

Salinity and temperature effects on sea lice over-wintering on sea trout (*Salmo trutta*) in coastal areas of the Skagerrak

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Both the salmon louse *Lepeophtheirus salmonis* and its close relative *Caligus elongatus* are ectoparasitic on Salmonidae in salt water in the northern hemisphere. In this study we monitored population dynamics of these parasites on anadromous brown trout, i.e. sea trout, on the Norwegian Skagerrak coast in the winters of 1998–1999 and 1999–2000. The low salinity was expected to reduce sea lice populations as lice do not tolerate sojourns of more than a few weeks, at most, in freshwater. Results confirmed the presence of both parasite species on estuarine sea trout in winter, and showed that the lice populations go through a bottleneck in this period. Prevalences of infection of both parasite species were very different in the two sampling periods, but fell below 10% in March in both winters. Median infection intensity was 1–2 fish⁻¹. Salinity was statistically related to the presence of *C. elongatus* both winters, and to *L. salmonis* in 1999–2000. Temperature appeared to be less important for the abundance of lice.

INTRODUCTION

The salmon louse *Lepeophtheirus salmonis* (Krøyer) is an ectoparasitic copepod which is specific for Salmonidae in seawater in the northern hemisphere (Kabata, 1979; Pike & Wadsworth, 1999). In Norwegian waters, the most abundant natural hosts are Atlantic salmon, *Salmo salar* L. and anadromous brown trout *Salmo trutta* L., hereafter called sea trout. However, the life cycles of these fish species make them challenging habitats for the parasite (Pike & Wadsworth, 1999), as both spend a limited time in coastal waters. Atlantic salmon, both smolts and adult fish, pass through the coastal zone in a matter of days in spring, to reach feeding grounds in the open ocean (e.g. Holm et al., 1982; Hvidsten, 1994; Nordeng, 1994). Here they stay 1–4 years before returning in April–October to spawn in their native river (e.g. Hansen & Quinn, 1998). Salmon lice reproduce on salmon in the open ocean (Jakobsen & Gaard, 1997), but the bulk of the homing salmon arrive at the coast too late for their parasites to infect spring-running salmonid smolts (Hansen & Quinn, 1998). Sea trout, which are found along most of the Norwegian coast, are generally believed to enter the marine environment in spring, and spend 3–6 months foraging near-shore. They then ascend rivers to spawn, if mature, and over-winter (e.g. Jensen, 1968; Jonsson, 1985; Berg & Berg, 1987, 1989). In winter, then, there would seem to be no natural host fish in Norwegian coastal areas. Salmon lice will not survive for more than a few weeks in freshwater (Hahnenkamp & Fyhn, 1985; McLean et al., 1990; Finstad et al., 1995), so there are no possible hosts in lakes and rivers. However, a recent study revealed that in March and April, 20% of Norwegian Skagerrak sea trout carried lice (Schram et al., 1998). Late autumn prevalence reached 90–100% (Schram et al., 1998), thus the parasite population apparently goes through a

bottleneck in winter. Our hypothesis in the present work has been that some sea trout remain in the marine environment through the winter.

We also report concomitant changes in the population of the closely related, sympatric copepod *Caligus elongatus*. This parasite, which has been found on more than 80 fish species (Kabata, 1979), provides a contrast to the relatively host-specific salmon louse. While it too appears to be intolerant to freshwater (Landsberg et al., 1991), it is also a good swimmer, and adult individuals have been hypothesized to switch hosts in the sea (Wootten et al., 1982). *Caligus elongatus* may therefore be expected to have different population dynamics to *L. salmonis*.

MATERIALS AND METHODS

Field sampling

The study area included the Norwegian Skagerrak coast from the Tromøy Sound at Langangselva (58°29'N 8°52'E) just north of Arendal, to Vikkilen (58°21'N 8°37'E) near the town of Grimstad (see Knutsen et al., 2001). Salinity in the area may fluctuate considerably as a function of freshwater run-off from nearby rivers. Sea trout were caught by 15.0×1.5-m floating monofilament gill nets at five permanent sampling stations: in bays on the sides of the Tromøy Sound, and in the bays of Hove, Søm, Grevstad and Vik. Ten different gill nets (9–17.5-mm bar mesh) were set at the precise same locations within sampling stations, and mesh widths were randomly distributed among locations. The first fishing period (Winter 1) started in October 1998 and continued through April 1999, and the second period (Winter 2) was from October 1999 to March 2000. Each month sampling lasted until a sample of approximately 30 fish was obtained. The fish were carefully removed from the nets and put individually in marked plastic bags. Salinity and temperature from 0–10 m depth were recorded

with a portable conductivity, temperature and depth (CTD) profiler in the place nearest to the nets permitting this depth range.

Sea lice

In the laboratory, the catch was either frozen immediately, or examined fresh with a 4× magnifying glass with good illumination. Fish weight and fork length were recorded. Thawed and fresh trout were submerged in a tray, and examined for parasites. Bags and tray water were subsequently inspected. The number and development stage of lice of each parasite species on each fish was determined using Schram (1993) and Piasecki (1996). Parasitological terms are used as recommended by Bush et al. (1997). Reported numbers may be regarded as underestimates, although Tully et al. (1999) showed that gill-netting not necessarily reduces lice numbers compared to electro-fishing. As sampling was standardized in the investigation, the error is expected to be the systematic and not influence the relative amounts of lice recovered.

Data treatment and statistics

As sea trout feed in the littoral zone (Lyse et al., 1998; Knutsen et al., 2001), the temperature and salinity recordings from the upper 2.5 m of the water column were assumed to cover the 'average environment' experienced by the trout. All readings from 0–2.5 m were thus averaged for each fishing date at each station, and subsequently these were averaged over each month of sampling. Underlying distributions of temperature and salinity were assumed to be approximately normal, so these variables were analysed with parametric analysis of variance and Pearson correlation. Parasite counts were presumed to be skewed (Schram et al., 1998) and consequently non-parametric Spearman correlations were used to test for association.

The relationship between temperature, salinity and parasite infection was investigated with logistic regression and Fisher exact tests. In the latter, separate 3×3 matrices of the total number of lice (0, 1 and >1 louse/fish) vs temperature (<3°C, 3–5°C, and >5°C) and salinity (<23 psu, 23–28 psu and >28 psu) were constructed. These intervals were based on the presumed salinity tolerance limits of the fish (Sigholt & Finstad, 1990) and on the recorded salinity levels on the sampling sites. The probability of obtaining the observed numbers in each cell of the matrices by chance was calculated. Effects were judged significant if the probability was less than 0.05.

RESULTS

Sampled fish

Altogether 367 fish were captured in the two study periods. Average fish weight was 328 g (±63 SD), and average fish age was 2.7 y (±1.0 SD). Catches were fairly evenly distributed in size, and their length distributions showed that they were smolts-of-the-year with a sea age of 6–9 months.

Lepeophtheirus salmonis infection

Sea lice were found at low intensities through both sampling periods. Altogether 141 *L. salmonis* were found on 189 fish sampled in Winter 1 and 59 were found on the 178 fish sampled in Winter 2. The prevalence of *L. salmonis* followed different trajectories through time in the two periods. In Winter 1, the prevalence was ~47% in October and November, and then fell continuously to reach a minimum of ~8% in March (Figure 1A). In April 1999 the prevalence climbed to ~25%. The median intensity of infection was relatively stable at about two to three lice per fish through Winter 1, except for February 1999. In this month only two infected fish were caught, carrying seven and 11 lice respectively. Median infection intensity reached a low in April 1999 at one louse per fish. In Winter 2, the prevalence of infection rose from 12% in October to reach a maximum of 43% in December, and subsequently decline to 0% in March 2000 (Figure 1B). The intensity was somewhat lower in Winter 2, peaking at two lice per fish in November.

More than 50% of the *L. salmonis* were adult females in both sampling periods, but the population structure was not similar. In Winter 1, chalimus stages were found only in October and November, and the last preadults were observed in December (Figure 2A). There seemed to be

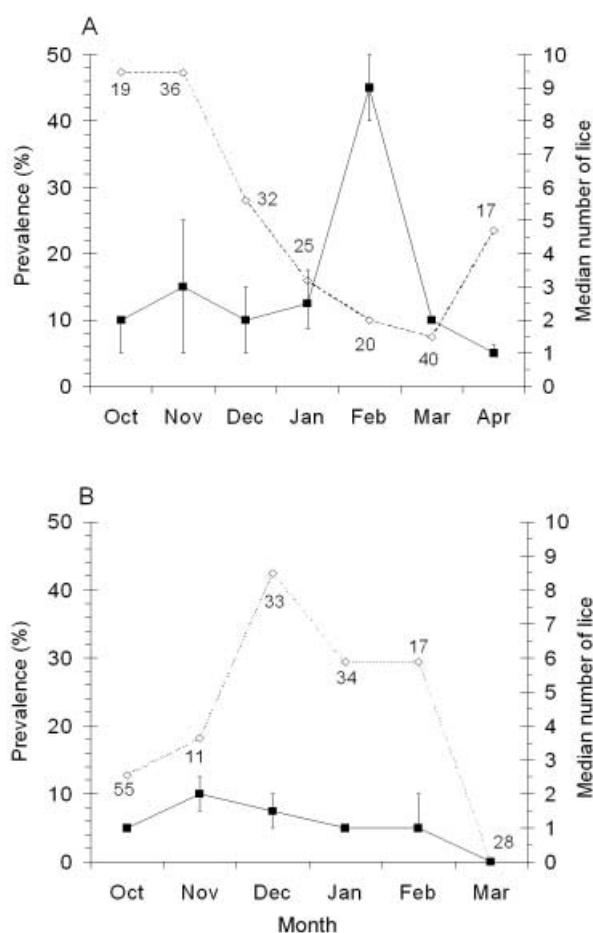


Figure 1. Prevalence (◇) and median intensity (■) ± Interquartile range of infection with *Lepeophtheirus salmonis* on sea trout (*Salmo trutta*) on the Skagerrak coast of Norway in (A) 1998–1999 and (B) 1999–2000. The number of fish caught each month is indicated above curve.

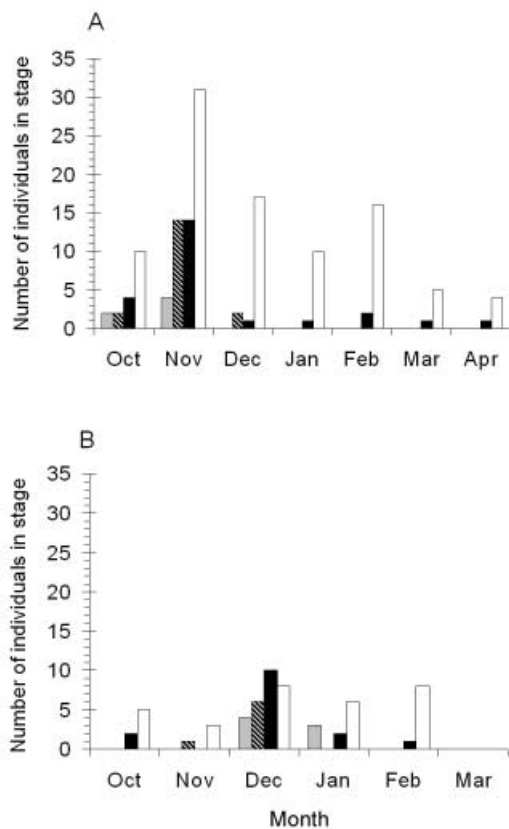


Figure 2. Population structure of *Lepeophtheirus salmonis* on sea trout (*Salmo trutta*) on the Skagerrak coast of Norway in (A) 1998–1999 and (B) 1999–2000. Copepodid and chalimus stages, grey bars; preadults, hatched bars; adult males, black bars; adult females, open bars.

no further recruitment to the parasite population in the four following months. In Winter 2, chalimus stages were found in December and January, but no preadults were recorded in February and March (Figure 2B). The absolute numbers of adults, however, remained approximately the same through to February 2000.

Caligus elongatus infection

The total number of *C. elongatus* on a host was correlated with the total number of *L. salmonis* on the same fish (Spearman's $\rho=0.57$, $P<0.0001$). Thirty *C. elongatus* were found in Winter 1, and 73 in Winter 2. The prevalence of this species also differed markedly between the two sample periods. In Winter 1, prevalence peaked in November, fell in December, then rose in January to fall to zero in March (Figure 3A). In Winter 2, prevalence was at its lowest in October, peaked in December at ~46%, and fell continuously through March (Figure 3B). This general pattern was similar for both parasite species in Winter 2. Median infection intensity of *C. elongatus* was one in October and November in both sampling periods, and subsequently oscillated between one and two lice per fish. *Caligus elongatus* adult females also made up 50 to 100% of the population of the species in both study periods, but clear differences in recruitment were noted. As with the salmon louse, chalimus stages were observed only in the autumn in Winter 1 (Figure 4A). In Winter 2, chalimi were found from December through March (Figure 4B).

Temperature and salinity

Monthly averages of temperature and salinity were correlated (correlation coefficient=0.186, $P<0.0001$). In Winter 1, temperatures generally fell through the sampling periods reaching a minimum in March 1999 at about 2°C, and in Winter 2 at about 3°C in February 2000. November and March averages were about 2°C lower in Winter 1 than in Winter 2. Monthly 1m depth temperature averages from the Institute of Marine Research's station at Flødevigen show that from August to January Winter 1 was 1–2°C colder than Winter 2.

In Winter 1, salinity increased from November to February, and decreased markedly in March, whereas in Winter 2 salinity averages were more variable. The relationship between temperature, salinity and sea louse infection was investigated using logistic regression and Fisher exact tests. In Winter 1, temperature was the only significant factor for the presence of *L. salmonis*, whereas in Winter 2, salinity was the only significant factor. Temperature was weakly significant for the occurrence of *C. elongatus* in Winter 1, but the variable was not significant in Winter 2. Salinity was significant in all tests in both periods for *C. elongatus*.

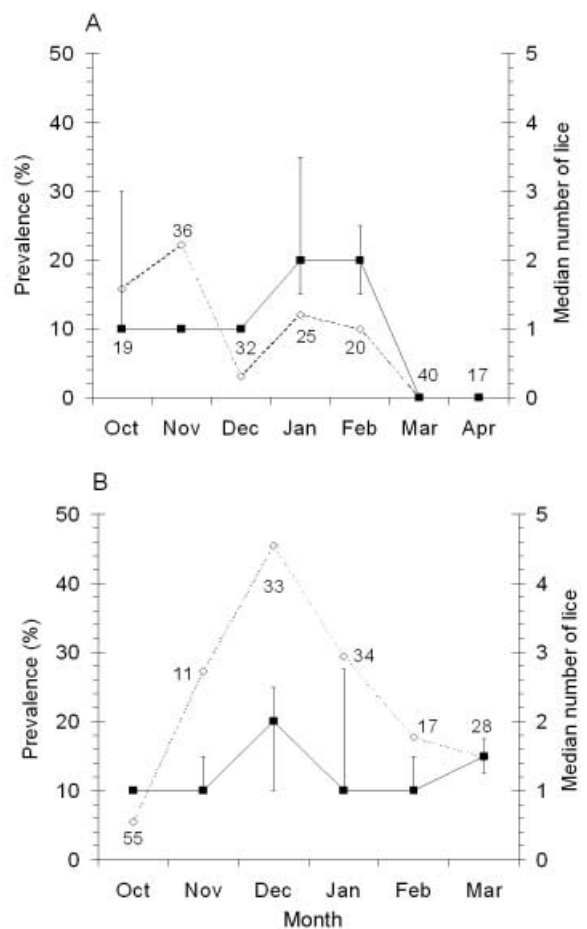


Figure 3. Prevalence (◇) and median intensity (■) ±Interquartile range of infection with *Caligus elongatus* on sea trout (*Salmo trutta*) on the Skagerrak coast of Norway in (A) 1998–1999 and (B) 1999–2000. The number of fish caught each month is indicated above curve.

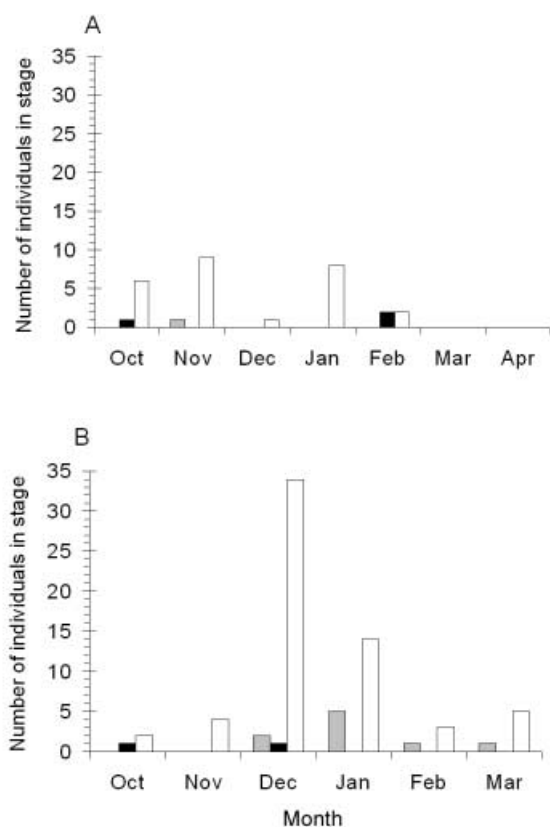


Figure 4. Population structure of *Caligus elongatus* on sea trout (*Salmo trutta*) on the Skagerrak coast of Norway in (A) 1998–1999 and (B) 1999–2000. Copepodid and chalimus stages, grey bars; adult males, black bars; adult females, open bars.

DISCUSSION

Lepeophtheirus salmonis

The present work shows that sea trout in the littoral zone of the Skagerrak coast of Norway harbour small numbers of *L. salmonis* in winter. However, the total number of *L. salmonis* recovered was very different in the two sampling periods. In Winter 1 (1998–1999), almost three times as many *L. salmonis* were sampled as in Winter 2 (1999–2000), on roughly the same number of fish. The difference was mainly due to a higher intensity and much higher prevalence of infection in October and November 1998 compared to the same months in 1999. Schram et al. (1998) found a similar difference between the October 1992 (50%) and 1994 (100%) prevalences of *L. salmonis* infection. Such differences may either be caused by reduced recruitment in late summer, or greater mortality of mature females. It was not possible to determine the influence of either of these from the data of the present study.

Schram et al. (1998) did not see signs of recruitment in winter between 1992 and 1996, thus the occurrence of chalimus larvae in December 1999 and January 2000 was surprising. It is possibly connected to the consistently higher temperatures of 1999. Water temperatures in November 1999 were higher than November 1998, and in addition, the sampling stations had higher salinity in this month. As sea lice grow faster at higher temperatures (Johnson & Albright, 1991; Nordhagen et al., 2000), it is

possible that the females matured and produced eggs earlier in 1999–2000.

Parasite prevalence in our samples fell to zero in March 2000, suggesting that the recruitment may not have been widespread enough to maintain prevalence, or that the new generation of lice did not succeed in establishing themselves. In both winters some females survived, and prevalence picked up in spring. This is congruent with Schram et al. (1998), who found that the autumn prevalence on sea trout of nearly 100% was reduced to ~20% in the spring. Both data sets consequently support the assumption that *L. salmonis* on the coast survive as adults through the winter, producing larvae in the spring which perpetuate the population.

Why do the lice populations decline so dramatically in winter? Our hypothesis was that most sea lice die when their hosts stay in freshwater-influenced areas in winter to compensate for their reduced ability to osmoregulate. Experiments indicate that Atlantic salmon osmoregulation in full strength seawater (33 psu) becomes a problem between 4° and 6°C (Sigholt & Finstad, 1990). If this result is valid for sea trout, the temperatures in the upper 2.5 m of the water column would have been sub-optimal during most of the two sampling periods at full salinity. Accordingly, the sampled fish were found in estuaries near river mouths. For sea lice, presumably the most important effect of decreasing temperature is that their hosts move to low salinity waters. Salmon lice will not survive for more than a few weeks in freshwater (Hahnenkamp & Fyhn, 1985; McLean et al., 1990; Finstad et al., 1995), so salinity is most likely of paramount importance for the development of lice populations.

This indirect mechanism may obscure the effects of temperature *per se*. Temperature as an explanatory variable was borderline significant for *L. salmonis* in Winter 1, suggesting that there was only a weak link between lice levels and this factor. In neither tests for Winter 2 temperature was significant. However, evidence suggests that temperature may have an impact directly on larval stages of *L. salmonis*. There is conflicting evidence as to whether normal development of embryos and larvae may take place at low temperatures. Whereas Boxaspen & Næss (2000) observed normal development down to 4°C, Ritchie (1993, in Pike & Wadsworth, 1999) and Wadsworth (1998, in Pike & Wadsworth, 1999) both state that successful development to copepodid is depressed in winter. However, the copepodids' ability to establish themselves on a host appear to be impaired. Tucker et al. (2000) showed in a laboratory experiment that a larger proportion of copepodids fail to establish themselves on the host at 7°C than at 12°C. If low temperatures generally impair copepodid development this would decrease winter infection pressure, and may explain the absence of recruitment in the coldest months of Winter 1. Winter infections of salmon in pens in full strength seawater on the Norwegian west coast have been observed (Boxaspen, 1997), but sea trout winter infections at temperatures below 6°C, as was found in the present study, have never before been recorded in nature.

The higher abundance of *L. salmonis* in the generally colder Winter 1 apparently contradicts the hypothesized correlation between low temperatures, low salinity and high mortality of lice. However, abundance was highest

in the autumn of 1998, and temperatures then rarely approached the presumed lower limit for effective host osmoregulation. Hence the fish have probably remained in salt water until winter, when a substantial population decline was recorded. Whereas recruitment rates appear to be reduced by low temperatures alone, this factor does not seem to explain the reduction in the number of adult lice. The low winter temperatures of the open Atlantic ocean do not prevent a build-up of substantial numbers of adult female lice on homing salmon (e.g. Berland, 1993; Jakobsen & Gaard, 1997; Todd et al., 2000). Low temperatures apparently only slow down the rate of development.

Caligus elongatus

The present data suggest that there are many similarities in the population dynamics of *C. elongatus* and *L. salmonis* on sea trout, although the latter was twice as abundant as the former. Both species showed similar development in prevalence through the two sampling periods, particularly in Winter 2. The median intensity of infection oscillated between 0 and 2 for both parasites. Furthermore, in the present study both seemed to disappear from our samples because of stochastic processes during the winter in which they were less abundant, *C. elongatus* in Winter 1, and *L. salmonis* in Winter 2. Finally, there were new recruitments in both species in Winter 2. These results agree with the data of Schram et al. (1998), where the monthly median intensities of the two parasite species were positively correlated. The similarities in the population dynamics between the relatively host-specific *L. salmonis* and the generalist *C. elongatus* suggest that there is little or no transfer of *C. elongatus* to sea trout from other fish species in winter.

Caligus elongatus was more abundant in Winter 2 than in Winter 1, however, temperature was not significant as an explanatory variable for *C. elongatus*. This conforms with Schram et al. (1998), who state that changes in *C. elongatus* infection parameters of this fish population do not seem to be tightly coupled to changes in surface temperature. The abundance of *C. elongatus* appeared to be closely related to salinity in both sampling periods, whereas *L. salmonis* was related to this parameter only in Winter 2. As discussed above, this suggests that the former is less tolerant to salinity reductions than the latter. It would also be in accord with previous studies of salinity tolerance (Landsberg et al., 1991) and occurrence of *C. elongatus* (Sharp et al., 1994; Mo & Heuch, 1998).

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