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The susceptibility of *Salvelinus namaycush* (Walbaum) to *Gyrodactylus salaris* Malmberg (Platyhelminthes; Monogenea) under experimental conditions

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The host specificity of *Gyrodactylus salaris* was studied with respect to its ability to infect Lake trout (*Salvelinus namaycush)* under experimental conditions. Lake trout exposed to heavily infected salmon for 6 days became infected but at a low intensity compared to previous results from salmon. The Lake trout were divided into two groups on basis of the course of infection and parasite survival on individually isolated fish: (1) Hosts receptive to parasite attachment but refractive to parasite reproduction (maximum infrapopulation survival time, 21 days post-isolation); (2) Hosts receptive to parasite attachment and reproduction, but which, after a short period of parasite population growth, eliminated the parasite (maximum infrapopulation survival time, 28 days post-isolation). The parasite population declined directly after isolation of two replicated groups of 50 Lake trout each, in contrast to ca. 50% of the individually isolated Lake trout (group 2 above). This shows the necessity of experimental observations of the course of infection on individually isolated hosts for information on parasite reproduction. No *G. salaris*-induced host mortality was observed.

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INTRODUCTION

The monogenean *Gyrodactylus salaris* Malmberg, 1957, has been shown experimentally to be capable of infecting and reproducing on Rainbow trout *Oncorhynchus mykiss* (Walbaum) and Brook trout *Salvelinus fontinalis* (Mitchill) (see Bakke et al. 1991a, In prep.), two salmonid species with a Nearctic origin which have been introduced to Europe (Grande 1982). Accordingly, these fish species may function as hosts under natural conditions, sustain the parasite and play a part in the epidemiology and dissemination of *G. salaris* on salmon in the Palaearctic.

A third non-indigenous salmonid, the North American Lake trout *Salvelinus namaycush* (Walbaum), was introduced to France in 1886 (Laurent 1972) and Switzerland in 1900 (Grimås & Nilsson 1962). It was imported directly from North America (Lake Superior, Lace Simco) to Finland and Sweden in the 1950's (Nilsson & Svärdsson 1968). The first introduction to Norway was probably in 1972, to mid-Norway, where they later became naturalized. A lake near Oslo was also stocked with Lake trout in 1985 (Langeland 1988, Grande 1988).

The Lake trout, which is a species of char, is most closely related to Brook trout and Arctic char (*Salvelinus alpinus*) (Martin & Olver 1980, Greve et al. 1990). Biologically it differs from these species by being more predatory, confined to the deeper parts of large lakes, and being rarely found in running water (Martin & Olver op.cit.). However, since the two Nearctic species, the Rainbow trout and the Brook trout, and the Arctic char (see Bakke & Jansen 1991a), have all been found susceptible to *G. salaris* it was suspected that Lake trout also may play a part in the epidemiology and dispersal of *G. salaris* in Europe, given the opportunity.

There are several reasons why the Lake

trout was introduced to Scandinavia (Mutenia et al. 1984, Gönczi & Nilsson 1984, Langeland 1988, Grande 1988): besides its importance as food and for angling, its predatory habit is thought to be a regulator of dwarf populations of Arctic char and other salmonids. This predatory behaviour also gives opportunities for direct transfer of ectoparasites such as gyrodactylids (Malmberg 1973, Bakke et al. 1991b). The aim of the present paper was to investigate experimentally the potential of Lake trout as a host for *G. salaris,* and to relate these findings to the possible importance of this fish as a host for *G. salaris* under natural conditions.

MATERIALS AND METHODS

Gyrodactylus salaris Malmberg was obtained from heavily infected Atlantic salmon (*Salmo salar*) collected from the river Lierelva in 1990 and maintained in the laboratory at 11—13 °C for two weeks prior to the experiments.

The Lake trout used were young of the year (0^+), hatched and raised in the fish laboratory at the Norwegian Institute for Water Research (NIVA), Oslo. They were imported in 1975 from Sweden and represented the F_3 generation of the original eyed eggs imported to Sweden (P generation) from Lake Superior in North America. The fish had a mean length of 8.1 cm (range 6.8—10.0 cm) and mean weight of 4.9 g (range 2.9—8.9 g), based on 20 randomly selected and measured specimens. The fishes had had no previous exposure to *G. salaris.*

Infections of *G. salaris* were initiated by placing 20 heavily infected *S. salar* parr (2^+, with the adipose fin removed for identification) with 150 uninfected Lake trout for 6 days in grey plastic tanks (1.0 x 1.0 x 0.2 m to water level). Fishes were kept in dechlorinated, charcoal-filtered, continuously circulating Oslo tap water, and were conditioned to a water temperature of 12—13 °C prior to the start of the experiments, which were run at 12.5 °C (see Jansen & Bakke 1991). The parasites spread throughout the Lake trout population during the period of exposure to infected salmon. The progress of the epidemic after the subsequent isolation of the Lake trout, was monitored regularly by examining, under a stereomicroscope, fishes anaesthetized by immersion in 0.4% chlorbutanol in hatchery water for ca. 3 mins. All experiments were carried out under conditions of constant dim illumination and the fishes were fed unmedicated pellet food (Ewos). Experimental protocol was as follows:

EXPT. 1: **Parasite population growth on grouped hosts**
After 6 days exposure the salmon parr were removed and the Lake trout divided into two batches of 50 fish each in parallel grey plastic tanks. Parasite population growth was followed by counting *G. salaris* on 10 randomly selected anaesthetized fishes every 7th day. After counting, the fishes were allowed to recover, then returned to the experimental tank.

EXPT 2: **Parasite population growth on isolated hosts**
Two replicates of 10 fishes each, individually isolated in two grey plastic tanks, were run in parallel. The 20 Lake trout were taken from the same batch of 150 fishes used to start Expt. 1. They were maintained in small floating boxes (11 x 17 cm x 5 cm to water level), made of transparent plastic with a mesh base, allowing free exchange of water with the tank. The fishes were examined weekly in the same manner as described for Expt 1.

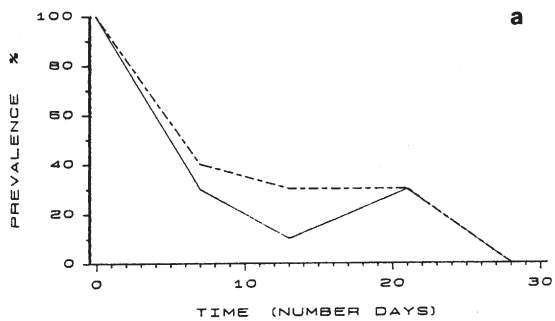
RESULTS

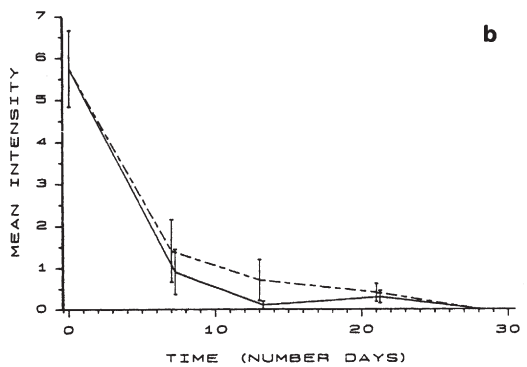
Parasite population growth on grouped hosts

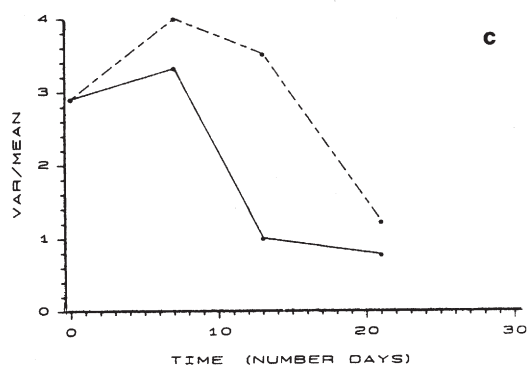
Mean intensity of *G. salaris* on the Lake trout after 6 days of exposure to infection (Day 0) was 5.8 (range 3—21), the prevalence was 100%. Immediately after the separation into two groups of 50 fish each at Day 0, both prevalence and mean intensity of infection decreased in each replicate group (Fig. 1a, b). After 21 days the infections were still present on ca. 30% of the fishes, but at a low intensity (1—4) per fish. In both replicates the *G. salaris* population was eliminated after 28 days of isolation, when the experiment was terminated. The distribution of *G. salaris* was slightly overdispersed as the variance to mean ratio exceeded unity initially (Fig. 1c).

Parasite population growth on isolated hosts

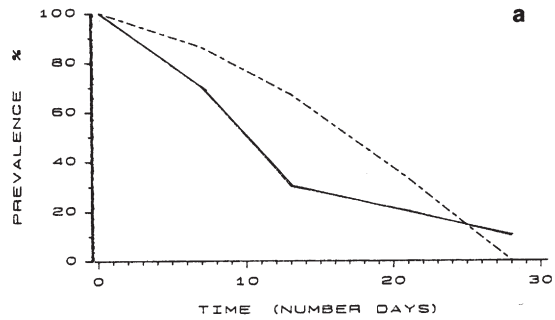
The pattern of *G. salaris* population growth in the pooled results of the individually isola-

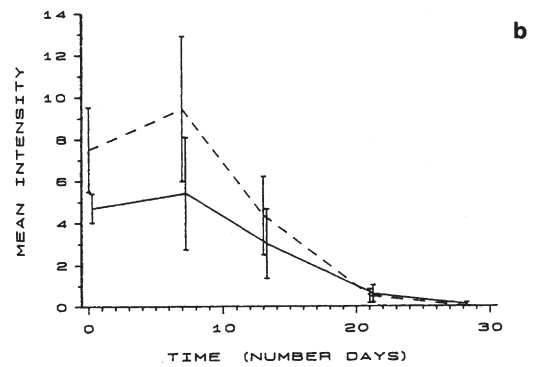


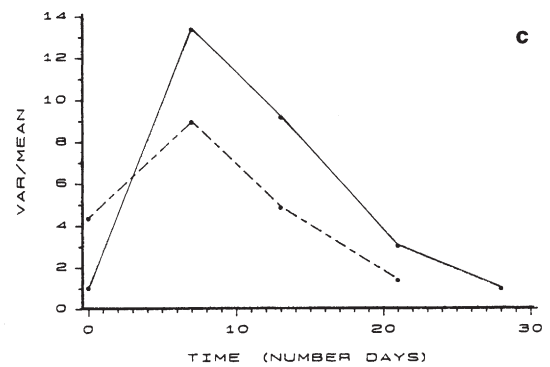




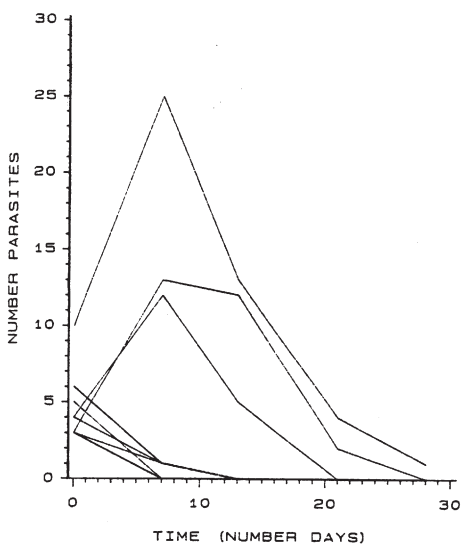
Figs. 1a—c. The course of infection of *G. salaris* on parr of *S. namaycush* up to 30d post-isolation. The parr were exposed for 6 days to a source infection, thereafter separated into two replicate batches, of 50 each, at 12.5 °C. (a) Prevalence; (b) Mean intensity; (c) Variance to mean ratio (s^2/mean). Replicate 1 indicated by solid line, replicate 2 by dashed line. (Bars = S.E.)

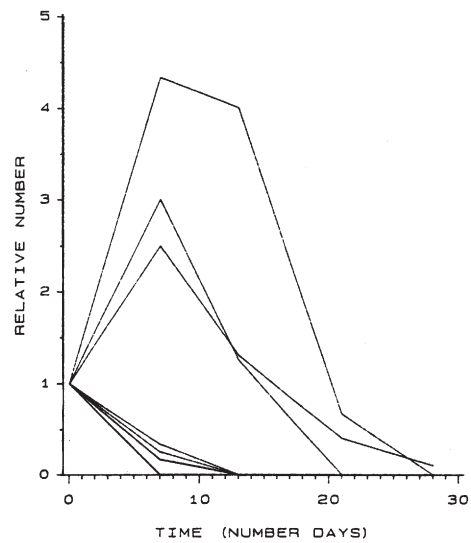




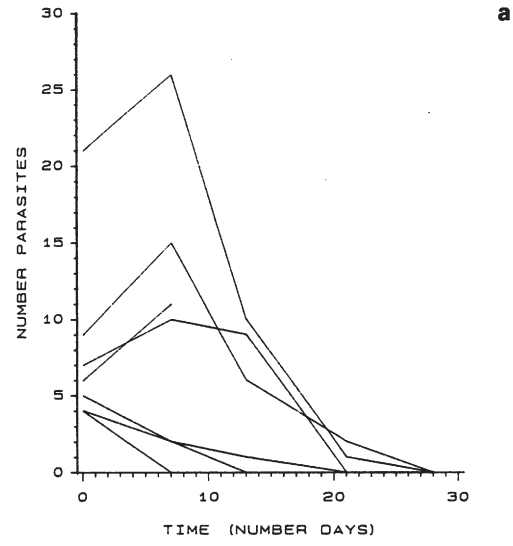


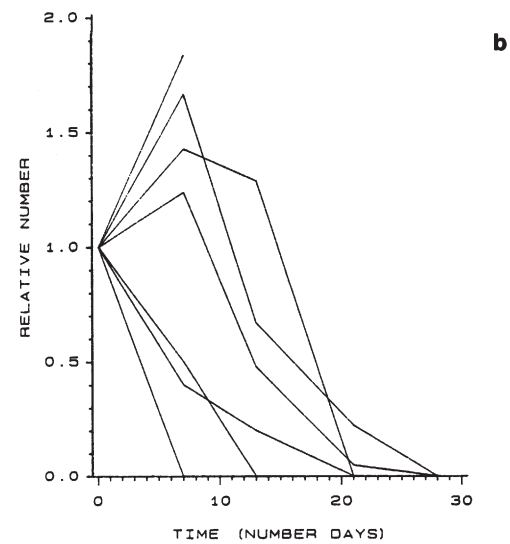
Figs. 2a—c. The course of infection of *G. salaris* on parr of *S. namaycush* up to 30d post-isolation. The parr were exposed for 6 days to a source infection, thereafter individually isolated separately into two replicate batches, at 12.5 °C. Each data point represents 10 (or 7) individually isolated fishes. (a) Prevalence; (b) Mean intensity; (c) Variance to mean ratio (s^2/mean). Replicate 1 indicated by solid line, replicate 2 by dashed line. (Bars = S. E.)





Figs. 3a,b. The intensity of infection of *G. salaris,* expressed as absolute and relative numbers (see text) of a group of 10 *S. namaycush* held individually isolated at 12.5 °C. The naive parr had been exposed to an infection source for 6 days before isolation. (Each line represents a single parr, except two lines each representing two fish.)





Figs. 4a,b. The intensity of infection of *G. salaris,* expressed as absolute and relative numbers (see text) of a group of 7 *S. namaycush* held individually isolated at 12.5 °C. The naive parr had been exposed to an infection source for 6 days before isolation. (Each line represents a single parr.)

ted fishes demonstrated a decrease in prevalence immediately after isolation (Fig. 2a). The mean intensity of infection also finally decreased in both groups and the infection was eliminated after approximately 30 days (Fig. 2a, b). The change in the variance/-mean ratio in the individually isolated fish, when the data were pooled, demonstrated increased overdispersion indicating an initial growth phase of infection, before the subsequent decline to unity (Fig. 2c).

The intensity and relative number (= number of parasites at time t in relation to initial infection at Day 0) of parasites per fish is shown for the 10 + 7 (3 fish died during first week, 1 during second week) individually isolated fish in Figs. 3a, b, 4a, b. Approximately half of the fishes were initially resistant to parasite reproduction (Figs. 3a; 4a). On the remainder there was a significant but restricted parasite population growth, with a peak up to about 4 times the initial population size (Fig. 3b), The maximum number of parasites observed on one fish was 26 (Fig. 4a).

The individual susceptibility and resistance to *G. salaris* varied in the Lake trout stock tested. However, in the initially susceptible Lake trout, only very restricted parasite reproduction was observed and a host response was mounted approximately one week post-isolation, eliminating the infection within four weeks. Although four individually isolated fishes accidentally died during the experiments, no *G. salaris* induced parasite mortality was observed.

DISCUSSION

The attachment rate and reproduction of *Gyrodactylus salaris* on Lake trout was restricted in comparison with other investigated salmonids (Bakke et al. 1990, 1991a, Bakke 1991, Bakke & Jansen 1991a, b), except Brown trout, which were found to have an almost total innate resistance to *G. salaris* infection (Tanum 1983, Bakke 1991, Unpublished). Approximately half of the tested *S. namaycush* were naturally resistant to parasite reproduction, although parasites persisted for up to 28 d. In the Lake trout, as in *O. mykiss* (Bakke et al. 1991a), and the anadromous *Salvelinus alpinus* (Bakke & Jansen 1991a), but not apparently in *S. fontinalis* (Bakke et al. in prep), a heterogeneity in innate resistance towards *G. salaris* was observed. However, the number of innately resistant individuals was resticted but the time requested to elicit an acquired response in the susceptible Lake trout was very short. This situation is comparable to that observed in the Baltic Neva salmon (Bakke et al. 1990), but the response is still more pronounced and efficient. It has previously been suggested that the variability in the infection patterns of *G. salaris* on salmonids is genetically determined and heritable (Bakke et al. 1990, Jansen et al. 1991, see Madhavi & Anderson 1985).

Lester (1972) reported shedding of mucus with attached parasites and proposed this as a mechanism for controlling parasite population growth. Mucus shedding or excess mucus production was not observed in the Lake trout. However, fish mucus contains a variety of components of the host immune system and probably only experimental analysis of this system can elucidate the mechanism of resistance by teleosts to gyrodactylid infection.

The variance/mean ratio of the pooled parasite population on isolated hosts increased slightly with the initial tendence of increase in mean intensity of infection. This indicates an increased overdispersion in the parasite frequency distribution probably due to differential parasite reproduction and/or mortality (see Cusack & Cone 1986). In the multihost system the similar tendence may be explained by low parasite numbers and mortality. However, the clear evidence of a slight parasite reproduction on ca. 50% of the individually isolated hosts, suggests that the same thing probably occurred on some of the 100 batched fish. It is not possible to deduce this from the course of mean intensity in the grouped fish (Fig. 1b). This demonstrates the importance of monitoring individually isolated fish in studies of host range and host specificity.

There seem to be no previous report of gyrodactylids from Lake trout in the Nearctic, except one unconfirmed report of *Gyrodactylus elegans* (Hoffmann 1967). Although *G. salaris* has been recorded from a range of cultured salmonids (Bakke et al., in prep.), the present experiments show that at least the present stock of Lake trout was quite resistant to infection.

At present, introduction of Lake trout to Norway is not allowed due to the general restrictions introducing new species. One

reason for these restrictions is that new species may be hosts for diseases and parasites which may be a threat to the native fish fauna. The present results and the ecology of Lake trout show that this salmonid species is relatively unimportant as host and disseminative agent for *G. salaris,* which is considered by some workers to be responsible for extensive mortalities of Atlantic salmon parr in Norway (Heggberget & Johnsen 1982, Johnsen & Jensen 1986, see also Dolmen 1987, Malmberg 1988 and Mo 1989), although this is questioned by others (Halvorsen & Hartvigsen 1989).

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SAMMENDRAG

Mottagelighet hos canadisk innsjørøye for infeksjoner av *Gyrodactylus salaris* under eksperimentelle betingelser.

Vertsspesifisiteten til *Gyrodactylus salaris* ble undersøkt med hensyn på parasittens evne til å infisere canadisk innsjørøye *(Salvelinus namaycush)* under eksperimentelle betingelser. Innsjørøye som ble eksponert til sterkt infiserte laks over 6 døgn ble infisert av parasitten, men med lave intensiteter sammenlignet med resultater fra laks. Innsjørøya ble delt inn i to grupper basert på infeksjonsutvikling og parasittenes overlevelse på individuelt isolerte fisk: (1) Verter som var mottagelige for parasitt fastheftelse, men motstandsdyktige mot parasitt reproduksjon (maksimal overlevelsestid for infrapopulasjoner, 21 dager etter isolasjon); (2) Verter mottagelige for parasitt fasteheftelse og reproduksjon, men som, etter en kort periode med parasitt populasjonsvekst, eliminerte parasitten (maksimal overlevelsestid for infrapopulasjoner, 28 dager etter isolasjon). På to grupper av 50 innsjørøye redusertes parasittpopulasjonene direkte etter isolasjon fra infiserte laks, i motsetning til ca. 50% av de individuelt isolerte innsjørøyene (gruppe 2 over). Dette viser behovet for eksperimentelle observasjoner av infeksjonsutviklingen på individuelt isolerte fisk, for informasjon om parasitt reproduksjon. *Gyrodactyklus salaris*-indusert vertsmortalitet ble ikke observert.

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