of an aquaculture industry around the world that is supplying an increasing world demand for seafood. It is controversial for scientific reasons and in some cases for ideological reasons. In British Columbia, one major concern is production of sea lice on farmed Atlantic salmon (Salmo salar) and the impact these sea lice may have on the abundance of juvenile Pacific salmon.

Lepeophtheirus salmonis is found on salmonids and recently, on three-spine stickleback (Gasterosteus aculeatus) [7]. Caligus clemensi was first described in 1964 where it was observed to cause “significant damage” to juvenile pink salmon (O. gorbuscha)[8]. C. clemensi is found on a number of coastal fishes and is not specific to salmonids. It has been reported on 13 species of fish including salmonids, but the parasite, apparently, may attach to any species of fish inhabiting coastal waters [8].

In recent years there have been about 26 salmon farms in the Broughton Island area and 14-17 among them may be active [9]. When Atlantic salmon smolts are added to the farms (at an average size of 160 mm) they are free of sea lice, having come from freshwater rearing tanks. Eventually these farmed salmon may become infected with one or both of these species of sea lice. Once the sea lice mature on the farmed salmon, the resulting copepods are potentially available to infect juvenile pink and chum (O. keta) salmon and three-spine stickleback.

*Corresponding authors: R. Beamish, 1Fisheries & Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo BC V9T 6N7, Tel: 250-756-7029; Fax: 250-756-7053; E-mail: Richard.Beamish@dfo-mpo.gc.ca

Received December 24, 2010; Accepted January 26, 2011; Published January 27, 2011

Citation: Beamish R, Gordon E, Wade J, Pennell B, Neville C, et al. (2011) The Winter Infection of Sea Lice on Salmon in Farms in a Coastal Inlet in British Columbia and Possible Causes. J Aquac Res Development 2:107. doi:10.4172/2155-9546.1000107

Copyright: © 2011 Beamish R, et al. This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.
We studied the sea lice infection cycle on three key salmon farms in the Broughton Island area as part of an effort to understand how these farms can be managed to ensure that they are not contributing to the sea lice-associated mortality of juvenile Pacific salmon in a way that substantially reduces the size of a population beyond natural levels of variation. The farms in our study are located at the junction of Knight Inlet and Tribune Channel (Figure 1). There are no salmon farms farther up the inlet. There is, however, a major source of juvenile Pacific salmon about 37 km up the inlet from these farms. The Glendale River and spawning channel (Figure 1) has been the major producer of pink salmon in the area since the mid 1990s, accounting for up to 80-90% of the total adult population returning to all rivers in the Broughton Island area in even numbered years and 40-50% in odd numbered years (Figure 2). A spawning channel is a series of artificial channels that are designed to let large numbers of Pacific salmon spawn in an optimal habitat, resulting in a large increase in the survival of eggs. Escapement is the term used for adult salmon that escape the fishery to spawn in their natal river. Thus, the salmon farms in our study are the first farms that most juvenile pink salmon in the area encounter on their route to the open ocean. Chum salmon also spawn in the Glendale River and other rivers in the area. Chum salmon are abundant but estimates of their abundances are not known as they spawn later in the year than pink salmon and are difficult to count. The Glendale spawning channel is closed after the desired number of pink salmon enters the channel, maintaining the use of the channel for pink salmon.

In 2005, 2006 and 2007 we studied the infection cycle of sea lice on one (Sargeaunt Pass) of the three farms (Figure 1). In the winter of 2007 and 2008 we conducted a study to determine how the farms in this area became infected. During this winter study in 2008, the three farms (Sargeaunt Pass, Humphrey Rock and Doctor Islets) were treated with SLICE® (emamectin benzoate) or had the fish removed so that sea lice production on the farmed salmon in February and March 2008 was greatly reduced. SLICE® treatments reduce approximately 90% of the parasitic stages of sea lice after about three weeks [10-12] when added to the feed for a seven-day period. In this paper we document how the winter infection developed and propose how the farmed fish could become infected.

Methods

Hook and line fish sampling - sargeaunt pass fish farm

Atlantic salmon from net pens at Sargeaunt Pass were caught by hook and line and sampled for sea lice. A total of 5 fish from 4 pens were sampled biweekly from April 2005 to February 2007. All fish were taken off the hook without handling and landed directly into individual plastic totes where they were killed with a blow to the head. All fish were lifted onto a measuring board from the inside of the mouth, reducing the possibility of removing parasites from the specimen. Sea lice enumeration was conducted on both sides of the fish in regions (head, dorsal, ventral and tail) described from [13]. Each individual fish was examined by a trained and experienced person using a 10x magnifying glass, necessary to locate and remove the small copepodid and chalimus stages. If sea lice were found, they were removed from the fish and put into labelled scintillation vials containing 70% ethanol. The tote was then examined for the presence of lice that may have detached from the host. Any loose lice were stored in the same labelled vial. The tote was then thoroughly cleaned. The preserved sea lice were brought back to the laboratory where the species and stage of development was determined by an expert using the criteria described by Kabata [14,15] and Johnson and Albright [16]. Sea lice abundance was calculated and expressed as the number of sea lice per individual fish. A second sample of fish was examined by the staff of the fish farm. Their samples included 20 fish from the same four net pens, but the fish were examined after being anaesthetized using Tricaine-S (MS222, Syndel Labs) and returned to the net pen [5]. Fish were seized within the net pen and individually dip-netted into a solution of Tricaine-S. Each fish was then examined for sea lice by an employee of the fish farm that was trained to detect and identify sea lice. Each fish was examined on all sides in a white, shallow, water-filled tote. Magnification was not used, and copepodids were not recorded. Chalimus stages were recorded, but not separated by species and gravid C. clemensi were included in the category for mobile C. clemensi.

Survey of sea lice on adjacent two fish farms by farm staff

Monitoring of sea lice on Atlantic salmon was conducted at two...
adjacent farms (Doctor Islets and Humphrey Rock) in the Broughton Island area at the junction of Knight Inlet and Tribune Channel (Figure 1) from 2005 to 2007 approximately biweekly. Twenty fish from three pens were caught individually and dip netted into an anaesthetic bath of Tricaine-S. Loose sea lice in the totes were identified and added to the total count of sea lice per sampled pen. Upon recovery, the fish were returned to their original net pens. The protocol used by the industry to monitor sea lice was similar to the well-established procedures used in Ireland and Norway of 20 to 30 fish from two to four cages [17,18]. An independent audit of the procedures found no significant differences between the farm estimates and the audit estimates in 28 of 32 comparisons in 2004 and 2005 [5].

**Salinity, temperature and current measurements**

Prior to March 2006, temperature was measured at the Sargeaunt Pass farm using an Oxygenicator Handy MK III meter and salinity measurements were made using a VISTA A365 refractometer. Prior to use, the refractometer was calibrated using freshwater to give a measure of 0. Measurements of salinity and temperature were made at depths of 0-1, 5 and 10 meters off the side of the fish farm float house. After March 2006, the salinity and temperature measurements were made using a digital YSI salinometer. A calibration check for the dissolved oxygen was done once a week using a HACH Kit. Salinity measurements were made at 0.5 m increments ranging from 0 to 14.5 meters. Current meters [19] were installed near the junction of Tribune Channel and Knight Inlet in the winter of 2007/2008.

**Trawl surveys**

Three trawl surveys using chartered commercial fishing vessels

### Table 1A: Sampling dates, number of fish sampled and the observed abundances and stages of sea lice (*L. salmonis* and *C. clemensi*) at the Sargeaunt Pass farm.

| Date       | Number of Fish Sampled | *L. salmonis* abundance by stages | *C. clemensi* abundance by stages |
|------------|-------------------------|-----------------------------------|-----------------------------------|
|            |                         | Cope-podid | Chalimus | Pre-adult | Adult* | Gravid | Chalimus | Pre-adult | Adult* | Gravid |
| April 14/05| 17                      | 0          | 0        | 0        | 0      | 0      | 0        | 0        | 0      | 0      |
| May 5/05   | 20                      | 0          | 0        | 0.20     | 0      | 0.15   | 0        | 0.15     | 0      | 0.10   |
| May 19/05  | 20                      | 0          | 0        | 0        | 0.05   | 0      | 0.15     | 0        | 0.10   | 0      |
| June 2/05  | 20                      | 0          | 0        | 0        | 0.05   | 0      | 0.15     | 0.05     | 0.25   | 0.05   |
| June 16/05 | 20                      | 0          | 0.05     | 0.05     | 0.05   | 0      | 0.40     | 0        | 0.20   | 0      |
| June 28/05 | 20                      | 0          | 0        | 0.05     | 0.05   | 0      | 0        | 0        | 0      | 0      |
| July 14/05 | 20                      | 0          | 0.05     | 0.05     | 0.05   | 0      | 0        | 0        | 0      | 0      |
| July 26/05 | 40                      | 0          | 0        | 0.03     | 0.03   | 0      | 0.03     | 0        | 0      | 0      |
| Aug 11/05  | 20                      | 0          | 0        | 0.05     | 0.05   | 0      | 0        | 0        | 0      | 0      |
| Aug 25/05  | 20                      | 0          | 0        | 0.05     | 0.05   | 0      | 0        | 0        | 0      | 0      |
| Sept 8/05  | 20                      | 0          | 0        | 0.05     | 0.05   | 0      | 0        | 0        | 0      | 0      |
| Sept 22/05 | 20                      | 0          | 0        | 0.05     | 0      | 0      | 0        | 0        | 0      | 0      |
| Oct 6/05   | 40                      | 0.03       | 0.08     | 0.05     | 0      | 0.05   | 0        | 0.10     | 0      |
| Oct 18/05  | 20                      | 0          | 0.10     | 0.10     | 0      | 0      | 0        | 0        | 0      | 0      |
| Nov 3/05   | 20                      | 0.05       | 0.10     | 0.30     | 0      | 0      | 0        | 0        | 0      | 0      |
| Nov 17/05  | 20                      | 0.05       | 0.10     | 0.40     | 0      | 0      | 0        | 0.05     | 0      |
| Nov 30/05  | 20                      | 0.05       | 0.10     | 0.25     | 0.05   | 0.05   | 0.10     | 0        |
| Dec 15/05  | 17                      | 0.12       | 0.10     | 0.10     | 0.50   | 0.06   | 0        | 0        | 0      |
| Jan 5/06   | 20                      | 0.80       | 0.05     | 0.55     | 0      | 0.20   | 0.15     | 0.20     | 0.15   |
| Jan 11-12/06 | 20                 | 0.10      | 1.55     | 0.45     | 0.55   | 0.15   | 0.25     | 0.20     | 0.50   | 0.25   |
| Jan 31-Feb 2/06 | 50                | 2.04     | 2.90     | 1.60     | 0.02   | 1.28   | 0.44     | 1.00     | 0.10   |
| Feb 9/06   | 20                      | 0.05       | 1.90     | 0.37     | 4.10   | 0.10   | 1.25     | 0.15     | 1.20   | 0.35   |
| March 8/06 | 20                      | 2.80       | 4.25     | 5.80     | 0.65   | 1.20   | 0.15     | 0.40     | 0.80   |
| March 22/06| 20                      | 1.80       | 0.70     | 3.30     | 0.65   | 0.50   | 0        | 0.20     | 0.15   |
| April 20/06| 20                      | 0          | 0.60     | 0.90     | 0.10   | 0.35   | 0        | 0.10     | 0      |
| May 4/06   | 20                      | 0          | 0.25     | 0        | 0      | 0.15   | 0        | 0.15     | 0      |
| May 18/06  | 20                      | 0          | 0        | 0.05     | 0      | 0.15   | 0.05     | 0.10     | 0      |
| June 1/06  | 20                      | 0          | 0        | 0.05     | 0.05   | 0.10   | 0.20     | 0        | 0      | 0.05   |
| June 15/06 | 20                      | 0          | 0        | 0.20     | 0.05   | 0.05   | 0        | 0        | 0      |
| June 29/06 | 20                      | 0.05       | 0.10     | 0.10     | 0.05   | 0      | 0        | 0        | 0      |
| July 13/06 | 15                      | 0          | 0        | 0        | 0      | 0      | 0        | 0        | 0      |
| Aug 14/06  | 20                      | 0          | 0.10     | 0        | 0.30   | 0      | 0        | 0        | 0      |
| Sept 7/06  | 20                      | 0          | 0        | 0.05     | 0.05   | 0      | 0        | 0        | 0      |
| Oct 5/06   | 15                      | 0.07       | 0.07     | 0.13     | 0      | 0.07   | 0        | 0        | 0      |
| Nov 2/06   | 20                      | 0.07       | 0.33     | 0.07     | 0.07   | 0.27   | 0        | 0        | 0      |
| Dec 19/06  | 10                      | 0          | 0        | 0.10     | 0.60   | 0      | 0.10     | 0        | 0      |
| Jan 17/07  | 10                      | 0.30       | 0.40     | 1.00     | 0.60   | 0.20   | 0.10     | 0.70     | 0.10   |
| Feb 13/07  | 10                      | 0          | 0.20     | 0.70     | 1.50   | 0.40   | 0        | 0.50     | 0.10   |

*Adult sea lice counts do not include counts of gravid individuals*
were conducted in the area of the three fish farms (Figure 1) to determine if there were fish in the vicinity of the farms that might be a source of sea lice in the winter. One survey was conducted in November of 2007 and one survey in each of February and March of 2008. The modified trawl net and the fishing and sampling procedures have been described in Beamish et al. [20]. The trawl has an average opening of approximately 14 by 32 m under normal fishing conditions with a cod end mesh of approximately 1.2 cm square mesh. Trawling began at daybreak and continued until after dark. Deep, mid-water and shallow sets were made. Sets were made at night to ensure that fish that may not be present in the daytime were sampled. All sets were 30 minutes in duration at a speed of 5 knots. Deep, mid-water and shallow sets were made. Sets were made at night to ensure that fish that may not be present in the daytime were sampled. All sets were 30 minutes in duration at a speed of 5 knots. Once the net was on board, the contents of the cod end were emptied directly into plastic tubs. Catches were carefully sorted by species and individuals were counted. All fish were handled by the head, to minimize the loss of sea lice. A sub-sample of each species was examined for the presence of sea lice using a dissecting microscope. The overall condition of the fish was noted and the location of the sea louse on the fish was identified using

| Date       | Fish Sampled | L. salmonis & C. clemensi | L. salmonis | C. clemensi |
|------------|--------------|---------------------------|-------------|-------------|
|            |              | Chalimus*                 | Pre-adult   | Adult       | Gravid      | Preadult, adult, gravid |
| May 24/05  | 60           | 0.03                      | 0.03        | 0           | 0           | 0                        |
| June 11/05 | 60           | 0.27                      | 0.07        | 0           | 0           | 0                        |
| Jul 14/05  | 80           | 0                         | 0.03        | 0           | 0           | 0                        |
| Jul 26/05  | 80           | 0.03                      | 0.01        | 0.01        | 0           | 0                        |
| Aug 11/05  | 80           | 0                         | 0.01        | 0           | 0           | 0                        |
| Aug 25/05  | 80           | 0.01                      | 0           | 0           | 0           | 0                        |
| Sept 8/05  | 80           | 0.01                      | 0.03        | 0.03        | 0           | 0                        |
| Sept 22/05 | 80           | 0                         | 0.03        | 0.04        | 0           | 0                        |
| Oct 6/05   | 80           | 0.06                      | 0.05        | 0.03        | 0           | 0                        |
| Oct 18/05  | 80           | 0                         | 0           | 0.03        | 0           | 0                        |
| Nov 5/05   | 80           | 0.04                      | 0.05        | 0.09        | 0           | 0                        |
| Nov 17/05  | 80           | 0.04                      | 0.03        | 0.06        | 0.01        | 0.01                     |
| Nov 30/05  | 80           | 0.04                      | 0.04        | 0.05        | 0.03        | 0.14                     |
| Dec 29/05  | 80           | 0.13                      | 0.06        | 0.13        | 0           | 0                        |
| Jan 11-14/06 | 80          | 1.44                      | 0.10        | 0.26        | 0           | 0.09                     |
| Jan 26/06  | 80           | 2.21                      | 0.69        | 0.30        | 0.11        | 0.45                     |
| Feb 7/06   | 80           | 1.00                      | 1.28        | 1.20        | 0.06        | 0.11                     |
| Feb 24/06  | 80           | 3.09                      | 2.73        | 4.95        | 0.25        | 0.48                     |
| March 3/06 | 80           | 2.20                      | 2.84        | 2.96        | 0.20        | 0.50                     |
| March 10/06| 80           | 1.30                      | 1.14        | 4.55        | 0.55        | 0.83                     |
| March 17/06| 80           | 1.39                      | 1.23        | 2.40        | 0.45        | 0.09                     |
| April 22/06| 80           | 0.03                      | 0.14        | 0.19        | 0.05        | 0.01                     |
| April 28/06| 60           | 0.08                      | 0.08        | 0.07        | 0.02        | 0                        |
| May 5/06   | 80           | 0.11                      | 0.01        | 0.13        | 0.06        | 0                        |
| May 18/06  | 80           | 0                         | 0.04        | 0.09        | 0.03        | 0.01                     |
| June 1/06  | 80           | 0                         | 0.01        | 0.08        | 0           | 0.03                     |
| June 8/06  | 80           | 0                         | 0.01        | 0.05        | 0.03        | 0                        |
| June 15/06 | 80           | 0                         | 0           | 0.01        | 0.01        | 0                        |
| June 29/06 | 80           | 0                         | 0.03        | 0           | 0.10        | 0                        |
| July 13/06 | 80           | 0                         | 0.03        | 0           | 0.05        | 0                        |
| July 27/06 | 80           | 0                         | 0.01        | 0.01        | 0.01        | 0                        |
| Aug 4/06   | 80           | 0                         | 0           | 0.03        | 0.03        | 0                        |
| Aug 26/06  | 80           | 0                         | 0.03        | 0.01        | 0.03        | 0.01                     |
| Sept 21/06 | 60           | 0                         | 0           | 0.02        | 0.05        | 0                        |
| Oct 5/06   | 60           | 0                         | 0.02        | 0.03        | 0.03        | 0                        |
| Nov 2/06   | 60           | 0.02                      | 0.13        | 0.03        | 0.03        | 0.02                     |
| Dec 2/06   | 60           | 0.05                      | 0.13        | 0.35        | 0.10        | 0.15                     |
| Jan 17/07  | 40           | 0.70                      | 0.20        | 0.33        | 0.33        | 0.03                     |
| Feb 12/07  | 40           | 0.68                      | 0.20        | 0.60        | 0.50        | 0.18                     |

*Chalimus stages included L. salmonis and C. clemensi.

Table 1B: The sampling dates, numbers of fish sampled, and observed abundances and stages of sea lice (L. salmonis and C. clemensi) sampled by the staff on the Sargeaunt Pass farm.
the same methodology as previously described for the farmed fish (i.e. head, dorsal, ventral and tail). If catches were small, all individuals in the catch were examined for presence or absence of sea lice. Any sea lice that were found were removed from the fish and put into a vial containing 70% ethanol. Following the completion of the set, each plastic tub was examined for loose sea lice. Any sea lice were preserved in separate vials. Identification of the species and stages were made in the laboratory.

Samples of sticklebacks were frozen for analysis of stomach contents for later laboratory analysis. Once in the laboratory, sticklebacks were thawed and their stomachs were removed and placed in 5% formalin in vials. Stomach contents of individual fish were then identified using a dissection microscope, by an expert trained to identify copepod life stages of individual fish were then identified using a dissection microscope, by an expert trained to identify copepod life stages.

Results

Sargeaunt pass fish farm

We sampled the Sargeaunt Pass fish farm 38 times from April 14, 2005 to February 13, 2007 (Table 1A). There were also 39 sampling dates in which the farm staff sampled for sea lice (Table 1B). Juvenile Atlantic salmon (180mm) were added to all net pens in mid-April, 2005. A major increase in sea lice infection started about 8 months later in December 2005 (Figure 3A-Figure 3C). The general pattern of infection was similar between our observations (Figure 3A) and the farm observations (Figure 3B). The abundance of all stages of *L. salmonis* and *C. clemensi* increased from 0.9/fish in mid December 2005 to 12.0/fish in February 2006. Fish were first treated with SLICE® on February 10, 2006 (Figure 3A-C) and *L. salmonis* abundance declined rapidly to 1.1/fish by mid-April 2006. In 2005, the estimated number of fish in all pens in the Sargeaunt Pass farm ranged from approximately 570,000 to 680,000. Estimates of the number of fish in all pens in 2006 from January to November ranged between 730,000 and 740,000. Fish in the farm were harvested from December 2006 to April 2007 with virtually no fish remaining by June 2007.

In 2005, surface salinity gradually increased from a minimum of 8%o in August to over 30%o in early December (Figure 3C); Note that the scale for salinity and temperature is the same. Salinity remained at this level through to about early May 2006. Sea surface temperature (SST) ranged from approximately 6.1°C in the winter to 12.0°C in the summer. The daily SST averaged 7.1°C (SD=0.52) from November 2006 through to early April 2007 with very little variation (Figure 3C).

Chalimus stages

The species of the chalimus stage of sea lice were identified and recorded in our study but not in the farm staff study, as they combined estimates for both species of sea lice. There were small, irregular infections of the chalimus stage of *L. salmonis* from April 2005 through to the end of November 2005 (Figure 4A). A major increase in the abundance of the chalimus stage of *L. salmonis* started in late November and reached maximum levels from mid-January to early March 2006. There were very few chalimus stages of *L. salmonis* found on the farmed salmon for the rest of the year. There was a small increase in mid-January of 2007.

There was a small initial infection of *C. clemensi* in May and June 2005 shortly after the fish were added to the farm, which did not persist (Figure 4B). A major infection of *C. clemensi* started at the end of November and reached the highest abundances in February. The abundances of chalimus stages of *C. clemensi* declined shortly after the SLICE® treatment in early February and virtually disappeared from about mid-June 2006 to early October 2006 (Figure 4B). There was a small increase in abundance beginning in early November 2007 that persisted into the winter as a small infection.

A linear regression fitted to the increasing abundance estimate late in 2005 and early in 2006 indicated that the beginning of the infection of the chalimus stage of both species started about November 25, 2005 (Figure 5A, Figure 5B). The rate of increase of the infection of the chalimus stage of *L. salmonis* (0.03 lice/day) was about twice as fast as...
for *C. clemensi* (0.015 lice/day). The combined estimate of abundance of the chalimus stage of both species was lower using the farm estimates than our estimates (Figure 5C) and the rate of increase was slower as indicated by the slopes of the regressions. If data from our study and the farm staff data are combined for both species, the estimated time of the increase in the infection of the chalimus stage started about December 5, 2007 and abundance increased at a rate of 0.03 chalimus per day (Figure 5C).

**Abundance of mobile stages**

There were very small infections of the mobile stage of *L. salmonis* from late April 2005 until the end of December 2005 (Figure 6A). Mobile stages increased rapidly in abundance in late December, with the largest abundances occurring at the end of February and early March 2006, immediately after the SLICE® treatment in February. Abundances remained low until January 2007 when they increased to approximately one half of the levels observed in January and February 2006. There were very small abundances of *C. clemensi* immediately after fish were added to the farm in the spring of 2005, but no infections of mobile stages were observed until late in 2005 (Figure 6B). The samples collected by the farm staff recorded the mobile stages of *L. salmonis* separately, but combined mobile and gravid stages for *C. clemensi*. The samples collected by the farm staff for mobile stages of *L. salmonis* showed an increasing abundance trend, similar to the trend in our sample (Figure 6C).

Our data indicated that the infection of mobile stages of *L. salmonis* began to increase about December 22, 2005 at a rate of 0.09 mobile sea lice per day (Figure 7A). The abundance estimates of the mobile stages of *L. salmonis* from the farm staff data were lower than our observation up to early February 2006, resulting in a slightly later date of January 7, 2006 for the beginning of the infection (Figure 7B). A combination of both data series identified December 27, 2005 as the date of the increasing abundance of the mobile stage of *L. salmonis* (Figure 7B). Because the counts of mobile *C. clemensi* in the farm staff data included gravid *C. clemensi*, we used only the data in our sample to estimate the date when the infection started to increase. The increase in the abundance of the mobile stage of *C. clemensi* occurred about December 14, approximately 8 days earlier than *L. salmonis* (Figure 7C). The rate of increase was 0.02 mobile sea lice per day.

**Gravid stages**

There were no gravid *L. salmonis* in our samples until the end.
of November 2005 (Figure 8A). On November 30 we recorded an abundance of gravid *L. salmonis* of 0.05 and it was not until January 11, 2006 that we again detected gravid *L. salmonis* (an abundance of 0.15). We did not detect gravid *C. clemensi* until January 5, 2006 at an abundance of 0.15 (Figure 8B). The farm sampling recorded gravid *L. salmonis* on November 17 at an abundance of 0.01 (Figure 8C). The abundance was 0.03 on November 30, but no gravid lice were detected in the farm sample on December 29 or the January 11-14 samples (Figure 8C). The largest abundances actually occurred after the SLICE® treatment. Small numbers of gravid *L. salmonis* occurred throughout 2006 with a large increase in mid-January 2007 (Figure 8C). In general, the abundance estimates of gravid *L. salmonis* from the farm staff data were similar to our estimates (Figure 8C). Gravid *C. clemensi* were rare after March 2006 and none were found in 2006 after mid-May (Figure 8B). There was a small number found in mid-January 2007. A linear regression fit to our samples indicated that the increase in gravid sea lice of both species started about late November and that the rate of increase was about four times faster for *L. salmonis* than for *C. clemensi* (Figure 9).

### Sea lice abundance on the Humphrey Rock and Doctor Islets fish farms

All net pens in the Humphrey Rock fish farm were stocked in April 2003 and in March 2004. The abundance of all stage of both species of sea lice on fish at the Humphrey Rock fish farm (Figure 10A) increased...
in each of the winters of 2003/2004, 2004/2005, and 2005/2006. In 2004, the fish were not treated with SLICE® until mid-May after the abundance of all stages of both species reached 23.0 lice/fish. Treatments of SLICE® in the other years were in early February and abundances declined after the treatment through to the next winter. There was an infection in the spring of 2004, immediately after the juvenile salmon were added to the net pens. Following this infection, there were two subsequent infections in the winters of 2004/2005 and 2005/2006. Fish were harvested in May 2005 and new fish added in September 2005. There were approximately 590,000 fish prior to harvesting and 710,000 fish in the pens in 2005. The abundances of gravid L. salmonis in October, November and December 2005 were 0.27, 0.43 and 0.37, respectively.

Following the introduction of Atlantic salmon smolts at the Doctor Islets fish farm in April 2004, there was an increase in infections in the winter of 2004/2005 and late in the year in 2005 (Figure 10B). Fish were harvested in December 2005 and January 2006. Juvenile fish were added to the net pens in the summer of 2006, with a sea lice infection starting to increase on these fish in the fall (Figure 10B). The number of fish ranged between approximately 550,000 and 580,000 during the study period in 2005. There were no gravid L. salmonis recorded in farmed fish in April and May 2005. The abundances of gravid L. salmonis in June, July, August, September, October and November 2005 were 0.07, 0.12, 0.42, 0.08, 0.45 and 0.88, respectively.

Fish farm treatments in the winter of 2008

The three farms in the study area were managed in early 2008 to reduce sea lice levels on all the farmed fish. Sargeant Pass and Humphrey Rock were treated with SLICE® on January 8, 2008. There were approximately 655,000 and 680,000 fish on the Sargeant Pass and Humphrey Rock farms, respectively from January to the end of March 2008. Sargeant Pass and Humphrey Rock farms, respectively from January to the end of March 2008 were treated with SLICE® on January 8, 2008. There to reduce sea lice levels on all the farmed fish. Sargeant Pass and

salmon farms (Figure 1). There were approximately 3,850 sticklebacks captured and 175 were examined for sea lice. There were 81 sticklebacks with sea lice, with an incidence of 1.1, a prevalence of 46.3% and an abundance of 0.6. Most (77.7%) were the chalimus stage of C. clemensi. There were a small number (14.6%) of pre-adult and adult stages of C. clemensi and a small number (7.8%) of pre-adult and adult L. salmonis (Table 2).

On February 27-29, 2008, 29 sets were made that captured 2972 fish (Table 2) of which 1,377 sticklebacks were captured and 176 were examined for sea lice. There were 125 sticklebacks that were infected with a total of 232 sea lice of all stages of both species. This represented a prevalence of 71.0%, an incidence of 1.9 and an abundance of 1.3 for the combined species and stages of sea lice. There were 83 L. salmonis and 149 C. clemensi. Most C. clemensi (N=146) were in the chalimus stage, however, there were 3 adults observed. All of the L. salmonis (N=83) were in the chalimus stage (Table 2).

In March 25-27, 2008, there were 29 sets that captured 3,457 fish. Included in the catch were 2,464 sticklebacks of which 412 were examined for sea lice. There were 248 that were infected with sea lice. The prevalence, intensity and abundance of all stages of both species of sea lice were 60.2%, 2.1 and 1.3. There were 115 L. salmonis and 416 C. clemensi. Most (94.8%) of the L. salmonis were in the chalimus stage; however, there were 6 mobile stages including one adult. The stages of C. clemensi were also mostly chalimus (95%) with 12 copepodid stages and 9 mobile stages including 8 adults (Table 2).

Stomach analysis

The contents of the stomachs of 30 sticklebacks were examined from the November 2007 catch and 74 in March 2008. Most of the stomach contents were copepods (Figure 11). There were relatively small numbers of amphipods, decapods (March sample only) and euphausiids. About one quarter of the contents was too digested to identify. There were no sea lice nauplii in any of the stomachs.

Other species in the trawl survey

Catches of all species of fishes in the February and March 2008 trawl surveys are listed in (Table 3). Stickleback were the most numerous fish in the catch in both surveys. No Pacific salmon were captured in the February or March surveys or in the single set on November 9, 2007.
Knight inlet currents

The east-west current in Knight Inlet was measured near the fish farms at 5.5 m, 34.5 m, 60 m and 95 m from September 2007 until March 2008. For most of the study, the flow at 5.5 m was out of the inlet (Figure 12). At 34.5 m, beginning in early November most of the flow is into the inlet at about <20 cm/s. At 60 m and 95 m, the currents are weak (<10 cm/s) but mostly flowing into the inlet (Figure 12).

Discussion

The rapid increase in the infection of sea lice in our study began in the winter. The pattern of infection was similar in our sample and in the samples taken by the farm staff. The pattern of infection was also similar among all three farms in the study area. This indicated that the timing of infection started in late November with an increase in the chalimus stage of both species at a surface salinity of about 30%. The increase in the rate of infection of mobile stages was difficult to identify but appeared to start in January even though the regression indicated an earlier date of increase. The regression fit was difficult to identify but appeared to start in January even though the timing of the increase in gravid lice data probably did not represent the dynamics of the infection because of the small sample. Inspection of the data indicated that it is likely that the infection of gravid lice occurred about four to five weeks after the increase in the mobile stages. The largest numbers of gravid lice occurred at the time of the SLICE™ treatment which quickly resulted in substantially lower abundances of sea lice on the farmed salmon. A similar pattern of increase in the abundance of all stages of both species of sea lice was reported by Brooks [21] for the Sargeant Pass and Humphrey Rock salmon farms in the late fall of 2003. Brooks [21] reported that the typical generation time of _L. salmonis_ in the study area was 106 days at a typical spring temperature (Figure 3) and 32 days at a typical summer temperature (Figure 3). He also cited the studies of Pike and Wadsworth [13] to show that the reduced surface salinities that are typical in the study area in the spring and summer (Figure 3) would reduce the development of the copepodid stage of _L. salmonis_. Saksida et al. [5] interpreted the decrease in the levels of lice on farmed fish in the summer to indicate that a re-infection of lice from within the farm was unlikely because of the duration of generation times at

Knight Inlet on a trawl survey.

Figure 11: The stomach contents of 30 stickleback captured on 9 Nov 2007 in Knight Inlet on a trawl survey.

Figure 12: Vertical profile of the observed Knight Inlet average flow (relative to surface) from September 2007 to March 2008.

Table 3: Catch of all species of fish captured in the February 27-29, 2008 and March 25-27, 2008 surveys in Broughton Island area.
the summer temperatures. There were low abundances of gravid lice observed in some samples from the three farms in the study area, indicating that it is possible that some of the lice contributing to the increase in the infection in the winter of 2005-2006 originated from farmed fish. However, because gravid sea lice were rarely found on the farmed salmon prior to the increase in the rate of infection of the chalimus stage, and there were very few gravid lice on the Sargeant Pass farm, we suggest that the major source of the infection at the study site in the winter of 2005-2006 was from outside of the farm area.

An increase in the abundance of mobile *L. salmonis* occurs in the winter on farmed salmon in some areas in the eastern North Atlantic [22-24]. This may indicate that in addition to a source of infection in the winter, the ocean conditions are also important. The rapid increase in the infection in the winter, therefore, appears to be a combination of a consistent supply of infectious copepodids, cooler temperatures and suitable ocean conditions.

The trawl survey in the winter of 2007 and 2008 did not catch any Pacific salmon. It is most likely that there were very few Pacific salmon in the sample area at the time of the trawl survey in February and March of 2008 as the net and the fishing method readily catch all sizes of Pacific salmon in other areas [20]. Low abundances of juvenile Pacific salmon in this area at this time would be expected because only chinook and coho salmon would be in this area at this time and their abundances in this area have been very low in recent years. Catches of species such as Pacific herring (*Clupea harengus pallasi*) known to host *C. clemensi* [6] were also small. The trawl survey in the winter of 2007 and 2008 did capture relatively large numbers of sticklebacks that were heavily infected with the juvenile stages of both species of sea lice. In March, 2008, the combined prevalence of 60.2% occurred at a time when there were no gravid sea lice in the samples from the salmon in the farms in the area. These farms had been treated with SLICE® in January 2008 which would greatly reduce the production of viable sea lice after approximately three weeks post treatment [10-12]. It is possible that even low levels of gravid lice on the farms contributed to the lice levels observed on the sticklebacks, but it is also likely that the infection on the sticklebacks in 2008 came from a source that was not in the immediate vicinity of these three farms.

We hypothesize that the diurnal vertical migratory behaviour displayed by the *L. salmonis* copepodid [25] provides an opportunity for the larvae to be transported by the deeper estuarine flow moving up the inlet. Brooks [21] and Brooks and Stucchi [26] noted that the strong surface currents in the study area could carry sea nauplii away from the farm sites, particularly in the spring and summer. However, as identified in the studies of Costello [27,28] and Gillibrand and Willis [29], deeper, counter currents can transport nauplii farther into an inlet. Also, the presence of a silt within an inlet can bring the deeper currents to the surface [30,31]. The circulation patterns in Knight Inlet have been extensively studied and modelled [32-34]. The estuarine circulation in response to the flows from the Klinaklini River at the head of the inlet and from other rivers draining into the inlet (Figure 1) results in surface flows down the inlet with deeper compensating flows up the inlet. The deeper flows appear to transport water up Fife Sound and Tribune Channel rather than from the mouth of Knight Inlet [34]. The current monitoring in the winter of 2007/2008 confirmed the observations of these previous studies that the general circulation in the winter in this area is estuarine, resulting in surface water flowing out of the inlet past the farms and the deeper water flowing into the inlet. As the deeper water flows past the study area and up Knight Inlet, it encounters a sill at Hoeya Head (Figure 1) that is 63 m below the surface. Studies have shown [30,31,34] that the sill could cause the deeper water to come close to the surface where it would be transported back down the inlet and past the three salmon farms in this study.

Thus, we speculate that a possible source of the chalimus stages that infects both the salmon in the farms in the winter and the resident sticklebacks could come from sources seaward of the study area. The hosts of the sea lice that produce these juvenile stages of sea lice could be wild or untreated farmed salmon farther down the inlet or other sources. It is possible that some of the *C. clemensi* originated from Pacific herring as Pacific herring are known to transport large abundances of sea lice into coastal areas when they spawn [6]. Winter is the expected time that Pacific herring migrate from offshore areas into coastal areas to spawn [35] and herring are known to spawn in the Fife Sound – Kingcome Inlet area [36]. Another possible source of the infection on the farmed fish might be the chum salmon that spawn in the Glendale River from mid October until early November. The timing of the spawning migration of chum salmon out of the ocean and into the Glendale River is not clear, but it is possible that few chum salmon remain in the ocean past mid November. Temperatures in the inlet at this time are about 7°C which indicates that the combined nauplii and copepodid stages could survive for about two weeks [21,37]. Because the increase in the chalimus stages started in late November 2006 and continued to increase through to mid January 2007, the infections in December and later in the winter would not be from the returning chum salmon.

A difficulty with the speculation of a seaward source of the sea lice that infect the farms in the study area is that we have been able to find only very small numbers of nauplii or copepodid stages of either species in our plankton samples collected in the winter in vertical hauls in and around the net pens and along the shore line (R.J. Beamish, unpublished data). However, the sticklebacks in the study area continually become infected with both species. Although stickleback appear to be an excellent host for the juvenile stages of sea lice of *L. salmonis* and *C. clemensi* [7], adult sea lice were rarely found on stickleback. This indicates that stickleback are an index of a fresh infection, but are not a major host for gravid sea lice and a source of planktonic copepodids which appear responsible for most of the infections on the farmed salmon reported here. We do not have estimates of abundances of sticklebacks, but their abundances in the study area, as estimated from the ship's echo-sounder, could be in the hundreds of thousands or even millions of fish. It is possible that stickleback become infected when they search for and feed on copepod nauplii as indicated by the diet of the fish we examined. Despite our inability to identify how they became infected, it appears that sticklebacks are an effective indicator of the abundances and distribution of juvenile stages of sea lice. Thus, studies of the feeding behaviour of sticklebacks may be an excellent method of studying the population ecology of lice nauplii. If a substantial number of lice originate from farms seaward of the study area, then the treatment of these seaward farms could minimize the winter infection in the study area. Research needs to continue to identify the sources of lice in the winter as part of any strategy to manage sea lice production on the farmed salmon and to protect juvenile Pacific salmon during their migration offshore.

**Acknowledgements**

We greatly appreciate the help provided by the many people who assisted in this field study. In particular, we thank Brad Boyce, Chris Bobb, Mark Brow and Eric Stoughton for their support and friendship. Tom McDonald identified the sea lice and Carol Cooper identified the contents of fish stomachs. Dario Stucchi and Mike Foreman provided current data as well as information on the ocean circulation patterns in the study area. Dario Stucchi provided Figure 12. Lana Fitzpatrick helped prepare the figures and manuscript. Funding was partially provided by the Pacific Salmon Forum. We appreciate the complete cooperation of the companies involved in the fish farming industry in the study area.
References

1. Ministry of Environment, Oceans and Marine Fisheries Branch (2010) British Columbia Seafood Industry Year in Review 2008.
2. Price Waterhouse Coopers (2009) Profile of the BC Farmed Salmon Industry in 2008. Report submitted to the British Columbia Salmon Farmers Association (BCSFA).
3. Beamish RJ, King JR, McFarlane GA (2006) Canada. P. 15-56 in R.J. Beamish (ed.) Impacts of climate and climate change on the key species in the fisheries in the North Pacific. PICES Sci Rep No 35. PICES Working Group on Climate Change, Shifts in Fish Populations, and Fisheries Management. N Pac Mar Sci Org (PICES), Secretariat, Sidney BC.
4. Beamish R, Jones S, Neville C, Sweeting R, Karremann G, et al. (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.
5. Saksida S, Constantine J, Karremann GA, McDonald A (2007) Evaluation of sea lice abundance levels on farmed Atlantic salmon (Salmo salar L.) located in the Broughton Archipelago of British Columbia from 2003 to 2005. Aquacult Res 38:219-231.
6. Beamish RJ, Wade J,Pennell W, Gordon E, Jones SRM, et al. (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.
7. Jones SRM, Prosperi-Porta G, Kim E, Calow P, Hargreaves NB (2006) 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.
8. Parker RR, Margolis L (1964) A new species of parasitic copepod, Caligus clemensi sp. Nov. (Caligoida: Caligidae), from pelagic fishes in the coastal waters of British Columbia. J Fish Res Bd Can 21: 873-889.
9. Marty GD, Saksida SM, Quinn II TJ (2010) Relationship of farm salmon, sea lice, and wild salmon populations. Supporting information. Proceedings of the National Academy of Science of the United States of America (PNAS) Early Edition.
10. Ramstad A, Colquhoun DJ, Nordro M, Sutherland IH, Simmons R (2002) Field trials in Norway with SLICE© (0.2% emamectin benzoate) for the oral treatment of sea lice infestation in farmed Atlantic salmon Salmo salar. Dis Aquat Org 44: 233-330.
11. Stone J, Sutherland IH, Sommerville C, Richards RH, Varma KJ (2000) Commercial trials using emamectin benzoate to control sea lice Lepeophtheirus salmonis infestations in Atlantic salmon Salmo salar. Dis Aquat Organ 41: 141-149.
12. Treasurer JW, Wallace C, Dear G (2002) Control of sea lice on farmed Atlantic salmon S. salar L., with oral treatment Emaemetic benzoate (SLICE). Bull Eur Aqu Fish Pathol 22: 375-380.
13. Pike AW, Wadsworth SL (1999) Sea lice on salmonids: Their biology and control. Adv Parasitol 44: 233-330.
14. Kabata Z (1972) Developmental stages of Caligus clemensi (Copepoda: Caligidae). J Fish Res Board Canada 29: 1571-1593.
15. Kabata Z (1973) The species of Lepeophtheirus (Copepoda: Caligidae) from fishes of British Columbia. J Fish Res Board Canada 30: 729-759.
16. Johnson SC, Albright LJ (1991) The developmental stages of Lepeophtheirus salmonis (Kroyer, 1837) (Copepoda: Caligidae). Can J Zool 69: 929-950.
17. O'Donohoe P, Kennedy S, Copley L, Kane F, Naughton O, et al. (2003) National survey of sea lice (Lepeophtheirus salmonis Kroyer and Caligus elongatus Nordmann) on fish farms in Ireland – 2002. Report of Aquaculture and Catchment Management Services, Marine Institute, Galway Technology Park, Parkmore, Galway.
18. Revie CW, Gettinby G, Treasurer JW, Wallace C (2005) Evaluating the effect of clustering when monitoring the abundance of sea lice populations on farmed Atlantic salmon. J Fish Biol 66: 773-783.
19. Stuchli DJ, Guo M, Foreman MGG, Czajko P, Galbraith M, et al. (2010) Modelling sea lice production and concentrations in the Broughton Archipelago, British Columbia. In S.R.M. Jones and R.J. Beamish (eds.) Salmon Lice: An integrated approach to understanding parasite abundance and distribution.
20. Beamish RJ, McCaughrain D, King JR, Sweeting RM, McFarlane GA (2000) Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. North Am J Fish Manage 20: 369-375.
21. Brooks KM (2005) The effects of water temperature, salinity, and currents on the survival and distribution of the infective copepodid stage of sea lice (Lepeophtheirus salmonis) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada. Rev Fish Sci 13: 177-204.
22. Tully O (1989) The succession of generations and growth of the caligid copepods Caligus elongatus and Lepeophtheirus salmonis parasitizing farmed Atlantic salmon snomls (Salmo salar L.). J Mar Biol Assoc UK 69: 279-287.
23. Baillie M, Lees F, Gettinby G, Revie CW (2009) The use of prevalence as a measure of lice burden: a case study of Lepeophtheirus salmonis on Scottish Atlantic salmon, Salmo salar L., farms. J Fish Dis 32: 15-25.
24. Lees F, Gettinby G, Revie CW (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.
25. Heuch PA, Parsons A, Boxaspen K (1995) Die vertical migration: a possible host-finding mechanism in salmon louse (Lepeophtheirus salmonis) copepods? Can J Fish Aquat Sci 52: 681-689.
26. Brooks KM, Stuchli DJ (2006) The effects of water temperature, salinity and currents on the survival and distribution of the infective copepodid stage of the salmon louse (Lepeophtheirus salmonis) originating on Atlantic salmon farms in the Broughton Archipelago of British Columbia, Canada (Brooks, 2005) – A response to the rebuttal of Krkocek et al. (2005). Rev Fish Sci 14: 13-23.
27. Costello MJ (2009) How sea lice from salmon farms may cause wild salmonid declines in Europe and North America and be a threat to fishes elsewhere. Proc Biol Sci 276: 3383-3394.
28. Costello MJ (2006) Ecology of sea lice parasitic on farmed and wild fish. Trends Parasitol 22: 475-583.
29. Gillibrand PA, Willis KJ (2007) Dispersal of sea louse larvae from salmon farms: modelling the influence of environmental conditions and larval behaviour. Aquat Biol 1: 63-75.
30. Gillibrand PA, Amundrud TL (2007) A numerical study of the tidal circulation and buoyancy effects in a Scottish fjord: Loch Tomlon. J Geophys Res 112: C05030.
31. Farmer D, Arni L (1999) The generation and trapping of solitary waves over topography. Science 283: 188-190.
32. Freeland HJ, Farmer D (1980) Circulation and energetics of a deep, strongly stratified inlet, Can J Fish Aquat Sci 37: 1398-1410.
33. Thomson RE, Huggett WS (1980) M. baroclinic tides in Johnstone Strait, British Columbia. J Phys Oceanogr 10: 1599-1539.
34. Foreman MGG, Stuchli DJ, Zhang Y, Baptista AM (2006) Estuarine and tidal currents in the Broughton Archipelago. Atmosph-Ocean 44: 47-63.
35. Hrountson AS, Haegle CW (1980) Herring on Canada's Pacific Coast. Can Spec Pub Fish Aquat Sci 48: 23.
36. Hay DE, McCarter PB (2008) Herring spawning areas of British Columbia: a review, geographic analysis and classification. Revised edition of Can MS Rep Fish Aquat Sci 2019.
37. Tucker CS, Sommerville C, Wooten R (2000) An investigation into the larval energetics and settlement of the sea louse, Lepeophtheirus salmonis, an ectoparasitic copepod of Atlantic salmon, Salmo salar. Fish Path 35: 137-140.