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Differing susceptibility of anadromous brown trout (*Salmo trutta* L.) populations to salmon louse (*Lepeophtheirus salmonis* (Krøyer, 1837)) infection

K. A. Glover, Ø. Skaala, F. Nilsen, R. Olsen, A. J. Teale, and J. B. Taggart

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Three Norwegian sea trout (*Salmo trutta* L.) stocks and a farmed Atlantic salmon (*Salmo salar* L.) stock were challenged with salmon lice (*Lepeophtheirus salmonis* (Krøyer, 1837)), in a "common garden" experiment. Sea trout from the River Guddal exhibited a significantly lower level of infection, as measured by louse abundance and louse density, than other stocks. In addition, salmon lice developed significantly more slowly on the Guddal stock than on the other stocks. Salmon louse abundance and density were similar for the Rivers Fortun and Sima stocks of sea trout, and abundance of lice, though not density, was highest for farmed Atlantic salmon. Within stocks, there were no differences in infection levels of salmon louse between mature and immature fish, between sexes, or between anal-fin-clipped and non-clipped salmon. Differences in infection level among the sea trout stocks may, it is suggested, reflect genetic differences.

Keywords: Atlantic salmon, genetic, salmon lice, sea trout.

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K. A. Glover, Ø. Skaala, F. Nilsen, and R. Olsen: Institute of Marine Research, Division of Aquaculture, Nordnesgaten 50, PO Box 1870, Nordnes, 5817 Bergen, Norway. A. J. Teale, and J. B. Taggart: Institute of Aquaculture, University of Stirling, Stirling FK9 4LA, United Kingdom. Correspondence to K. A. Glover: tel.: +47 55236357; fax: +47 55236379; e-mail: kevin.glover@imr.no.

Introduction

The brown trout (*Salmo trutta* L.) is a salmonid fish native to Eurasia and north Africa. Occurring as many ecotypes, the species displays extensive phenotypic variation (Day, 1887; Yevsin, 1976; Skaala and Jørstad, 1987; Pakkasmaa and Piironen, 2001) and is characterized by a high level of electrophoretically detectable genetic differentiation (Taggart *et al*., 1981; Ryman, 1983; Ferguson, 1989; Skaala, 1992). In comparison with other salmonids, a greater component of the genetic diversity in brown trout is observed among, as opposed to within, populations (Ryman, 1983).

Anadromous populations of brown trout (henceforth referred to as sea trout) are subject to infection in the marine stage of their life cycle by the salmon louse (*Lepeophtheirus salmonis* (Krøyer, 1837)), an external parasitic copepod. This parasite feeds on the surface of the fish, causing skin damage that may result in mortality as a consequence of osmoregulatory failure (Wootten *et al*., 1982; Pike, 1989; Dawson *et al*., 1998). Furthermore, wild infected sea trout may return prematurely to freshwater with potentially serious consequences for individual fish growth and survival (Birkeland, 1996). Salmon lice have received increased attention in the past decade owing to the economic losses they cause in cultured Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Costello, 1993), and also because of a possible link between infection at marine farms and high levels of infection levels in local wild populations of sea trout (Tully and Whelan, 1993; Tully *et al*., 1999).

Genetic variation in susceptibility to a close relative of the salmon louse (*Caligus elongatus*) has been reported for Atlantic salmon (Mustafa and MacKinnon, 1999). Furthermore, differences in susceptibility to salmon louse infection have been observed among salmonid species (Johnson and Albright, 1992a; Johnson, 1993; Dawson *et al*., 1997), as well as between sea trout and freshwater resident brown trout (Glover *et al*., 2001). In the latter report, fish from a land-locked stock that could not have been exposed to infection by the salmon louse in its natural habitat,

displayed a significantly higher level of infection than trout from an anadromous stock with a history of infection by the salmon louse. It was suggested in that paper that the observations may reflect genetic differences in susceptibility to infection by lice between the two stocks. However, because the freshwater resident brown trout needed to be reared and infected in saltwater, it was not possible to exclude the possibility that the fish were osmotically challenged and consequently stressed, and that this may have caused, or at least contributed to, the reported higher infection susceptibility to the louse.

Here, we report on the susceptibility to salmon louse infection among different sea trout populations. By comparing only anadromous fish, stock-specific differences in salinity tolerance are likely to be minimized. Fish from three Norwegian stocks of sea trout were reared and subjected to a salmon louse challenge in a common environment. A concurrent challenge of Atlantic salmon provided a reference point for infection levels.

Material and methods

Adult sea trout were collected from three river systems from which sampling of synchronous spawning fish was logistically feasible: the River Guddal, draining into the middle of the Hardanger fjord (59°58′N, 6°00′E), the River Sima, draining into the innermost part of the Hardanger fjord (60°30′N, 7°08′E), and the River Fortun, draining into the innermost part of the Sogne fjord (61°29′N, 7°35′E). Figure 1 shows the fjords and the location of the rivers. The Atlantic salmon used in the study were of farmed origin from a major Norwegian strain.

Experimental design

Detailed rearing conditions for the sea trout used in this study have been described elsewhere (Glover *et al*., 2003). In short, wild adult sea trout were collected from the three rivers in autumn 1998 and crossed within stocks. Fish were hatched and reared in the Statkraft hatchery on the River Sima. In May 1999, all fish were fin-clipped to permit identification (Table 1), then transferred to communal tanks, where stocks were mixed. On 19 March 2000, all fish were graded into presumptive smolts and non-smolts according to size criteria (see Glover *et al*., 2003). The presumptive non-smolts were reared for a further year, in a single tank.

On 13 June 2001, a sample of 97–102 fish between 18 and 23 cm total length were sampled from each of the three stocks of sea trout. Fish representing each stock were selected randomly among the presumptive age-2 smolts, based on the individual size criteria of Glover *et al*. (2003). Compared with Atlantic salmon, sea trout show limited and highly variable changes associated with the process of smoltification (Soivio *et al*., 1989; Tanguy *et al*., 1994; Pirhonen and Forsman, 1998). Consequently, no physiological measurement of smoltification was made in the present study. The selected trout were transported to the Institute of Marine Research in Bergen, where they were divided between two identical outdoor 1500-l tanks, each containing 150 sea trout. Each tank then contained between 48 and 51 fish from each stock. Salinity in the tanks was increased from 0 to 32 over a period of 3 weeks. A gradual transition from fresh- to saltwater was chosen to simulate that experienced by sea trout in the wild. On 26 July, 65 farmed Atlantic salmon of 19–24 cm were added to each of the two replicate tanks containing sea trout. These salmon had been gradually acclimatized to seawater 8 weeks earlier and were presumed to be fully smoltified (based on body silvering and individual size) at the date of transfer. Just before addition, all were anaesthetized with benzocaine, and 15 of the 65 salmon per tank were marked by clipping their anal fins. This subgroup of fin-clipped salmon was intended to serve as a control to investigate whether removal of a single fin may affect salmon lice infection levels.

Throughout the entire experimental period, tanks were supplied filtered louse-free seawater pumped from a depth of 90 m running at 25 l min^{-1}. Temperature and oxygen were maintained at 9±1°C and 85–95% saturation, respectively. Fish were kept under natural light intensities and a Bergen (60°N) light regime. All fish were hand-fed to satiation once daily on a mixture of 3- and 4-mm commercial pellet food (EWOS). Mortalities were removed once daily.

Infection and sampling of fish with salmon lice

On 7 August 2001, gravid salmon lice were collected from farmed rainbow trout immediately after death at a fish slaughterhouse. Egg strings were incubated and hatched as described by Glover *et al*. (2001). On 13 August, the presence of copepodids was confirmed by stereomicroscopy and then they were mixed into a 20-l bucket. No quantitative estimate of the numbers of copepodids was made. Water flow in the two replicate tanks containing the fish was stopped, and the total volume reduced from 1500 to 200 l. Oxygen was delivered directly to the tanks and held over 85% saturation during the entire infection period. Copepodids were divided equally between the two tanks by alternately pouring 2 l samples into each. After 1 h the original water flow and level were reinstated. One week later, on 20 August, a sample of salmon and trout was taken randomly from the two tanks (three salmon all with anal fin and four Guddal trout). Attachment of lice was briefly checked to confirm that infection had been induced. These fish were removed from the experiment.

On 17 September, 35 days post-infection, the experiment was terminated. Fish were removed from each tank in small groups by net and placed immediately into a 50 l bath containing an overdose of anaesthetic (1 ml benzocaine per litre of water). Heavily anaesthetized fish were immediately placed into individual plastic bags and killed with a single

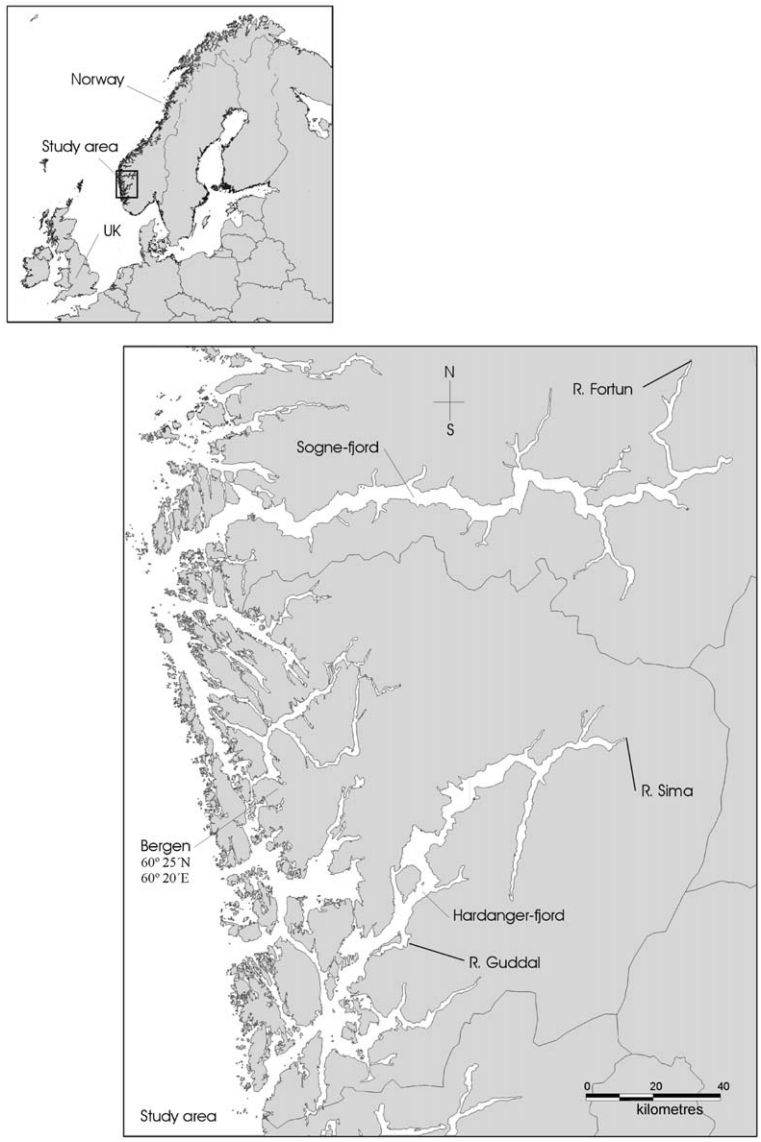

Figure 1. Map of the study area and the location of the sampling rivers within the fjords.

Table 1. Numbers of fish of each stock sampled (n), fin-clip code (Fin.), mean total length and weight, mean condition factor (CF), and calculated surface area (cm^2) for the stocks at the end of the experiment. Data in parentheses represent standard errors and different superscript letters denote stocks different from each other at the 5% significance level. Data are pooled from both tanks.

Stock	n	Fin.	Length (cm)	Weight (g)	CF	Surface area (cm^2)
Guddal	92	Anal	22.8 (0.17)^a	133.3 (3.2)^a	1.10 (0.01)^a	243 (3.6)^a
Sima	102	Ventral	23.6 (0.17)^b	139.9 (3.2)^a	1.05 (0.01)^b	250 (3.5)^a
Fortun	101	Adipose	24.3 (0.15)^c	164.4 (3.8)^b	1.13 (0.01)^a	276 (3.9)^b
Salmon	96	None	26.0 (0.17)^d	171.3 (3.6)^b	0.96 (0.01)^c	283 (3.7)^b
Salmon	29	Anal	26.3 (0.27)^d	177.8 (6.0)^b	0.97 (0.01)^c	290 (6.0)^b

sharp blow to the head. This operation was carried out in a quick and efficient manner to reduce loss of salmon lice during the sampling process. The numbers of lice remaining in the anaesthetic bath were counted at the end of sampling each tank. Individual fish were stored at −18°C until they were examined. From each fish the following parameters were noted: stock, length, weight, sex, and any obvious signs of maturity (clearly enlarged gonads compared with immature fish). All salmon lice were removed from the fish and the gills were checked for infection. Numbers, sex, and stage of development of the lice were recorded in accordance with Schram (1993). Parasitological terms were used in accordance with Margolis *et al.* (1982).

Statistical analysis

All data analysis was carried out in Statistica version 5.0, except for the G-tests of independence that were performed in an Excel 2000 spreadsheet. Length frequency analysis showed the raw data (lice abundance) to be slightly skewed to the right. Therefore, lice abundance data were normalized by transforming by $\log(x+1)$ prior to parametric statistical analysis. To investigate differences in lice abundance between replicate tanks for the pooled material and each stock independently, as well as to compare the abundance of lice on fin-clipped and non-fin-clipped salmon, t-tests were used.

The density of salmon lice on individual fish was calculated by three methods: number of lice divided by fish total length, number of lice divided by fish weight, and number of lice divided by fish surface area, according to a model for Atlantic salmon surface area developed by Hamre and colleagues (unpublished), where surface area = $12.339206\text{Weight}^{0.6104678}$. Among the stocks, louse abundance, louse density, fish weight, fish length, fish condition factor, and fish surface area were all tested separately by ANOVA. Significant ANOVA tests were examined further using the Tukey *post hoc* test for unequal n.

Potential effects of sex and sexual maturation on the abundance of lice were tested within stocks using a Kruskal–Wallis non-parametric ANOVA. A non-parametric test was chosen for this comparison owing to the relatively small numbers of fish within sex maturity categories. Potential correlation between louse abundance and fish size, and between louse density (estimated by all three methods) and fish size, were tested by regression analysis. Development of lice was compared among the stocks for each louse sex-independently using a rows × columns G-test of independence on the raw data (Sokal and Rohlf, 1981).

Results

When the experiment was terminated 35 days post-infection, significant differences in total length ($p < 0.0001$), weight ($p < 0.0001$), condition factor ($p < 0.0001$), and calculated surface area ($p < 0.0001$), were detected among the fish representing the stocks (Table 1). The Guddal fish were on average smallest, followed by Sima, Fortun, and the two salmon groups, which were the largest. At the end of the experiment, density of fish was approximately 21.5 kg m^{-3} for the two replicate tanks.

Overall mortality was low (<1%) during the entire period in which the fish were reared in the replicate tanks (approximately 12 weeks). One Guddal trout and two salmon made up the three mortalities 6, 12, and 24 days post-infection, respectively. Cause of death was not determined. When the experiment was terminated, some fish had developed small patches of exposed skin. This was particularly noticeable in the head region, presumably as a result of feeding by salmon lice.

No significant differences in louse abundance were detected between the two replicate tanks for the overall pooled material ($p > 0.1$), for Fortun fish ($p > 0.4$), for Guddal fish ($p > 0.5$), for Sima fish ($p > 0.2$), for salmon ($p > 0.9$), or for fin-clipped salmon ($p > 0.2$; Table 2). Data from the replicate tanks were therefore pooled for subsequent analyses. No significant difference in louse abundance was detected between the fin-clipped and the non-fin-clipped salmon groups ($p > 0.5$; Table 2), so these two groups were pooled for subsequent analyses.

Overall, significant differences ($p < 0.0001$) in louse abundance were observed among the stocks (Table 2). *Post hoc* tests revealed that the Guddal fish had significantly fewer lice than the other stocks (Guddal vs. all other groups independently; least significant $p < 0.0003$; Table 2). The Fortun and Sima stocks had similar abundances of lice ($p > 0.3$), both being significantly lower in terms of abundance of lice than the pooled salmon stock (Fortun vs. pooled salmon $p < 0.046$; Sima vs. pooled salmon $p < 0.0002$; Table 2).

Although significant differences in infection level, as measured by louse abundance, were observed among stocks, differences in mean fish size, by length, weight, or surface area, were also observed among the stocks. Furthermore, there were significant positive correlations between fish length and louse abundance ($r^2 = 0.123$, $p < 0.0001$; Figure 2), and fish weight and louse abundance ($r^2 = 0.069$, $p < 0.0001$) for the pooled fish material. Clearly, differences in mean fish size biased the comparisons of lice abundance among the stocks. In order to counteract this, salmon louse abundance was converted to salmon louse density by adjusting for fish length, fish weight, and fish surface area independently. After adjustment for fish length, a very weak, but significant, positive correlation between salmon louse density, and fish length ($r^2 = 0.0346$, $p < 0.0002$; Figure 3a) and weight ($r^2 = 0.0133$, $p < 0.02$) remained. After adjustment for fish weight, there was a very weak but significant correlation between salmon louse density, and fish length ($r^2 = 0.0114$, $p = 0.028$; Figure 3b), and weight ($r^2 = 0.053$, $p < 0.0001$).

Table 2. Salmon louse infection parameters for stocks, replicate tanks, and tanks pooled.

Group	n	Abundance[a] Mean (±s.e.)	Range	Density[b] Mean (±s.e.)	Density[c] Mean (±s.e.)	Density[d] Mean (±s.e.)	% Density[e]
Guddal	92	7.6 (0.4)	1–20	0.33 (0.02)	0.058 (0.003)	0.031 (0.002)	100
Fortun	101	11.4 (0.6)	3–29	0.47 (0.02)	0.072 (0.004)	0.042 (0.002)	135
Sima	102	10.3 (0.4)	1–25	0.44 (0.02)	0.077 (0.004)	0.042 (0.002)	135
Salmon	96	12.9 (0.5)	1–32	0.50 (0.02)	0.079 (0.003)	0.046 (0.002)	148
Salmon (-anal)	29	13.2 (0.7)	7–21	0.50 (0.03)	0.075 (0.003)	0.046 (0.002)	148
Salmon pooled	125	13.0 (0.4)	1–32	0.50 (0.01)	0.078 (0.003)	0.046 (0.001)	148
Tank 1	208	11.2 (0.4)	1–32	NA	NA	NA	NA
Tank 2	212	10.4 (0.3)	1–29	NA	NA	NA	NA
Pooled tanks	420	10.8 (0.2)	1–32	NA	NA	NA	NA

[a]Numbers of lice per fish.
[b]Abundance of lice/individual fish length (cm).
[c]Abundance of lice/individual fish weight (g).
[d]Abundance of lice/individual fish surface area (cm^2).
[e]Relative infection level compared with the Guddal stock.
NA, not applicable.

However, in contrast to the positive correlation between fish length and louse density as adjusted for by fish length, the relationship between fish length and louse density as adjusted for by fish weight was negative (cf. Figure 3a and b). Finally, louse abundance was converted to louse density by adjusting for fish surface area. Following adjustment for fish surface area, no correlation between louse density and fish length ($r^2 = 0.0053$, $p > 0.1$; Figure 3c), or individual weight ($r^2 = 0.0018$, $p > 0.3$) was observed. All measures of louse density were subsequently used to compare infection level among stocks.

Significant differences were observed in infection level among the stocks, as calculated by the mean salmon louse density as a function of fish length ($p < 0.0001$), fish weight ($p < 0.0001$), and fish surface area ($p < 0.0001$; Table 2). However, in contrast to the results obtained by comparing salmon louse abundance among the stocks, *post hoc* tests revealed that only the Guddal stock remained significantly different in infection level compared with all other stocks (Table 3). Interestingly, despite three different estimates of louse density being used to compare the stocks, the pattern of among-stock louse density (Table 2), and its statistical significance (Table 3), was similar between all

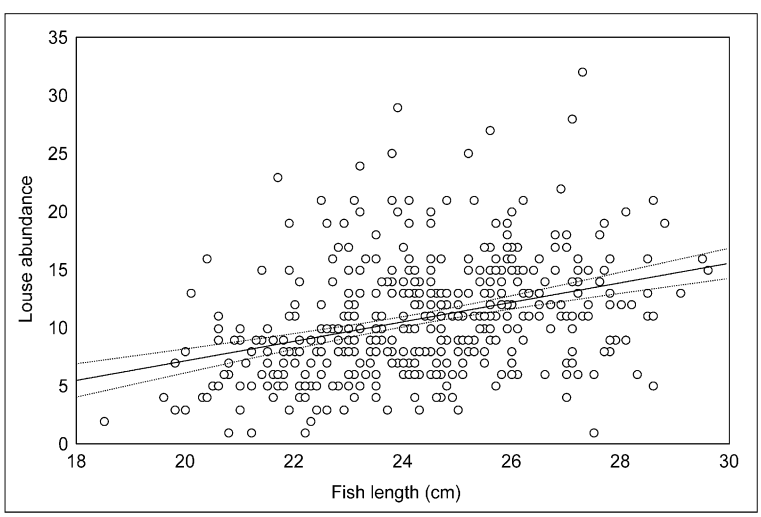

Figure 2. Relationship between abundance of salmon lice and fish length for pooled material. The dotted lines represent the 95% confidence intervals.

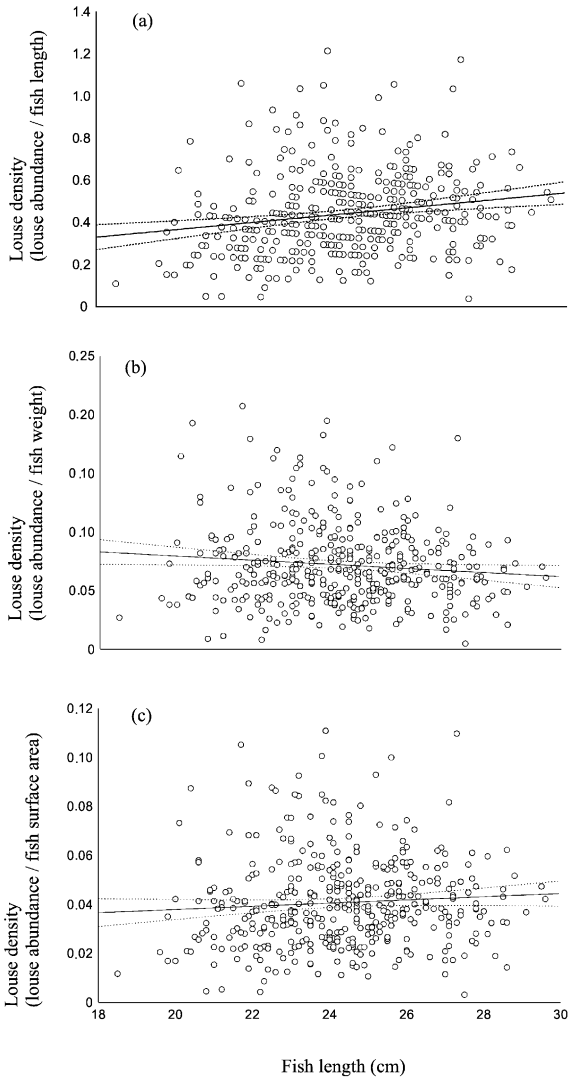

Figure 3. Relationship between the density of salmon lice calculated by dividing louse abundance by (a) fish length, (b) fish weight, and (c) fish surface area, and fish length for pooled material. The dotted lines represent the 95% confidence intervals.

estimates. There were no significant differences in louse density among any of the other stocks, and again this pattern was similar for all three estimates of louse density (Table 3).

Maturation of the fish varied greatly between sexes and stocks (Table 4). Male maturation was considerably higher than female maturation, whereas incidence of maturation was higher for the Guddal and Sima stocks than for the Fortun and salmon stocks. However, no differences in louse abundance were observed between males, females, mature males, and mature females for the Guddal stock ($p > 0.9$), between males, females, and mature males for the Sima stock ($p > 0.9$), or between males and females for the Fortun ($p > 0.7$) or salmon stocks ($p > 0.9$; Table 4).

Table 3. Values of p for pairwise comparisons (Tukey *post hoc* test for unequal n) between the stocks for salmon louse density as adjusted by fish length, fish weight, and calculated fish surface area.

Pairwise stock comparison	Louse density parameter		
	Length (cm)	Weight (g)	Surface area (cm^2)
Guddal × Fortun	<0.0001	<0.016	<0.0003
Guddal × Sima	<0.0005	<0.0006	<0.0003
Guddal × Salmon	<0.0001	<0.0002	<0.0001
Fortun × Sima	>0.6	>0.7	>0.9
Fortun × Salmon	>0.5	>0.5	>0.2
Sima × Salmon	>0.6	>0.9	>0.2

At the end of the experiment, most male lice had grown to adult stage (Figure 4a) and most female lice to pre-adult female II stage (Figure 4b). Significant differences in the distribution of male lice between pre-adult II and adult stages were noted among the stocks ($p < 0.05$). Similarly, significant differences in the distribution of female lice between pre-adult I and pre-adult II stages were noted among the stocks ($p < 0.05$). Both male and female lice developed more slowly on the Guddal fish than on all other groups (Figure 4a, b).

Loss of salmon lice during sampling was minimal. In all, 64 and 78 lice were lost from replicate tanks 1 and 2, respectively, during the sampling procedure, a mean of 0.31 (2.8%) and 0.35 (3.4%) lice lost per fish, respectively. No lice were found attached to the gills of the fish at the end of the experiment.

Discussion

There were significant differences in infection level of salmon lice among fish representing three sea trout stocks and a farmed Atlantic salmon stock. Sea trout from the River Guddal displayed a significantly lower abundance and density of salmon lice than all other stocks, among which there were only small and insignificant differences in louse density. In addition, both male and female salmon lice developed more slowly on the Guddal fish than on fish of the other stocks. All fish were reared and infected in communal tanks, and were naive to salmon lice infection prior to challenge; replicate tanks showed highly similar results, and environmental variables were carefully controlled throughout the study. It is therefore suggested that this result reflects genetic differences among the stocks.

Sea trout from the River Guddal exhibited the lowest infection level of salmon lice as well as the slowest developing lice of all stocks challenged. Glover *et al.* (2001) suggested that differences in infection levels of salmon lice among brown trout populations may reflect differences in the history of exposure to this parasite.

Table 4. Numbers of observations (n) and mean abundance of lice recorded in fish of different sex and maturation category within stocks.

	Number of observations and mean abundance							
	Guddal		Sima		Fortun		Pooled salmon	
Sex and maturity	n	Abundance	n	Abundance	n	Abundance	n	Abundance
Immature ♂	18	7.4 (0.8)	24	11.0 (1.2)	49	11.1 (0.7)	68	13.2 (0.6)
Mature ♂	34	7.5 (0.7)	28	10.1 (0.8)	5	–	3	–
Immature ♀	31	7.7 (0.7)	50	10.1 (0.5)	45	11.8 (0.9)	54	12.8 (0.4)
Mature ♀	9	7.7 (1.4)	0	–	2	–	0	–

Note: – = not calculated. Data in parentheses are ±s.e. For any given category where n is ≤5, the mean louse abundance has not been calculated.

Salmon lice do not develop in salinity less than 22 (Heuch, 1995; Vikeså, 2000), and although the time taken for lice to die or fall off infected fish when exposed to freshwater has been reported to vary (Hahnenkamp and Fyhn, 1985; McLean *et al*., 1990; Finstad *et al*., 1995), mobile adult stages may start to die within 8 h (Hahnenkamp and Fyhn, 1985; McLean *et al*., 1990). Periodically, salinity drops greatly in the inner fjords, a situation caused by river discharge, coastal current, wind-directed surface currents, barometric pressure and tidal currents (Helland-Hansen and Nansen, 1909; Dick, 1975). This reduction in salinity is less marked and less frequent in the middle and outer areas of fjords, where greater exchange with full salinity seawater buffers to a greater extent the water-freshening effects. It is therefore suggested that, as a consequence of prevailing hydrographic conditions, and the biology of the salmon louse, the numbers of infectious salmon lice larvae, and consequently, the intensity of natural selection via louse-induced fish mortality, may vary considerably between inner and outer fjords over a given period of time. This idea is supported by the fact that infection levels of salmon lice on salmonid fish in Norwegian net pens located in inner fjords are often lower than those in middle and outer fjord areas (pers. obs.).

Although data on the exact migration patterns of sea trout representing the stocks used in the present study do not exist, available data on other Norwegian stocks of sea trout suggest that few fish undertake migrations as far as 100 km, and that the vast majority make significantly shorter migrations (Jensen, 1968; Jonsson, 1985; Berg and Berg, 1987; Lund and Hansen, 1992). Fish migrating from the River Guddal enter the middle of the Hardanger fjord, whereas fish from the Rivers Sima and Fortun enter the very innermost parts of their respective fjords. It is suggested that, historically, the sea trout stock originating from the River Guddal may have been exposed to more frequent and to more intensive infections by salmon lice than the stocks originating from the Rivers Sima or Fortun.

Data for this experiment were obtained from a single sample taken 35 days post-infection. It is therefore not possible to indicate whether the differences in abundance of salmon lice observed among the groups were the result of differences in settlement of lice (Dawson *et al*., 1997), differences in mortality of lice after settlement (Johnson and Albright, 1992a; Johnson, 1993), or a combination of these factors (Dawson *et al*., 1997). Furthermore, pre-adult and adult salmon lice can actively transfer between hosts, and this may have an unknown effect on the data. However, Guddal fish not only had the lowest abundance of salmon lice, but also lice developed significantly more slowly on them than on fish of the other stocks. The implication here is that there is a role for post-settlement factors.

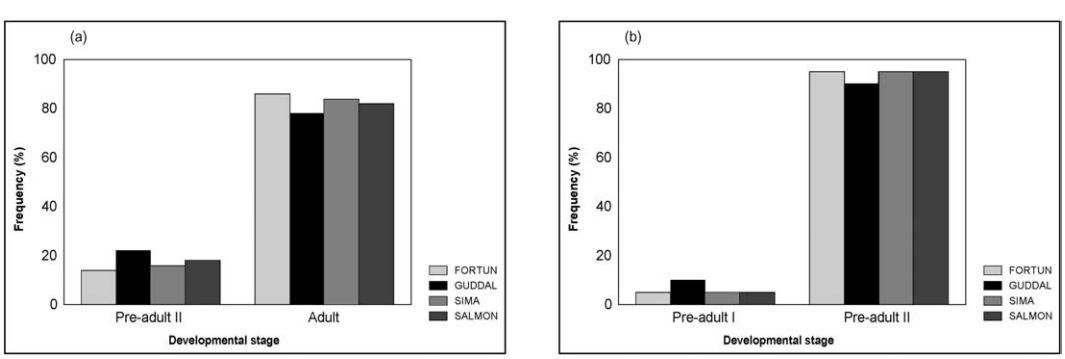

Figure 4. Development of (a) male and (b) female salmon lice on three sea trout stocks and a farmed Atlantic salmon strain.

Johnson and Albright (1992b) and Johnson (1993) suggested that host nutritional factors, in addition to non-specific immune responses, may be involved in resistance mechanisms to salmon louse infection. Although these may have played a role in the present experiment, it is not possible to disentangle other stock-specific differences, some of which may also display an underlying genetic distribution, from having had an influence on the present result. For example, other factors may include skin thickness, mucous development or behavioural reaction to the challenge. The latter point may be of great importance considering that fish moving about to a greater degree while under infection may attract a greater number of lice.

There were large differences in the extent of male and female maturation among the stocks. Unfortunately, it is not known whether the fish were mature prior to transfer to saltwater, or whether this was the result of post-smolt maturation. The Guddal stock displayed not only the lowest overall level of infection, but also the greatest degree of maturation. Salmonid fish undergo significant changes during maturation, including skin properties (McBride and Van Overbeeke, 1975; Aksnes *et al*., 1986; Mork *et al*., 1989). However, when infection levels were compared between mature and immature fish within stocks, there were no differences in louse abundance for either male or female fish. The same observation was made by Glover *et al*. (2001), and it represents an interesting observation considering that skin provides both a barrier to the external surroundings of the fish and a source of nutrition for salmon lice.

Fish size differed among stocks. There was also a weak but significant overall correlation between fish size and salmon louse abundance. Similar observations have been documented in other studies (Jaworski and Holm, 1992; Glover *et al*., 2001; Tucker *et al*., 2002). In the present experiment, differences in fish size among stocks were compensated for by creating three independent estimates of salmon louse density. All three density estimates reduced or, as for the surface area density estimate, eliminated completely the correlation between individual fish size and infection level. This allowed unbiased comparisons of infection levels among stocks. Because the surface area model eliminated the effect of fish size on infection level, this method of calculating density may be the most suitable of the three methods described. Irrespective of the differences between the density estimates, all gave identical results. In other words, the Guddal stock displayed a significantly lower infection level than the other stocks. Agreement between the density estimates is most likely to be caused by differences in fish size between the groups being relatively small and inconsequential. For example, the Sima stock was only 4% longer, 5% heavier, and had a 3% larger surface area than the Guddal stock, but the Sima stock displayed 33–36% greater abundance or density of lice, using all estimates of louse density, than the Guddal stock.

Atlantic salmon displayed the highest abundance and density of lice among all the experimental groups, but only the difference between the salmon and the Guddal stock was statistically significant. In a challenge experiment, Dawson *et al*. (1997) observed a greater abundance of salmon lice on a single sea trout stock than on a farmed Atlantic salmon strain. Owing to differences in experimental procedure between the two studies, it is difficult to make direct comparisons. Moreover, because the salmon were not reared in the same tanks as the trout during their entire life cycle, it is difficult to indicate to what extent the differences observed represent genetic rather than environmental effects.

Fins are important sites for attachment of salmon lice (Tucker *et al*., 2002). A single fin-clip was used to identify the stocks in the present study. Although this could have influenced the result, no differences were observed in infection level between salmon with their anal fin intact and the control salmon group that had been fin-clipped. The anal fin was clipped on the Guddal fish. There is no evidence to suggest that the differences in infection level observed among the stocks were influenced by the marking method chosen.

In summary, significant differences in abundance, density, and development rate of salmon lice were observed among three sea trout stocks and one farmed Atlantic salmon stock. It is suggested that the observed differences in infection level of salmon lice among the three sea trout stocks reflect genetic differences, and may also be linked with adaptation.

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