

Susceptibility of Baltic and East Atlantic salmon *Salmo salar* stocks to *Gyrodactylus salaris* (Monogenea)

T. A. Bakke^{1,*}, P. D. Harris², H. Hansen¹, J. Cable³, L. P. Hansen⁴

¹Zoological Museum, The Natural History Museums and Botanical Garden (NHM), University of Oslo, Oslo, Norway

²Department of Continuing Education, University of Nottingham, Nottingham NG7 2RD, UK

³School of Biosciences, Cardiff University, Cardiff CF10 3TL, UK

⁴Norwegian Institute for Nature Research (NINA), PO Box 736, Sentrum, Oslo, Norway

ABSTRACT: The susceptibility of a Baltic salmon stock *Salmo salar* (Indalsälvs, central Sweden) to Norwegian *Gyrodactylus salaris* (Figga strain, central Norway) was experimentally tested and compared with previously obtained results on East Atlantic salmon (Lierelva, SE Norway). Contrary to expectation, the Baltic salmon, which had no prior exposure to this parasite strain, appeared almost as susceptible as the Norwegian salmon parr that naturally experience *G. salaris*-induced mortality. Individually isolated salmon of both stocks sustained *G. salaris* infections with little evidence of innate resistance. A few individuals of the Indalsälvs stock controlled their infection from the beginning, but overall there was considerable heterogeneity in the course of infection in both stocks. On individual hosts, *G. salaris* growth rates declined steadily throughout the infection, a trend which was particularly marked amongst the Lierelva stock. On shoaling Lierelva fish, there was some evidence of reduced parasite population growth towards the end of the infection; this was not apparent in Indalsälvs fishes. These results reflect a growing awareness that not all Baltic salmon may be resistant to Norwegian *G. salaris*, and that Norwegian and Baltic *G. salaris* strains may differ in virulence. Consequently, management decisions concerning this parasite–host system should be based upon the actual, and tested, susceptibility of stocks under consideration and not upon identification of stocks as either Atlantic or Baltic.

KEY WORDS: *Gyrodactylus salaris* · Host-specificity · Resistance · Salmonids

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INTRODUCTION

The ectoparasite monogenean *Gyrodactylus salaris* is epidemic on East Atlantic salmon *Salmo salar* in Norway and has devastated fish stocks over the last 25 yr (Heggberget & Johnsen 1982, Johnsen et al. 1999). Average density of salmon parr in infected rivers has been reduced by 86%, leading to an annual loss of 250 to 500 t of salmon (NOU 1999). The total cost now exceeds 500 million US dollars.

When originally described from a hatchery near to the Indalsälvs river in Sweden (Malmberg 1957), *Gyrodactylus salaris* was not considered pathogenic in the wild, and it has since been recorded on several occa-

sions within the Baltic watershed without being associated with disease (Malmberg & Malmberg 1991, 1993). This led to the hypothesis that Norwegian salmon were particularly susceptible to this pathogen, and that *G. salaris* was a recent introduction into Norway (Johnsen & Jensen 1991, Mo 1994). In support of this, Bakke et al. (1990) showed that 2 Norwegian stocks of salmon succumbed readily to the parasite in the laboratory, while the parasite was not pathogenic in Baltic salmon (the Russian Neva stock). Hybrids between Norwegian Imsa and Baltic Neva stocks showed intermediate susceptibility (Bakke et al. 1999, 2002). Further support for the anthropochore spread of *G. salaris* across national borders comes from the recent epidemic in a

White Sea salmon stock in Russia, which is known to have been caused by introduction from Finland (Malmberg 1993, Mo 1994, Johnsen et al. 1999).

Introduction does not however fully explain the relative susceptibility of different salmon stocks to *Gyrodactylus salaris*. Detailed study has revealed a patchwork of pathogenicity, which does not reflect the Baltic/Eastern Atlantic split in salmon stocks (reviewed in Bakke et al. 2002). Although Bakke et al. (1990) did show a clear difference between Neva and 2 Norwegian salmon stocks during a 4 wk experiment, 3 further Eastern Atlantic stocks, 2 from Scotland and 1 from Norway (Lierelva), showed a range in susceptibilities, and some individual Norwegian fish were able to limit *G. salaris* infection (Bakke & MacKenzie 1993). Subsequently, Jansen & Bakke (1993a) showed that some wild Lierelva parr, individually constrained in the river throughout the year, could successfully control parasite population growth. Experimentally, Altaelva

salmon parr have also mounted a response to *G. salaris*, with a decline in parasite population growth late in the infection (Bakke et al. 1999). There is therefore a previously unappreciated degree of heterogeneity of resistance within and between Norwegian salmon stocks.

Although several Norwegian salmon stocks have been assessed with respect to their susceptibility/resistance to *Gyrodactylus salaris* and recently 3 salmon stocks from the west coast of Sweden (Karlsson et al. 2003), only 2 Baltic stocks (Rivers Neva and Lule) have been tested in detail. All fish of the Neva stock mounted a host response (Bakke et al. 1990, 2002), whereas the Swedish Lule stock was susceptible, but to a lesser extent than a Scottish salmon stock (Dalggaard et al. 2003). This indicates that susceptibility to *G. salaris* might not be restricted to East Atlantic salmon. To further investigate the spectrum of specificity found in Baltic salmon stocks, we have therefore compared the susceptibility of the Indalsälvs stock from the Baltic coast of Sweden with that of the extensively studied Lierelva stock from SE Norway (Jansen & Bakke 1991, 1993a,b, Bakke & Mackenzie 1993).

MATERIALS AND METHODS

Naïve Swedish salmon *Salmo salar* of the River Indalsälvs stock, hatchery-reared from artificially spawned eggs, were obtained from Bergforsens Kraft AB Laksodling, Sweden. The parr (average length/weight of 9.1 cm/5.4 g) were transported to Vikan AkvaVet (Veterinary Station for Contract Research in Fish Diseases, Norway) in February 1992, and on arrival, conditioned for 1 wk to a water temperature of $12^{\circ}\text{C} \pm 0.5$, and an 8 h light: 16 h dark regime. The salmon ($n = 150$) were infected over 2 d by exposure to 10 killed and 35 living marked parr (River Namsen stock) that were artificially infected with the River Figga (central Norway) strain of *Gyrodactylus salaris*. This resulted in an epidemic spread of *G. salaris*, and all fish acquired infections (range 77 to 161 parasites). The experimental fish of each stock were then separated from the naturally infected fish (Day 0) and transferred to two 500 l holding tanks with a constantly flowing water supply of 5 l min^{-1} . Each tank held 50 fish in a pooled group plus another 12 fish individually isolated in small floating grey plastic cages ($47 \times 37 \text{ cm}$, 10 cm water level) with wire-mesh floors. The pooled fish were fed unmedicated pellet food (EWOS), the isolated fish were unfed. At weekly intervals from Day 0, all isolated fish and 10 fish randomly selected fish from each pooled group were anaesthetized (2 min in 0.04 % chlorobutanol), and the numbers of *G. salaris* counted using a stereomicroscope (intensities from 500 to 1000

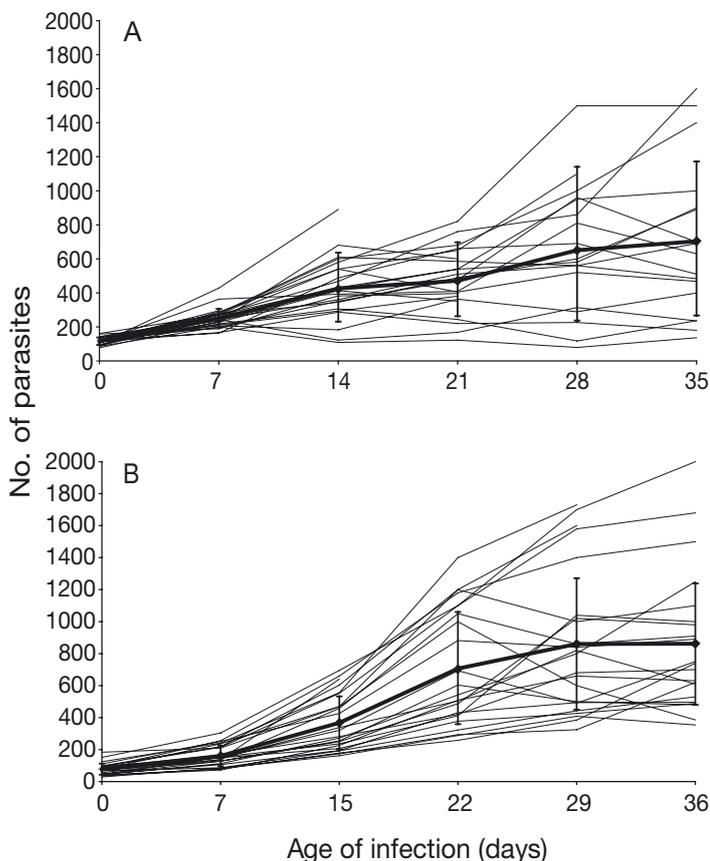


Fig. 1. *Gyrodactylus salaris* (Figga strain) infecting *Salmo salar*. Individual trajectories of intrapopulation growth of *G. salaris* on isolated salmon parr of (A) Indalsälvs (Baltic) and (B) Lierelva (Norwegian) stock. Thick line: mean ± 1 SD of natural logarithm-transformed data; fine lines: trajectories of parasite population growth on individual parr; lines terminating before Day 35 indicate mortality

were counted to the nearest 10, and those over 1000 to the nearest 100). The above experimental procedures were identical to those of Bakke & MacKenzie (1993), who assessed reproduction of the same parasite strain on Norwegian Lierelva parr 4 mo earlier at Vikan AkvaVet. The data from this study were re-analysed for comparison with the parasite growth on Swedish salmon.

Analysis of parasite populations was carried out using a natural logarithm transformation ($\log_e N + 1$) to confer normality. This was the most appropriate transformation in the absence of specific data on the value of k , the overdispersion coefficient. Analyses were performed using SPSS for Windows Version 11.0.

The reproductive rate (r) of *Gyrodactylus salaris* on individual parr was calculated from the equation:

$$N_t = N_0 e^{rt}$$

where N_t = the number of parasites recorded at Time t , and N_0 = the number of parasites recorded at Time 0. Reproductive rates were normally distributed at each time point, allowing parametric statistics (Student's t -test and Pearson's correlation coefficient) to be applied without transformation.

RESULTS

The initial prevalence of *Gyrodactylus salaris* on both individually isolated and grouped Indalsälvs and Lierelva fishes was 100% on Day 0. The initial intensity of infection varied between stocks, with the Indalsälv hosts being infected with 86 to 161 parasites (mean 115.9) and the Lierelva parr harbouring 29 to 184 parasites each (mean 77). This variation in parasite burden did not appear to influence the outcome of the infection. During the first week, parasite infrapopulations increased on all Indalsälv fishes, but heterogeneity was evident subsequently. Thus, on some Indalsälv hosts the parasite burden increased continuously throughout the infection, while on others the infrapopulations reached their peak size after a variable time period of up to 4 wk. Some Indalsälv fish controlled their infections at relatively low parasite burdens (200 to 300 worms fish⁻¹) as early as 7 to 14 d post-infection, p.i. (Fig. 1). On isolated Lierelva parr, the initial pattern of parasite population growth was similar, with some infections increasing throughout the experiment. However, on some fishes, the *G. salaris* infrapopulations attained a peak intensity of ca. 800 parasites after 28 to 35 d and then declined (see Bakke & Mackenzie 1993). Both stocks of fish also contained a small proportion of hosts on which parasite population growth continued until either the fish died or the experiment was terminated. Fewer Indalsälv parr (5 out of 24) were

able to limit parasite reproduction compared to the Lierelva population (10 out of 24), and the proportion of fish on which the *G. salaris* population grew without check within the experimental period was correspondingly greater amongst the Indalsälv stock. However, the spectrum of individual host responses to the parasite was similar in the 2 salmon stocks.

Reproductive rate was calculated for each successive 7 d period. The average initial reproductive rate (r) of *Gyrodactylus salaris* on Lierelva fish in this experiment was 0.1021 (SD = 0.0499, $n = 24$), while that on Indalsälv fish was only 0.0825 (SD = 0.0607, $n = 24$). This difference between initial reproductive rates (Fig. 2) was barely significant at the $p > 0.1$ level (1-tailed Student's t -test: critical value for 10% significance = 1.319, calculated value for experimental data = 1.332). However, even such a small difference can be important as population size increases as the exponent of r . The proportion of Indalsälv fish in which r was initially negative was greater than the proportion for Lierelva fishes, and conversely the proportion of Lierelva fish with an initial rate of reproduction in excess of 0.15 was correspondingly greater (Fig. 2). On Lierelva fish, parasite population growth rates declined steadily, becoming negative on many (11 out of 24) hosts 30 to 35 d p.i. (Fig. 3). This decline in population growth rate was correlated with infection age (Pearson's $r = 0.726$, $n = 140$, $p < 0.001$), but not infection size. This pattern of decline in parasite population growth rate is typical of *G. salaris* infections on Norwegian salmon stocks (Bakke et al. 2002). On Indalsälv fish a similar trend of declining population growth rate was noted, with 13 out of 24 fish showing a negative rate after 30 to 35 d, but the correlation between population growth rate and age of infection was not as strong (Pearson's

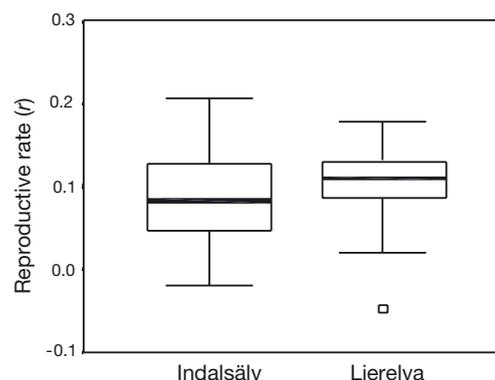


Fig. 2. *Gyrodactylus salaris* (Figga strain) infecting *Salmo salar*. Boxplots showing reproductive rate (r) after 7 d for *G. salaris* on both Lierelva (Norwegian) and Indalsälv (Baltic) salmon parr. Boxes represent dispersion of data points up to 1 SD of mean (marked by thick line); whiskers represent data points extending from mean ± 1 variance; (□) outlier

$r = 0.4287$, $n = 103$, $p < 0.001$). This was because many of the trajectories were curvilinear, with several declining rapidly in the first weeks after infection but then increasing again towards the end of the study period.

No significant differences (Student's t -test on means of \log_e -transformed data) were noted in the population growth of *Gyrodactylus salaris* on Lierelva or Indalsälv shoals (Fig. 4), although in general populations

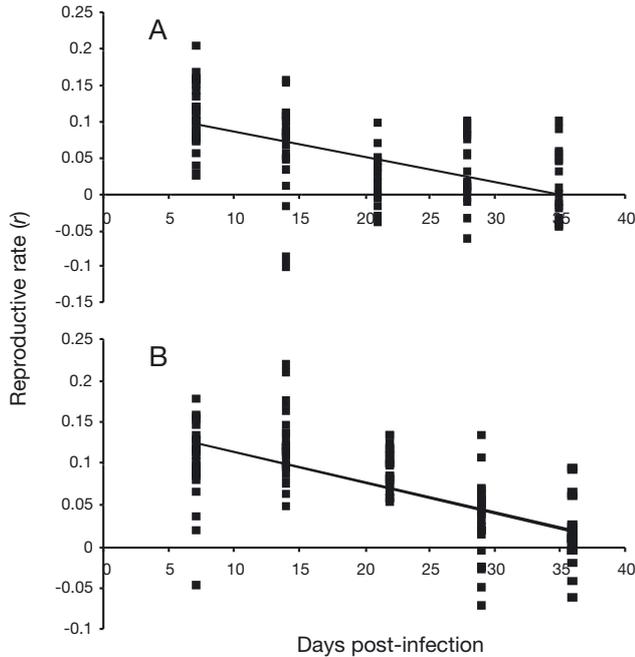


Fig. 3. *Gyrodactylus salaris* (Figga strain) infecting *Salmo salar*. Relationship between population growth rate of *G. salaris* on (A) Indalsälv (Baltic) salmon parr and (B) Lierelva (Norwegian) salmon parr and days post-infection

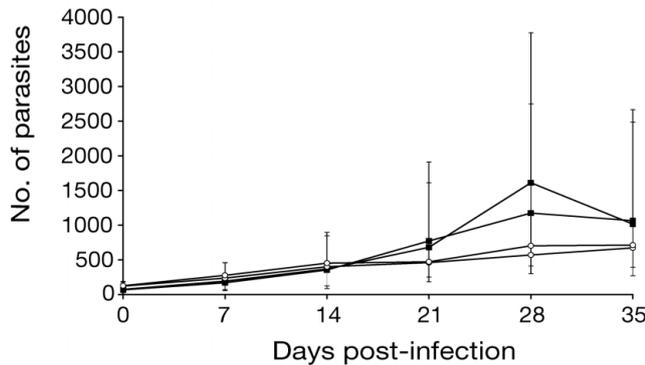


Fig. 4. *Gyrodactylus salaris* (Figga strain) infecting *Salmo salar*. Growth of *G. salaris* populations on shoaling populations of Lierelva (■) and Indalsälv (○) salmon parr; 2 replicate populations of 50 fish examined for each salmon strain. Data points represent means \pm 1 SD of natural log-transformed data

achieved a larger size after 35 d on the Lierelva fishes. *G. salaris* growth on the shoals continued throughout the infection with little evidence of a host response, although population growth on Lierelva fishes did slow 28 d p.i. In contrast, there was no evidence of declining population growth in the slower-growing *G. salaris* populations on Indalsälv parr (Fig. 4).

Mortality amongst individually isolated parr was similar for both salmon strains, with 30% of Indalsälv and 40% of Lierelva fishes dying within 35 d (Fig. 5). The onset of parasite-induced mortality occurred at 25 to 28 d p.i.

DISCUSSION

The present results show that the level of success of the parasite and the host mortality of the Indalsälv stock due to Norwegian *Gyrodactylus salaris* is comparable to that of the Norwegian stock from Lierelva (see Bakke & MacKenzie 1993). This is surprising, as the Baltic salmon stocks have previously been regarded as resistant to *G. salaris* (Bakke et al. 1990, 2002), although Dalgaard et al. (2003) found that the Swedish Lule stock was susceptible to the Norwegian River Laerdalselva strain of *G. salaris*. During 1952 to 1956, Indalsälv was restocked with salmon of the Umeälva stock (Larsson et al. 1979). Since 1956, when a hydroelectric dam was constructed, natural reproduction of salmon in the river has ceased, and the population is totally dependent on annual restocking with offspring from a brood stock of only 25 to 30 native wild adults. In 1958 only 1 pair of adult salmon were used for restocking and the stock has therefore been severely bottlenecked. As a consequence, polymorphic disease-resistance alleles may have been lost, resulting in reduced *G. salaris* resistance compared to the original

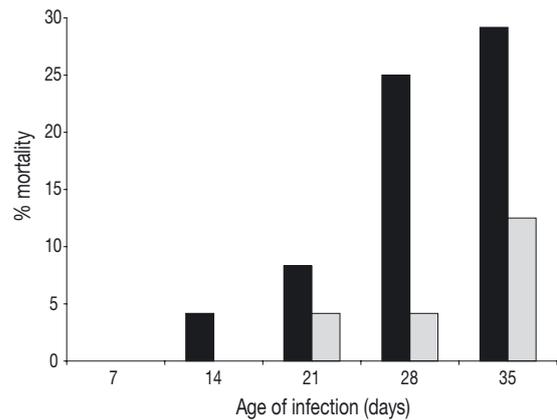


Fig. 5. *Salmo salmar* infected by *Gyrodactylus salaris*. Mortality of parr individually isolated after infection. Black bars: Indalsälv strain (Baltic); grey bars: Lierelva strain (Norwegian)

Indalsälvs salmon. However, we observed heterogeneity over the course of infection, and parasite population growth declined on some individually isolated salmon, suggesting that some genetic diversity may have been retained.

The initial growth rates of *Gyrodactylus salaris* populations on Indalsälv and Lierelva parr were similar, and consistent with the maximum rate calculated for this species (Jansen & Bakke 1991, Harris et al. 1994, Cable et al. 2000, Bakke et al. 2002). The intrinsic population growth rate (r) of *G. salaris* on individually isolated salmon parr of both stocks declined from the start of infection, but at different rates, and parasite populations began to decline after 28 to 35 d. This pattern of decline in population growth rate suggests that in spite of the initial growth of infection on both salmon stocks, a response occurs from the start of infection before a decline is noticed (P. D. Harris et al. unpubl.), supporting observations that the host response is more closely related to infection age rather than size (Bakke et al. 2002).

In shoals of both salmon stocks, some *Gyrodactylus salaris* infrapopulations increased without check until the hosts died. This difference in the course of infection between individually isolated and pooled fish has been observed for other gyrodactylids (Lester & Adams 1974, Scott & Anderson 1984, Harris 1989) and may be related to transmission strategy. Parasites that are not killed by a host reaction may re-infect other hosts, and so, in the confined conditions of the experimental aquarium, populations may build up to lethal levels. During the present experiments, fish were not removed immediately after death but could lie on the tank bottom overnight; hence, reinfection by dislodged parasites (Bakke et al. 1991, 1992) may have been a major cause of the higher growth rate of *G. salaris* populations in the pooled fish. Immunity cannot control parasite population growth in homogenous environments unless it is synchronous in all fish. This was also shown in long-term infection by *G. turnbulli* of guppies (Scott & Anderson 1984, Richards & Chubb 1996), and only *Oncorhynchus mykiss* (see Bakke et al. 1991) and *Salvelinus fontinalis* (see Bakke et al. 1992) responded to *G. salaris* infection sufficiently synchronously to eliminate the infection. Mortality of individual salmon in natural environments due to *G. salaris* does not automatically imply a lack of an immune response in the fish concerned.

If the present results do represent the natural salmon susceptibility to *Gyrodactylus salaris* in Indalsälv, this either reflects variability in *G. salaris* susceptibility among Baltic salmon, and/or variation in parasite virulence, which is probably influenced by micro- and macro-environmental factors. Although ecological river conditions related to both water chemistry and

water physics are known to influence the epidemiology of *G. salaris* (see Jansen & Bakke 1991, Soleng et al. 1999, Bakke et al. 2002), no studies have been undertaken investigating the influence of macro-environmental factors on *G. salaris* epidemiology in the Baltic area.

Atlantic salmon stocks are well known to exhibit genetic variation. Thorpe & Mitchell (1981), Ståhl (1987) and Ståhl & Hindar (1988), using allozymes, found genetic differences between populations from rivers draining the East Atlantic and Baltic Seas. Recently, Nilsson et al. (2001), using mitochondrial markers, found the greatest genetic diversity amongst the Atlantic populations, followed by Baltic populations from the Gulf of Bothnia (including Indalsälv). Populations in the Southern Baltic (including Neva and most landlocked salmon) included only a single unique haplotype. One haplotype prevalent in a Norwegian stock (Numedalslågen, SE Norway) also dominated in the Indalsälv Baltic salmon, but differed markedly from that of the Neva stock (Nilsson et al. 2001). This indicates that stocks from the Gulf of Bothnia may be more similar to Norwegian stocks than to those from the Gulf of Finland. This could be important in explaining the present observed similarity of the Swedish and Norwegian stocks in their susceptibility to *Gyrodactylus salaris*. However, the extant geographical pattern of susceptibility may be very complicated, as populations in individual rivers may be affected to differing degrees by genetic drift and founder events, and disrupted by stocking and stock transfer both in and between Sweden and Norway (Larsson et al. 1979, Johnsen et al. 1999, Nilsson et al. 2001). Furthermore, many Baltic Sea salmon populations exist only as hatchery populations, with attendant inherent risks to their genetic integrity. It appears that a patchwork of resistance and susceptibility to *G. salaris* exists in salmon stocks from different rivers in the Baltic, as has previously been found for Norway (Bakke et al. 2002), and that absolute distinctions do not exist between the major East Atlantic and Baltic clades. This patchwork of susceptibility would also explain why salmon parr in some infected Norwegian rivers seem to survive better (Mo 1992, Jansen & Bakke 1993b) than those in others (Johnsen & Jensen 1991, 1992).

The biological diversity of *Gyrodactylus salaris* strains from the East Atlantic and the Baltic has not yet been tested. However, we have recently demonstrated significant molecular heterogeneity between different Norwegian populations of *G. salaris* (Hansen et al. 2003, J. Cable, P. D. Harris and T. A. Bakke unpubl.), which may also be reflected in biological differences in infectivity, virulence and pathogenicity. The present results indicate an urgent need to increase our knowledge concerning the potential for differences in viru-

lence of *G. salaris* strains to East Atlantic and Baltic salmon.

In conclusion, these results show that the Indalsälva stock, a Baltic salmon generally assumed to be resistant to *Gyrodactylus salaris*, is almost as susceptible as Norwegian salmon under laboratory conditions, but appearing to possess a non-sterile immunity that can be epidemiologically effective when hosts are maintained at low density. The results indicate that outbreaks of gyrodactylosis can be due to stock variability in the susceptibility of both Atlantic and Baltic salmon stocks and/or strain differences in *G. salaris* virulence. Recently, a genetic *G. salaris* variant from Denmark on rainbow trout *Oncorhynchus mykiss* was shown by Lindenstrøm et al. (2003) to have a very restricted reproduction on Atlantic salmon. The current results have clear implications for management of the disease, as relative resistance/susceptibility of a stock cannot be assumed without experimental evaluation.

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