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Seasonal occurrence of *Lepeophtheirus salmonis* and *Caligus elongatus* (Copepoda: Caligidae) on sea trout (*Salmo trutta*), off southern Norway

T. A. Schram, J. A. Knutsen, P. A. Heuch, and T. A. Mo

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The occurrence of the parasitic copepod *Lepeophtheirus salmonis* Krøyer and *Caligus elongatus* Nordmann on sea trout *Salmo trutta* L. was investigated in the Arendal archipelago, southern Norway, an area without salmon farms. The occurrence of both parasite species followed a seasonal pattern. Prevalence (percent infested fish) and median intensity (median number of lice on the infested fish) of both species increased in the spring, and declined in the winter. A prevalence of 100% was reached in 1993, 1994 and 1995 for *L. salmonis*, while the prevalence of *C. elongatus* generally peaked at about 90%. In March, only adult *L. salmonis* were found, and small numbers of pre-adults appeared in April. The proportion of chalimi of *L. salmonis* never reached more than 15% each month of the study. The infected fish were without wounds and apparently in good condition. Neither the condition factor of the host, nor host age were correlated with the intensity of *L. salmonis* or *C. elongatus*.

Key words: sea trout, salmon lice, *Lepeophtheirus salmonis*, *Caligus elongatus*, fish farms, natural infestation, season cycles.

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T. A. Schram: Department of Biology, Section of Marine Zoology and Marine Chemistry, University of Oslo, PO Box 1064 Blindern, N-0316 Oslo, Norway. J. A. Knutsen: County Governor of Aust-Agder, Department of Environmental Affairs, Fylkeshuset, N-4800 Arendal, Norway. P. A. Heuch and T. A. Mo: National Veterinary Institute, Fish Health Section, PO Box 8156 Dep., N-0033 Oslo, Norway. Correspondence to T. A. Schram: tel: +47 2285 4507; fax: +47 2285 4438; e-mail: t.a.schram@bio.uio.no

Introduction

Recently, high numbers of *Lepeophtheirus salmonis* Krøyer larvae have been observed on sea trout *Salmo trutta* L. smolts returning in the early spring to west and north-west coast rivers in Norway (Birkeland, 1996a, b). Similar observations have been made in Ireland (e.g. Tully and Whelan, 1993; Tully *et al.*, 1993a, b). The trout in these studies have been mainly smolts or post-smolts in a poor physical condition which is often associated with severely damaged tail and dorsal fins.

It has been suggested that these unusual infestations are caused by increased *L. salmonis* reproduction on farmed salmon (Tully *et al.*, 1993b; Birkeland, 1996a, b). However, data on lice infestation on sea trout from Norway are scarce. Knowledge of natural infestation levels in areas both close to and remote from salmon farms would be necessary to draw conclusions about the potential impact of salmon lice from farms on wild fish stocks.

This paper reports data from a 3.5 year study of *L. salmonis* and *Caligus elongatus* Nordmann infestations on sea trout from the Arendal archipelago, southern Norway, an area without salmon farming. Further data from the inner Oslo Fjord are presented in an accompanying paper (Mo and Heuch, 1998).

Materials and methods

Study area

Sea-run brown trout, *Salmo trutta* m. *trutta*, henceforth named sea trout, were collected around the Tromøy island off the town of Arendal on the Norwegian Skagerrak coast (Fig. 1). The most important sea trout

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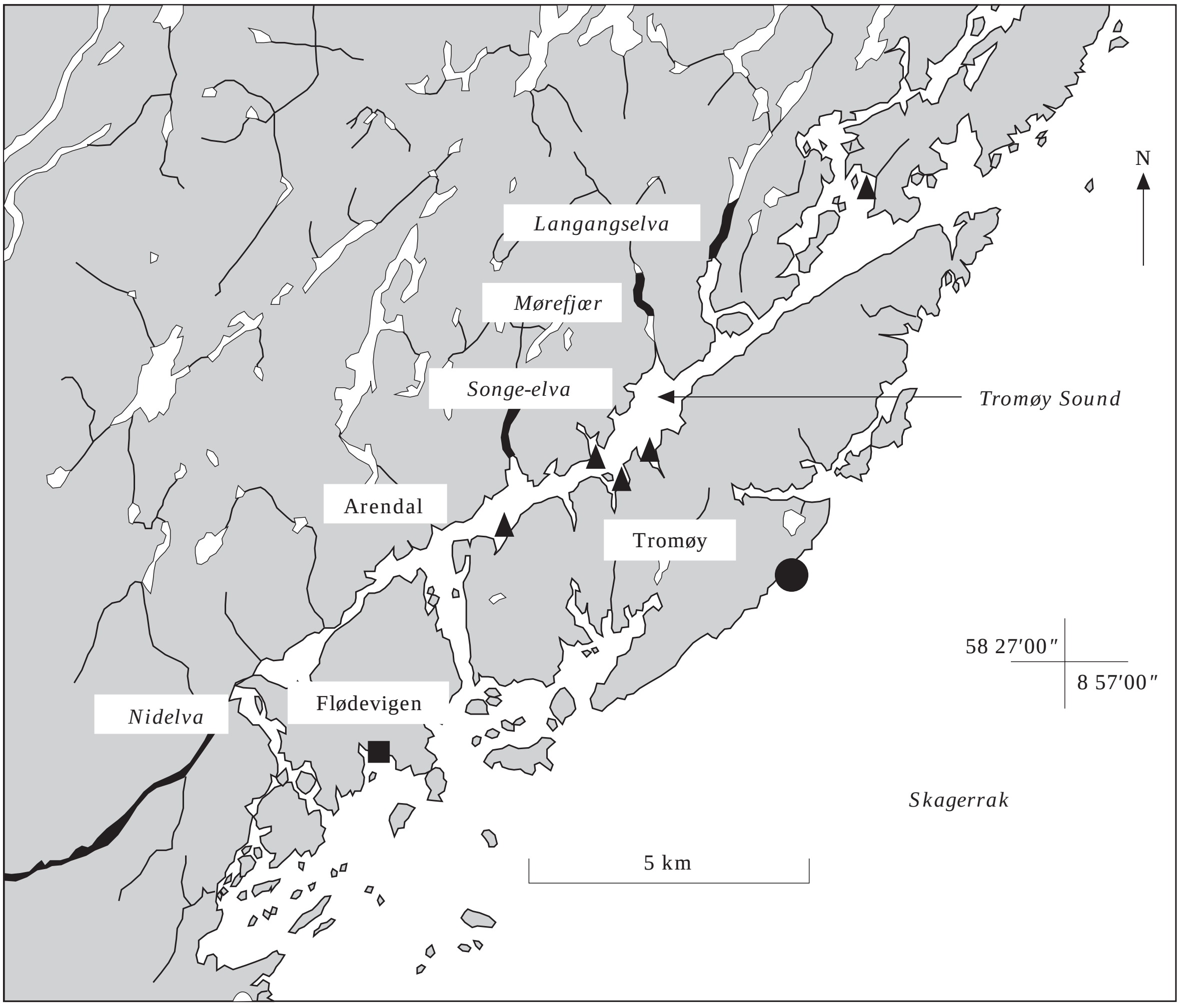

Figure 1. Map of the Arendal archipelago showing the sampling locations for beach seine (▲) and bag net (●). Major sea trout rivers are indicated by heavy black lines.

rivers here are Nidelva, Songe-elva, Mørefjær and Langangselva. The salmon farm closest to the sampling locations at Tromøy is about 40 km southwards of Lillesand, which is downstream in the Norwegian coastal current. No farming of salmonids on a commercial scale occurs along the coast north of the sampling area. Hence, the observed copepod parasite infestation patterns are expected to reflect natural population cycles in the host-parasite system. Daily records of temperatures from 0.5 m below the surface were kindly supplied by the Flødevigen Marine Research Station (see Fig. 1). These data were used to calculate monthly temperature means.

Collection of sea trout and sea lice

Sea trout were sampled within the period from March to December in the years 1992–1995. Most fish were caught with a nylon beach seine, which was 65.0 m long, 5.5 m deep, and had a stretched mesh size of 30 mm. One side of the seine was made especially for closing in and catching the fish, with mesh size 8.0 mm. This gear was used on the inside of the island (the Tromøy Sound) in the spring and autumn. In the summer, fishing was almost exclusively done with a moored bag-net on the outside of the island. This was 60.0 m long and 6.0 m deep, and had a stretched mesh size of 19–20 mm. Fishing with this equipment has been described by Dannevig and Van der Eyden (1986). The distance between the southernmost station in the Tromøy Sound and the bag-net locality is approximately 10 km. A few trout were also captured with 35.0 mm 15.0×1.5 m floating monofilament gill nets in the Tromøy Sound.

Special care was taken to avoid lice loss when taking the fish out of the nets. Each fish was immediately put into a separate plastic bag and killed by a blow to the

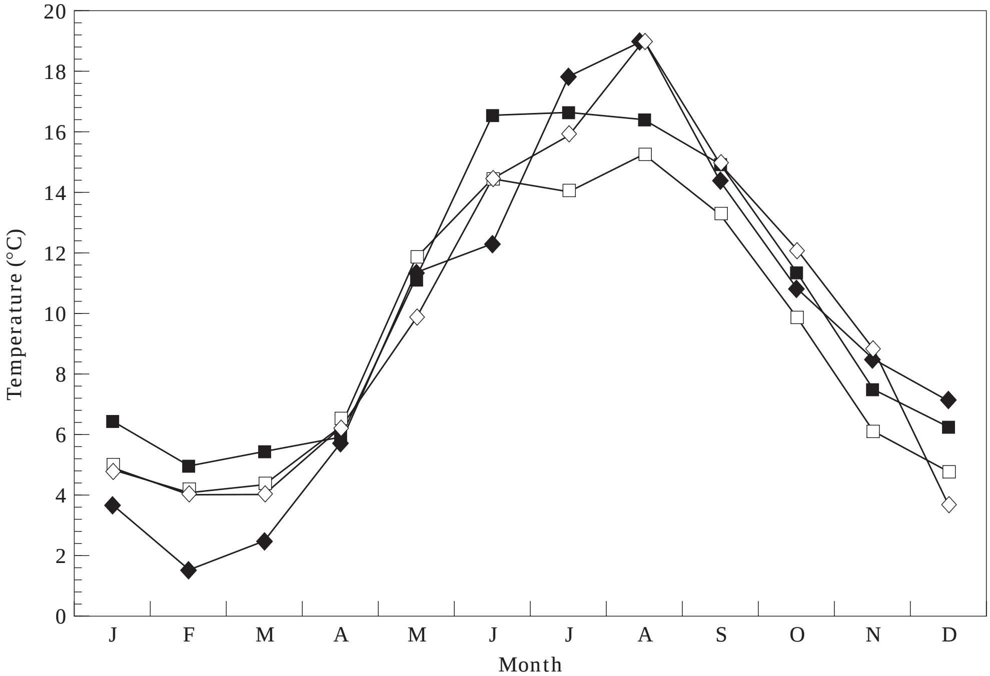

Figure 2. Monthly average water temperature at 0.5 m depth calculated from daily recordings from the Flødevigen Marine Research Station (see Fig. 1). 1992 (■); 1993 (□); 1994 (◆); 1995 (◇).

head. All trout were examined for the presence of lice within 24 h of capture. Examination was done in good illumination, with fish submerged in a tray. The water in the tray was filtered and examined after each fish. The bag was also inspected for detached parasites. Fish fork length (mm), wet weight (g) and age were recorded. Age was determined from otoliths and scales as described by Jonsson (1976) and Skurdal and Andersen (1985).

Ecological terms are used as follows: Prevalence is defined as the percentage of infested fish, and median intensity is the median number of parasites per infested fish, of a sample. The distribution of parasites in the host population is described by the variance to mean ratio of infestation intensity. The ratio is below unity if the parasites are evenly distributed (under-dispersed) and approximately unity if the distribution is random. If the parasites are aggregated (over-dispersed), that is, most hosts have few or no parasites and a few have very many, the ratio will exceed unity. As the lice in general had an aggregated distribution on their hosts (Fig. 4), non-parametric Kruskal-Wallis tests or Spearman's Rank correlations were used, with the significance level set at 0.05. The value of Spearman's correlation coefficient ρ indicates the strength of the association, where $\rho = 1$ signifies a 100% positive correlation, and $\rho = -1$ a 100% negative correlation.

The distribution of parasites within the host population is of crucial importance to the outcome of host-parasite interactions (e.g. Anderson and May, 1978; Anderson and Gordon, 1982; Scott, 1987, 1994; Esch and Fernández, 1993; McCallum and Scott, 1994), since the pathogenicity of the parasite depends on the number of parasites present on a host. For example, sudden changes in parasite aggregation may be a result of increased mortality among the most heavily infested fish (Lester, 1984).

Results

Surface temperature

The monthly averaged temperatures for the four years of sampling are presented in Figure 2. The temperatures in the period January to March were highest in 1992 and lowest in 1994. The warmest water was recorded in August in 1993–1995, and in June in 1992; subsequently there was a constant decline in temperature until December in all years.

The host population

A total of 502 sea trout were sampled. The average age was 3.11 years (± 1.02 s.d., range 1–7 yr), the average wet weight 440.3 g (± 475.7 s.d., range 28–4000 g), and average length was 319.7 mm (± 89.4 s.d., range 140–725 mm). The average fish length in the samples differed significantly between months within each year (Table 1). Fish length and age were generally lower in

Table 1. Monthly catch data of sea trout *Salmo trutta* around Tromøy, Norway. Age data are missing for 10 fish as indicated.

Year	Month	n	Mean fish length (mm) (± s.d.)	Mean fish age (± s.d.)
1992	August	10	282.2 (59.7)	2.3 (0.5)
	September	8	253.4 (45.2)	1.8 (0.5)
	October	16	282.4 (53.6)	2.2 (0.5)
	December	26	315.9 (33.2)	2.2 (0.5)
1993	March	17	301.9 (21.8)	3.4 (0.5)
	April	29	324.3 (39.0)	3.6 (0.5)
	May	26	229.8 (90.4)	2.7 (0.7)
	June	41	278.6 (100.7)	2.9 (1.1) (n = 36)
	July	5	267.0 (54.0)	2.3 (0.6) (n = 3)
	August	28	326.3 (90.0)	2.6 (0.7)
1994	April	37	319.4 (69.7)	3.8 (0.9) (n = 36)
	May	18	318.7 (60.8)	3.7 (1.0)
	June	35	369.4 (86.5)	3.9 (1.1)
	July	29	393.4 (95.7)	3.8 (0.7)
	August	32	267.4 (66.4)	2.6 (0.8)
	September	15	261.6 (61.2)	2.1 (0.7)
	October	18	298.9 (51.3)	2.2 (0.5)
1995	March	24	354.9 (90.9)	3.6 (1.0)
	April	34	348.1 (62.3)	3.5 (0.7)
	May	10	418.5 (94.9)	4.0 (1.2)
	June	29	415.6 (115.7)	3.5 (1.0) (n = 28)
	August	7	291.4 (57.7)	2.3 (0.5)
	September	8	262.8 (26.6)	2.4 (0.8) (n = 7)

the Tromøy Sound, mainly due to the presence of more 2-year-old fish there, while there were more 5–7-year-olds on the outside of the island. However, more than 60% of the catch were 3- and 4-year-old fish in both areas.

Seasonal changes in prevalence and median intensity

In general, the percentage of fish infested with *L. salmonis* (prevalence) increased from about 20–35% in March–April to about 100% in the late summer or autumn (Fig. 3). The prevalence of 62% in December 1992 showed that the largest drop in infestation occurred between December and March. Although no fish were obtained in the period from November to Febraury of 1993–1995, the low lice levels in March and April suggest that both prevalence and intensity decreased in January and February.

In 1992, we found a median of one salmon louse per infected fish (Fig. 3), and there were no significant differences in median intensity of infestation between months ($p = 0.56$). In 1993, 1994 and 1995, the median intensity of infestation generally increased from less than three in March–April to a maximum of eight salmon lice per fish in the period from May to August (Fig. 3). In 1994 the intensity decreased between August and September, and subsequently levelled out. These patterns produced significant differences between months in 1993 ($p < 0.001$) and 1994 ($p < 0.001$), but not in 1995 ($p = 0.18$).

In the first sample each year the distribution of *L. salmonis* on hosts was under-dispersed, as the ratios of variance to mean intensity were below one every month (Fig. 4a). The ratio increased the following months, and the distribution became overdispersed (aggregated) in the period from May to June. When the median intensity fell from August to September 1994 (Fig. 3), there was a rise in aggregation (Fig. 4a). A similar increase occurred in 1994 and 1995, but levelled off between July and August in 1993. Generally, the changes in aggregation resembled the changes in prevalence and median intensity through time.

With few exceptions, the prevalence and median intensity of *C. elongatus* followed each other closely in the four years of study (Fig. 5). In general, there was a gradual build-up of the *C. elongatus* population from 0–2 individuals per host in the first sample of the year to a maximum of 4–10 in July–September. At this time the prevalence reached about 90% in 1993–1995, and subsequently fell. The infestation intensity was not recorded after August in 1993, but in 1994 it fell markedly between July and August, and in 1995 it peaked in September, the last sampling month. *Caligus elongatus* was not found in April 1994 and March 1995. In 1992, the peak in both prevalence and median intensity occurred in October. The intensity of *C. elongatus*

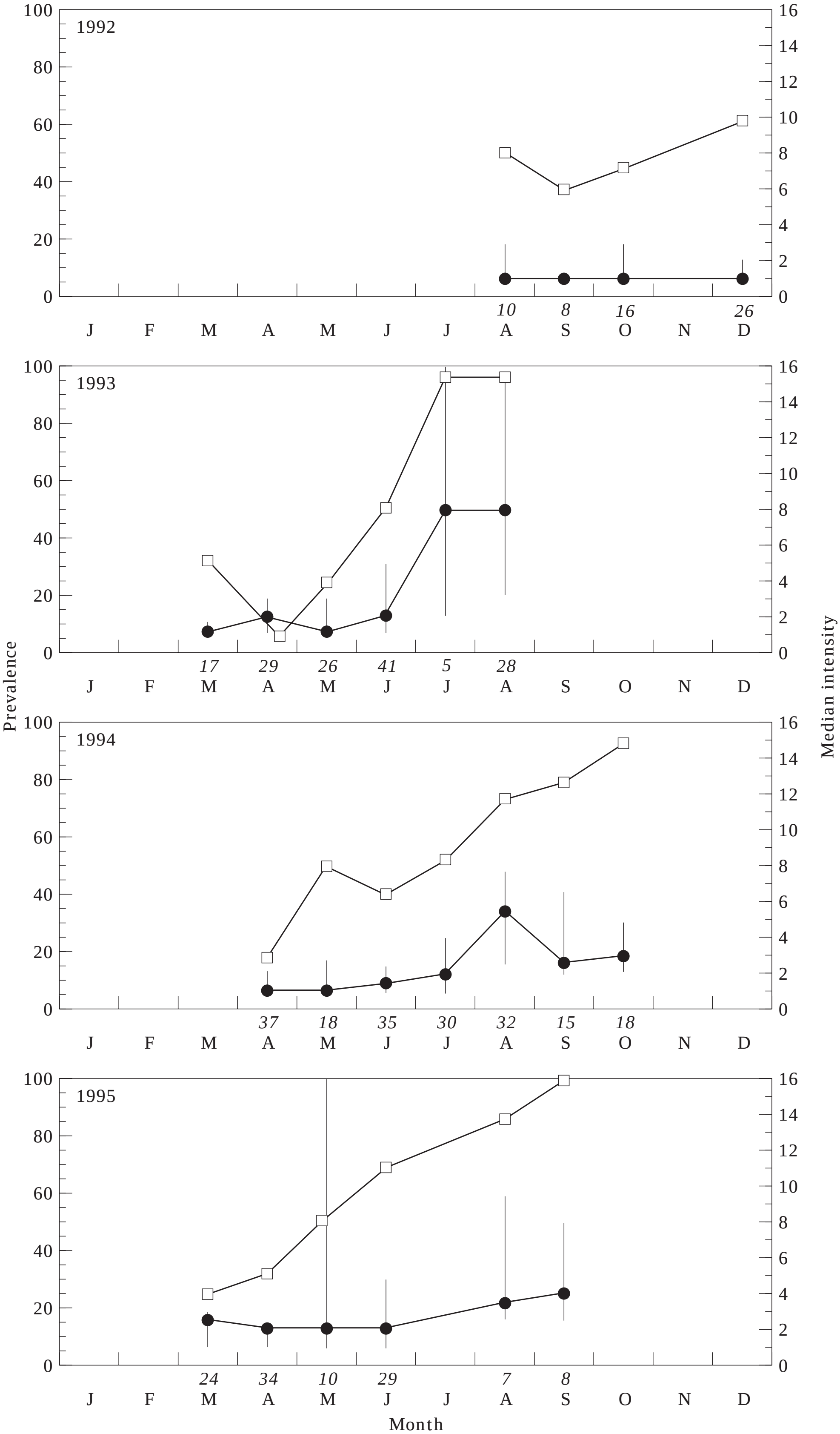

Figure 3. Prevalence (□) and median intensity (●) with IQR (Interquartile range, the span between the 25th and 75th percentile) of *Lepeophtheirus salmonis* infestation on sea trout in 1992–1995. The number of sea trout caught each month is indicated below the abscissa axis.

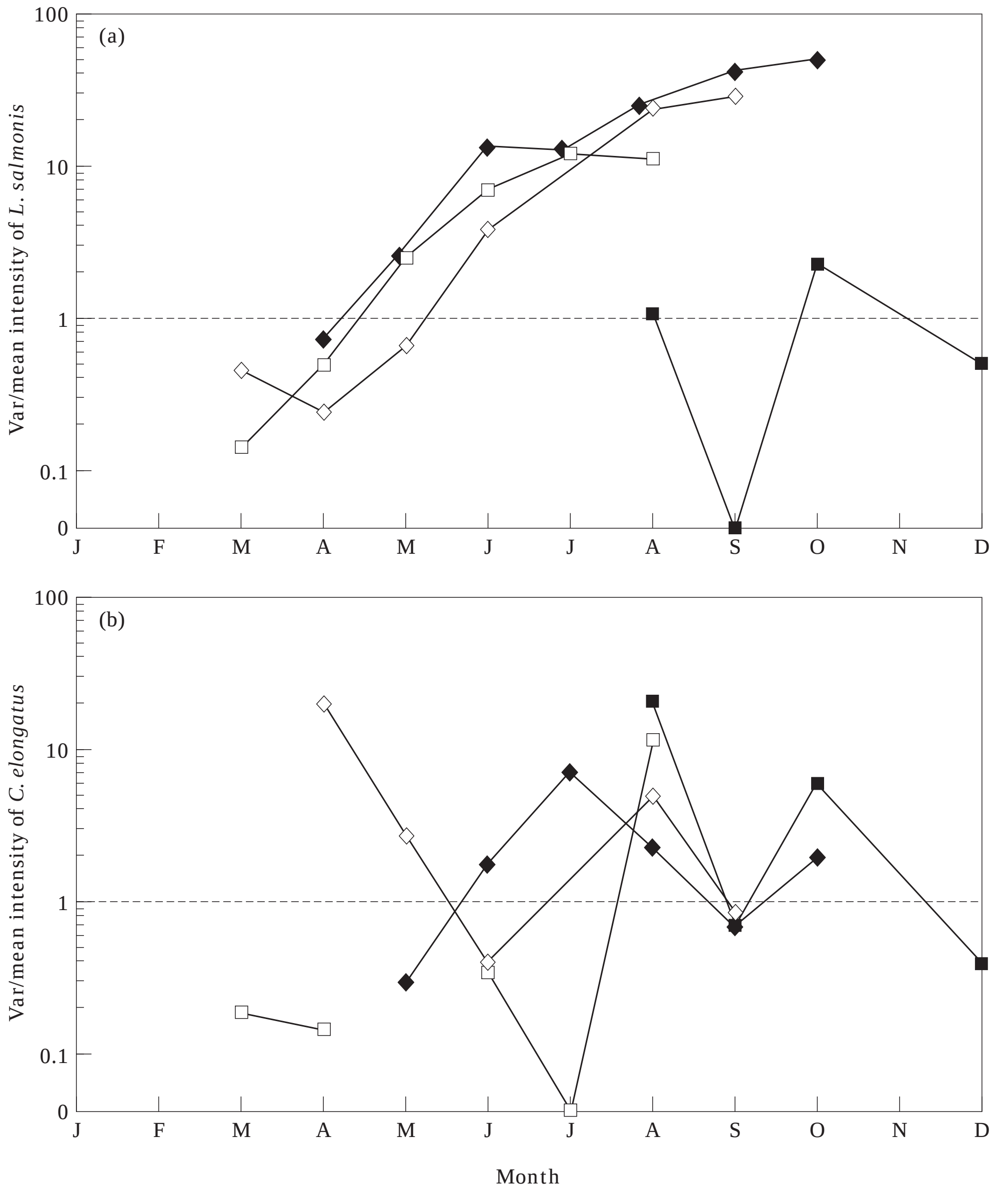

Figure 4. (a) Ratio of the variance to mean intensity of *Lepeophtheirus salmonis* infestation on seat trout in 1992–1995. The value for September 1992 is based on three *L. salmonis* only, one on each of three fish. (b) Ratio of the variance to mean intensity of *Caligus elongatus* infestation on sea trout in 1992–1995. The value of May 1993 is not plotted as there was only one *C. elongatus* in the sample. The value for July 1992 is based on four *C. elongatus* only, one on each of four fish. 1992 (■); 1993 (□); 1994 (◆); 1995 (◇).

infestation was significantly different between months in 1992 ($p=0.0086$), 1993 ($p<0.001$) and 1994 ($p=0.001$), but not in 1995 ($p=0.26$).

Caligus elongatus was generally less aggregated in the trout population, and had larger variations in the degree of aggregation than *L. salmonis* (Fig. 4b). The variance to mean ratio did not follow prevalence or intensity of infestation.

Seasonal changes in population structure

Adult lice, mainly females, dominated the infestations of *L. salmonis* on sea trout (Fig. 6). Egg-producing females were found in December 1992, March–June 1993, April–October 1994 and April–September 1995. In March, the parasite population consisted of adult females and males only, with pre-adults

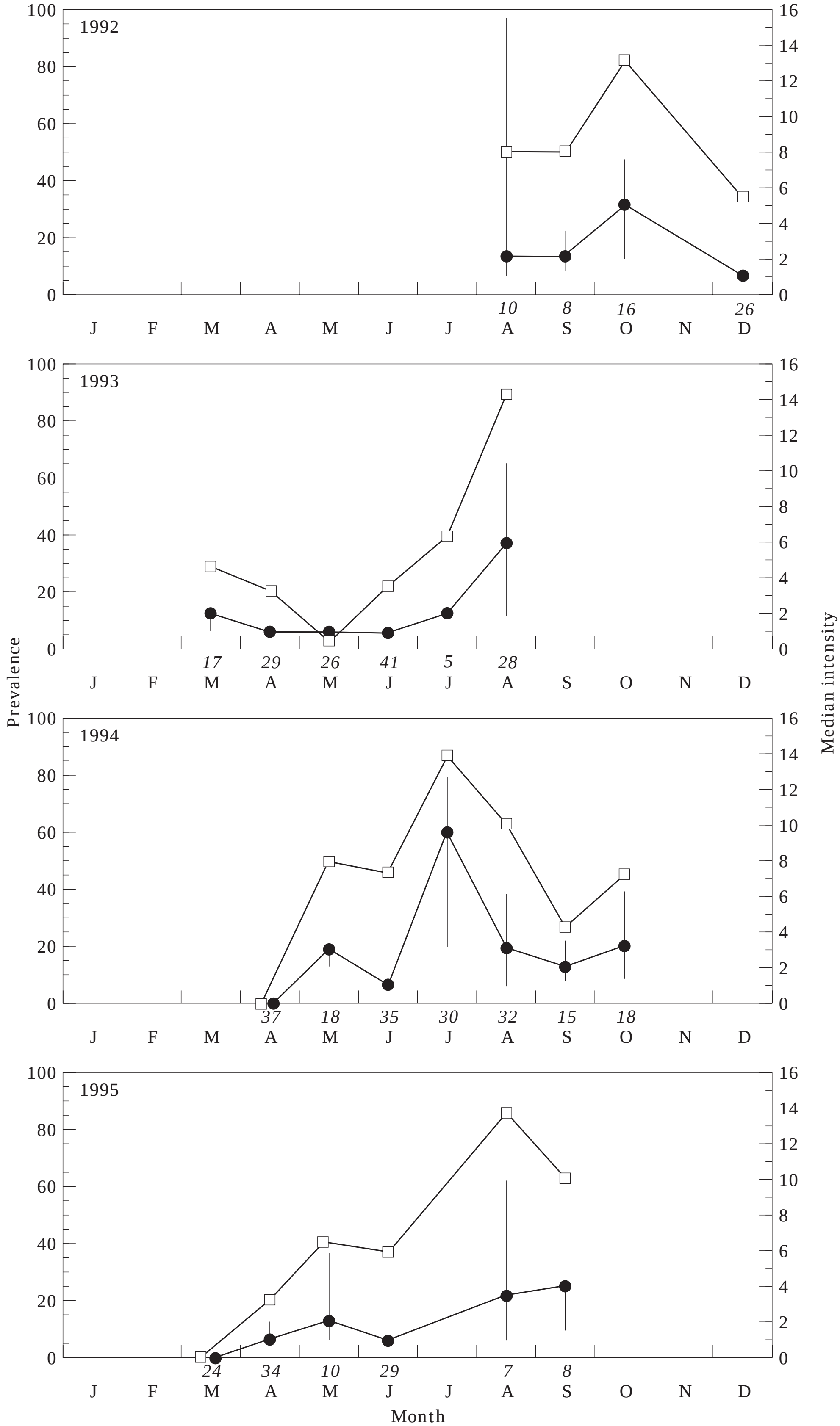

Figure 5. Prevalence (□) and median intensity (●) with IQR (Interquartile range, the span between the 25th and 75th percentile) of *Caligus elongatus* infestation on sea trout in 1992–1995. The number of sea trout caught each month is indicated below the abscissa axis.

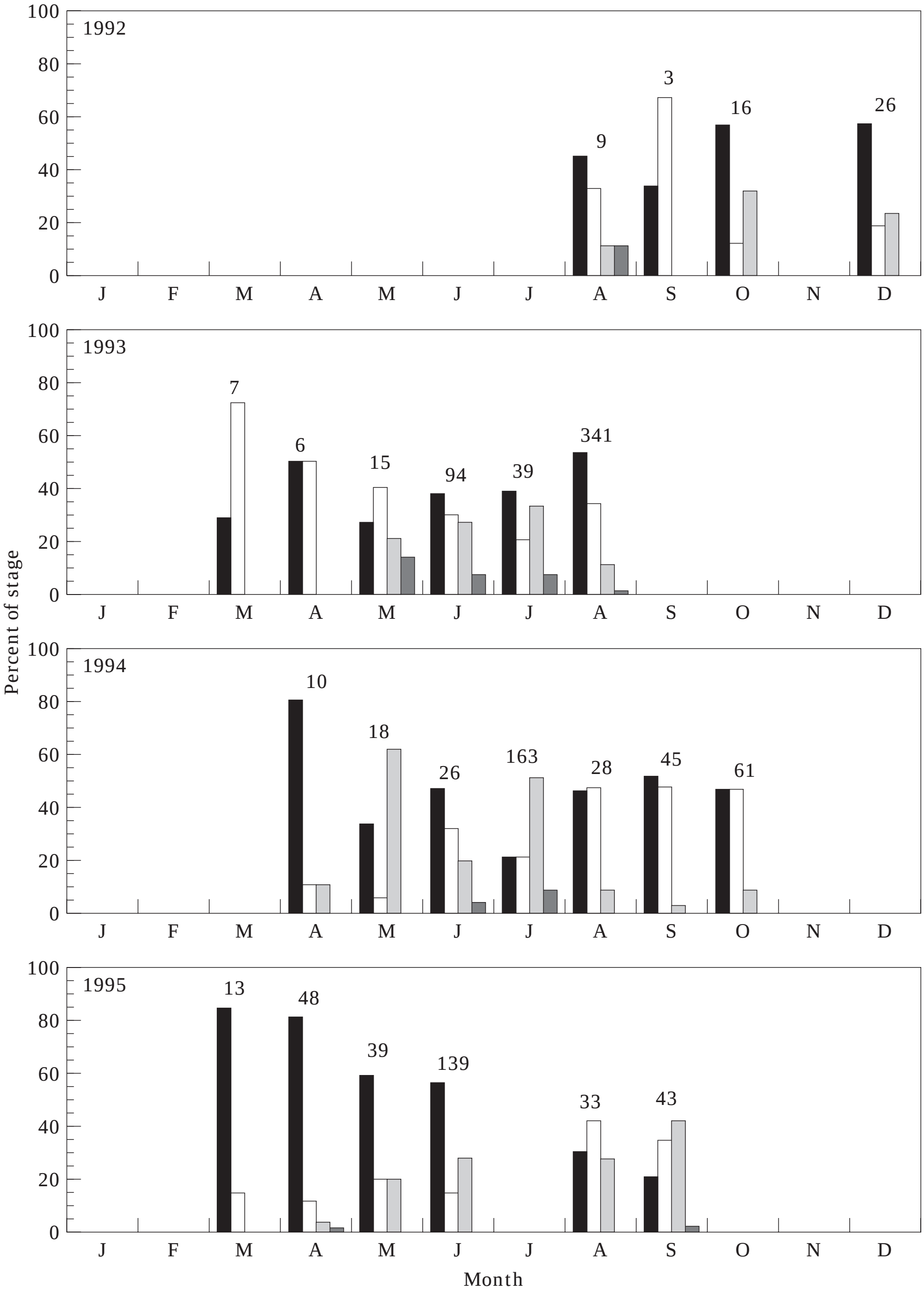

Figure 6. Relative abundance of groups of developmental stages of *Lepeophtheirus salmonis* on sea trout in 1992–1995. The number of parasites collected each month is indicated above the bars. Adult females (■); adult males (□); pre-adults (▨); chalimus (▨).

appearing in April in small amounts. The pre-adult proportion then increased through the summer, and declined in the autumn in 1993 and 1994. In 1992 and 1995, substantial amounts of pre-adults were observed in the autumn. Pre-adults were also found in December 1992, but no chalimus larvae were found after August. Chalimus larvae were first found in May in 1993, in June in 1994 and in April in 1995. The proportion of chalimus larvae in the monthly samples never exceeded 15%.

The population of *C. elongatus* was completely dominated by adult females in all years (Fig. 7). Small numbers of chalimus larvae were observed in March 1993, May 1994 and April 1995, indicating that recruitment may occur at 5–10°C in this area.

General trends in parasite-host associations

All catches from the four years of sampling were pooled for analysis by non-parametric Spearman's Rank correlation. The median intensities of *L. salmonis* and *C. elongatus* were not correlated with the condition factor of the host ($\rho=0.02$, $p=0.75$ and $\rho=-0.038$, $p=0.66$, respectively), nor with host age ($\rho=-0.086$, $p=0.18$ and $\rho=-0.107$, $p=0.14$). However, the intensity of *C. elongatus* was positively correlated with host weight ($\rho=0.217$, $p=0.0024$) and length ($\rho=0.232$, $p=0.0011$).

On the fish that harboured both parasite species, the median intensity of *C. elongatus* was positively correlated with the median intensity of *L. salmonis* ($\rho=0.303$, $p<0.001$). The differences in median intensity between age groups were not significant ($p=0.23$ for *L. salmonis* and $p=0.49$ for *C. elongatus*), and the two parasites were similarly distributed on hosts age groups (Fig. 8). The median intensity of *L. salmonis* was lowest in one-year-olds, at one parasite per infected fish.

Discussion

Seasonal occurrence of *L. salmonis* and *C. elongatus*

The river of origin of individual fish caught in this study is not known, but the similarity in age structure of the samples caught at different locations and with different gear suggests that the fish can be regarded as originating from sea trout populations with comparable behaviour at sea. About 60% of the trout caught both inside and outside of Tromøy were aged 3 to 4 years. It would therefore, appear reasonable to assume that the recorded infestations are independent of changes in sampling locality and gear.

Both parasites studied were present in small numbers in March and April, and then increased in numbers during the spring and summer. A prevalence of 100% was reached in 1993, 1994 and 1995 for *L. salmonis*, while the prevalence of *C. elongatus* generally peaked at about 90%. Maximum prevalence of salmon lice was reached later than for *C. elongatus*. Pemberton (1976) found a similar pattern for the occurrence of salmon lice on sea trout from Loch Etive on the Scottish west coast. In the winter the infestation was markedly reduced, and the trout generally seemed to be infested on their seaward migration outside the loch proper, the prevalence reaching 95% in August. The salinity of Loch Etive is strongly influenced by rain and river run-off, so this may have influenced the infestation pattern (Pemberton, 1976). An increase in infestation to a maximum in the late summer or autumn was found for both parasite species on farmed salmon in Ireland from May to September 1991 (Jackson and Minchin, 1993). A study of the infestation changes in an untreated salmon pen in Ireland from July 1987 to January 1988 (Tully, 1989) showed a markedly different pattern. There, the abundance of *L. salmonis* peaked in August, then fell in the autumn and rose in December and January, the prevalence reaching 100% in December. Another difference is that pre-adult females in Ireland did not mature to any great extent before December (Tully, 1989), whereas we found egg-producing females in most of our samples.

No *C. elongatus* were found in the first catches in 1994 and 1995, whereas female adults of *L. salmonis* were recorded in small numbers. Low water temperature is most likely not the reason for this, as 1994 and 1995 were not similar with respect to winter temperature. Furthermore, *C. elongatus* may be more tolerant to cold water than salmon lice (Hogans and Trudeau, 1989). A possible explanation is that the first *C. elongatus* infestation in the spring originates from other host species than trout, and that these arrived later in 1994 and 1995. *Caligus elongatus* has a very low host specificity (Kabata, 1979), and the adults are good swimmers and may transfer between hosts (Wootten *et al.*, 1982; Bruno and Stone, 1990). Indeed, Wootten *et al.* (1982) hypothesize that maximum intensity of *C. elongatus* on farmed salmon in Scotland may be associated with the time of occurrence of wild reservoir hosts in the vicinity of the sea cages. Transfers between hosts of different species may also explain the large variation in aggregation of *C. elongatus*. If the parasite uses other host species within a life cycle, a variance to mean index based on sea trout only would clearly give an incomplete picture of its distribution, as the most infested host could be other fish species.

In the Oslo Fjord, which does not have full strength sea water, *C. elongatus* was very rarely found on sea trout, and it was never found in a stream running into the fjord (Mo and Heuch, 1998). Sharp *et al.* (1994) found *C. elongatus* in only one of 13 rivers in Scotland. Their trout was sampled with rod and line in the lowest parts of the rivers. It is possible that *C. elongatus* is less tolerant than the salmon louse to fresh water, and that it leaves its host before they enter brackish or fresh water. This may be easier to accomplish for *C. elongatus* than for *L. salmonis*, because the former has better faculties of swimming (Wootten *et al.*, 1982; Neilson *et al.*, 1987). Also, it has repeatedly been found in plankton tows (Wootten *et al.*, 1982; Neilson *et al.*, 1987; T. A. Schram, pers. obs.), which implies that periods of free swimming in the water might be a natural part of the life cycle of this parasite.

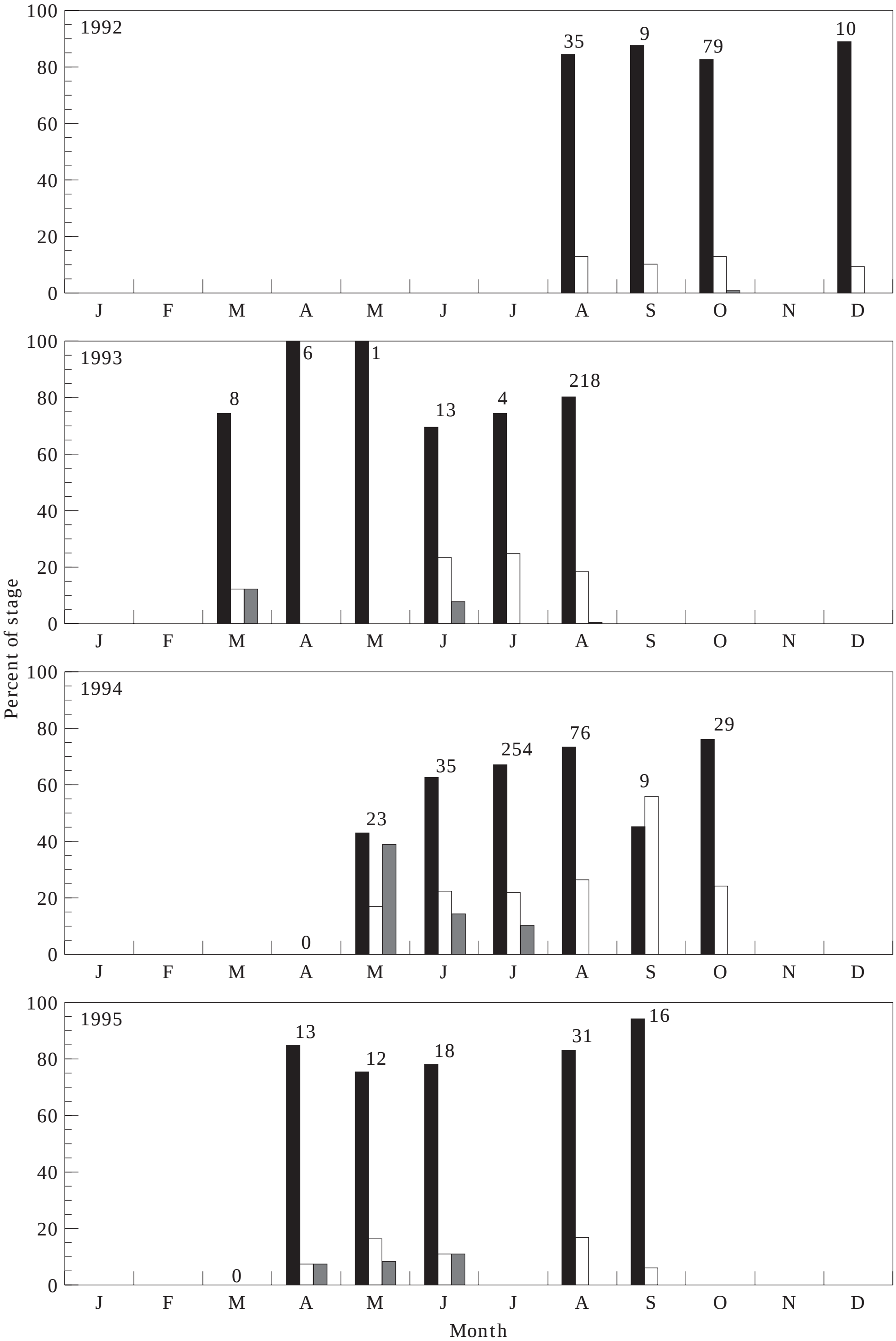

Figure 7. Relative abundance of groups of developmental stages of *Caligus elongatus* on sea trout in 1992–1995. The number of parasites collected each month is indicated above the bars. Adult females (■); adult males (□); chalimus (▨).

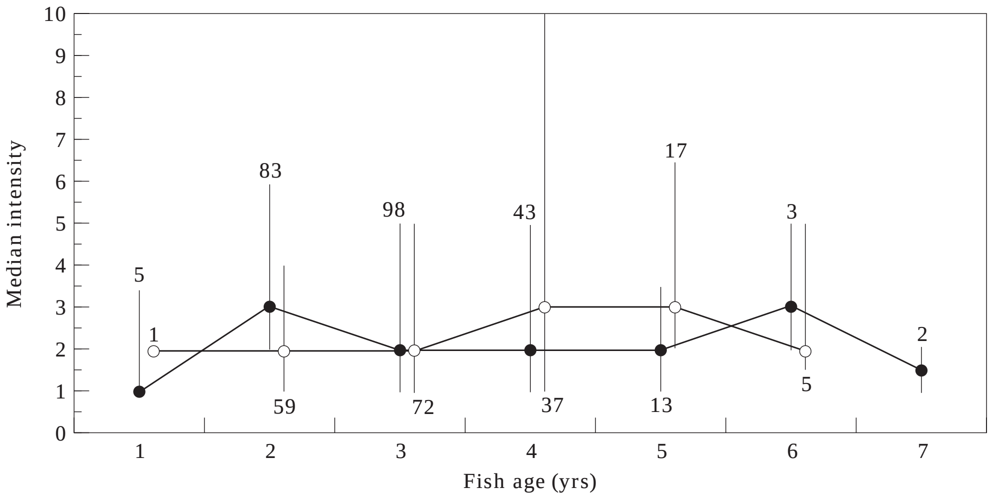

Figure 8. Median intensity with IQR (interquartile range, the span between the 25th and 75th percentile) of *Lepeophtheirus salmonis* and *Caligus elongatus* on sea trout of different age classes in 1992–1995. The number of fish collected each month is indicated above/below the bars. *L. salmonis* (●); *C. elongatus* (○).

The infestation of sea trout on the Norwegian south coast with *C. elongatus* is more similar to Tully's (1989) observations on caged salmon in Ireland, where the infestation seemed to decline in the winter. In 1993–1995, the occurrence of *C. elongatus* on sea trout off Arendal also seemed to be reduced in September, but there are no data for the winter these years. Hogans and Trudeau (1989) followed the occurrence of *C. elongatus*, which accounted for more than 97% of the caligid parasites, on farmed Atlantic salmon in the Bay of Fundy, Canada. They recorded a peak in copepod abundance and intensity in September–October, when the water temperatures were highest, and a subsequent decline. In the present material, the changes in infestation parameters do not seem to be tightly coupled to changes in surface temperature. The increase in both prevalence and median intensity of *C. elongatus* from September to October 1992 happened when the temperature was falling, and the decline in both parameters in 1994 and 1995 occurred before the temperature dropped. The reason for this uncoupling may be that sea trout can choose water depths with an optimal (stable) temperature, whereas caged salmon are restrained by the net bottom, which is usually at ca. 6 m depth. Differences in the availability of other hosts may also have influenced the infestations. Wootten *et al.* (1982) recorded *C. elongatus* infestation through a year on farmed salmon in Scotland. The parasite did not appear on the fish until June, and maximum numbers in their study occurred in November. This is remarkably different from the situation on wild sea trout at Tromøy and on farmed salmon in the Bay of Fundy in Canada. Although temperature data were not included in the Scottish work, it would be reasonable to assume that this increase in intensity has taken place on falling temperatures. This again would indicate that the occurrence of *C. elongatus* is not strongly correlated with sea-surface temperature.

The data show that the occurrence of the two parasites are correlated. This was also found by Jackson and Minchin (1992) on farmed Atlantic salmon in Ireland. Thus it would appear that there is no competitive exclusion by either species.

A difference between *L. salmonis* and *C. elongatus* in median intensity of infestation appeared between August and September 1994. Whereas median intensity followed the decline in prevalence in *C. elongatus*, the intensity of *L. salmonis* dropped as the prevalence continued to rise. As reproduction in the latter species is strongly positively correlated with temperature (Tully, 1989, 1992; Johnson and Albright, 1991), and the temperature continued to rise in the period, a continued increment could be expected. There may be several reasons for the fall in intensity. Mortality among adult lice may have been higher than recruitment, the most heavily infested trout may have mounted effective responses, or they may have had a higher mortality than the uninfected or lightly infected fish. Finally, the change in fishing method and location might have biased the infestation parameters. If the adult salmon lice mortality rate had been higher than the rate of new infestations, the population of lice could have been expected to contain a larger proportion of chalimus and pre-adult stages after the fall in median intensity. In 1994 the proportion of these stages decreased between August and September, suggesting that heavy mortality of adults alone did not cause the decline in median intensity.

If present, effective host responses against lice would most likely be seen in the most infected fish, i.e. those fish which have the strongest stimulation of their immunological defence. This would result in a reduction of lice loads on these fish, and consequently a less aggregated distribution of the parasites in the host population (Anderson and Gordon, 1982). The same would be expected if the fish with most parasites are more likely to die than lightly infested fish (Anderson and Gordon, 1982). However, from August to September 1994 the reduction in median intensity of infestation was accompanied by a rise in the value of the index of aggregation. Development of resistance to the parasitic copepod *Lernea cyprinacea* has been demonstrated in the fish *Helostoma temmincki* (Woo and Shariff, 1990), but no conclusive evidence for a strong specific immunity against *L. salmonis* in sea trout has been put forward (Grayson *et al.*, 1995). We conclude that neither an increased adult mortality among the lice, nor a density-dependent disappearance of lice can explain the decline in median intensity of infestation in 1994. This is supported by the finding that louse burden and condition factor of the host are not correlated. Furthermore, similar patterns of prevalence, median infestation and aggregation in 1992, 1993 and 1995 suggest that *L. salmonis* cause little damage to sea trout.

At no time were large numbers of chalimi found in our samples. The dominance of adults in the samples was expected, since the time from egg to adult of both species is probably much shorter than the duration of adult life. The adult life span of *L. salmonis* in nature is not known, but Nordhagen (1997) recorded a maximum duration of life from copepodid to death of adult of 191 days at 7.4°C, where the first eggstrings were produced after about 79 days. Observations of epiphytes on adult female lice indicate that they may live for half a year (authors' observations). In the closely related species *L. pectoralis* females may live for 4–6 months (Boxhall, 1974), and it seems reasonable that the larger salmon lice females would live for just as long.

Sea lice and premature return of sea trout

Most sea trout caught during the present investigation were 2–4 years old, but catches included both younger and older fish. There was very little external damage due to lice, and the fish appeared healthy. The condition factor of the host was not correlated with the intensity of infestation with either *L. salmonis* or *C. elongatus*. This is in agreement with the studies of *L. salmonis* on sea trout from Scottish rivers (Sharp et al., 1994), and from the Oslo fjord in Norway (Mo and Heuch, 1998). No similar study from salmon farming areas exist, so the impact of sea lice from farms on marine populations of sea trout is difficult to evaluate. These two data sets contrast sharply with other studies from Norway (Birkeland, 1996a, b) and Ireland (Tully *et al.*, 1993a, b) of the occurrence of salmon lice on sea trout returned in the early summer to rivers in areas with intensive salmon farming. These fish were in the smolt or post-smolt stage, probably 1–2 years-old, and in a poor condition. However, the situation is not directly comparable to the present data, which comes from a relatively open marine environment.

In our material, 1-year-old fish had fewer parasites than 2-year-old fish, probably due to the shorter duration of exposure to infective larvae. The infested 2–6-year-old trout had a median of 2–3 *L. salmonis* and *C. elongatus*. In Loch Etive, Pemberton (1976) found that sea trout larger than 21 cm were ''clearly more infested'' with salmon lice than fish below this size. This was explained by the fact that the smaller fish stayed within the loch where the salinity is low, and that the larger fish came from the marine environment outside (Pemberton, 1976).

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