Disease induced by the sea louse (*Lepeophtheirus salmonis*) (Copepoda: Caligidae) in wild sockeye salmon (*Oncorhynchus nerka*) stocks of Alberni Inlet, British Columbia

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Abstract: The occurrence of the marine ectoparasitic copepod *Lepeophtheirus salmonis* and the prevalence of lesions caused by its feeding activities were monitored on sockeye salmon (*Oncorhynchus nerka*) adults returning to the Sproat and Stamp rivers through Alberni Inlet, British Columbia, in 1990 and 1992–1993. All sockeye examined were infected with *L. salmonis* and had higher intensities of infection than previously reported. The presence of high numbers of early developmental stages of *L. salmonis* suggests a high rate of infection for sockeye in coastal waters. Lesions attributable to *L. salmonis* ranged from minor skin discoloration to large open lesions that exposed the musculature. In 1990, when escapement into these river systems was delayed, sockeye holding in the inlet developed severe lesions and suffered high mortalities. High percentages of fish with open lesions entered both river systems in 1990, but few fish with open lesions were observed on the spawning grounds, suggesting additional prespawning mortality. In 1992 and 1993, when escapement patterns were more normal than in 1990, the severity of lesions owing to *L. salmonis* was reduced and no mortalities were observed. Throughout the study, fish in the Sproat River escapement had more severe lesions than those in the Stamp River escapement.

Résumé : Nous avons surveillé l'occurrence du copépode marin ectoparasite *Lepeophtheirus salmonis* et la prévalence des lésions causées par son activité alimentaire chez des adultes de saumon rouge (*Oncorhynchus nerka*) retournant aux rivières Sproat et Stamp en passant par l'inlet Alberni (Colombie-Britannique) en 1990 et en 1992–1993. Tous les saumons rouges examinés étaient infestés par *L. salmonis*, et présentaient des infestations plus intenses que ce qui avait été observé jusque-là. La présence d'un nombre important de parasites aux premiers stades du développement indique probablement un fort taux d'infestation des saumons dans les eaux côtières. Les lésions attribuables à *L. salmonis* allaient de simples altérations de la couleur de la peau à de grandes lésions ouvertes qui exposaient la musculature. En 1990, alors que la remonte vers ces cours d'eau a été retardée, les saumons rouges qui demeuraient dans l'inlet ont subi de graves lésions et une forte mortalité. Des pourcentages importants de poissons portant des lésions ouvertes ont pénétré dans les deux réseaux en 1990, mais rares étaient les individus atteints de lésions observés sur les frayères, ce qui permet de penser qu'il se produit une mortalité additionnelle avant la fraye. En 1992 et 1993, alors que les patrons des échappées étaient plus normaux qu'en 1990, la gravité des lésions dues à *L. salmonis* a baissé, et on n'a observé aucune mortalité. Tout au long de l'étude, les poissons de l'échappée de la rivière Sproat présentaient des lésions plus graves que ceux de l'échappée de la rivière Stamp.
[Traduit par la Rédaction]

Introduction

The marine ectoparasitic copepod *Lepeophtheirus salmonis* (Krøyer), often referred to as the salmon or sea louse, is commonly found on most species of wild and sea-farmed salmonids of the genera *Oncorhynchus*, *Salmo*, and *Salvelinus* in the northern hemisphere (Kabata 1979, 1988; Wootten et al. 1982; Pike 1989). The life cycle is direct, consisting of five phases and 10 stages. These include two free-swimming naupliar stages, one free-swimming infectious copepodid stage, four attached chalimus stages, two preadult stages, and an adult stage (Johnson and Albright 1991*a*). Attached copepodids,

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chalimus larvae, preadults, and adults feed on host mucus, skin, and blood (Kabata 1974; Brandal et al. 1976).

Epizootics of *L. salmonis* commonly occur in sea-farmed salmonids, causing serious disease and high mortality rates if untreated (Brandal and Egidius 1979; Wootten et al. 1982; Pike 1989). This disease is characterized by extensive areas of skin erosion and hemorrhaging on the head and back and a distinct area of erosion and subepidermal hemorrhage in the perianal region (Brandal and Egidius 1979; Wootten et al. 1982). Death may be caused by secondary bacterial infections (e.g., vibriosis), fungal infections acquired when fish return to fresh water, or, in severe cases, osmotic stress (Wootten et al. 1982).

Lepeophtheirus salmonis is common on wild salmonids but generally present only in low abundance and responsible for only minor host tissue damage (abrasion, dark coloration, and hemorrhages of the perianal region) (Wootten et al. 1982; Nagasawa 1987; Nagasawa et al. 1993; Nagasawa and Takami 1993). However, in certain situations, *L. salmonis* may be associated with disease conditions. Lesions that range in severity from discoloration to complete removal of the skin from the heads and backs of wild Atlantic salmon (*Salmo salar*) have been reported (Calderwood 1906; Huntsman 1918; White 1940, 1942) and attributed to sea louse feeding (Huntsman 1918; White 1940, 1942). In addition to forming foci for secondary fungal infections (Huntsman 1918), the presence of severe sea louse lesions coupled with high water temperatures were reported to cause the death of Atlantic salmon in Moser River, Nova Scotia, over the period of 1939–1942 (White 1940, 1942). Recently, high levels of mortality in wild postsmolt sea trout (*Salmo trutta*) in waters off the west coast of Ireland have been attributed to sea lice (Tully et al. 1993*a*, 1993*b*). These infections resulted in extensive tissue damage to the fins and dorsal body surfaces. Gilhousen (1989) reported that sockeye salmon caught in the Fraser River, British Columbia, were only lightly infected with *L. salmonis* during July and August of 1971. However, during September and October of the same year, he reported extensive parasitism by sea lice that resulted in the development of large abraded areas and open wounds, especially behind the dorsal fin and in the perianal region.

This paper documents the dynamics and severity of the sea louse disease outbreak in sockeye salmon stocks of Alberni Inlet, British Columbia, that occurred in 1990 when migration into the Somass River was delayed, as well as the dynamics and severity of sea louse disease in these stocks in years with normal migration patterns (1992 and 1993). These data provide the baseline information necessary to assess the causes and the impact of future sea louse disease outbreaks in these and other wild stocks of salmonids.

Materials and methods

Study area, stocks, and sampling

Alberni Inlet is a typical fjord situated on the southwest coast of Vancouver Island opening into the Pacific Ocean through Barkley Sound. Oceanographic conditions of the inlet are given in Morris and Leaney (1980). Within the Alberni watershed, Sproat, Great Central, and Henderson lakes support sockeye stocks (Hyatt and Steer 1987). The Stamp and Sproat rivers drain Great Central and Sproat lakes, respectively. These rivers join to form the Somass River, which drains into the head of Alberni Inlet. Sampling was conducted at fishways located approximately 0.5 km below the outlet of Sproat Lake and at a dam that forms the outlet of Great Central Lake. Details concerning sockeye abundance, annual run timing, and the fisheries they support are found in Hyatt and Steer (1987).

In 1990, samples of sockeye from Alberni Inlet were caught using a commercial gill-net boat equipped with a 11-cm mesh gill net. In 1991–1993, samples were obtained from commercial seine and gill-net boats. In all years, samples from the fishways of the Sproat and Stamp rivers were caught in traps that form part of the fishways. Beach seining was used to collect samples from the spawning grounds within Sproat and Great Central lakes in 1990.

Data on the abundance of sea lice were obtained from samples of fish collected by gill net (1990 and 1991), longline, trawl, or seine (1992). Upon landing, fish were placed immediately in individual plastic bags and stored frozen prior to examination. Whole fish were examined under a dissecting scope. All sea lice were counted and the general developmental stage (copepodid, chalimus, preadult, or adult) was noted. Preadult and adult stages were identified to species.

The terms prevalence and abundance as used in this paper are defined by Margolis et al. (1982). The term escapement refers to those fish that escape capture and enter the the lake systems.

Lesion classification

Data on the prevalence and severity of sea louse lesions and other wounds and scars were collected in the fall and winter of 1990. Samples obtained from the fishways of the Sproat and Stamp rivers in September were classified as (*i*) unmarked, (*ii*) open lesions (dorsal lesions extending through to the dermis, exposing underlying musculature), and (*iii*) other marks (this category includes lesions in which the dermis was not breached, as well as fungal disease, predator wounds, and marks attributed to commercial fishing activities). Lesions on samples collected from the spawning grounds in the fall and winter were classified as having mild (one open lesion), moderate (two or three open lesions), or severe (more than three open lesions) external damage.

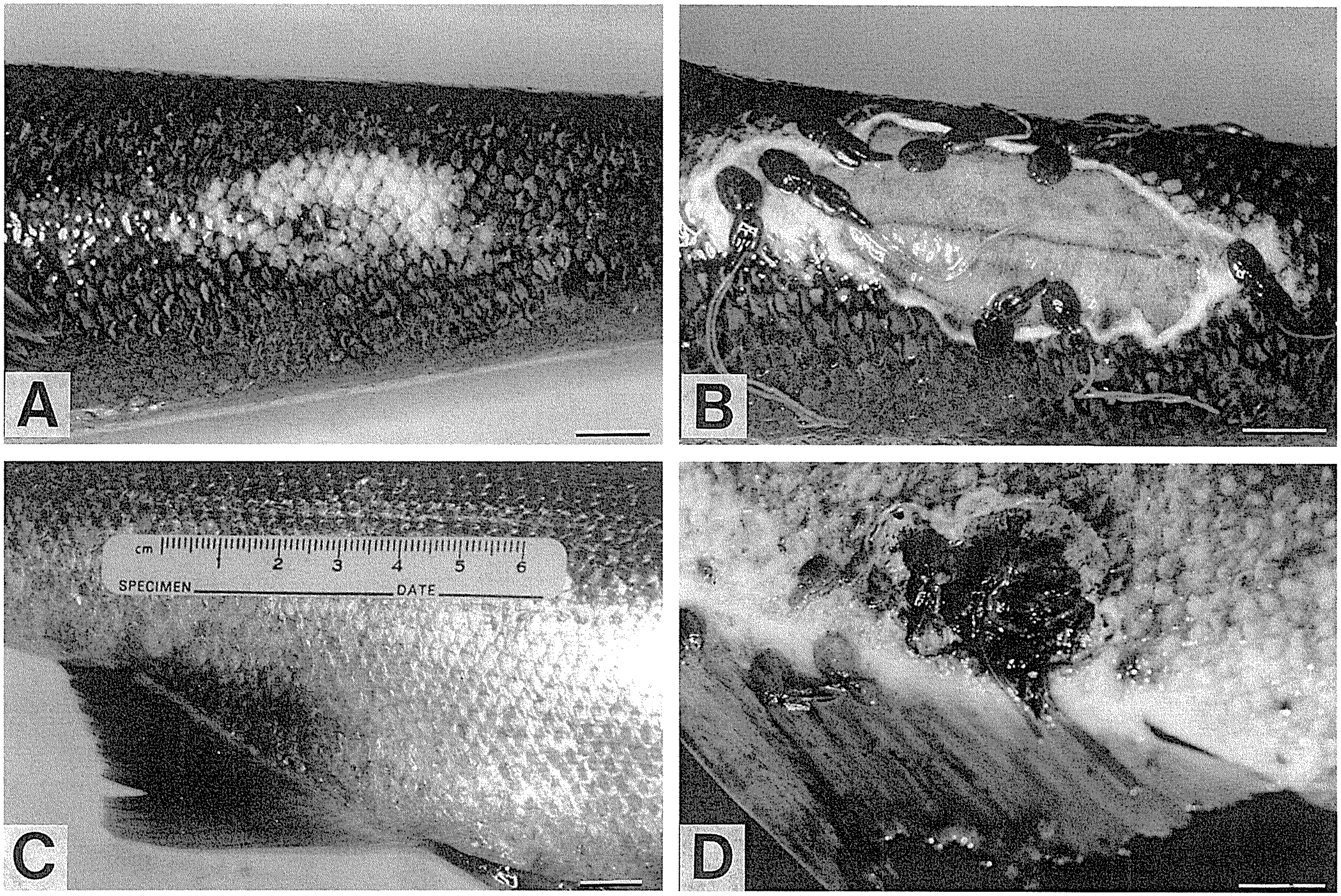
In the summer and fall of 1992 and 1993, data on the prevalence and severity of sea louse lesions were collected from test fishery samples obtained from Alberni Inlet by gill net or seine and from escapement samples from the fishways of the Sproat and Stamp rivers. Lesions attributable to sea lice occurred on the head, at the base of and posterior to the dorsal fin, and in the perianal region, and were ranked as follows. (A) Posterior to dorsal fin, base of dorsal fin, and head: rank 0, unmarked; rank 1, grazing evident, with discoloration of skin surface, and in some cases mild descaling and hemorrhaging; rank 2, early white lesion, with partial removal of epidermis and scales resulting in patches of grayish to whitish necrotic tissue; rank 3, white lesion, with epidermis and scales removed, lesions covered with continuous whitish necrotic tissue, and no breaks in skin exposing musculature (Fig. 1A); rank 4, early open lesion, white lesion with small (1–2 mm) point lesions open to musculature; and rank 5, open lesion, with epidermis and dermis removed exposing musculature (Fig. 1B). (B) Perianal region: rank 0, unmarked; rank 1, grazing evident, characterized by discoloration of skin surface and in some cases blood seepage from the scale pockets; rank 2, mild descaling and hemorrhaging; rank 3, extensive discoloration, descaling, and hemorrhaging (Fig. 1C); rank 4, early open lesion, with extensive descaling and hemorrhaging with small point lesions (1–2 mm) open to the musculature; and rank 5, open lesion, with epidermis and dermis removed, exposing musculature (Fig. 1D).

An overall lesion score (LS) of sea louse wounds was calculated for each fish by summing the rank for each of the four regions above. The LS could have a value of 0–20, with 20 representing the most severe damage.

Microbiology and histology

Because of high levels of mortality in 1990, samples of gill, kidney,

Fig. 1. Lesions caused by *Lepeophtheirus salmonis* on sockeye salmon (*Oncorhynchus nerka*). (A) Rank 3, white lesion posterior to the base of the dorsal fin. (B) Rank 5, open lesion posterior to the base of the dorsal fin. Note the exposed musculature and several adult female *L. salmonis* feeding within the lesion. (C) Rank 3, perianal region with extensive discoloration, descaling, and hemorrhaging. (D) Rank 5, perianal region with open lesion. Note the exposed musculature. Scale bars = 1.0 cm.



spleen, and pyloric ceca were collected from freshly killed sockeye adults caught in the inlet and rivers and assayed for the presence of bacteria and viruses according to standard techniques (Anonymous 1984). Bacteriological samples were streaked on plates of TSA and TSA plus salt, incubated in air at 20°C, and checked for growth after 2 and 8 days. Bacterial isolates as well as smears of kidney and gut were examined by employing standard biochemical techniques (Anonymous 1984). Virological samples were homogenized in Earle's balanced salt solution and centrifuged. Supernatants were collected, serially diluted, inoculated onto an epithelial papilloma cyprinid cell line, and monitored for 2–3 weeks for the formation of plaques. Samples of external lesions, gill, kidney, pyloric ceca, lower intestine, liver, and spleen were also collected from freshly killed individuals, fixed in Davidson's solution, and dehydrated through to 100% alcohol. Tissues were wax embedded, cut to a thickness of 5 μm, and stained with hematoxylin and eosin. Sections of lesions from fish collected in fresh water were also stained with periodic acid Schiff's and Gram's stains.

Statistical analysis

The distribution of LS on fish collected from Alberni Inlet between years (1992 and 1993) was compared using Pearson's χ^2 statistic. Lesion scores on the escapement samples from Sproat and Stamp rivers were compared both between years and between systems using Pearson's χ^2 statistic. The effects of host sex, hypural length, and sea age on lesion sums were investigated using Spearman's rank correlation.

Results

Lepeophtheirus salmonis was the dominant parasitic copepod collected during this study, although a few *Caligus clemensi* chalimus larvae and adults were found. In all samples, the prevalence of *L. salmonis* was 100% and all developmental stages, except for the free-swimming naupliar stages, were found (Table 1). Sockeye collected in September 1990 were the most heavily infected, with a mean of 300 *L. salmonis*/fish (range 49–1372). Observation of copepods made in the field on other dates in 1990 estimated up to approximately 300 preadults and adults present. The mean abundance of *L. salmonis* in 1991 and 1992 was considerably lower, ranging from 7.4 to 77.1 copepods/fish. Sockeye collected offshore, near the Queen Charlotte Islands, and from the surf zone at the mouth of Alberni Inlet in 1992 had mean abundances of 22.5 and 71.7 copepods/fish, respectively (Table 1). Copepodids and chalimus larvae were found most commonly on the body (68.4 and 52.6%, respectively), followed by the fins (29.0 and 43.3%, respectively) and then the gills (2.6 and 4.0%, respectively).

Alberni Inlet

In early to mid-September 1990, moribund sockeye with heavy infections of *L. salmonis* were commonly observed swimming at the surface of Alberni Inlet. Almost 100% of sockeye collected from Alberni Inlet during this time were heavily infected with *L. salmonis* and had lesions caused by sea louse feeding. In 87% of these fish the ulcers extended through the dermis, exposing the underlying musculature. These ulcers occurred most commonly on the dorsal and lateral surfaces of the head and the dorsal surface posterior to the dorsal fin. In addition, most fish had multiple shallow ulcers, epithelial abrasions, and scale loss that could not be attributed to netting.

Table 1. Abundance of *Lepeophtheirus salmonis* developmental stages on maturing sockeye salmon (*Oncorhynchus nerka*) in Alberni Inlet and offshore waters.

Date and locality	Sampling method	Sample size	Copepodids		Chalimus larvae		Preadults		Adults		Total copepods	
			Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range
Sept. 17, 1990,[a] Alberni Inlet	Gill net	9	95.4±210.5	0–633	141.2±223.2	12–721	17.6±17.8	4–63	45.8±27.6	9–85	300.0±424.8	49–1372
July 23, 1991,[b] Alberni Inlet	Gill net	15	1.1±2.4	0–9	9.6±10.6	0–40	0.6±0.7	0–2	15.5±10.7	1–35	26.9±13.1	3–59
June 28, 1992, Alberni Inlet mouth	Trawl	3	11.3±11.0	5–24	15.3±0.6	15–16	12.7±5.5	7–18	32.3±11.0	25–45	71.7±14.6	55–82
July 1, 1992, Alberni Inlet	Seine	21	0.6±1.6	0–6	2.3±2.4	0–6	1.0±1.3	0–5	3.5±2.7	0–9	7.4±4.7	0–18
July 7, 1992, Alberni Inlet	Seine	22	28.5±41.5	0–180	28.6±30.4	4–106	5.3±8.2	0–39	14.2±11.7	0–41	77.1±61.1	15–220
July 19, 1992, offshore	Longline	2	3.5±5.0	0–7	1.0±1.4	0–2	6.0±2.8	4–8	12.0±2.8	10–14	22.5±3.5	20–25
July 20–21, 1992, Alberni Inlet	Seine	33	0.2±0.5	0–2	10.7±13.1	0–58	0.6±0.8	0–2	4.9±3.4	1–17	16.5±13.6	3–64

[a]Some sample bags were torn, which may have resulted in copepod loss.
[b]Body of fish was not examined for copepodids and chalimus larvae.

Fig. 2. Distribution of lesion scores (see text) for Alberni Inlet sockeye (*Oncorhynchus nerka*) collected in July and August of 1992 and 1993. Examined fish were from test fishery samples collected in July and August of each year.

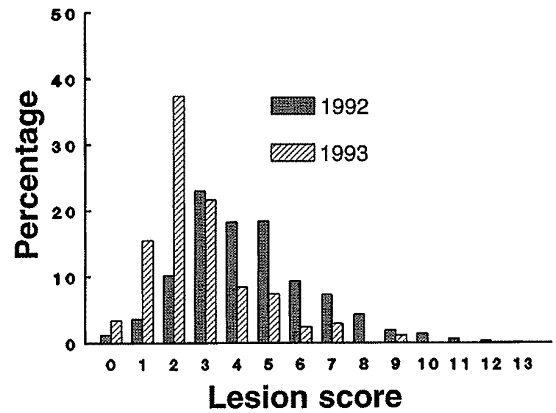
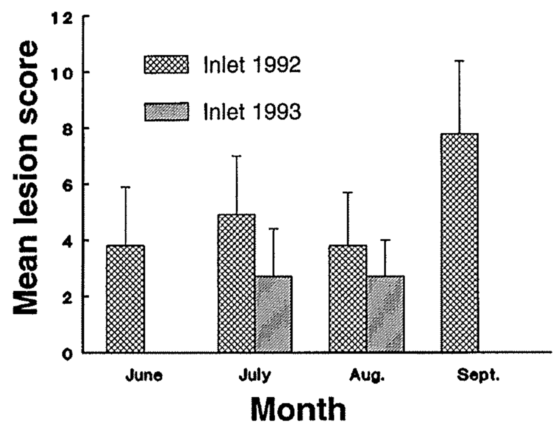


Fig. 3. Mean (+SD) monthly lesion scores for Alberni Inlet sockeye (*Oncorhynchus nerka*) collected in 1992 and 1993.



Scale removal, blood seepage, and tissue darkening occurred in the perianal region of most fish.

Examination of tissue samples collected for bacteriology and virology revealed no disease organisms that might account for the morbidity. Tissue sections of fins where chalimus larvae were feeding revealed mild epithelial hyperplasia associated with the frontal filaments, epidermal erosion at the feeding sites, and a small amount of inflammatory infiltrate. Tissue sections of the large open lesions revealed a progressive deepening of the lesions toward the center where both the epithelium and dermis were removed and the underlying muscle was exposed. Congestion occurred in the blood vessels of the exposed muscle, but little inflammation was observed. A small amount of filamentous bacteria was present on the surface of approximately 15% of the lesions and within the tissue (dermis or muscle) immediately beneath it.

Histological examination of the gills revealed no abnormalities. Examination of the internal organs revealed only a mild inflammatory response associated with a normal level of infection (5–20 worms) by the nematode *Philonema oncorhynchi*.

Table 2. Percentage of Alberni Inlet sockeye salmon (*Oncorhynchus nerka*) with lesions (see text) attributed to the feeding activities of *Lepeophtheirus salmonis* by body region and month for 1992 and 1993.

Lesion position and month	Lesion ranking						No. of fish examined
	0	1	2	3	4	5	
Posterior to dorsal fin							
June 1992	6.8	39.5	31.1	19.2	2.3	1.1	177
July 1992	0.5	15.1	58.4	17.9	1.8	6.3	397
August 1992	10.7	32.6	26.5	20.8	0.7	8.7	298
September 1992	0	11.2	14.4	54.4	4.8	15.2	125
July 1993	22.5	55.7	12.1	7.1	1.1	1.4	280
August 1993	7.0	70.0	8.0	10.0	1.0	4.0	100
Base of dorsal fin							
June 1992	93.2	2.3	2.3	1.1	0	1.1	177
July 1992	63.0	24.2	8.8	3.8	0	0.3	397
August 1992	48.0	46.0	3.4	2.0	0	0.7	298
September 1992	0.8	87.2	2.4	5.6	0.8	3.2	125
July 1993	72.9	25.7	1.1	0.4	0	0	280
August 1993	76.0	23.0	0	1.0	0	0	100
Head							
June 1992	97.7	0.6	1.7	0	0	0	177
July 1992	99.7	0	0	0	0	0.3	397
August 1992	94.3	0.3	1.7	2.3	0.3	1.0	298
September 1992	18.4	40.8	8.8	13.6	6.4	12.0	125
July 1993	99.3	0.4	0	0.4	0	0	280
August 1993	100.0	0	0	0	0	0	100
Perianal							
June 1992	9.6	44.6	0	44.6	0	1.1	177
July 1992	0.8	48.6	0	46.9	0.5	3.3	397
August 1992	2.3	86.9	9.1	1.3	0	0.3	298
September 1992	0.8	68.6	0.2	24.0	2.4	3.2	125
July 1993	9.6	67.1	12.9	8.9	0.4	1.1	280
August 1993	1.0	95.0	4.0	0	0	0	100

Lesions similar to those seen in 1990 occurred on fish examined in 1992 and 1993, although their severity was not as great, and moribund and dead fish were not observed. Fish collected in July and August of 1992 had higher LS than fish collected in July and August of 1993 (Pearson's χ^2, $P < 0.001$; Figs. 2 and 3), and in 1992 the LS increased over time from approximately 4 in June to approximately 8 in September (Fig. 3). In both 1992 and 1993 the severity of lesions at the base of the dorsal fin, on the head, and in the perianal region was low, with the majority of fish being either unmarked (rank 0) or only mildly damaged (rank 1) in these regions (Table 2). With respect to the region posterior to the dorsal fin, there were more severe lesions (rank 2 or higher) in 1992 than in 1993 (Table 2).

Escapement samples

In September 1990, there were higher percentages of fish with open or severe lesions in the Sproat River than in the Stamp River (Tables 3 and 4). From 47 to 100% of the Sproat fish had open lesions compared with 13 to 34% of the Stamp fish (Table 3). The severity of lesions on fish in the escapement samples collected from both rivers in 1992 and 1993 was less than in 1990, and the severity of lesions, as measured by the mean monthly LS, was greater in 1992 than in 1993 (Fig. 4).

Table 3. Percentage of sockeye salmon (*Oncorhynchus nerka*) from the Sproat and Stamp rivers with dorsal lesions and (or) other marks in September 1990.

Date (in 1990)	Location	Sampling method	*n*	Unmarked	Open lesions	Other marks
Sept. 12	Sproat	Observer	ns		100	
Sept. 12	Stamp	Observer	143	79	13	8
Sept. 13	Sproat	Trap	50	2	78	20
Sept. 13	Stamp	Trap	50	10	34	56
Sept. 17	Sproat	Observer	51	30	47	23
Sept. 17	Stamp	Observer	195	65	24	11
Sept. 24	Stamp	Observer	86	53	19	28

Note: Lesions were ranked as follows: unmarked; open lesions, dorsal lesion extending through the dermis exposing underlying musculature; other marks, dorsal lesions in which the dermis was not breached, fungal lesions, predator wounds, and marks attributed to commercial fishing. ns, sample size not specified.

For both river systems, the percentage of open lesions (rank 5) also was higher in 1992 than in 1993 (Table 5). In both 1992 and 1993, fish from the Sproat River had higher percentages of the higher LS and higher mean monthly LS than fish from the Stamp River (Figs. 4 and 5). Open lesions occurred behind the dorsal fin in 21.8 and 19.2% of the fish examined from the Sproat River in 1992 and 1993, respectively. In the Stamp River, open lesions occurred behind the dorsal fin in 10.4 and 4.4% of the fish in 1992 and 1993, respectively. For both river systems and years, the severity of lesions at the base of the dorsal fin, on the head, and in the perianal region was generally low (rank 0 or 1) (Table 5).

The majority of fish collected on the spawning grounds in both Sproat and Great Central lakes in October and November of 1990 were unmarked (Table 4). For the Sproat Lake fish, between 0 and 14% had a single open dorsal lesion, and between 0 and 4% had two or more open dorsal lesions. For the Great Central Lake fish, between 8 and 15% had a single open dorsal lesion, and between 0 and 7% had two or more open dorsal lesions.

For both the Sproat and Stamp rivers in 1992, there were significant correlations between LS and hypural length (Spearman rank; $P < 0.01$, $n = 212$ for Sproat River; $P < 0.001$, $n = 273$ for Stamp River) and sea age (Spearman rank; $P < 0.001$, $n = 184$ for Sproat River; $P < 0.001$, $n = 53$ for Stamp River). In addition, there was a marginally significant correlation (Spearman rank; $P < 0.04$, $n = 273$) with host sex in the Stamp River, with males having a marginally higher LS than females. In 1993 there were no significant correlations between LS and host sex, hypural length, or sea age in either system.

Discussion

All sockeye examined for the presence of sea lice were infected with *L. salmonis* and had higher levels of infection than previously reported for sockeye. Prevalences between 0.6 and 12.5% and abundances between 0.02 and 0.32 copepods/fish have been reported previously for sockeye collected with longlines on the high seas of the North Pacific Ocean (Nagasawa 1987; Nagasawa et al. 1993; K. Nagasawa, National Research Institute of Far Seas Fisheries, Fisheries Agency of Japan, Shimizu, Japan, personal communication). However, Nagasawa's counts were based on either total adult or adult female *L. salmonis* only. The higher prevalences and intensities of infection reported here are due in part to our enumeration of the previously unreported earlier developmental stages and in part to the fact that our samples were taken in coastal waters. The presence of high numbers of early developmental stages (copepodids and chalimus larvae) suggests a high rate of infection by *L. salmonis* in coastal waters. However, our use of gill nets and seines to collect fish most likely resulted in an underestimation of the actual number of preadult and adult copepods. Nagasawa (1985) estimated that 77% more adult *L. salmonis* were lost because of net abrasion from gill-netted chum salmon (*Oncorhynchus keta*) than from those caught by longline.

The lesions seen in this study are the same as those reported from wild and farmed Atlantic salmon infected with *L. salmonis* (Huntsman 1918; White 1940, 1942; Brandal et al. 1976; Wootten et al. 1982; Jónsdóttir et al. 1992). The prevalence and severity of sea louse lesions in this study were greater than previously reported for sockeye. In this study the majority of fish had lesions that could be attributed to sea louse feeding. Abrasions and open wounds caused by sea lice were reported previously on the dorsal surface and in the perianal region of late-run sockeye in the Fraser River; however, data on lesion prevalence were not given (Gilhousen 1989). In contrast, Ishida and Nagasawa (1993) examined 2038 sockeye from the North Pacific Ocean, Bering Sea, and Ohkotsk Sea and found no lesions attributable to sea lice.

In 1990, low river flows and high river temperatures forced a high percentage (approximately 60%) of sockeye to remain in the inlet until September, thereby exposing the fish to an extended period of crowding, high water temperatures, and low dissolved oxygen levels (K.D. Hyatt, unpublished data). In our 1990 abundance samples, the highest proportion of adult *L. salmonis* present was ovigerous females. Each female carried high numbers of eggs (440 ± 120; mean ± SD) and was capable of extruding a second pair of egg strings within 2 days of the eggs hatching (S.C. Johnson, unpublished data). This strongly female sex ratio, high fecundity, and rapid development at higher temperatures (egg to infectious copepodid stage in 7.4 days at 15°C; Johnson and Albright 1991*b*) combined with the presence of a large number of hosts in a restricted area most likely allowed the population of *L. salmonis* to increase rapidly, resulting in the development of serious lesions while the fish were holding in the inlet. In 1992 and 1993, escapement to both Sproat and Great Central lakes followed a more normal pattern, with approximately 65% of the escapement entering the lakes before September 1 (K.D. Hyatt, unpublished data), and damage from sea lice was less severe.

In both the inlet and river samples of 1992 and 1993, the severity of sea louse lesions increased towards the end of the runs (September). A similar trend was reported by Gilhousen (1989), who found no sea louse lesions on Fraser River sockeye collected in July and August but abraded areas and open lesions on sockeye collected in September and October. It is possible that the longer period of residence in coastal waters allows a greater proportion of the copepods to develop to the preadult and adult stages. It is these stages that are most commonly responsible for disease because of their larger size and capability of moving on the host.

It is highly probable that sockeye, as they mature or are exposed to other stresses such as adverse environmental

Table 4. Percentage of sockeye salmon (*Oncorhynchus nerka*) with open lesions (i.e., extending to the musculature) in the fall of 1990.

Date (in 1990)	Location	Sampling method	*n*	Unmarked	Mild external damage	Moderate external damage	Severe external damage
				Sproat Lake			
Sept. 14	Fishway	Trap	50	10	28	48	14
Oct. 26	Two Rivers Arm	Seine	100	88	9	2	1
Oct. 25	Taylor Arm	Seine	100	82	14	4	0
Nov. 5	Two Rivers Arm	Seine	100	94	4	2	0
Nov. 5	Taylor Arm	Seine	100	96	1	3	0
Nov. 19	Two Rivers Arm	Seine	100	100	0	0	0
Nov. 19	Taylor Arm	Seine	100	97	3	0	0
				Great Central Lake			
Sept. 14	Fishway	Trap	50	22	44	35	0
Sept. 25	Fishway	Trap	50	32	48	20	0
Oct. 26	Forestry Camp	Seine	82	84	12	4	0
Oct. 26	Fawn Point	Seine	100	82	9	7	2
Nov. 6	Forestry Camp	Seine	100	89	8	3	0
Nov. 7	Fawn Point	Seine	100	88	11	1	0
Nov. 26	Forestry Camp	Seine	100	83	12	5	0
Nov. 21	Fawn Point	Seine	100	85	13	2	0

Note: Fish were sampled at the fishways of the Sproat and Stamp rivers and various lake locations. Fish were ranked as having mild (one open lesion), moderate (two or three open lesions), or severe (more than three open lesions) external damage.

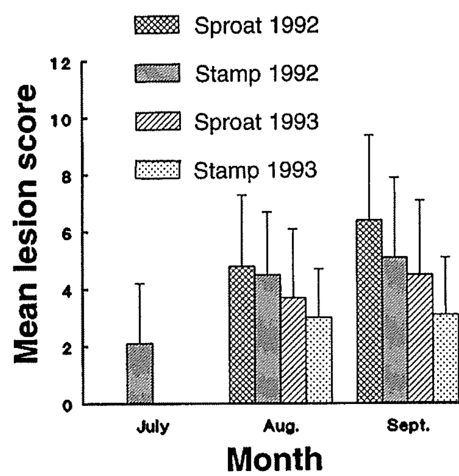
conditions (i.e., high temperature, low dissolved oxygen levels, or toxic plankton blooms), become more susceptible to infection with *L. salmonis*. Stress factors such as sexual maturation and exposure to deleterious environmental conditions are known to cause immunosuppression resulting in increased susceptibility of salmonid fishes to infection with a variety of parasites (reviewed in Pickering 1987). Immunosuppression of coho (*Oncorhynchus kisutch*) and chinook salmon (*Oncorhynchus tshawytscha*), induced by implantation of hydrocortisol, increased their susceptibility to infection by *L. salmonis* (Johnson and Albright 1992; S.C. Johnson, unpublished observation).

Throughout the study, sockeye returning to Sproat Lake were more severely affected by sea lice than those returning to Great Central Lake. There are several reasons that may account for this difference. The longer migration into Great Central Lake may cause fish with more severe lesions to die before they reach the lake. This is unlikely, however, because (*i*) the passage into Sproat Lake is more difficult because of river topography and (*ii*) transit times into the two lakes do not differ substantially (Manzer et al. 1985). Furthermore, high numbers of heavily affected, moribund, or dead fish were not observed in either the Stamp, Sproat, or Somass rivers in 1992 or 1993.

Differences in patterns of migration on the high seas, timing of the return to coastal waters and the inlet, or other behaviors may expose Sproat or Great Central stocks to different levels of infection with *L. salmonis*. However, available data provide no consistent, demonstrably significant differences between these stocks with respect to migration patterns or timing of return to coastal waters and Alberni Inlet (K.D. Hyatt, unpublished data).

It is also possible that the two stocks differ in their susceptibility to infection with *L. salmonis* because of genetic differences. Differences in susceptibility to infection with parasites between stocks of coho and chinook salmon have been shown to have a genetic basis (Hemmingsen et al. 1986; Ching and Parker 1989). Great Central and Sproat stocks have been

Fig. 4. Mean (+SD) monthly lesion scores for sockeye (*Oncorhynchus nerka*) from the Sproat and Stamp rivers collected in August and September of 1992 and 1993.



shown to consistently differ in both electrophoretic and DNA patterns (Quinn et al. 1987; Beacham et al. 1995; Taylor et al. 1996).

In 1990, samples collected on the spawning grounds of both lakes contained a higher percentage of fish without lesions than the river samples. These data suggest that lesions caused by sea lice may contribute to prespawning mortality during their stay in fresh water. Fish with open lesions would be more susceptible to secondary fungal and bacterial infections, as well as being osmotically compromised. In addition to direct mortality, there may be other subtle effects of sea louse damage on reproductive success. Berg et al. (1986) noted that wounded Atlantic salmon exhibited behavioral differences that decreased their reproductive success.

Table 5. Percentage of sockeye salmon (*Oncorhynchus nerka*) from the Sproat and Stamp rivers with lesions attributed to the feeding activities of *Lepeophtheirus salmonis* by body region and river system in 1992 (July–September) and 1993 (August–September).

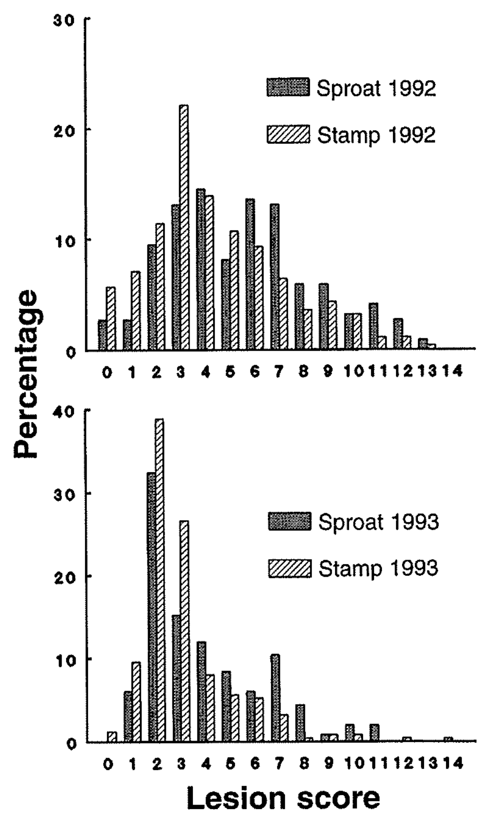
Lesion position, river system, and year	Lesion ranking						No. of fish examined
	0	1	2	3	4	5	
Posterior to dorsal fin							
Sproat River, 1992	5.5	34.1	20.0	10.0	8.6	21.8	220
Stamp River, 1992	13.3	33.7	28.3	10.4	3.9	10.4	279
Sproat River, 1993	9.6	54.4	7.2	6.8	2.8	19.2	250
Stamp River, 1993	14.0	68.4	7.2	2.8	3.2	4.4	250
Base of dorsal fin							
Sproat River, 1992	23.2	70.9	2.7	1.8	0	1.4	220
Stamp River, 1992	38.0	59.1	1.4	1.1	0	0.4	279
Sproat River, 1993	55.6	42.0	0.4	0	0.4	1.6	250
Stamp River, 1993	65.6	32.8	0.8	0.4	0	0.4	250
Head							
Sproat River, 1992	72.3	10.9	1.8	4.1	4.1	6.8	220
Stamp River, 1992	82.8	2.5	1.8	2.9	2.5	7.5	279
Sproat River, 1993	99.2	0	0	0.4	0	0.4	250
Stamp River, 1993	98.8	0	0	0.8	0	0.4	250
Perianal							
Sproat River, 1992	4.1	72.4	6.8	15.4	0.5	0.9	220
Stamp River, 1992	10.8	76.0	2.2	10.4	0	0.7	279
Sproat River, 1993	0	68.8	17.2	8.8	2.4	2.8	250
Stamp River, 1993	2.0	74.4	14.4	7.2	0.8	1.2	250

Because our samples were taken in September 1990, it is possible that we missed a large percentage of undamaged fish entering the lakes during earlier periods of escapement. However, a large percentage of the run would have had to occur prior to September to account for the observed low prevalence of open lesions on the spawning grounds. This was not the case in 1990, when approximately 69% of the run passed from Alberni Inlet into the Somass River after September 1 (K.D. Hyatt, unpublished data).

Nagasawa et al. (1993) observed slight increases in the prevalence, mean intensity, and abundance of *L. salmonis* on sockeye with increasing age and host size. However, sockeye in their study had very low intensities of infection (≤3 copepods/host) and did not have lesions induced by sea lice. Significant positive correlations between LS and hypural length and sea age were observed in both the Stamp and Sproat rivers in 1992; however, these were not repeated in 1993. The positive relationship demonstrated for 1992 is expected because fish with a longer sea residence would accumulate more sea lice and suffer more damage from their feeding activities. The lack of significant correlations in 1993 may be due to the broad categories used in our ranking system. Subtle differences in lesion severity within ranks, therefore, are not distinguished. In years such as 1993 when the majority of fish had only very mild lesions (rank 0 or 1), our ranking system may not be sensitive enough to identify correlations.

In summary, we saw higher prevalences and intensities of *L. salmonis* on mature sockeye in Alberni Inlet than reported for immature and maturing sockeye collected on the high seas. Sockeye may become infected with *L. salmonis* as they pass through coastal wateres or hold in inlets prior to entering fresh water. It is also possible that immunosuppression concomitant with maturation makes sockeye more susceptible to infection with sea lice as they come ashore. Stocks of Alberni sockeye

Fig. 5. Distribution of lesion scores for sockeye (*Oncorhynchus nerka*) from the Sproat and Stamp rivers collected in August and September of 1992 and 1993.



were shown to differ in the severity of lesions caused by sea lice. The reasons for this difference are unknown. In years, such as 1990, when unfavorable river conditions force the fish to remain in the inlet longer than normal, serious disease and mortality induced by sea lice can occur. In extreme cases, disease induced by sea lice appears to cause prespawning mortality in freshwater environments, thereby further affecting the reproductive success of these stocks. This observation highlights the important role that diseases may play in the population dynamics of fish stocks.

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References

Anonymous. 1984. Fish health protection regulations: manual of compliance. Misc. Spec. Publ. Fish. Mar. Serv. Can. No. 31 (revised).

Beacham, T.D., Withler, R.E., and Wood, C.C. 1995. Stock identification of sockeye salmon (*Oncorhynchus nerka*) using minisatellite DNA variation. N. Am. J. Fish. Manage. **15**: 249–265.

Berg, M., Abrahamson, B., and Berg, O.K. 1986. Spawning of injured compared to uninjured female Atlantic salmon, *Salmo salar* L. Aquacult. Fish. Manage. **17**: 195–199.

Brandal, P.O., and Egidius, E. 1979. Treatment of salmon lice (*Lepeophtheirus salmonis* Krøyer, 1838) with Neguvon[R]: description of method and equipment. Aquaculture, **18**: 183–188.

Brandal, P.O., Egidius, E., and Romslo, I. 1976. Host blood: a major food component for the parasitic copepod *Lepeophtheirus salmonis* Krøyer, 1838 (Crustacea: Caligidae). Norw. J. Zool. **24**: 341–343.

Calderwood, W.L. 1906. "The white spot" affecting salmon in the Island of Lewis. *In* Annual report of the Fisheries Board of Scotland, Glasgow. Part II. Report on salmon fisheries. Vol. 24. James Hedderwick & Sons Limited, Glasgow, Scotland. pp. 78–80.

Ching, H.L., and Parker, L. 1989. Experimental exposure of trout and salmon from 12 British Columbian stocks to the myxozoan parasite *Ceratomyxa shasta*. J. Aquat. Anim. Health, **1**: 205–208.

Gilhousen, P. 1989. Wounds, scars and marks on Fraser River sockeye salmon with some relationships to predation losses. Int. Pac. Salmon Fish. Comm. Prog. Rep. No. 42.

Hemmingsen, A.R., Holt, R.A., and Ewing, R.D. 1986. Susceptibility of progeny from crosses among three stocks of coho salmon to infection by *Ceratomyxa shasta*. Trans. Am. Fish. Soc. **115**: 492–495.

Huntsman, A.G. 1918. Report on affected salmon in the Miramichi River, New Brunswick. Contrib. Can. Biol. 1917–1918: 169–173.

Hyatt, K.D., and Steer, D.J. 1987. Barkley Sound sockeye salmon (*Oncorhynchus nerka*): evidence for over a century of successful stock development, fisheries management, research and enhancement efforts. *In* Sockeye salmon (*Oncorhynchus nerka*) population biology and future management. *Edited by* H.D. Smith, L. Margolis, and C.C. Wood. Can. Spec. Publ. Fish. Aquat. Sci. No. 96. pp. 435–457.

Ishida Y., and Nagasawa, K. 1993. The incidence of external injuries and wounds on salmonidis [sic] caught by Japanese research vessels in the North Pacific Ocean in 1992. *In* Reports of the research of salmon resources in the North Pacific Ocean in 1993. Document submitted to the Annual Meeting of the North Pacific Anadromous Fish Commission, Vancouver, B.C. November 1993. National Research Institute of Far Sea Fisheries, Fisheries Agency of Japan, Shimizu, Shizuoka 424, Japan.

Johnson, S.C., and Albright, L.J. 1991*a*. The developmental stages of *Lepeophtheirus salmonis* (Krøyer, 1837) (Copepoda: Caligidae). Can. J. Zool. **69**: 929–950.

Johnson, S.C., and Albright, L.J. 1991*b*. Development, growth, and survival of *Lepeophtheirus salmonis* (Copepoda: Caligidae) under laboratory conditions. J. Mar. Biol. Assoc. U.K. **71**: 425–436.

Johnson, S.C., and Albright, L.J. 1992. Effects of cortisol implants on the susceptibility and the histopathology of the responses of naive coho salmon *Oncorhynchus kisutch* to experimental infection with *Lepeophtheirus salmonis* (Copepoda: Caligidae). Dis. Aquat. Org. **14**: 195–205.

Jónsdóttir, H., Bron, J.E., Wootten, R., and Turnbull, J.F. 1992. The histopathology associated with the pre-adult and adult stages of *Lepeophtheirus salmonis* on the Atlantic salmon, *Salmo salar* L. J. Fish Dis. **15**: 521–527.

Kabata, Z. 1974. Mouth and mode of feeding of Caligidae (Copepoda), parasites of fishes, as determined by light and scanning electron microscopy. J. Fish. Res. Board Can. **31**: 1583–1588.

Kabata, Z. 1979. Parasitic Copepoda of British fishes. The Ray Society, London, U.K.

Kabata, Z. 1988. Copepoda and Branchiura. *In* Guide to the parasites of fishes of Canada. Part II. Crustacea. *Edited by* L. Margolis and Z. Kabata. Can. Spec. Publ. Fish. Aquat. Sci. No. 101. pp. 3–127.

Manzer, J.I., Morley, R.B., and Girodat, D.J. 1985. Terminal travel rates for Alberni Inlet sockeye salmon (*Oncorhynchus nerka*). Can. Tech. Rep. Fish. Aquat. Sci. No. 1367.

Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M., and Schad, G.A. 1982. The use of ecological terms in parasitology. J. Parasitol. **68**: 131–133.

Morris, S., and Leaney, A.J. 1980. The Somass River estuary: status of environmental knowledge to 1980. *In* Special estuary series. No. 9. Fisheries and Oceans Canada and Environment Canada, Vancouver, B.C.

Nagasawa, K. 1985. Comparison of the infection levels of *Lepeophtheirus salmonis* (Copepoda) on chum salmon captured by two methods. Jpn. J. Ichthyol. **32**: 386–370.

Nagasawa, K. 1987. Prevalence and abundance of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on high-seas salmon and trout in the North Pacific Ocean. Nippon Suisan Gakkaishi, **53**: 2151–2156.

Nagasawa, K., and Takami, T. 1993. Host utilization by the salmon louse *Lepeophtheirus salmonis* (Copepoda: Caligidae) in the Sea of Japan. J. Parasitol. **79**: 127–130.

Nagasawa, K., Ishida, Y., Ogura, M., Tadokoro, K., and Hiramatsu, K. 1993. The abundance and distribution of *Lepeophtheirus salmonis* (Copepoda: Caligidae) on six species of Pacific salmon in offshore waters of the North Pacific Ocean and Bering Sea. *In* Pathogens of wild and farmed fish: sea lice. *Edited by* G.A. Boxshall and D. Defaye. Ellis Horwood, Chichester, U.K. pp. 166–178.

Pickering, A.D. 1987. Stress responses and disease resistance in farmed fish. *In* Proceedings of the Aqua Nor 87 International Conference, Tronheim, Norway. Norske Fiskeoppdretternes Forening, Tronheim, Norway. pp. 36–49.

Pike, A.W. 1989. Sea lice: major pathogens of farmed Atlantic salmon. Parasitol. Today, **5**: 291–297.

Quinn, T.P., Wood, C.C., Margolis, L., Riddell, B.E., and Hyatt, K.D.

1987. Homing in wild sockeye salmon (*Oncorhynchus nerka*) populations as inferred from differences in parasite prevalance [sic] and allozyme allele frequencies. Can. J. Fish. Aquat. Sci. **44**: 1963–1971.

Taylor, E.B., Foote, C.J., and Wood, C.C. 1996. Molecular genetic evidence for parallel life history evolution within a Pacific salmon (sockeye salmon and kokanee, *Oncorhynchus nerka*). Evolution, **50**: 401–416.

Tully, O., Poole, W.R., Whelan, K.F., and Merigoux, S. 1993*a*. Parameters and possible causes of epizootics of *Lepeophtheirus salmonis* (Krøyer) infesting sea trout (*Salmo trutta* L.) off the west coast of Ireland. *In* Pathogens of wild and farmed fish: sea lice. *Edited by* G.A. Boxshall and D. Defaye. Ellis Horwood, Chichester, U.K. pp. 202–213.

Tully, O., Poole, W.R., and Whelan, K.F. 1993*b*. Infestation parameters for *Lepeophtheirus salmonis* (Kroyer) (Copepoda: Caligidae) parasitic on sea trout, *Salmo trutta* L., off the west coast of Ireland during 1990 and 1991. Aquacult. Fish. Manage. **24**: 545–555.

White, H.C. 1940. "Sea lice" (*Lepeophtheirus*) and death of salmon. J. Fish. Res. Board Can. **5**: 172–175.

White, H.C. 1942. Severe injuries from *Lepeophtheirus salmonis* occur during drought years. Report No. 21. *In* Atlantic salmon and trout investigations 1942. Fish. Res. Board Can. Manuscr. Rep. Biol. No. 329.

Wootten, R., Smith, J.W., and Needham, E.A. 1982. Aspects of the biology of the parasitic copepods *Lepeophtheirus salmonis* and *Caligus elongatus* on farmed salmonids, and their treatment. Proc. R. Soc. Edinb. Sect. B Biol. Sci. **81**: 185–197.