Sea lice, *Lepeophtheirus salmonis*, transfer between wild sympatric adult and juvenile salmon on the north coast of British Columbia, Canada

A S Gottesfeld[1], B Proctor[2], L D Rolston[2] and C Carr-Harris[1]

1 Skeena Fisheries Commission, Hazelton, BC, Canada
2 Oona River Resources Association, Prince Rupert, BC, Canada

Abstract

We examine sea lice, *Lepeophtheirus salmonis*, on juvenile and adult salmon from the north coast of British Columbia between 2004 and 2006 in an area that does not at present contain salmon farms. There is a pronounced zonation in the abundance of *L. salmonis* on juvenile pink salmon, *Oncorhynchus gorbuscha*, in the Skeena and Nass estuaries. Abundances in the proximal and distal zones of these estuaries are 0.01 and 0.05 respectively. The outer zones serve as feeding and staging areas for the pink salmon smolts. Returning Chinook, *Oncorhynchus tshawytscha*, and coho salmon, *Oncorhynchus kisutch*, concentrate in these areas. We collected data in 2006 to examine whether *L. salmonis* on returning adult salmon are an important source of the sea lice that appear on juvenile pink salmon. Nearly all (99%) of the sea lice on returning Chinook and over 80% on coho salmon were *L. salmonis*. Most of the *L. salmonis* were motile stages including many ovigerous females. There was a sharp increase in the abundance of sea lice on juvenile pink salmon smolts between May and July 2006 near the sites of adult captures. As there are no salmon farms on the north coast, few sticklebacks, *Gasterosteus aculeatus*, and very few resident salmonids until later in the summer, it seems that the most important reservoir of *L. salmonis* under natural conditions is returning adult salmon. This natural source of sea lice results in levels of abundance that are one or two orders of magnitude lower than those observed on juvenile pink salmon in areas with salmon farms such as the Broughton Archipelago.

Keywords: Chinook salmon, *Lepeophtheirus salmonis*, pink salmon, sea lice, sea lice epizootiology, wild salmon.

Correspondence *A S Gottesfeld, Skeena Fisheries Commission, PO Box 166, 1525A Hankin Street, Hazelton, BC V0J 1Y0, Canada*
(e-mail: gottesfeld@skeenafisheries.ca)

Introduction

There are two species of caligid sea lice, *Lepeophtheirus salmonis* (Krøyer), and *Caligus clemensi* Parker and Margolis, which are common on salmonids in the coastal zone of British Columbia (Kent 1992). *Caligus clemensi* is a generalist species found on many teleosts and is especially common in inshore areas of the north coast on the ubiquitous herring, *Clupea harengus pallasi* (Valenciennes). *Lepeophtheirus salmonis* is mostly restricted to salmonid fish, of which the vast majority in this area belong to the six North American species of Pacific salmon, *Oncorhynchus* spp. *L. salmonis* also occurs on three-spined sticklebacks, *Gasterosteus aculeatu,* L., common in other parts of the British Columbia coast (Jones, Prosperi-Porta, Kim & Hargreaves 2006) but uncommon on the north coast.

While *C. clemensi* is the most common caligid on the north coast, *L. salmonis* is of special interest because it is the species that is most abundant in salmon farms of southern and central British Columbia. *Lepeophtheirus salmonis* has been implicated in the morbidity and death of wild juvenile pink, *O. gorbuscha* (Walbaum), and chum salmon, *O. keta* (Walbaum), (Krkošek, Lewis, Morton, Frazer & Volpe 2006; Morton & Routledge

2006; Krkošek, Gottesfeld, Proctor, Rolston, Carr-Harris & Lewis 2007) in the Broughton Archipelago near the north end of Vancouver Island, as well as of wild Atlantic salmon, *Salmo salar* L., and sea trout, *Salmo trutta* L., of the North Atlantic Ocean (Tully, Poole, Whelan & Merigoux 1993; Tully & Whelan 1993; Bjorn, Finstad & Kristoffersen 2001; Bjorn & Finstad 2002; Gargan, Tully & Poole 2003). Although salmon farms have been proposed for the north coast, none were established at the time of writing. This area thus provides an opportunity to examine the autecology of *L. salmonis* under natural conditions and to establish baseline conditions prior to the introduction of salmon farms.

The life history of *L. salmonis* is fairly well known. After hatching from the egg strings of ovigerous females, sea lice progress through two planktonic nauplius stages before developing into copepodids which attach to a host. After successful attachment, *L. salmonis* development proceeds through four chalimus and two preadult stages before reaching sexual maturity (Kent 1992). Transmission from infested fish is direct and achieved by attachment of the copepodids (Johnson & Albright 1991b; Tully & Whelan 1993). Direct passage of individual adult sea lice from infected to naive fish is also a possibility, one that has been demonstrated in the laboratory (Ritchie 1997; Hull, Pike, Mordue (Luntz) & Rae 1998).

On the north coast of British Columbia, pink salmon are produced principally in the lower reaches of the Skeena and Nass Rivers and their major tributaries. The Skeena River accounts for 60 to 70% of the north coast production of pink salmon. Most of the remainder come from the Nass River. The two rivers have a common estuary in Chatham Sound although much of the Skeena flood flows are directed southward through Ogden Channel (Fig. 1).

Pink salmon arrive on the coast lice-free and remain in the littoral zone for two to three months. Sea lice levels increase in prevalence and intensity during this interval (Gottesfeld, Ryan, Rolston & Proctor 2005; Krkošek *et al.* 2007). During our baseline studies in 2004 and 2005, we found that *L. salmonis* infection is largely a phenomenon of the outer estuary. This zone is utilized by returning adult salmon from May to October. In 2006, we researched the possibility of louse transfer between adult returning salmon and juvenile pink salmon occupying closely adjacent habitat.

Materials and methods

Study area

Our collections in 2006 encompassed the islands along the west margin of Chatham Sound, from the north side of Dundas Island to Qlawdzeet Anchorage on the north end of Stephens Island (Fig. 2). These islands on the outer north coast divide the coastal waters of Chatham Sound from the open waters of Dixon Entrance in the west. This is historically an important location for commercial net and troll fleets, and is still heavily exploited by the recreational fishing fleet for Chinook, *Oncorhynchus tshawytscha* (Walbaum), and coho salmon, *Oncorhynchus kisutch* (Walbaum), during the summer months. We observed high concentrations of juvenile pink salmon in the western portion of Chatham Sound during sampling in 2004 and 2005.

Sampling and analysis

Collections of juvenile pink salmon were made in 2004 and 2005 throughout the Skeena and Nass estuaries between the months of April and July. Collections were made using dip nets early in the season, during April and May when pink salmon were easily captured in shallow water. Dip netting occurred as close to shore as possible. The dip net was 5 mm knotless mesh, 45 cm in diameter, and attached to a 2.45 m pole.

Different sampling techniques were necessary later in the season because by June, the concentrations of juvenile pink salmon had moved to the deeper waters outside the kelp zone (> 10 m depth) where they were inaccessible by beach sampling methods. We used a surface trawl net that was modified from the OFL Atlantic salmon smolt net design of Holst & McDonald (2000). The trawl net was 18 m long with an opening 5 m wide and 4.6 m deep. The fish were collected into a rigid holding box at the cod end designed for live capture and to minimize the loss of scales and ectoparasites. Dip net and trawl samples were transferred into 5-gallon buckets and sorted by species. Juvenile salmonids were individually bagged and frozen for further analysis in the laboratory. Temperature and salinity data were recorded at each trawl and dip net site using an YSI-30 SCT meter.

Adult and juvenile samples were collected during May, June and July 2006. Sampling of

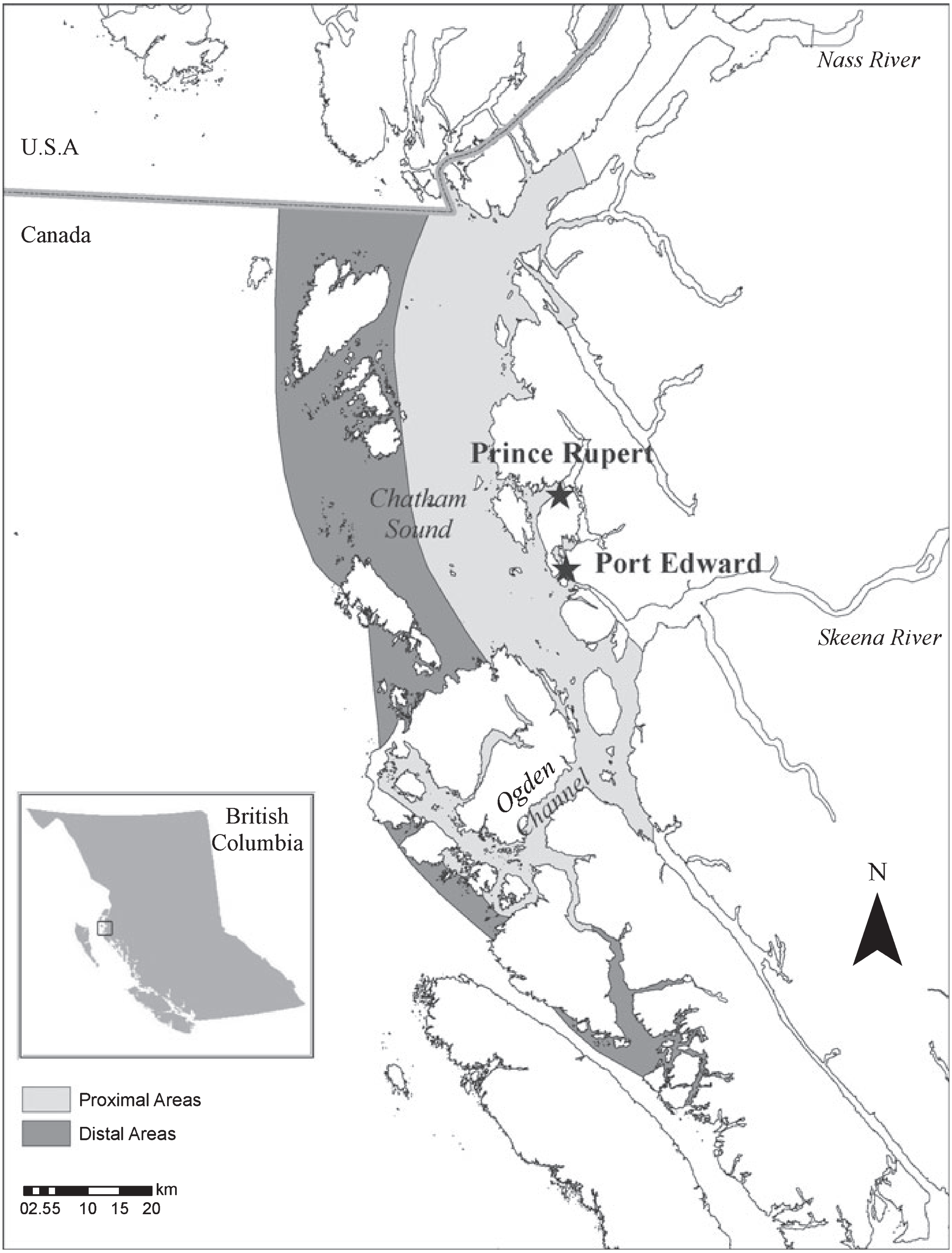

Figure 1 The north coast of British Columbia showing proximal and distal zonation of the Skeena and Nass estuaries.

adults occurred once per month for four to six consecutive days. Juvenile salmon were collected during 4–5-day periods in the weeks immediately following periods of adult sampling. We selected adult and juvenile collection areas that were as closely adjacent to one another as possible (Fig. 2).

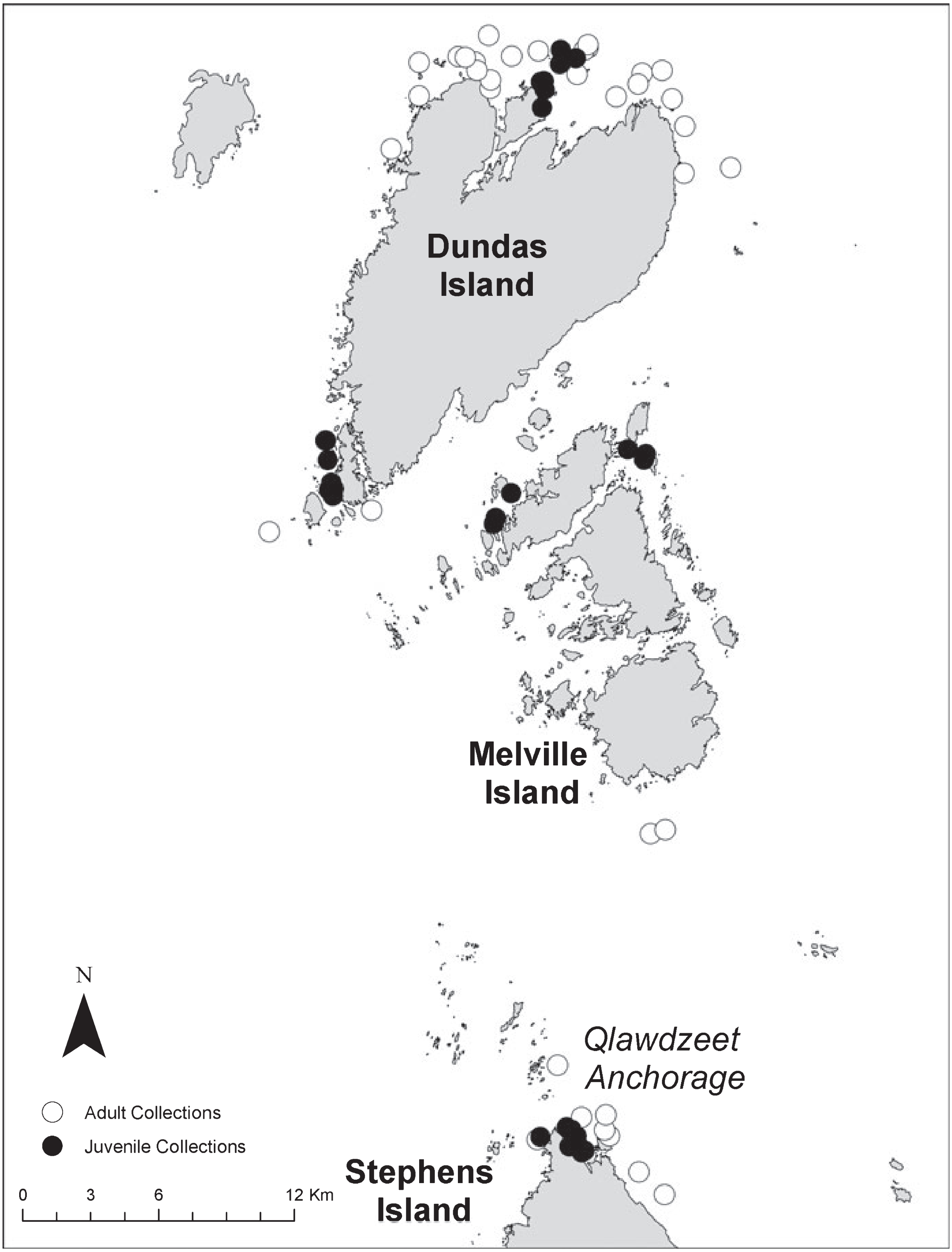

Figure 2 Map of 2006 collection sites in the northern part of the distal region of the Skeena Estuary.

Juvenile pink salmon were collected in 2006 using the same techniques as in the 2004 and 2005 field seasons.

Adult sampling was conducted within popular traditional troll sites for Chinook salmon on the north coast, within a kilometre of the islands along the western and northern rim of Chatham Sound. Salmon were collected with two commercial salmon trolling vessels, the M.V. Diane B in May and July, and M.V. Salten in June. Trolling occurred at a depth of approximately 40 m along the shoreline. Salmon were caught using a variety of fishing gear including flashers, spoons and bait fish. Trolling occurred continuously during daylight hours except while the vessel was underway between sampling sites.

Adult salmon were landed directly into plastic tubs and killed with a single blow to the head in such a manner as to reduce blood loss and to minimize the loss of scales and lice (Beamish, Neville, Sweeting & Ambers 2005). When fish captures were frequent enough that examination did not keep up with the capture, fish were held in separate tubs. The fish were measured and examined for sea lice using a 10x hand lens. The plastic tubs were carefully examined for lice that had been detached from the salmon. In the few examples where lice were found in the collection tubs, they were identified and added to the totals recorded for the salmon they came from. Sea lice were identified to stage and species (Kabata 1972; Johnson & Albright 1991a; Galbraith 2005) and preserved in 10% formalin for further analysis in the laboratory where field identifications were later confirmed.

In the laboratory, juvenile fish were weighed, measured and examined for sea lice using a dissecting microscope. The motile stages of lice from adult and juvenile collections were determined according to morphological characteristics outlined in Kabata (1972) and Johnson & Albright (1991a). Copepodid and chalimus stages from both the adult and juvenile fish samples were mounted on permanent slides and identified to species and stages using a compound microscope.

Results

In 2004 and 2005, pink salmon were initially found at high densities in the proximal parts of the estuary where salinities averaged 19–25‰ (Fig. 3). The fish that were caught soon after they first left fresh water in April were 37–39 mm long with an average weight of 0.42–0.52 g (Table 1). Over the ensuing months the juveniles moved to staging areas in the outer estuary where salinities averaged 26–30‰ (Fig. 3). Temperatures were similar in both parts of the estuary and averaged from 9–13 °C (Fig. 4). During May and June the density of juveniles

Table 1 Lengths and weights of pink salmon smolts collected in the Skeena estuary in 2004, 2005, and 2006

	n	April	May	June	July	August
Length (mm)						
2004	6252	39	45	72	93	109
2005	12162	37	46	76	98	
2006	2941		39	84	95	
Weight (g)						
2004	6252	0.52	0.97	3.97	7.97	13.67
2005	12068	0.42	0.93	4.53	9.63	
2006	2931		0.5	6.6	8.89	

increased in the staging areas. Juvenile densities declined in all areas in July and August.

In 2006, collections of juvenile pink salmon were made from May through July in the northern portion of the distal estuary along the western part of Chatham Sound (Fig. 2). Juvenile pink salmon were relatively plentiful during May and June 2006 throughout the study area, and target samples were easily exceeded during each month. We collected 1016 juvenile pink salmon in May and 1055 in June. By July, the density of juvenile fish had decreased, and the total collection for that month was 871. The mean lengths and weights of juvenile pink salmon in May, June and July were similar to those in the larger collections of 2004 and 2005.

Overall, 21427 pink salmon were examined for sea lice between 2004 and 2006. The lice increased in abundance as the season progressed (Tables 2 and 3). The abundance of *L. salmonis* was 0.003 (Table 3) in April 2004 and 2005; by July abundance was 0.318. Sea lice abundance also rose sharply on juvenile salmon between May and July 2006 (Table 3). In May the abundance was 0.007, entirely of larval forms. By late July the abundance increased to 0.099, predominantly of motile forms. The intensity of *L. salmonis* on juvenile pink salmon was low in all 3 years, ranging from 1.03 to 1.37 (Tables 2 and 3). Most of the lice on juvenile salmon were single parasites with annual proportions ranging from 76% to 91% (Tables 2 and 3).

There was a geographic as well as a temporal pattern of distribution of *L. salmonis* infection. The geographic pattern showed a marked zonation from the inshore areas near the river mouths to the outer estuary areas (Fig. 1). The relatively inshore proximal zone had an average abundance of 0.011 and the outer distal zone 0.048 to 0.060 (Table 3). In Table 4 the 2006 juvenile data is compared to collections made in the equivalent portion of the

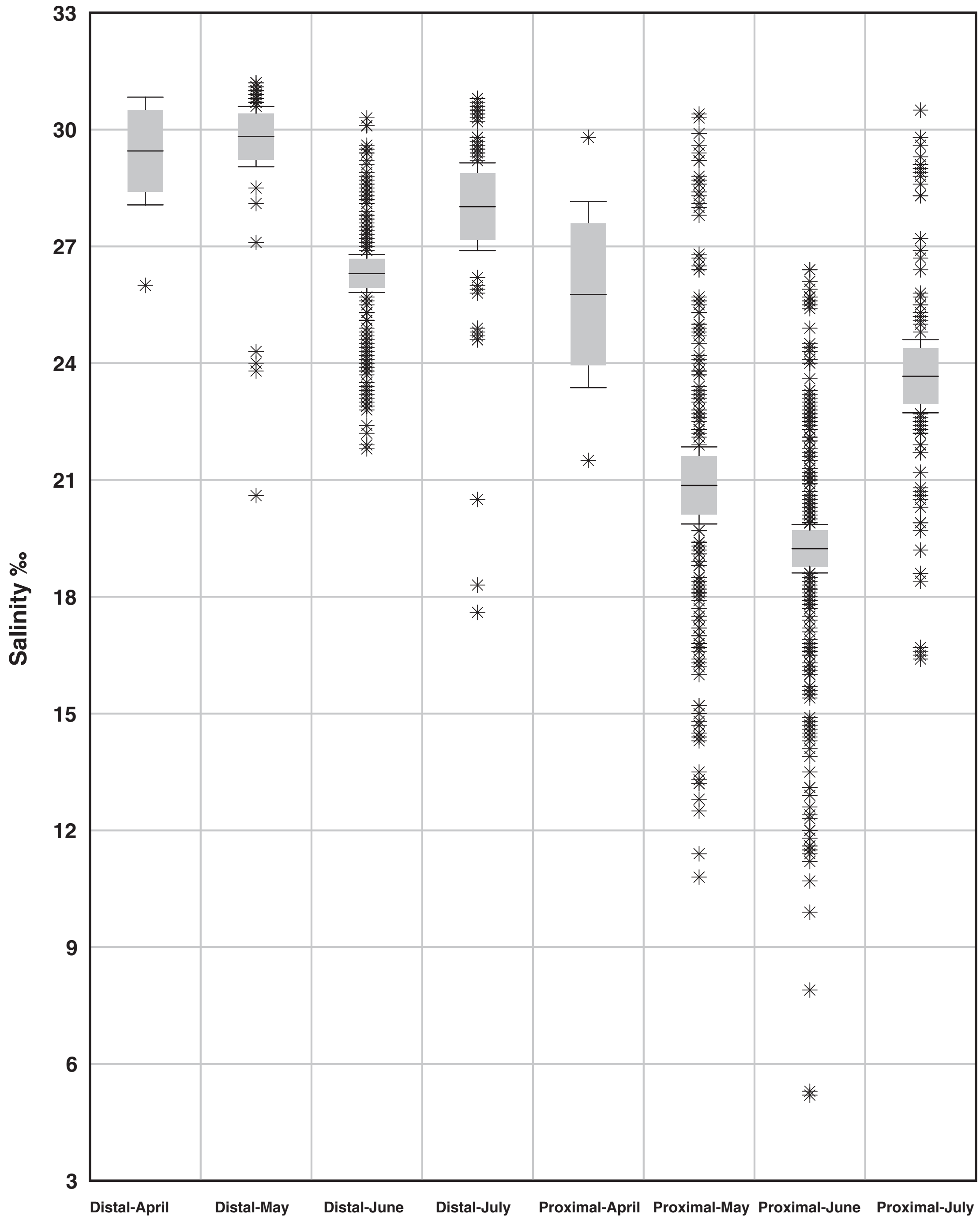

Figure 3 Box plots showing distribution of surface salinities recorded in 2005; the black horizontal line is the mean value, the grey box represents the 95% confidence limits, the whisker limits are 99% confidence limits; asterisks are outlying values.

distal zone in 2004 and 2005 where juvenile pink salmon had abundances of *L. salmonis* ranging from 0.049 to 0.098. The distal portions of this early juvenile marine habitat have significantly higher levels of *L. salmonis* (means of 2004 collections $P < 0.01$, 2005 $P < 0.\ 001$). It appears that lice

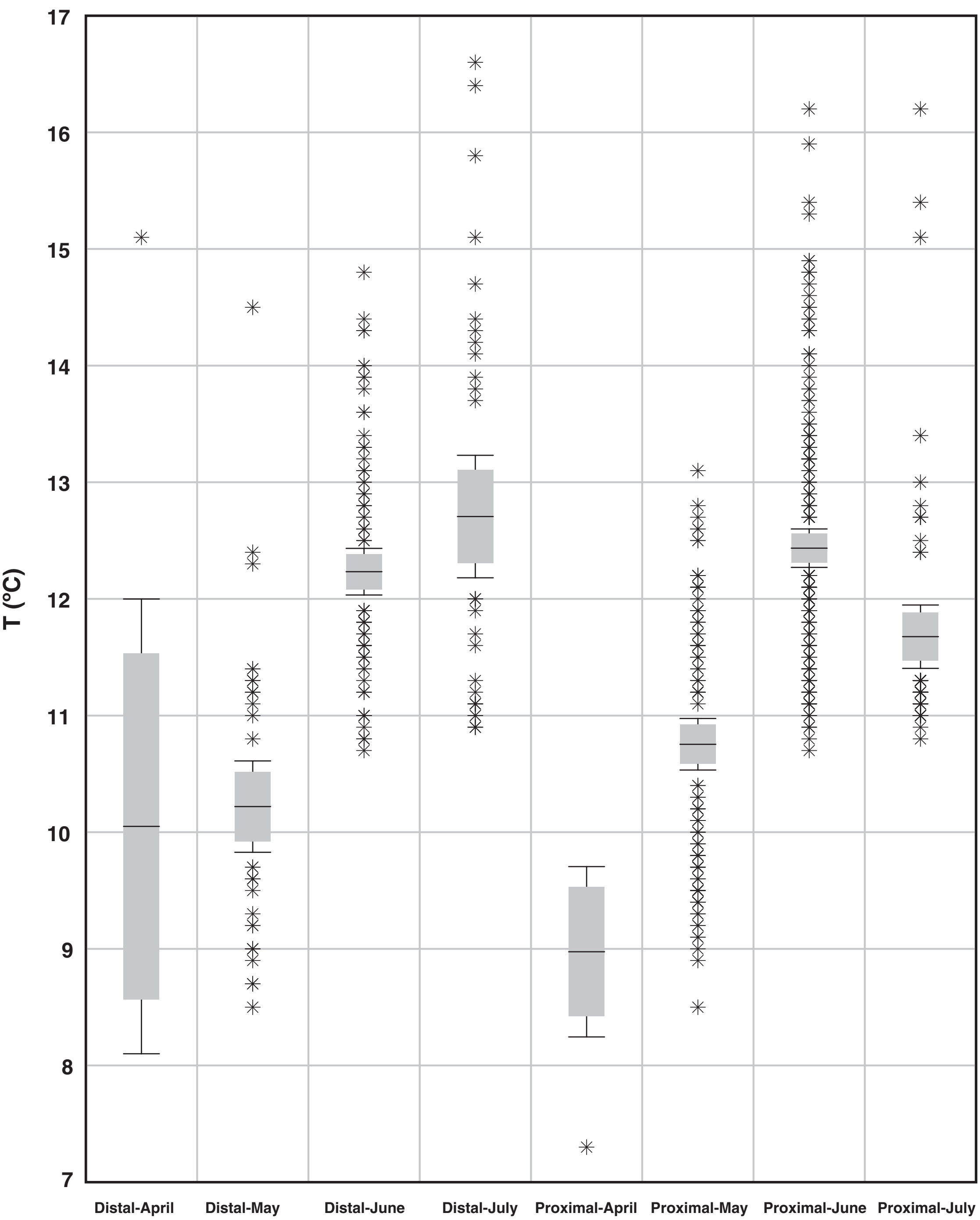

Figure 4 Box plots showing distribution of surface temperatures recorded in 2005; the black horizontal line is the mean value, the grey box represents the 95% confidence limits, the whisker limits are 99% confidence limits; asterisks are outlying values.

levels increase throughout the season, and that a large majority of *L. salmonis* infection is limited to the outer zones of the estuary.

Returning adult Chinook salmon first appear on the northwest British Columbia coast in May. There are usually about 100 000 fish returning to

Table 2 Abundance and average intensity of *Lepeophtheirus salmonis* on juvenile pink salmon from the Skeena estuary collected in 2004 and 2005; The column '% single L.s' is the proportion of the total lice infection where the intensity is 1

Collection dates	*n* Fish	*L. salmonis*	Cop& Ch1	Ch2, Ch3, Ch4	Motile stages	Average intensity	% Single L.s.	Total abundance
April	3738	11	0.001	0.002	0.000	1.000	100	0.003
May	6678	98	0.002	0.012	0.002	1.022	99	0.015
June	6186	132	0.002	0.003	0.016	1.031	97	0.021
July	1883	570	0.105	0.054	0.158	1.508	69	0.318
2004	6240	164	0.002	0.005	0.020	1.107	90	0.026
2005	12245	647	0.018	0.014	0.023	1.380	76	0.055

Table 3 Abundance and average intensity of *Lepeophheirus salmonis* on juvenile pink salmon collected in the 2006 study area; The column '% single L.s' is the proportion of the total lice infection where the intensity is 1

Collection dates	*n* Fish	*L. salmonis*	Cop& Ch1	Ch2, Ch3, Ch4	Motile stages	Average intensity	% Single L.s.	Total abundance
May 21–23	1016	7	0.004	0.003	0	1.000	100	0.007
June 26–29	1055	52	0.012	0.001	0.036	1.136	86	0.049
July 11–22	871	86	0.026	0.001	0.071	1.078	93	0.099
2006	2942	145	0.014	0.002	0.034	1.094	91	0.049

Table 4 Comparison of sea lice abundance on juvenile pink salmon in the proximal and distal zones of the Skeena estuary in 2004 and 2005 with the area selected for detailed study in 2006

	Proximal Zones		Distal Zones		2006 Study Area	
Year	Abundance	*n*	Abundance	*n*	Abundance	*n*
2004	0.014	2839	0.048	3413	0.059	2088
2005	0.009	4321	0.060	6497	0.098	3716
2006	–				0.049	2942

the Skeena and Nass Rivers and a larger group travelling along the coast to more southerly rivers (Department of Fisheries and Oceans 2006). Chinook salmon catches in this area were relatively small in 2006 compared to previous years (I. Winther, Canada Department of Fisheries and Oceans, personal communication 2006). The success rate of trolling increased greatly once the relatively numerous coho salmon appeared. The Chinook salmon that were sampled measured 72.52 ± 3.92 cm in fork-snout length (Table 5). All but two were > 60 cm in length and probably returning to their spawning rivers in 2006, but not necessarily to the Skeena River. The coho salmon were smaller and averaged 63.53 ± 1.10 cm. It is probable that most of the coho were from north coast stocks.

All but three of the adult salmon that were collected in 2006 carried sea lice. *Lepeophtheirus salmonis* appeared on all but two of the Chinook salmon. In May, all the lice found on Chinook were *L. salmonis*. The prevalence of *L. salmonis* on Chinook declined slightly to 99.5% in June and 99.0% in July (Table 5). Coho salmon first appeared in July with a similar lice load but a higher proportion of *C. clemensi*. The proportion of *L. salmonis* on the coho sampled was 85.1%. Almost all of the sea lice we observed remained attached to the salmon. Only 40 motile sea lice, or 1.3% of the total lice and 1.8% of the motile lice, were recovered from the salmon landing tubs.

Most of the *L. salmonis* (83%) on returning salmon were motile stages (Table 6). The proportion of motile to larval stages of *L. salmonis* ranged from 96% on returning Chinook in May to 75% on Chinook and 83% on coho in July. Of the motile stages the largest component were adult females. Of these 76% had egg strings attached. In contrast, most of the *C. clemensi* (71%) were early larval stages. Only a single adult *C. clemensi* was observed on the returning Chinook; 11 adult *C. clemensi* were found on returning coho.

Discussion

Pink salmon fry emerge from the gravel redds in April and May and immediately migrate to the coast (Heard 1991). In April 2004, we found that before they began feeding on the coast, the pink

Table 5 2006 Adult salmon lengths and sea lice prevalence. Abundance values are the combined values for *Lepeophtheirus salmonis* and *Caligus clemensi*

Date	*n* Chinook	*n* Coho	Length	*n* lice	Prevalence	Abundance %	*L. salmonis*
13–20 May	17	–	79.39 ± 7.80	307	100%	18.06	100.0
19–22 June	35	–	73.82 ± 5.03	629	100%	18.06	99.5
11–15 July	17	–	62.94 ± 7.87	294	88%	17.47	99.0
11–15 July	–	101	63.53 ± 1.10	1659	100%	15.85	85.1
All Chinook	69	–	72.52 ± 3.92	2934	100%	17.91	99.5

Table 6 Abundance of *Lepeophtheirus salmonis* on returning adult salmon captured in 2006. Stages are copepodid (COP), chalimus 1 (CH1), chalimus 2 (CH2), chalimus 3 (CH3), chalimus 4 (CH4), preadult (PA), adult male (AM), adult female (AF)

	Chinook				Coho	
	May	June	July		July	
Stage	*n* fish = 17	*n* fish = 35	*n* fish = 17	*n* Lice	*n* fish = 101	*n* Lice
COP	0	0.2	0.824	21	1.218	123
CH 1	0.118	0.286	0.353	18	0.248	25
CH 2	0.059	0.371	0.294	19	0.317	32
CH 3	0.294	0.743	0.824	45	0.248	25
CH 4	0.176	1.686	2.059	97	0.257	26
PA	1.647	3.00	4.882	216	2.119	214
AM	4.294	3.286	3.00	239	4.188	423
AF	11.471	8.40	5.059	575	4.891	494
Total	18.059	17.971	17.294	1230	13.485	1362

salmon were about 32 mm long and weighed about 0.25 g. The fry moving down the Skeena River and through the estuary are essentially plankton as the current velocity (1–4 m sec^{-1}) is more than an order of magnitude greater than their swimming speed of about 0.11 m sec^{-1} (Videler & Wardle 1991). We observed that the fry accumulate on the rocky shores of the islands of the coast, frequently in depths of 1–2 m early in the season and that when they reach a length of about 50 mm they move into deeper shoreline habitat. Frequently this means they move from inside the kelp band at 5–10 m depth to outside the band. The juvenile pink salmon can be easily observed in May in small schools feeding at favoured spots along the shallows of the rocky coast. Seaward migration is difficult to observe but is probably intermittent (Parker 1968), perhaps as a response to food depletion.

We conceptualize the outer estuary areas as staging zones where pink salmon smolts accumulate, feed intensively and grow rapidly, gaining up to 4.5% weight per day (Heard 1991). By late July, the juvenile pink salmon leave on their northward migration along the Alaska coast (Healey 1991; Fisher, Trudel, Ammann, Orsi, Piccolo, Bucher, Casillas, Harding, MacFarlane, Brodeur, Morris & Welch 2007). Between May and July, returning adult Chinook salmon, and later coho, are present only tens to hundreds of metres away from the areas where juvenile pinks aggregate in the shallow littoral zone. The lice levels we report on the returning adult Chinook salmon in 2006 and coho are closely comparable to those reported by Beamish *et al.* (2005) for the 2004 season. They found average values of 15.7 and 16.2 for both species of sea lice (combined abundance) on Chinook and 18.5 on coho. The prevalence of *L. salmonis* was 99% of the total for Chinook and coho. The similarity of these to our observations is encouraging. Despite being collected over 500 km apart, it is likely that both collections were adult salmon that had recently returned from the Gulf of Alaska. The abundance of sea lice on other species of returning salmon is not relevant to this study because they do not reach the north coast of British Columbia until nearly all the pink salmon juveniles have left.

The abundance of *L. salmonis* increases one hundredfold in juvenile pink salmon during the months that they occupy the staging areas on the west side of Chatham Sound. The source of the infectious stages of *L. salmonis* responsible for this increased abundance remains open to discussion. Salmon farms may be ruled out as a potential source for sea lice on the north coast, the nearest being over 300 km away from our study areas. Sticklebacks have been suggested as an important reservoir of *L. salmonis* (Jones *et al.* 2006), but there are few on the north coast. We collected no sticklebacks in our 2006 trawl samples. In 2004 and 2005 we found that sticklebacks were readily accessible at only a single location, the shallow mud-bottomed Big Bay on the east side of Chatham Sound. Resident Chinook and coho salmon are apparently a source for sea lice on the south coast of British Columbia (Beamish, Dawe, Sweeting, Gordon, Ambers, Hurst & Neville 2003), where some fish delay their northward migration or do not migrate at all. The life history pattern of delayed or non-migration is infrequent on the north coast, where resident Chinook and coho salmon are rare. The low level of overwintering salmon on the north coast can be seen in the data of Trudel, Theiss, Bucher, Farley, MacFarlane, Casillas, Fisher, Morris, Murphy & Welch (2007b), Fisher *et al.* (2007) and Morris, Trudel, Theiss, Sweeting, Fisher, Hinton, Fergusson, Orsi, Farley & Welch (2007). The few resident Chinook salmon that may be observed on the north coast prior to the return migration period are usually strays from the south coast. Resident sea-going trout, *Oncorhynchus clarki clarki* (Richardson), and Dolly Varden char, *Salvelinus malma* (Walbaum), are rare on the north coast. We caught only six trout and char in our trawl collections of more than 50 000 fish in 2004 and 2006.

There is thus a conspicuous geographic pattern to *L. salmonis* infection and a temporal pattern whereby *L. salmonis* increases in abundance between April and July in all 3 years sampled (Krkošek *et al.* 2007; $P = 0.05$). It is noteworthy however, that Krkošek *et al.* (2007) (in their supplementary material) found no significant relationship between salinity and the abundance of *L. salmonis* in the Skeena/Nass estuary in 2004 and 2005.

The timing of the increase in louse abundance that we observed in juvenile pink salmon compares well with the arrival of abundant ovigerous female *L. salmonis* observed on returning Chinook salmon at sites adjacent to the rearing habitat of the juvenile pink salmon. A conservative estimate is that tens of thousands of Chinook and coho salmon travelled through and/or fed in the area we sampled in 2006. The returning Chinook and coho, with the high levels of salmon lice that we observed, were a potent source of transmission of *L. salmonis*. Other salmon travelled by nearby routes during this time and may have contributed to the infection.

Using data from the central coast of British Columbia and elsewhere, Beamish, Neville, Sweeting, Jones, Ambers, Gordon, Hunter & McDonald (2007) emphasize the importance of returning salmon as reservoir hosts of *L. salmonis* that transfer to coastal Pacific salmon populations. In the multi-host context (Haydon, Cleaveland, Taylor & Laurenson 2002) of northern Bitish Columbia, it appears that returning adult salmon are the most important source population of *L. salmonis* under natural conditions. The first salmon to return, Chinook, are present in coastal waters from May through July. The experience of commercial troll fishermen is that returning Chinook are normally plentiful along the western and northern margins of Chatham Sound. These Chinook salmon have the greatest overlap in residence time with pink salmon juveniles.

We have documented the level of lice on emigrating pink juveniles. There are several reports of *L. salmonis* levels on pink salmon captured with trawl nets in their first 6 months at sea as they move up the Pacific coast. To the south, Beamish *et al.* (2007) reported results from trawls in August on the central coast of British Columbia with an abundance of 0.12. To the north, Wertheimer, Fergusson, Focht, Heard, Orsi, Sturdevant & Wing (2003) reported levels in Icy Strait in southern Alaska as an abundance of 0.038. Trudel, Jones, Theiss, Morris, Moss, Wing, Farley, Murphy, Baldwin & Jacobson (2007) reported levels of 0.16 for pink salmon in their first winter on the coast of northern British Columbia in 2003.

Nagasawa, Ishida, Ogura, Tadakoro & Hiramatsu (1993) reported an abundance of 5.35 for mature female *L. salmonis* in the central Pacific Ocean from later in the 1-year marine residence of pink salmon. In 2005, the abundance of all stages in the central Pacific was 17.7 (Beamish *et al.* 2007). In the final months of pink salmon life at sea, Trudel *et al.* (2007a) reported an abundance of 12.1 in 2003 on pink salmon in northern British Columbia. The highest levels are reported by Beamish *et al.* 2005 on returning pink salmon with a 51.1 abundance in Queen Charlotte Strait (31% larval stages) and 56.7 abundance in Smith & Rivers Inlets (51% larval stages).

It is evident from these data that much of the *L. salmonis* reproduction occurs at sea. Pink salmon return to coastal areas with lice abundances that are two orders of magnitude higher than those they leave with. Some of the sea lice transmission to adult salmon may occur in the relatively near-shore marine environment transited as the maturing salmon return, as seems likely from the Beamish *et al.* (2007) data, but most of the transmission to adult Chinook probably occurs prior to their arrival in coastal waters. Relatively few of the juvenile pink salmon we observed had lice intensities of >1. The proportion of lice that were solitary residents on host pink salmon ranged from 64% to 100%. As caligid lice have two sexes, reproduction must require effective colonization at sea, via the settling of either copepodids or free swimming adults or both. The abundance of motile stages in July samples with apparently few earlier stages suggests that some adult transfer occurs. Hull *et al.* (1998) show interhost transfer of adult lice under experimental conditions, Transfer in the ocean seems more likely if adults can survive for long periods unattached to a host. Hogans (1995) reported that under laboratory conditions adult female *L. salmonis* survive at least 49 days in sea water without feeding. It may be that transfer of sea lice in the coastal zone is not a requirement for continuation of *L. salmonis* populations, but a minor part of the species' reproductive spectrum.

The geographic and temporal pattern of *L. salmonis* infection in juvenile pink salmon suggests that returning Chinook and coho salmon are predominant sources of sea lice on the north coast. This natural source of sea lice results in levels of abundance of 0.05 to 0.10. In the Broughton Archipelago of central British Columbia, an area with a high density of salmon farms, sea lice levels on migrating pink salmon are one or two orders of magnitude higher. Morton, Routledge & Williams (2005) reported abundances of 6.8 in 2002 and 9.75 in 2004. When salmon farm fallowing was planned and effected to some degree in 2003, lice levels were reported as 0.64 (Morton *et al.* 2005) and 0.22 to 0.48 (Beamish, Jones, Neville, Sweeting, Karreman, Saksida & Gordon 2006). The epizootiology of *L. salmonis* infection is more complex on the central coast, but these data agree with the suggestion that a large proportion of the sea lice infection in the Broughton Archipelago comes from salmon farms (Krkošek, Lewis & Volpe 2005; Orr 2007).

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