ICES Journal of Marine Science, 54: 1113–1119. 1997

Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.)

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Jacobsen, J. A. and Gaard, E. 1997. Open-ocean infestation by salmon lice (*Lepeophtheirus salmonis*): comparison of wild and escaped farmed Atlantic salmon (*Salmo salar* L.). – ICES Journal of Marine Science, 54: 1113–1119.

Salmon lice (*Lepeophtheirus salmonis*) infestation was investigated in 128 salmon (*Salmo salar* L.) caught on floating long-lines in the Norwegian Sea during November–March 1993–1995. Overall prevalence was 99.2% and abundance 29.5 lice per salmon. Most lice were adults (90%), and 72% of these were ovigerous females. These adult lice were estimated to be at least 3 months old based on prevailing sea-surface temperatures at the sampling site: 7°C in November and 3°C in March. The prevalence and abundance of lice on one sea winter (1SW) salmon were significantly higher on escaped farmed fish than on wild salmon. However, no difference in abundance was observed between 2SW farmed and wild salmon. The average number of lice per surface area of fish (density) was significantly higher in 2SW wild salmon than in 1SW wild salmon, indicating an accumulation of lice on the salmon in the oceanic phase. No differences in density were observed between 1SW and 2SW farmed salmon. The prevalence of *Caligus elongatus* was low (5.5%), with an abundance of 0.9 lice per salmon.

Key words: Atlantic salmon, *Caligus elongatus*, escaped farmed salmon, *Lepeophtheirus salmonis*, open-ocean infestation, *Salmo salar*, sea age, sea lice, wild salmon.

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Introduction

Two species of sea lice, *Lepeophtheirus salmonis* (Krøyer, 1938) and *Caligus elongatus* von Nordmann, 1832, infest the Atlantic salmon (*Salmo salar* L.) in the North Atlantic and adjacent seas. The salmon louse (*L. salmonis*) is an important pathogen responsible for high losses of sea-farmed Atlantic salmon (Brandal and Egidius, 1979; Grimnes and Jakobsen, 1996). In wild stocks, sea lice are commonly present in low numbers and are rarely the cause of severe pathological symptoms (White, 1940; Nagasawa, 1987; Johnson *et al.*, 1996). In spite of their known presence on wild salmon returning from the sea, there is a paucity of good data on the infestation of Atlantic salmon in the open ocean. For *L. salmonis*, abundance estimates of less than eight lice per fish have been reported from the high seas on fish caught by gillnet and pelagic trawl (Pippy, 1969; Holst *et al.*, 1993) and less than 20 lice per fish from gillnet samples from the coastal areas of Norway (Berland, 1993). In the North Pacific, abundance estimates of less than 13 have been reported on Pacific salmon (*Oncorhynchus* spp.) (Nagasawa, 1985, 1987; Nagasawa *et al.*, 1993). Some of these estimates suffer from a downward bias of infestation levels due to the sampling methods. Nagasawa (1985) showed that Pacific salmon caught by long-line carried over four times as many lice as salmon from comparable gillnet catches and Holst *et al.* (1993) found an inverse correlation between scale losses and prevalence of lice on post-smolts from trawl catches, suggesting loss of lice during capture by these gears as a result of skin abrasion.

Salmon from most countries bordering the North Atlantic utilize the area north of the Faroes during their oceanic feeding phase (Jacobsen and Hansen, 1996; ICES, 1997). This feeding area is characterized by a front that separates the warmer Atlantic waters from the south-west and the colder and less saline Arctic waters from the north-west (Hansen, 1985). Salmon are typically distributed in or close to the frontal areas (Jákupsstovu, 1988; Jacobsen and Hansen, 1996), and in recent years large numbers (20–40%) of fish-farm escapees have been observed in this feeding area (Hansen *et al.*, 1993; ICES, 1997). It is possible that escaped farmed salmon transfer increasing numbers of sea lice to wild salmon in the open ocean but

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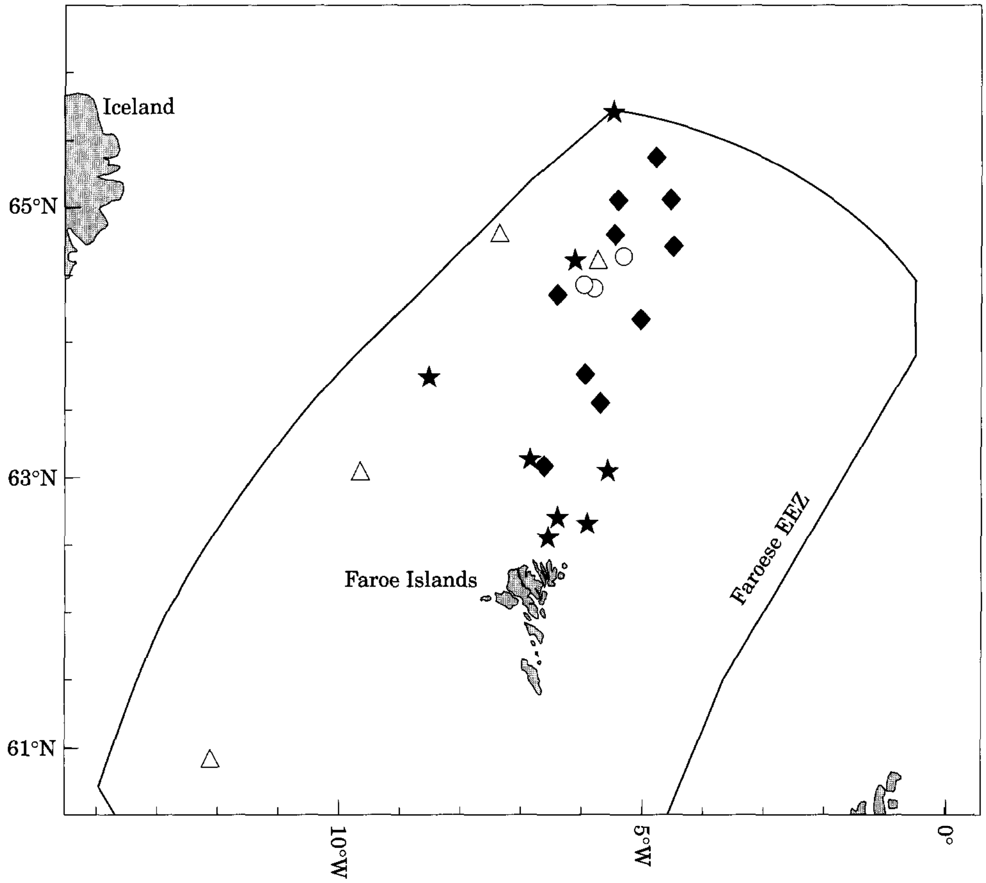

Figure 1. Sampling locations of 128 Atlantic salmon caught using long-lines during the period from March 1993 to March 1995: March 1993—3 salmon (○), February–March 1994—13 salmon (△), November–December 1994—50 salmon (★), and February–March 1995—62 salmon (◆).

unfortunately no historic infestation data are available from the high seas to study this question.

The level of infestation of salmon in the feeding areas and post-smolts in the sea may provide information about possible causes of mortality during the oceanic phase. Moreover, basic information, which is necessary for understanding the epizootiology of the salmon lice, is still lacking. Of special interest are life-history parameters such as the longevity and mortality of adult lice under the conditions experienced by salmon in the open ocean. Such knowledge is important in understanding the possible interactions between escaped farmed salmon as lice carriers and wild salmon in feeding areas in the open sea.

This paper describes the infestation of *L. salmonis* and *C. elongatus* on Atlantic salmon caught by long-line in the open ocean during the winter. The sea lice burdens of wild and escaped farmed salmon are compared, the rate of infestation in the sea is estimated, and possible mechanisms of transmission of lice in relation to the distribution of salmon in the sea are discussed.

Materials and methods

In total, 128 salmon caught on 25 long-line sets in the Norwegian Sea (north of the Faroes) between 62°30′N–66°00′N and 10°00′W–2°00′W during November–March 1993–1995 (Fig. 1) were examined for sea lice. This sample was part of a larger research programme in the Faroes area ongoing since 1992 (ICES, 1997). Most of the fish were caught in November–December 1994 (50 salmon) and February–March 1995 (62 salmon). In addition, three fish from March 1993 and 13 from February–March 1994 were examined. To minimize the loss of sea lice, live salmon were taken directly from the long-line with a gaff and, without touching the side of the vessel or deck, were placed in individual plastic bags. The snood was cut off, leaving the hook in the fish. The salmon to be examined for sea lice were randomly selected off the line. Sea-surface temperature (SST) was measured four times a day, before and after setting and hauling of the long-line.

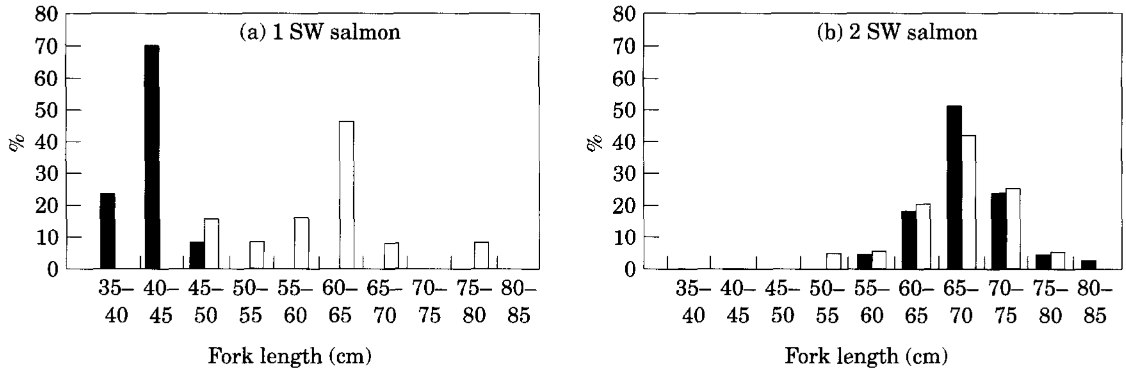

Figure 2. Length distribution of wild and escaped farmed salmon, (a) 1 sea winter (■ Wild, n=13; □ Farmed, n=13) and (b) 2 sea winter fish (■ Wild, n=56 □ Farmed, n=24). Data from November 1994 to March 1995.

Salmon were examined under a magnifying glass and a dissecting microscope, and all sea lice were removed and stored in 70% ethanol. Species and developmental stages were identified according to Johnson and Albright (1991a) for *L. salmonis* and Piasecki (1996) for *C. elongatus*. Fork lengths, total lengths, and weights were obtained for all salmon caught. In addition, for the 112 fish caught in the 1994/1995 season, smolt age, sea age, and origin (wild or escaped farmed fish) were determined from scale samples following the procedure of Lund *et al.* (1989). The age reading of 2SW farmed fish might have been overestimated due to the inclusion of false zones on the scales, however, less than 8% are expected to be incorrectly classified (Lund *et al.*, 1989). The body surface area of the salmon was calculated according to the formula $S=9.5864\ W^{0.629}$, where S is the body surface area (cm^2) and W is the wet weight (g) (Jaworski and Holm, 1992).

Mann–Whitney U-tests were used to test for differences in abundance and density between sea ages and between wild and farmed salmon. Three sea winter fish were excluded from this analysis due to inadequate samples (five salmon).

The terms prevalence, mean intensity, and abundance are defined by Margolis *et al.* (1982). Density is defined as "the number of parasites per unit area of all hosts examined". Salmon in the first winter in the sea, i.e. from May the first year to August the following year, are referred to as one sea winter (1SW) salmon, and fish caught from September in the second year to August in the third year at sea are referred to as two sea winter (2SW) salmon.

Results

Mean sea-surface temperature (SST ± s.d.) at the sampling locations was 7°C (±1.6°C) in November–December and 3°C (±1.3°C) in February–March. Fork lengths of salmon caught during the 1994/1995 season ranged from 38 to 85 cm (Fig. 2). The mean fork length of 1SW escaped farmed salmon was significantly greater than that of 1SW wild salmon (Mann–Whitney U-test; $p<0.001$). There was no significant difference in the mean fork length of 2SW escaped farmed and wild salmon.

The overall prevalence of *L. salmonis* was 99.2%, the mean intensity was 29.7 lice per salmon, and the abundance was 29.5 lice per salmon with a range of 0–187. The prevalence of *C. elongatus* was very low (5.5%) with a mean intensity of 17 lice per salmon and an abundance of 0.9 lice per salmon with a range of 0–112.

One escaped farmed fish (sea age 0+, river age 1) was found to carry 299 lice in all, 187 *L. salmonis* and 112 *C. elongatus* (94% of all *C. elongatus* observed). This individual differed significantly from the other fish with regard to the abundance of chalimus stages of both *L. salmonis* and *C. elongatus* and was excluded from further analysis.

The distribution of the different developmental stages of *L. salmonis* on the salmon is shown in Figure 3. The age distribution of lice within the host infrapopulations is characterized by a very low abundance of young stages and a predominance of adult stages, with most of the adult females being ovigerous (Fig. 3). The abundance and the density of lice on 1SW salmon were significantly higher on escaped farmed fish than on wild salmon ($p=0.001$ and 0.009, respectively) (Tables 1 and 2). In particular, the chalimus and pre-adult stages occurred in much higher numbers on the escaped farmed salmon than on the wild salmon (Table 1). No significant difference was observed in abundance ($p=0.663$) or in density ($p=0.941$) between 2SW wild and farmed salmon (Tables 1 and 2). Abundance and density increased with the sea age of the wild salmon ($p<0.001$ for both measures), but not for farmed salmon ($p=0.916$ and 0.861, respectively) (Tables 1 and 2).

On the basis of external examination, the average abundance of about 30 lice did not cause damage to the

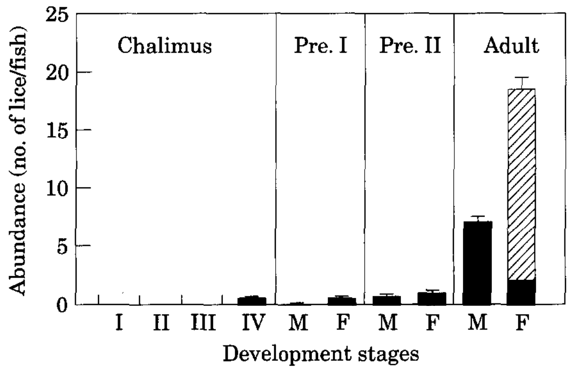

Figure 3. Abundance (+standard error) of *Lepeophtheirus salmonis* on 127 salmon, from March 1993 (3 salmon), February–March 1994 (13 salmon), and from November 1994 to March 1995 (111 salmon). Excluding one farmed salmon with an atypically high burden of lice. Notation: Pre.=preadult, M=male, and F=female. Hatched bar represents ovigerous females.

host, even though 90% of the lice were adults and 72% of the adults were females (Fig. 3).

The positively skewed frequency distribution of *L. salmonis* among the 1SW fish is evident from Figure 4. The information presented in Figures 4(b) and (c) for 2SW fish indicates a dome-shaped distribution. The frequency distribution for 1SW wild salmon is skewed compared to the distribution for 2SW wild salmon (Fig. 4a and b). The 1SW farmed salmon also differ from the 2SW farmed fish, but with a less pronounced difference (Fig. 4c and d).

Discussion

The presence of both chalimus and pre-adult stages of *L. salmonis* on wild salmon throughout the winter months and the increasing abundance and density of lice with sea age indicate that infestation occurs in the open-ocean. Infestation on the high seas is common for other caligid copepods (Boxshall, 1974; Neilson *et al.*, 1987). However, the difference between 1SW and 2SW salmon could be explained in part by differences in lice levels experienced by salmon in coastal areas in 1993 and 1994.

The observation of the high abundance of adult lice compared with the number of the younger stages on the hosts indicates an accumulation of adult stages in the oceanic phase. The significant increase in density of lice with sea age suggests this. The less positively skewed frequency distribution of lice on 2SW salmon, as compared with 1SW fish, also indicates a "stabilizing tendency" (Anderson and Gordon, 1982). Furthermore, the similar density of adult lice stages of about 0.02 cm^{-2} on 2SW wild and farmed salmon and 1SW farmed salmon compared to the lower density on 1SW wild salmon may indicate a regulatory mechanism in the open-ocean, e.g. death of heavily infected fish or lice mortality. High abundance of juvenile lice (more than 30 chalimus) becomes lethal to smolts when the lice develop into the first pre-adult stage (Grimnes and Jakobsen, 1996).

The significantly higher lice burden observed on 1SW escaped farmed fish than on 1SW wild salmon suggests that the escapees might carry lice from the coastal areas in higher abundance than wild smolts. An alternative explanation could be that the escaped farmed salmon are more susceptible to infestation on the high seas. We expected, however, that the escaped farmed fish would carry higher lice burdens than the wild salmon when they migrated to the high seas for the following reasons. Wild smolts are observed to migrate directly out into the open sea (Jonsson *et al.*, 1993; Lacroix and McCurdy, 1996), and thus spend a shorter time in areas where there is a high probability of being infected, while escaped farmed fish have been observed to stay in the vicinity of the site of escape for up to 3 weeks (Hansen and Lund, 1992). The significantly higher number of the internal parasite *Anisakis simplex* observed in escaped farmed salmon, compared with wild salmon (B. Berland, University of Bergen, Bergen, Norway, pers. comm.) indirectly supports the idea of residence in coastal areas prior to seaward migration. Furthermore, the highly skewed frequency distribution of lice on 1SW wild salmon as compared with the less positively skewed distribution for 1SW farmed salmon, a typical difference in dispersion patterns between wild and farmed fish (Costello, 1993), supports the view that the initial parasitic load on farmed fish is higher when they leave coastal waters. Wild smolts are only in coastal areas long enough for the infective copepodid stage to develop to the chalimus stages (Finstad *et al.*, 1994) while escaped farmed salmon are more likely to carry all stages. The greater size of 1SW escaped farmed salmon than of 1SW wild salmon in the sea suggests that most of the farmed fish were of a larger size when they escaped compared to the size of wild smolts when they migrate to the sea (Fig. 2). Thus it is possible that the farmed fish experience lower mortality from the louse burden than wild salmon smolts.

One escaped farmed fish (excluded from the analysis) with an atypically high number of lice (299 lice) was caught in an area far to the north of the traditional fishing areas in November (Fig. 1). This fish is thought to have left coastal areas shortly before capture, either directly from a fish farm or from an inshore area with high levels of infection.

Our findings suggest that adult female lice survive on salmon during the winter period in the sea, since they were found on wild salmon in our spring samples. They also survive on farmed salmon over the winter in northern Norway (A. Nylund, University of Bergen,

Table 1. Abundance of *Lepeophtheirus salmonis* on Atlantic salmon by sea age (SW) and origin. Lice stages grouped into chalimus (stages III and IV), pre-adult, and adult lice. Data from November 1994 to March 1995, excluding one farmed salmon with an atypically high number of lice. Abundance is defined as the total number of parasites divided by the total number of hosts examined (Margolis *et al.*, 1982).

	Wild salmon			Farmed salmon			
Stages	1 SW	2 SW	1+2 SW	1 SW	2 SW[a]	1+2 SW	Total
Chalimus III–IV	0.1	0.6	0.5	0.6	0.5	0.6	0.5
Pre-adult I–II	0.1	2.9	2.3	4.4	2.0	2.8	2.5
Juveniles	0.2	3.5	2.9	5.0	2.5	3.4	3.1
Adult males	2.3	7.6	6.6	5.5	10.3	8.6	7.3
Adult females[b]	3.5	22.4	18.8	16.5	20.0	18.8	18.8
Adults both sexes	5.8	30.0	25.4	21.9	30.3	27.4	26.1
All stages	5.9	33.5	28.3	26.9	32.9	30.8	29.2
No. of fish	13	56	69	13	24	37	106

[a]The sea age of farmed fish may be biased upwards because of inclusion of false zones in the age reading.
[b]About 90% of the females were ovigerous.

Bergen, Norway, pers. comm.). Boxshall (1974) estimated the total lifespan of *L. pectoralis* (Müller, 1776) to be 10 months on plaice (*Pleuronectes platessa* L.), with an overwintering population of adult lice ready to shed their eggs in early spring when the sea temperature increases. Hogans and Trudeau (1989) found overwintering *C. elongatus* on salmon at temperatures below 5°C in Canada.

Laboratory investigations of *L. salmonis* indicate that the generation time of lice is between 1 and 4 months, and is inversely related to temperature (Johannesen, 1978; Johnson and Albright, 1991b; Tully, 1992). However, no growth experiments of the entire life cycle of *L. salmonis* at temperatures below 7°C have been reported in the literature and the longevity of ovigerous females is not known.

By using a combination of the reported temperature relationships we estimate the generation time from chalimus to adult to be about 3 mo in the autumn (7°C ambient temperature) and 4–6 mo in the early spring (3°C), thus the infestation rate in the sea during the winter months is likely to be low. The average abundance of 30 adult lice on 2SW wild salmon compared to the average abundance of only 6 lice on 1SW wild salmon (Table 1) is higher than we would have expected from the assumed low infestation rate during the winter period. The infestation rate might be higher in late spring and summer as compared to the winter months at sea and the ambient temperature in the sea is unknown for the period other than November–March. An increase in infestation rates through the late spring and early fall is recognized for farmed fish (see e.g. Tully

Table 2. Density of *Lepeophtheirus salmonis* on Atlantic salmon by sea age (SW) and origin. Lice stages grouped into chalimus (stages III and IV), pre-adult, and adult lice. Data from November 1994 to March 1995, excluding one farmed salmon with an atypically high number of lice. Density is expressed as number of lice × 10^3 per surface area of fish (cm^2).

	Wild salmon			Farmed salmon			
Stages	1 SW	2 SW	1+2 SW	1 SW	2 SW[a]	1+2 SW	Total
Chalimus III–IV	0.1	0.4	0.4	0.5	0.4	0.4	0.4
Pre-adult I–II	0.1	1.9	1.8	3.7	1.4	2.1	1.9
Juveniles	0.2	2.4	2.2	4.2	1.7	2.5	2.3
Adult males	3.7	5.1	5.0	4.6	7.1	6.3	5.5
Adult females[b]	5.6	15.1	14.2	13.8	13.7	13.8	14.1
Adults both sexes	9.3	20.2	19.2	18.4	20.9	20.1	19.5
All stages	9.5	22.6	21.4	22.5	22.6	22.6	21.8
No. of fish	13	56	69	13	24	37	106

[a]The sea age of farmed fish may be biased upwards because of inclusion of false zones in the age reading.
[b]About 90% of the females were ovigerous.

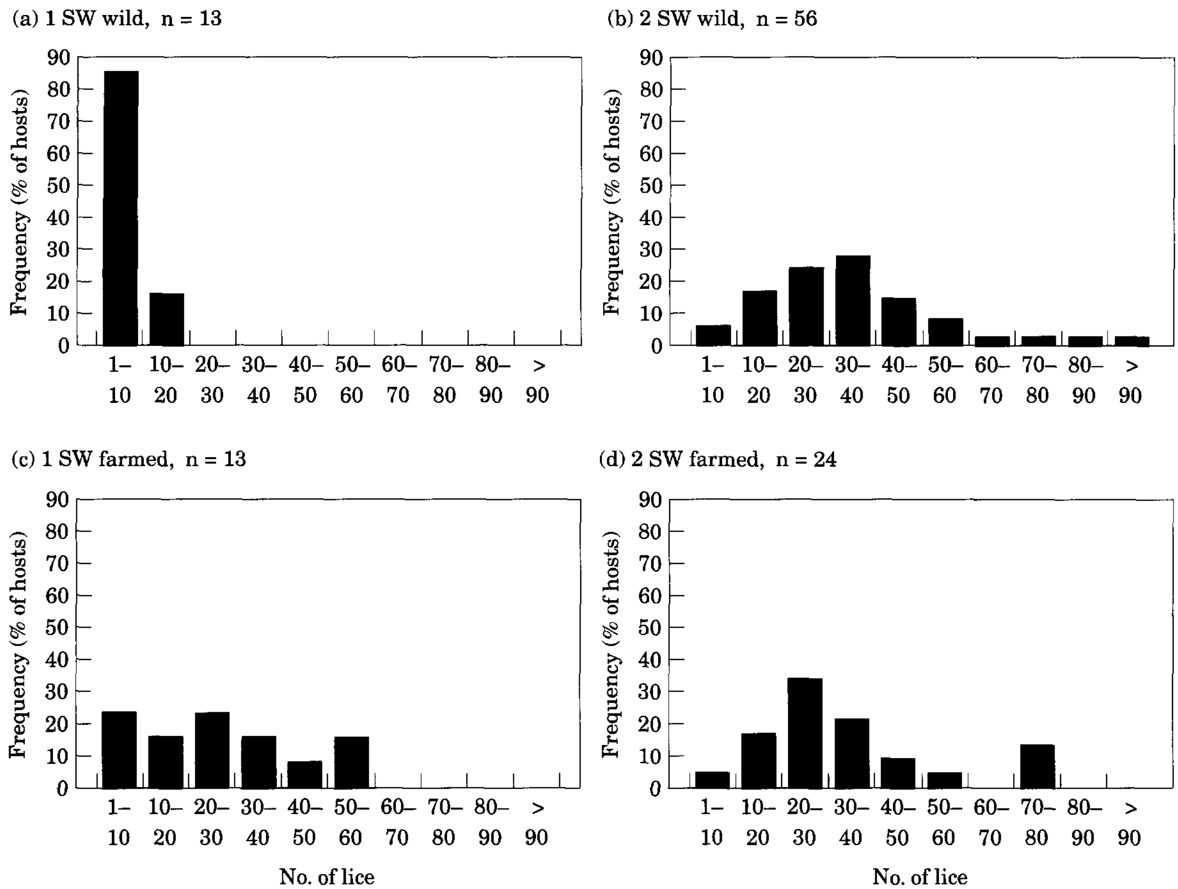

Figure 4. Frequency distribution of observed number of salmon with different numbers of *Lepeophtheirus salmonis.* (a) Wild 1 sea winter (1SW) salmon, (b) wild 2SW salmon, (c) escaped farmed 1SW salmon, excluding one farmed salmon with an atypically high burden of lice, and (d) escaped farmed 2SW salmon. Data from November 1994 to March 1995.

et al., 1993). Furthermore, the 1SW and 2SW fish might experience different environmental conditions due to spatial separation.

Acknowledgements

Thanks to S. Lamhauge, R. Mourtisen, and A. Hendriksen for the collection and recording of material onboard M/S "Hvítiklettur" and to E. Poulsen, A. Johansen, and H. Debes for technical assistance at the Faroese Fisheries Laboratory. A. Nylund, E. Karlsbakk, P. Jakobsen, L. P. Hansen, G. Nævdal, and B. Berland made valuable comments on earlier drafts. Gunnel M. Østborg at the Norwegian Institute for Nature Research kindly provided age readings of the scale samples. The sampling was part of a joint Nordic project on salmon in the Faroese area receiving grants from the Nordic Council of Ministers (66.05.04), the Norwegian Directorate for Nature Management and the Faroese Home Government. One of the authors (J.A.J.) is in receipt of a personal grant from NorFa (Nordic Academy for Advanced Study) during 1996/1997.

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