

A proposed life history strategy for the salmon louse, *Lepeophtheirus salmonis* in the subarctic Pacific

R.J. Beamish^{a,*}, C.M. Neville^a, R.M. Sweeting^a, S.R.M. Jones^a, N. Ambers^a,
E.K. Gordon^a, K.L. Hunter^a, T.E. McDonald^b

^a Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, B.C. Canada V9T 6N7

^b 3350 Uplands Drive, Nanaimo, B.C. Canada V9T 2T5

Received 16 June 2006; received in revised form 20 December 2006; accepted 31 December 2006

Abstract

The sea louse, *Lepeophtheirus salmonis*, is commonly found on Pacific salmon that are rearing in the central North Pacific Ocean and adjacent seas (subarctic Pacific). Large numbers of sea lice have also been observed on all species of adult Pacific salmon when they return to coastal marine areas in the summer during their spawning migration. We propose that the transport of sea lice into coastal areas is a strategy employed by *L. salmonis* to improve their productivity by improving the transmission potential of the infectious stage when host densities are decreased in the open ocean and increased in the coastal areas. Juveniles of the species of Pacific salmon inhabit the same areas at the same time as the returning adult salmon and, according to the proposed strategy, will become infected from sea lice on the adult Pacific salmon. Juvenile pink, chum and sockeye salmon will carry these sea lice into the open ocean when they migrate away from the coastal areas later in the year. The offspring of these sea lice on pink, chum and sockeye would infect Pacific salmon on the high seas and thus maintain high abundances of sea lice. Juvenile coho and chinook salmon that remain in the coastal areas would serve as hosts for the sea lice over the winter. The sea lice on these resident coho and chinook salmon would infect juvenile Pacific salmon that enter the ocean in the early spring. The strategy would result in the infection of juvenile Pacific salmon throughout their range in all coastal areas.

Crown Copyright © 2007 Published by Elsevier B.V. All rights reserved.

Keywords: *Lepeophtheirus salmonis*; Sea lice life history; Pacific salmon; British Columbia

1. Introduction

Salmon farming is an important and developing industry in the province of British Columbia, producing 70–80,000 t in 2003 and 2004. This compares to a wild Pacific salmon catch of all species of 38.4 t in 2003 and 25.6 t in 2004. In 2005, there were 126 salmon farms

licensed of which 86 were growing salmon. Farmed salmon is currently the major agricultural export in the province.

There is concern that salmon farming may harm wild Pacific salmon (*Oncorhynchus* spp.). One concern is that sea lice produced on farmed salmon will cause a mortality of wild salmon that is additive and not compensatory to their natural mortality. Understanding and managing any impact of sea lice produced from salmon in farms requires an understanding of the natural production of sea lice. There are two species of sea lice that are found on farmed

* Corresponding author. Tel.: +1 250 756 7029; fax: +1 250 756 7053.

E-mail address: beamishr@pac.dfo-mpo.gc.ca (R.J. Beamish).

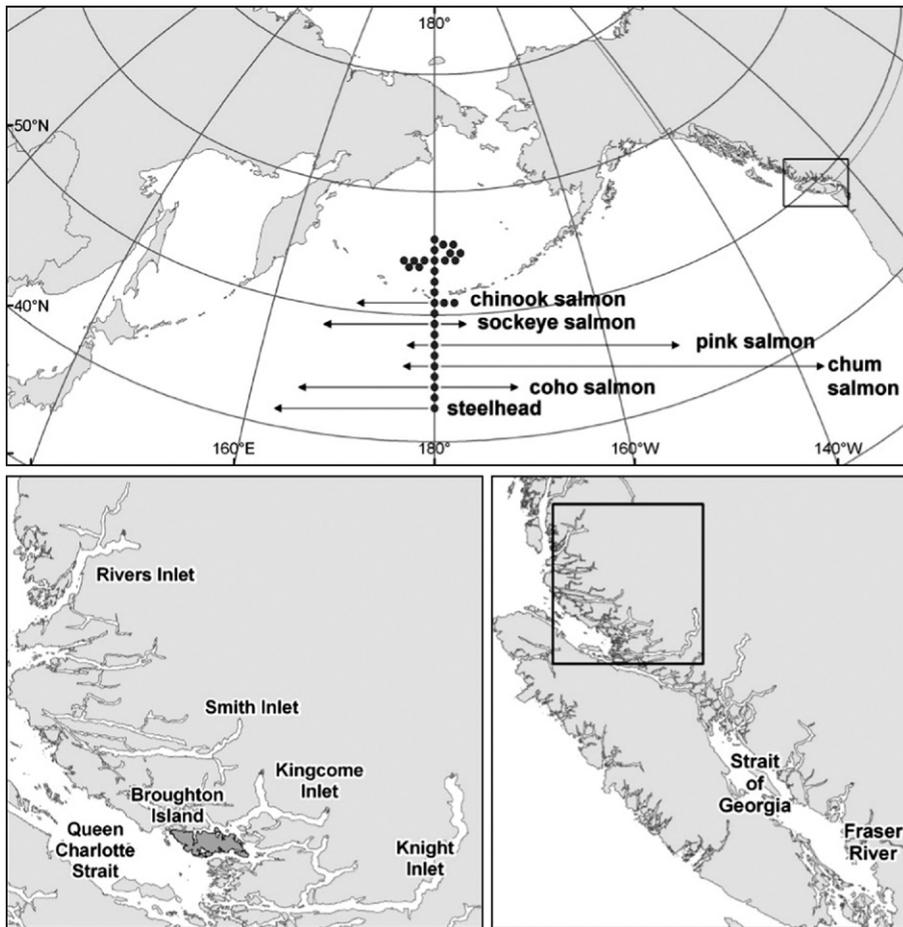


Fig. 1. (A) Study area showing the location of the sets (●) fished in the central North Pacific in this study and by Nagasawa (2001). The horizontal arrows show the extent of the distribution of Pacific salmon of Asian origin east of the fishing locations (→) and the extent of the distribution of Pacific salmon of North American origin west of the fishing locations (←). Also shown is the sampling area off the coast of British Columbia, inset (B). The study area in the central coast region of British Columbia showing the Strait of Georgia, Fraser River, inset (C). Location of sampling areas.

salmon in British Columbia (Beamish et al., 2006); however, it is *Lepeophtheirus salmonis* that is of immediate concern. Despite the widespread distribution of *L. salmonis* and the early recognition of its potential impact on commercial mariculture (Kabata, 1973), little is known about the natural factors that affect its population dynamics (Tully and Nolan, 2002). This is particularly notable in the subarctic Pacific (North Pacific Ocean and adjacent seas) where Pacific salmon dominate the daytime fish biomass in the surface waters (Beamish et al., 2005a).

L. salmonis, the salmon louse, is a common parasite on Pacific salmon in the North Pacific and on the species in the genus *Salmo* in the North Atlantic (Kabata, 1979). The life cycle has five phases and ten stages (Johnson and Albright, 1991; Schram, 1993), with the survival of an individual sea louse depending on the relatively short-lived and planktonic copepodid stage finding a suitable host. After the egg hatches there are two nauplii stages that

develop in 4 days at 10 °C into the infectious copepodid stage (Johnson and Albright, 1991). It is not known how long the copepodid may live at different temperatures but at temperatures of about 10 °C to 15 °C, which occur in the central North Pacific in the summer, the copepodid may live approximately 5 days (Wooten et al., 1982; Voth, 1972; Brooks, 2005). Recognizing that there is a short time available for the copepodid to find a host, it is impressive that *L. salmonis* is so successful. Its success is even more remarkable when one considers that the host Pacific salmon are highly migratory and anadromous. In particular, there is a major reduction in the biomass of all Pacific salmon in the open ocean after the adult fish leave the high seas in the spring and summer and begin their spawning migration. Beamish et al. (2005a) estimated that between 1990 and 1999 the average annual biomass of adult Pacific salmon returning to coastal areas around the subarctic Pacific was 1.42 million t. Because large

Table 1

Comparison of the prevalence and intensity of sea lice on adult Pacific salmon, from Queen Charlotte Strait and Rivers and Smith inlets, August 4–19, 2004 (Beamish et al., 2005b) and from Queen Charlotte Strait, Aug 8–15, 2005

Species	Number of fish		Length (mm)±S.D.		Prevalence (%)		Intensity		Intensity of mobile stages		Intensity of non-mobile <i>L. salmonis</i>		Intensity of mobile <i>L. salmonis</i>		Intensity of non-mobile <i>C. clemensi</i>		Intensity of mobile <i>C. clemensi</i>	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
Pink salmon	132	91	488±30.5	522±22.8	100	100	52.3	24.6	19.1	19.5	7.9	3.5	13.3	19.0	19.3	1.5	5.8	0.5
Sockeye salmon	124	50	590±41.0	575±28.4	100	100	45.1	39.0	21.1	27.3	12.6	10.7	20.1	26.9	5.7	1.0	1.0	0.3
Chum salmon	62	1	710±46.3	749	100	100	41.5	5.0	15.3	5.0	4.0	0	7.3	5.0	18.8	0	8.0	0
Coho salmon	208	100	639±80.5	608±81.4	99.0	96.0	18.6	10.8	10.6	6.6	1.9	0.8	9.3	6.4	5.0	2.9	0.9	0.3
Chinook salmon*	140	100	502±156.7	528±163.1	99.3	98.0	16.1	13.8	12.4	11.9	1.9	1.3	12.1	11.9	0.2	0.3	0.3	0.1

* Chinook salmon included adults and sub-adults.

increases in individual weight occur just before adults return to the coast (Ricker, 1964) and because total catches in the 1990s by all countries have not fluctuated extensively, it was possible to conclude that about one half of the total biomass in the open ocean was lost during the coastal migration. This reduction in host biomass on the high seas would decrease the opportunity of the copepodids to find a host.

Beamish et al. (2005b) showed that sea lice commonly occur on virtually all adult Pacific salmon in a coastal marine ecosystem in British Columbia, Canada. We show here that large abundances of juvenile Pacific salmon coexist with these returning adult Pacific salmon. Most of these juvenile salmon will migrate into the open ocean, but many coho salmon (*O. kisutch*) and chinook salmon (*O. tshawytscha*) will remain in the coastal areas during the winter. It is during this period of overlapping distribution of adult and juvenile Pacific salmon that the offspring of sea lice on adult salmon can infect juvenile salmon.

This paper identifies a possible life history strategy of the salmon louse that maximizes its transmission potential. According to the strategy, transmission potential within salmon lice populations would be improved when the parasites are carried into coastal areas where their

habitat area is smaller and host density is higher. The life history strategy of the salmon louse is completed when the parasites are carried offshore by the newly infected juvenile salmon and become part of the open ocean population of all Pacific salmon species. Importantly, the proposed strategy helps to explain the natural infections of salmon lice observed on juvenile Pacific salmon throughout the coastal areas of the subarctic Pacific.

2. Methods

Sea lice were categorized according to the general development stages of chalimus, pre-adult and adult. We report pre-adult and adult individuals as mobile stages. Sea lice were identified in the laboratory and at sea by two experts using the criteria described by Kabata (1972, 1973) and by Johnson and Albright (1991). We used the term prevalence as the percentage of fish with sea lice and the term intensity to categorize the number of sea lice per infected fish according to the recommendations of Margolis et al. (1982). The study was conducted in the Central Coast area of British Columbia and the central North Pacific Ocean (Fig. 1). We use the term juvenile for Pacific salmon in their first marine year

Table 2

Prevalence and intensity of sea lice on juvenile Pacific salmon sampled using troll gear in Queen Charlotte Strait, August 4–19, 2004

	Number of fish	Average length (mm)±S.D.	Number of sea lice	Prevalence (%)	Intensity	Prevalence (%) non-mobile <i>L. salmonis</i>	Prevalence (%) mobile <i>L. salmonis</i>	Prevalence (%) non-mobile <i>C. clemensi</i>	Prevalence (%) mobile <i>C. clemensi</i>
Coho salmon	36	246±42.4	36	100	1.0	13.9	80.6	2.8	2.8
Chinook salmon	10	215±48.5	10	90.0	1.1	20.0	70.0	10.0	0

Table 3

Prevalence and intensity of sea lice on juvenile Pacific salmon sampled using troll gear in Queen Charlotte Strait, November 30 to December 5, 2004

	Number of fish	Average length (mm)±S.D.	Number of sea lice	Prevalence (%)	Intensity	Prevalence (%) non-mobile <i>L. salmonis</i>	Prevalence (%) mobile <i>L. salmonis</i>	Prevalence (%) non-mobile <i>C. clemensi</i>	Prevalence (%) mobile <i>C. clemensi</i>
Coho salmon	151	295±29.6	549	93.0	3.9	1.8	84.8	6.8	6.6
Chinook salmon	90	246±34.1	330	87.0	4.2	15.5	79.9	3.0	1.5

(ocean age 0) and the term sub-adult for immature fish that were in the ocean at least one winter.

A troller was used to collect juvenile, sub-adult and adult Pacific salmon in a manner that provided accurate estimates of sea lice prevalence and intensity (Beamish et al., 2005b). The hook and line gear fished during the day included flashers (rectangular metal plates used to attract Pacific salmon) and a variety of hook sizes, lure colours and types. Gear was fished at a variety of depths. Fish were landed directly into individual tubs without handling. Sea lice in the tub were added to the counts on the fish. In general, there were relatively few sea lice in the tubs.

Juvenile Pacific salmon were also captured using a rope trawl (Beamish and Folkes, 1998; Beamish et al., 2000) fished from a chartered trawler, the F/V *Frosti* and the R/V *W.E. Ricker*. Trawl studies were used to determine if there were overlapping distributions of adult and juvenile Pacific salmon. The gear and the sampling methods are now commonly used to sample juvenile Pacific salmon throughout the North Pacific and Bering Sea (NPAFC, 2001). Sets were chosen along transects so that the fishing operation lasted about 12 to 14 h during daylight, with most sets being 30 min. All juvenile Pacific salmon from each trawl catch were emptied from the net into tubs and subsequently identified. Abundances of juvenile Pacific salmon were determined in July and September 2003, 2004 and 2005 in the Strait of Georgia (Fig. 1) using the methods reported in Beamish et al. (2000). These abundances and corresponding catch per unit effort (CPUE) were compared to the CPUE in the area of the troll study to show that large numbers of juvenile Pacific salmon occurred in the same area as adult Pacific

salmon. CPUE was the number of fish that were caught in one set and standardized to 1 h. Abundances were not determined for the Queen Charlotte Strait area (Fig. 1) because the area surveyed was proportionally much smaller than the survey area in the Strait of Georgia.

Juvenile Pacific salmon collected from the Queen Charlotte Strait area were examined for sea lice in 2003. In most cases the total sample was examined for all stages of sea lice using dissecting microscopes with up to 22× magnification. When the total sample could not be processed because of time constraints or the catch was too large, a sample of the catch was taken from the fish at the top of the container without selection. The species of sea lice were determined at sea for samples collected in the trawl study. All identifications were made by experts onboard the vessel. Identifications made at sea were confirmed in the laboratory by the same experts that identified all other sea lice reported in this paper.

Samples of sub-adult Pacific salmon were obtained from purse seines and beach seines in the spring of 2003 from the waters around the archipelago of islands in the vicinity of Broughton Island and in Knight and Kingcome inlets (Fig. 1C). Each fish was removed from the seine with a dip net and placed directly into a plastic bag.

3. Sea lice on Pacific salmon from the central subarctic Pacific

Nagasawa (2001) reported the results of a study of the prevalence and intensity of *L. salmonis* on Pacific salmon from the central North Pacific Ocean. Pacific salmon were caught using baited hooks attached to surface longlines. All samples were collected from mid-June to mid-July 1991 to 1997, at stations from 38°30'N to 58°30'N along a transect at 179°30'W (Nagasawa et al., 1993; Fig. 1A). Only adult female *L. salmonis* were counted. In 2005, we repeated the sampling conducted by Nagasawa (2001) so that the juvenile stages of all species of sea lice could be recorded. We sampled on board the Japanese research vessel, R/V *Wakatake maru* and along the same transect line as in the Nagasawa (2001) study (Fig. 1A). Pacific salmon collected from the longline gear as well as in the gillnets were sampled for sea lice as described by Nagasawa (2001), except that all stages and species of

Table 4

Prevalence and intensity of sea lice on sub-adult Pacific salmon collected with purse seines, April 2–May 30, 2003

	Number of fish	Average length (mm) ±S.D.	Prevalence (%)	Intensity
Coho salmon	10	337±62.2	70.0	3.4
Chinook salmon	25	233±58.2	72.0	3.4
Dolly Varden	21	185±48.4	57.1	2.1
Steelhead salmon	4	184±12.7	25.0	1.0

Species and stages of sea lice were not identified.

Table 5A

Abundance ($\times 10^6$) of juvenile Pacific salmon in 2003, 2004, 2005 in the Strait of Georgia and + 2 S.D.

		Pink salmon	Sockeye salmon	Chum salmon	Coho salmon	Chinook salmon	Total
2003	September	0.06±0.036	1.82±1.18	2.97±1.31	1.19±0.49	2.26±0.63	8.30
2004	July	5.20±4.10	2.32±2.31	11.57±6.45	2.77±0.74	4.92±5.32	26.78
2004	September	1.30±0.88	0.95±0.41	2.77±1.46	0.80±0.42	1.94±0.69	7.76
2005	July	0.03±0.02	0.31±0.15	12.18±4.97	0.57±0.24	0.93±0.33	14.02
2005	September	0.08±0.05	0.85±0.48	12.47±8.10	0.87±0.47	4.95±2.55	19.22

No samples were available for July 2003.

sea lice were counted. Sea lice information collected from fish captured using gillnets will be biased (Nagasawa, 1985); however, the data do provide information relating to the species and stages of sea lice. We included the information from salmon captured with gillnets only for comparison with the data collected from fish captured using longline gear. All sea lice were removed, preserved in 70% ethanol and transported back to our laboratory in Canada where identifications were made by the same experts that identified all sea lice reported in this paper.

4. Results

4.1. Comparison of the prevalence and intensity of sea lice on adult Pacific salmon captured on troll gear in August 2004 and 2005

The results of the 2004 troll-caught samples have been reported in Beamish et al. (2005b). Here we compare the 2004 results with the new observations from this study in 2005 that was conducted in the same area and at a similar time as in 2004. The prevalence of both species of sea lice and all stages was virtually identical in both years (Table 1). The intensities of all stages of both species of sea lice in 2004 compared to 2005 (Table 1) were not significantly different (Mann–

Whitney test, $P>0.05$). There was a higher intensity of mobile stages of *L. salmonis* on pink and sockeye salmon in 2005 (Table 1) compared to 2004, but the intensities on all species of Pacific salmon were not significantly different (Mann–Whitney test, $P>0.05$). The intensity of non-mobile and mobile *Caligus clemensi* was lower in 2005 than in 2004; however, only the intensity of mobile *C. clemensi* was significantly lower (Mann–Whitney test, $P<0.05$; Table 1).

4.2. Troll and purse seine samples of juvenile and sub-adult Pacific salmon examined for sea lice

In early August 2004, the sample of 46 juvenile coho and chinook salmon captured using troll gear in the Queen Charlotte Sound area had a high prevalence of sea lice ranging from 90% to 100%, but a low intensity of about 1 (Table 2). Most sea lice were mobile stages of *L. salmonis*. A second, larger, sample of 241 juvenile coho and chinook salmon caught on troll gear late in 2004 also had a high prevalence of sea lice ranging from 87% to 93% (Table 3). Most sea lice were *L. salmonis* and most were in the mobile stage (Table 3). The intensity of sea lice on coho (3.9) and chinook (4.2) salmon was higher (Table 3) than observed from the sample collected in August 2004 (Table 2).

Table 5B

Catch and catch per unit effort (CPUE) of juvenile Pacific salmon in trawl surveys in July and August 2003, 2004 and 2005 in Queen Charlotte Strait and Strait of Georgia

		Pink salmon		Sockeye salmon		Chum salmon		Coho salmon		Chinook salmon		Total number of Pacific salmon	Total CPUE
		Number	CPUE	Number	CPUE	Number	CPUE	Number	CPUE	Number	CPUE		
Queen Charlotte Strait	2003 Jul 30–Aug 8	1123	30.8	168	4.6	8315	228.0	521	14.3	179	4.9	10306	282.6
	2004 Jun 24–Jul 3	12740	249.8	10205	200.1	8903	174.6	680	13.3	61	1.2	32589	639.0
	2005 Jul–Aug *	308	10.9	88	3.1	1028	36.3	125	4.4	94	3.3	1643	58.0
Strait of Georgia	2004 Jul 4–13	4776	63.7	2345	31.3	10262	276.9	2679	59.5	3864	77.2	23926	508.6
	2005 Jul 14–21	26	0.4	317	453.7	11473	4.8	416	10.9	694	18.1	12926	487.9

* July 12, 13, 29, 31, Aug 1, 2.

Table 5C

Catch and catch per unit effort (CPUE) of juvenile Pacific salmon in September and October trawl surveys in 2003, 2004 and 2005 in Queen Charlotte Strait and Strait of Georgia

		Pink salmon		Sockeye salmon		Chum salmon		Coho salmon		Chinook salmon		Total number of Pacific salmon	Total CPUE
		Number CPUE		Number CPUE		Number CPUE		Number CPUE		Number CPUE			
		Number	CPUE	Number	CPUE	Number	CPUE	Number	CPUE	Number	CPUE		
Queen Charlotte Strait	2003 Sep 23–27	620	45.9	53	3.9	256	19.0	58	4.3	90	6.7	1077	79.8
	2004 Sep 22–Oct 1	1386	40.2	82	2.4	887	25.7	51	1.5	109	3.2	2515	73.0
	2005 Sep 7–13	1987	67.4	89	3.0	2686	91.1	278	9.4	169	5.7	5209	176.6
Strait of Georgia	2003 Sep 13–20	51	1.4	1558	40.6	2592	67.7	841	21.9	1260	31.1	6302	162.7
	2004 Oct 7–18	788	24.7	636	20.1	1800	56.6	402	12.6	736	22.9	4362	136.9
	2005 Sep 14–21	64	2.4	737	27.3	11075	410.2	507	18.0	2467	81.1	14850	53.9

The sample of 60 fish representing four species of sub-adult Pacific salmonids caught in seines in 2003 in the vicinity of Broughton Island had a high prevalence of sea lice (57.1%–72.0%) except for steelhead (*O. mykiss*, 25%, Table 4). The prevalence on coho and chinook salmon was similar at 70% and 72% respectively (Table 4). Dolly Varden (*Salvelinus malma*) are not commonly found in the more open ocean areas, but were relatively abundant in this sample. The intensity of sea lice on coho and chinook salmon was identical at 3.4 sea lice per fish (Table 4). The species and stages of sea lice were not determined for this sample.

4.3. Juvenile Pacific salmon abundance studies

Juvenile Pacific salmon of all five species of Pacific salmon were common in the trawl catches in the Central Coast and Strait of Georgia in 2003, 2004 and 2005 (Tables 5A B C) with pink and chum salmon dominant in all years. Juvenile pink salmon were most abundant in even numbered years (2004) when juvenile pink salmon from the Fraser River entered the ocean. Pink salmon virtually all spawn in the Fraser River only in odd numbered years (Neave, 1952), which results in their offspring entering the ocean in even numbered years. Thus, very low catches of juvenile pink salmon

Table 6

Prevalence and intensity of sea lice on juvenile Pacific salmon sampled using trawl gear in the Broughton Island area, Queen Charlotte Strait and Rivers and Smith inlets, August 2003

		Species				
		Pink salmon	Sockeye salmon	Chum salmon	Coho salmon	Chinook salmon
Broughton Area	Number of fish	422	41	202	99	80
	Average length (mm)	135	142	148	190	156
	Prevalence (%)	7.8	80.5	5.0	24.2	13.8
	Intensity	1.0	6.5	1.1	1.8	1.2
Queen Charlotte Strait	Number of fish	154	109	388	129	2
	Average Length (mm)	135	151	171	208	243
	Prevalence (%)	14.9	88.1	26.8	44.2	50.0
	Intensity	1.7	7.4	2.0	1.5	1.0
Smith and Rivers inlets	Number of fish	53	81	104	61	65
	Average length (mm)	107	102	173	222	176
	Prevalence (%)	17.0	51.9	24.0	59.0	20.0
	Intensity	1.0	2.0	1.0	1.4	1.5
Total	Number of fish	629	231	694	289	147
	Prevalence (%)	10.3	74.0	20.0	40.5	17.0
	Non-mobile stages (%)	2.9	72.3	16.1	12.1	4.8
	Mobile <i>L. salmonis</i> (%)	7.2	4.8	3.7	30.4	18.4
	Mobile <i>C. clemensi</i> (%)	0.8	1.7	0.6	1.4	0
	Intensity	1.2	5.9	1.7	1.5	1.3

occur in odd numbered years. Catches of coho and chinook salmon were generally smaller than the other species, with their combined abundances averaging 28% of the catch in July and September. Abundance estimates for juvenile Pacific salmon in the Strait of Georgia in 2004 and 2005 in July totaled 26.78 million and 14.02 million, respectively (Table 5A). In September 2003, 2004 and 2005, the total abundances were 8.30 million, 7.76 million and 19.22 million, respectively (Table 5A). The abundance in September 2005 was more than double the abundance in September 2004 and 2003. A comparison of the standardized catches in Queen Charlotte Strait with the Strait of Georgia (Tables 5B C) showed that there were large numbers of juvenile Pacific salmon in Queen Charlotte Strait at the same time as in the Strait of Georgia, although the species composition differed between the two areas. The trawl catches in Queen Charlotte Strait indicated that juvenile Pacific salmon were abundant relative to the Strait of Georgia. The CPUE of pink salmon and sockeye salmon was substantially larger in Queen Charlotte Strait in July 2004 than in the Strait of

Georgia. Coho and chinook salmon were less abundant in Queen Charlotte Strait as indicated by the comparisons of CPUE. In September, in Queen Charlotte Strait, pink salmon CPUE remained high relative to the Strait of Georgia (Table 5C). The CPUE of the other four species in Queen Charlotte Strait was generally lower in September (Table 5C).

4.4. Sea lice on juvenile Pacific salmon captured using trawl gear in the Central Coast area, August 2 to 6, 2003

In August 2003, 629 juvenile pink salmon, 694 juvenile chum salmon and 231 juvenile sockeye salmon were captured in the Central Coast area. The prevalence of all species of sea lice on these juveniles was 10%, 20% and 74%, respectively (Table 6). The intensity for pink, chum and sockeye salmon was 1.2, 1.7 and 5.9, respectively. Most mobile sea lice were *L. salmonis* and chalimus were the dominant stage. Juvenile sockeye salmon were heavily infected with sea lice. The prevalence of 74.0% consisted of almost all chalimus stages (Table 6). Juvenile coho and juvenile/sub-adult

Table 7
Prevalence and intensity of sea lice observed from fish sampled from longlines and gillnets on the R/V *Wakatake maru*, July 2005

Species	Gear	Number of fish	Length (mm) ±S.D.	Number of sea lice	Prevalence (%)	Intensity	Prevalence (%)	Prevalence (%)	Prevalence (%)	Prevalence (%)	Prevalence (%)	Prevalence (%)
							copepodid <i>L. salmonis</i>	chalimus <i>L. salmonis</i>	mobile <i>L. salmonis</i>	mobile male <i>L. salmonis</i>	non-gravid female <i>L. salmonis</i>	gravid female <i>L. salmonis</i>
Pink salmon	Longline	45	474±30.7	803	100	17.7	2.2	7.5	90.3	18.2	50.3	33.8
	Gillnet	62	479±27.1	341	85.5	6.4	3.2	5.6	91.3	8.0	76.3	44.5
Sockeye salmon	Longline	4	552±90.0	3	25.0	3.0	0	100	0	0	0	0
	Gillnet	9	489±95.6	2	11.1	2.0	0	0	100	50.0	0	0
Chum salmon	Longline	30	493±48.4	109	76.7	4.7	0	1.9	98.1	21.5	63.6	39.3
	Gillnet	10	444±84.8	3	20.0	1.5	0	100	0	0	0	0
Coho salmon	Longline	20	519±37.5	48	70.0	3.5	0	8.3	91.7	20.8	62.5	47.9
	Gillnet	5	560±22.2	7	40.0	3.5	0	0	100	0	100	100
Chinook salmon	Longline	3	496±116.5	31	100	10.3	0	0	100	3.2	96.8	51.6
	Gillnet	1	–	7	100	7.0	0	14.3	85.7	14.3	42.9	28.6
Steelhead salmon	Longline	3	593±48.8	11	100	3.7	18.2	36.4	45.5	9.1	27.3	18.2
	Gillnet	1	–	9	100	8.0	0	0	100	25.0	62.5	50.0
Total or Average	Longline	105	495±50.5	1005	84.5	11.3	1.9	7.4	90.7	18.0	53.4	35.0
	Gillnet	88	482±54.3	369	68.2	6.1	3.0	6.3	90.7	8.5	74.7	44.8

chinook salmon were also sampled for sea lice. The prevalence observed on these trawl-caught samples was lower (Table 6) than observed when coho and chinook salmon were captured with troll gear (Table 2), but the intensity was similar.

4.5. Samples collected on the R/V *Wakatake maru*

There were 193 Pacific salmon sampled from the central subarctic Pacific for sea lice of which 88 were captured using gillnets and 105 were captured on longlines (Table 7). All sea lice were *L. salmonis*. The average prevalence on all salmonids captured on longlines was 84.5% with an intensity of 11.3. Most of the *L. salmonis* were mobile stages of which 53.4% were females and 35.0% of the females were gravid (Table 7). Chalimus and copepodid stages represented 9.3% of all sea lice. Pink salmon were the most heavily infected (intensity of 17.7), but the intensity of 10.3 for chinook salmon was also high. The prevalence and intensity of *L. salmonis* on fish captured using gillnets was smaller (Table 7).

The observations of sea lice prevalence and intensity of adult female *L. salmonis* on Pacific salmon (excluding steelhead trout) collected in the central subarctic Pacific by Nagasawa (2001) were compared with the observations from adult Pacific salmon in the coastal

waters in 2004 and 2005 (Table 8) using a Mann–Whitney test. There were no differences in the intensity of adult female *L. salmonis* between the Nagasawa (2001) study and the intensities observed in the coastal area ($P > 0.05$). The prevalence of adult *L. salmonis* on Pacific salmon in the coastal area was significantly higher than observed in the Nagasawa (2001) study ($P < 0.05$) in 2005 but not in 2004 ($P > 0.05$).

5. Discussion

5.1. Evidence that sea lice are transported into all coastal areas

Our studies of the prevalence and intensity of sea lice on adult Pacific salmon in 2004 (Beamish et al., 2005b) and repeated in this study for 2005 indicate that sea lice in general, and *L. salmonis* in particular, are commonly found on adult Pacific salmon in the Central Coast area of British Columbia. The prevalence in both years was virtually identical. The intensity observed in 2005 differed from 2004, as there were fewer *C. clemensi*. However, the average intensity of the mobile stages of both species of sea lice in both years on all salmon combined was not significantly different. These reports of the prevalence and intensity of sea lice on all species of adult Pacific salmon in a coastal ecosystem are the

Table 8
Comparison of observations of sea lice by Nagasawa (2001) and observations of sea lice in coastal British Columbia

Species	Number of fish		Prevalence of adult female <i>L. salmonis</i> (%)				Intensity of adult female <i>L. salmonis</i>			
	Nagasawa (2001)	R/V <i>Wakatake maru</i> (2005)	Nagasawa (2001)	R/V <i>Wakatake maru</i> (2005)	Coastal British Columbia (2004)*	Coastal British Columbia (2005)	Nagasawa (2001)	R/V <i>Wakatake maru</i> (2005)	Coastal British Columbia (2004)*	Coastal British Columbia (2005)
Pink salmon	1664	45	93.8	95.6	85.6	96.7	5.9	8.9	5.2	9.0
Sockeye salmon	528	4	7.8	0	96.8	98.0	1.0	0	8.8	11.5
Chum salmon	4807	30	36.4	60.0	80.6	100	2.1	3.0	3.0	2.0
Coho salmon	495	20	63.9	55.0	79.6	79.0	2.4	2.1	4.8	3.7
Chinook salmon	108	3	80.6	100	80.0	84.0	5.3	10.0	6.5	6.0
Steelhead trout	90	3	91.5	66.7	–	–	6.1	1.0	–	–
Total or average	7692	105	49.9	73.3	83.3	88.0	3.8	6.4	5.9	7.2

Observations from Nagasawa (2001) and the R/V *Wakatake maru* (2005) are for longline catch only. Coastal British Columbia samples are from troll catches.

– not caught.

* Calculated from Beamish et al. (2005b).

first such comprehensive studies. It is clear that sea lice are commonly found on adult Pacific salmon at the time of their coastal migration.

The study of Nagasawa (2001) showed that Pacific salmon in the Central North Pacific Ocean had a high prevalence of adult *L. salmonis*. A total of 7692 Pacific salmon were examined in the Nagasawa (2001) study (Table 8). The results of our study that repeated the Nagasawa (2001) study confirmed that the prevalence of sea lice is high on Pacific salmon in the mid-subarctic Pacific. Our sample was small, but the prevalence and intensity of comparable stages of sea lice observed in our study were similar (Table 8) to those reported by Nagasawa (2001). The intensities of adult female *L. salmonis* on Pacific salmon on the high seas were also similar to those from the coastal samples of adult Pacific salmon (Table 8). The occurrence of non-mobile *L. salmonis* on samples collected in the mid-Pacific is evidence for high-seas transmission of this parasite. However, the non-mobile stages were much less abundant on the high seas samples than on the coastal samples, indicating that there is a higher rate of infection in the coastal areas than in the open ocean. There also were no *C. clemensi* in our sample, possibly indicating that *C. clemensi* is restricted to coastal habitats.

The survey in the mid-subarctic Pacific was in an area of overlapping distribution of Asian and North American origin Pacific salmon (Beamish et al., 2005a). Extensive tagging studies by a number of investigators have shown that the survey area used by Nagasawa (2001) was at the outer area of the distribution of stocks of both North American and Asian origin (Fig. 1; Groot and Margolis, 1991; Myers et al., 1996; Gritsenko, 2002). The overlap in Asian and North American stocks was greatest for pink and chum salmon and it is these two species of Pacific salmon that are the most abundant and most wide spread (Groot and Margolis, 1991). The common occurrence of *L. salmonis* on Pacific salmon at the outer margins of North American and Asian stocks indicates that the parasite could be carried back into coastal areas of the North Pacific where adult Pacific salmon aggregate before entering fresh water to spawn. We are not aware of any genetic comparisons for *L. salmonis* from coastal areas off Asia and North America. The results of such genetic differentiation studies might clarify the population structure of *L. salmonis*.

5.2. Evidence that sea lice occur on juvenile and sub-adult Pacific salmon in the coastal areas

The results of sea lice counts on the troll-caught juvenile coho and chinook salmon confirm that these

fish commonly are infected with sea lice. Counts of sea lice on these fish may be as accurate as possible because the individual fish were captured with hook and line and landed directly into a container that was inspected for any sea lice that may have been removed during capture. The high prevalence of sea lice on juvenile coho and chinook through to late November and early December indicates that it is probable that the sea lice remained on the fish throughout the winter. The sample of sub-adult Pacific salmon caught in seines in the spring of 2003 also showed that sea lice possibly were carried by these fish through the winter.

We were not able to catch juvenile pink, chum and sockeye salmon on hooks. Thus, we used samples of these juveniles collected by trawl gear to show that they were hosts for sea lice. Sea lice observations from Pacific salmon captured using trawls would not represent accurate estimates of intensity or prevalence, but the observations provide useful information relating to the occurrence of sea lice on these juvenile fish. The trawl samples showed that both non-mobile and mobile stages of *L. salmonis* were found on an average of 26% of all three species. Therefore, it is evident that juvenile pink, chum and sockeye salmon as well as coho and chinook salmon are infected with *L. salmonis* prior to migrating into the subarctic Pacific.

5.3. Evidence of sea lice on juvenile and sub-adult Pacific salmon in other areas

In southeastern Alaska in 2003, Wertheimer et al. (2003) reported observations of sea lice infections for 900 pink salmon, 657 chum salmon and 108 sockeye salmon captured from late July to late August using trawls. The average prevalence of sea lice on the combined samples for pink, chum and sockeye salmon was 4.5%, 8.4% and 23.2%, respectively. The average prevalence for 128 juvenile coho salmon was quite high at 57.8%. Bugaev (2005) reported the prevalence of sea lice on immature Pacific salmon from gillnet catches in the southwestern Bering Sea and off the east coast of Kamchatka from June to September. Only mobile stages were reported and all were *L. salmonis*. The average sizes of the Pacific salmon in the Bugaev (2005) study would indicate that the immature fish were not juveniles, but sub-adults. The prevalence for sockeye, chum and chinook was 2.4%, 10.2% and 70.4% respectively. Sviridov et al. (2004) reported sea lice levels on Pacific salmon captured in a trawl survey in the western Bering Sea and adjacent Pacific waters over a period from July 15 to October 23, 2005. They reported

that the percentages of immature chinook, pink, coho, chum and sockeye salmon that had sea lice was 36.0%, 29.7%, 24.0%, 4.8–8.1% and 1.1–1.7% respectively. The species and stages of sea lice were not identified. Ho and Nagasawa (2001) concluded that adult chum salmon that returned to the coastal waters off Japan in the late fall were the source of *L. salmonis* that infected juvenile rainbow trout (*O. mykiss*) that were cultivated in net pens in the coastal waters off Japan. We suggest that it is possible to conclude on the basis of the existing published observations that sea lice probably are commonly found on juvenile Pacific salmon during their residence in coastal waters.

5.4. Evidence that there is an overlap in the distributions of juvenile and adult Pacific salmon

Our trawl surveys showed that large numbers of juvenile Pacific salmon were in the same areas of the coast at the time that adult Pacific salmon were returning with the high levels of sea lice. Our surveys showed that juvenile Pacific salmon were commonly found in the coastal areas when adults are returning to spawn and at the time we sampled adult Pacific salmon for sea lice prevalence and intensity. We used a combination of absolute abundance estimates and relative abundance estimates using CPUE to show that the various species of juvenile salmon were abundant in two major juvenile salmon rearing areas from early July to late September. The abundances varied among species and years as might be expected. For example, in 2004, the relative abundances of pink, chum and sockeye salmon in the early summer in Queen Charlotte Strait were higher than in the Strait of Georgia. Chinook and coho salmon were also abundant in the Strait of Georgia at this time. It is useful to put estimates of abundance into perspective. To do this, we compared total juvenile abundances in the Strait of Georgia to total commercial catches. In 2004 and 2005 the total commercial catch of all species of Pacific salmon by Canada was 7.71 million and 9.97 million fish, respectively. The combined abundances of all juveniles in the Strait of Georgia in July 2004 and 2005 were 26.78 million and 14.02 million respectively. There is a natural mortality that occurs over the winter (Beamish et al., 2005b) between the juvenile stages we assessed and the return of adults. Also the total catch is for all species of Pacific salmon for all areas of the province. However, a comparison between the commercial catch and the juvenile abundance estimates provides a perspective that indicates that the juvenile abundances could be considered to be large. In general we concluded from the trawl studies in 2004 and

2005 that juvenile Pacific salmon were abundant in the coastal areas in July and August.

There also are a number of Russian and Japanese studies that showed that large abundances of juvenile chum and pink salmon remained inshore at the southern part of the Okhotsk Sea through to the fall (Karpenko, 2003; Mayama and Ishida, 2003). Thus, it is known that there is an overlap in the coastal distributions of returning adult Pacific salmon and juvenile pink, chum and sockeye salmon throughout the distribution of Pacific salmon.

5.5. Proposed life history strategy for *L. salmonis*

Tully and Nolan (2002) explored the concept that *L. salmonis* was distributed as a metapopulation within a region. In such a case, the survival of the metapopulation depended on immigration and colonization of new habitats within the metapopulation. There would be a cut-off distance between populations that would be defined by the longevity of the pre-chalimus stages and the particular ecosystem as defined by ocean conditions such as currents, salinity and temperature. Tully and Nolan (2002) suggested that the risk of extinction could be a function of habitat area that they considered was the population size of the host. We follow from their insights and suggest that the extinction risk of *L. salmonis* is related to ocean habitat size and host density. We propose that the transport of mobile and mature sea lice into coastal areas by adult Pacific salmon that are returning to spawn is part of a life history strategy of *L. salmonis* that brings the parasite into coastal waters where it can infect juvenile Pacific salmon. Infected juvenile salmon would transport the parasite into the high seas where the life cycle of the parasite would continue. Infected juvenile salmon would also carry the parasite over winter in coastal areas where the offspring of these sea lice can infect juvenile Pacific salmon when they enter the ocean in the spring (Fig. 2). The strategy is needed to compensate for the reduced sea lice transmission potential associated with reduced host densities in the open ocean when adult Pacific salmon return to the coastal areas and their spawning rivers.

Migration times vary according to species, stocks and location (Groot and Margolis, 1991), but it is common for most adult Pacific salmon to begin to leave the open ocean in time to arrive in the coastal areas in July, August and September (Fig. 2). It is the arrival of these adults that supports most commercial fisheries in coastal areas and particularly in Queen Charlotte Strait and the Strait of Georgia. In the coastal areas, we showed that there is an overlapping distribution of juvenile and adult

Pacific salmon of all species. *L. salmonis* does not survive more than several weeks in fresh water (McLean et al., 1990; Finstad et al., 1995) and is therefore not expected to survive on adult Pacific salmon following entry into spawning rivers in the late fall. Rather, the offspring of sea lice on the adult Pacific salmon would infect juvenile Pacific salmon during the period of overlapping distribution. These juvenile salmon generally move from the shallow near-shore areas in April and May into the coastal areas in June, July and August (Fig. 2). Pink, chum and sockeye salmon would begin to leave the coastal areas in August, September and October where they would carry the sea lice into the open ocean into the winter where the lice would mature. At the time of the migration into the open ocean, coho and chinook salmon would either migrate with the pink, chum and sockeye salmon or remain in the coastal areas. The fish that remained inshore would carry the sea lice over the winter. In the early spring in April and May, coho and chinook salmon would move into the near-shore area where they may feed on the juvenile salmon entering the ocean or on Pacific herring (*Clupea harengus pallasii*) that are also in the near shore. The offspring of the sea lice on these coho and chinook salmon would infect the juvenile Pacific salmon in the near-shore and coastal areas. Chinook salmon would carry sea lice for a number of years as they generally spend an average of 2 to 4 years in the ocean (Healey,

1991). Coho salmon would carry the sea lice through to the fall of the second year in the ocean when they mature and return to spawn in fresh water (Sandercock, 1991).

We conclude that the transport of *L. salmonis* into coastal areas is an evolutionary adaptation to ensure the parasite optimizes production during periods of reduced host densities in the open ocean when adult Pacific salmon return to the coastal areas. The overlapping distribution of adult and juvenile Pacific salmon in the coastal areas in the summer transfers *L. salmonis* to juvenile Pacific salmon that carry the parasite into the open ocean and into the nearshore areas in the following spring. The importance of our proposed life history strategy is that some juvenile Pacific salmon would be infected by resident salmon almost immediately after they entered the ocean. Infections from returning adult salmon would continue in the coastal areas where juvenile salmon grow prior to migrating into the high seas. According to this life history strategy, sea lice would infect juvenile Pacific salmon throughout their range in coastal areas. The strategy also insures that sea lice remain abundant on Pacific salmon that reside in the open ocean.

Acknowledgments

This research was partially funded by the Innovation Council of British Columbia and the Aquaculture

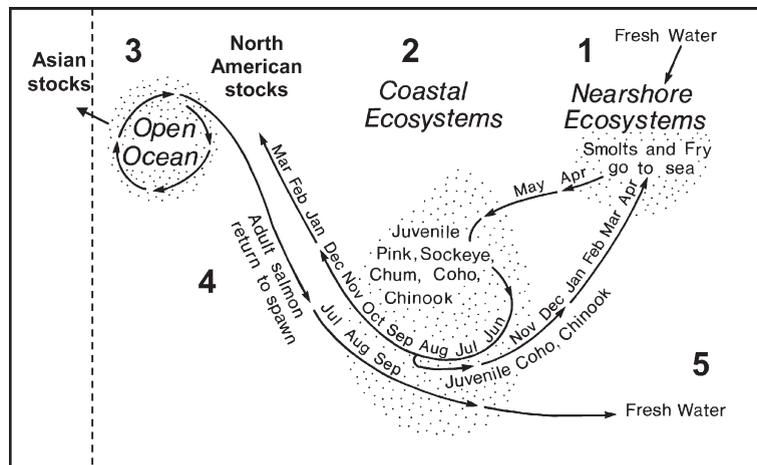


Fig. 2. Summary of the proposed life history strategy. The general migration and timing of juvenile Pacific salmon from the coastal areas to the open ocean and return. Stippled areas represent the areas where sea lice infection occurs on Pacific salmon. 1. The nearshore ecosystem is the area where juvenile Pacific salmon first enter the ocean. Infections in this area would come from sea lice on resident juvenile coho and chinook salmon that spend the fall, winter and spring (November to April) in the coastal and nearshore areas and may be feeding on the young salmon. 2. The coastal ecosystem is the area of overlapping distributions of adult and juvenile Pacific salmon. It includes the larger marine areas off the coast of British Columbia such as Queen Charlotte Strait which is also a major fishing area for returning Pacific salmon. 3. The open ocean is the high seas area where Pacific salmon stocks from both North America and Asia feed and grow. 4. Most adult salmon leave the open ocean and return to the coastal areas by July through to September. 5. Adult Pacific salmon finish their migration by entering their natal rivers and streams. Any *L. salmonis* remaining on the salmon will die in the fresh water.

Collaborative Research and Development Program. We appreciate the support of the Fisheries Research Agency of Japan for permitting us to sample sea lice onboard the R/V *Wakatake maru* and Dr. Masa-aki Fukuwaka for his support and guidance. We appreciate the comments on an earlier draft by Dr. Bob Kabata and Dr. Alasdair McVicar. Lana Fitzpatrick and Maria Surry assisted in the preparation of the manuscript.

References

- Beamish, R.J., Folkes, M., 1998. Recent changes in the marine distribution of juvenile chum salmon off Canada. *N. Pac. Anadr. Fish. Comm. Bull.* 1, 443–453.
- Beamish, R.J., McCaughran, D., King, J.R., Sweeting, R.M., McFarlane, G.A., 2000. Estimating the abundance of juvenile coho salmon in the Strait of Georgia by means of surface trawls. *N. Am. J. Fish. Manage.* 20, 369–375.
- Beamish, R.J., McFarlane, G.A., King, J.R., 2005a. Migratory patterns of pelagic fishes and possible linkages between open ocean and coastal ecosystems off the Pacific coast of North America. *Deep-Sea Res., Part 2, Top. Stud. Oceanogr.* 52, 739–755.
- Beamish, R.J., Neville, C.M., Sweeting, R.M., Ambers, N., 2005b. Sea lice on adult Pacific salmon in the coastal waters of Central British Columbia, Canada. *Fish. Res.* 76, 198–208.
- Beamish, R.J., Jones, S., Neville, C., Sweeting, R., Kareman, G., Sakida, S., Gordon, E., 2006. Exceptional marine survival of pink salmon that entered the marine environment in 2003 suggests that farmed Atlantic salmon and Pacific salmon can coexist successfully in a marine ecosystem on the Pacific coast of Canada. *ICES J. Mar. Sci.* 63, 1326–1337.
- Brooks, K.M., 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.
- Bugaev, A.V., 2005. Sea lice *Lepeophtheirus salmonis* (Caligidae) infestation of Pacific salmon *Oncorhynchus* spp. on the data from driftnet catches in the Russian Economic Zone in 2004. *N. Pac. Anadr. Fish. Comm. Doc.* 865, 14 pp. KamchatNIRO, Kamchatka Fisheries and Oceanography Institute, Fisheries State Committee of Russia, Naberezhnaya Street 18, Petropavlovsk–Kamchatsky, Russia.
- Finstad, B., Bjørn, P.A., Nilsen, S.T., 1995. Survival of salmon lice, *Lepeophtheirus salmonis* Krøyer, on Arctic charr, *Salvelinus alpinus* (L.), in fresh water. *Aquac. Res.* 26, 791–795.
- Gritsenko, O.F., 2002. Atlas of Marine Distribution of Pacific Salmon during the Spring–Summer Feeding and Pre-Spawning Migrations. VNIRO Publishing, Moscow. 189 pp.
- Groot, C., Margolis, L., 1991. Preface. In: Groot, C., Margolis, L. (Eds.), *Pacific Salmon Life Histories*. U.B.C. Press, Vancouver, Canada, pp. ix–xi.
- Healey, M.C., 1991. The life history of chinook salmon (*O. tshawytscha*). In: Groot, C., Margolis, L. (Eds.), *Pacific Salmon Life Histories*. U.B.C. Press, Vancouver, Canada, pp. 313–393.
- Ho, J., Nagasawa, K., 2001. Why infestation by *Lepeophtheirus salmonis* (Copepoda: Caligidae) is not a problem in the coho salmon farming industry in Japan. *J. Crustac. Biol.* 21, 954–960.
- Johnson, S.C., Albright, L.J., 1991. The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). *Can. J. Zool.* 69, 929–950.
- Kabata, Z., 1972. Developmental stages of *Caligus clemensi* (Copepoda: Caligidae). *J. Fish. Res. Board Can.* 29, 1571–1593.
- Kabata, Z., 1973. The species of *Lepeophtheirus* (Copepoda: Caligidae) from fishes of British Columbia. *J. Fish. Res. Board Can.* 30, 729–759.
- Kabata, Z., 1979. Parasitic Copepoda of British fishes, 152. Ray Society, London, U.K., Publ., 468 pp.
- Karpenko, V.I., 2003. Review of Russian marine investigations of juvenile Pacific salmon. *N. Pac. Anadr. Fish. Comm. Bull.* 3, 69–88.
- Margolis, L., Esch, G.W., Homes, J.C., Kuris, A.M., Schad, G.A., 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). *J. Parasitol.* 68, 131–133.
- Mayama, H., Ishida, Y., 2003. Japanese studies on the early ocean life of juvenile salmon. *N. Pac. Anadr. Fish. Comm. Bull.* 3, 41–67.
- McLean, P.H., Smith, G.W., Wilson, M.J., 1990. Residence time of the sea louse, *Lepeophtheirus salmonis* K., on Atlantic salmon, *Salmo salar* L., after immersion in fresh water. *J. Fish Biol.* 37, 311–314.
- Myers, K.W., Aydin, K.Y., Walker, R.V., Fowler, S., Dahlberg, M.L., 1996. Known ocean ranges of stocks of Pacific salmon and steelhead as shown by tagging experiments, 1956–1995. *N. Pac. Anadr. Fish. Comm. Doc.* 192, FRI-UW-9614, Fisheries Research Institute, University of Washington, Seattle, 4p.+ figs.
- Nagasawa, K., 1985. Comparison of the infection levels of *Lepeophtheirus salmonis* (Copepoda) on chum salmon captured by two methods. *Jpn. J. Ichthyol.* 32, 368–370.
- Nagasawa, K., 2001. Annual changes in the population size of salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas Pacific salmon (*Oncorhynchus* spp.), and relationship to host abundance. *Hydrobiologia* 453/454, 411–416.
- Nagasawa, K., Ishida, Y., Ogura, M., Tadakoro, K., Hiramatsu, K., 1993. The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on six species of Pacific salmon in offshore waters of the North Pacific Ocean and Bering Sea. In: Boxshall, G.A., DeFaye, D. (Eds.), *Pathogens of Wild and Farmed Fish: Sea Lice*. Ellis Horwood Ltd., West Sussex, U.K., pp. 166–178.
- Neave, F., 1952. ‘Even-year’ and ‘odd-year’ pink salmon populations. *Proc. Trans. R. Soc. Can. Ser.* 3 46, 97–105.
- North Pacific Anadromous Fish Commission (NPAFC), 2001. Plan for NPAFC Bering–Aleutian Salmon International Survey (BASIS) 2002–2006. *N. Pac. Anadr. Fish. Comm. Doc.* 579, Rev. 2, 27 pp.
- Ricker, W.E., 1964. Ocean growth and mortality of pink and chum salmon. *J. Fish. Res. Board Can.* 21 (5), 905–931.
- Sandercock, F.K., 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In: Groot, C., Margolis, L. (Eds.), *Pacific Salmon Life Histories*. U.B.C. Press, Vancouver, Canada, pp. 396–445.
- Schram, T.A., 1993. Supplementary description of the developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). In: Boxshall, G.A., DeFaye, D. (Eds.), *Pathogens of Wild and Farmed Fish: Sea Lice*. Ellis Horwood Ltd., West Sussex, U.K., pp. 30–47.
- Sviridov, V.V., Glebov, I.I., Ocheretyanny, M.A., Kulik, V.V., 2004. Traumatization and infestation of the Pacific salmon in the western Bering sea and adjacent waters during summer–autumn period of 2003. *N. Pac. Anadr. Fish. Comm. Doc.* 752, Pacific Science Research Fisheries Center (TNIRO-center), Shevchenko Alley 4, Vladivostok 69095 Russia, 16pp.
- Tully, O., Nolan, D.T., 2002. A review of the population biology and host–parasite interactions of the sea louse, *Lepeophtheirus salmonis* (Copepoda: Caligidae). *Parasitol.* 124, S165–S182.

- Voth, D.R., 1972. Life history of the caligid copepod *Lepeophtheirus salmonis* Fraser, 1920 (Crustacea: Caligoidae). Diss. Abstr. Int., B. Sci. Eng. 33, 5547–5548.
- Wertheimer, A.C., Fergusson, E.A., Focht, R.L., Heard, W.R., Orsi, J.A., Sturdevant, M.V., Wing, B.L., 2003. Sea lice infection of juvenile salmon in the marine waters of the northern region of south-eastern Alaska, May–Aug 2003. N. Pac. Anad. Fish Comm. Doc. 706, Auke Bay Lab., Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, U.S. Dept. of Commerce, 11305 Glacier Highway, Juneau Alaska, 99801-8626, 13pp.
- Wooten, R., Smith, J.W., Needham, E.A., 1982. Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongates* on farmed salmonids and their treatment. Proc. R. Soc. Edinb. 81B, 185–197.