

# Population growth of *Gyrodactylus salaris* (Monogenea) on Norwegian and Baltic Atlantic salmon (*Salmo salar*) stocks

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## SUMMARY

Reproductive success of *Gyrodactylus salaris* from River Lierelva was compared experimentally on 3 stocks of salmon (12.5 °C ± 0.2). Isolated fish from 2 susceptible Norwegian stocks (Rivers Lier and Alta) and 1 resistant Baltic stock of salmon (River Neva) were infected with a single gravid worm in order to record the temporal sequence of births and age at death of individual parasites. Establishment success (proportion of worms surviving to give birth) was generally low and mortality high, but significantly fewer worms survived on Neva (45% with mean survival of 3.5 days) compared to Alta and Lier fish (60%, mean survival 7.9 and 5.2 days, respectively). There was a dramatic difference in parasite fecundity between the host stocks: only 2 births occurred on Neva fish compared to third and fourth births on both Alta and Lier hosts. The timing of the first birth was more variable on Neva hosts and was significantly extended (mean 2.3 days) relative to that on Alta and Neva fish (1.8 days). However, timing of the second birth did not vary on any of the 3 salmon stocks. Age-specific mortality and fecundity data are consistent with exponential population growth of *G. salaris* on Alta and Lier fish but eventual extinction on Neva hosts. This is the first demonstration that gyrodactylids maintained on different host stocks exhibit variations in fecundity, development and mortality, which may in turn account for the variable virulence noted when *G. salaris* infects different salmonid hosts.

Key words: gyrodactylid, reproduction, viviparity, host immunity, resistance, susceptibility.

## INTRODUCTION

*Gyrodactylus salaris* Malmberg, 1957 is responsible for a serious epidemic of wild Atlantic salmon (*Salmo salar* L.) in Norway and other parts of Scandinavia (Bakke & Harris, 1998). Nevertheless, it has a wider distribution, coexisting endemically on salmon in several Baltic watersheds (Malmberg, 1993). This difference in population behaviour is considered to reflect differences in the susceptibility of the Baltic race of Atlantic salmon when compared to the Atlantic race (Bakke, Jansen & Hansen, 1990; Bakke & MacKenzie, 1993). The accordance between *G. salaris* geographical distribution and restocking with salmon from infected hatcheries (Johnsen & Jensen, 1986), and the differing susceptibility of Baltic and Norwegian fish, was interpreted as evidence that *G. salaris* had been introduced to Norway from Sweden (Johnsen & Jensen, 1991; Mo, 1994; Johnsen, Moekkelgjerd & Jensen, 1999). This hypothesis became generally accepted and was used to justify rotenone treatment as a strategy for eradication of the parasite (Anonymous, 1995; Bakke & Harris, 1998). More recently, however, *G. salaris*

has been found to have complex specificity and can infect most salmonids with varying success (Bakke, 1991; Bakke & Jansen, 1991; Bakke, Harris & Jansen, 1992a; Bakke *et al.* 1992b; Bakke, Jansen & Grande, 1992c; Bakke & MacKenzie, 1993; Jansen & Bakke, 1995; Bakke, Jansen & Harris, 1996). Susceptibility is increased in hydrocortisone-treated salmonids (Harris, Soleng & Bakke, 2000) and a genetic component has been demonstrated using trout-salmon hybrids (Bakke, Soleng & Harris, 1999). It appears therefore that specificity is determined by both host genotype and phenotype, and that immune status influences susceptibility.

Gyrodactylid monogeneans have a unique reproductive biology, giving birth to single fully-grown offspring which already contain a developing embryo *in utero*. Population modelling studies of gyrodactylids have stressed the importance of parasite mortality (e.g. Lester & Adams, 1974; Scott, 1982), but have not considered the effects of reproductive rate which are usually assumed to be constant. Studies on the mechanism of the immune response (e.g. Harris, Soleng & Bakke, 1998; Buchmann, 1999) have also stressed the importance of mortality, while ignoring fecundity. However, given the nature of gyrodactylid reproduction, changes in fecundity could potentially have a major effect on population growth rates, and may be more

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important in regulating gyrodactylid populations than changes in mortality. Fecundity and mortality schedules have been studied in *G. salaris*, but only on the susceptible Norwegian hosts from River Lone (Jansen & Bakke, 1991; Harris, Jansen & Bakke, 1994). To test the hypothesis that both fecundity and mortality can be influenced by host stock, we conducted a series of experiments examining the reproductive success of *G. salaris* on the relatively resistant Neva host (a Baltic stock), and on 2 susceptible Norwegian stocks, from the Lier and Alta rivers.

#### MATERIALS AND METHODS

*Gyrodactylus salaris* were collected from heavily infected wild salmon parr electrofished from Lierelva (Buskerud County, 40 km west of Oslo), transferred to hatchery reared Lier fish and maintained at 12 °C in the laboratory for up to 1 month before experiments began in June 1999. Basic experimental protocols, including infection and disinfection procedures, have been reported elsewhere (Bakke *et al.* 1990). Alta and Neva stocks were obtained from the Ims Research Station (NINA, Stiftelsen for Naturforskning), Sandnes, autumn 1998, and Lier fish from the DOFA's (Drammen og Omegns Fisker-administrasjon) salmon hatchery, Lier, spring 1999. Fish were routinely treated with formaldehyde (1:4000) and subsequent immersion in salt water upon arrival to the aquarium, the last treatment occurring 50 days before the start of experiments. Naive fish ranged in size (Alta 50–89 mm, Lier 63–101 mm, and Neva 71–118 mm), and therefore the stocks were subdivided into small (50–70 mm), medium (71–90 mm) and large (91–118 mm) size classes ensuring potential effects of host size were controlled. All fish were maintained in dechlorinated, charcoal filtered, continuously running (2 l/min) Oslo tapwater under constant dim illumination. Fish were fed unmedicated pellet food (Ewos).

#### *Collection of parasites and infection of naive hosts*

Experimentally infected hatchery salmon were anaesthetized in 0.04% chlorobutanol, placed in a deep Petri dish containing clean dechlorinated water and viewed using a stereo-microscope with fibre-optic epi-illumination. Individual gravid parasites (containing a large embryo) were removed using insect pins and transferred to a Petri dish. An experimental host was anaesthetized and its tail brought into contact with the detached parasite. Through careful positioning of parasite and fish (monitored using a stereo-microscope), it was possible to ensure that the parasite always attached to the central region of the caudal fin. The fish was transferred to clean water in

a deeper dish. Successful attachment, normal activity, and position of the parasite on the tail was recorded. The fish was then placed individually in an experimental floating arena (0.37 × 0.28 m, 0.12 m water level, see Bakke *et al.* (1999) for full description). A total of 18 arenas were maintained in each 100 litre tank (1 × 1 m, 0.3 m water level), and fish were assigned randomly with respect to race in each tank. Temperature in the tanks during the experiment ranged from 12.2 to 12.6 °C (mean 12.5 °C).

#### *Infected Neva hosts*

An additional group of 11 medium to large (86–107 mm) Neva fish were exposed to *G. salaris* prior to infection with individual worms. The fish which were allowed to swim freely with infected Lier fish for 24 h, acquired a mean infection of 4 worms/host. The fish were maintained together in a single tank (1 × 1 m, 0.25 m water level). Their infection levels were monitored after 3 weeks, and then at approximately weekly intervals, by anaesthetizing each fish in turn and recording the total number of parasites under a stereo-microscope. After an initial rise to a mean of 36 worms/host, infection levels stabilized at 35–38 worms/host (s.e. 5.0–8.7). After 47 days, the fish were anaesthetized again and all remaining parasites were removed with forceps. These hosts were then immediately re-infected with individual gravid worms (as described above). Although Neva salmon are referred to in this study as resistant, there is as yet no comprehensive analysis of the extent or mechanisms of resistance in this stock.

#### *Observation of individual parasites*

Each fish was anaesthetized every 24 h following infection and the external surface scanned using a stereo-microscope. When the parasite had given birth, it was killed and the daughter allowed to remain on the fin. The first birth of the initial gravid worm was defined as successful establishment. The position of the daughter on the fish, and the size of its contained embryo, was recorded subsequently every 24 h using the developmental series outlined in Table 1. When the daughter gave birth, its offspring were killed. All parasites were followed in this way until they were found attached but dead, or had disappeared from the surface of the fish. When worms were lost from a host, the fish was checked 3 times in the following 12 h–2 days, and if still uninfected, it was reinfected with a fresh individual parasite. Individual hosts were reinfected up to 7 times as previous studies indicate that single worm gyrodactylid infections do not induce an immune response (unpublished data). Furthermore, there was no evidence of decreased parasite establishment

Table 1. *Gyrodactylus salaris* embryo development on Atlantic salmon from River Lier at 12.5 °C as discerned using a stereo-microscope at ×30 magnification

Age (post-birth)	Embryological development
Birth	Contracted uterus – small translucent circle surrounded by the gut.
1 day	As above, no obvious increase in size but uterus often tear-shaped.
2 days	Rounder, larger, uterus often with square neck in region of seminal receptacle.
3 days	Small/medium F1 embryo (oval shape with haptor hooks just visible as refractive blur).
4 days	Medium/large F1 embryo (points of F1 hamuli formed and shaft elongation commenced. A fold in the embryo may be present) equivalent stage to newborn parasite.
5 days onwards	Near-term F1 embryo characterized by opaque haptor and F2 hooks just visible as refractive blur.

Table 2. Establishment success for *Gyrodactylus salaris* on different Atlantic salmon stocks

Fish stock	No. of initial infections	No. of initial infections surviving to give birth	% establishment	% of daughters lost within 24 h of their birth
Alta	82	49	59.7	18.4
Lier	137	86	62.8	19.8
Neva	163	74	45.4	31.5
Refractory Neva	18	6	33.3	16.7

and survival, or changes in parasite fecundity on individual hosts which were reinfected during the course of these experiments.

## RESULTS

### *Initial establishment of individual G. salaris infections*

A total of 382 parasites were used to infect salmon parr, and a clear difference was noted in the success of initial *G. salaris* infections on the different host stocks (Table 2). Of 82 flukes used to infect naive Alta fish, 49 survived to give birth once representing an initial establishment success of 59.7%. On naive Lier fish, establishment was similar, 62.8% of 137 worms surviving to give birth once. On naive Neva fish, however, fewer parasites (45.4% of 163) survived to the first birth compared to both Alta and Lier stocks. Contingency tables showed establishment success was significantly reduced on Neva compared to Alta and Lier fish ( $\chi^2 = 11.9$ , 2 D.F. = 2,  $P < 0.005$ ). Establishment on previously infected Neva fish did not differ significantly from that on naive Neva fish (Contingency Table,  $\chi^2 = 1.00$ ). The Neva fish were substantially larger than those of the other 2 stocks, but  $\chi^2$  analysis did not indicate a size related effect.

### *Differences in parasite fecundity and embryonic development on different host stocks*

A maximum of only 2 parasite births occurred on Neva fish (mean births/worm  $0.55 \pm 0.64$ ), whereas third and fourth births were also observed on Alta

and Lier fish (mean births/worm  $1.33 \pm 1.09$  and  $0.97 \pm 0.82$ , respectively). Differences in fecundity were also observed in the time required for embryos to develop in parasites on the 3 stocks of fish (Fig. 1). The first-born daughter begins development while its mother is still an embryo: the median period between birth of any worm and the birth of its first born daughter was therefore only 2 days. On the other hand, the second-born and subsequent daughters which complete their entire development in a mature parent, had a median gestation period of 6–7 days. On Alta and Lier fish, the development period of the first daughter after the mother's own birth was 1.8 days, with very little variation (Fig. 1A). On Neva, however, mean developmental period was 2.3 days, a significant extension in gestation relative to both Lier and Alta fish (Mann-Whitney,  $P < 0.05$ ), principally because of a marked skew on Neva fish towards longer development (Fig. 1A). This difference occurred despite the common initial development of all first-born daughters within their mothers while their grandmothers infected a susceptible Lier fish. Interestingly, there was no apparent developmental retardation of the second-born daughter on Neva fish (Fig. 1B), even though this generation had completed its entire development while the mother was feeding on a Neva fish. Only 6 parasites survived on Neva fish to give birth a second time, and 3 of these had experienced a delayed first birth (2 worms giving birth at 4 days and 1 at 5 days). Parasites on Neva fish did not survive long enough to give birth a third or fourth time, and there were no differences in development time for the third or fourth births on Alta or Lier fish.

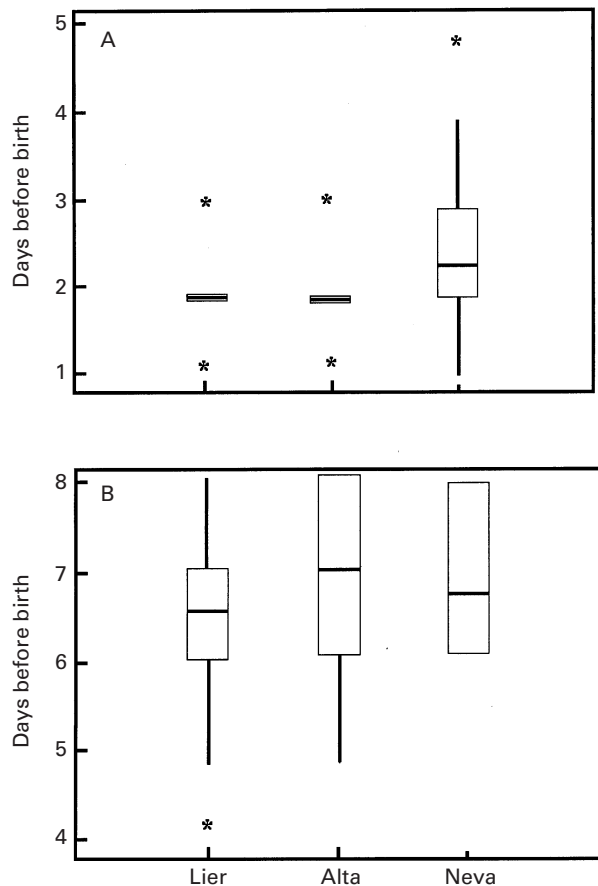


Fig. 1. Developmental period for first (A) and second (B) births of *Gyrodactylus salaris* maintained on Lier, Alta and Neva salmon, expressed as boxplot. Horizontal line in each box represents mean developmental period, box encloses 50% of observations (from 25% up to 75%). Whiskers connect observations lying within 1.5 box lengths of box limits. Outliers (★) lie more than 1.5 box lengths outside of box limits. The first birth Lier and Alta outliers represent multiple data points. Note that for parasites maintained on Neva fish, the first birth is significantly delayed (Mann-Whitney,  $P < 0.05$ ) compared to those on either Alta or Lier, with a distinct skew apparent. This delay was not apparent in the case of the second birth.

#### Differences in parasite age-specific mortality and survivorship

Parasite mortality was high in all experiments, giving concave survivorship curves (Fig. 2). The 50% survival times for *G. salaris* on Lier, Alta and Neva fish were 5.2, 7.9 and 3.5 days, respectively. Maximum longevity was extended to 24 and 26 days, respectively, for Alta and Lier fish (allowing up to 4 births), but was only 17 days for Neva fish (giving time for only 2 births). Age-specific mortality showed an unusual pattern of increase and decline throughout life on all 3 salmon stocks, being highest at the time of each birth, and declining to a minimum when the contained embryo was small (Fig. 3). Further analysis, pooling data for all births on all stocks, showed this to be due to a large increase in

parasite mortality 1–2 days after giving birth (Fig. 4). Parasite mortality subsequently declined until the next generation of births which began from day 5 onwards (see Table 3): the apparent low mortality of parasites more than 7 d after birth may merely reflect the small number of worms in which births are delayed to this time-point. No long-term trends in age-specific mortality were noted: therefore, an exponential model of survivorship, based on an assumption of constant age-specific mortality, was used to calculate the regression lines shown in Fig. 2. This model assumes that the number of parasites ( $N_t$ ) surviving to time  $t$  is equal to:

$$N_t = N_0 \exp^{-\mu t},$$

where  $N_0$  is the number of parasites at time 0, and  $-\mu$  is the constant daily parasite mortality. Mortality rates ( $\mu$ ) calculated for *G. salaris* infecting Alta, Lier and Neva salmon were 0.144, 0.210 and 0.279 per day respectively, giving correlation coefficients ( $r$ ) for the fitted line to data points of 0.98, 0.96 and 0.98, respectively. If mortality calculations were restricted to the first 10 days of parasite life (which included 85% of observations and avoided the increasing amplitude of variations in age-specific mortality seen in very old worms), daily mortality rates showed even greater differences between host stocks than noted for the complete data set (0.107 on Alta fish, 0.214 on Lier fish, and 0.313 on Neva fish). Over the first 10 days of life, these estimates of mortality also gave slightly improved correlations with observed data ( $r = 0.97, 0.98, 0.99$ ).

#### Population growth simulation

The data on age-specific mortality and fecundity for *G. salaris* infecting all 3 stocks of salmon derived above were incorporated into Life Tables (Deevey, 1947; Begon, Harper & Townsend, 1996) and used to calculate basic reproductive rates ( $R_0$ ) using a population growth simulation in which fecundity and mortality schedules were held constant. An initial cohort size of 1000 parasites was chosen, and the simulation run for 100 days to minimize effects due to an unstable age structure. Population growth was then calculated directly from the growth curves of the simulated populations. This simulation showed that the relatively small differences in fecundity and mortality schedules on the 3 hosts were sufficient to allow exponential growth on Lier and Alta fish ( $R_0 = 1.073$  and  $1.082$  respectively), but that on Neva fish, population growth would decline until extinction ( $R_0 = 0.9401$ ).

#### Migration of individual parasites on the host

During daily observation periods, parasites frequently moved short distances (ca 2–3 body lengths/min) on a particular fin or region of skin. Migration

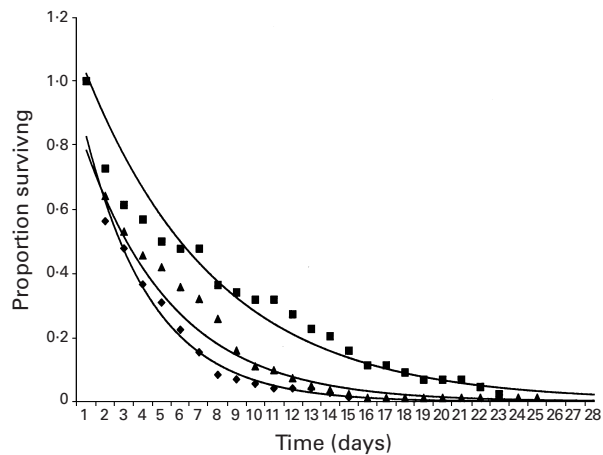


Fig. 2. Survivorship of *Gyrodactylus salaris* maintained on Alta (■, fitted curve A), Lier (▲, fitted curve B), and Neva (◆, fitted curve C) Atlantic salmon stocks, with best-fit exponential model regression curves. Estimated daily mortality (from regression curve) 0.144 for Alta, 0.210 for Lier, and 0.279 for Neva fish. Fitted curves not constrained to pass through 0 when cohort becomes extinct.

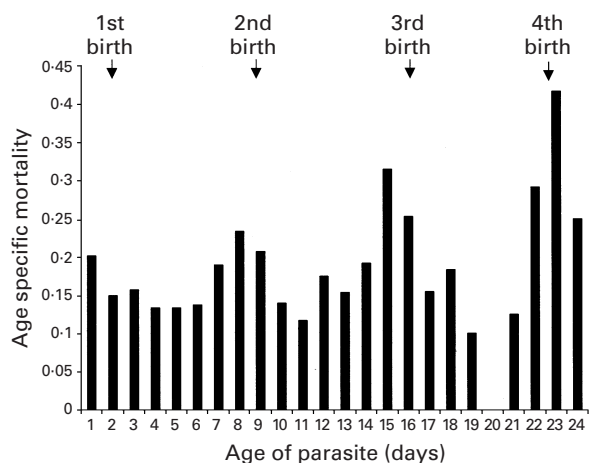


Fig. 3. Age-specific mortality for cohort of *Gyrodactylus salaris* on 3 stocks of Atlantic salmon ( $n = 196$ ). Mortality smoothed by taking 2 day running average. Age-specific mortality peaks at regular intervals corresponding with the times at which offspring are born.

was defined as a movement from one body region to another (i.e. fin to skin, fin to fin) in a 24 h period. All infections commenced with a single gravid worm attached to the central region of the caudal fin. This appeared to be a preferred site of attachment as (i) detached parasites attached here within a few seconds, (ii) if worms did not migrate from the caudal fin, the majority of their life-span was spent within the central region of this fin, and (iii) pre-first birth worms which were not born on the tail (in the

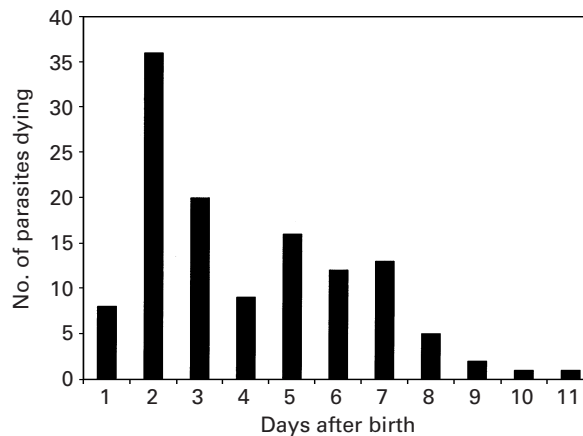


Fig. 4. Mortality of *Gyrodactylus salaris* in the days following a birth. Data summed for *G. salaris* on all stocks of Atlantic salmon, and for all births after the first.

few cases in which their gravid mother had migrated away from the tail before giving birth) actively migrated to this site. Most pre-first birth worms born on the caudal fin, remained on this fin, but did occasionally move on to the peduncle. Those parasites which did migrate, most commonly re-located immediately after each birth (Table 4) with the majority of worms migrating anteriorly and not returning to posterior sites. Migration, and distance from the caudal fin, increased with parasite age. With the exception of the peduncle immediately adjacent to the caudal fin, migrating worms were not found on the skin for more than 2 consecutive daily observations. Worms migrating from the tail were normally found on the peduncle (42%), adipose (33.3%), and anal (10.5%) fins, only post-second birth and older worms were found on the pectoral (7%), or more rarely, on the pelvic or dorsal fins (each 3.5%). Occasionally, worms migrated on the flank between fins, particularly the adipose and anal fins. Table 4 indicates a difference in mobility of *G. salaris* on the 3 stocks of salmon, but when the data is subdivided according to host size the proportion of non-migrating worms is only significantly different between Lier and Alta medium sized hosts (71–90 mm, Mann-Whitney,  $P < 0.05$ ). Apparent parasite inactivity on Neva fish may have been biased by the larger number of worms which died shortly after the first birth, and the larger size of these fish (24 out of 32 parasites which survived beyond their first birth on Neva hosts were maintained on large, 91–118 mm, fish). However, Lier parasites appeared more active than Alta parasites even though they had a shorter mean life-span so the observed differences between stocks cannot be accounted for entirely by differences in parasite mortality. Similarly, migration after the first birth was higher among parasites maintained on Lier, rather than those on Alta salmon.

Table 3. Timing of *Gyrodactylus salaris* births (12.5 °C) on 3 stocks of Atlantic salmon (sample size and standard error given in parentheses, before and after mean age at birth in days)

Host stocks	1st Birth	2nd Birth	3rd Birth	4th Birth
Lier	(59) 1.88 (0.52)	(20) 8.35 (1.06)	(2) 16 (1.0)	(1) 23
Alta	(34) 1.85 (0.49)	(19) 9.05 (0.99)	(8) 16.4 (0.99)	(2) 22.5 (0.5)
Neva	(35) 2.34 (0.89)	(6) 10.00 (1.9)		

Table 4. Migration of individual *Gyrodactylus salaris* on 3 stocks of Atlantic salmon (included only those individuals which survived beyond the first birth and expressed as percentages)

	Lier (n = 48)	Alta (n = 34)	Neva (n = 32)	Total (n = 114)
Anterior migration on the host				
None	27.1	44.1	56.2	40.3
Immediately after birth	62.5	32.4	34.4	45.7
Between births	10.4	23.5	9.4	14.0
Return migrations to caudal fin	6.2	5.9	9.7	7.0

## DISCUSSION

In an earlier study, Bakke *et al.* (1990) established that *Gyrodactylus salaris* parasite population growth was high upon Norwegian stocks of Atlantic salmon, while Baltic Neva fish were able to limit and eventually eliminate their infections. On fish of the susceptible Norwegian Lone stocks, individual *G. salaris* could give birth up to 4 times in a month long life-span (Jansen & Bakke, 1991), but these observations on the influence of temperature were not extended to a comparison with life-history parameters on other fish stocks. The current work confirmed Jansen & Bakke's (1991) observations that *G. salaris* can give birth up to 4 times on the susceptible Norwegian Lier and Alta salmon stocks. On Neva fish, on the other hand, parasite age-specific mortality was considerably greater than on susceptible stocks, and developmental periods for embryos were extended. As a consequence no parasites survived to give birth more than twice on this host stock.

Parasite age-specific mortality on all 3 host stocks was greater than that observed by Jansen & Bakke (1991) on Lone fish, with particularly poor survival and establishment success amongst newly attached worms. This may be a host effect, Lone fish being more suitable as a host than either Lier or Alta fish. However, it is more likely to reflect batch-to-batch differences in viability of *G. salaris* following removal from a host, possibly due to the action of host complement (Harris *et al.* 1998). Worms can become coated with complement prior to removal from a host, and damage from this source could account for the high initial mortality of *G. salaris* in these experiments. Nevertheless, there were significant differences in parasite survivorship observed be-

tween the 3 host stocks in the current work where the experimental design allocated parasites randomly to host stocks ( $n > 80$ ) and to positioning within cages.

Unusually, age-specific mortality of *G. salaris* on salmon is related to the birth cycle. Although this was previously noted by Harris *et al.* (1994), the current work has confirmed this pattern on a much larger sample of parasites which has allowed smoothing to remove short-term statistical fluctuations. The pattern is quite different to the age-related, exponentially increasing model of age-specific mortality observed for *G. turnbulli* (see Scott, 1982) which is widespread for detached, free-living stages of parasites (Anderson & Whitfield, 1975). However, exponentially increasing age-specific mortality does appear characteristic of detached *G. salaris* (see Harris *et al.* 1998) when food resources are excluded or limited. On the basis of detachment data, Harris (1993) suggested that age-specific mortality of other gyrodactylids may also be related to the developmental cycle of embryos, but the mechanisms involved are unknown. Birth is itself a costly process, but the peak in age-specific mortality occurs a day or so after birth. Diversion of resources to the energetically costly embryo may reduce survivorship of the adult, but a more likely explanation is that mortality is linked to migration of the parasites on the host which, in turn, is related to embryo developmental cycles. Harris *et al.* (1994) recorded a predominance of worms with small embryos detached in the water, at approximately the stage at which the majority of worms disappeared from the host in this study. A similar phenomenon was observed by Scott (1985) in relation to transmission processes which suggests that accidental dislodgement during movement is a major risk for these parasites.

Although the differences between fecundity, developmental time and mortality of *G. salaris* on different host stocks were slight, they were sufficient to cause substantial differences in population growth. When age-specific mortality and fecundity schedules were incorporated into an exponential growth model, positive population growth was predicted for both Alta and Lier fish, as demonstrated experimentally by Bakke & MacKenzie (1993) and Bakke *et al.* (1999), respectively. On the other hand, negative growth, with eventual elimination, was predicted for *G. salaris* infecting individual Neva fish. This supports previous findings indicating that Neva fish exhibit both a restricted susceptibility (Bakke *et al.* unpublished results) and innate or acquired resistance to *G. salaris* (see Bakke *et al.* 1990). Population studies (Bakke *et al.* 1990) suggest that Neva fish can support *G. salaris* more effectively than is predicted by the data derived here from single worm infections. However, this is partly a population phenomenon: infections on individual fish do rapidly dwindle, whereas the parasite is able to survive in a host population for at least 2.5 months (Bakke *et al.* 1990). More importantly, the initial high mortality of *G. salaris* on all stocks of fish in the current study may have masked the fact that naive Neva fish can normally support positive parasite population growth before the host response becomes effective (Bakke *et al.* 1990; unpublished results). Future experiments should compare age-specific mortality schedules during positive and negative growth phases of the parasite population cycle.

Gyrodactylid reproduction is unusual in that fecundity is particularly low, and this work highlights the importance of relatively small differences in fecundity and mortality schedules when total fecundity is less than 5. Such differences, which are probably under the control of genetic, biotic and abiotic environmental factors, can determine whether gyrodactylid infections grow pathogenically, coexist asymptotically, or are eliminated. Stock differences seem to be genetic (see Bakke *et al.* 1996, 1999, unpublished results), but stress-related corticosteroid hormones also influence salmonid susceptibility to gyrodactylids (Buchmann, 1998; Harris *et al.* 2000). Slight increases in stress, caused by environmental factors or even social interactions (Bakke & Harris, 1998) could increase parasite population growth, via changes in fecundity and mortality. The precise mechanisms responsible for changes in parasite development time such as those observed on Neva fish are not known. Typically, analyses of gyrodactylid population biology have simplified birth-death processes to a situation of varying mortality with constant reproduction (Lester & Adams, 1974; Scott & Anderson, 1984). The current work is the first to demonstrate that differences in fecundity and reproductive rate influence gyrodactylid population

growth. In particular, development time of the first-born embryo on Neva fish was extended by up to 0.5 days relative to that on the Norwegian salmon. However, the sample size for these fish was small, and the effect was not statistically significant. The physiological mechanisms involved in reducing survival and delaying development are unknown, but may involve complement (Harris *et al.* 1998), which is ingested and would therefore be able to act against the parasite's gut lining. Repair of complement-mediated damage to the tegument of the adult worm may also divert resources from reproduction, slowing development time. Differences in complement titre exist between different salmon strains, and have been implicated in resistance to a range of pathogens (Røed *et al.* 1992). We are currently investigating further the relationship between strain-specific complement titres and resistance to *G. salaris* on Atlantic salmon strains (Bakke *et al.* 2000).

The pattern of reproduction in *G. salaris* is quite different to that observed previously in *G. gasterostei*, highlighting the diversity which exists in the genus. In the latter species, which infects sticklebacks, parasites regularly give birth to only 2 daughters (Harris, 1998), while the third oocyte remains within the seminal receptacle and fails to develop further. The uterus of such worms becomes blocked i.e. inflated and fluid filled (Harris, 1985, 1998). No such block was noted in *G. salaris* in the current study: reproduction was limited by poor survival, and although differences in developmental time were noted on resistant hosts, the oocytes continued to enter the uterus normally. Nevertheless a block may eventually occur, as Harris *et al.* (1994) recorded worms with an inflated uterus and an oocyte in the seminal receptacle, principally detached at the bottom of the aquarium.

We noted a consistent pattern of *G. salaris* migration. Parasites placed in the central region of the caudal fin moved anteriorly on the body. Two components of migration were noted. Firstly, activity increased throughout life, beginning after the first birth. Secondly, there was a peak in migratory behaviour in the first 24 h after each birth. One function of this dispersal strategy on the host may be to prevent mothers cross-inseminating their own offspring. Similar migration patterns have been noted in *G. salmonis* (see Cone & Cusack, 1989), and *G. turnbulli* migrates from the fins to the peduncle at the start of an infection (Harris, 1988). Although slight differences in migration on different host stocks were noted, their significance is not clear.

This work has shown for the first time small differences in fecundity, development time and mortality of a gyrodactylid maintained on different host stocks. These findings may partly explain why a gyrodactylid such as *G. salaris* can be a significant pathogen of Norwegian stocks of Atlantic salmon (see Bakke *et al.* 1990, 1999), while coexisting on

some hosts (e.g. Neva salmon, see Bakke *et al.* 1990) and being eliminated from others (e.g. Brown trout, see Jansen & Bakke, 1995). Our findings may also be significant in terms of gyrodactylid reproductive strategies. The first 2 daughters can develop asexually and parthenogenetically, and isolated flukes reproduce indefinitely (Braun, 1966; Harris, 1998). At the same time, *G. salaris* is frequently inseminated (Harris *et al.* 1994), and it is possible that the third-born and subsequent daughters develop sexually. Different host stocks may have a major impact on the extent of parasite sexual reproduction. On Lier and Alta fish, large populations would develop which could reproduce sexually, because individual parasites survived long enough to give birth to sexually derived offspring. On Neva fish, however, no parasites survived to reproduce sexually, and the parasite could survive only by asexual reproduction or parthenogenesis. Such differences in strategy on different hosts could have a major impact on patterns of gyrodactylid speciation and host–parasite coevolution.

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